Exploration of the links between baleen whales and forage fish in the Celtic Sea:

assessing spatial distribution and energy content

Mareike Volkenandt

B.Sc. Biology
M.Sc. Marine Biodiversity and Conservation

Galway-Mayo Institute of Technology

Submitted in fulfilment
of the requirements for the
degree of Doctor of Philosophy

Supervisors:
Dr. Ian O'Connor (GMIT)
Dr. Simon Berrow (GMIT)
Prof. Jean-Marc Guarini (UPMC)

Submitted to the Galway-Mayo Institute of Technology
December 2014

Mareike Volkenandt was part of the Marine and Freshwater Research Centre at the Galway-Mayo Institute of Technology and
the Laboratoire d' Ecogéochimie des Environnements Benthiques / UMR 8222 at the Observatoire Océanologique de Banyuls-sur-Mer.

This study is part of the **MARES** Doctoral Programme on Marine Ecosystem Health and Conservation.
MARES is a joint doctorate programme selected under Erasmus Mundus coordinated by Ghent University (FPA 2011-0016).

Support was given by the Irish Whale and Dolphin Group (IWDG) and the Marine Institute Networking Initiative, funded under the Marine Research Sub-programme by the Irish Government, co-financed by the European Union via the European Regional Development Fund.

Declaration

I hereby certify that this material, which I now submit for assessment on the programme of study leading to the award of PhD is entirely my own work and has not been taken from the work of others save and to the extent that such work has been cited and acknowledged within the text of my work.

Signed: ______________________ Candidate

ID No.: G00295009

Date: 16. 12.2014

Für Mama und Papa

Dedicated to Mom and Dad

— ♡ —

Exploration of the links between baleen whales and forage fish in the Celtic Sea: assessing spatial distribution and energy content

Mareike Volkenandt

Abstract

Forage fish are small pelagic fish that are energy pathways from low to high trophic levels and their high stock biomass makes them a profitable target for large scale fisheries. An ecosystem-based approach to fisheries management (EBFM) is necessary if the objective is to maintain a functional ecosystem by avoiding disruption in the food-chain while ensuring profitable resource exploitation. The general objective of this study is to develop the base for such a fishery approach, linking forage fishes, (mainly herring, *Clupea harengus*, which is a key forage fish species), and baleen whales (fin, minke and humpback whale; *Balenoptera physalus, Balenoptera acutorostrata, Megaptera novaengliae*) in the Celtic Sea ecosystem. The spatial distribution of the annual Celtic Sea herring stock was analysed from acoustic survey data using geostatistics. Herring was randomly distributed in patches, influenced by coastal spawning grounds without correlation with temperature and salinity. Observed spatial distribution of baleen whales was fund to be influenced by the distribution of herring and sprat (*Sprattus sprattus*) suggesting that baleen whales actively targeted these two species. To establish the transfer of energy between prey and predators, energy content of herring, sprat and mackerel (*Scromber scombrus*) were first measured with bomb-calorimetry. Measures exhibited a high variation pattern caused by maturation status. A significant drop in energy content of fish after spawning is assumed to be an important factor for the quantification of the predation pressure on fish stocks. A simplified individual dynamic energy budget was combined with a model of whale behaviour, in order to quantify their predation on herring. Such modelling allows for testing of different scenarios regarding ecosystem functioning and can help understanding ecosystem links between predator and prey species.

Atlantic herring • baleen whales • ecology • EBFM • forage fish

Exploration of the links between baleen whales and forage fish in the Celtic Sea: assessing spatial distribution and energy content

Résumé

Les poissons "fourrage" sont des petits pélagiques qui sont une voie de transfert d'énergie des bas vers les hauts niveaux trophiques. Cependant, la forte biomasse des stocks halieutiques qu'ils représentent en fait une cible privilégiée et à fort profit pour les pêcheries industrielles. La conséquence de ces deux constats est que, pour maintenir l'écosystème fonctionnel (et éviter une perturbation dans la chaîne trophique) tout en maintenant une exploitation profitable, une approche écosystémique de la gestion des pêches (ecosystem-based approach to fisheries management, EBFM) est nécessaire. L'objectif général de cette étude est de développer une base pour une telle approche, en reliant les poissons "fourrage" (principalement les harengs, *C. harengus*, qui est une espèce clé) aux baleines (rorqual commun, *B. physalus*, petit rorqual, *B acutorostrata*, et baleine à bosse, *M. noveaenglia*) dans l'écosystème de la Mer Celtique. La distribution spatiale du stock de harengs a été analysée à partir des suivis acoustiques annuels en utilisant les géostatistiques. Le stock de harengs a une distribution aggrégative aléatoire, influencée par les zones de pontes, mais sans correlation avec la température ou la salinité. La distribution observée des baleines est influencée par la distribution des stocks de harengs et de sprats (*S. sprattus*), suggérant que les baleines ciblent activement ces deux espèces dans sa recherche de nourriture. Pour quantifier le transfert d'énergie entre proies et prédateurs, premièrement, les contenus énergétiques des harengs, sprats et maquereaux (*S. scombrus*) ont été mesurés par calorimétrie. Les mesures présentent de larges variations causées par l'état de maturation. Principalement, elle permettent de faire l'hypothèse que la chute de contenu énergétique des poissons après les pontes est telle qu'elle doit être prise en compte dans la quantification de la pression de prédation des baleines sur les stocks de poissons. Dans un deuxième temps, un bilan de la dynamique énergétique individuelle a été combiné à un modèle de comportement des baleines. Il est utilisé dans la quantification de leur prédation sur le stock de harengs. Cette modélisation permet de tester différents scénarios concernant le fonctionnement des écosystèmes, et peut contribuer à une meilleure connaissance des liens prédateurs-proies dans le context de baleines consommant les petits pélagiques.

Acknowledgements

To begin, I want to thank my supervisors, Ian O'Connor, Simon Berrow and Jean-Marc Guarini for support and supervision over the years. Thank you for giving me the possibility to do this thesis and the opportunity to take part in several cruises. I want to thank you for all the proof reading and efforts to tackle the bureaucratic challenges involved with a co-tutelle PhD project. Thank you to the thesis committee, Jason Link, Vincent Ridoux and Cilian Roden for evaluating and reading this thesis. Further I want to thank the MARES programme for funding this thesis, and Pieter Blondeel, Tim Deprez and Magda Vincx for the kind support. I acknowledge the provision of the time series data from the Marine Institute and the Irish Whale and Dolphin Group.

It has been exciting three years and I had the chance to meet great people along the way. Working at two universities, taking part at different training course and presenting at conferences made this time very lively and involved making a lot of new connections. To keep it short, I want to say that I am very thankful for the welcoming atmosphere during all the MARES meetings and workshops.

Struggling with understanding the Irish ”English”, I was put on the Celtic Explorer for my first CSHAS survey. ”Thank you” to the helpful (and patient) crew and the scientific crew from the Marine Institute. Thank you, Rob Bunn, Tobi Rapp, Turloch Smith, Macdara O'Cuaig, Graham Johnston and Cormack Nolan for introducing me to the work on boat and the handling of fish. I want to thank Helen McCormick for showing me how to age fish and the help with all otolith work. Ciaran O'Donnell, thank you for your patience with me on the boat and for your amazing support long after the cruise was finished. Thank you for showing me the world of fisheries acoustic. Further I would like to thank all the good souls at the Marine Institute, who were always willing to help as much as they could: Caroline Cusack, Sinead O'Brian (what would have I done without those cheese rolls!), Rafael Salas and Dave Clarke. I want to thank Trevor Alcorn, Glenn Nolan, Kieran Lyons, Hans Gerritsen and Maurice Clarke for technical support and the kind replies to my emails full of questions. Thanks to Ciaran, Cormack, Tobi and Dave Stokes for providing me with all kind of fish samples over the years.

I want to thank all the birders on CSHAS'12 and CSHAS'13 for all the hours

on deck, counting enthusiastically all the birds under sometimes nasty conditions: Sarah Ingham, Eamonn O'Sullivan, Stephen McAvoy, Garry Robinson, Caoimhe Muldoon (RIP) and Niall Keogh. I want to thank my "own" scientific crew, Simon Berrow, Stephen Newton, Simon Dedman, Niall Keogh, Conor Ryan, Teresa Martin and Laurence Manning, for sticking with me for one week and to check all the survey aims and also the crew of the Celtic Voyager for their patience with me. A big "thank you" to the Irish Whale and Dolphin Group for providing data and support over the years and BirdWatch Ireland for collaboration.

I had the opportunity to visit several other working groups during my PhD thesis to analyse samples and to learn new methods. I want to thank the "Departamento de Biología de Organismas y Sistemas" at the University of Oviedo in Spain for hosting me for a few weeks, even though the results finally did not make it into the thesis. An enormous "Thank you" to Fernando Gonzales Taboada for being the best "R" emergency contact I can imagine and building the foundation of my "R" skills. Further I want to thank the "Ecologie et Modèles pour l'Halieutique (EMH)" group at IFREMER Nantes in France for a very instructive stay, especially Pierre Petitgas and Mathieu Woillez; and Laurence Fauconnet for such a nice introduction to France. Finally, I want to thank Anna Soler-Vila and the "Irish Seaweed Research" group at the National University of Ireland Galway for the kind provision of their laboratories. Thank you, Svenja Heesch for staying longer just so that I could finish my samples and for the cups of coffee afterwards.

Back at my base working place, I want to thank all my colleagues at the Marine and Freshwater research centre at GMIT. Thank you for a nice, collegial working atmosphere and great discussions during and after work hours. Thank you Cóilín Minto for being there for all kind of "simple" R questions, and for your encouraging scientific discussions, ending with your kind "Viel Spass" and "Tschuss" that always made me smile. Thank you Melanie Zölck, Conor Ryan and James Keating for your support even though you were busy with your own work. Thanks to Joanne O'Brien and Suzanne Beck for being there for me, with a cup of cappuccino, when I needed it most (!) and all the chats. Most of all, thank you to Larry Manning. I don't know if you are even aware of how much you helped me with just being you and your cups of tea. Thank you!

I was nervous to move to Banyuls-sur-Mer. Yet another move, yet another beginning and mon dieux another language ... but you could not have made it easier for me! Thank you for a great welcome and making the integration for me so easy. I want to thank the group LECOB for all the support. Thank you for coffee breaks, after-work refreshments at the beach and enjoying Banyuls during all seasons. Especially I want to thank Mariana Paldron, Sandra Baksay, Margot Doberva, Elsa Stetten, Anne-Sophie Gicquiaux and Tatiana Severin. And thank you to my "gamers" for making us forget time and worries and for being great friends: Rémy Van Geersdaele, Hugo Lebredonchel, Océane Haranger, Marine Blanchet and Sheree Yau. A big "Thank you" Sheree for all the (last minute) proof reading!!! An extra special thanks goes to Sandrine Fanfard. I don't know how I could have survived in France without your friendship and help and your patience with me!

Being part of such an international programme with the aim of networking, you meet a lot of people, which all leave traces in me and my work. There is always a team behind, which supports you in one way or another. I remember meeting Paula Ní Ríogaín the first time, on the boat, introducing herself with "I'm the one here to help you" and the entire time after you have done exactly that! I don't know in how many ways you helped, learning how to throw a net, counting blows, proof reading, and not to forget all the cups of tea, listening to all my worries and having a reasonable answer ready. Thank you, and Julia Baer, for always having an open door for me and for climbing mountains with me! Danke to Jessica Kegel, who became such a good friend in such a short time. Thank you for motivating me, when I thought it is not going anywhere. Thank you to all my friends "back home". Every phone call, text message, virtual hug was an encouragement.

Finally, I want to thank my parents and Tobias for their full support and encouragement for this thesis and always, for accepting my moods, for keeping track with every telephone number and address change, for trying to make everything a little bit easier for me and for protecting me. I know this life style and the many changes of plans are not the easiest to go along with. I am asking for a lot of patience and you give me the best return I could wish for.

I am very lucky to have been able to go this path, thank you for joining me during the different stages!

If I have seen further

it is by standing on the shoulders of giants.

— *Isaac Newton*, 1676

Abbreviations

B	Stock biomass
$\mathbf{B_{lim}}$	Biomass limit for when recruitment is impaired, which can lead to overexploitation
$\mathbf{B_{MP}}$	Biomass target according to the fishery management plan
$\mathbf{B_{PA}}$	Biomass target of a precautionary management plan
CG	Center of gravity
CSF	Celtic Sea Front
CSHAS	Celtic Sea Herring Acoustic Survey
E	Energy content per fish
EBFM	Ecosystem-based fisheries management
EEZ	Exclusive economic zone
ED	Energy density per gram dry mass
EDSU	Elementary distance sampling unit
EW	Energy density per gram wet mass
EU	European Union
F	Fishing mortality
$\mathbf{F_{0,1}}$	Fishing mortality when the increase in yield per recruit is a 10th of the maximum increase in yield per recruit
FAO	Food and Agriculture Organisation
FEAS	Fisheries Ecosystem Advisory Services group at the Marine Institute
$\mathbf{F_{lim}}$	Fishing mortality limit for when recruitment is impaired, which can lead to overexploitation
$\mathbf{F_{MP}}$	Fishing mortality providing the maximum yield per recruit
$\mathbf{F_{PA}}$	Fishing mortality target of a precautionary management plan
IBM	Individual based model
ICC	Irish Coastal Current
ICES	International Council for the Exploration of the Sea
ISF	Irish Shelf Front
$\mathbf{I_{G}}$	Gonado-somatic index
M	Natural mortality
MARES	Doctoral Programme on Marine Ecosystem Health and Conservation
MSC	Marine Stewardship Council
MSY	Maximum Sustainable Yield
NAC	North Atlantic Current
NASC	Nautical area scattering coefficient
PCA	Principal component analysis

RSW . . .	Refrigerated seawater vessel
SSB	Spawning stock biomass
SST	Sea surface temperature
TAC	Total allowable catch
UK	United Kingdom
UN	United Nations
VPA	Virtual population analysis

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Chapter 1

Introduction

> “An EBFM is a holistic management approach and before implementation,
> decisions on the desired ecosystem state and socio-economic output
> have to be made based on discussions with all stakeholders. [...]
> As key species in ecosystems and with the biomass fluctuations,
> an EBFM is especially important for small pelagic fisheries.”
>
> (p. 5 & 6)

1.1 Thesis Introduction

Marine fisheries, the exploitation of target species from the sea, have been an important part of human history; however the modernisation of fishing fleets and an increasing demand for fish protein has lead to high fishery levels which alter pristine ecosystems. In 1996 global marine fisheries were five times higher compared to 1950 (increase from 16.8 million tonnes to 86.4 million tonnes) and now stabilized at 80 million tonnes (FAO, 2014). In 2011, 29% of the world's fish stocks were overexploited, meaning, that the fishing yield is below its original potential and strict management is needed to restore and recover their potential productivity. Fully exploited fish stocks are those at the maximum yield, no further increase is possible without effective management and a careful prevention of stock decline. The majority of all fish stocks, that is 61%, are already fully exploited. Only 10% of stocks are under low fishing pressure allowing for an increase in exploitation with a proper management plan (FAO, 2014). After analysing the world's fisheries statistics, the Food and Agriculture Organisation (FAO) states: *"The declining global marine catch over the last few years together with the increased percentage of overexploited fish stocks and the decreased proportion of non-fully exploited species around the world convey the strong message that the state of world marine fisheries is worsening and has had a negative impact on fishery production. Overexploitation not only causes negative ecological consequences, but it also reduces fish production, which further leads to negative social and economic consequences."* (FAO, 2012, p. 59).

The apparent stability in global marine catches gives a false impression because it overshadows the increased fishing effort on under-fished stocks due to the limitations of fully exploited fish stocks. It is an indication of a shift in effort, which can be seen in the search for new fishing grounds and stocks in i.e. the deep sea or the open ocean (FAO, 2014). Thus, overfishing, the exploitation of a stock above its sustainable limit, remains a cause for a complex of problems for all oceans. The impacts of fisheries on the ecosystem are vast and can vary due to the applied fishing method. Bottom trawling can have direct physical effects on sea floor structure, increase post-trawling mortality and have long-lasting effects on the benthic ecosystem (Jones, 1992). Bycatch, the unintended fishing of non-target species, often results in incidental mortality, mainly of marine top predators e.g. seabirds, marine mammals and sharks, or fish with low economic value (Hall et al., 2000). It can influence biodiversity due to the removal of individuals of top predator species, thereby affecting trophic dynamics in an ecosystem (Hall et al., 2000). Similar to bycatch, discards, the dumping of unwanted catch back into the sea before landing, increases fisheries-induced mortality. However, discards can contain individuals of the target species with a low market value that are unprofitable to sell. If there is uncertainty concerning the level of discard in a fishery, which is usually the case, then mortality is underestimated in the stock assessment and the fishing yield is lower than assumed (Jennings et al., 2009; Hilborn and Hilborn, 2012). Equally, ghost fishing (lost fishing gear in the sea that traps animals without ever being recovered) and the catch taken illegally will cause uncertainties in yield estimation.

Fishing and overfishing can alter the ecosystem structure via the removal of predators or prey whose place in the ecosystem will be filled by another species. The species composition and biodiversity will be different to the pre-fishing status, e.g. via the domination of jellyfish or algae with low exploitation interest (e.g. Pace et al., 1999; Cury and Shannon, 2004; Folke et al., 2004). Once an ecosystem has turned, it is difficult or even impossible to recuperate the previous state. The loss of biodiversity reduces the resilience potential and increases ecosystem vulnerability to disturbance. The removal of higher trophic levels ("Fishing down the food web") and trophic cascades compress the food pyramid, increase predation pressure on lower trophic levels and shorten food chains (Pauly et al., 1998; Pauly and Palomares, 2005). Following the market demands and economic interests, fishing is selective and bigger individuals are exploited first. Thereby the size, age and maturity structure of a stock is altered, which can influence reproduction rates and stock growth (Borrell, 2013). Fundamentally, fisheries are a global business and thus overfishing can also have economic and social implications. Hilborn and Hilborn (2012, p. 111) state: *"Fact is, fishing changes ecosystems. [...] Environmental impacts exist on a continuous gradient. Very little fishing produces very little food and has very little impact on the ecosystem. Sustainable fishing produces a lot of food and changes the ecosystem considerably. Severe overfishing produces little food and completely transforms the ecosystem"* .

According to the scientific fisheries assessments, a third of all stocks are overfished and half are below a level that would produce a maximum sustainable yield (Worm et al., 2009; FAO, 2014). It should be noted however, that fishing pressure had been reduced significantly and that fisheries management is in the process of change (Cardinale et al., 2013). In view of the increasing world population and the according demand for food security, attempts are being made for more sustainable fish exploitation. Governments, scientists, the fisheries sector and the public are more aware of the problems and impacts arising from overfishing. During the World Summit on Sustainable Development (WSSD) in 2002 the United Nations (UN) committed to maintain and restore stocks and to the development of an ecosystem approach to fisheries management. They reinforced their commitments ten years later at the United Nations Conference on sustainable Development (Rio +20). An ecosystem-based fisheries management (EBFM) focuses on the full ecosystem, recognises that species are interconnected, takes the ecological impact of the fisheries into account and goes far beyond a single species fisheries approach (Garcia and Cochrane, 2005; Curtin and Prellezo, 2010; Link and Browman, 2014). EBFM supports fishing on maximum sustainable yield without jeopardising ecosystem state sustainability (Browman and Stergiou, 2004). An EBFM is a holistic management approach and before implementation, decisions on the desired ecosystem state and socio-economic output have to be made based on discussions with all stakeholders. EBFM stands on sound and broad scientific knowledge of ecosystem interactions spanning fisheries, cybernetic, food web and community metrics but also the sensitivity to climate change and oceanographic characteristics (Link, 2002; Levin et al., 2009; Curtin and Prellezo, 2010).

The development of forage fish fishery, the fishery of small pelagic shoaling fish, is given careful attention. Forage fish, like anchovy, sardines, mackerel and herring, are within the top ten of most fished species according to landings in tonnes (FAO, 2014). As trophic middle players, forage fish are important key species in the ecosystem. As zooplankton consumers they are the pathway of energy to high trophic levels including top predators like seabirds and marine mammals. Thus they have a central role for ecosystem stability. Forage fish occur in high biomass and form large schools, therefore they are easily detectable and their harvesting is particularly facile with convenient fuel efficiency (in average 20 tonnes per tonne of fuel) (Alder and Pauly, 2006a; Pikitch et al., 2012). Forage fish are fished for direct human consumption in some selected countries, however the majority of landings is used for fishmeal production (Tacon and Metian, 2013). As the aquaculture sector grows rapidly, the demand for fishmeal will increase and hence the demand for forage fish (Alder et al., 2008; FAO, 2014). However forage fish are short-lived species that show a strong coupling to environmental conditions causing large fluctuations in their biomass (Pikitch et al., 2012). As key species in ecosystems and with the biomass fluctuations, an EBFM is especially important for these small pelagic fisheries.

This PhD study specialises on the Atlantic herring (*Clupea harengus*) stock in the Celtic Sea, its distribution and the trophic interactions with baleen whales as top predators. Herring stocks, the most fished pelagic stocks in the North Atlantic, have been overexploited and fisheries collapsed in the past (FAO, 2014; Dickey-Collas et al., 2014). Now, most stocks in the North Atlantic show signs of recovery. Using different geostatistical and ecological modelling techniques, the central role of herring in the Celtic Sea ecosystem is explored. This thesis should provide valuable knowledge of the ecosystem functioning to contribute to the scientific base of an EBFM development for sustainable herring harvesting without disturbing the ecosystem balance.

1.2 Forage fish in the Celtic Sea

Small pelagic fish that occur in high abundance are called forage fish because of their role as prey for higher trophic levels. Forage fish transport the energy from zooplankton up the food chain to higher trophic levels including charismatic top predators (Engelhard et al., 2014). Forage fish stocks show large natural fluctuations in biomass, which can often be correlated to changes in temperature or other atmosphere-ocean climate proxies or exploitation and predation dynamics (Hjermann et al., 2004; Harma et al., 2012; Peck et al., 2013; Leitão et al., 2014; Trenkel et al., 2014). A well-known example is the coupling of el Niño events with Peruvian anchovies (*Engraulis ringens*) in the Humboldt current ecosystem. The Peruvian anchovy fishery is the largest in the world and the stock collapsed due to high fishing effort during el Niño times, when the stock had a naturally low biomass. With the decline in anchovy availability, seabird populations suffered from the difficulties in finding sufficient food causing a drastic decline in several seabird abundances (Pikitch et al., 2012).

About 50 - 80% of forage fish landings are processed to fish meal (Alder et al., 2008; Tacon and Metian, 2009). Yet, in selected countries, particularly for people with low income, forage fish are important for direct human consumption, which has to be considered for the outlook in increasing fish meal production (Alder et al., 2008; FAO, 2014). Forage fish fisheries directly contribute 20% to the total value of the world fisheries, but if the contribution of forage fish to the growth of other exploited fishes via predation is included, the percentage is much higher (Pikitch et al., 2014). Forage fish species are among the most exploited species (by weight) with 12 out of the 20 most fished species in all oceans (FAO, 2014) and 9 out of the top 10 within European fisheries (Figure 1.1) (European Union, 2014). Natural fluctuations in forage fish biomass due to environmental conditions, their importance as prey for top predators, many of which are endangered, and their high economic value for fish meal and direct consumption, call for the implementation of sustainable forage fish exploitation following an EBFM approach to maintain ecosystem integrity and sustainability (Smith et al., 2011; Engelhard et al., 2014; Pikitch et al., 2014). In the Celtic Sea ecosystem, Atlantic herring, European sprat (*Sprattus sprattus*) and young Atlantic mackerel (*Scromber scombrus*) often form shoals together and form the diet of many species in the Celtic Sea (Trenkel et al., 2005; Ryan et al., 2013). The species are introduced in the following chapters, with more emphasis given to herring as the most economically important forage fish species in the Celtic Sea.

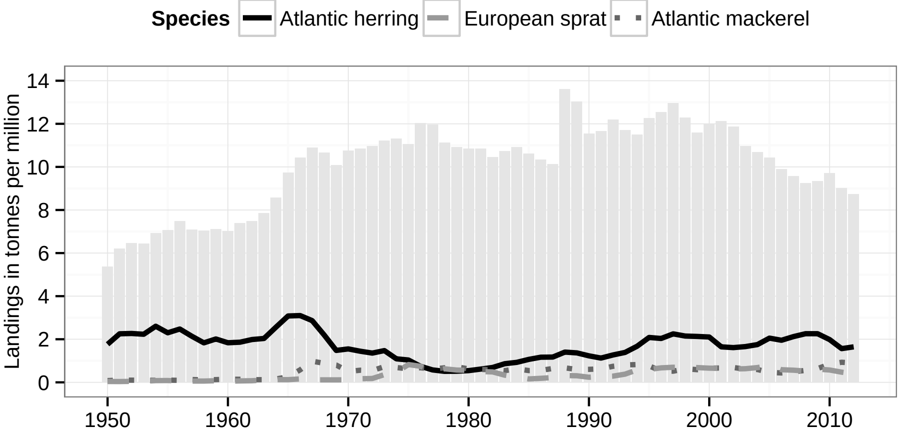


Figure 1.1: Atlantic herring, European sprat and Atlantic mackerel landings statistics from the North Atlantic taken by the European fleets are shown from 1950 to 2012. The grey bars indicate the landings for marine fishes by the European fleets in the North Atlantic. Data are taken from FAO Fishery Statistical Collections and selected for marine fishes, herring, sprat and mackerel landings in the North Atlantic by European fleets.

1.2.1 Atlantic herring (*Clupea harengus* L.)

Herring, the genus Clupea, belongs into the family of Clupediae. *Clupea harengus* (Linnaeus, 1758) is the Atlantic herring with a wide distribution in temperate waters in the North Atlantic from the Bay of Biscay to the Barents Sea. Within the North Atlantic, herring stocks are in the North Sea, Norwegian Sea, Barents Sea, west of Scotland and in Irish waters. Atlantic herring is a highly migratory fish with a migration according to season and life stage (McQuinn, 1997; Trenkel et al., 2014). During summer, all adult herring carry out their gonadal development at the feeding grounds. In autumn, the migration continues to the spawning grounds for autumn and winter spawning components of the stock, while the spring spawning component migrates to wintering grounds. Herring prefer to spawn over gravel and rocky grounds to which they can attach their eggs. After spawning, adults return to the feeding grounds to regenerate. The duration of egg and larval development depend on spawning time and environmental conditions (Brunel and Dickey-Collas, 2010; Peck et al., 2012b). Larval characteristics indicate maternal and parental effects (Geffen, 2009) and, together with food availability and quality, can influence the metamorphose from larvae to juvenile herring. Larvae are pelagic and are able to swim short distances. Juvenile herring are on average 40 mm in total length (Klinkhardt, 1996), form shoals on nursery grounds close inshore and have sufficient swimming capacities to migrate offshore in the winter months (Klinkhardt, 1996). Depending on the stock, fish reach maturity with 2 - 5 years and life expectancy can be up to 12 - 13 years (Klinkhardt, 1996; Molloy, 2006).

Herring fisheries have been an important part of European history. As large herring shoals reliably returned to the fishing grounds, towns were created along the coastline living of fishing and trading the "silver from the sea" (Klinkhardt, 1996), which was supported by the Hanseatic league in the 14th - 16th century (Alder and Pauly, 2006b). Herring were barrelled and cured giving it a long storage life and the possibility for international trading without risking a loss in product quality (Alder and Pauly, 2006b; Molloy, 2006). If we fast-forward to the mid-20th century, when the catch statistics began, herring stocks were increasing after years of low biomass. In the 1950s, herring was the main species contributing to fish meal production (Alder and Pauly, 2006b; Molloy, 2006; Alder et al., 2008). The fisheries became highly industrialized, catches strongly increased and fisheries expanded (Figure 1.2). Norwegian spring spawning and North Sea herring started to decline in the early 1970s, which lead to an increase in fishing effort in the Celtic Sea (Figure 1.2). The exclusive economic zone (EEZ) for nations was extended and first total allowable catch (TAC) quotas were installed in the mid-1970s but quotas were never reached because the stocks were decreasing more rapidly than expected (Molloy, 2006). Between the late 1970s and early 1980s herring stocks were depleted and the fisheries were closed (Molloy, 2006; Dickey-Collas et al., 2010).

In the mid-1980s, after the closure, the interest in frozen fish increased, consumers developed a taste for different species and other species were used for fish meal production (Molloy, 2006; Alder et al., 2008; Dickey-Collas et al., 2010). A change in the market demand was causing a change in the herring target (more juveniles and roe fishery), leading to fisheries with large ecological impact due to

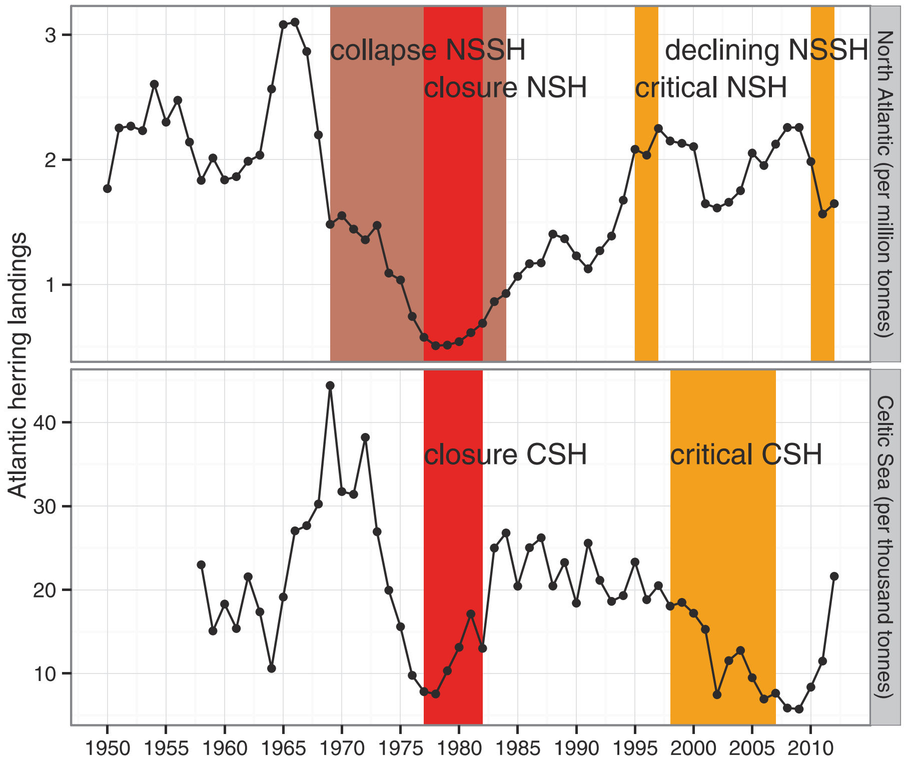


Figure 1.2: Atlantic herring landings statistics from the North Atlantic and explicitly for the Celtic Sea are shown from 1950 to 2012. Fishery closures are indicated in red, critical phases are indicated in orange. NSSH = Norwegian Spring Spawning Herring; NSH = North Sea Herring; CSH = Celtic Sea Herring. Data are taken from FAO Fishery Statistical Collections and selected for herring landings in the North Atlantic by European fleets.

high discards and reduced reproductive potential (Molloy, 2006; Dickey-Collas et al., 2010). Mortality due to fishing was high in the early 1990s, and a stricter TAC regulation was installed for North Sea herring (Simmonds, 2007). Recruitment was generally low in the mid-2000s, however some stocks showed signs of increasing spawning stock biomass (Figure 1.2). After the mid-2000s all European herring stocks were managed with a careful decision on TACs following a precautionary approach, meaning that quotas were set lower than what could be sustained by the stock, to support recruitment and biomass increase (Molloy, 2006; Dickey-Collas et al., 2010). Up to now, fishing mortality has been decreased and stock biomass stabilized, even showing signs of increase. The baseline of the 1970s is needed to understand that European herring catches are still half of what they were then (Figure 1.2). Hence, considering its history, herring stocks seem to be still in a state of rebuilding (Toresen and Ostvedt, 2000; Dickey-Collas et al., 2010). In 2011, herring was the main species caught by the European fishing fleet with 509,951 t (European Union, 2014) and fifth most fished species worldwide according by weight with 1 780,268 t (FAO, 2014). Within the EU fisheries policy, European herring fisheries are well managed and stocks well assessed, however the inclusion of natural stock variability and the role of herring in the ecosystem is still absent from management plans.

The Celtic Sea Herring

In the Irish EEZ, three herring stocks, the North West, the Irish Sea and the Celtic Sea herring, encompass the Irish herring population and underlie separate fishery management plans. However, all Irish stocks are connected to a degree due to stock mixing during the larval and juvenile phase (Molloy, 2006; Burke et al., 2009) but return to their natal spawning grounds for reproduction (Brophy and Danilowicz, 2002). Natal homing behaviour is well known for herring species (Geffen, 2009). Across its borders, the Irish herring population shows a level of connectivity to stocks in the Shetlands, the English Channel, the central North Sea and the southern Norwegian stock (Limborg et al., 2012). Juveniles use the Irish Sea and the bays and inlets along the south and west coast as nursery grounds (Brophy and Danilowicz, 2002; Molloy, 2006) (Figure 1.3). The Celtic Sea herring spawning grounds are inshore along the Irish south coast and partly in Bantry Bay. The stock contains autumn and winter spawning components with a spawning time from October to January. Recruitment starts in the western area and follows an eastward movement (Molloy, 2006). After the recruitment phase, herring migrate to the offshore feeding grounds extending from the Labadie Bank across to the Smalls (Molloy, 2006) (Figure 1.3). Compared to other herring stocks, the Celtic Sea herring shows a migration pattern with a rather modest distance (Molloy, 2006). Within 2 - 3 years (when they measure 220 mm) juveniles reach maturity and become part of the spawning stock biomass (Lynch, 2011). Mean fish length and weight at age peaked in the 1970s and then declined, together with a decline in general fish condition, however the length/weight relationship stayed constant (Lynch, 2011).

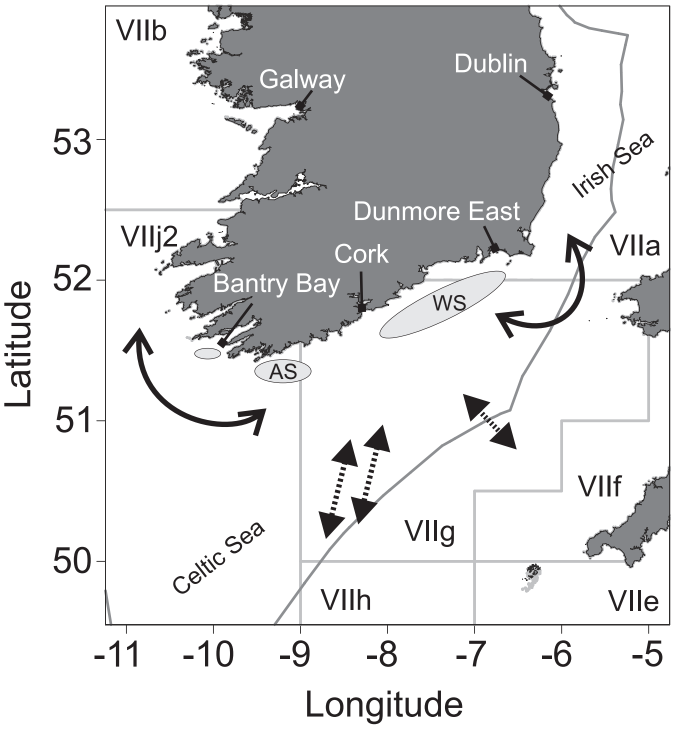


Figure 1.3: The Celtic Sea herring stock is connected to the Irish Sea and North West herring stock (black arrows). Celtic Sea juvenile herring use the Irish Sea and bays and inlets along the south and west coast as nursery grounds. For spawning, herring migrate from the central Celtic Sea to the inshore spawning grounds (dotted arrow). Spawning grounds are inshore along the south coast for autumn (AS) and winter spawners (WS) (grey circles). The Irish EEZ (dark grey line) and ICES management boundaries (light grey lines) are shown.

John Molloy summarised the history of Irish herring fisheries in one of his books (Molloy, 2006). The big herring fisheries of the mid-1950s in the Celtic Sea along the Irish South coast lead to the development of fishing ports and an associated industry in the south of the country. The high biomass in the late 1950s attracted many international and northern Irish vessels causing some friction between local and foreign fishermen. Hence the Irish fishery limits were extended in 1960 and access denied for continental fleets. Herring export increased due to the exclusive Irish fishing rights, but so did illegal fishing activities and conflicts with northern Irish and Dutch fishermen. From the mid-1960s onwards, the fishery expanded rapidly and management was taken over by a local fishermen association. In 1970, scientists saw the first signs of change in the stock due to missing fish at some known locations and a change in size per landed fish. Landings decreased drastically after, albeit 1972/73 was a successful season, which lead to a further increased fishing effort. The assessment body of the International Council of the Exploration of the Sea (ICES) proposed strong TAC regulations, but catches fell below the quota, which were further reduced in every season. In 1977, with the installation of the 200 miles EEZ, the Irish government and the EU managed the herring fishery. The EU Council of Fisheries Ministers banned herring fishing in the Celtic Sea as part of the Common Fisheries Policy from 1977 to 1982 (Molloy, 2006).

The closure was not controlled and small catches continued. Fisherman officially fished sprat and mackerel but were aiming for the herring bycatch. The stock showed signs of recovery in early in 1982, but the fishery stayed closed until the end of the year, which caused large political conflicts with the fishermen communities. After the re-opening for the 1982/83 season, a new management committee was installed introducing TAC quotas and boat restrictions. The market demand for fresh or cured herring was low, hence the Irish fishery switched to a roe fishery for the Japanese market. For the roe fishery, herring had to be fished exactly at the right moment of maturity, which caused a high level of discards because fish were of insufficient quality. To combat the high fishing mortality, the "rotational spawning ground closure" was first introduced in 1988. For some years, the stock recovered due to good recruitment in the early 1990s, but by the end of the 1990s the stock decreased and shoals became scarce. Fishermen criticized the scientific assessment methods and it was agreed that a new management approach and committee was needed. The new committee was eager to install conservative measures like an individual size limitation and again the closure of the spawning grounds. In 2003, the committee became a formal body, the Celtic Sea Herring Management Advisory Committee (CSHMAC), which is still active. The fishery was still poor and the acceptance of low TACs was difficult for the industry (Molloy, 2006).

Present Celtic Sea Herring fishery management and status

The CSHMAC is integrative and contains representatives from the fisher association, fishing co-operatives, scientists and non-governmental organisation representatives (Molloy, 2006). CSHMAC provides management advice to the Department of Agriculture, Food and Marine. Also, ICES provides advice on the annual TAC and revises the stock assessment regularly. A rebuilding plan was followed in the mid-2000s, which was modified to a long-term management plan in accordance with the precautionary approach in 2011. See Appendix A for a full description of the long-term management plan and Section 1.3 for an introduction into the fisheries management and terminology. The stock is assessed from the 1st April to the 31st March each year to include the new recruitment in spring, but for management purposes the TAC is set annually for the 1st January to the 31st December. The management aim is to keep SSB above 41,000 t. If SSB is above a trigger biomass ($B_{trigger}$) the target fishing mortality is set (F_{target} 0.23). If SSB is below $B_{trigger}$, the TAC will be reduced accordingly. The TAC may not differ more than 30% from one year to another. Over time, the MSY management plan can lead to sustainable yield and stability in catches.

Celtic Sea herring is managed as one stock for the ICES areas VIIaS, VIIg and VIIj (Figure 1.3). Irish vessels dominate the fishery with 86% of the TAC. The remaining quota is allocated to Germany, France, Netherlands and the United Kingdom. The Celtic Sea herring fishery is a pelagic trawl and pair trawled fishery with dry hold polyvalent vessels and larger refrigerated seawater vessels (RSW). The fishing season is regulated and opens only for registered vessels participating in the fishery for several weeks from September to January, or until the quota is filled. The closure of the spawning grounds north of 52°N Latitude for vessels larger than 15 m has become a constant stock conservation measurement (Figure 1.3). The Celtic Sea stock is considered to be data rich with a full analytical assessment (Marine Institute, 2013). The quantitative assessment includes commercial catch data, annual biological stock characteristics and data from the acoustic survey. The annual acoustic survey with the RV Celtic Explorer is conducted by the group for Fisheries Ecosystem Advisory Services (FEAS) at the Marine Institute. The Celtic Sea Herring Acoustic Survey (CSHAS) covers part of the West coast, the entire South coast and can reach into UK waters. It is designed to assess the herring stock during the inshore spawning migration and to collect co-incident oceanographic data (O'Donnell et al., 2013). Simultaneously, non-governmental environmental organisations visually observe marine mammals and seabirds for distribution and abundance estimates (O'Donnell et al., 2013).

Due to the low stock biomass, the TAC was low (5,918 t in 2007), but has increased to 15,140 t for 2015. After 2007, with a careful TAC limitation and strong recruitment years, SSB has been increasing and is now above MSY $B_{trigger}$ and B_{PA}. Fishing mortality has increased, but is below F_{MSY}. ICES confirmed with a bench mark assessment in 2014 that the plan still follows a precautionary approach (ICES, 2014). ICES advises to continue protecting the spawning habitat of Celtic Sea herring via obviation of mining and marine constructions on the spawning grounds. Herring from the Celtic Sea, fished by Irish vessels, has been certified as sustainable sea food by the Marine Stewardship Council (MSC) in 2012. The herring fishery in the Celtic Sea is one of the most valuable fishery of the entire Irish fishing quota with an estimated value of €7,770,000 for 2012 (Marine Institute, 2013).

1.2.2 Other forage fish species in the Celtic Sea

Seabirds are selective predators on forage fish and selection can occur based on foraging distance to the colony or beak size for themselves or their young (Ashmole, 1968; Marchetti and Price, 1989; Barrett et al., 2007), while baleen whales are less selective when engulfing forage fish. Hence, predation on forage fish can be species specific and if one species is less available, predation on the other forage fish species could increase. Awareness of those species interactions and trophic linkages are important within an EBFM approach. Thus, even if the main focus of this study lies on herring in the Celtic Sea, two more forage fish species, sprat and mackerel, which are simultaneously present with herring, shall be introduced here. Mixed shoals of herring and sprat as well as herring and mackerel have been observed (e.g.

O'Donnell et al., 2013). Species can be differentiated during the acoustic assessment due to their characteristic schooling behaviour and their specific acoustic signal due to the presence or absence of a swim bladder (Simmonds and MacLennan, 2005). Mackerel have no swim bladder, which results in a different acoustic back scatter signal compared to herring or sprat during acoustic surveys.

European sprat (*Sprattus sprattus*, L.)

European sprat belongs to the family Clupeidea. Sprat are common throughout the North Atlantic and form large shoals inshore. Adult sprat, with an average maximum length of 12 cm, resemble juvenile herring and both species can often form mixed shoals. The misidentification of the two species can cause errors in landing statistics when actual herring catches are reported as sprat (Marine Institute, 2013). Sprat populations in the north-east Atlantic show weak genetic division, however fine-scale population structures should be taken into account (Limborg et al., 2009). Insufficient biological information exists to differentiate between stocks and populations, hence the Celtic Sea and the west of Scotland are managed as one ”stock”, but preliminary studies suggest discrete populations for the south, west and northwest coast of Ireland (Marine Institute, 2013). Only scarce information exists for sprat migration routes, spawning grounds and spawning season in the Celtic Sea, but sprat are known to be multiple spawners with pelagic eggs (Alheit, 1988; Peck et al., 2012a). The sprat fisheries in Irish waters of the Celtic Sea are not subject to quotas and fisheries restrictions only exist for fishing gear and bycatch.

Atlantic mackerel (*Scromber scombrus*, L.)

Atlantic mackerel belong to the family Scombridae. Adult mackerel have a mean length of 30 cm, similar to larger herring, and can have a maximum length of 60 cm, which is much larger than herring. Hence, from an ecological viewpoint, young mackerel can be compared to adult herring, but the appearance of both species is very different and a misidentification is unlikely. Mackerel often shoal together or in proximity to herring and mackerel fisheries can often contain herring bycatch (e.g. Misund and Aglen, 1992; Beare et al., 2003; Marine Institute, 2013). Mackerel is a highly migratory fish and managed as one stock for the entire north-east Atlantic even though it comprises different spawning components (Jansen et al., 2012; Jansen and Gislason, 2013). Spawning areas are spread over the north-east Atlantic with a separate spawning component in the North Sea; however all stock components mix on the feeding grounds in the Nordic seas and the North Sea and the straying of individuals outweighs spatial segregation (Jansen and Gislason, 2013). The Irish share of the EU TAC allocation provided the highest estimated value of all Irish fisheries quotas in 2013 (Marine Institute, 2013).

1.3 Basic principals of stock assessment

This section is based on Jennings et al., 2009 and Haddon, 2011.

A stock is defined as a management unit with jurisdictional boundaries. A stock contains part of a population, or in some cases the entire population is managed as one stock. For example, Atlantic mackerel is managed as one stock for the entire North Atlantic because less information about migration patterns and population dynamics is available. In contrast, different characteristics of the Atlantic herring population are known which facilitates the division of the population into several stocks. Stakeholders and decision makers then decide on the development of a stock within its boundaries based on advice provided by a stock assessment. Within EBFM, the management board should contain representatives of all stakeholders interested or influenced by the stock; hence besides fishermen, fish processing companies, politicians, scientists, environmental agencies or local spokespersons can be part of the management board. The management board decides on targets and management strategies to achieve those targets. Usually targets are set with a long-term perspective and should maximise profit without unbalancing ecosystem health for EBFM. However for overfished stocks, a set target could be the rebuilding of stock biomass under a precautionary approach, as for example for the Celtic Sea herring fisheries in the mid-2000s. Working groups for species and ecosystems within ICES produce regular stock assessments and formulate management advice based on the set targets and pre-defined management plans. The advice is communicated to the EU, which finally decides on respective fishing quotas. While a stock assessment provides the necessary foundation, the final application and implementation lies with the decision makers. Thus a stock assessment has three main objectives:

- Evaluate stock status by estimating fish abundance, biomass and recruitment strength in comparison to historical data and reference points.
- Evaluate uncertainties around stock status by estimating the accuracy of previous estimates and performing sensitivity analyses.
- Predict how different management strategies could impact stock status by testing different scenarios and calculating their respective probabilities.

Stock assessments are based on theoretical ecological principles applied to empirical data. As it is impossible to get an exact abundance estimate for a dynamic, moving stock without physical boundaries in the ocean, those theoretical approaches are needed as much as biological information. The more biological information is available for a stock, the more detailed a stock assessment can be. For fisheries of data poor stocks, the uncertainties in the model outputs are higher and the stock assessment usually more general. Data feeding into stock assessments can be fisheries dependent (e.g. catch-at-age, standardised fishing effort, historical landing records, bycatch estimates) or can come from scientific surveys as fisheries independent data. Both are needed to increase the accuracy of the stock assessment.

Due to the mathematical complexity of stock assessments, reference points have been defined to ease the comparison of stock status between fisheries and to follow the development of a stock. Reference points are used to describe the status of a fishery and give an indication if the stock could be overfished or is fished unsustainably. Reference points are also used to set targets relating to the development of the fishery. Today, reference points are set in view of a long-term productivity, described as maximum sustainable yield (MSY). MSY is defined as the level of exploitation where stock growth and reproduction will be at the maximum. Fishing below MSY indicates that a fishery has a higher potential and theoretically could increase fishing, and with that fishing yield, without reducing the stock production. However fishing above MSY indicates that a stock is exploited above its potential and that stock production is below the exploitation rate, which can lead to a decreasing stock size. Reference points are given either in relation to fishing mortality, F (”How hard can we fish?") or in relation to stock biomass, B or SSB ("How much can we fish?"). The following reference points are typically presented in a stock assessment:

- B_{MSY} / F_{MSY} exploitation at a sustainable level, balancing exploitation and stock production
- B_{lim} / F_{lim} below these levels, a stock is defined as overfished and protection measurements according to the management plan have to be activated (e.g. closing of the fishery)
- B_{MP} / F_{MP} exploitation according to the agreed management plan. B_{MP} / F_{MP} can be the same or below MSY, but never above
- B_{PA} / F_{PA} exploitation at a precautionary approach to either rebuild the stock or if in-sufficient stock information is available
- F_{MAX} exploitation that provides the largest yield. Due to density dependence, the growth of a population actually increases when population size is small because more resources are available for the remaining fish. Hence, the more fish are taken out, the higher the reproductive success and biomass for further fishing will be higher. In other words, with increasing fishing mortality due to exploitation, the yield (biomass per recruit) increases. However, if exploitation is too high, the rate of production is too small to compensate exploitation rate, i.e. the biomass produced by the stock equals the biomass taken from the stock. The stock is exploited at its maximum, F_{MAX}. However, F_{MAX} is difficult to estimate.
- $F_{0,1}$ describes exploitation where the increase in yield is lowered to a 10^{th} of its original potential. In summary, $F_{0,1}$ is very close to F_{MAX}, with the advantage to be easier to calculate and more stable.

Reference points for a fishery are calculated in the stock assessment and then agreed on by the management board. Within a stock assessment, the development of B and F are shown graphically in relation to the defined reference points, e.g. for the Celtic Sea herring fishery (Figure 1.4).

A stock assessment includes five basic steps and can be extended according to the management requirements (Figure 1.5):

1. Calculating components of production based on fundamental ecological principles. Production of a stock is described as the growth of the previous biomass (using von Bertalanfy growth models), subtracting loss of individuals due to death (natural mortality, M), adding the new recruitment (population growth models according to e.g. Beverton Holt or Ricker) and then subtracting the loss of animals due to fishing (F).

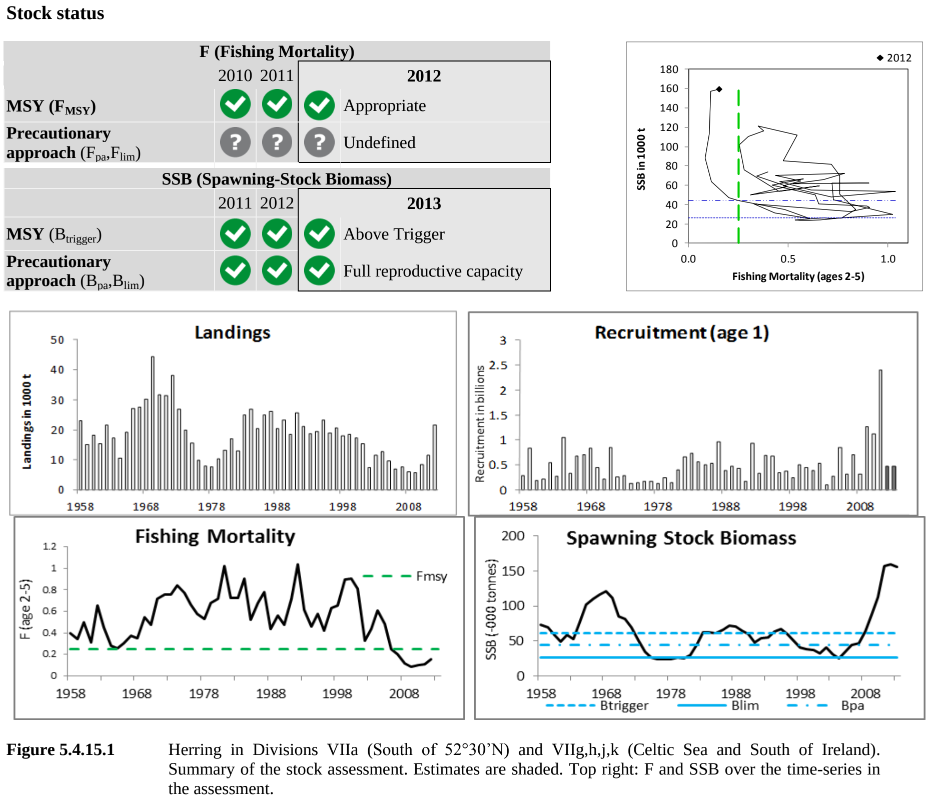
2. Integrating all the previous calculations into a population dynamics model with the structure of population growth models, where M and F are combined to a total mortality. The output are values of total number of individuals per year. This approach is used for data poor assessments, when no information about age structure of the stock exists.

3. For data rich stocks, the population dynamics model is split into age classes and F and M are age-specific. With the same approach as in 2. the population dynamics model produces estimates of number of individuals per age class and year. These values can be multiplied with the average weight-per-age to get total stock biomass or spawning stock biomass. The output includes best fitted, estimated values for the population components (see step 1) and reference points can be calculated.

4. To increase the certainty in the model output, step 3 is repeated many times and sensitivity to changes in model components is tested e.g. how does abundance change if natural mortality is increased or individual growth decreased? How dependent are model components? The models are fitted to historical catch data and can be calibrated with survey abundance indices.

5. Then, the model components can be applied within a virtual population analysis (VPA), which analyses historical stock abundance estimates and allows predictions of stock development in time under the same model conditions. Different scenarios in the interest of the management board can be tested for example if fishing pressure is increased, what would be the probability to deplete the stock within the next 10 years? Reference points can be adjusted based on the stock history.

These are the basic steps within a stock assessment. However, each step can be described in more detail so that when more biological and ecological information is available, the better are the estimates of the principal components of population dynamics and subsequently the better are the following population dynamics models. Accordingly, the accuracy for stock abundance estimates, biomass and reference points needed for management decisions are improved.



Stock status

F (Fishing Mortality)			
	2010	2011	**2012**
MSY (F_{MSY})	✓	✓	✓ Appropriate
Precautionary approach (F_{pa},F_{lim})	?	?	? Undefined
SSB (Spawning-Stock Biomass)			
	2011	2012	**2013**
MSY ($B_{trigger}$)	✓	✓	✓ Above Trigger
Precautionary approach (B_{pa},B_{lim})	✓	✓	✓ Full reproductive capacity

Figure 5.4.15.1 Herring in Divisions VIIa (South of 52°30'N) and VIIg,h,j,k (Celtic Sea and South of Ireland). Summary of the stock assessment. Estimates are shaded. Top right: F and SSB over the time-series in the assessment.

Figure 1.4: Representation of a stock assessment, which would be included in an ICES fishery management advice, here for Celtic Sea herring assessed in 2012. © Marine Institute, taken from Marine Institute (2013).

1.4 Cetaceans as forage fish predators

Cetaceans, commonly known as whales, dolphins and porpoises, are marine mammals that belong to the order of Cetacea and are further divided into two suborders: the Mysticeti and the Odontoceti. The suborder Mysticeti (or Baleen whales) contains whale species that engulf large volumes of sea water and filter zooplankton and small pelagic fish through their baleen plates. They are bulk feeders and predation in areas of high prey densities is believed to be unselective (Bannister, 2002). The

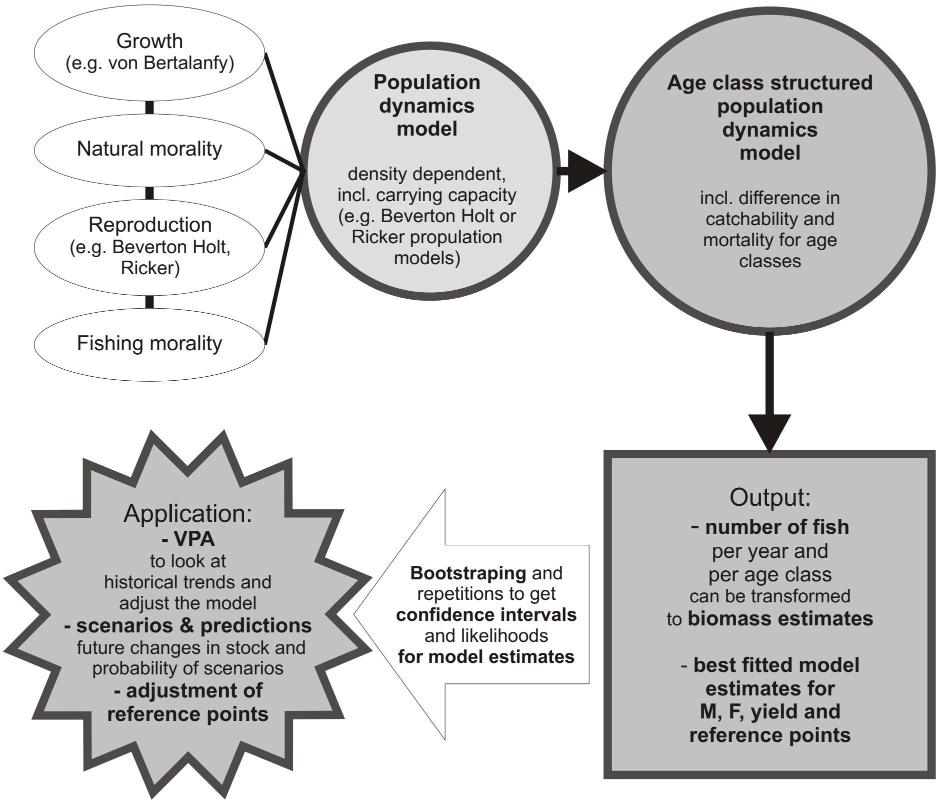


Figure 1.5: Flowchart of processes in a stock assessment. VPA = Virtual population analysis.

suborder Odontoceti (or toothed cetaceans) is taxonomically more diverse, containing toothed whales, dolphins and porpoises. Odontoceti use echolocation to find and select their prey; then they catch the prey with their teeth and bite of smaller chunks or swallow the prey as a whole (Hooker, 2002). Many countries engaged in whaling both within their own waters and in remote locations. The level of exploitations of whales increased with increasing demand for products derived from the fishery, particularly oils. However, the effort increase with industrial whaling reduced population levels of many species close to extinction in the early 1900s. In the mid-1900s, the first whaling regulation and species conservation attempts were put in place and in 1986 commercial whaling of all species was set on hold with exceptions for traditional whaling countries and scientific whaling (Clapham and Baker, 2002). Many species are still considered endangered and population levels are still well below pre-whaling times, however some species show signs of slow recovery (IWC, 2014). The status according to the IUCN list of threatened species for cetaceans in Irish waters is shown in Appendix B. Today, cetaceans are in danger of non-directed human induced injuries and mortality via pollution with noise and waste, ship strikes, entanglements in fishing gear and, for small cetaceans, also bycatch.

The top-down impact of cetacean predation on forage fish is believed to be considerably small. In a global meta-study, cetaceans consumed 12 million tonnes of forage fish, which is one quarter of the global fisheries landings (Kaschner et al., 2006). Forage fish made up only 20% of the cetacean diet, predominantly that of baleen whales, and only 10% of the diet of toothed whales. Thus, globally, due to the wide distribution of cetaceans, predation on forage fish is assumed to be homogeneous over the large forage fish distribution and resource competition and exploitation overlap with fisheries is believed to be small (Kaschner et al., 2006; Engelhard et al., 2014). Yet, the small-scale local foraging of cetaceans can cause high mortality of single fish aggregates or schools, so called high-intensity predation events (Temming et al., 2007). The summation of those small local wipe-outs can have a significant effect on stock dynamics (Temming et al., 2007; Engelhard et al., 2014). On a local scale, competition between cetacean predators and fisheries can occur, leading to discussions about local actions e.g. culls to reduce predation competition with the fishing industry (Kaschner et al., 2006). However, forage fish can have significant influence on top predators via a bottom-up control (e.g. Cury et al., 2011; Smith et al., 2011), where the impact is largest for less mobile predators with a specialised diet and distribution restrictions (e.g. seabirds during breeding or seal colonies). Cetaceans are mobile and able to switch prey and feeding area at times of low prey availability; hence low forage fish abundance could lead to reduced general condition of cetaceans, but not necessarily to mortality.

Cetaceans, especially large whales, have been identified as ecosystem engineers, shaping an ecosystem due to their role as top predator and as a vector of nutrients (Roman et al., 2014). The presence of cetaceans can be seen as a good ecosystem health indicator. Most baleen whales, the main cetacean predator of forage fish, are under protection and some populations show signs of recovery (IWC, 2014). With an increase in predator abundance and increase in local foraging, the dynamics of small pelagic fish stocks could be altered; competition with fisheries could increase; if exploitation is at maximum sustainable levels, the fishing yield would be reduced and the competition between other forage fish predators would be increased, leading to changes in ecosystem balance. On the other hand, if forage fish biomass is low, the body condition of whales could be reduced, whales would leave the area to find richer feeding grounds, which could influence ecosystem dynamics as well as a potential ecotourism economy. Therefore, a good understanding of the spatial overlap of predators, prey and the fishery must be a fundamental basis for management operations within the fishery management strategy. Within an EBFM, these will not only aim to maximise fishing yield, but also to protect species under special attention and to maintain the ecosystem balance. In view of the different scenarios, reliable, and most importantly, local, information on cetacean predators, forage fish dynamics and the ecosystem predator-prey dynamics is a requirement for an EBFM for herring in the Celtic Sea.

1.4.1 Baleen whales in the Celtic Sea

In Irish waters whales were hunted opportunistically by Norwegian operators with an increased effort from 1908 to 1922 for industrial whaling (Went, 1968). 718 whales were landed of which 525 were fin whales and 5 humpback whales, showing the already global decline of the humpback whale population in the early 1900s. After the stop, Norwegian vessels continued whaling up to 1976, after which it was forbidden to whale within the Irish EEZ (Fairley, 1981). Today, cetaceans are under full protection within the Irish EEZ through the EU Habitats Directive and international conventions (O'Brien et al., 2009). Five baleen whale species are recorded in Irish waters, of which two, the blue whale (*Balaenoptera musculus*) and the sei whale (*Balaenoptera borealis*), are more abundant in deeper waters and the open ocean (Bannister, 2002). Blue and sei whales are rarely seen in Irish waters with low abundance estimates (Berrow et al., 2010; Wall et al., 2013). Due to their low and offshore occurrence, they are believed to have low impact on Celtic Sea forage fish population. The other three species, humpback whales, fin whales and minke whales, are potential predators of forage fish in the Celtic Sea and are often observed forming foraging associations (Piatt and Methven, 1992; Skern-Mauritzen et al., 2011). Foraging of baleen whales comes with high metabolic costs as lunge feeding is very energy demanding (Goldbogen, 2009; Goldbogen et al., 2012). Therefore sympatric feeding can be observed in areas with high prey densities, as all species depend on high prey density to guarantee a positive energy balance (Piatt and Methven, 1992; Goldbogen et al., 2011). In the North Atlantic baleen whale distribution has been linked to the availability of pelagic fish as prey (e.g. Anderwald et al., 2012). Prey species found in whale stomachs, or when feeding has been observed, are sandeels (*Ammodytes* sp.), capelin (*Mallotus villosus*), herring, sprat and krill, but also non-pelagic prey as for example cod (*Gadus morhua*) or haddock (*Melanogrammus aeglefinus*) has been found, however in much lower quantity compared to pelagic prey (e.g. Watkins and Schevill, 1979; Piatt et al., 1989; Lydersen et al., 1991; Sigurjónsson et al., 2000; Olsen and Holst, 2001; Lindstrøm et al., 2002; Pierce et al., 2004).

Humpback whale (*Megaptera novaengliae*, Borowski)

Humpback whales are a global species with separate populations in the Atlantic and Pacific (Clapham, 2002). Individuals have a unique fluke colouration, which is used for photo identification and facilitates studies on ecology, life history and migration of the species. Adults have an average length of 14 - 15 m and juveniles are between 8 - 10 m long. Maturity is reached at an age of 5 years. Humpback whales are highly mobile with seasonal migration between feeding and breeding grounds. The North Atlantic population has two main breeding grounds, in the West Indies and around Cape Verde. Mating and breeding takes place in the winter months. From spring to autumn, animals are in higher latitudes at the feeding grounds in the Gulf of Maine, Gulf of St. Lawrence, Newfoundland, Labrador, Greenland, Iceland and Norway (Clapham, 2002). Individuals show general site fidelity in respect to feeding and breeding grounds but not all animals migrate every year to the breeding grounds (e.g.Wenzel et al., 2009). Humpback whales use deeper water for migration and travelling; however, during foraging and breeding they stay in coastal shelf areas. Individuals travel alone or in small, unstable groups. The North Atlantic humpback whale population has been estimated to be 12,000 animals with the majority belonging to the West Indies breeding grounds in the western North Atlantic (IWC, 2014). In Irish waters, 33 individual humpback whales have been photo-identified from a large set of photos since 1995 with inter-annual resightings of animals in and outside of Irish waters (Norway and Netherlands) (IWDG, 2014). Sightings are more frequent along the Irish South coast from June to February, with peaks in September to December (Berrow et al., 2010; Wall et al., 2013). During the absence from March to May, Irish humpback whales are believed to be at the Cape Verde breeding ground, but no photo-identification match has been found to date. The migration distance of 4,000 km from Irish waters to the Cape Verde Islands could take ca. 32 days for a travelling humpback whale according to swimming speed measured in the western North Atlantic (Kennedy et al., 2014).

Fin whale (*Balenoptera physalus*, L.)

Fin whales are a cosmopolitan species that can be found in all oceans, but preferably in temperate to cold waters (Aguilar, 2002). Adults have an average length of 21 - 22 m and juveniles are between 11 - 13 m long. Maturity is reached at 6 - 8 years of age. Fin whales show seasonal migration between feeding and breeding areas. Mating takes place in winter months, but breeding grounds remain unknown. Some animals stay in the higher latitudes and show no signs of migratory behaviour. Animals travel alone or in small groups of up to 7 animals. Fin whales are the fastest baleen whale with swimming speeds of 5 - 8 knots with bursts up to 15 knots and an average of 36 km per day according to tagging experiments (Watkins et al., 1996; Aguilar, 2002). A rough estimate of 35,000 animals exists for the North Atlantic (IWC, 2014). Fin whales rarely fluke or breach, therefore it is difficult to obtain suitable pictures for photo-identification; however, 63 individuals have been identified according to fin shape characteristics within Irish waters (IWDG, 2014). Some individuals have been resighted over the years (Whooley et al., 2011). Fin whales are sighted from May to February along the Irish coast, with peak abundance along the South coast from October to December (Berrow et al., 2010; Wall et al., 2013).

Minke whale (*Balenoptera acutorostrata*, Lacepede)

Minke whales are abundant in all oceans. The common Minke whale with its charismatic white marks on both flippers, is found in the North Atlantic, while smaller subspecies, without the flipper marks, are abundant in the North Pacific and Antarctica (Perrin and Brownell, 2002). Minke whales are the smallest baleen whale with a maximum length of 8 m. Maturity is reached within 6 - 7 years (Perrin and Brownell, 2002). Migration routes are less known for minke whales, but it is believed that the animals feed in higher latitudes e.g. northern Svalbard, Barents Sea and Scotland and mate in warmer southern waters. Minke whales are solitary or can form small groups or feeding aggregations (Perrin and Brownell, 2002). Due to their small size, minke whales have not been in the focus of commercial whaling as much as other baleen whales in the North Atlantic. The minke whale population in the northeast and central North Atlantic and Greenland is in a healthy state with population estimates of 180,000 animals (IWC, 2014). Minke whales are the most sighted baleen whale in Irish waters, however their short surfacing behaviour and inconspicuous blow prohibits good photo-identification. Only 11 animals are identified in Irish waters, but number of sightings exceeds 2000 and therefore abundance is believed to be much higher (Berrow et al., 2010; Wall et al., 2013; IWDG, 2014). Recordings peak from May to October, but whales are also seen in the autumn and winter months but in smaller numbers (Berrow et al., 2010). Minke whales are seen all along the Irish coast and predominantly in shallow waters (Wall et al., 2013).

1.4.2 Other cetaceans in the Celtic Sea

Other cetaceans in the Celtic Sea belong to the Odontoceti. For many of those species e.g. sperm whales (*Physeter macrocephalus*), beaked whales (*Ziphiidae* spp.), northern bottlenose whales (*Hyperoodon ampullatus*) or pilot whales (*Globicephala melas*), forage fish are not an important part of the diet, their distribution does not overlap with forage fish and/or they occur in very low numbers within Irish waters (Hooker et al., 2001; MacLeod et al., 2003; Berrow et al., 2010; Santos et al., 2014). Therefore they are believed to have no significant impact on forage fish populations within Irish waters. Killer whales (*Orcinus orca*) around Norway and Iceland are known predators of herring and mackerel (Foote et al., 2012; Kuningas et al., 2013), however killer whales in Irish waters exhibit a more mammal-based diet (McHugh et al., 2007). Killer whales are more often sighted along the north and west coast of Ireland (Berrow et al., 2010) and individuals have been matched to a killer whale population in Scotland (Beck et al., 2014; Wall et al., 2013). The population size is small and animals have a core area in the Hebrides, west of Scotland. They only transit in Irish waters for short periods with a peak in sightings in the summer months (Berrow et al., 2010). During the passage, killer whales could opportunistically feed on pelagic fish, however their preferred prey are marine mammals for example seals (Beck et al., 2012), hence impact of killer whales on forage fish populations should be minimal in Irish waters.

Striped dolphins (*Stenella coeruleoabla*) are common in off-shore waters (Berrow et al., 2010). Not much is known about their diet, but cephalopods, crustaceans and fish remains have been found in stomachs (Würtz and Marrale, 1993). According to their distribution, striped dolphins diet could include pelagic fish species that are commonly found along the shelf break e.g. blue whiting and mackerel. Atlantic white-sided dolphins (*Lagenorhynchus acutus*) have as well an off-shore distribution and are more often sighted in northwest Irish waters. Strandings have been associated to mackerel fishery, which suggests mackerel are part of their diet (Couperus, 1997). Common Bottlenose dolphins (*Tursiops truncatus*) have a distinct off-shore and in-shore population within Irish waters (Berrow et al., 2010; Louis et al., 2014). The diet of coastal bottlenose dolphins appears to contain predominately demersal fishes and crustaceans (Blanco et al., 2001; Santos et al., 2001), but the offshore bottlenose dolphin population could have a diet comparable to striped or white-sided dolphins. Short-beaked common dolphins (*Delphinus delphis*), which are often seen in feeding aggregations with baleen whales in Irish waters, are common throughout Irish waters and the Celtic Sea (Berrow et al., 2010; Wall et al., 2013). The diet of common dolphins in the Bay of Biscay contained many forage fish species e.g. anchovies and sardines, and predation appeared to depend on prey availability (Meynier et al., 2008; Santos et al., 2013). Common dolphin foraging on pelagic fish in the Celtic Sea is very likely. Abundance estimates for common dolphin along the Irish coast and Celtic Sea are 11,660 animals out of 56,220 for European waters (Hammond et al., 2013).

Harbour porpoises (*Phocoena phocoena*) are the smallest, but most abundant cetacean species in Irish waters. Population estimates for European waters are 375,360 animals, with 25,950 animals within Irish waters (Hammond et al., 2013). Porpoises are a very coastal species and hardly sighted in off-shore areas in the Celtic Sea (Wall et al., 2013). According to stomach content analysis, forage fish are a preferred prey for harbour porpoises (Spitz et al., 2006; MacLeod et al., 2007; Víkingsson et al., 2014) and the distribution of harbour porpoises in the North Sea could be explained by prey distribution (Sveegaard et al., 2012), supporting the dependence of the small marine mammals on forage fish. Within EBFM, predation of all sources on the chosen forage fish species should be included for an as accurate as possible approximation of natural mortality (e.g. Read and Brownstein, 2003; Overholtz and Link, 2007). Common dolphins and harbour porpoises are probable predators on forage fish, especially herring and sprat, in the Celtic Sea and due to their large abundance, predation levels could be reasonably high. However, a detailed in depth analysis of dolphin and porpoise predation on forage fish within the Celtic Sea is beyond the scope of this study, which focuses on predation by baleen whales.

1.5 The Celtic Sea

The Celtic Sea is a shelf area in the eastern North Atlantic, under influence of the North Atlantic Current (NAC). The NAC is an extension of the Gulf Stream and transports relatively warm and saline subtropical waters to the north-east Atlantic (Figure 1.6). The position and strength of the NAC is influenced by the wind field and the relative strength of the subpolar and subtropical gyres. When the subpolar gyre is very strong, relatively cool and saline waters reach the European continental shelf (Hátún et al., 2005). The Shelf Edge Current (SEC) determines the conditions at the Irish shelf edge and plays an important role in transportation of passive biota e.g. eggs and larvae of fishes (Cannaby and Nolan, 2009). The SEC flows along the continental margin from Portugal to Norway and is influenced by the NAC and the North Atlantic Oscillation (NAO) (Pingree and LeCann, 1990; Pingree, 2002). The Irish Coastal Current (ICC) is a stable oceanographic feature going clockwise around the coast due to density gradients with offshore waters (McMahon et al., 1995). The Irish Shelf Front (ISF) between the Irish coastal waters and North Atlantic waters is stable over the year (Huang et al., 1991; McMahon et al., 1995). The strength of the ICC in winter is driven by location of the ISF, wind conditions and freshwater input via rivers and rainfall (Nolan, 1997; Raine and McMahon, 1998).

In the Celtic Sea, the shallow areas remain vertically mixed throughout the year due to tidal movement, however in deeper regions the surface layer warms during summer while bottom waters remain cooler, creating a seasonally stratified water column. Frontal zones are created at the boundary of vertically mixed coastal waters and stratified water masses (Cannaby and Nolan, 2009). During summer, stable, baroclinic bottom jets of up to 30 cm/s are described for the central Celtic Sea, when cold and dense water is trapped beneath the thermocline (Brown et al., 2003; Fernand et al., 2006; Hill et al., 2008). A cyclonic baroclinic circulation pattern is present in the Celtic Sea, which can extend northward along the west coast (Nolan, 2002; Brown et al., 2003). It is believed that the summer circulation in the Celtic Sea is dominated by these bottom jet-like flows and that the warming trend in the Celtic Sea may lead to earlier stratification and more persistent currents (Brown et al., 2003; Cannaby and Nolan, 2009). Given the same direction of the ICC and baroclinic bottom jets, they could be jointly referred to as Irish Coastal Current

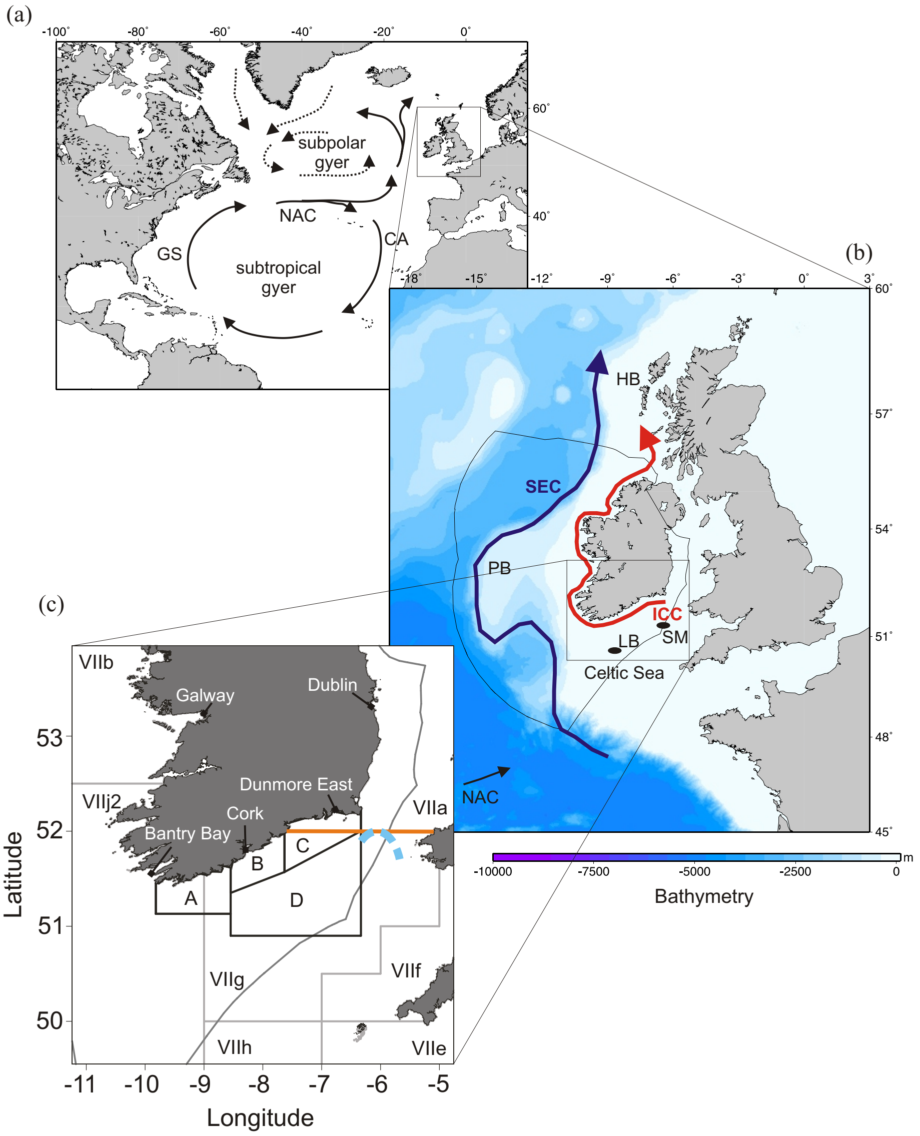


Figure 1.6: The Celtic Sea and the study area in the North Atlantic are shown. (a) The Celtic Sea is influenced by the North Atlantic Current (NAC) and branches of the subpolar gyer. (b) The Celtic Sea is on a shallow plateau. The Shelf Edge Current (SEC, blue line) forms a barrier between the shelf and the open North Atlantic. The Irish EEZ is shown with a fine black line around Ireland. The Irish Coastal Current (ICC, red line) is an important current for larval dispersion along the Irish coast. The Labadie Bank (LB) and ”the Smalls” (SM) are feeding grounds for Celtic Sea herring. (c) The study area is along the Irish South coast (black line) and has been divided into subareas A,B,C and D for different aspects of this study. ICES areas and the Irish EEZ are shown in grey. The herring spawning box in North of 52°N Latitude, where fishing is prohibited for large vessels (orange line). The Celtic Sea front (broken blue line) forms the barrier between the Celtic and the Irish Sea. Additional abbreviations are: GS = Gulf Stream; CA = Canary Current; PB = Porcupine Bank; and HB = the Hebrides.

(Figure 1.6), however the driving mechanism is seasonally different with a horizontal pressure gradient and according Coriolis force in winter and buoyancy friction balanced currents in summer (G. Nolan unpublished). Additionally, the Celtic Sea Front (CSF) is an important oceanographic feature in the Celtic Sea (Figure 1.6). The front forms in summer due to the high degree of stratification, which breaks down abruptly at the entrance to the Irish Sea and the Bristol Channel (Simpson, 1976; James, 1977). During winter, Celtic Sea and Irish Sea are well mixed.

Simultaneously to global warming and the warming of the North Atlantic (e.g. Polyakov et al., 2010; Rhein et al., 2013), Irish waters exhibit a warming trend in sea surface temperature (SST) between 1850 and 2008 of 0.3°C, with the strongest warming trend observed in south-western waters (Cannaby and Hüsrevoğlu, 2009). Average SST ranges are for winter, 6 - 8°C; for spring, 7 - 12°C; for summer, 12 - 16°C and for autumn, 14 - 8°C (Cannaby and Nolan, 2009). Salinity at the water surface shows year to year variability and a freshening linked to increased winter rainfall, however no significant trend in freshening was found for water masses below 200 m on the Irish continental shelf (Cannaby and Nolan, 2009).

1.6 Thesis objectives and study outline

The overall aim of this thesis is to explore the position and trophic links of forage fish, especially Atlantic herring, in the Celtic Sea. The predator-prey relationship between baleen whales and forage fish is investigated. Geostatistics, energy content analysis and modelling techniques were used to widen the knowledge base of forage fish, particularly herring, and baleen whales in the Celtic Sea ecosystem. This study contributes to ecosystem understanding, identifies current knowledge gaps and discusses possibilities for developing an EBFM of the herring fishery in the Celtic Sea.

This thesis contains a general introduction, followed by four consecutive chapters and closes with a general discussion of the application of the results produced by this study. Within the discussion, a general conceptual model on the trophic links between baleen whales and forage fish is presented. This model shows the importance of the previous chapters to increase the ecosystem understanding in the

Celtic Sea and the trophic links between baleen whales and forage fish. The methods are explained in each chapter and a list of the software used for analysis and presentation of the results is given in Appendix C. Contributions to international conferences presented within the framework of this thesis are shown in Appendix D. A brief overview of chapter aims and content is given below.

Chapter 2. *Prespawning herring distribution in the Irish Celtic Sea between 2005 and 2012*

This chapter analyses the Atlantic herring distribution within the Irish part of the Celtic Sea during prespawning migration. The aim of this chapter is: (i) to describe the spatial distribution pattern; (ii) to identify any possible distribution shift; and (iii) to analyse environmental distribution constrains. The modelling of variograms and the centre of gravity, as well as linear regression for the realized habitat are the geostatistical methods applied to data collected during the annual acoustic stock assessment from 2005 to 2012. The acoustic back-scattering coefficient (NASC) on a resolution of one nautical mile has been used to analyse the distribution pattern of herring, while temperature and salinity at the sea surface and bottom have been used to describe habitat and potential environmental distribution constrains.

This chapter has been published as: Volkenandt, M., Berrow, S., O'Connor, I., Guarini, J.-M. and O'Donnell, C. (2014). Prespawning herring distribution in the Irish Celtic Sea between 2005 and 2012. ICES Journal of Marine Science, doi:10.1093/icesjms/fsu143

Chapter 3. *Fine-scale spatial association between baleen whales and forage fish in the Celtic Sea*

Is the Celtic Sea a prey hot spot for baleen whales? In this chapter, the spatial co-occurrence of forage fish (being Atlantic herring, European sprat and Atlantic mackerel) and the most abundant baleen whales (fin, minke and humpback whales) were analysed. The aim of this chapter is: (i) to make the link between forage fish and baleen whales in the Celtic Sea and consequently (ii) to highlight the importance of the Celtic Sea as a prey hot spot for baleen whales and (iii) to identify any foraging biomass threshold and prey selectivity for baleen whales. Data from the annual acoustic fish survey were aligned with the synoptic obtained marine mammal observations from 2007 to 2013. First, the distance between predator and prey was calculated and compared to a simulated data set. Then, forage fish biomass densities and average fish length were calculated for the prior defined foraging distance to identify a foraging biomass threshold and prey selectivity.

This chapter is submitted to the Canadian Journal of Fisheries and Aquatic Sciences.

Chapter 4. *Energy content of Atlantic herring (Clupea harengus) driven by reproductive status*

Here the relationship of the reproductive status to energy content of Atlantic herring is analysed. Reproductive status is defined as juvenile, pre- and post-spawning and the energy content has been measured using a bomb calorimeter. The aim of this chapter is: (i) to provide an estimate of energy content for herring; and (ii) to analyse variability in energy content due to body size and reproductive status. Linear regression models based on body length and maturity were fitted to the energy measurements to explore variability in the data. The results have been compared to energy contents found in literature for Atlantic, Baltic Sea and Pacific herring.

This chapter is in preparation for submission to the Journal of Fish Biology.

Chapter 5. *Comparison of energy content of forage fish from the Celtic Sea*

Following the same approach as in the previous chapter, the energy content of European sprat and Atlantic mackerel is analysed. The aim of the chapter is: (i) to provide estimates of energy content for sprat and mackerel; and (ii) to compare energy content of co-occurring forage fish species (i.e. herring, sprat and mackerel). A linear regression model was fitted to the data to explore the relationship of water content to energy densities and compared to literature. The prey quality defined by the energy content and its variability due to reproductive status is presented and discussed for the three forage fish species.

This chapter is in preparation for submission to the Journal of Fish Biology.

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Chapter 2

Prespawning herring distribution in the Irish Celtic Sea between 2005 and 2012

> "Understanding [herring] spatial distribution can help protecting
> the herring stock and therewith the ecosystem equilibrium. [...]
> The aggregated, randomized herring distribution pattern during migration
> can find application in predator - prey ecosystem modelling."
>
> (p. 68)

Abstract

Knowledge of species spatial distribution is fundamental to understanding trophic interactions and ecosystem structure. Intraspecies-specific dynamics and environmental factors shape species distribution within an ecosystem. Distribution patterns and the realized habitat of Atlantic herring (*Clupea harengus*), a key fish species in the Celtic Sea, were examined using distribution data collected during annual acoustic stock assessment surveys during 2005 to 2012. Distribution patterns during migration to spawning grounds were analysed using geostatistical methods, including modelling of variograms and comparing the centre of gravity (CG). Distribution patterns were further linked to oceanographic variables collected with the acoustic data to describe habitat. Herring density was greatest inshore along the spawning grounds and lower farther offshore. Herring shoals were clustered and randomly distributed during spawning migration. Variograms of fish densities described the global structure, with high local variability of the same order of magnitude as variability at a regional scale, indicating that no continuous structure can be found within the study area. The CG-values showed that the average position of the population was located northeast. The realized habitat for herring encompassed a wide range of temperatures and salinities; therefore, oceanographic features were not a limiting factor for herring distribution during spawning migration. The present study changes the perception of the spatial distribution of the Celtic Sea herring stock from a more continuous distribution to a discrete model, with implications for trophic ecosystem modelling on local scales. Future studies of herring distribution and its influence within the Celtic Sea ecosystem would benefit from using the approach employed in the present study for analysing aggregation patterns.

Keywords:
acoustic backscatter survey · Celtic Sea · geostatistics · herring (*Clupea harengus*) · spatial distribution

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This chapter has been published as: M. Volkenandt, S. Berrow, I. O'Connor, J.-M. Guarini and C. O'Donnell, 2014. *Prespawning herring distribution in the Irish Celtic Sea between 2005 and 2012*. ICES Journal of Marine Science. doi: 10.1093/icesjms/fsu143

2.1 Introduction

The understanding of species distribution is an important element in the development of ecosystem-based fishery management (EBFM) (Johnson et al., 2013). An EBFM describes sustainable fishery management which maximizes economic profitability, but without decreasing marine ecosystem health and functioning (Browman and Stergiou, 2004). Spatial distribution data are valuable within an EBFM for directing fishing effort and as an indication of regions of high management impact i.e. for the allocation of fishing quotas per area and the introduction of marine protected areas (Babcock et al., 2005; Johnson et al., 2013). Under an ecosystem approach, the distribution and foraging behaviour of predators can be linked to prey distribution. Subsequently, prey distribution and availability can be integrated into dynamic, bioenergetics, ecosystem models. Thus, spatial distribution of target species can feed into an EBFM framework directly via the installation of spatial regulations and indirectly via trophic web models to sustain ecosystem health. However, current gaps in knowledge exist within aspects of the biotic (e.g. population densities, life stages and migration cycles) and abiotic (e.g. environmental conditions, predator and prey availability) variables affecting species distribution and the spatial scale over which these habitat variables may act (Planque et al., 2011; Johnson et al., 2013; Sharples et al., 2013; Le Pape et al., 2014).

Atlantic herring (*Clupea harengus* L.) is a highly migratory species that occupies nursery grounds during the early life stages and then migrates to spawning, wintering, and feeding grounds (Blaxter and Holliday, 1963). Understanding its multifarious distribution can feed into the implementation of an EBFM for herring fisheries. Atlantic herring, a small pelagic forage fish, is a key species within the Celtic Sea ecosystem, transferring energy from low to high trophic levels (Peck et al., 2014). It is an important prey for marine top predators such as seabirds and cetaceans (Chivers et al., 2012; Ryan et al., 2014). The Celtic Sea herring fishery is one of the most economically valuable fisheries in Ireland, with 86 % of the total allowable catch (TAC) in the Celtic Sea (Marine Institute, 2013). The Celtic Sea stock is considered to be data rich, with a full analytical assessment (Marine Institute, 2013). In recent years, stock biomass has undergone a constant increase (Figure 2.1), and fishing mortality (F) is well above the level of maximum sustainable yield (F_{MSY}). Management tools in this fishery include a strictly regulated fishing season (open for several weeks from September to December), a TAC quota allocated to the boats participating in the fishery, and a constant closure of one of the key herring spawning grounds (spawning box north of 52°N, Figure 2.2) for vessels larger than 15 m (Marine Institute, 2013).

The Celtic Sea herring stock is spatially and temporally complex due to exchange with other stocks in the North Atlantic and within the Celtic Sea. The stock shows genetic exchange within Irish waters (i.e. Northwest herring and Irish Sea herring, Figure 2.2), but also extending to the wider North Atlantic, including Shetland, North Sea and Norwegian stocks (Brophy and Danilowicz, 2002; Molloy, 2006; Limborg et al., 2012). The Celtic Sea stock is comprised of autumn- and winter- spawning components, with a protracted spawning period from October to January (Molloy, 2006). The stock components mix throughout their life cycle on the offshore feeding grounds as well as on the nursery grounds (Brophy and Danilowicz, 2002). Spawning begins inshore at the western Irish south coast and follows an eastward movement (Molloy, 2006). Natal homing and a natal area imprint are suggested for Celtic Sea herring based on otolith microstructure and genetic markers (Brophy and Danilowicz, 2002; Ruzzante et al., 2006). After the spawning period, herring migrate to the offshore feeding grounds that extend from Labadie Bank across to the Smalls (Figure 2.2; Molloy, 2006). Juvenile herring use the Irish Sea and the bays and inlets along the south and west coasts as nursery grounds (Brophy and Danilowicz, 2002; Molloy, 2006). Compared to other North Atlantic herring stocks, Celtic Sea herring exhibit a migration pattern with a rather modest distance (Molloy, 2006).

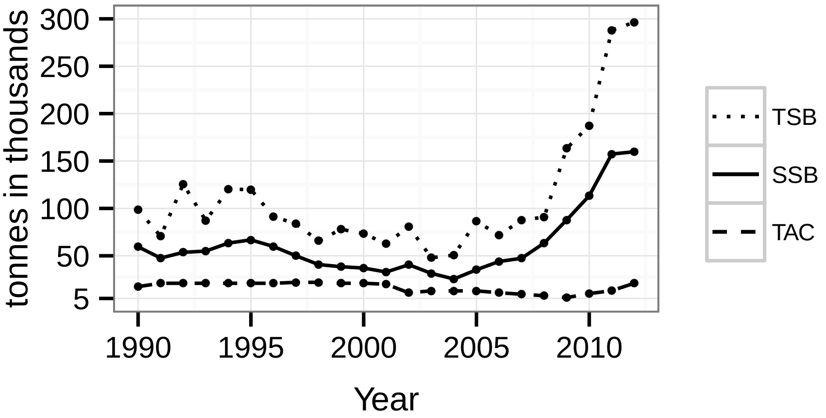

Figure 2.1: Total stock (TSB, dotted line) and spawning stock (SSB, solid line) biomass in tonnes and total allowable catch (TAC, dashed line) over time for the Celtic Sea herring in ICES area VIIg (according to the stock assessment, HAWG, 2013).

This study aims to quantify the spatial structure and distribution of pre-spawning herring during the migration to inshore spawning grounds in the Celtic Sea by applying geostatistical methods (variograms) to the existing survey time series data. The analysed

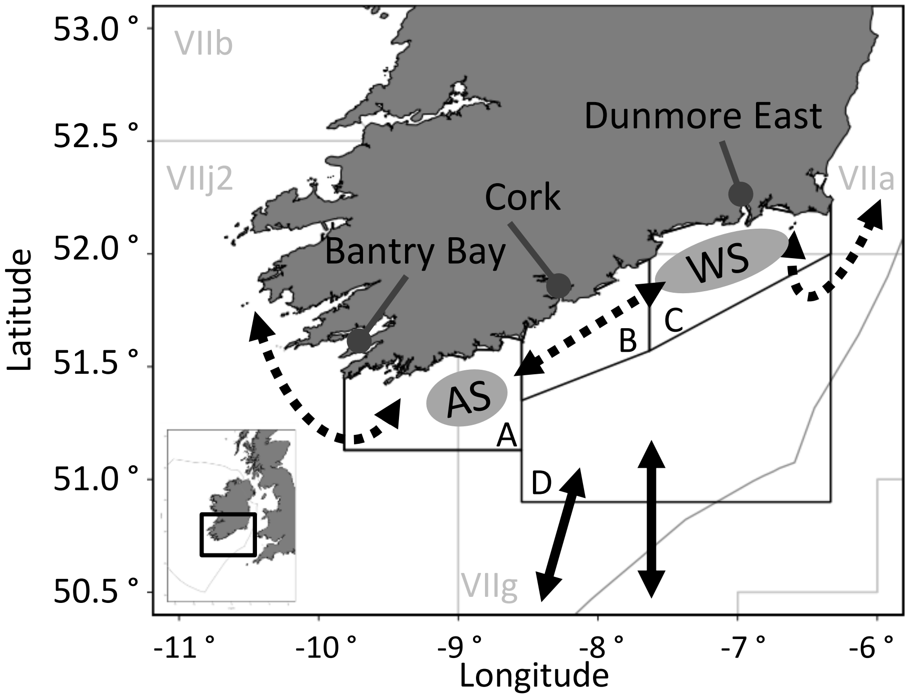

Figure 2.2: Research area in the Irish Celtic Sea (black box) divided into four areas: A. western South coast, B. inshore around Cork, C. inshore around Dunmore East and D. offshore. The herring spawning box closure is north of 52°N (thick grey line), where no vessels larger than 15 m are allowed to fish. ICES areas and the Irish EEZ are shown (light grey lines). Herring coming from the feeding grounds in the central Celtic Sea migrate into the coastal areas for spawning (black arrows). The stock contains autumn and winter spawner components, with spawning grounds all along the south coast and in Bantry Bay (light grey shaded areas). Autumn spawners are more abundant in the western South coast (AS) with a later winter spawning towards the east (WS). The Celtic Sea stock mixes with the Irish Sea Herring and the North West Herring during the larval and juvenile phase (black, dotted arrows).

distribution data were collected during the annual acoustic surveys carried out between 2005 and 2012. The centre of gravity was calculated to help identify any visible trends in the herring distribution over time. Oceanographic variables such as temperature and salinity were used to describe the realized habitat and to identify distribution constraints due to the abiotic environment. The realized habitat describes where fish are actually observed and can be compared to the potential habitat, which is defined by variables within the range where a species can survive (Röckmann et al., 2011).

2.2 Material and Methods

Study area and data acquisition

The geographic coverage of the survey (Figure 2.2) is focused on the Celtic Sea plateau with a maximum depth of 125 m and reaches shallow depths of ca. 40 m close to the coast. The study area was limited to the annual survey coverage of the Celtic Sea Herring Acoustic Survey (CSHAS) programme. Transects were parallel and perpendicular to the coast line with 2 - 4 nautical mile spacing in offshore and 1 nautical mile in inshore areas (O'Donnell et al., 2012). The research area was divided into four areas: A. the western South coast, B. inshore Cork (Co. Cork), C. inshore Dunmore East (Co. Wexford) and D. offshore (Figure 2.2). This division corresponds to the change in the survey transect resolution. The survey was carried out each year over 21 days in October from 2005 to 2012. A calibrated Simrad EK60 echosounder with four frequencies (18, 38, 120 and 200 kHz) collected acoustic data continuously along the ship route. The Nautical Area Scattering Coefficient (NASC) is the backscattered acoustic signal of objects in the water column (Simmonds and MacLennan, 2005). NASC values are dimensionless but can be converted to fish abundance and biomass with species specific transformations (Dalen and Nakken, 1983), however within the frame of this study, the NASC values were used as an untransformed density index of pelagic fish distributions. NASC values were integrated over depth and 1 nautical mile into effort blocks known as elementary distance sampling units (EDSUs), which are routinely used for biomass interpolation within the stock assessment. The echograms were identified to a species level, based on species specific acoustic signals, shoal shapes and directed trawling. Haul composition of trawls performed in proximity to the shoals were used to validate the identification of herring categories on the echogram. Only shoals identified as "definitely" and "probably" herring were analysed in this study, see O'Donnell et al. (2012) for a detailed survey description. In average 44

CTD stations placed along N - S- transects were sampled per year. Temperatures and salinities were collected using a calibrated Seabird 911 CTD sampler (O'Donnell et al., 2012). The upper 10 m in the water column and the 10 m above sea floor were used to describe environmental conditions at the sea surface and bottom respectively.

Data analysis NASC percentage distribution

The NASC percentage for each sub-area and for the spawning box (north of 52°N) has been calculated for each year. The average percentage per area was calculated as a weighted average.

Variograms

A variogram quantifies the spatial structure of the data by calculating the average square spatial difference of a regionalized variable as a function of distance and direction (Matheron, 1971; Oliver and Webster, 2014). Variograms are usually described by a set of criteria, as the local variability (called "nugget"), a range beyond which the data becomes spatially independent ("range") and a maximum value for the average square differences ("sill") (Matheron, 1971; Oliver and Webster, 2014). Variogram models are used to interpolate the data by kriging (Matheron, 1971; Rivoirard et al., 2000; Oliver and Webster, 2014). Here, the EDSU NASC data were used to compute empirical semi-variograms under an intrinsic hypothesis (stationary of the increments only). Coordinates were projected to nautical miles for the analysis. A lag distance of 30 nautical miles with a distance interval of 2 nautical miles was applied as variogram parameter and the model structure investigated for anisotropy. Models that ensure positivity of variance were adjusted to the data using ordinary least square criterion and the best fit was retained. If cross-validation (using the model to re-estimate successively each of the points by the actual neighbours) validated the data (i.e. providing a regression coefficient not significantly different to 1 for the regression between observed and predicted data), then the average stock value and its spatial distribution field were calculated using a 2D kriging. The standard error (SE) for the regression coefficient and the proportion of variation explained by the best-fit line (r^2 value) were calculated. The program GS+ (Geostatistics for the Environmental Sciences, Version 5.1.1, Gamma Design Software) was used to perform all calculations.

The centre of gravity

The centre of gravity (CG) is an estimator for the theoretical centre of the sampled population (Woillez et al., 2009). It does not indicate actual positions of fish, but rather provides a first spatial distribution overview allowing for comparison between years. Because of an uneven transect spacing in the study area, the area of influence (spatial weight) was calculated for each sampling point before the CG was calculated (Woillez et al., 2009). A CG of the sampling effort was first calculated. This CG- value should not differ significantly over the years, showing that the sampling plan remained unchanged. Then the CG of the herring stock was calculated and a linear model was fitted to test for the existence of significant trends in the stock's average distribution. The methods and R script given in Woillez et al. (2009) were used for all calculations.

Average and ambient environmental conditions

Temperature and salinity values, recorded by a CTD probe at defined sampling stations, were used to interpolate by kriging the environmental conditions over the study area. For each variable (bottom and surface temperatures and salinities respectively) models were fitted to empirical variograms and cross-validation was performed to select the best model. The mean and standard deviation of each variable was calculated to describe the average condition in the study area. The mean ambient condition (Con) and standard deviation for herring in the Celtic Sea were calculated as average temperature or salinity weighted by the NASC value at the position(x,y):

$$\overline{Con}_{\mathrm{amb}} = \sum \left(\frac{NASC_{(\mathrm{x,y})}}{\sum NASC} \right) \times Con_{(\mathrm{x,y})} \tag{2.1}$$

Average and ambient conditions at the bottom and surface for temperature and salinity were compared with a Tukey t-test. All analyses were done with the open-source statistical software "R" (`http://cran.r-project.org`). Kriged maps for temperature and salinity can be found in the respective CSHAS report available on the Marine Institute internet page (`http://marine.ie`), e.g. for 2012 see O'Donnell et al. (2012).

2.3 Results

NASC percentage distribution

The NASC distribution from 2005 to 2012 is shown in Figure 2.3. Starting with the western area, none or only few herring were found in area "A" in all years, besides in 2007 and 2009 when 12 % and 8.9 % of NASC were estimated respectively (Figure 2.3). The distribution from the mid to the eastern South coast can be described as either "overall" with high densities in- and offshore (2005, 2008, 2009, 2012) or as "inshore" with high densities mainly close to the coast (2006, 2007, 2010, 2011). In the offshore area "D" the distribution pattern varied from a wide distribution of a high number of small shoals (2008 and 2009) to a dense aggregation on a transect line (2005 and 2012). In years with a pre-dominantly "inshore" distribution, the area "C" around Dunmore East generally contained higher percentages of fish than area "B" around Cork. Within area "C", high percentage of herring was found north of 52°N within the protected spawning box (in average 60 % of all fish in area C; Figure 2.3). Thus in average, the western area had the least percent of NASC with 2 ±4 %. The inshore area around Cork and the offshore area had comparable percentages of NASC with 18 ±23 % and 21 ±20 % respectively. Herring was predominantly found in the inshore area around Dunmore East with 59 ±24 % . The standard deviations for each area were high, indicating an uneven distribution during the study period.

Variograms

No anisotropy was detected in the variograms and all fitted variograms had an isotropic structure. Only the variograms for 2005, 2006, 2010 and 2012 indicated the presence of a stationary structure and thus a spherical model could be fitted to the variograms. A spherical model shows a steady increase of variability up to the sill and remains on a plateau. For other years, a linear model was fitted, which included a linearly increasing variability with distance without reaching a sill (Table 2.1 and Figure 2.4). For 2007 a gaussian model was fitted, which includes a gradual increase of the intercept and an exponential structure but without reaching a sill. Even though 2005, 2006, 2010 and 2012 had a better fit, none of the analysed variogram models were statistically significant and the cross-validation could not be accepted because of the low r^2 and high standard error (Table 2.1). The global structure of the NASC values showed a very high variability at a local scale (nugget), comparable to the variability at a regional scale (sill). Thus, based on the 1 nautical mile EDSU resolution, migrating herring appeared to be randomly distributed within the study region with high variability in the NASC values. No continuous structure could be detected.

The centre of gravity

The centre of gravity (CG) for survey effort showed no significant difference across the time series, indicating a similar survey effort between years and therefore the CG of the herring stock could be compared (Figure 2.5). Using the CG of the survey effort to indicate the centre of the study area, the positions of the herring CG was examined. In all years, the herring CG-values were distributed north-eastern of the centre, indicating an uneven distribution of the herring CG. The north-eastern position was in accordance with

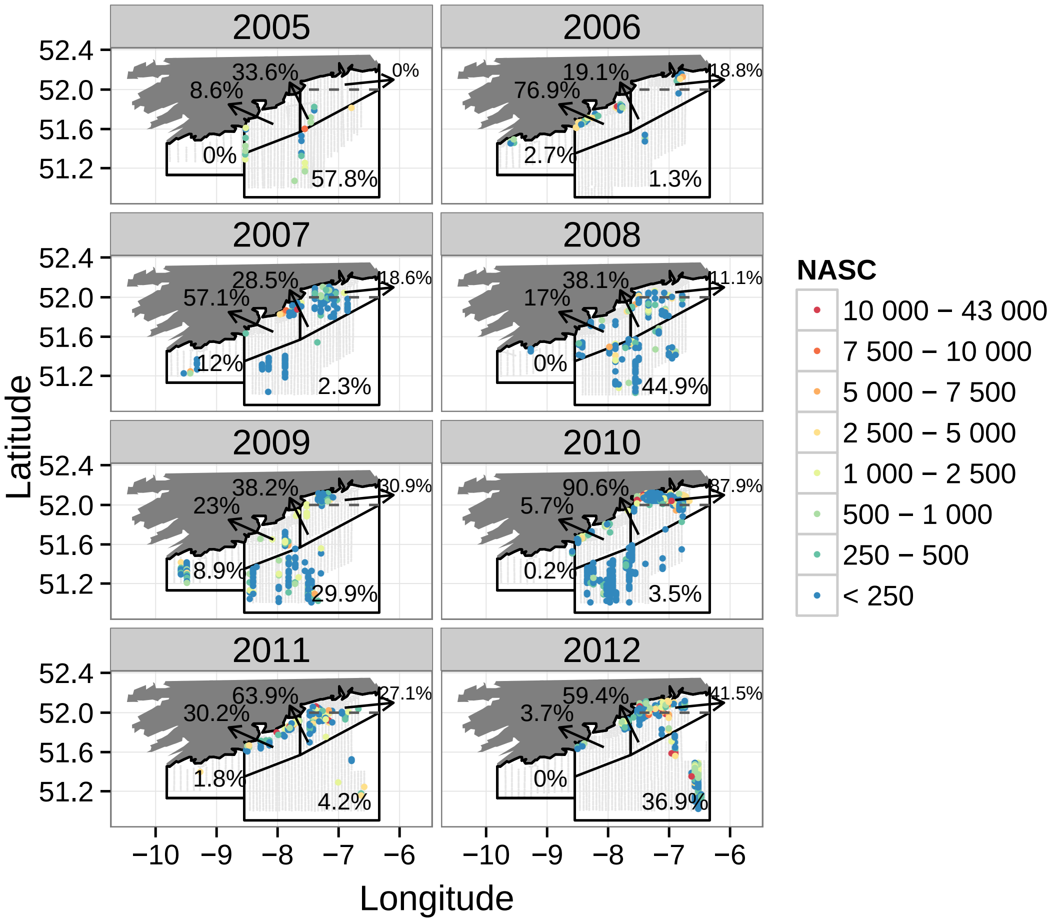

Figure 2.3: Herring NASC distribution from 2005 to 2012 (coloured points). The numbers give the percentage of NASC per area and year. The percentage of NASC within the herring spawning box (north of 52°N, grey dotted line) is shown.

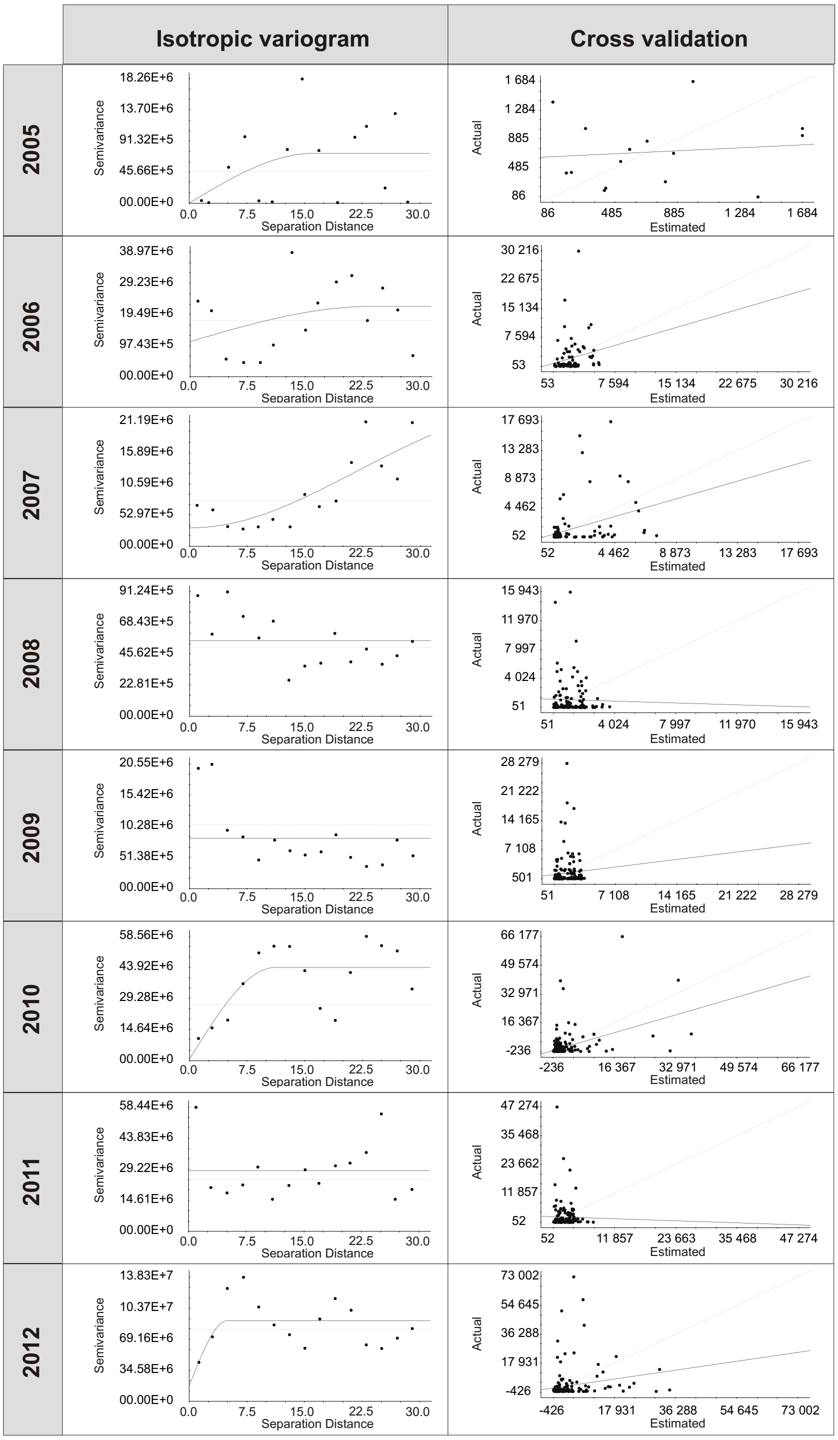

Figure 2.4: Variograms and cross validation plotted for each year. Parameters of the model fit are shown in Table 2.1.

Table 2.1: Variogram models with respective r^2 to estimate NASC variance for each survey year. Model fit was compared with cross-validation and the according regression coefficient (slope), r^2 value and standard error (SE). RSS = residual sum of squares.

		variogram		cross validation		
year	model	r^2	RSS	slope	r^2	SE
2005	spherical	0.155	4.04E+14	0.102	0.013	0.245
2006	spherical	0.089	1.51E+15	0.621	0.004	0.335
2007	gaussian	0.688	1.63E+14	0.613	0.129	0.145
2008	linear	0.392	5.11E+13	-0.062	0.001	0.244
2009	linear	0.468	3.74E+14	0.264	0.006	0.242
2010	spherical	0.507	1.85E+15	0.617	0.205	0.061
2011	linear	0.000	2.43E+15	-0.069	0.000	0.264
2012	spherical	0.216	7.92E+15	0.309	0.037	0.111

the higher fish densities along the eastern South coast. Only the CG for 2009 was westerly compared to all other years, which was due to the high percentage of fish mid-offshore (Figure 2.3). The CG latitude and longitude for the herring stock showed a fluctuation of 0.2°- 0.3° respectively around the mean CG of 51.6°N / -7.5°E. A linear model was fitted to the longitude and latitude CG, however no significant linear trend was found (Figure 2.5). This indicated that the general herring distribution varied over the years but no distribution shift could be shown using the CG.

Average and ambient environmental conditions

For temperature (T) as well as salinity (S), the conditions at the bottom of the water column were significantly different to the conditions at the sea surface and showed a higher variability ($p < 0.001$ respectively, Figure 2.6). For a small number of years and single variables, a significant difference could be found between the average and ambient condition (i.e. T bottom in 2006); however there was no significant overall difference between the "average" and "ambient" for either temperature or salinity ($Tbottomp = 0.05$, $Tsurfacep = 0.42$; $Sbottomp = 0.12$, $Ssurfacep = 0.45$). A decreasing trend with time for surface temperature ($p < 0.05$) and an increasing trend for surface salinity with time ($p < 0.01$) were detected during the study period. No significant trends for the bottom conditions were found ($p > 0.05$).

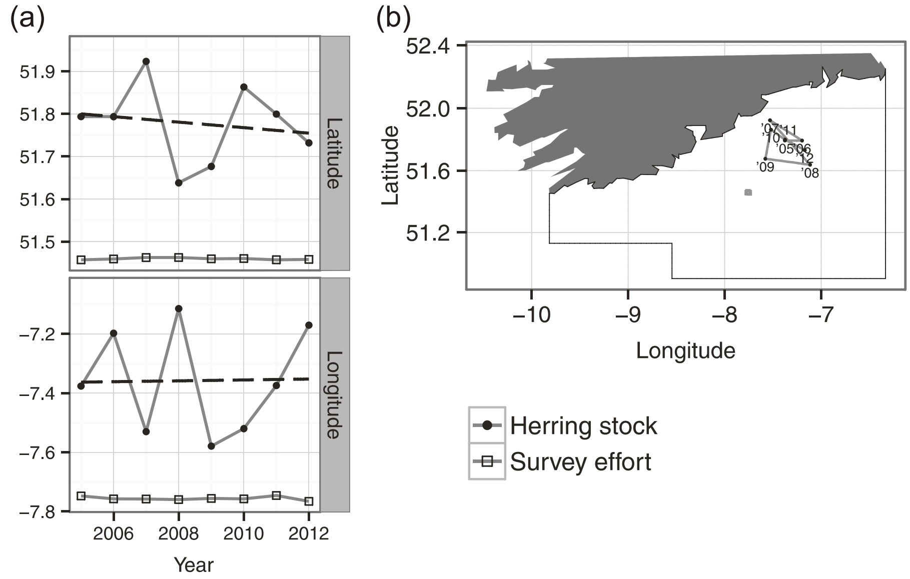

Figure 2.5: The centre of gravity (CG) for the herring stock (black points) and the survey effort (open squares) for 2005 - 2012. (a) The CG showed no significant linear trend (dashed black line). In (b) the theoretic mean position of the herring population over time in the research area is shown.

2.4 Discussion

General herring distribution

The results of the present study showed where and how herring was distributed in the Celtic Sea during spawning migration, followed by an exploration of distribution shift and distribution constraints. Herring abundance increased from the west to the east coast and was generally very high inshore; however in four out of eight analysed years, herring was also abundant offshore. The variance in NASC was high, indicating an overall random distribution without spatial dependence. No statistical significant distribution shift could be found using the CG index and the herring distribution was not constrained by temperature or salinity. The Celtic Sea herring stock contains autumn and winter spawning components, with a decreasing proportion of autumn spawners (Harma et al., 2012) and the autumn spawning grounds are predominantly along the western South coast (Figure 2.2). The low herring densities encountered in the west during the surveys could be due to a mismatch of survey time in October with the already decreasing proportion of autumn spawners. Even though the western area contained in average only 2 % of NASC, it is an area for stock exchange and mixing. Larvae from the South coast are transported into the Southwest and West coast via the coastal currents to reach the nursery grounds (Figure 2.2; Brophy et al., 2006; Molloy, 2006; Clarke et al., 2010). With low fish densities, the western area is uninteresting for commercial fishing; however it is important to keep

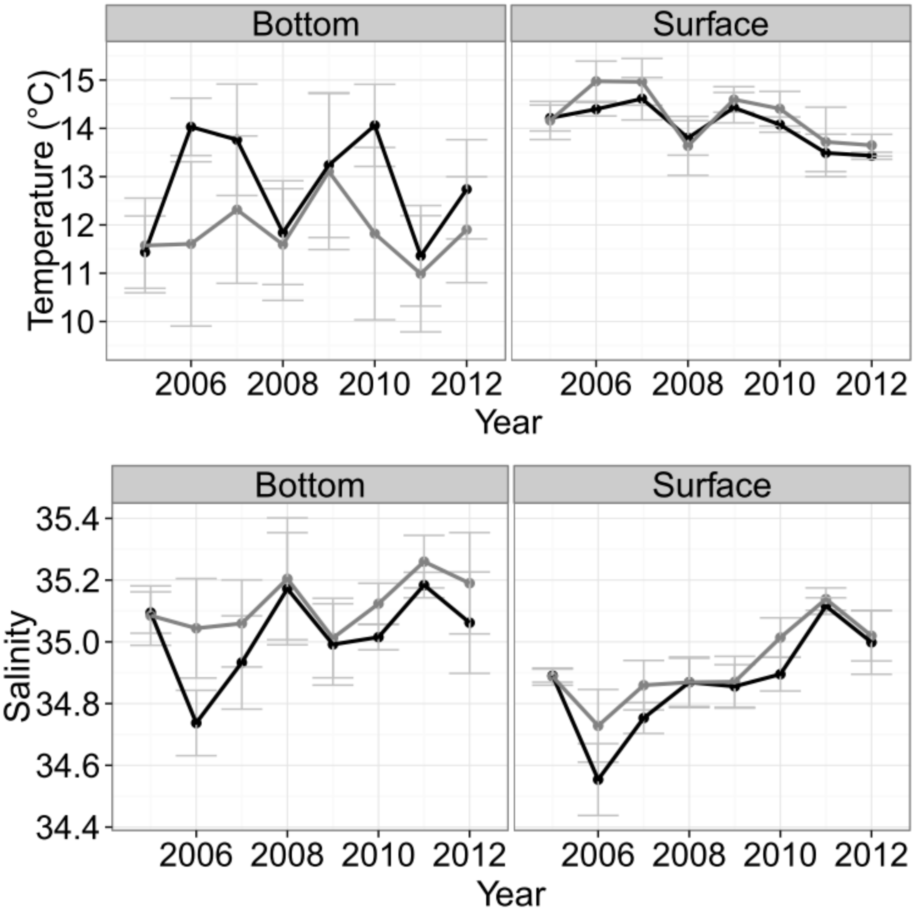

Figure 2.6: Ambient (black line) and average (grey line) temperatures and salinities with standard deviations, given for the bottom and surface over time.

surveying because of its high biological significance for stock complexity.

The most spawning grounds and the largest spawning bed with 36 km^2 are around Dunmore East (O'Sullivan et al., 2013), which contained generally the highest herring abundance. Thus, the eastern coastal area, including the spawning box is of high importance for the herring stock and its management. The spawning box closure protects the high abundance of spawning fish from fishing induced mortality. Protection of spawning grounds allows for undisturbed spawning and, if post larval conditions allow, an increased chance of recruitment success and accordingly more recruits with spawning side fidelity for the following years. The fishery yields outside the spawning box should benefit via connectivity and export of fish and larvae from protected to fished areas via the so called "spill over effect" (Gell and Roberts, 2003; Le Pape et al., 2014). In the North Sea, at low abundance, herring remained within the main spawning grounds and expanded to surrounding areas as stock size increased (Dickey-Collas et al., 2010). The Celtic Sea herring year classes 2007, 2009 - 2011 showed positive recruitment to the spawning stock biomass.

With the current increase in biomass in the Celtic Sea, herring could expand from the protected area into the neighbouring spawning grounds along the south coast. O'Sullivan et al. (2013) showed that due to the oceanographic circulation, larvae from the South coast are transported all along the Irish coast, increasing stock mixing, connectivity and complexity, which are important components of stock resilience and recolonisation of new spawning grounds (Dickey-Collas et al., 2010; Petitgas et al., 2011). If a strong proportion of the year classes return to their natal spawning grounds to recruit, the density around Dunmore East could further increase in the following years boosting the stock further.

Variogram analysis

Acoustic techniques are suitable to survey pelagic fish stocks (Simmonds and MacLennan, 2005) with the integration into geostatistical analyses for biomass interpolation over the region. At the same time the global distribution structure and aggregation patterns can be analysed using survey data feeding into variographic analysis (Mello and Rose, 2005). However a temporally and spatially fixed survey could lead to a mismatch with the migration period because it prohibits a spontaneous reaction to the system (i.e. flexible survey onset). For the Celtic Sea, October has been chosen as a suitable time to encounter most winter spawning herring during the inshore migration (O'Donnell et al., 2012). The herring fishing season generally starts in October; hence no information about herring distribution is available prior to the survey. Thus, the survey design is broad, covering the entire South coast and allow only for small flexibility to react to information about herring distribution from commercial fishing vessels (O'Donnell et al., 2012). The survey output, the NASC values with EDSU resolution, can be influenced by the back scatter of the sea floor, the weather conditions and the identification of species to the acoustic mark (Simmonds and MacLennan, 2005). Finally, escape behaviour as a reaction to the vessel intrusion could lead to an underestimation of fish densities (Simmonds and MacLennan, 2005). Here, a silent research vessel, a high resolution transect design in core areas and skilled personnel during the acoustic survey operations has kept the uncertainty of stock underestimation and misidentification to a minimum (O'Donnell et al., 2012). The survey design and the EDSU are accepted by ICES and used for the annual stock assessment.

For the geostatistical analysis of Celtic Sea herring the EDSU resolution was used; however herring were aggregated in dense shoals with sharp boundaries and no spatial dependence was detected with this resolution. Due to the patchiness of herring shoals, the variance above 1 nautical mile already reflected the scale of the global variance, masking a fine scale distribution pattern. The EDSU could be too coarse to detect a distribution structure mainly based on aggregates, even though herring shoals can be very large and have already extended over 2 nautical miles in the study area (O'Donnell et al., 2012). The herring distribution during migration appears on a macro-scale of 1 nautical mile to be a random distribution of aggregates. A clearer distribution pattern would benefit from a survey design suitable for non-continuous distributions. While the survey design is used to minimize variance in stock estimation, an adaptive survey design would be more suitable for assessing a more detailed distribution map including more than a basic structure (Mello and Rose, 2005; Simmonds and MacLennan, 2005). In the perspective of foraging models, the fine scale distribution, where hunting behaviour predominates, could become more important than global distribution or total abundance. Fishing pressure and predation have a large local impact, therefore modelling the prey source as a non-continuous, discrete aggregated herring distribution will improve further ecosystem simulations. In addition, in non-stationary cases, geostatistical tools combined to general additive models (GAMs) or empirical orthogonal functions (EOFs) could minimise the variance (e.g. Petitgas, 2001, 2008; Loots et al., 2010; Le Pape et al., 2014) and produce a finer distribution map. Here, limited to the survey design and representing a snap shot in time of the herring distribution, variograms provided a spatial overview of the herring distribution and a basic spatial stock structure during spawning migration, which can be applied to ecosystem modelling.

Distribution shift and constrains

The CG-values indicated a strong attraction to the spawning grounds along the eastern South coast, but no shift in the average herring distribution over time. Within the study area, the herring distribution was not constrained by oceanographic conditions and the realized habitat (i.e. the ambient conditions) did not differ to the potential habitat (i.e. average conditions). This supports the findings of the variograms that herring make use of the total study area and that distribution during spawning migration is not influenced by temperature or salinity but rather by the physical properties of the spawning grounds and spawning ground fidelity. In the Barents Sea, 0-group herring showed maximum fish densities at 7° C (Eriksen et al., 2012), and Röckmann et al. (2011) identified realized habitats for early-stage North Sea herring according to temperature and salinity. Broms et al. (2012) showed that temperature was of secondary importance during feeding migration of Norwegian spring spawning herring, but herring avoided waters colder than 1-2° C, indicating a temperature barrier at the lower end of the temperature range of North Atlantic herring (Brunel and Dickey-Collas, 2010). With an average ambient temperature of 14° C and 13° C at the sea surface and bottom respectively in the Celtic Sea, herring face conditions at the higher end of its temperature range. The SST in Irish waters is exhibiting a warming trend (Cannaby and Hüsrevoğlu, 2009) and with temperatures close to its range limits, herring could be affected in future. However the attraction to the spawning grounds is so strong, that herring, at least at present, tolerate a wide range of temperatures while passing the Celtic Sea. It is important to keep monitoring theses basic parameters to identify impending changes from increasing sea temperature or other changes in habitat.

Other distribution drivers

The variable distribution of migration herring within the study area could be due to a variation in the onset of migration from the feeding grounds and consequently lead to variation in the arrival time at the spawning grounds. This raises the question of what triggers migration, and if oceanographic conditions and prey depletion at the feeding grounds could influence the herring migration pattern and distribution? During summer, stable, baroclinic bottom jets of up to 30 cm/s are described for the central Celtic Sea, when cold and dense water is trapped beneath the thermocline (Brown et al., 2003; Fernand et al., 2006; Hill et al., 2008). It is believed that the summer circulation in the Celtic Sea is dominated by these bottom jet-like flows and that the warming trend in the Celtic Sea may lead to earlier stratification and more persistent currents (Brown et al., 2003; Nolan et al., 2010). A visual comparison of herring distribution and average depth during spawning migration showed the overlap of herring migration routes with an area known for bottom currents (Hill et al., 2008). The currents could give an impulse for migrating herring, which could use the currents as a lift to arrive early at the spawning grounds. Further, changes in prey composition and density could lead to an earlier onset of spawning migration, visible in higher abundances inshore at the spawning grounds. *Calanus* species are the main prey species for herring in the Irish and Scottish Sea with *Calanus helgolandicus* and *Calanus finmarchicus* having the highest proportion in the diet (Rice, 1963; De Silva, 1973), but both species showed a decreasing trend in abundance for the Celtic Sea (McGinty et al., 2011), leading to an earlier departure of the feeding grounds . Spatial and temporal prey dynamics, especially of *C. finmarchicus*, were affecting the feeding migration of Norwegian spring-spawning herring, which left an area before their prey was depleted (Broms et al., 2012). Further diet studies in the Celtic Sea and a direct comparison of zooplankton biomass at the feeding grounds and fish biomass at the spawning grounds could help to understand the trigger for herring migration in the Celtic Sea.

Herring, as forage fish, is an important middle player in the Celtic Sea ecosystem.

Understanding its spatial distribution can help protecting the herring stock and therewith the ecosystem equilibrium. This study highlighted the strong importance of the eastern spawning grounds, which can, when kept undisturbed and protected, further support stock biomass. The aggregated, randomized herring distribution pattern during migration can find application in predator - prey ecosystem modelling, where local availability can be more important than the overall prey abundance (Peck et al., 2014). Global change impacts on the stock and stock dynamics can show in distribution and realized habitat shifts. Monitoring variables like the centre of gravity and realized habitats and being alert in case of changes, can provide valuable information for an adaptive, sustainable, ecosystem based, stock management in the Celtic Sea. For a deeper understanding of herring distribution in the Celtic Sea and possible interaction with zooplankton abundance or oceanographic features, the study area and period should be enlarged to also include the summer conditions at the feeding grounds in the central Celtic Sea.

Acknowledgement

We want to thank the chief scientists and captains, as well as the crew and scientists on board the *RV Celtic Explorer* for their help during the CSHAS surveys. We are thankful to Glenn Nolan, Hans Gerritsen and the "Ecologie et Modèles pour l'Halieutique (EMH)" group at IFREMER Nantes for technical support. MV was funded through a MARES Grant. MARES is a Joint Doctorate programme selected under Erasmus Mundus coordinated by Ghent University (FPA 2011-0016). Further support for this study was given by the Euromarine Mobility Fellowship and the NETWORKING INITITATIVE under the SeaChange strategy with the support of the Marine Institute and the Marine Research Sub-programme of the National Development Plan 2007-2013. Data used in this study belong to the Marine Institute (Rinville, Ireland) and was used under the Data agreement 2011/252, 2011/254 and 2013/045. Our thanks go to the Editor and two anonymous reviewers whose comments greatly improved the manuscript.

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Chapter 3

Fine-scale spatial association between baleen whales and forage fish in the Celtic Sea

“Within an ecosystem-based management, predator, prey and their interactions have to be accounted for. After acknowledging the importance of the Celtic Sea as a prey hotspot [for baleen whales], further research on predator populations and their foraging decisions as well as on prey population dynamics is necessary.”

(p.93)

Top and bottom right picture courtesy of Conor Ryan.

Abstract

The Celtic Sea is a productive area, which attracts large baleen whales to feed, however little is known about their foraging behaviour. The study aim was to know whether or not baleen whales actively target forage fish or, on the contrary, is predation on the Celtic Sea plateau driven by random encounters between prey and predator? Concurrent sighting surveys for fin, minke and humpback whales (*B. pysalus*, *B. acutorostrata* and *M. novaeangliae*) were carried out simultaneously during a dedicated fisheries acoustic survey assessing the abundance and distribution of forage fish from 2007 to 2013. Probabilities of spatial overlap on a resolution up to 30 km between baleen whales and forage fish were analysed and compared to the probability of a random encounter. For estimations of foraging threshold and prey selectivity, average fish biomass and fish length were calculated when baleen whales and forage fish co-occurred. Whales were found to actively search in areas with herring (*C. harengus*) and sprat (*S. sprattus*), while areas with mackerel (*S. scombrus*) were not targeted. A foraging distance and prey detection range of up to 8 km was found, which enables baleen whales to track their prey to minimise search effort. Fish densities within the defined foraging distance ranged from 0.001 to 3 $kg\ m^{-2}$ and were correlated to total fish abundance. No prey size selectivity according to fish length was found. Selectivity and active foraging behaviour in whale predation modify the forage fish mortality and should be considered in an ecosystem-based management of the Celtic Sea resources.

Keywords:

Fin whale (*Balenoptera physalus*) · foraging · foraging distance · Herring (*Clupea harengus*) · Minke whale (*Balenoptera acutorostrata*) · Sprat (*Sprattus sprattus*)

3.1 Introduction

Baleen whales undergo annual long distance migrations from mating grounds to nutrient rich feeding grounds at high latitudes to feed on zooplankton and small pelagic fish (Corkeron and Connor, 1999; Clapham, 2001; Kennedy et al., 2013). Within a conceptual foraging model, large migrations of several thousands of kilometres can be seen as the first spatial scale of foraging strategies (Kenney et al., 2001; Hazen et al., 2009). The spatial meso-scale is within hundreds of kilometres to select a prey hot spot (an area with potentially high prey densities), while individual foraging events take place on the scale of less than 10 km (Kenney et al., 2001; Hazen et al., 2009). As prey abundance decreases in space and time, it can become advantageous for an animal to leave and to explore new areas, if the potential value of the new area promises a net energetic gain (Charnov, 1976; Pyke et al., 1977). Tagging and mark/recapture studies have shown that baleen whales visit several prey hot spots within the same region, but also leave an area to discover new hot spots which involves longer travelling distances (Watkins et al., 1996; Zerbini et al., 2006; Witteveen et al., 2008; Olsen et al., 2009; Silva et al., 2013; Feyrer and Duffus, 2014; Kennedy et al., 2014). Prior knowledge due to matrilineal learning and site fidelity (the recurring search within a certain area) can help baleen whales to accept or reject possible areas before visiting, thereby attempting to prevent a negative energy balance (Pyke et al., 1977; Kenney et al., 2001).

Baleen whales can shape an ecosystem on multiple levels for instance by acting as nutrient vectors and apex predators (Roman et al., 2014; Willis, 2014). Therefore baleen whales should be given attention within the assessment of an ecosystem as top predator and baleen whale impacts on prey population dynamics should be explored within an ecosystem-based fishery management (Engelhard et al., 2014; Link and Browman, 2014; Travis et al., 2014). Results from photo-id surveys within the Celtic Sea have demonstrated inter-annual resighting of both humpback (*Megaptera novaeangliae*) and fin whale (*Balaenoptera pysalus*) (Whooley et al., 2011; Ryan et al., 2015), suggesting some seasonal site fidelity within and between years. A predation impact assessment requires an understanding on local, small-scale baleen whale foraging decisions including prey selectivity, foraging thresholds, foraging duration and habitat utilisation.

Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*) and Atlantic mackerel (*Scromber scombrus*) are abundant pelagic fish species in the Celtic Sea which support large scale fisheries (Marine Institute, 2013). Small pelagic fish are defined as forage fish because of their dense schooling behaviour and position in the trophic food web as common prey for higher trophic levels (Engelhard et al., 2014; Pikitch et al., 2014). The only reported in-situ diet analysis of baleen whales in the Celtic Sea showed a preference by fin and humpback whales for sprat and juvenile herring (Ryan et al., 2014). Are whales intermittently preying on forage fish while coincidently passing the Celtic Sea during migration? Or is the Celtic Sea plateau a prey hot spot where baleen whales directly and reliably target herring, sprat and mackerel?

Referring to seven years of synoptic observed predator and prey distribution, we analysed the spatial overlap of fin, minke (*Balaenoptera acutorostrata*) and humpback whales, which are the most common baleen whales recorded in the Celtic Sea, with the presence of herring and sprat. Further, where spatial overlap occurred, we calculated the average biomass and average fish length of forage fish in proximity to the whale sighting. The results provide information on:

1. prey selectivity and habitat use of baleen whales, which can help to understand and quantify foraging decisions;
2. potential predation of forage fish stocks, which can contribute to mortality rate estimations in stock assessments;
3. trophic chain characterization in the Celtic Sea to improve ecosystem modelling allowing for different set-ups e.g. increase of prey or predator abundances and different bottom-up or top-down scenarios.

3.2 Material and Methods

Fish data acquisition

Acoustic data were collected from 2007 to 2013 during the annual Celtic Sea Acoustic Herring Survey which occurs over 21 consecutive days each October in the Celtic Sea along the Irish South coast. A calibrated Simrad EK60 echosounder recorded acoustic data continuously along pre-determined transect lines with four frequencies (18, 38, 120 and 200 kHz). NASC (Nautical Area Scattering Coefficient) data were obtained and integrated over the local depth and 1.85 km intervals into effort blocks known as elementary distance sampling units (EDSUs). Echograms were identified to species level based on species-specific acoustic signals and echotrace recognition, and ground-truthed with directed fishing tows (O'Donnell et al., 2013). Only herring and sprat echotraces positively identified were analysed in this study (O'Donnell et al., 2013). The average fish length (L, in cm) per species from the closest geographical trawl to the respective EDSU was used to calculate the target strength (TS) per fish species at 38 kHz with $TS = 20logL - 71.2dB$ [1] for herring and sprat.

No 38 kHz frequency data were available from 2010 due to a technical defect, so the 18 kHz signal and an adjusted TS/length relationship was used instead (Saunders et al., 2012). No abundance was estimated in 2010 for sprat, however the echotraces were used for the presence/absence analysis. NASC values for herring and sprat were transformed into fish abundance per square metre and multiplied with the average fish weight taken from the closest haul to obtain fish biomass per square meter (B, in $kg\ m^{-2}$) (Simmonds and MacLennan, 2005). NASC values for mackerel were used as indication for presence only and no biomass was calculated. No distribution data for mackerel were available for 2010 and 2012.

Simultaneous baleen whale observations

During the survey, one observer kept a daylight watch recording marine mammal sightings from the crow's nest (18 m above sea level) or from the bridge (11 m above sea level). All sightings in an area up to 90 degrees to either side of the vessel were recorded. The field of view was constantly scanned during watch hours by eye and through binoculars. For each sighting the following data were recorded: time, location, species, distance, bearing, number of animals and behaviour. Only fin, humpback and minke whale sightings recorded up to a maximum sea state of 5 were used in this analysis. Whale sightings that could not be identified to species level (i.e. no body but the blow was seen) were recorded as unidentified large whale sightings. A total of 113 baleen whale sightings were recorded from 2007 to 2013 (Table 3.1). Here sightings were used as unit to describe the presence of a whale, irrespective of group size per sighting. Generally most individuals were solitary, but groups of up to 10 individuals were recorded within one sighting.

Analysis of spatial co-occurrence and fish biomass within proximity

Whale sightings were aligned with the acoustic data set from the respective year and fish biomass (B_{area} in $kg\ m^{-2}$) was calculated for a circular area with different radii (R with 2, 4, 6, 8, 10, 14, 16, 18, 20, 25 and 30 km) centred to the whale sighting. Fish biomass within the area around the observed whale sighting can identify a biomass target and foraging threshold of baleen whales. To calculate B_{area} the average acoustic density

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[1] For the year 2010: $TS = 20logL - 69.7dB$ for 18kHz and only for herring.

Table 3.1: Overview of cetacean watch effort (in hours) and sightings per unit effort (n per hour) from 2007 to 2013 with the respective number of sightings of baleen whales on species level.

	total	2007	2008	2009	2010	2011	2012	2013
hours of effort	626	96	79	78	88	78	110	97
Sightings per unit effort	0.18	0.15	0.18	0.22	0.10	0.36	0.15	0.15
total baleen whale sightings	113	14	14	17	9	28	16	15
Fin whale	61	3	9	4	3	24	12	6
Minke whale	30	8	5	8	1	4	2	2
Humpback whale	2	1			1			
Unident. baleen whale	20	2	0	5	4	0	2	7

over each transect (B_t) was weighted by the transect length (l), summed and applied to the surface area:

$$B_{area} = \pi \times R^2 \sum^{transect} \frac{B_t \times l}{\sum l} \tag{3.1}$$

with R and l in meters and B_t as:

$$B_t = \sum \frac{B \times 1852}{l} \tag{3.2}$$

For each whale sighting, the presence of fish (defined as $B_{area} > 0$) was recorded for each radius and target fish species. The proportion of positive co-occurrence between whale sighting and fish was calculated for a total of 113 sightings over seven years. To test if any spatial overlap of baleen whale and pelagic fish species was coincidental, whale sightings were replaced by random points on the ship transect. Presence/absence analysis for each radius was repeated 200 times for the simulated random whale presences. The probabilities of a positive fish biomass per whale location (observed vs. simulated sighting) being significantly different to random were tested with a two-sided probability test of success (R function prob.test, "stats" package). When the test of disparity of probabilities was significant ($p < 0.05$), the null-hypothesis was rejected, meaning that spatial co-occurrence was not coincidental.

Analysis on size selection by baleen whales

Average fish length ($\overline{TL}$) and standard deviation were calculated for fish proximal to a whale sighting to explore if whales preferentially associate with or select certain prey sizes. The total length values recorded from the fishing trawls during the survey were averaged:

- $\overline{TL}_{obs}$: average length of the trawl geographically closest to the whale observation; here called "observations";

- $\overline{TL}_{sim}$: average length of the trawl geographically closest to the simulated whale location; here called "simulations";
- $\overline{TL}_{full}$: average length of all trawls in the study area; here called "full survey";

$\overline{TL}_{obs}$ provided information on the size distribution close to a whale sighting and thus could indicated a possible prey size selection by baleen whales. $\overline{TL}_{sim}$ represented a random selection from the stock and therefore should be similar to $\overline{TL}_{full}$. $\overline{TL}_{obs}$, $\overline{TL}_{sim}$ and $\overline{TL}_{full}$ were calculated for each survey year and compared using a Tukey's test. All analyses were carried out using the open source statistical software "R" (http://cran.r-project.org).

3.3 Results

Spatial co-occurrence of baleen whales and forage fish

The proportion of positive co-occurrence was calculated for a circular area centred on a whale sighting with increasing distances (2 to 30 km). With increasing distance, the proportion of spatial overlap increased (Figure 3.1). The proportion of spatial overlap with herring and sprat was very similar, however when all fish species were combined, the spatial overlap of whale sightings within proximity to fish was highest (Figure 3.1). Proportions obtained from simulated random whale sightings showed the same pattern of increasing spatial overlap with distance (Figure 3.1). However, a comparison of proportions of overlap showed significant differences between observed and simulated data up to a distance of 8 km (Figure 3.1 and Table 3.2). Within 8 km to a sighting, the null-hypothesis could be rejected suggesting that occurrence of a whale sighting in proximity to herring and sprat did not occur by chance (Table 3.2). For distances larger than 8 km, no difference between observed and simulated co-occurrence events was detected ($p > 0.05$, Table 3.2), implying that any spatial overlap of predator and prey over larger distances was coincidental. The proportion of co-occurrence was highest with 0.83 within an 8 km radius, thus 94 of 113 whale sightings were seen in proximity to potential prey (Table 3.2). The spatial overlap between mackerel and whale sighting was not significant for any distances ($p > 0.05$, Table 3.2). In the Celtic Sea, baleen whales appeared to actively search in the proximity to forage fish without differentiation between herring and sprat, while mackerel did not appear to be targeted (Figure 3.2).

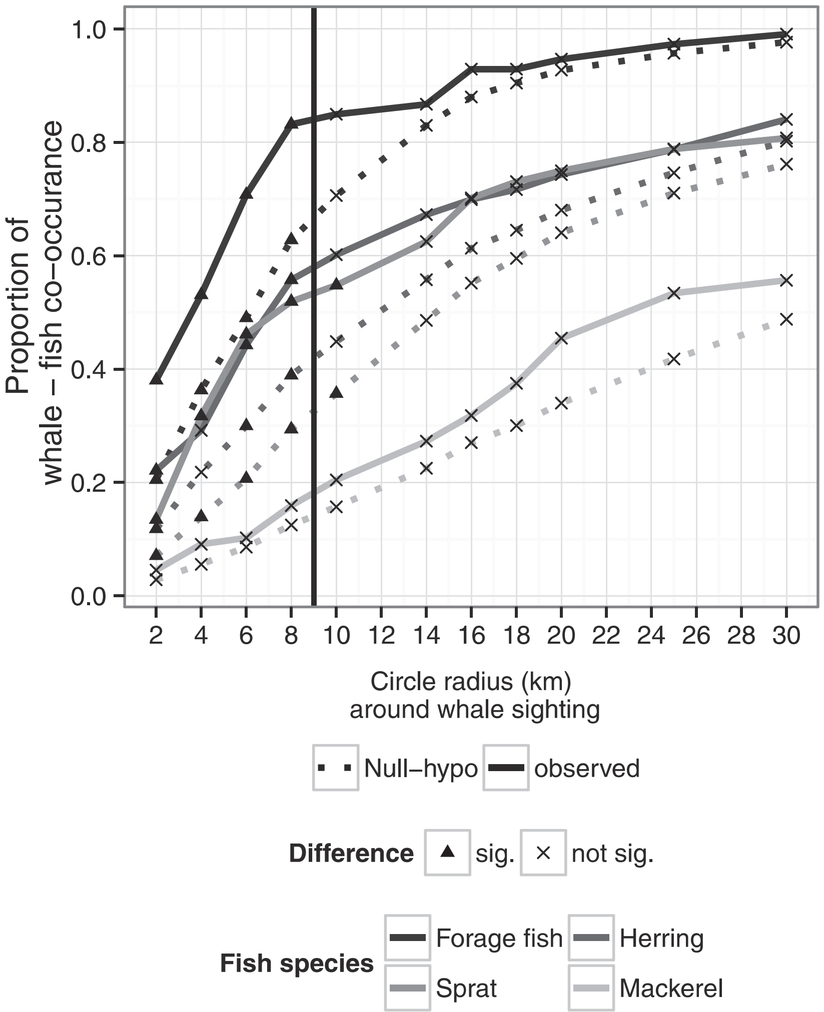

Figure 3.1: The proportion of positive spatial overlap of a whale sighting and the presence of fish is shown for herring, sprat and mackerel and their combination here defined as forage fish. Observed proportions of overlap are shown (closed lines) and compared to simulated data (dotted lines) with increasing distance to the whale sighting. Significant differences ($p < 0.05$) between the two models are shown. The black vertical line indicated the break in significance with distances larger than 8 km.

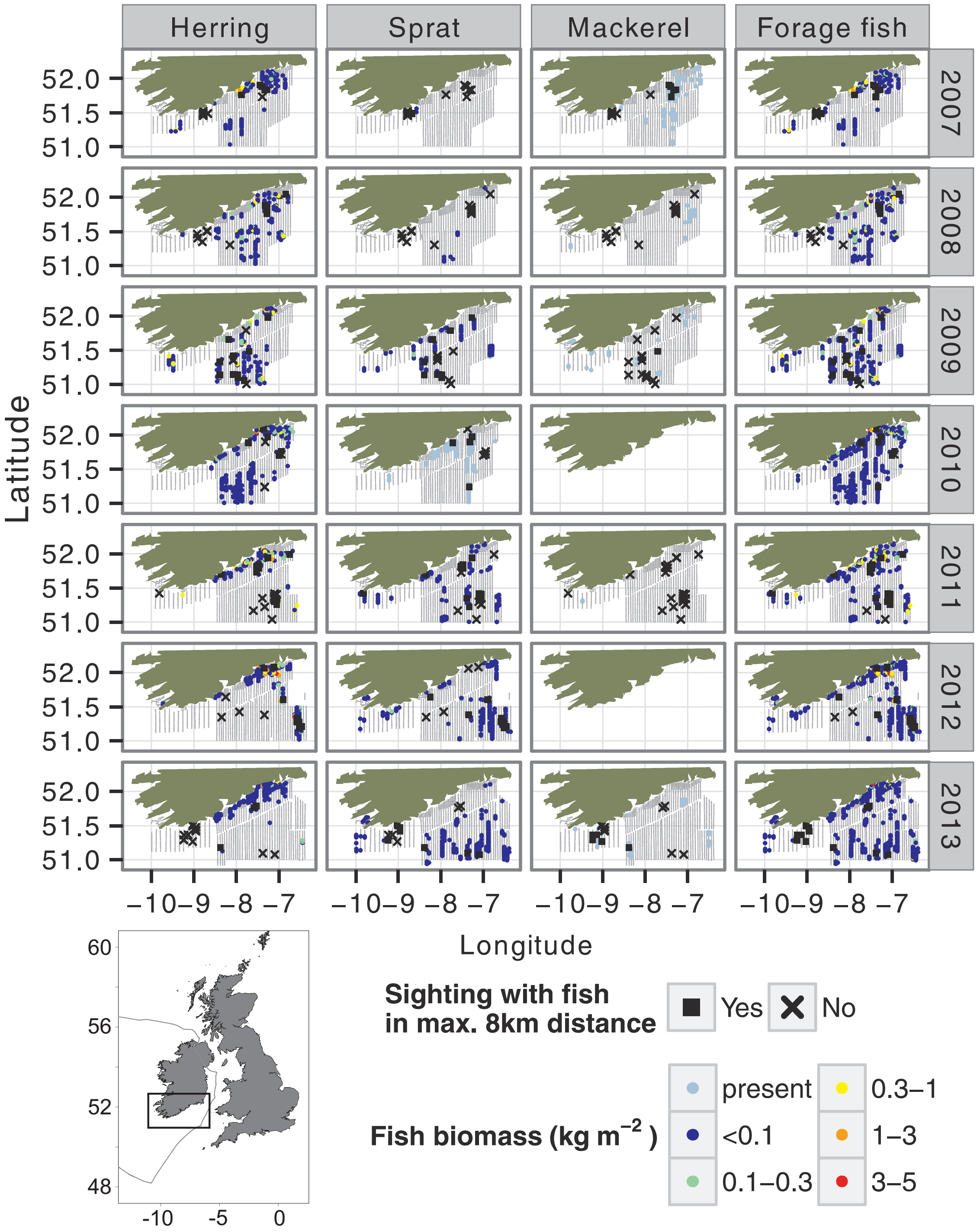

Figure 3.2: Visualisation of the fish and whale sighting distribution in the Celtic Sea from 2007 to 2013. Whale sightings with fish within 8 km to the sighting are indicated (black squares), while no spatial overlap is indicated with a cross. Fish biomass (coloured points) has been calculated based on the NASC values per EDSU from the acoustic survey (grey points). No biomass was calculated for sprat in 2010 and mackerel at any year; NASC values were seen as presence only (light blue point).

Table 3.2: Number of events of spatial co-occurrence between baleen whales and forage fish, herring, sprat and mackerel for increasing radii (in km) centred to the whale. The total number of observed (obs.) and simulated (sim.) whale sightings are given as "n". Significant differences of probabilities between observation and simulation were calculated, p-value rounded to two decimals and significant events are highlighted in bold ($p < 0.05$).

		forage fish			herring			sprat			mackerel		
		obs.	sim.	p	obs.	sim.	p	obs.	sim.	p	obs.	sim.	p
n		113	22600		113	22600		104	20800		88	17600	
radius (km)	2	**43**	**4630**	**<0.01**	**25**	**2671**	**<0.01**	**14**	**1473**	**0.03**	4	501	0.54
	4	**60**	**8206**	**0.02**	33	4928	0.17	**33**	**2895**	**<0.01**	8	978	0.26
	6	**80**	**11086**	**0.01**	**50**	**6779**	**0.03**	**48**	**4300**	**<0.01**	9	1541	0.76
	8	**94**	**14191**	**0.05**	**63**	**8797**	**0.03**	**54**	**6116**	**<0.01**	14	2197	0.49
	10	96	15966	0.21	68	10142	0.07	**57**	**7421**	**0.01**	18	2765	0.38
	14	98	18759	0.80	76	12607	0.23	65	10111	0.13	24	3960	0.47
	16	105	19890	0.74	79	13861	0.41	73	11479	0.13	28	4755	0.52
	18	105	20449	0.90	81	14581	0.52	76	12382	0.20	33	5287	0.33
	20	107	20963	0.93	84	15380	0.59	78	13325	0.33	40	5984	0.15
	25	110	21637	0.95	89	16868	0.76	82	14779	0.53	47	7354	0.20
	30	112	22077	0.97	95	18133	0.79	84	15840	0.74	49	8586	0.51

Fish biomass within foraging distance

Because mackerel may not be a target species for baleen whales in the Celtic Sea, only the acoustic biomass of herring and sprat was calculated within the circular area with an 8 km radius. Sightings of the three whale species were in proximity to fish biomass of 0.001 to 0.2 $kg\ m^{-2}$ (Figure 3.3), representing 0.2 to 4 tonnes of fish within an 8 km radius. In years of high herring biomass recorded during the acoustic survey (2010 to 2012, Figure 3.4) whales were more frequently observed in areas with high herring biomass densities (Figure 3.3). In some years single, large herring schools were recorded (Figure 3.2) and whales were seen in proximity to those schools, explaining the higher fish biomass for 2008, 2011 and 2012 for fin whales and for minke whales between 2010 and 2012. Total sprat biomass was much lower compared to the total herring biomass recorded during all surveys (Figure 3.4). Sprat was targeted by fin whales only in the years with higher sprat biomass survey estimates, while minke whales were observed in proximity to sprat irrespective of sprat biomass, i.e. during all years (Figures 3.3 and 3.4).

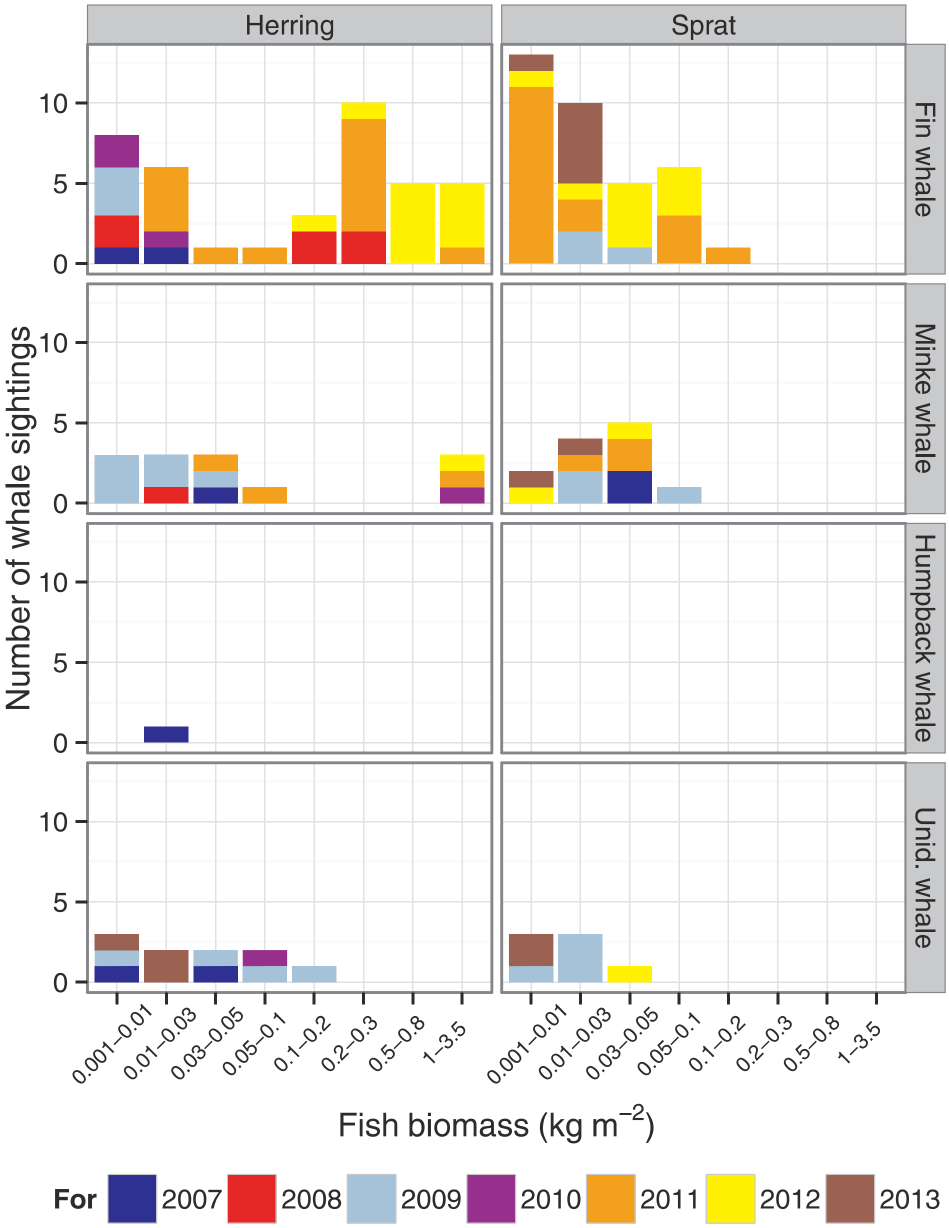

Figure 3.3: Calculated fish biomass by year for herring and sprat over the circular area of 8 km distance to the whale sighting is shown for respective whale species.

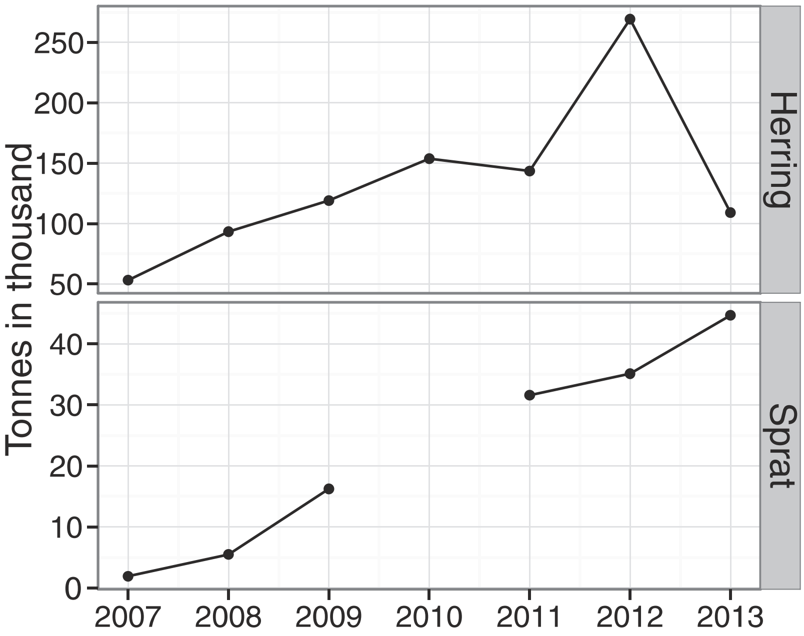

Figure 3.4: Total herring and sprat biomass observed during the surveys in tonnes per thousand over the entire survey area. No biomass was estimated for sprat in 2010. Note different scales on the y-axis.

Fish size in proximity to the whale sightings

Average fish length for herring and sprat was calculated for fish within 8 km to the whale sighting and the simulated data, and then compared to the total average fish length of the survey per year. No significant difference was detected for $\overline{TL}_{sim}$ compared to $\overline{TL}_{full}$ for neither herring nor sprat ($p = 0.68$ and $p = 0.78$ respectively; Figure 3.5). $\overline{TL}_{obs}$ in proximity to the observed whale sightings followed the distribution of the surveys, without general significant differences to $\overline{TL}_{full}$ (p = 0.99 for herring and p = 0.53 for sprat). Only in selected years, $\overline{TL}_{obs}$ for herring was smaller (2008) and larger (2013) compared to the herring $\overline{TL}_{full}$ from the survey (Figure 3.5).

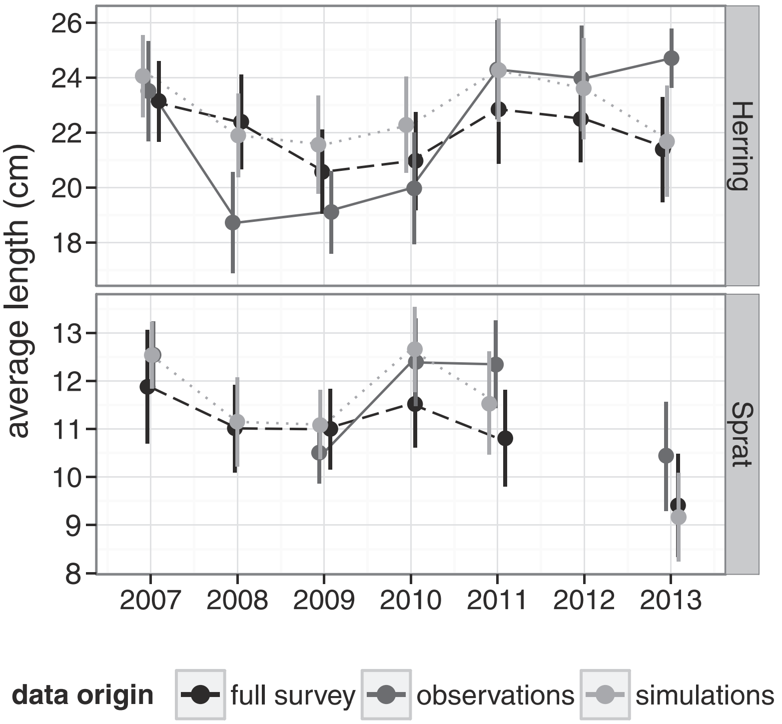

Figure 3.5: Average fish length for herring and sprat within 8 km to the observed and simulated sighting compared to the average length of fish recorded for the full survey. No whale sightings were recorded within proximity to sprat in 2008 and no data was available for sprat in 2012.

3.4 Discussion

Over 80 % of the baleen whale sightings were recorded in close proximity to herring and sprat (56 % and 52 % respectively), which are therefore likely to be actively search out by whales. No significant spatial overlap was found for mackerel and baleen whales; hence mackerel does not appear to be actively targeted by baleen whales in the Celtic Sea. Direct observations of mackerel made over successive years during the survey found this species to form low density scattering and widely dispersed layers as compared to the larger, higher density localised schools formed by herring and sprat. The highest proportion of significant spatial overlap of prey and predator occurred within a distance of 8 km. Fish biomass within the 8 km radius ranged between 0.2 and 4 tonnes (or 0.001 - 0.2 $kg\ m^{-2}$). Fin and minke whales were actively targeting localised areas with the high herring density in years where acoustic densities of herring were correspondingly high. Sprat was targeted in all years by minke whales; however only in years with high sprat biomass survey estimates was sprat also targeted by fin whales. This suggests a density-driven relationship of predator-prey co-occurrence which is different for different whale species. No significant difference in the length distribution of fish was found between herring and sprat in proximity to whales (to 8 km) and fish that were encountered without a simultaneous baleen whale sighting. This suggests that, based on spatial proximity that fin, humpback and minke whales engage in feeding without an explicit prey size selection while in the Celtic Sea.

Spatial co-occurrence of baleen whales and forage fish

A set of circular areas with increasing radii around a whale sighting were tested to find the spatial resolution of overlapping distribution. Overlap with fish further than 8 km to the sighting statistically resembled a coincidental spatial overlap. However whale sightings were predominantly recorded in close proximity to fish; but not all whale sightings in proximity to fish correspond to actual observed foraging behaviour. In fact, foraging was only observed in 20 out of the 113 sightings. Diving and foraging have a high metabolic cost (Goldbogen et al., 2006, 2008) and single foraging dives are often separated by several minutes of rest close to the surface (Goldbogen et al., 2013). Considering that both the whale and the prey target are mobile, foraging events can occur on the scale of several kilometres (Kenney et al., 2001; Hazen et al., 2009; Friedlaender et al., 2014). Minke and humpback whales have swimming speeds of 3 to 6 $km\ h^{-1}$ and could cover 2 to 8 km within 30 minutes to 2 hours respectively, while fin whales have faster swimming speed of up to 20 $km\ h^{-1}$ thus could swim 8 km in less than 30 minutes (Markussen et al., 1992;

McDonald et al., 1995; Goldbogen et al., 2006; Kennedy et al., 2013; Silva et al., 2013; Risch et al., 2014).

Within the concept of prey detection and foraging on a local small-scale (Kenney et al., 2001), a maximum distance between predator and prey of less than 10 km could be the limit of baleen whale detection range. Visual and acoustic cues originating from forage fish and other predators like foraging seabirds and dolphins (Anderwald et al., 2011) could be received within this distance and attract baleen whales to the prey source. Additionally, fish schools can be detected, tracked and preyed on, while energetic costs for a new search effort and relocation may be reduced. A distance of less than 10 km appears to be a profitable, easy reachable distance for foraging by staying close - but not too close - to prey. Significant spatial overlap of baleen whales with prey was found for herring and sprat, which are known prey items of baleen whales in the region (Ryan et al., 2014), the North Atlantic and the North Sea (Haug et al., 1997; Olsen and Holst, 2001; Pierce et al., 2004). Mackerel was not targeted by baleen whales in the Celtic Sea even though it has been found as prey together with other species in one minke whale stomach and been mentioned as prey for humpback whales (Olsen and Holst, 2001; Clapham, 2002). Their infrequency in stomach contents of baleen whales together with the non-significant spatial overlap in the Celtic Sea, indicates that mackerel itself is not a prey target, but may be consumed while preying on mixed fish schools. Unlike mackerel, herring and sprat contain a swimbladder, which can produce sounds and can give visual cues (Wahlberg and Westerberg, 2003; Wilson et al., 2004; Hahn and Thomas, 2008) which could facilitate the detection of Clupeids species for baleen whales. At the time of sampling, in October, mackerel are more dispersed, forming scattered foraging layers as opposed to dense schools, which are known for herring and sprat. Hence foraging on mackerel could be less rewarding energetically compared to the high density of herring and sprat schools.

Prey density distribution and environmental descriptors like sea surface temperature have been used as explaining factors for whale distribution on feeding grounds using multivariate models (e.g. generalized additive models, GAMs) (e.g. Friedlaender et al., 2006; Ingram et al., 2007; Hazen et al., 2009; Laidre et al., 2010; Anderwald et al., 2012; Nøttestad et al., 2014). In some studies, no or only weak spatial overlap of forage fish and baleen whales was found, which could be due to non-matching spatial and temporal resolution in the data (Laidre et al., 2010; Nøttestad et al., 2014). Here the acoustic survey for the Celtic Sea herring provided a valuable opportunistic platform of obtaining high-quality fish distribution and abundance information with synoptic baleen whale occurrence. Herring is known to be randomly distributed in patches with a strong attraction to coastal spawning grounds but without being influenced by temperature or salinity in the region (Volkenandt et al., 2014). Following a random, patchy, prey distribution, we suggest that baleen whale distribution would be less influenced by a continuous variable like temperature, which has less variability in this area compared to that encountered by baleen whales during migration (Piatt et al., 1989). Based on high-resolution spatial distribution data of predator and prey with high level of synchrony, a general comparison between distances of observed and simulated baleen whale sightings to prey abundance as single variable has highlighted the importance of the Celtic Sea plateau as a prey hot spot for baleen whales.

Fish biomass and average length within an 8 km foraging distance

Fish densities of herring and sprat within an 8 km radius to the whale sighting were variable and skewed to lower fish densities. To calculate fish densities, biomass observations with a 1.85 km resolution were extrapolated over the circular area. Hence low biomass densities can still represent a single large school surrounded by zero values due to the patchy distribution of forage fish schools (Volkenandt et al., 2014). With calculated daily consumption rates for baleen whales (Fin whales 981 kg; Minke whales 165 kg and Humpback whales 621 kg with respective large confidence intervals, see Smith et al., 2014) the observed low fish densities equalling 0.2 to 4 tonnes over the 8 km radius could still sustain an energetic return on foraging. Sprat was targeted by fin whales in years when total stock biomass as determined by the acoustic survey data was also high, supporting a suggested prey biomass- and foraging threshold for baleen whales (Piatt and Methven, 1992; Goldbogen et al., 2011; Feyrer and Duffus, 2014; Friedlaender et al., 2014), especially for fin whales but less for minke whales.

No significant differences were found between average fish length in proximity to baleen whales and the overall fish length distribution. Hence baleen whales approach forage fish that are abundant in the environment without apparent prey size selection. Exceptions occurred in 2008 and 2013 for herring which could be due to a high abundance of one-year old herring in 2008 and the respective higher abundance five years later (Figure 3.6); however no selectivity could be found for other years even with a higher abundance of young herring. An in-depth analysis of length-frequencies and year class abundances is necessary to explore possible selectivity by prey size. We suggest that baleen whales non-selectively target herring and sprat according to their availability in the Celtic Sea based on spatial correlation, which does not necessarily imply actual foraging. To date the only available dietary data originating from stable isotope analysis in the Celtic Sea indicated a selectivity for smaller sized fish (sprat and juvenile herring) followed by larger size herring (age 2 to 4) by baleen whales (Ryan et al., 2014), which could support the deviation to the overall abundant prey sizes in certain years.

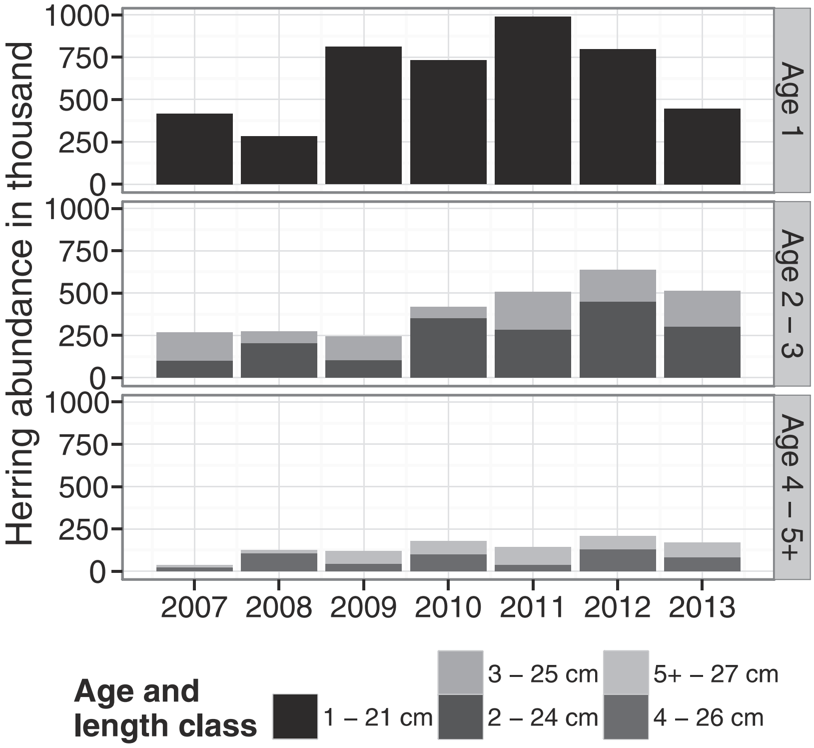

Figure 3.6: Herring abundance by age class and average length per age is given. Numbers were obtained from the Celtic Sea herring stock assessment (HAWG, 2014).

Ecosystem implication

The current study showed that baleen whales actively search for forage fish in the Celtic Sea, which can be identified as a prey hot spot. This is a first and necessary initial step for future studies on baleen whale foraging on small pelagic fish in the Celtic Sea. After the spatial link between predator and prey, predation will have to be further specified. Geographic memories and site fidelity could be directing foraging decisions of baleen whales on larger spatial scales, while acoustic and visual cues together with prey densities and energetic net gain could be local drivers on a small-spatial scale (Kenney et al., 2001). Residency, and hence predation pressure on forage fish, could be linked to the net-energetic gain. Optimal foraging depends on the time spent in a patch as the net-energetic gain decreases with the removal of prey (Charnov, 1976; Pyke et al., 1977). A negative energy balance, e.g. via prey depletion and an increase effort for foraging (due to less dense fish schools occurring after the spawning period) could result in the decision to leave the Celtic Sea plateau to travel to more distant, zooplankton rich foraging areas along the Celtic Sea shelf edge (Ryan et al., 2014). Tagging experiments could provide further valuable information on habitat use and foraging ecology of baleen whales in the Celtic Sea and if whales remain longer in patches of high fish densities (Goldbogen et al., 2013).

While no prey size selectivity was evident, predation can influence the natural mortality estimates of all age classes. Notably, when fish species were treated separately, spatial overlap occurred for 56 % and 52 % of the whale sightings for herring and sprat respectively, while the percentage was increased to 80 %, when species were combined to resemble a forage fish community. Herring is well-studied in the Celtic Sea, but much less is known about sprat. In a changing ecosystem with increasing herring and sprat total stock biomass, the inter-species specific fish population dynamics will become important together with the impact it could have on baleen whale foraging decisions. Here, sprat became a more attractive target for fin whales with increased biomass . Within an ecosystem-based management, predator, prey and their interactions have to be accounted for (Link and Browman, 2014). Hence, after acknowledging the importance of the Celtic Sea as a prey hotspot for baleen whales, further research on predator population and their foraging decisions as well as on prey population dynamics is necessary.

Acknowledgement

We are grateful to the chief scientists, crew and scientific crew of the CSHAS'07 to CSHAS'13 surveys from the Marine Institute for data collection. We thank the Irish Whale and Dolphin Group for the use of the cetacean data set and Dave Wall, Paula Ní Ríogaín, Enda McKeogh and David Williams for collecting the marine mammal data during the Celtic Sea Herring Acoustic Survey. Biological and acoustic data used in this study belong to the Marine Institute (Rinville, Ireland) and were used under the Data Agreements 2011/252, 2013/045, 2014/118 and 2014/161. M. Volkenandt was funded through a MARES Grant. MARES is a joint doctorate programme selected under Erasmus Mundus coordinated by Ghent University (FPA 2011 0016). Thanks to Cóilín Minto and Conor Ryan whose comments helped to improve this manuscript.

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Chapter 4

Energy content of Atlantic herring (*Clupea harengus*) driven by reproductive status

“The proposed linear relationship should be implemented in ecological models [which] can be used as a primary tool for EBFM, providing a link between predation and fisheries catches, emphasizing eventual competition between both.”

(p. 120)

Abstract

Atlantic herring (*Clupea harengus*) form the basis of several commercially important fisheries and is an ecosystem key species. Based on the balance between metabolic costs of predators and prey energy values, energy contents of herring are calculated to estimate predation thresholds within foraging models and food web studies. The objective of this study was to estimate herring energy content and explore their variance due to fish reproductive status. Herring samples were collected in March, October and December 2012 from the Celtic Sea and bomb-calorimetry was used to measure energy content. Samples were pooled according to the size and reproductive status, defined as pre-spawning and post-spawning. A principal component analysis (PCA) and linear regressions were performed to identify factors affecting energy content variability. Post-spawning fish lost up to 46 % in energy density during spawning and migration compared to pre-spawning fish. We proposed two linear regressions to describe the dependence of energy content (E, kJ per fish) to the total fish length (TL, in cm) while taking fish reproductive status into account: $lnE = 2.176 + 0.204 \times TL$ for pre-spawning fish and $lnE = 3.846 + 0.09 \times TL$ for post-spawning fish. These results allow more accurate estimations of prey energy density, which is an important parameter to estimate predation biomass thresholds of herring in ecosystem and foraging models. In agreement with what is found in the literature, energy content was significantly correlated to water content of the fish.

Keywords:
bomb-calorimetry · Celtic Sea · energy density · maturation · North Atlantic · water content

4.1 Introduction

Forage fish are small pelagic fish that occur in large abundance, form dense aggregations and are important prey for higher trophic levels (Alder et al., 2008; Smith et al., 2011; Peck et al., 2014). Nine out of the top ten species of fish caught by the European Union fleet fall into this category (European Union, 2014). Only three out of these nine species are consumed directly while the others are used in fishmeal production (Alder et al., 2008; Smith et al., 2011; European Union, 2014). Due to their central role in marine food webs, forage fish species are important dietary components for several trophic groups such as seabirds and cetaceans (Wanless et al., 2005; Alder et al., 2008; Peck et al., 2014). This central role, when combined with commercial importance could lead to resource competition between apex predators and industry (Smith et al., 2011; Engelhard et al., 2014). Therefore, a rational exploitation of forage fish species should adopt an ecosystem-based fisheries management (EBFM), which optimises the economic profitability without impairing the functioning of marine ecosystems (Browman and Stergiou, 2004; Peck et al., 2014).

Quantifying predation on forage fish is a key component of EBFM (Smith et al., 2011); however, prey consumption by large predators is often difficult to assess. Bioenergetics models, based on energy densities, have been used as an alternative method (Leaper and Lavigne, 2007). Metabolic costs are calculated for predator functions (e.g. predation, reproduction, growth), and balanced with the energy density of their prey, which is then used to find the biomass threshold that satisfies the energy requirements of the predator (Stevick et al., 2008; Spitz et al., 2012; Goldbogen et al., 2012). Errors in energy density estimation can bias the output of bioenergetics models and quantification of predation, which could have significant consequences for EBFM. For example, Mårtensson et al. (1996) showed an increase of 10 % to 15 % in joule, hence 300,000 tonnes in biomass intake, needed to fulfil the requirements of a minke whales (*Balaenoptera acutorostrata*, Lacepede 1804) population, when seasonal variation of prey energy density was taken into account.

Previous authors have reported energy density values for several species of small pelagic fish (Hislop et al., 1991; Hartman and Brandt, 1995; Mårtensson et al., 1996; Paul et al., 1998; Anthony et al., 2000; Pedersen and Hislop, 2001; Tierney et al., 2002; Wanless et al., 2005; Van de Putte et al., 2006; Dubreuil and Petitgas, 2009; Spitz et al., 2010; Vollenweider et al., 2011). Despite the considerable amount of published material, estimates of energy density are often incomplete, for example information about variability due to location, age, season, and maturity is often missing. Vollenweider et al. (2011) report differences in energy density values of up to 300 % for a single species (Pacific herring, *Clupea pallasii* Valenciennes 1847). Such variation represents a source of error when estimating energy densities at the stock or population level. Energy density can be estimated experimentally using a bomb-calorimeter. This produces accurate results but is time consuming and unsuitable for the rapid assessment of large numbers of samples (Cummins and Wuycheck, 1971).

Alternatively, Hartman and Brandt (1995) present a linear regression model for estimating energy density of many fish species. The model relies on water content of the fish and Van de Putte et al. (2006) verified it for a wide range of fish species. Therefore the model is considered a suitable substitute for experimental energy content estimations or species-oriented data mining. However, given the fact that the model relies on water content as an input variable and the inherent variation caused by age, season and maturity, water content should be measured explicitly for the ecosystem in question before implementing it into energy density calculations. When establishing a large data set on the energy density of forage fish from fisheries landings, the measurement of water content is not feasible for large surveys or long time series. An energy regression model based on variables measured routinely for fisheries assessment could facilitate energy density calculations from large data sets and their use in bioenergetics models.

Atlantic herring (*Clupea harengus*, L. 1758) is an important prey species in the North Atlantic (Engelhard et al., 2014) and a sub-species can be found in the Baltic Sea (Baltic Sea herring, *C. harengus membras*, Wulff 1765). In the western Northern Hemisphere, Pacific herring is a separate Clupeidae species (Figure 4.1). Atlantic herring is widely distributed and managed as several stocks separated by location and spawning behaviour in the North Atlantic (HAWG, 2013). The stock shows strong seasonal migration to feeding, spawning and overwintering grounds. Individuals are iteroparous (Murua and Saborido-Rey, 2003) and spawn in shallow water zones during winter, spring or autumn, depending on the stock-specific spawning components. Stocks mix to a small degree in common feeding and nursery grounds; however they remain genetically and phenotypically divergent due to differences in spawning location and time (Bekkevold et al., 2005; Brophy et al., 2006; Ruzzante et al., 2006; Limborg et al., 2012). Growth rates and age at maturity can vary within and between stocks and range between 2 and 5 years (ICES, 2011).

The aim of this study was to use bomb-calorimetry to provide an estimate of the reproductive status variability of energy content in Atlantic herring. Energy densities (in relation to dry and wet mass) as well as whole energy content were provided in the perspective of their integration into specific bioenergetics models for future ecosystem studies. For this, a regression model based on length and maturity was fitted to data and compared with others found in literature.

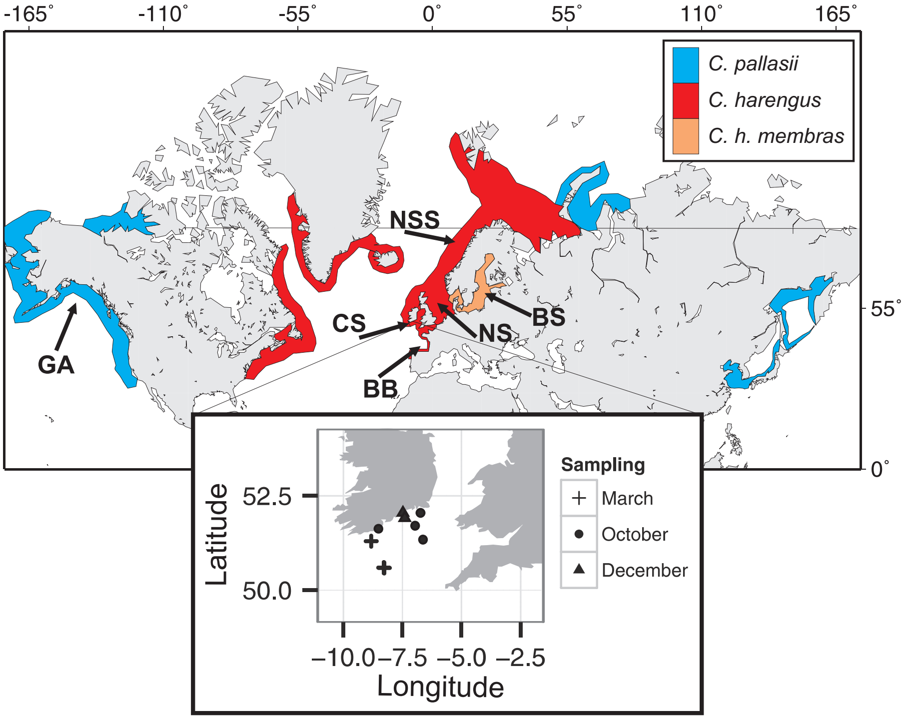


Figure 4.1: Approximate distribution of Pacific, Atlantic and Baltic Sea herring (according to *Aquamaps* `http://aquamaps.org`) and the indication of sampling stations per month in the Celtic Sea. The spatial distribution of different Atlantic herring stocks mentioned in the ecosystem comparison are shown: BB = Bay of Biscay, BS = Baltic Sea herring; CS = Celtic Sea herring; GA = Gulf of Alaska; NS = North Sea herring; NSS = Norwegian spring spawning herring.

4.2 Material and Methods

Sampling procedure

Atlantic herring samples were collected from the Celtic Sea (Figure 4.1) during March, October and December 2012 (n= 174). In March, herring were sampled from opportunistic bycatches on commercial whitefish and pelagic trawlers (n= 42). Bycatch samples were collected to retrieve samples outside of the fishing season (from October to January), which otherwise would not be accessible. Due to the life-cycle of Celtic Sea herring, March samples represent the previous cohort to October and December samples from the same stock. In October, herring were collected during the Celtic Sea Herring Acoustic Survey using a single pelagic midwater trawl (O'Donnell et al., 2012). Samples of 20 herring each were taken from four randomly chosen trawls (n= 82). In December, herring were sampled using a GOV (Grande Ouverture Verticale) trawl during the Irish Groundfish Survey (Marine Institute, 2012) and samples of 25 herring were taken from two trawls (n= 50). Upon retrieval from their respective nets fish were wrapped in sealed plastic bags to minimize water loss and were stored at -20°C before analysis.

Fish preparation

Individuals were thawed and measured for total length (TL, in cm) and wet mass (W, in g) with a precision of 0.01 cm and 0.1 g respectively. Otoliths were extracted for the age determination. Maturity stage was recorded based on the eight stage- scheme (juvenile, developing virgin, ripening I, II and III, running, recently spend and recovering) proposed by Landry and McQuinn (1988), see Figure 4.2. Gonads were removed and weighed with a precision of 0.1 mg (OW, in g) for all maturity stages except juvenile herring, where the gonads were under-developed and could not be fully removed. Each fish was handled within a previously weighed aluminium cup to minimize any loss of liquids. Individual fish, including stomach and gonads, were dried for 24h at a constant temperature of 105°C. After drying and cooling in a dry chamber, the total dry weight (DW, in g) was determined. Each dried fish was homogenized with a common kitchen blender. Ten fish per haul were pooled according to sampling month, reproductive stage (based on Brown-Peterson et al., 2011) and length class to reduce the inter-individual variability (n = 15; Table 4.1). A subsample of 1 g of the dried, pooled fish powder was used per replicate to measure energy density (ED, in kJg^{-1} per dry mass) with an adiabatic bomb-calorimeter (Parr Instrument Company, model 6100). The average value of three combustions was taken as the energy density estimate for each sample.

Statistical analysis

For each individual fish, water content (%H_2O), expressed as percentage of wet mass, and a gonado-somatic index (I_G, expressed in %) was calculated as in Domínguez-Petit et al. (2010):

$$I_G = 100 \times \frac{OW}{W - OW} \tag{4.1}$$

For the juvenile herring samples the I_G could not be calculated because no OW could be obtained. Average length, weight, age, I_G and water content were calculated for each sample. The table crossing samples with quantitative variables that describe them (TL,

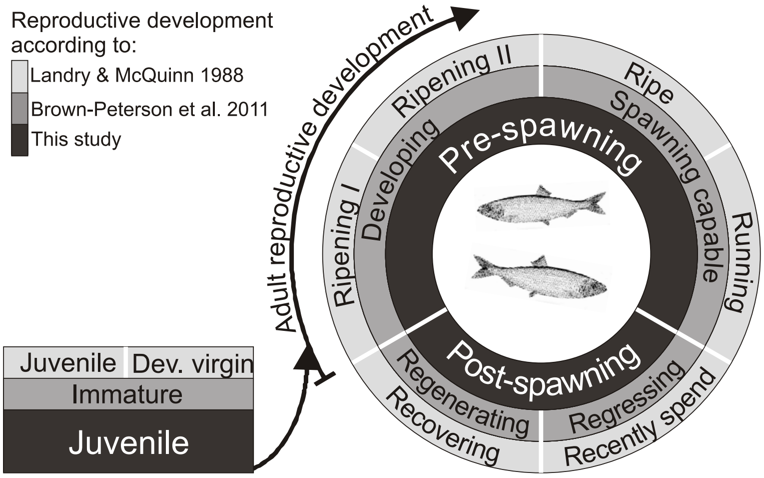


Figure 4.2: Maturity stages of herring individuals determined after Landry and McQuinn (1988) in light grey shading, and maturity stages after Brown-Peterson et al. (2011) in dark grey shading. This typology was used to categorize samples used for bomb calorimetric and to pool samples for establishing linear regressions to explain variation in energy density in black shading.

W, age, %H_2O and energy density) was analysed using Principal Component Analysis (PCA), for which observations were centred and reduced. Two ancillary estimators were calculated for each sample:

- Energy density per gram wet mass (EW, in kJg^{-1}) was calculated using the proportion of water:
$$EW = ED \times (1 - \frac{\%H_2O}{100}) \tag{4.2}$$
- Total energy content per fish (E, in kJ) was calculated as:
$$E = EW \times W \tag{4.3}$$

Hartman and Brandt (1995) proposed a linear regression with EW dependent on percent dry mass, here expressed with water content, for a wide range of fish species with:

$$EW = -3.419 + 0.375(100 - \%H_2O) \tag{4.4}$$

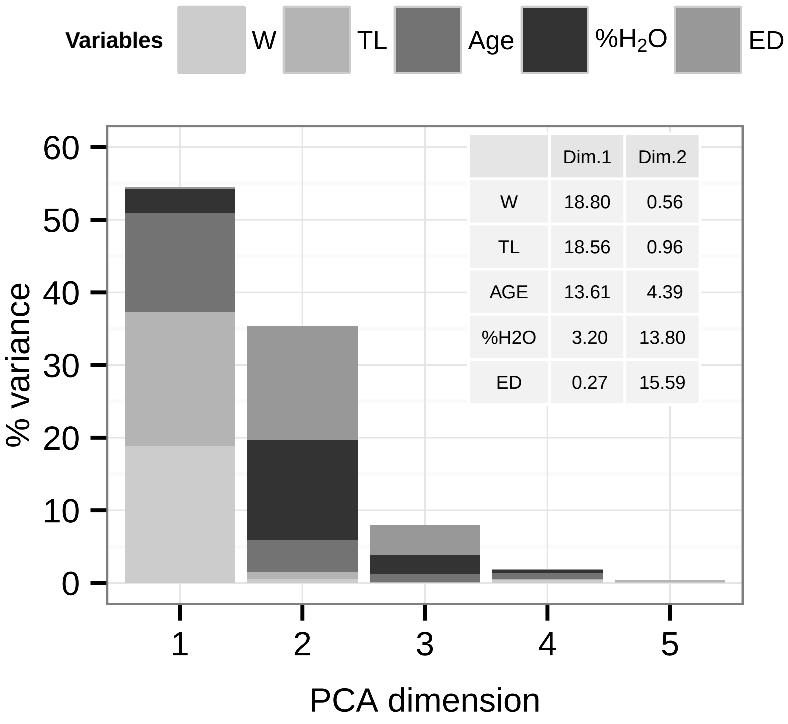
Where intercept and slope are empirically derived constants. Equation (4.4) has been fitted to Clupeid fish with a different intercept and slope by Hartman and Brandt (1995) and Pedersen and Hislop (2001). A linear regression model has been applied to the herring samples from the current study and was compared with parameters estimated in Hartman and Brandt (1995) and Pedersen and Hislop (2001) using an ANOVA. Further, to analyse the influence of reproductive status and body length on energy density, linear models were fitted with ED, EW and E (log-normal transformed) as dependent variables (energy descriptor) and TL as explanatory variable. The linear models were fitted for pre- and post-spawning stages and model parameters were compared using an ANOVA. For the PCA and linear regression, due to the absence or low abundance of some maturity stages in the fishing hauls, samples had to be grouped into three groups according to the reproductive status in the spawning season: i. juveniles, ii. pre-spawning and iii. post-spawning (Figure 4.2). For the purpose of this study, pre-spawning were samples with maturity stages "developing", "spawning capable" or "spawning". Post-spawning were all samples with maturity stages "spent" and "recovering". Sample volume for pre- and post-spawning herring was similar and samples were supposed to be taken from the same stock, thus the comparison of the two reproductive statuses was assumed to be possible.

If not stated otherwise, energy is presented in kilo joule (kJ) throughout the text. All analyses were performed using the open-source statistical software "R" (`http://cran.r-project.org`).

4.3 Results

Sample variation

During the three surveys, a wide range of herring lengths was sampled. Juvenile herring, according to maturity stages, were only sampled during the dedicated herring survey in October due to different fishing methods. 89.7 % of the total variance was explained by the first two Principal Components (PC). The first PC explained 54.4 % of the variance and was influenced by a combination of W, TL and age (Figures 4.3 and 4.4). The second PC explained 35.3 % variance and was influenced by water content and ED (Figures 4.3 and 4.4). A negative correlation between water content and ED was found in the PCA (Figure 4.4). Samples are grouped according to their reproductive status. The first PC opposed samples of juveniles and adults, with expected significant difference in W, TL and age (Figure 4.4), while the second PC separated pre- and post-spawning herring according to their water and energy content. With a third PC, the cumulative explained variance reached 97.8 % (Figure 4.3). Variance on the third principal component was due to a residual correlation of all factors W, TL and age (for a cumulative value of 1.3 %), water content (2.3 %) and ED (4.1 %). Reproductive status was a significant structuring factor for the first and second PC ($r^2 = 0.68$, $p = 0.001$ and $r^2 = 0.61$, $p = 0.003$ respectively), while sampling month was only significant for the second PC ($r^2 = 0.52$, $p = 0.01$).



	Dim.1	Dim.2
W	18.80	0.56
TL	18.56	0.96
AGE	13.61	4.39
%H2O	3.20	13.80
ED	0.27	15.59

Figure 4.3: Results of the Principal Component Analysis performed on the samples vs. fish characteristics (mass, length, age, water content, energy density) matrix. It shows the percentage of variance explained by each PC and the influence of each variable. The contributions to the first and second components are inserted in the main figure. W = wet weight, TL = total length, Age = age according to winter rings, %H$_2$O = percentage of water content, ED = energy density per dry mass.

Averages of TL, W, age, I_G, %H$_2$O and energy descriptors per reproductive status are shown in Table 4.1. Juveniles were significantly different in W, TL and age from adults (Table 4.1 and Figure 4.4). Adults had comparable TL and age for pre- and post-spawning status (Table 4.1 and Figure 4.4), but differed significantly in W, I_G and water content. The I_G- value of post- spawning herring was much lower than the I_G of pre-spawning herring, underlining differences due to maturation stage in the grouping of our samples. Since all statuses had similar average ED (juvenile 24.5 kJg^{-1}; pre-spawning 24.7 ±2.0 kJg^{-1}; post-spawning 21.2 ±2.0 kJg^{-1}), the observed significant differences in EW and E resulted from variation in fish weight and water content (Table 4.1). Post-spawning herring had much lower energy values compared to juvenile and pre-spawning

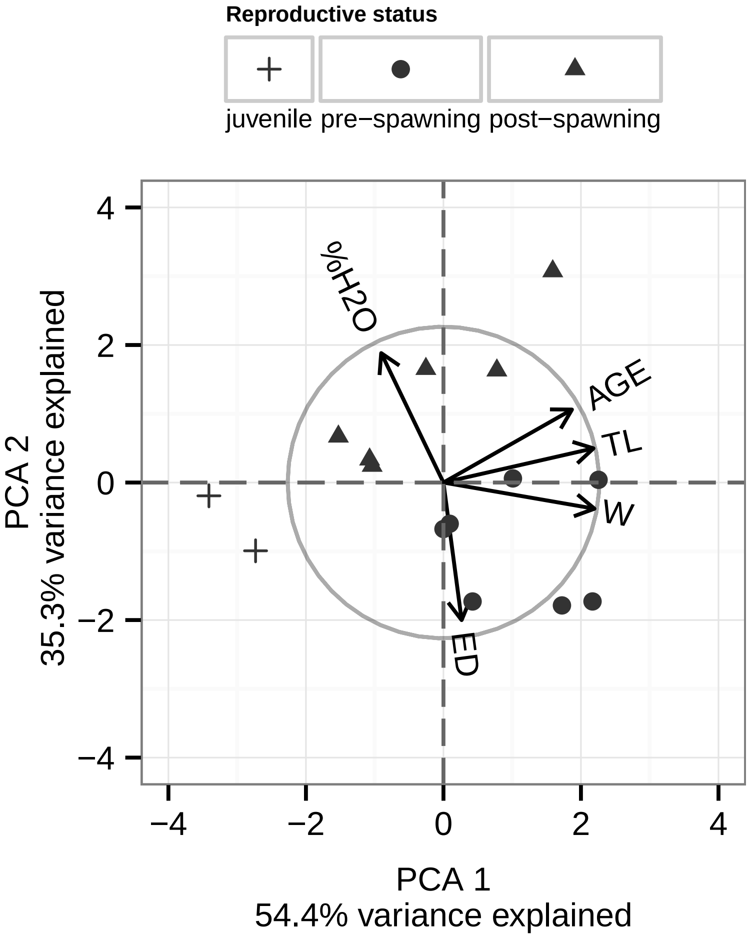


Figure 4.4: First and second components for the centred and reduced PCA. They explain together 89.7 % of variance. Sample points are labelled according to the reproductive status of the samples. W= wet weight, TL = total length, Age = age according to winter rings, $\%H_2O$ = % water content, ED = energy density per dry mass.

herring (Table 4.1). W, TL and age are correlated, therefore only the correlation between water content, ED and length was further explored using linear regression models.

Table 4.1: Basic statistics of estimates performed on the available samples (means and standard deviation). *ED* stands for energy density per dry mass and was measured; *EW* is the energy density per wet mass and was calculated according to Equation (4.2); *E* is the total energy content per fish calculated according to Equation (4.3). Samples were pooled according to length and maturity stage (according to Brown-Peterson et al., 2011) and were grouped in a second step into juvenile, pre- and post-spawning categories.

Spawning group	Maturity	month	n	TL (cm)	W (g)	winter rings	I_G	%H_2O	ED (kJg^{-1})	EW (kJg^{-1})	E (kJ)
juvenile	juvenile	Oct	10	13.5 ±0.6	18.6 ±3.5	0	-	75.8 ±1.8	23.3	5.7 ±0.4	105.7 ±25.1
		Oct	6	15.3 ±1.8	30.7 ±12.2	0	-	72.4 ±2.6	25.6	7.1 ±0.7	223.1 ±115.1
average			**2**	**14.4**	**24.7**	**0**	-	**74.1**	**24.5**	**6.4**	**164.4**
pre-spawning	developing	Oct	9	22.6 ±2.8	91.5 ±29.2	2 ±1	2.5 ±2.4	65.5 ±11.8	24.3	8.4 ±2.9	778.3 ±400.0
	spawning capable	Oct	10	21.9 ±1.6	101.5 ±20.0	2 ±1	8.2 ±2.2	55.1 ±10.2	25.3	11.4 ±2.6	1190.7 ±494.6
		Oct	10	24.2 ±0.3	136.7 ±10.2	3 ±1	13.8 ±4.4	55.3 ±12	26.6	11.9 ±3.2	1637.3 ±506.7
		Oct	10	25.3 ±0.4	146.9 ±19.7	4 ±1	12.8 ±6.3	57.8 ±13.2	27.5	11.6 ±3.7	1735.2 ±667.3
	spawning	Dec	9	22.0 ±0.8	92.9 ±14.5	2	14.6 ±3.6	59.8 ±9.3	22.6	9.1 ±2.1	862.9 ±321.8
		Dec	10	24.5 ±0.4	121.0 ±11.1	3 ±1	17.8 ±3.7	62.2 ±16.1	21.4	8.1 ±3.4	995.8 ±475.0
		Dec	3	26.2 ±0.4	150.8 ±21.3	5 ±1	17.8 ±2.4	69.3 ±8.5	25.0	7.7 ±2.1	1187.5 ±477.5
average			**7**	**23.8** ±2.0	**120.2** ±25.0	**3.5** ±1	**12.5** ±5.0	**60.7** ±5.0	**24.7** ±2.0	**9.7** ±2.0	**1198.3** ±368
post-spawning	spend/ recovering	Mar	5	19.3 ±0.7	47.1 ±7.5	3 ±1	0.1 ±0.2	68.8 ±4.2	22.2	6.9 ±0.9	326.1 ±64.4
		Dec	10	19.8 ±1.2	54.9 ±9.9	1	0.3 ±0.2	71.5 ±5.7	20.3	5.8 ±1.2	317.9 ±84.8
		Mar	10	19.9 ±1.4	53.4 ±10.8	3 ±1	0.4 ±0.2	76.2 ±2.6	24.6	5.9 ±0.6	313.3 ±73.8
		Dec	9	23.4 ±0.6	82.6 ±8.7	3 ±1	0.8 ±0.8	79.8 ±0.6	20.6	4.2 ±0.1	344.1 ±73.8
		Mar	10	24.4 ±1.2	93.1 ±13.4	5 ±1	1.7 ±3.2	75.5 ±4.6	21.1	5.2 ±1.0	486.3 ±147.3
		Dec	2	26.5 ±0.7	106.0 ±4.2	7 ±1	0.7 ±0.1	80.7 ±1.4	18.7	3.6 ±0.3	382.0 ±11.6
average			**6**	**22.2** ±3.0	**72.9** ±24.0	**4** ±2	**0.7** ±1.0	**75.4** ±5.0	**21.2** ±2.0	**5.3** ±1.0	**361.6** ±66.0

Energy density regression and comparison

The parameters of the linear regression model for estimating EW from water content have been compared to model parameters proposed by Hartman and Brandt (1995) for a wide range of fishes and Clupeidae, and to a model proposed by Pedersen and Hislop (2001) for Atlantic herring (Table 4.2). No significant difference was found between the four models (ANOVA, $F(3,240) = 1.03$, $p = 0.38$). For our study, the linear model describing changes of EW as a function of water content was:

$$EW = -1.747 + 0.292(100 - \%H_2O)$$

The correlation between energy density and content (ED, EW and E) and total length (TL) was different between the energy descriptors (Figure 4.5). Without taking the reproductive status into account, no significant relationship between ED (Energy per gram dry mass) or EW (Energy per gram wet mass) and TL was found (Table 4.3). But TL was significantly correlated with energy content per fish (linear regression, $r^2 = 0.53$, $F(1,13) = 16.85$, $p = 0.001$). The regression improved, when reproductive status was considered (Table 4.3). The regression for E of post-spawning herring was significantly different to the regression for pre-spawning herring (tHSD, $p = 0.00001$), while the difference between the global regression (all reproductive status confounded) and regression for pre-spawning herring was not significant (tHSD, $p = 0.134$). The regression for energy content per herring with TL (in cm) as explanatory variable for pre-spawning herring was: $lnE = 2.176 + 0.204 \times TL$ and for post-spawning herring: $lnE = 3.846 + 0.09 \times TL$.

Table 4.2: Parameters of linear regressions performed on energy densities per wet mass (in kJg^{-1}) as a function of percent of dry mass, here represented with percentage of water content: EW = intercept + slope x (100 - $\%H_2O$). Results of our study are highlighted in bold. [1] Hartman and Brandt (1995); [2] Pedersen and Hislop (2001).

model	r^2	N	Intercept	SE	Slope	SE	P	source
all fish	0.95	587	-3.419		0.375			[1]
Clupeidae	0.95	82	-2.532		0.329			[1]
Herring	0.99	20	-4.6395	0.189	0.417	0.007	< 0.0001	[2]
Herring	**0.93**	**15**	**-1.747**	**0.684**	**0.292**	**0.021**	**< 0.0001**	

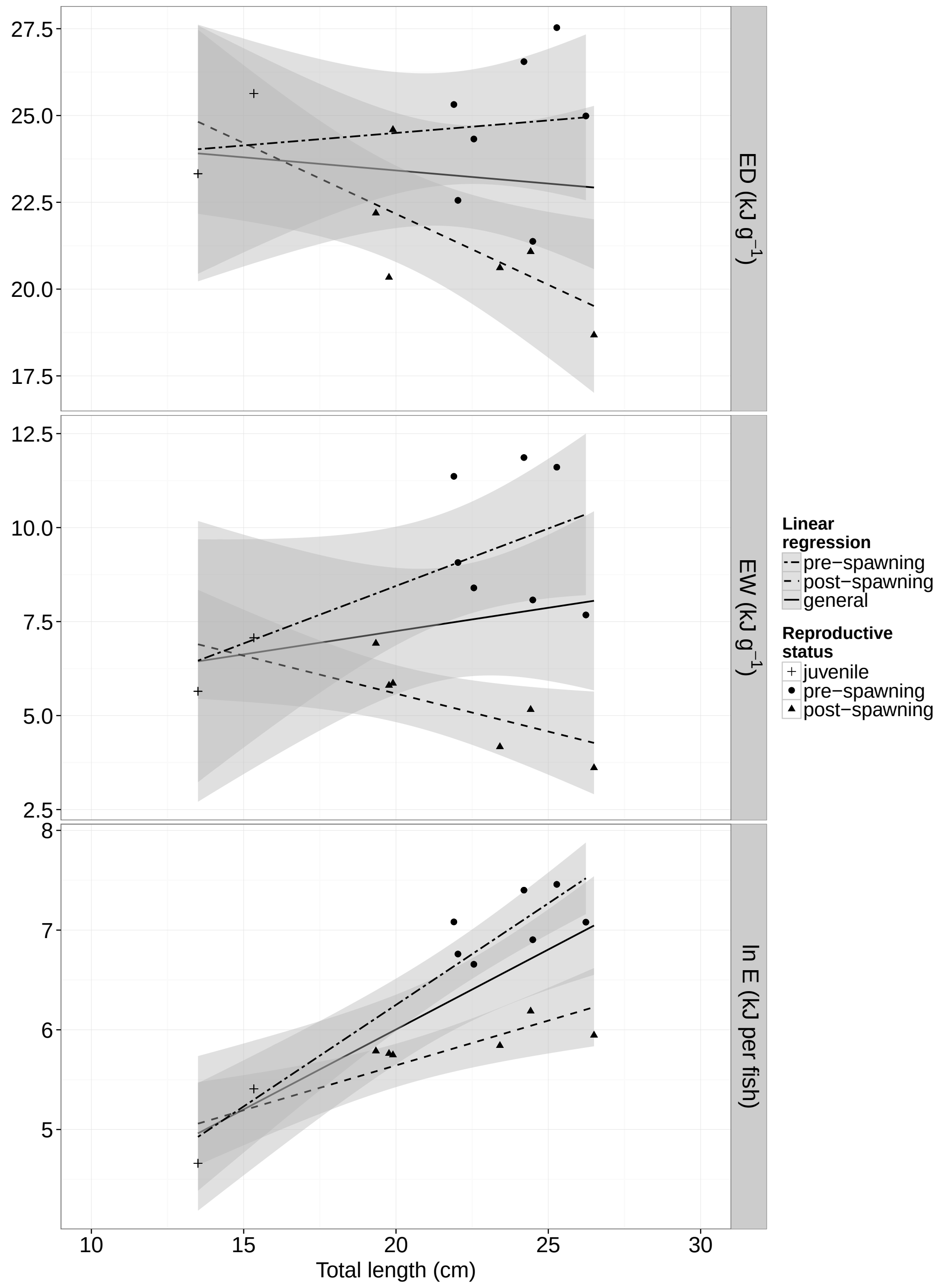


Figure 4.5: Energy density descriptors (*ED* for density per gram dry mass, *EW* for density per gram wet mass and *E* for total energy content) as a function of length. Linear regression models were fitted to the data, splitted according to the reproductive status of samples. A global regression was performed on the pooled data, regardless of the reproductive status of individuals. The values for *E* have been transformed with the neperian logarithm. Regression parameters and significance values are given in Table 4.3.

Table 4.3: Parameters of linear regressions linking energy density per gram dry mass (*ED*), energy density per gram wet mass (*EW*) and the log of total energy content per individual (*lnE*) with total length in cm. Regression curves and data are shown in Figure 4.5. Note that the model for *E* is based on the normal-logarithmic transformed values for energy density. Significant regressions (with $\alpha = 0.05$) are highlighted in bold.

	model	r^2	N	Intercept	SE	Slope	SE	P	sig
ED	general	-0.06	15	24.928	4.128	-0.076	0.186	0.691	
	pre-spawning	-0.11	9	23.056	3.642	0.072	0.165	0.675	
	post-spawning	**0.53**	**8**	**30.334**	**2.825**	**-0.408**	**0.137**	**0.024**	*
EW	general	-0.04	15	4.770	4.183	0.124	0.188	0.522	
	pre-spawning	0.29	9	2.335	3.276	0.306	0.148	0.078	.
	post-spawning	**0.47**	**8**	**9.619**	**1.544**	**-0.202**	**0.075**	**0.035**	*
E	**general**	**0.53**	**15**	**2.796**	**0.868**	**0.160**	**0.039**	**0.001**	***
	pre-spawning	**0.89**	**9**	**2.176**	**0.548**	**0.204**	**0.025**	**<0.001**	***
	post-spawning	**0.70**	**8**	**3.846**	**0.443**	**0.090**	**0.021**	**0.006**	**

4.4 Discussion

The main objective of this study was to measure the energy content of Atlantic herring using bomb-calorimetry. This is the first study that attempts to directly link reproductive status to energy content for Atlantic herring. Three descriptors of energy content were used: energy density per gram dry mass, energy density per gram wet mass and energy content per fish. The energy content of samples collected in October, December and March differed due to variability in characteristics between juveniles and adults. Some of this variability was explained by reproductive status, which was a better predictor than sampling month. Energy densities of juvenile and pre-spawning herring were high, while the energy density for post-spawning adults was comparably lower. The linear relationship between water content and energy density per gram wet mass was comparable with results presented in the literature (Hartman and Brandt, 1995; Pedersen and Hislop, 2001). A linear regression to estimate energy content per fish based on total length and reproductive status is proposed.

Seasonal variation explained with the influence of reproductive status

Seasonal variations in energy density for herring are known and often associated with feeding or spawning season and the respective utilisation cycle in protein and fat content for gonad development and metabolism (Hislop et al., 1991; Arrhenius, 1996; Paul et al., 1998; Slotte, 1999; Varpe et al., 2005; Varpe and Fiksen, 2010; Vollenweider et al., 2011). Sampling month was sufficient to explain variability in energy density of herring, but reproductive status was a better predictor of energy content. Temporal variation in energy density estimates would coincide with observed differences due to reproductive status, as long as all individuals of the population are synchronic for reproduction, which is not always the case for Atlantic herring. For example Celtic Sea herring have a prolonged spawning season lasting from autumn through winter (Molloy, 2006). Based on catch statistics, in October the stock was composed of juveniles and pre-spawning fish (O'Donnell et al., 2012). Based on the sampling in December, only half of the fish had spawned, while the other half was still in a pre-spawning state. March is assumed to be outside the spawning season and all bycatch samples were post-spawning fish. The spawning stock biomass (excluding juveniles) for Celtic Sea herring was estimated to be 159,776 tonnes in the season 2012/2013 (HAWG, 2013). For the ease of this example, taking the average energy density per gram wet mass and solely the variability due to reproductive status in a heterogenic population (hence, neglecting variation due to fish size), the herring spawning stock biomass would have represented 1539 $\pm 328\,TJ$ (tera joule) in October. Due to the presence of fish representing two reproductive status in December the estimate would be lowered to 1191 $\pm 182\,TJ$ and would be as low as 842 $\pm 157\,TJ$ in March. Without considering reproductive variability, energy density would be 7.7 ±2.8 kJg^{-1} wet mass and the entire spawning stock would provide an estimate of 1254 $\pm 454\,TJ$ in any month. For the purpose of a deterministic food web modelling, it would be important to consider the abundances and variation in energy content of groups with different reproductive states in order to avoid significant uncertainties in energy values.

Slotte (1999) found that Norwegian spring spawning herring used 30-50 % of their energy resource during spawning migration and spawning. In the current study, after spawning and migration, post-spawning herring contained an average of 46 % less energy in kJg^{-1} wet mass, which is similar to the values estimated by Slotte (1999). When the energy content per fish (E) was compared, the difference between reproductive stages was 70 % less energy. However, the differences in energy density per gram dry mass between pre- and post-spawning herring and juveniles were not significant. For pre-spawning herring, weight and I_G increased due to gonad production and water content decreased, leading to higher energy density per gram wet mass and energy per individual. The correlation of water content to energy density per gram wet mass has been shown for a wide range of fish species by Hartman and Brandt (1995) and was further confirmed for other forage fish by e.g. Hislop et al. (1991); Van Pelt et al. (1997); Anthony et al. (2000) and Dubreuil and Petitgas (2009). The relationship of water content and energy density per gram wet mass for Atlantic herring showed no significant variation to the relationship of other species. Thus, the relationship of water content and energy density per gram wet mass for Atlantic herring appears to be general.

Lower water content was found in high-lipid and high-protein fish (Anthony et al., 2000). An increase in lipid levels and energy during summer and autumn was found for forage fish and linked to food availability (Vollenweider et al., 2011). Reproductive status was not examined explicitly, but Vollenweider et al. (2011) showed that the peak in energy density over the season occurred in months prior to spawning, and was followed by a decrease in energy density, which was thought to be a result of lipid utilization during spawning. Thus, the lower water content and higher energy content in pre-spawning Atlantic herring could be linked to high lipid and protein levels during maturation. Anthony et al. (2000) found the opposite relationship between reproductive status and energy density per gram wet mass for capelin (*Mallotus villosus*, Müller 1776), where resting and developing stages had higher lipid content and energy densities compared to individuals classified as ripe, running or spent stages. The difference between those results and our study could be due to the definition of pre-and post-spawning fish (here being the integration of the developing-stage into the pre-spawning category) and the different methods applied in energy density estimation (bomb-calorimetry as opposed to the summation of energy equivalents for the proximate composition) rather than a biological characteristic. However, energy densities and lipid content for different forage fish species are variable (Anthony et al., 2000); hence energetic differences and relationships between energy density with water content and lipid levels could be species specific and result from different strategies in energy allocation to maintenance, growth, reproduction and migration in forage fish species. Analysis of biomolecule composition in different tissues would be necessary in order to verify pathways of energy allocation and reallocation during maturation.

Ecosystem comparison

Atlantic herring energy content estimates found in the literature are often incomplete due to missing information about season, weight, length, age, or water content (Table 4.4). Compared to Celtic Sea herring, energy values for Norwegian herring were much higher (Varpe et al., 2005). This could indicate that Atlantic herring exhibit strong spatial variation in energy content throughout its range; but it could also be due to temporal and/or methodological differences in energy estimation and disregarded reproductive status variability for the samples in Norway. Atlantic herring in the Bay of Biscay had similar energy density to Celtic Sea herring of the same length and season, but no information was given on their reproductive status (Spitz et al., 2010). Mårtensson et al. (1996) have shown that a seasonal variation can be observed in herring from the Barents Sea, where immature herring had energy density values in the range of what we reported for juvenile Celtic Sea herring. For adult herring, energy density values were comparable between the Celtic Sea and the Barents Sea with slightly higher values in autumn and winter for individuals from the Barents Sea. Pedersen and Hislop (2001) sampled herring of less than 15 cm in the North Sea and reported values comparable to the Celtic Sea herring juveniles. Hislop et al. (1991) presented energy densities per gram dry and wet mass, however their calculations were not in accordance with Celtic Sea herring, albeit energy densities per dry mass were comparable, e.g. 25 cm herring from the North Sea in November had $27.4\,kJg^{-1}\,ED$ and $7.5\,kJg^{-1}\,EW$, while a fish of the same length in October from the Celtic Sea had $27.5\,kJg^{-1}\,ED$ and accordingly $11.6\,kJg^{-1}\,EW$. Once again, inconsistencies in the results could likely be due to errors in water content estimation demonstrating the importance of presenting energy values per gram dry mass, wet mass and water content to allow intra-species comparisons. To sum up, it is possible to conclude that, because of the variability due to seasonality, size and maturation and because of the lack of ancillary information, energy density values for Celtic Sea herring were within the range of values presented for the Bay of Biscay, the North Sea and the Barents Sea (Table 4.4).

The energy densities of Pacific and Baltic Sea herring range between 2 to $13\,kJg^{-1}$ wet mass, including larval and juvenile fish (Arrhenius, 1996; Paul et al., 1998; Anthony et al., 2000; Vollenweider et al., 2011). Values given for the Baltic Sea population are comparable to post-spawning herring in the Celtic Sea (Paul et al., 1998). Adult Pacific herring from the Gulf of Alaska were in the range of values for the Celtic Sea herring for the autumn season (Paul et al., 1998). Pacific herring with similar average length to Celtic Sea herring exhibited similar energy density values, but it is not mentioned if fish sampled by Anthony et al. (2000) were also in a post-spawning phase. Pacific herring from the Gulf of Alaska showed seasonal variation, due to seasonality in lipid content and a mirrored pattern in water content (Vollenweider et al., 2011). Without knowing the exact reproductive status, but aligning the seasonality with the spawning cycle, energy density values for Pacific herring from the Gulf of Alaska are in the range of Atlantic pre- and post-spawning herring from the Celtic Sea. The lack of information given about length or maturity status blurs any identification of energy content variability within the genus Clupea (Table 4.4). However, when considering variability due to seasonality, body size and reproductive status, the energy value of herring can be assumed to be independent of the characteristics of the ecosystems. We based this conclusion on similar estimated energy values within and between herring species and with energy densities being in good agreement with the water content - energy density relationship given by Hartman and Brandt (1995). Our study suggests that additional measures of herring energetics should be carried out to improve the length to energy equation, in order to increase the significance of sample size per maturity stage and region. In addition, biomolecule composition analysis could provide information about seasonality and maturity affecting the energy allocation and energy loss during migration and spawning.

Ecosystem modelling implication

Due to the high individual and seasonal variability in body size and maturation, no single value of energy density could be used for herring (Paul et al., 1998). As discussed, water content provides a good estimation for herring energy density; but its estimation is time consuming and cannot always be performed. Based on the positive correlation between total length and energy content, a linear relationship to calculate energy per fish is proposed (Table 4.3). Introducing the reproductive status of the individuals improves the relationship between the energy content per fish and total length. To our knowledge, this is the first attempt to estimate energy per herring using both total length and reproductive status. The estimates of energy content per individual fish has a much higher ecological importance for food web studies than energy density per gram dry or wet mass, because in predator-prey relationship, the whole prey individual is eaten and the total energy can be metabolized.

The proposed equation can be used to estimate energy densities with historical herring data sets, if the length-weight relationship of herring has not changed over time. In the case of Celtic Sea herring, mean length has declined since the 1970s, however the length-weight relationship has been relatively stable over time (Lynch et al., 2004). Information about length-weight relationships for herring in the North Atlantic can be found in the respective stock assessment documentation e.g. HAWG (2013) for Celtic Sea herring. However annual variability, caused by changing habitat quality has to be considered. Wanless et al. (2005) linked seabird breeding failure to low quality sprat and sandeels, which had less than 25 % of the expected energy content compared to previous years. Studies that explicitly sampled multiple years found inter-annual variation in energy densities, however without being statistically significant (Hislop et al., 1991; Vollenweider et al., 2011). Celtic Sea herring sampled in 2012, showed comparable values with overlapping confidence intervals to studies in 1987, 1993, 1996 - 1998 and 2002 - 2008 (Table 4.4), (Hislop et al., 1991;

Table 4.4: Literature overview of energy content (*ED* for energy density per gram dry mass and *EW* for energy density per gram wet mass), with age, size, weight and water content, for Atlantic, Baltic and Pacific herring. TL = total length in cm, W = mass in g, %H_2O = percentage of water content; Ages are described in term of winter rings, or qualitative statements as YOY = young of the year; imm. = immature; mat. = mature. References are [1] Hislop et al. (1991); [2] Arrhenius (1996); [3] Mårtensson et al. (1996); [4] Paul et al. (1998); [5] Anthony et al. (2000); [6] Pedersen and Hislop (2001); [7] Varpe et al. (2005); [8] Spitz et al. (2010); [9]Vollenweider et al. (2011).

	season	age	TL	W	%H_2O	$ED\ kJg^{-1}$	$EW\ kJg^{-1}$	source
Atlantic herring	-	-	3 - 7	-	-	-	4.6 - 6.0	In [1]
	July Sep.	-	4 - 4.9	-	-	-	4.1	[6]
	July Sep	-	5 - 5.9	-	-	-	4.2	[6]
	July Sep.	-	6 - 7.9	-	-	-	3.9	[6]
	-	-	6.5	-	-	18.55	-	[1]
	-	-	7.5	-	-	19.5	-	[1]
	-	-	8.5	-	62.8	20	-	[1]
	July Sep.	-	8 - 9.9	-	-	-	4.5	[6]
	April - June	-	10 - 11.9	-	-	-	4.6	[6]
	July Sep	-	10 - 11.9	-	-	-	4.4	[6]
	April June	-	12 - 14.9	-	-	-	4.5	[6]
	July Sep	-	12 - 14.9	-	-	-	5.2	[6]
	Oct.- Dec.	-	12 - 14.9	-	-	-	6.3	[6]
	January	imm.	-	-	-	-	6.6	[3]
	April	imm	-	-	-	-	4.4 / 4.2	[3]
	Mai	imm.	-	-	-	-	5.2	[3]
	July	imm.	-	-	-	-	8.8	[3]
	August	imm.	-	-	-	-	7.0	[3]
	September	imm.	-	-	-	-	7.6	[3]
	October	imm.	-	-	-	-	5.3	[3]
	November	imm.	-	-	-	-	6.1 / 6.9	[3]
	April June	-	15 - 19.9	-	-	-	4.4	[6]
	July Sep	-	15 - 19.9	-	-	-	10.1	[6]
	Oct.- Dec.	-	15 - 19.9	-	-	-	7.1	[6]
	-	-	20	-	-	-	10.2	[8]
	April June	-	20 - 24.9	-	-	-	5.7	[6]
	July Sep	-	20 - 24.9	-	-	-	11.0	[6]
	Oct.- Dec.	-	20 - 24.9	-	-	-	8.5	[6]
	April - June	-	25 - 29.9	-	-	-	4.9	[6]
	July Sep	-	25 - 29.9	-	-	-	11.9	[6]
	Oct.- Dec.	-	25 - 29.9	-	-	-	8.8	[6]
	January	mat.	-	-	-	-	10.3 / 10.1 / 11.0	[3]
	February	mat.	-	-	-	-	6.0	[3]
	March	mat.	-	-	-	-	6.0 / 8.0	[3]
	April	mat.	-	-	-	-	7.9 / 3.9	[3]
	August	mat.	-	-	-	-	12.4 / 13.0	[3]
	November	mat.	-	-	-	-	11.2 / 12.6	[3]
	Full season	-	8.5 - 30	3.3 - 197	-	-	4.0 - 11.0	[1]
	full season	-	-	-	-	-	8.0 - 16.0	[7]
Baltic Sea herring	-	0	2 - 4	<0.13	-	-	2.2 - 2.8	[2]
	-	0	-	0.13 - 0.25	-	-	2.8 2.9	[2]
	-	0	-	-	-	4.8	-	[2]
	-	1	-	-	-	-	4.8 - 5.5	[2]
	-	2	-	-	-	-	5.0 - 6.0	In [2]
Pacific herring	Spring	YOY & 1	-	-	-	-	4.4	[4]
	Spring	2	-	-	-	-	5.2 - 6.5	[4]
	Spring	Adult	-	-	-	-	5.6 - 6.0	[4]
	Autumn	YOY	-	-	-	-	5.7	[4]
	Autumn	1	-	-	-	-	8.0	[4]
	Autumn	2	-	-	-	-	9.4 - 10.2	[4]
	Autumn	Adult	-	-	-	-	9.6 - 9.8	[4]
	-	-	19.3 ±4.2	87.5 ±51.1	58.2 - 80.8	-	3.48 - 12.75	[9]
	-	>0	<10	3.5	77.6	-	3.69	[5]
	-	>0	>10	23.5	72.3	-	5.84	[5]

Mårtensson et al., 1996; Pedersen and Hislop, 2001; Spitz et al., 2010). Inter-annual sampling was impossible within the timeframe of this study; however we acknowledge that annual variation is part of the total variation including body size, seasonality and reproductive status.

Conclusion

Our study estimated energy content values for Atlantic herring using bomb-calorimetry and attempted to link the variability of these estimates to a plausible series of explanatory factors. Reproductive status appeared to have more potential to explain the variability than evoking a generic seasonality. Water content was the main driver of energy density (per gram of wet mass) and the relationship that we established between water content and energy density was in good concordance with results found in the literature. We also found a linear relationship between the energy content of an individual fish and its length and reproductive status. This relationship is shown to be useful, since water content estimations are rarely available for historical samples. This relationship should be implemented in ecological models requiring the total energy available to predators of Atlantic herring. Once these models can be validated, they can be used as a primary tool for EBFM, providing a link between predation and fisheries catches, emphasizing eventual competition between both.

Acknowledgement

We would like to express our deep gratitude to Ciaran O'Donnell, David Stokes, Tobias Rapp and the crew of the CSHAS'12 and IGFS'12 surveys for collecting the fish samples. Thanks to Anna Soler-Vila and the "Irish Seaweed Research" group at the National University of Ireland Galway for the kind provision of their laboratories and usage of the bomb calorimeter. Cormack Nolan and the crew of the NWHAS'12 are thanked for collecting trial samples prior to the study and Clodagh Russell for assistance in the laboratory. This study was funded through a MARES Grant. MARES is a Joint Doctorate programme selected under Erasmus Mundus coordinated by Ghent University (FPA 2011-0016).

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Chapter 5

Comparison of energy content of forage fish from the Celtic Sea

"Herring, sprat and mackerel are considered as high quality prey.
Changes in prey energy content [...] can have implications on the
forage fish community due to shifting predation pressure as well as on
the predator population if no alternative higher quality prey is available."

(p. 140)

Abstract

As an energy carrier to higher trophic levels, forage fish play a key role in ecosystem functioning. Using bomb-calorimetry, energy densities per gram dry mass (ED in kJg^{-1}) and per gram wet mass (EW in kJg^{-1}) and energy content per individual (E in kJ) were measured for European sprat (*Sprattus sprattus*) and Atlantic mackerel (*Scromber scombrus*) from the Celtic Sea. Energy values were compared to values of Atlantic herring (*Clupea harengus*) to obtain baseline energy data of Celtic Sea forage fish. Energy densities for sprat were $ED = 27.1 \pm 2.7$ kJg^{-1} and $EW = 8.8 \pm 3.1$ kJg^{-1}. Respective values for mackerel were 28 kJg^{-1} and 10.5 kJg^{-1}. Water content was negatively correlated to energy density and could be used as a proxy for energy density. The high variability in sprat energy values was due to the presence of different reproductive stages in the samples. The forage fish species were defined as high quality prey, however with reduced quality depending on gonad development. This quality loss can be significant in foraging decisions. These data can be used to monitor prey quality and can be implemented in trophic ecosystem modelling for the Celtic Sea.

Keywords:

Atlantic herring · Atlantic mackerel · bomb-calorimetry · energy densities · European sprat · optimal foraging

5.1 Introduction

Forage fish, like Atlantic herring (*Clupea harengus*, L.), European sprat (*Sprattus sprattus*, L.) and Atlantic mackerel (*Scromber scombrus*, L.) are economically important species often used in fish meal production. However as carrier of energy from low to higher trophic levels, these species are important players in ecosystem structure and should therefore be exploited within an ecosystem-based fisheries management (EBFM) scheme. These fish species have a similar trophic level of 3 to 4 based on their nitrogen isotopic ratio (δ^{15}N) (Jennings et al., 2002; Ryan et al., 2014). Forage fish are preyed on by other fishes or apex predators like seabirds and cetaceans (Alder et al., 2008; Cury et al., 2011; Engelhard et al., 2014; Pikitch et al., 2014). Following the principles of optimal foraging theory, animals forage to maximise their fitness on an individual and a population level (Pyke et al., 1977). Successful foraging depends on the optimization of searching, pursuing, capturing and consuming prey (Pyke et al., 1977). In the field of "metabolic ecology", including the areas of bioenergetic models, foraging and food web theory and consumer-resource equations among others, most models refer to energy values as currency where optimal foraging is defined as predators maximising their net rate of energy intake (Pyke et al., 1977; Humphries and McCann, 2014).

Atlantic herring, European sprat and Atlantic mackerel (hereafter called herring, sprat and mackerel, respectively) are major forage fish species in the Celtic Sea ecosystem. Schools are often found in close proximity to the other species and mixed shoals are formed (Misund and Aglen, 1992; Saunders et al., 2012; Sveegaard et al., 2012). Even though herring, sprat and mackerel have similar trophic levels and position in the ecosystem, their population dynamics are very different. Herring is managed as one stock with fishery regulations within the Celtic Sea. From their offshore feeding grounds, herring migrate inshore to the Irish south coast in autumn and winter months for spawning (Molloy, 2006; Volkenandt et al., 2014). Sprat abundance in the Celtic Sea is highest in November to December and in spring, when sprat come inshore for spawning. No regulations exist for sprat fisheries in the Celtic Sea and the sprat stock structure is unknown (HAWG, 2013). Mackerel undergo feeding migrations to the Nordic Seas and the North Sea and thus are managed as one large, dynamic stock for the north-east Atlantic (Marine Institute, 2013; Jansen and Gislason, 2013). Understanding prey selection by predators can help defining the natural mortality rate within the respective stock assessment of the forage fish species.

Energy values of prey can be obtained by adding energy equivalents for the proximate body composition (see for example Van Pelt et al., 1997; Anthony et al., 2000; Vollenweider et al., 2011) or by measuring the heat capacity with a bomb-calorimeter (e.g. in Hislop et al., 1991; Paul and Paul, 1998; Spitz and Jouma'a, 2013, Chapter 4). Both methods are considered to be accurate, however a long preparation time is required prior to the actual measurement, which is less suitable for large sample volumes (Cummins and Wuycheck, 1971). Alternatively linear regression models that estimate energy content based on known water content can be applied (Hartman and Brandt, 1995; Van de Putte et al., 2006). In the literature, many energy density values can be found; yet because of incomplete information on variability due to location, age, seasonality or maturation, values often cannot be applied to the ecosystem in question. The choice of the most suitable method therefore depends on the research question, the level of accuracy needed and the energy descriptors desired.

Three common energy descriptors are often used within an ecological framework: 1. Energy density per gram dry mass (*ED*), which is an unbiased value, can be accurately measured and allows for comparison between species and ecosystems. However, the ecological importance of ED is low as dried prey is not consumed (Hislop et al., 1991). 2. Energy density per gram wet mass (*EW*) depends on water content, which can be underestimated due to unaccounted evaporation. *EW* benefits from ease of comparison and speed of data availability and is for these reasons, the main energy descriptor presented in literature. 3. The total energy per animal (*E*), which has high ecosystem relevance as it shows how much energy can be obtained during foraging. Information on the size of the animal has to be presented along with *E* before between-species comparison is possible.

A central part of ecology is to understand how energy flows govern ecosystem function and stability (Humphries and McCann, 2014). The aim of this study was to estimate energy values for sprat and mackerel and compare those values with energy estimates for herring from the Celtic Sea. Energy data are provided as energy densities (*ED* and *EW*) as well as *E* to present complete baseline information. Bomb-calorimetry was used to obtain energy values. Knowledge of energy contribution of forage fish species to the ecosystem will help to identify possible factors influencing prey selection and foraging decisions of apex predators. This information is necessary within an EBFM of forage fish and to maintain a high quality habitat for charismatic top predators like seabirds and cetaceans.

5.2 Material and Methods

Fish acquisition and preparation

European sprat and Atlantic mackerel samples were caught from the Celtic Sea in October 2012 (Figure 5.1) with a pelagic midwater trawl during the Celtic Sea Herring Survey (n= 61 sprat from 3 trawls; n=31 mackerel from two trawls). Sprat were also caught during the Irish Groundfish Survey in December 2012, however no mackerel samples were obtained. A GOV (Grande Ouverture Verticale) trawl was used and sprat were taken from five trawls (n= 76). Fishes caught in October were stored in individual zip bags at -20°C, while December samples were frozen in batches per trawl. In the laboratory, individuals were thawed and measured for total length (TL, in cm) and wet mass (W, in g) with a precision of 0.01 cm and 0.1 g respectively. Otoliths were extracted for age determination via otolith reading. Gonads were extracted and weighed with a precision of 0.001 g (OW, in g). Maturity stages were recorded for sprat and mackerel. The macroscopic identification of maturity stages for sprat is impeded by freeze-thawing (ICES, 2011) so no certain differentiation between maturity stages was possible. Therefore the gonado-somatic index was used in further analyses (explained below). All mackerel individuals were identified as juvenile fish based on the scale by Walsh et al. (1990). Each fish was handled with an aluminium cup with known weight to minimize any loss of liquids. The entire fish was dried for 24 h at a constant temperature of 105°C. After drying and cooling in a dry chamber, the total dry weight (DW, in g) was determined and the fish was homogenized with a common kitchen blender. Fish powder of up to ten fish of the same trawl and length class were pooled to reduce inter-individual variability (n=8 for sprat; n=2 for mackerel). Per combustion, a sub-sample of 1 g of the pooled fish powder was used to measure energy density per gram dry mass (ED, in kJg^{-1}) with an adiabatic bomb-calorimeter (Paar Instrument Company, model 6100). The average of three combustions was taken as energy density estimate per sample.

Statistical analysis

For each individual fish of both species, a gonado-somatic index (I_G, expressed in %) with:

$$I_G = 100 \times \frac{OW}{W - OW} \qquad \text{(eq. (4.1))}$$

and water content (%H_2O) expressed as percentage of wet mass was calculated. A higher I_G can indicate an advanced maturity stage because further developed gonads occupy a higher proportion of the total mass. Then, average length, weight, age, I_G and %H_2O

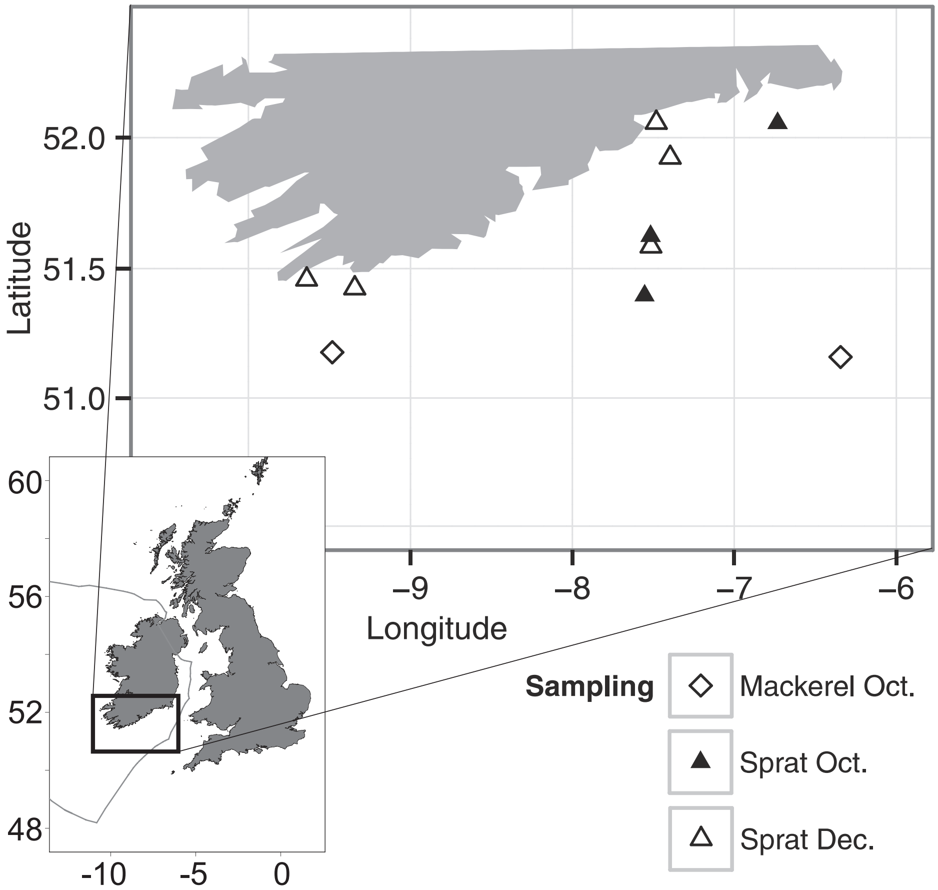

Figure 5.1: Sampling stations along the Irish south coast in the Celtic Sea. Sprat and mackerel samples were collected in October 2012 and additional sprat samples were collected in December 2012.

were calculated for each sample used for the bomb-calorimetry. The table containing quantitative variables (TL, W, age, %H_2O, ED, I_G) across all samples was analysed using Principal Component Analysis (PCA), for which observations were centred and reduced. Due to the small sampling volume of mackerel (n= 2), only sprat were analysed by PCA. A set of three energy descriptors were used to present energy values for sprat and mackerel:

- Experimentally obtained ED
- Energy density per gram wet mass (EW, in kJg^{-1}) calculated as:

$$EW = ED \times (1 - \frac{\%\mathrm{H_2O}}{100}) \qquad \text{(eq. (4.2))}$$

- Total energy content per fish (E, in kJ) calculated as

$$E = EW \times W \qquad \text{(eq. (4.3))}$$

.

Using an ANOVA, the linear relationship of water content and EW for sprat and mackerel were compared to the linear relationship proposed by Hartman and Brandt (1995) for an extended range of fish species: $EW = -3.419 + 0.375(100 - \%\mathrm{H_2O})$. Energy values for Atlantic herring from the same area and sampling month (October and December 2012) were obtained from Chapter 4. In relation to total length, the three energy descriptors (ED, EW and E) of herring, sprat and mackerel were compared to identify energetic difference at identical total length. Energy values are presented in kilojoules (kJ) throughout the text. All analyses were performed using the open-source statistical software ”R” (`http://cran.r-project.org`).

5.3 Results

Sample variation

The first two principal components (PC) explained 81% of variability in the sprat samples (Figure 5.2). The first PC explained 57.2% of the variance, influenced by a combination of ED, %H_2O, I_G and age (Figure 5.2), while ED was negatively correlated with %H_2O (Figure 5.2). The second PC explained 23.8% of the variance in the sprat data set and was driven by TL and W (Figure 5.2). With a third PC, the cumulative explained variance reached 93.8% including the contribution of W (8%), TL (3%) and ED

and age with a cumulative value of 1.3%. Samples collected in October were influenced by ED, I_G and age, while sprat taken in December had generally a higher water content compared to the October samples (Figure 5.2 and Table 5.1). Averages for TL, W, age, I_G, %H_2O and energy descriptors are shown in Table 5.1 for sprat and mackerel samples. The group of sprat samples with a low I_G ($I_G < 0.7$) had a mean ED of 24.2 ±1.3 kJg^{-1} (n=3), and sprat with an I_G bigger than 0.7% had a higher mean ED of 28.9 ±1.3 kJg^{-1} (n=5). Mackerel samples with a mean ED of $28kJg^{-1}$ (n=2) were composed of juvenile fish according to the stage of gonad development.

Energy density regression

The linear relationship between EW and %H_2O for sprat samples was:
$EW = -3.121 + 0.375 \times (100 - \%H_2O)$ ($r^2 = 0.99$, $p < 0.001$). With only two values, no linear relationship could be estimated for mackerel, however the EW values for mackerel ($EW = 9.2\ kJg^{-1}$ and $EW = 11.7\ kJg^{-1}$) were close to the estimation of Hartman and Brandt (1995) ($EW = 9.3\ kJg^{-1}$ and $EW = 11.8\ kJg^{-1}$) (Figure 5.3). Further, the linear regression for sprat was compared to the regression coefficients given by Hartman and Brandt (1995) and to the coefficient for herring ($EW = -1.747 + 0.292 \times (100 - \%H_2O)$, Chapter 4). No significant differences between the regression coefficients was found for the three linear models (ANOVA, F(2, 180) = 2.180, $p = 0.12$). EW for herring, sprat and juvenile mackerel could be accurately estimated by substituting the respective %H_2O into the equation given by Hartman and Brandt (1995).

Table 5.1: Mean and standard deviation of characteristics measured for European sprat and Atlantic mackerel. Total means (in bold) were calculated for sprat samples with $I_G >= 0.7$ and $I_G < 0.7$ as well as for mackerel samples.

Species	Month	n	TL (cm)	W (g)	winter rings	I_G	%H_2O	ED (kJg^{-1})	EW (kJg^{-1})	E (kJ)
Sprat	Oct	10	12 ±0.1	15.4 ±2.3	1	0.7 ±0.3	60.5 ±5.0	29.6	11.7 ±1.5	177.7 ±20.3
	Oct	10	12.7 ±0.3	17.8 ±1.8	2 ±1	0.8 ±0.5	55.7 ±4.0	30.6	13.5 ±1.2	239.8 ±21.4
	Oct	6	13.6 ±0.5	21.6 ±1.6	3 ±1	1.1 ±0.2	62.5 ±3.2	29.2	11.0 ±0.9	237.3 ±33.1
	Dec	10	7.6 ±0.6	25.5 ±15.7	-	-	75.7 ±4.3	25.6	6.2 ±1.1	159.5 ±100.7
	Dec	10	9.2 ±0.3	21.3 ±25.7	0	0.8 ±0.2	70.8 ±1.6	27.5	8.0 ±0.4	176.2 ±215.5
	Dec	10	10.7 ±0.6	10.1 ±1.8	1	1.2 ±0.3	67.0 ±3.2	27.6	9.1 ±0.9	92.8 ±23.0
	Dec	10	13.2 ±0.4	16.8 ±1.8	0	0.4 ±0.6	76.7 ±4.4	23.7	5.5 ±1.0	93.4 ±22.5
	Dec	10	14.3 ±0.4	21.4 ±2.9	0	0.1 ±0.1	77.2 ±1.5	23.2	5.3 ±0.4	113.5 ±22.2
average	$I_G < 0.7$	**3**	**11.7** ±3.6	**21.2** ±4.4	**0**	**0.25**	**76.5 0.9**	**24.2** ±1.3	**5.7** ±0.5	**122.1** ±33.9
	$I_G >= 0.7$	**5**	**11.6** ±1.7	**17.2** ±4.7	**1** ±1	**0.92** ±0.2	**63.3** ±5.8	**28.9** ±1.3	**10.7** ±2.2	**184.76** ±59.9
Mackerel	Oct	10	20.9 ±0.7	66.3 ±6.1	0	0.3 ±0.1	66.2 ±3.8	27.3	9.2 ±1.0	613.1 ±104.2
	Oct	4	23.4 ±1.1	98.1 ±14.6	1	0.5 ±0.2	59.3 ±8.6	28.7	11.7 ±2.5	1172 ±386.9
average	**juveniles**	**2**	**22.2**	**82.2**	**-**	**0.5**	**62.8**	**28**	**10.5**	**892.6**

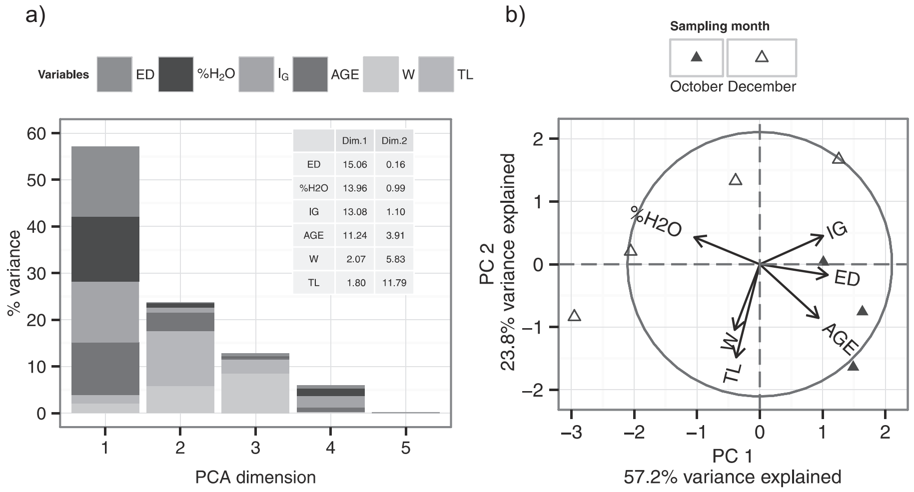

Figure 5.2: a) Overview Principal Component (PC) composition explaining the variance of the sample characteristics (mass, length, age, I_G and water content). The contributions to the first and second component are inset in the main figure. b) First and second component of the PCA performed on centered and reduced data explained a total of 81% of variance. Sample points are labelled according to the sampling month. W = wet mass, TL = total length, age = age according to winter rings, %H_2O = % water content, ED = energy density per dry weight.

Species comparison

Figure 5.4 shows a comparison of energy descriptors for herring, sprat and mackerel according to fish length. Each species showed an increase in energy densities and content with increasing body size. Irrespective of the smaller size, sprat contained similarly high ED compared to pre-spawning herring or juvenile mackerel. Small fishes of the same length (12 - 15 cm), i.e. juvenile herring and sprat samples, showed two distinct EW groups: sprat with a high I_G ($I_G >= 0.7$, here defined as "developing") had higher EW values than sprat with a low I_G ($I_G < 0.7$, here defined as "undeveloped") together with juvenile herring. Fishes of larger size, i.e. adult herring and 21 - 26 cm juvenile mackerel showed a similar pattern of high EW densities, while the values for post-spawning herring were much lower (Figure 5.4). As expected, smaller fishes of 7 - 15 cm contained lower E compared to larger fishes of 20 - 26 cm. Although post-spawning herring were much larger in size than sprat or juvenile herring, E was only marginally higher (Figure 5.4).

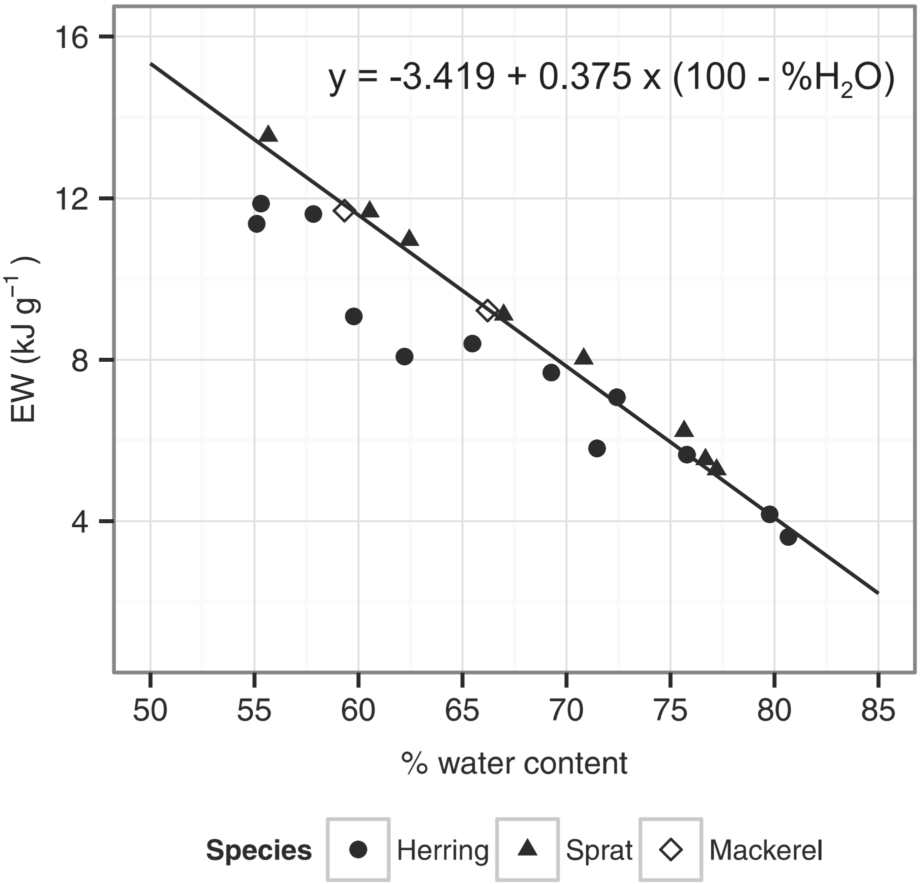

Figure 5.3: The linear regression of energy density per gram wet mass (EW) to water content presented by Hartman and Brandt (1995) is shown and the equation given. Energy densities of sprat and mackerel from this study as well as herring energy densities (see Chapter 4) are plotted. No significant differences between regression coefficients of herring and sprat compared to the given equation were found.

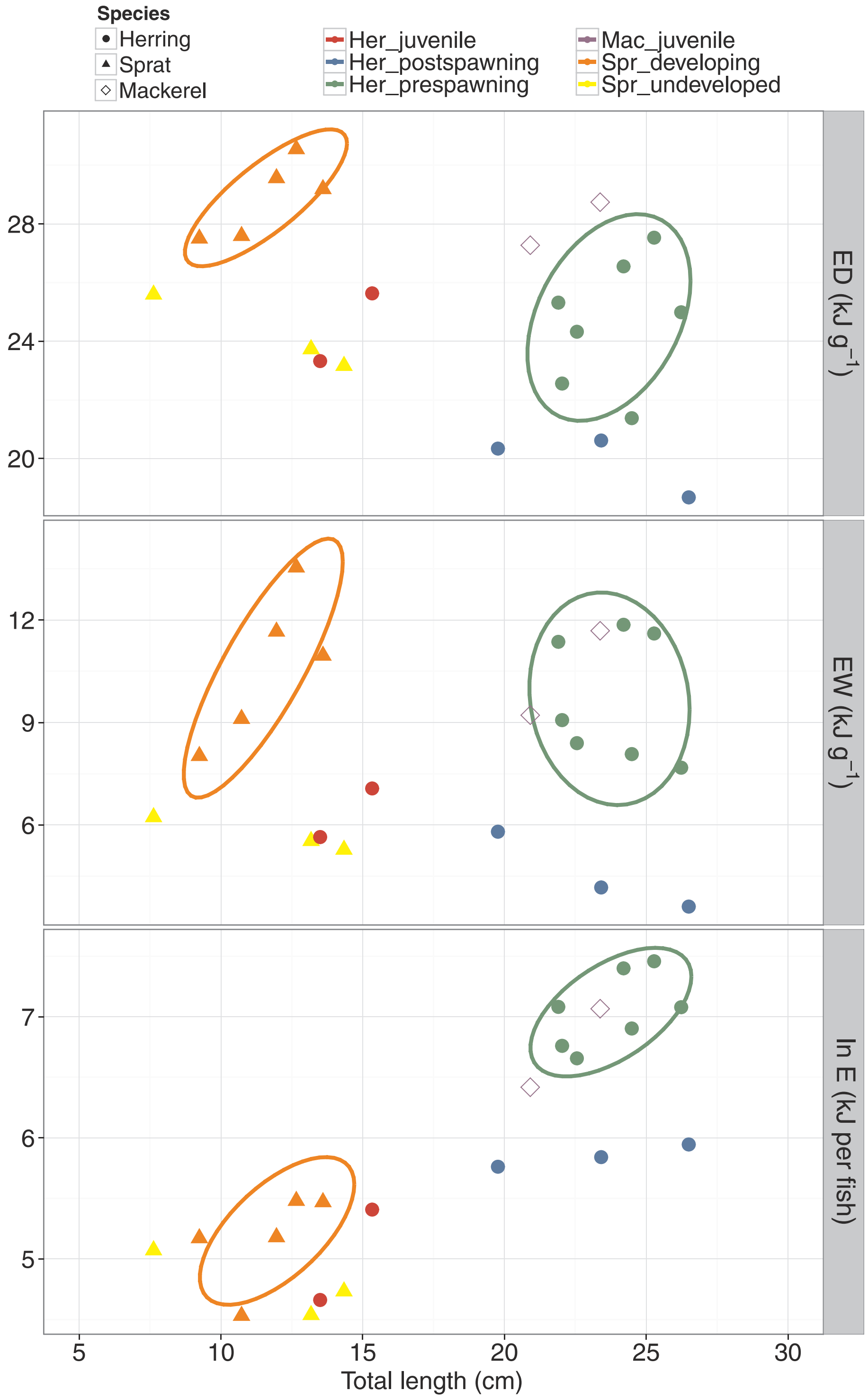

Figure 5.4: Energy descriptors (ED, EW and E) are shown in relation to length for herring, sprat and mackerel samples. The values for E have been transformed with the neperian logarithm. While different point shapes indicate fish species, a colour code was used to describe different sample characteristics: Her juvenile = juvenile herring samples; Her postspawning = herring with a regressing gonadal stage; Her prespawning = herring with developing or ripe gonads; Mac juvenile = juvenile mackerel of this study; Spr developing = sprat of this study with $I_G >= 0.7$ and Spr undeveloped = sprat of this study with $I_G < 0.7$. The coloured circles indicate a 0.95 confidence level for the respective group.

5.4 Discussion

Energy density values for sprat and mackerel were determined and compared to herring. For all three forage fish species, EW, were in agreement with a general linear regression presented in literature, which supports the accuracy of our results. Irrespective of the total length, sprat samples had ED on the same scale as herring and mackerel or even exceeding those values. Mackerel energy densities were within the range of pre-spawning herring of the same size. Overall, the importance of gonad development on energy content and densities was apparent. Energy values for herring and sprat with less developed or regressing gonads were much lower than for more developed fish.

Sprat maturation

The spawning season for Atlantic and Baltic sprat ranges from early spring to late autumn with a peak in May to June (ICES, 2011). Due to differences in the I_G values, sprat samples collected in October and December likely showed different progress in maturation for the spawning period. Two groups were identified according to the I_G values: developing sprat samples with an $I_G >= 0.7$ and undeveloped sprat samples with an $I_G < 0.7$. Sprat from the Kattegat and Skagerrak showed an I_G from 0.25 - 1 between August to December that increased to 6.25% from January to May (Mittermayer, 2007). A similar seasonality has been shown for Baltic Sea sprat (*S. sprattus balticus*, S.) that spawn from January to June and have I_G values of 8 - 10% for females (Haslob et al., 2013). The different reproductive stages were not apparent macroscopically, hence individuals were pooled for the bomb-calometric measurements according to length class and sampling month under the assumption that they originated from the same cohort. Pooling the samples according to the I_G values could reduce the variability caused by the mixture of reproductive stages in the samples.

Energy densities of sprat

Sprat sample variation was dominantly driven by water content, ED, length and gonad development (Figure 5.2). Strong influence of gonad development and maturation on energy density has been shown for Clupeidae (Paul et al., 1998; Slotte, 1999; Anthony et al., 2000 and Chapter 4) and could have been a driver of energy density variation in sprat from the Celtic Sea. No information on maturation was obtained for North Sea samples; however the energy density values (EW = 5.6 - 6.7 kJg^{-1}) were comparable to "undeveloped" Celtic Sea sprat of the same length and one sample showed an identical value compared to the Celtic Sea (EW = 11.5 kJg^{-1} compared to 11.7 kJg^{-1} respectively) (Pedersen and Hislop, 2001). Energy densities from the Celtic Sea had slightly higher values than those from the Bay of Biscay (Spitz et al., 2010; Spitz and Jouma'a, 2013), which was caused by a lower water content in some of the Celtic Sea samples. When comparing our results to North Sea sprat coming from seabird prey and fisheries samples (Hislop et al., 1991), some values for ED, EW and E were inconsistent. The discrepancy between the studies could be due to sampling a mixture of reproductive stages in both studies and unaccounted water loss during sample preparation. Water content measurement can be used for energy density estimation (Hislop et al., 1991; Hartman and Brandt, 1995 and Chapter 4). Notably, energy densities (ED and EW) based on water content were similar between this study and Hislop et al. (1991). Further validating our results, the EW-values for sprat from the Celtic Sea were in agreement with calculated values according to Hartman and Brandt (1995).

Comparison of forage fish energy values

Three functional groups, also called "quality groups" (QG) within a foraging context, were defined according to EW of prey to generalize and quantify ecosystem functions and predator-prey interactions (Spitz et al., 2010):

- Low QG with $EW < 4kJg^{-1}$
- Moderate QG with $4 < EW > 6\ kJg^{-1}$
- High QG with $EW > 6\ kJg^{-1}$.

Herring, sprat and mackerel from the Celtic Sea fall into the high quality group (Figure 5.4), which is typical for forage fish species (Spitz and Jouma'a, 2013). Prey species selection could be interchangeable when based on theoretical energy profitability to fulfil predator energetic requirements; however different reproductive stages of forage fishes can occur together causing a downgrading to moderate or low quality prey. From an ecological viewpoint, it could be beneficial for predators to switch from preying on post-spawning herring to the co-occurring developing sprat with a similar energy content per fish, even though they are of much smaller size (Figure 5.4). In the framework of optimal foraging and metabolic ecology, prey selection cannot be defined exclusively by prey energy content. Variables such as special nutrient requirements, prey encounter rate, dispersal and abundance influence prey selection and prey profitability (Österblom et al., 2008; Spitz et al., 2010). In addition, post-spawning herring schools are less dense and could be more difficult to detect; while on the other hand escape response to predator presence is less coordinated that can delay the formation of dense bait balls (Rieucau et al., 2014). Different schooling behaviour could be disadvantageous depending on the predator foraging abilities and can lead to a switch of prey thereby increasing predation pressure on other forage fish species. The inability to switch to prey of higher quality can have severe influence on the population dynamics of apex predators (Wanless et al., 2005; Österblom et al., 2008).

This study presented energy densities and energy content baseline data for highly abundant forage fish species in the Celtic Sea. Even though Atlantic herring, European sprat and Atlantic mackerel are considered as high quality prey, this status can be substantially lowered when several reproductive stages occur together. Changes in prey energy content together with a resulting change in foraging behaviour can have implications on the forage fish community due to shifting predation pressure, as well as on the predator population if no alternative higher quality prey is available. Within trophic ecosystem models and ecosystem based fisheries management for the Celtic Sea, these dependences of energy content, prey availability and consequent foraging decisions have to be accounted for.

Acknowledgement

We would like to thank Anna Soler-Vila and the ”Irish Seaweed Research” group at the National University of Ireland, Galway for providing the bomb calorimeter and for allowing the usage of their laboratories. Ciaran O’Donnell and David Stokes together with the respective crews of the CSHAS’12 and IGFS’12 surveys are thanked for sample collection. Thanks to Clodagh Russell for assistance during sample processing. This study was funded through a MARES Grant. MARES is a Joint Doctoral programme selected under Erasmus Mundus coordinated by Ghent University (FPA 2011-0016).

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Chapter 6

General discussion

“We do not know how to manage ecosystems [...]. What we do attempt to manage [...] is human activities. [...] now, nearly 20 years after [...] we do try to take ecosystem characteristics into account and fisheries management is becoming a more collaborative approach between decision makers, fishery scientists and ecologists.”

(p. 182)

Bottom right picture courtesy of Pádraig Whooley, Irish Whale and Dolphin Group.

6.1 Discussion introduction

An ecosystem-based approach to fisheries management (EBFM) is a relatively short and often-heard phrase, but its meaning is complex and its implementation is elaborately interwoven with other factors. In practice, there is no task list for scientists and decision makers that can be checked off with a final "Congratulations! Your fishery is now managed ecosystem friendly"- pop up window. Managing a resource in consideration of environmental and biological influences cannot be a simple "yes" or "no" process; however fishery management already can incorporate a wide range of biological processes, inter-specific dynamics and account for environmental influences. Shelton et al. (2014) summarises: *"the effect of different types of harvest of a given species or population within a species will depend strongly on the biological details of recruitment, growth, and mortality. [...] Decisions about how much harvest is too much harvest on anyone life stage are complicated by many factors, not the least of which are socio-economic and political consequences generated by biological constraints."* Accounting for ecosystem dynamics does not always imply modifications and confutation of a management in place (Shelton et al., 2014). However, one should not merely rely on fortunate ignorance of variability covered up by a precautionary fishery management, but encourage work towards the understanding of ecosystem processes.

This thesis contributes and broadens our knowledge base of biological processes in the Celtic Sea ecosystem. Focus was given to Celtic Sea herring in view of predation pressure by baleen whales and the existence of a regional herring fishery management. Two other forage fish species, sprat and mackerel, were considered briefly regarding the links between baleen whales and forage fish in the Celtic Sea ecosystem. First, the spatial distribution of herring on the Celtic Sea plateau was analysed and linked to environmental variables like temperature and salinity. This set the important background to link herring to other species and their placement within the Celtic Sea ecosystem. Second, statistical support was given to what has been historically observed, namely that baleen whales repeatedly target forage fish in the Celtic Sea and use it recurrently for foraging. Then the energy contribution of forage fish as prey in the Celtic Sea ecosystem was explored, highlighting the role of reproductive development as important factor for variability in energy content.

EBFM implies the extension of the traditional single-species management approach and consequently the field of fishery science has to be extended to a multidisciplinary scientific framework. Within the scope of this thesis, the multidisciplinary topics include: (i) forage fish, principally herring, from a fishery science perspective; (ii) cetaceans, essentially baleen whales, from an ecological viewpoint and (iii) the resulting interactions and dependencies within the Celtic Sea ecosystem. In the subsequent sections, I will touch on the following overarching ecological issues and their respective relevance within an EBFM for the Celtic Sea:

- Role of forage fish population dynamics
- Role of baleen whales as predators
- Energy content as currency to describe inter-specific dynamics
- Predation as driver of population dynamics
- Opportunities arising from modelling techniques
- Theoretical baleen whale distribution driven by forage fish in the Celtic Sea - a conceptual model on trophic links
- Prospects in fisheries management
- Avenues for EBFM

An outlook for future work and the conclusion closes the discussion on the exploration of the links between baleen whales and forage fish in the Celtic Sea: assessing spatial distribution and energy content.

6.2 Forage fish population dynamics

Recruitment projections for forage fish are already challenging without consideration of cetacean predation due to the strong variability in year class strength under the influence of oceanographic and environmental factors (Rice and Duplisea, 2014). Within a single-stock management and assessment strategy, one has to refer to the fundamental science of fish population dynamics that comprises subjects such as larval survival, larval transport, maturity at age, stock integrity (i.e. stock mixing) and density-dependent effects on population dynamics. Many of these processes have been previously studied for Celtic Sea herring and changes in population dynamics can be followed based on a long time series of landings data originating from the 1950s (Brophy and Danilowicz, 2002; Brophy et al., 2006; Burke et al., 2009; Lynch, 2011; Harma et al., 2012; O'Sullivan et al., 2013). The historical development of the herring fisheries in the Celtic Sea has been described by Molloy (2006). Hence, a conceptual framework of Celtic Sea herring population dynamics is already available for use in further scientific advancements. The present work contributes to the scientific knowledge of Celtic Sea herring by analysing their spatial distribution and energy content.

Understanding and observing changes in spatial distribution are important components in stock assessment. Spatial distribution and more importantly, the change in spatial distribution, involves central stock-specific characteristics of population dynamics, such as abundance, demography and behaviour, which can influence trophic interactions (Petitgas et al., 2014). Variability in distribution can cause fish to become more difficult or impossible to access for some predators e.g. seabirds that are bound to nesting areas (Engelhard et al., 2014) and hence spatial distribution can influence predation pressure on the fish stock. Further, distribution variability is closely linked to population dynamics and recruitment in the following year (Casini et al., 2014; Petitgas et al., 2014). Celtic Sea herring distribution was strongly oriented towards the coastal spawning grounds during pre-spawning migration and environmental influence was less strong compared to the spawning ground attraction (Chapter 2). A distribution shift was statistically non-existent based on survey data from 2005-2012, and data from 2013 indicated again a close inshore distribution (Figure 3.2). Preliminary data for 2014 suggest that herring were predominantly outside the research area within a delay of a few weeks (C. O'Donnell pers. communication). This highlights the need for further analysis of the spatial distribution of Celtic Sea herring and to understand the drivers of spawning migration initiation and the distribution range outside the spawning season.

A delay in migration could have particular consequences on predator populations within the match-mismatch concept (see Section 6.5). Because many baleen whales are bound to seasonal migration, their residence time within Irish waters is presumably limited. A delay in herring migration, which could also be due to a higher proportion of winter spawners and an offset of spawning time (Harma et al., 2012), could lead to food constrains for baleen whales (Ryan, 2012). Implications would be strongest, if herring were the primary prey source for baleen whales in the Celtic Sea, however Ryan et al. (2014) and Chapter 3 highlight the importance of sprat within the baleen whale-forage fish interaction. If sprat were "filling the gap" spatially and temporally by replacing herring, sprat could be an equivalent compensation with similar energy content (Chapter 5). In this regard, the inter-species specific dynamics between herring and sprat become especially interesting. As an aggravating circumstance, very little is known about sprat distribution, abundance and population dynamics in the Celtic Sea compared to herring.

Importantly for stock assessment and population dynamics, density dependence acts already within a species and can influence cannibalism, fecundity, growth rates and other population characteristics (Hixon and Carr, 1997; Rose et al., 2001; Lorenzen and Enberg, 2002; Rice and Duplisea, 2014). A primary example is the Baltic Sea, where interspecific density dependent control has been shown for herring and sprat (Casini et al., 2006, 2010). Due to food competition, Baltic Sea herring growth was triggered by sprat abundance (Casini et al., 2010). Information on zooplankton abundance for the Celtic Sea is sparse, however the zooplankton abundance in the neighbouring Western Channel has been relatively stable in the last decades (Eloire et al., 2010). A decline of copepod species was found for the larger Celtic Sea ecoregion, however data exist only up to 2008 and hence do not cover the time period of the recent increase in herring biomass (McGinty et al., 2011, 2012). Stomachs of co-occurring herring and sprat on the Celtic Sea plateau were empty in October and December (personal observation, sampling described in Chapters 4 and 5). However, samples were taken in the winter time when feeding of both species is less likely. It is unknown how much the two species overlap during the feeding period in spring to autumn in the Celtic Sea because of the limited information on sprat. Therefore, it is necessary to survey distribution and abundance of the two forage fish species with zooplankton abundance to understand inter-species density dependence and food competition.

Next to sprat, mackerel falls into the same functional group as herring (Reecht et al., 2013). Mackerel and herring have different predators in the Celtic Sea, i.e. baleen whales did not target mackerel, but rather herring (Chapter 3). Hence increasing predation pressure on the one species would not necessarily resemble a decreased predation on the other. For the Norwegian Sea, herring, blue whiting and mackerel showed spatial disparity and small diet overlap (Langøy et al., 2012), while in the Celtic Sea herring and mackerel co-occur and species interactions could be possible. Mackerel can impact the herring population via predation on juveniles or via density-dependent food competition between juvenile mackerel and herring. Spatial overlap with blue whiting could occur on the feeding grounds on the Celtic Sea plateau. Together with sprat and mackerel, other forage fish species and predatory fish can be in competition for resources with herring, increasing herring mortality or influencing their population dynamics (Engelhard et al., 2014; Trenkel et al., 2014).

Celtic Sea herring has its own population dynamics, which can be affected by spatial distribution and changes of spatial distribution. Further, Celtic Sea herring can be influenced by other fish species sharing a common habitat. Spatial co-occurrence can be a first indication of inter-species dynamics and can be a tool (together with dietary analysis) to study food competition. Knowledge on forage fish population dynamics in the Celtic Sea is strongly skewed towards herring and much less is known about sprat or mackerel. To better understand forage fish inter-species dynamics and partitioning, it is necessary to strengthen research on other fish species within the Celtic Sea pelagic ecosystem. For the development of an EBFM for Celtic Sea herring, it will be important to place herring spatially and conceptually within a piscivorous ecosystem network and include impacts of food competition, density dependence and predation on Celtic Sea herring population dynamics.

6.3 Role of baleen whales as predators

How much do baleen whales eat? Acknowledged as apex predators with the abilities to influence ecosystems via the removing of large volumes of prey, baleen whale predation should be included in mortality estimates of pelagic fish. Using different approaches, several ecosystem studies tried to answer the opening question, especially with focus on commercially exploited prey in light of resource competition between baleen whales and fisheries (Leaper and Lavigne, 2007). From a global viewpoint, baleen whale consumption is only a small proportion compared to the total landings from global forage fish fisheries (Kaschner et al., 2006), but this could be different on the scale of regional ecosystems concerning single stocks. Information on the habitat use of baleen whales in the Celtic Sea is sparse. This study showed a direct spatial link of baleen whales and forage fish in the Celtic Sea (Chapter 3). The use of the Celtic Sea as foraging ground for baleen whales is presented, which now opens the way for discussion on current knowledge gaps concerning baleen whales in the Celtic Sea.

Population estimates for fin, minke and humpback whales for the North Atlantic and European waters are 19 751, 30 410 and 11 570, respectively (Stevick et al., 2003; Hammond et al., 2011). Further, average individual daily consumption has been estimated as 981 kg for fin whales, 165 kg for minke whales and 621 kg for humpback whales (Smith et al., 2014). Assuming the abundance of baleen whales in the Celtic Sea is a proportion of the above estimated population and accounting for their different residence times (in days), the annual consumption of baleen whales in the Celtic Sea could be calculated using the concept of the rule of three [1] (Figure 6.1). Then by simply comparing total stock biomass and fishery quota, one concludes that if whale abundance stays below 60 individuals per year, predation impact would be comparable to the Celtic Sea herring fishery (fish consumption for 60 whales with a residency of 270 days equals 8 210 t, compared to a TAC of 17 200 t in 2013 for Celtic Sea herring), but more than a 1000 whales could diminish the stock (herring consumption over 270 days equals 144 580 t compared to a TSB of 163 500 t)) (Figure 6.1). This approach is purely mathematical and does not account for any uncertainties in any variable nor is it based on actual ecosystem observations. I clarify again, that Figure 6.1 should not be used as reference for any management decisions. The purpose of the above example is to highlight the importance of variability and the need for sound knowledge of ecosystem parameters, especially because any changes in parameters can lead to widely varying outcomes.

The above example shows the importance of three main parameters to estimate predation pressure by baleen whales on forage fish:

1. Realistic abundance estimation per whale species
2. Daily consumption or metabolic requirements of an individual and
3. Residency or foraging duration on the prey species in question

The three topics are further connected to population structure and migration behaviour.

6.3.1 Difficulties in abundance estimation of baleen whales

More important than the total number of baleen whales in the North Atlantic is the proportion of the population that forages in the Celtic Sea. Not much is known about whale migration routes for most of the baleen whale species. Trophic niche studies indicate that only a fraction of the north-east Atlantic fin whale population forage in the inshore waters of the Celtic Sea (Ryan, 2012; Ryan et al., 2013b). Fin whales are present from summer to winter and it is believed that they migrate to the Azores and lower latitudes along shelf breaks and the Mid-Atlantic Ridge in spring (Mikkelsen et al., 2007; Ryan et al., 2013b; Silva et al., 2013). Minke whales are absent in the winter months in Irish waters and are likely to migrate to wintering grounds in lower latitudes as shown for minke whales along the American east coast and Icelandic waters (Risch et al., 2014; Víkingsson and Heide-Jørgensen, 2014). Minke whale populations mix on the feeding grounds in the

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[1] Number of whales X consumption per day X days of residence

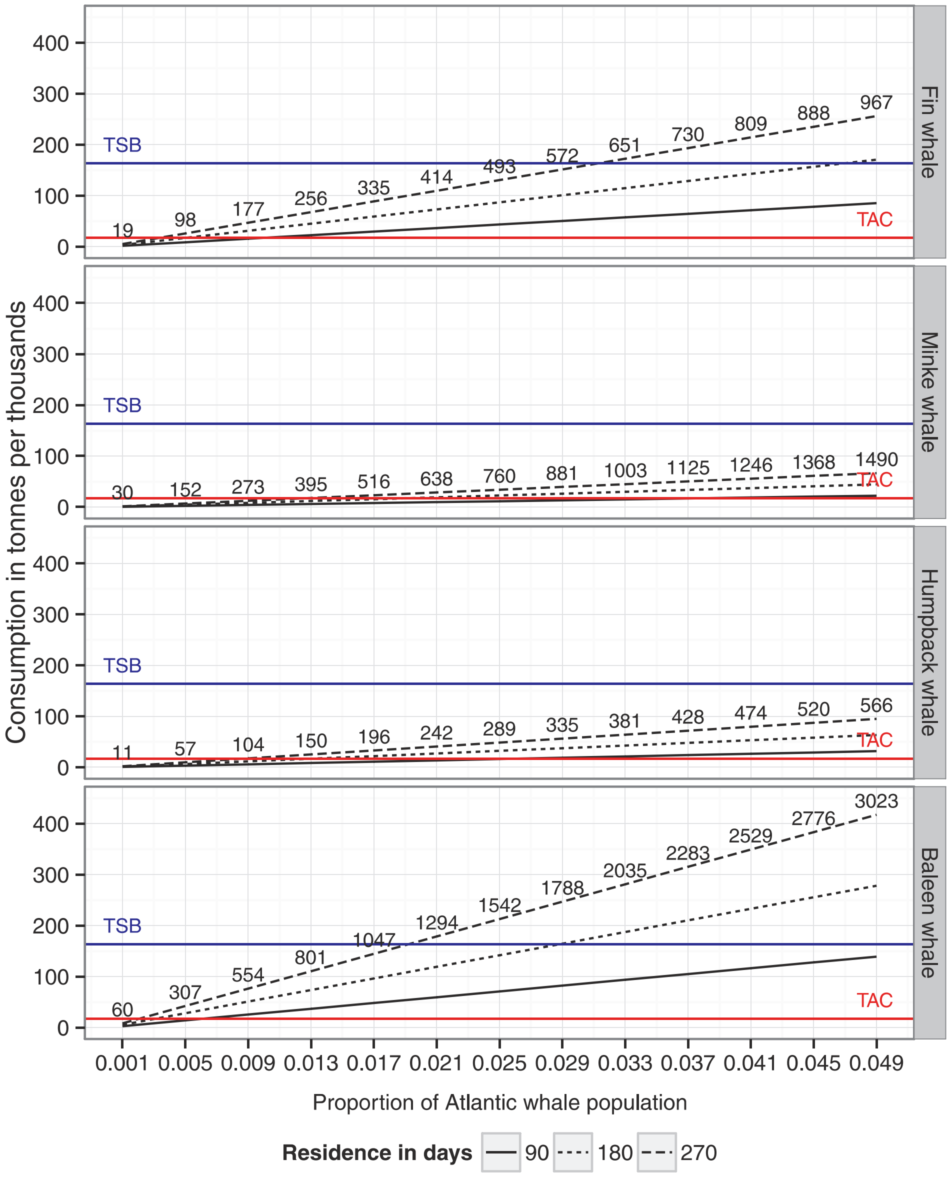

Figure 6.1: Simple mathematical approach to calculate annual whale consumption based on average individual daily consumption estimates by Smith et al. (2014) and population estimates for the North Atlantic given by Stevick et al. (2003) and Hammond et al. (2011). The numbers indicate the number of individuals comprising a given proportion of the North Atlantic whale population. Three different residence times of 3, 6 and 9 months were used for the calculations (closed, dotted and dashed line respectively). Baleen whale is the sum of fin, minke and humpback whale. Total Celtic Sea herring biomass estimated for 2013 is shown (TSB, blue line) and the corresponding total allowable catch (TAC, red line) according to HAWG (2014). This figure does not include any uncertainties in the variables and should not be used for management purposes.

northern Hemisphere (Anderwald et al., 2011a) and it is unknown if minke whales use the Celtic Sea as an enclosed feeding ground or if they originate from Icelandic and Norwegian waters. Humpback whales migrate from two breeding grounds in the West Indies and the

Cape Verdes to the feeding grounds in the northern Hemisphere where populations mix (Figure 6.3) (Clapham, 2002; Stevick et al., 2003; Wenzel et al., 2009). Even though migration routes of humpback whales are better studied, it is unknown to which breeding grounds whales in Irish waters belong to. It is suggested that "Irish" humpback whales migrate to the Cape Verde breeding grounds and use eastern Atlantic feeding grounds for foraging (Ryan et al., 2013b,a).

For baleen whale abundance estimates with respect to predation estimation on a certain forage fish stock, it is important to consider the number of individuals actually co-occurring with the fish species in question. For instance, fin whales are sighted often along the shelf edge in summer months, where they forage on zooplankton rather than forage fish (Wall et al., 2006, 2013). Therefore more information on population affiliation is needed to unfold migration routes, migration behaviour and habitat use. Delays, stops or suspense of migration may have implications on the metabolic requirements of baleen whales (see section below) and their foraging behaviour. Suspended migration is suggested for some fin whales in the Azores prior to the northward migration (Silva et al., 2013). Population affiliation can indicate if whales forage in the Celtic Sea as a "stop-over" during the southward migration; however not all whales migrate every season (e.g. Wenzel et al., 2009), which needs to be considered when linking predator and prey distribution. Abundance estimates exist for the North Atlantic (Stevick et al., 2003; Hammond et al., 2011) and local surveys can contribute time-limited density estimates (Wall et al., 2006, 2013). Further, stable isotope analysis, telemetry tagging studies and passive acoustic monitoring can provide valuable information on abundance estimates of baleen whales in the Celtic Sea, population identity and migration behaviour (e.g. Ryan et al., 2013b,a; Risch et al., 2014; Víkingsson and Heide-Jørgensen, 2014).

6.3.2 Energy requirements and foraging decisions of baleen whales

Every individual whale has unique energy requirements depending on body size, age, sex, maturation, behaviour and feeding strategy (e.g. Leaper and Lavigne, 2007; Goldbogen et al., 2011; Tyson et al., 2012; Spitz et al., 2012; Friedlaender et al., 2014). Observations in the Celtic Sea showed a higher abundance of immature male humpback whales compared to females (Ryan et al., 2013a), but the sex ratio could be biased due to difficulties in obtaining tissue samples of whales for genetic sexing. On top of that, a pregnant female was observed and resighted together with a calf in the following year (IWDG, 2014).

Mother-calf pairs of fin whales have been observed foraging in the Celtic Sea (Ryan, 2012), however information on minke whale population structure in the Celtic Sea is non-existent. Because population structure data are very difficult to obtain, perhaps referring to number of individuals without accounting for sex or life stage variability is a more general and feasible - but still challenging - approach to estimation baleen whale consumption with respect to forage fish EBFM. Integrating higher uncertainties and variability in abundance estimates could account for missing information on population structure.

An often-applied approach for consumption and energy acquisition is based on individual body mass and species-specific consumption parameters. Evidently variability in final estimates results from difficulties in estimation of those parameters (Leaper and Lavigne, 2007; Smith et al., 2014). Metabolic cost to maintain vital functions (the "basal metabolic rate") and cost for reproduction, growth, swimming and foraging comprise the individual energy requirements. Costs for swimming are believed to be relatively low, while fast swim, for instance during migration, decreases the total cost of transport (Williams and Noren, 2009). Longer periods of starvation during migration could alter the metabolism of a migrating whale. Hence, for energy requirement estimation it is important to know if baleen whales foraging on the Celtic Sea plateau are within a migrating phase, which could influence energy assimilation efficiency. Foraging dives are energetically costly (Goldbogen et al., 2011, 2012; Potvin et al., 2012) and energetic gain can be variable; in some case only be marginally higher than the foraging costs (Goldbogen et al., 2011). Within bioenergetics modelling, which can support EBFM decisions, it is important to estimate energy assimilation and foraging success. More information on foraging thresholds and decisions is needed to understand foraging success in baleen whales and to be able to integrate this information into bioenergetics models.

Inter-species competition between different baleen whale species is another important factor for predation estimation of forage fish. Whales in the Celtic Sea occupied different niches, even though mixed feeding aggregations are observed (Ryan et al., 2013b), which indicates that baleen whales show a general partitioning of the Celtic Sea resources. Feeding aggregations could be beneficial for baleen whales as cues to locate high prey densities, while different foraging behaviour decreases actual competition while foraging on a prey patch (Friedlaender et al., 2006, 2009; Goldbogen et al., 2013; Friedlaender et al., 2014). Visual, acoustic, chemical and environmental cues, together with communication between whales, can be methods for tracing prey; however it is still unknown how exactly baleen whales detect prey (Kenney et al., 2001; Anderwald et al., 2011b). Multisensor tags attached to baleen whales are promising tools to provide valuable information on foraging physiology and foraging behaviour of baleen whales, which will be invaluable for bioenergetics modelling and consumption estimation of baleen whales with applications for many ecosystem studies (Goldbogen et al., 2013).

6.3.3 Importance of baleen whale residence time on foraging grounds

To include baleen whale predation on forage fish in a stock assessment, it is important to recognise that whale abundance and residency on the foraging grounds are closely linked. Abundance can be overestimated if residency is not accounted for. Identification of individuals can be carried out either by comparison of photographs of characteristic marks on the body and an available photo catalogue or via genetic identification, with both methods relying on suitable sampling conditions. Tagging studies in Iceland showed that minke whales remained within an area for two months (Víkingsson and Heide-Jørgensen, 2014). Fin whales are observed from summer to winter in the Celtic Sea, however individuals were resighted on average within 33 days and a maximum residency of 165 days (Whooley et al., 2011). It is important to use the actual time of residence within a foraging ground for the implementation in prey stock assessment. For instance, baleen whales observed outside the herring season are more likely to be foraging on different prey, therefore only the residency and abundance of baleen whales in temporal and spatial accordance with the prey species in question should be included in the respective forage fish management.

An interesting question in relation to residence time is what triggers the decision for baleen whales to leave a foraging area? Are baleen whales restricted to a time schedule based on seasonal migration and thereby have to leave the Celtic Sea in a certain period to arrive ”on time” at the breeding grounds? Could the depletion of resources in the area lead to an onset of migration? Prey quality has been linked to foraging decisions in cetaceans (Spitz et al., 2012) and the low energy content of post-spawning fish (Chapters 4 and 5) together with less dense and spread out schools could motivate some species of baleen whales (e.g. fin whales) to a diet shift to zooplankton along the shelf edge (Ryan et al., 2013b) or to continue the migration to lower latitudes. Passive acoustic monitoring, individual identification and telemetry studies can help to improve the understanding of baleen whale habitat use and residence time.

6.3.4 Threats to baleen whales and research opportunities

Baleen whales have an important role in ecosystems as ecosystem engineers and are believed to contribute to climate regulations by supporting carbon fixation (Roman et al., 2014). However even after the end of commercial whaling (in most countries), baleen whales are still impacted by human induced threads. This is not only of concern for marine mammologists, environmentalist and the ecotourism community, but it can be also influential on predation pressure of baleen whales on forage fish. Noise pollution and changes in water quality can lead to difficulties in detecting prey, disorientation and, in the worst case scenario, result in an increase of strandings (e.g. Croll et al., 2001; Tyack, 2008). Chemical pollution can cause illness, infertility or death, which can reduce predation pressure of forage fish (e.g. Aguilar and Borrell, 1994; Zala and Penn, 2004; Jenssen, 2006). Plastic pollution, can block the digestive system leading to starvation, and entanglement in fishing gear and general waste could hinder mouth opening and foraging or lead to drowning (e.g. Hall et al., 2000; Read, 2008; Jacobsen et al., 2010; Fossi et al., 2012; de Stephanis et al., 2013). Further, the increased sea traffic and resource exploitation in off-shore areas can influence baleen whale migration, behaviour and well-being (Halpern et al., 2008).

Baleen whales are protected by law and different international agreements within Irish waters (O'Brien et al., 2009) and collaborating in conservation-orientated projects can provide valuable information on the above mentioned open questions concerning baleen whale ecology within the Celtic Sea. Baleen whale abundance estimates have to be refined and the connection to breeding grounds has to be made to improve the understanding of migration routes, migration behaviour and residence time within the Celtic Sea, for example by using acoustic monitoring, photo-identification or telemetry tagging. More dietary data from stable isotope analysis or stomach contents as well as telemetry tagging can provide new insights into feeding ecology and foraging behaviour. Even if baleen whales pass through the Celtic Sea during the southward migration, it has been shown that baleen whales actively target herring and sprat on the Celtic Sea plateau (Chapter 3). Therefore the impact assessment of baleen whale predation pressure on the forage fish community in the Celtic sea should be undertaken.

6.4 Energy content as currency to describe inter-species specific foraging dynamics

Prey consumption of baleen whales can be described by either the volume of the digestive system, the prey biomass or the energy gain. From an ecological viewpoint, prey volume, biomass and energy gain are connected. Stomach fullness and engulfment capacity will physically define how much prey can be obtained and could drive foraging duration and number of lunges during foraging dives (Goldbogen et al., 2012; Potvin et al., 2012). This sets limits on how much biomass can be ingested. However, finally prey energy content and energy assimilation efficiency define the energy gain after balancing basal and foraging metabolic costs (Goldbogen et al., 2011). For forage fish management purposes, prey biomass and number of deaths are the important units that can be integrated into VPA analysis in stock assessments.

Cetacean prey selectivity has been linked to metabolic predator requirements and prey energy content (Spitz and Jouma'a, 2013; Spitz et al., 2014). Herring and sprat have been identified as important prey for baleen whales in the Celtic Sea (Chapter 3 and Ryan et al. 2014). Their variability in energy content was analysed (Chapters 4 and 5) and demonstrated that the reproductive development of herring and sprat significantly influenced energy content variability. This showed that baleen whale predation on herring later in the season (i.e. after spawning) would result in a much lower energy gain based on equal biomass consumption of pre-spawning fish. However, post-spawning herring schools are less dense and more spread out, which could lead to low success in foraging dives and accordingly the need for additional lunges and respectively higher foraging costs without the promise of an actual net energy gain. Herring and sprat of similar length had similar energy contents (Chapters 4 and 5) and hence could be of the same importance for baleen whales considering that foraging effort does not differ significantly by fish species in respect to school density, school size and fish escape behaviour. In other words, if predation costs and energy intake are inter-changeable, baleen whales could forage on both herring and sprat and replace one species by the other as reaction to energy variability in prey species.

A trait-based approach to describe predator-prey relationships has been suggested by Spitz et al. (2014), concluding that prey selectivity according to species or size could be less important compared to prey, as well as predator, functional traits. Highly active marine mammals were associated to high-energy prey and the correlation was stronger compared to prey size (Spitz et al., 2014). Energy density, horizontal habitat, protein content, skeleton and water content were key functional traits that describe marine mammal prey, while predator traits included prey detection and foraging characteristics, e.g. echolocation, swimming speed and diving capabilities (Spitz et al., 2014). Albeit from an ecological and predator viewpoint, prey species is of less importance compared to the overall functional traits of the prey group, within a single stock assessment the actual mortality on species level should be known. Hence, energy content variability can help understand foraging decisions, but a transformation into species specific prey biomass has to be performed for predation estimates. Further, surveying energy content of prey is necessary to draw conclusions on prey impact on predator fitness, which is described with the "junk food"-hypothesis highlighting the importance of prey quality in predator-prey relationships (Österblom et al., 2008). Water content proved to be an accurate and fast measurable proxy for energy content and can be referred to for prey quality estimation (Chapters 4 and 5).

6.5 Predation as driver of population dynamics

Predator and prey populations are closely linked and described by ecological processes like "bottom-up" and "top-down" control (e.g. Krebs et al., 1995; Frank et al., 2007; Frederiksen et al., 2006). "Bottom-up" are processes where a predator population is influenced by prey or environmental factors (e.g. temperature or wind conditions on larval survival Rijnsdorp et al., 2009). "Top-down" are the reverse processes where predators directly affect prey population dynamics. Forage fish populations display high variability driven by oceanographic characteristics and are preferred prey for several top predators as well as large scale fisheries, hence forage fish are faced with bottom-up and top-down impacts. However due to their central position as key species, forage fish additionally shape ecosystems via so called "wasp-waist" processes in which forage fish populations impact on both their predators and prey (Jordán et al., 2005; Bakun, 2006). Thus several ecological processes are simultaneously present in an ecosystem (Figure 6.2) and maintain ecosystem stability and resilience. If one element of the trophic network is disrupted, resilience could be impaired, which could lead in the worst case to irreversible regime shifts (Folke et al., 2004; Casini et al., 2008).

For the Celtic Sea herring stock, zooplankton dynamics at the offshore feeding grounds and environmental conditions may affect stock abundance and stock structure (Chapter 2). Changes in zooplankton phenology could impact herring migration to spawning grounds or

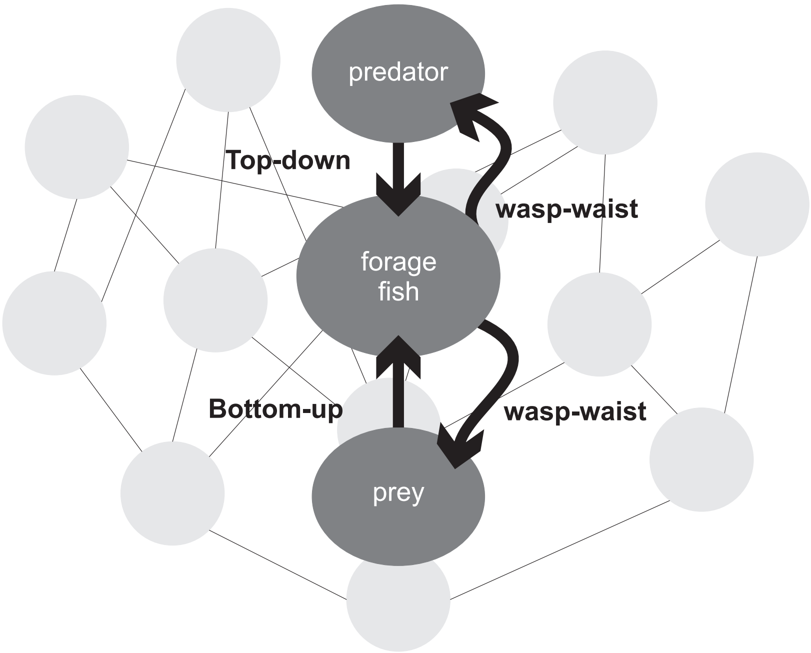

Figure 6.2: Conceptual description of ecological processes in a trophic web centred on forage fish. Top-down processes (consumer-driven) occur from predators on forage fish, while bottom-up processes (resource-driven) are the reverse impact from lower trophic levels and environmental conditions on the forage fish population. Forage fish can influence predator as well as prey populations with so called wasp-waist processes. An ecosystem network is built-up of several species and their interactions maintain ecosystem stability and resilience.

deteriorate conditions, which might reflect in reduced reproductive success (Edwards and Richardson, 2004). Temperature could motivate a distribution shift (Chapter 2) or impact larval development and thus larval survival (Rijnsdorp et al., 2009; Hinrichsen et al., 2012; Peck et al., 2013). Predation pressure by cetaceans, fisheries and other predators like seabirds and predatory fish could control or diminish the herring stock (Bakun, 2006). A strong prey size selectivity was not apparent for baleen whales (Chapter 3), which could help stabilize ecosystem resilience due to minimizing the risk of trophic cascades by impacting single size classes (Folke et al., 2004). The following thought experiment highlights the position of herring and forage fish in general in the Celtic Sea ecosystem and indicated trophic connections and concepts that should be considered within an EBFM.

A delay in herring inshore migration caused by unusual conditions on the feeding grounds could cause a mismatch of herring and baleen whales, which are within coastal waters. The Celtic Sea is a relatively small area, which could be crossed by baleen whales in few days. Assuming that baleen whales did not encounter the expected high herring biomass, they would probably leave the Celtic Sea to continue migration or the search for richer foraging grounds. This would reduce predation pressure on the later arriving

Celtic Sea herring stock, which itself could increase spawning success and eventually larval survival with the possibility of an increased spawning stock biomass in two years from then. On the predator side, baleen whale fitness and condition could be reduced during long starvation times, if no herring substitution could be found. Additionally, whale behaviour could be modified. A whale could chose different foraging grounds in following years based on unsuccessful foraging experience, so called "risk effects", which describe a behavioural mediated indirect interaction on trophic cascades (Creel and Christianson, 2008; Heithaus et al., 2008). However, the ecosystem could be shaped differently, if baleen whales find an alternative to herring, for instance sprat, in this fictitious scenario[2].

Recently, increased discontent was expressed by the Irish ecotourism sector claiming that baleen whales were "gone" (i.e. out of reach for smaller whale watching boats operating in coastal waters) due to the intense fishing effort on sprat [3]. In the Baltic Sea, the cod population has had difficulties to recover because of high predation pressure on cod eggs by sprat (Casini et al., 2009), and an increased harvesting of sprat could be discussed to help the recovery of cod in the interest of the fishing industry (Pikitch et al., 2012). This shows that within an EBFM, management goals and targets have to be clearly defined, including possible trade-offs for general ecosystem formation. In the Celtic Sea ecosystem, sprat fishery is an unpredictable top-down process due to the missing information on sprat ecology and fisheries. To achieve the desired ecosystem state defined by threshold biomass of certain species or reference points, decision makers can only refer to fishery regulations because radical actions like culls of predator species are generally prohibited (e.g. all cetacean are protected within Irish waters O'Brien et al. (2009) and less effective (Yodzis, 2001; Morissette et al., 2012). Considering the important position of forage fish in ecosystems, sprat fishery should not remain non-regulated in the Celtic Sea. With the mentioned interactions between herring and sprat (e.g. density dependence, Section 6.2), a non-regulated sprat fishery could also have implications for the Celtic Sea herring stock and the respective fishery. Uncontrolled harvesting adds additional top-down pressure on the ecosystem with uncertain consequences which could harm ecosystem stability and resilience. Ecosystem modelling, comparing different ecosystem scenarios and ecosystem monitoring can help the understanding of predation impacts spread over the ecosystem (i.e. trophic cascades) and the setting of ecosystem management targets (Daskalov, 2002).

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[2] In this thought experiment only two trophic players are considered without linking them to other species in the ecosystem and additional natural variability.

[3] Statement in the local newspaper "The Southern Star", 28. November 2014, http://www.southernstar.ie/News/West-Corks-whale-watching-under-threat-28112014.htm

6.6 Opportunities arising from modelling techniques

What is a model, especially the often-mentioned, ecosystem model? A model is a representation of a particular thing and it can be of any kind of shape, from conceptual to complex mathematical programming (Jackson et al., 2000). Stock assessments in fishery science strongly depends on models (Whipple et al., 2000; Haddon, 2011; Dickey-Collas et al., 2014). For example, analytical models that describe theoretical processes of populations, such as the Ricker or Van Bertalanffy growth models, form the base of every VPA analysis (Haddon, 2011; Dickey-Collas et al., 2014). A model is always a simplification of processes and by reducing complexity to a manageable form, makes processes comprehendible (Dickey-Collas et al., 2014). Due to the numerous processes and connections in an ecosystem, ecosystem modelling is challenging and there is no default structure. Generally ecosystem models use a generic approach to describe ecosystem functions or a single process is selected for detailed description (Hannah et al., 2010; Fulton et al., 2011).

Widely used ecosystem models, like for example EcoPath/EcoSim and OSMOSE (Pauly et al., 2000; Christensen and Walters, 2004; Shin and Cury, 2004; Travers et al., 2010), are suitable methods to describe dominant relationships in an ecosystem, but these models require comprehensive information on trophic levels starting by phyto- or zooplankton and ending with top predators. If sufficient data on the trophic levels exist, these models can provide a broad overview of ecosystem processes and can make projections into the far future, which could be of interest for ecosystem management (Christensen and Walters, 2004). However, in the common case, data quality for all trophic levels is unequal, and thereby an additional level of uncertainty is introduced to the ecosystem models. Further, EcoPath/EcoSim models are equilibrium models that assume a stable state of an ecosystem, which is a general assumption and deviations to a stable state equilibrium can cause uncertainty in the results (Plagányi and Butterworth, 2004).

The above mentioned models, including analytical models for population dynamics, represent broad processes in ecosystems or populations, which work well if the behaviour of an individual is not different to the behaviour of the group or population (e.g. fish populations). However, if behaviour is different between individuals and influences general population dynamics, behaviour should be modelled separately with so called individual based models (IBM) (e.g. Grimm, 1999). IBMs try to understand how ecosystems function based on interactions of individuals (Grimm, 1999). This is a suitable approach to apply to ecosystem models that include baleen whales, which are often solitary or occur in small groups (Bannister, 2002).

A model framework needs to be appropriate for the question posed and results will be strongly dependent on the quality of parameter estimates, especially for the use of IBMs (Grimm, 1999; Schmolke et al., 2010; Dickey-Collas et al., 2014). The more interactions and processes are included, the more the model will resemble the actual ecosystem. But adding more levels and increasing model resolution requires availability and accuracy of more parameters to support the increased resolution. In Section 6.7 ”only” two players of the ecosystem are presented, predator and prey, but the resulting complexity and difficulty in model parameter estimation and acquisition are illustrated. Thus, an ecosystem model can contribute to ecosystem studies by indicating where knowledge gaps exist and can direct research efforts (Whipple et al., 2000; Fulton et al., 2011; Dickey-Collas et al., 2014). The aim of modelling is not to give a blueprint of the ”real” ecosystem, but to capture dominant features in ecosystem processes (Grimm, 1999; Dickey-Collas et al., 2014). Section 6.7 is in the early stage of development and not yet intended for management decisions. Models constructed for management purposes require a high level of accuracy in parameter estimation, respective uncertainty analyses and validations. But, ecosystem models like in Section 6.7 can visualise and simplify relationships in the Celtic Sea ecosystem that are difficult to observe *in situ*, and are a valuable improvement to our understanding of ecosystem processes.

6.7 Theoretical baleen whale distribution driven by forage fish in the Celtic Sea - a conceptual model on trophic links

This section presents the first results of an conceptual model on trophic links in the Celtic Sea ecosystem. This model should provide information on a theoretical baleen whale distribution in the Celtic Sea driven by the present forage fish distribution. The model contains the main findings of the previous chapters and could be used to further explore the trophic links between forage fish and baleen whales in the Celtic Sea.

Baleen whales (Balenoptera) are known predators of small pelagic fish in the Celtic Sea. Atlantic herring (*Clupea harengus*) is one pelagic prey species of baleen whales; furthermore it is targeted by a large scale fishery in the Celtic Sea. For a sustainable exploitation of Celtic Sea herring, the impact of whale predation on stock dynamics and fishing yield must be explored. A lack of information on abundance and origin of baleen whales in the Celtic Sea hinders estimations of predation impact of baleen whales on the small pelagic fish community in the Celtic Sea. The here presented ecosystem model can increase the understanding of baleen whale habitat utilisation. The model simulates the interactive dynamics of two functional groups: 1. the baleen whale behaviour depending on 2. the distribution of a mobile prey source. Baleen whale behaviour includes foraging and movement and is based on individual modelling (IBM), a dynamic energy budget and a random walk movement trajectory. Prey resource is presented based on stock characteristics of Celtic Sea herring, which includes a seasonal migration from offshore feeding to coastal spawning grounds and energy density variability caused by reproductive investment. Two scenarios with low and high prey biomass were examined. This ecosystem model shows a theoretical, simplified simulation of baleen whale and herring interactions in the Celtic Sea and can contribute to predator-prey impact assessments.

6.7.1 Background information and incentive for model construction

Recent studies highlight the importance of baleen whales (Balenoptera) for ecosystem (Pershing et al., 2010; Roman and McCarthy, 2010; Roman et al., 2014; Lavery et al., 2014). These whales can remove large quantities of prey while foraging by enlarging their buccal cavity (Goldbogen et al., 2007, 2012). Baleen whale diet consists of forage fish, which are small pelagic fish, and zooplankton like krill, that occur in high densities (Pauly et al., 1998). At the same time, forage fish are targeted by large scale fisheries contributing to fish meal production and direct human consumption. Forage fish fisheries contribute with approximately 20% (measured by landings in weight) to the global marine catches (FAO, 2014). Hence the apprehension of competition between whale consumption and fisheries led to comparisons of marine mammal feeding rates and fishing mortality (e.g. Lavigne, 1996; Alder and Pauly, 2006; Leaper and Lavigne, 2007; Overholtz and Link, 2007; Morissette et al., 2012; Ruzicka et al., 2013; Smith et al., 2014). To avoid negative implications like regime shifts and trophic cascades in ecosystems caused by unsustainable fishing, fisheries management evolves towards an ecosystem-based management approach (EBFM) considering ecological, environmental and human factors in resource management (Curtin and Prellezo, 2010; Fogarty, 2013).

Influence of whale predation on forage fish stocks and food web structure are especially important for ecosystems at higher latitudes and the local EBFM of the respective fisheries. Baleen whales undertake large seasonal migrations from breeding grounds in warmer waters at lower latitudes in winter and spring where foraging is reduced, to feeding grounds at higher latitudes benefiting from high productivity in summer and autumn (e.g. Corkeron and Connor, 1999; Clapham, 2001). Migration routes have been assessed using individual identification based on characteristic body marks, stable isotope tracing, passive acoustic monitoring and following individuals equipped with satellite tags (e.g. Craig et al., 2003; Witteveen et al., 2009; Simon et al., 2010; Stanistreet et al., 2013; Risch et al., 2014). All analyses have in common that a trend in a usually small number of observations is extracted to generalize behaviour of populations or sub-populations. Common baleen whale feeding grounds in the North Atlantic are the Gulf of Maine, Gulf of St. Lawrence and the Labrador, Greenland, Norwegian and Barents Sea (Figure 6.3) and migration routes appear to be orientated along the mid-continental ridge, dominant currents like the gulf stream and depth contours (Watkins et al., 1996; Clapham, 2002; Mikkelsen et al., 2007; Olsen et al., 2009; Silva et al., 2013; Prieto et al., 2014; Risch et al., 2014; Víkingsson and Heide-Jørgensen, 2014).

The Celtic Sea is a species-diverse, productive ecosystem (Pinnegar et al., 2002; Trenkel et al., 2005, 2014) and baleen whales, dominantly fin, minke and humpback whales (*Balenoptera physalus, Balenoptera acutorostrata, Megaptera novaengliae*) are sighted year-to-year from summer to winter, but absent in spring (Wall et al., 2013). Foraging has been observed and spatial distribution of baleen whales was linked to forage fish distribution (Chapter 3). Atlantic herring (*Clupea harengus*) and European sprat (*Sprattus sprattus*) have been identified as important prey of baleen whales in the Celtic Sea (Ryan et al., 2014). Comparable to other feeding grounds in the North Atlantic, the Celtic Sea appears as a relatively small foraging area which can support a small proportion of the North Atlantic whale population. Baleen whales could travel to the Celtic Sea within the feeding season from other feeding grounds or during the north or southward migration from or towards breeding grounds. Baleen whales could divert to the Celtic Sea following branches of the North Atlantic Current (NAC) and profit of high productivity along the Celtic Sea shelf edge or swim against the Shelf Edge Current (SEC) and the Irish Coastal current (ICC) which are important currents for larval transport in the Celtic Sea (Figure 6.3). Until now, it is unknown from where the whales arrive, how many individuals annually feed in the Celtic Sea and to which whale populations these animals belong to.

Herring and sprat are abundant forage fish species in the Celtic Sea and form part of

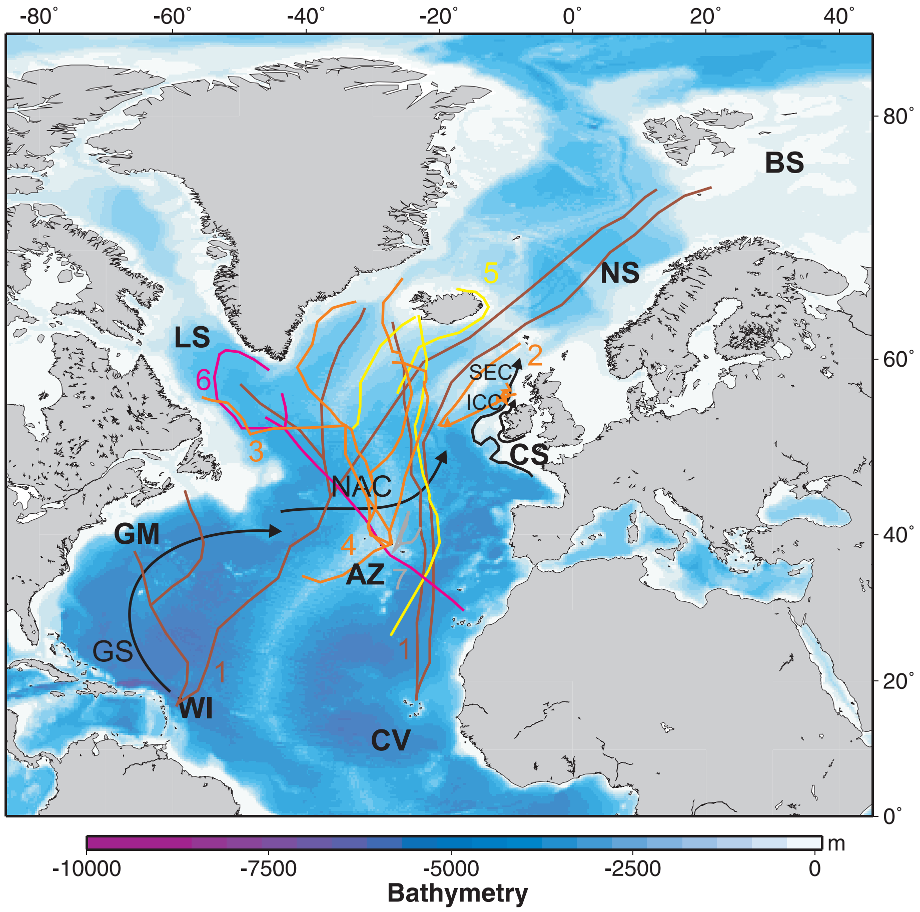

Figure 6.3: Approximate baleen whale migration trajectories obtained from literature and dominant water currents. 1. Humpback whales (red line; Clapham, 2002); 2.-4. Fin whales (orange line; Mikkelsen et al., 2007; Olsen et al., 2009; Silva et al., 2013); 5. Minke whales (yellow line; Víkingsson and Heide-Jørgensen, 2014); 6. Sei whales (pink line; Prieto et al., 2014); 7. Blue whales (grey line; Silva et al., 2013). Abbreviations stand for AZ = Azores; BS = Barents Sea; CS = Celtic Sea; CV = Cape Verde Islands; GM = Gulf of Maine; LS = Labrador Sea; NS = Norwegian Sea; WI = West Indies. Black lines indicate currents: ICC = Irish Coastal Current, GS = Gulf stream; NAC = North Atlantic Current and SEC = Shelf Edge Current.

baleen whale diet (Ryan et al., 2014). To the moment, sprat fisheries in the Celtic Sea has no catch limits, while the Celtic Sea herring fishery underlies the restrictions of a total allowable catch (TAC) and spatial as well as temporal limitations (Marine Institute, 2013). For the current herring stock assessment and a possible future management of sprat in the Celtic Sea, an estimation of the partitioning of resources with baleen whales and fishery is important and can lead towards an EBFM of forage fish fishery in the Celtic Sea. However an assessment is hindered due to open questions on habitat utilization of baleen whales. Here a simplified dynamic energy budget was combined with an individual based model of whale behaviour in order to simulate whale movement and predation pressure on herring in the Celtic Sea. Two scenarios were compared, one with low herring stock biomass as in 2005 and one with high herring stock biomass as it was estimated for 2013. The simplified behaviour and movement model can help the understanding of a complex ecosystem by demonstrating general traits of trophic links.

6.7.2 Model organisation and structure

The model contains two main elements: first a simulation of whale behaviour and movement and second a mobile prey source represented by characteristics of the Celtic Sea herring stock (Figure 6.4). It must be pointed out, that this model contains basic parameters to resemble whale behaviour, therefore it should be considered with caution when extrapolating to the actual ecosystem or during comparisons to real observations. Henceforth the term ”whale” is used as description of the simulated whale, if not stated otherwise. The model uses the bathymetry provided by the National Oceanic and Atmospheric Administration (NOAA, `http://www.ngdc.noaa.gov/mgg/global/global.html`) with a definition of 1 arc-minute (Amante and Eakins, 2009). A grid resolution of 1 cubic nautical mile was used as background and time step of simulations was 30 minutes over an overall duration of six months.

Simulated whale behaviour The general model set-up consists of 100 individual whales that are placed on the Rockall plateau in the North Atlantic as start position. An individual-based model (IBM) was developed, which represents the local behaviour of the whale, being swimming and feeding. Whales move in terms of horizontal movements and vertical motions (i.e. diving) are represented within energetic acquisition during foraging. Whales move constantly and stop only for acquiring energy when they encounter prey patches. Whale perception of the environment (depth and fish availability) is limited to one neighbouring grid cell, in practice to a maximum of one cubic nautical mile. If

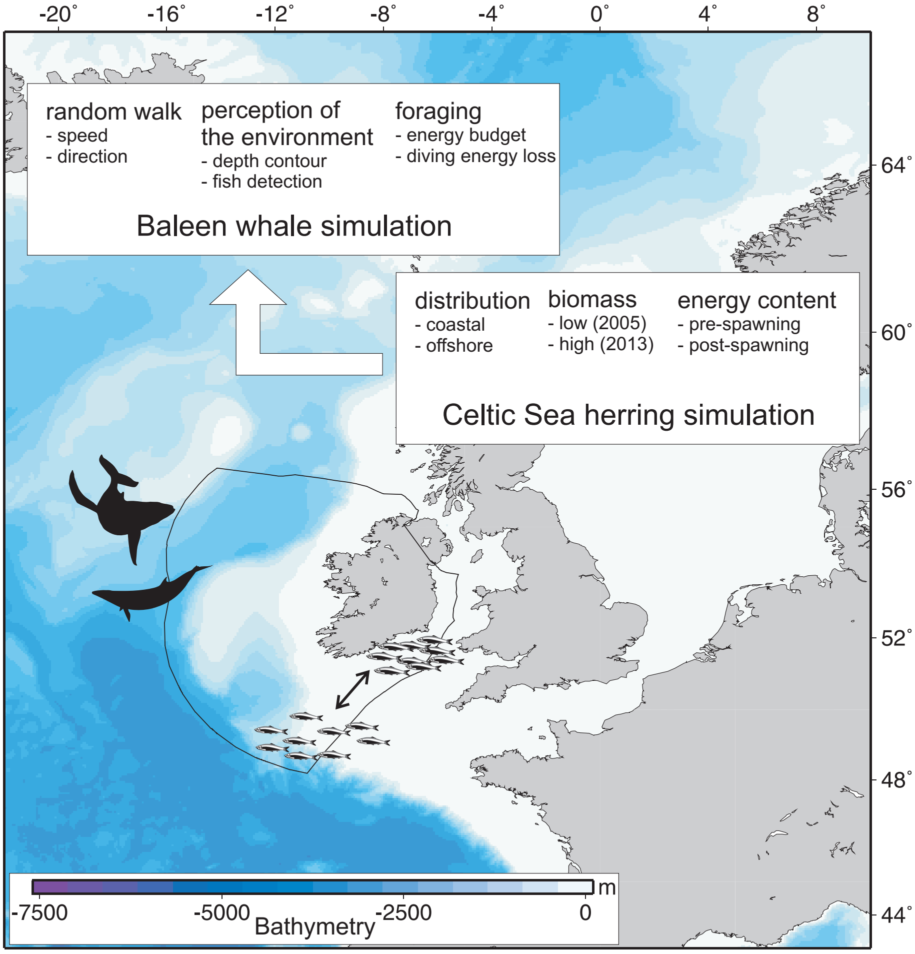

Figure 6.4: Conceptual model structure. The model simulates movement of 100 whales originating from the Rockall Plateau. Individual whales are described by position (directed by depth contours), swimming speed and direction and state of energy density. Whales can forage on pelagic fish represented by Celtic Sea herring stock, which includes a season inshore-offshore migration from spawning grounds and a variable energy density based on dominant maturity status. Two scenarios with low and high herring stock biomass were tested corresponding to total stock biomass in 2005 and 2013.

a whale reaches shallow waters, it turns direction away from the coast line. In the open ocean travel speed is high, while it decreases in coastal zones and is reduced to zero during foraging. In the case of a constant negative energy balance, whale movement is directed south, representing a continuation of migration to breeding grounds. Available and stored energy of an animal is represented explicitly in a simplified energy budget model.

Simplified energy budget model for whales A simple relationship of surface of the whale and food acquisition as well as volume of the whale and energy use was used to represent the energy budget in a minimalistic way. Assessing that the energy content is a linear function of the biovolume of the organisms, the dynamics of energy is represented by:

$$\frac{dE}{dt} = aE^{2/3} - rE \tag{6.1}$$

Where a represents energy acquisition, and r represents the energy spent for metabolic activities. The dynamics reaches an asymptotic steady-state value (stable equilibrium) equal to:

$$E^* = \left(\frac{a}{r}\right)^3 \tag{6.2}$$

This model would be sufficient for an organism that feeds constantly, however, to take into account that whales can stock a high quantity of energy in the form of blubber, a two compartments model was designed:

$$\begin{cases} \frac{dE}{dt} = aE^{2/3} - (s+r)E + kR \\ \frac{dR}{dt} = +sE - kR \end{cases} \tag{6.3}$$

where R representing the lipid reserve, s represents the stocking process, and k the destocking process (use of the reserve). The asymptotic ratio between reserve and rest of the energy content (mainly in muscles), is:

$$\left(\frac{R}{E}\right)^* = \left(\frac{s}{k}\right) \tag{6.4}$$

which can be seen as an index of condition for the individuals.

Celtic Sea herring simulation Two scenarios differing in total fish stock biomass were tested with the model. The first scenario termed "low" is comparable to the estimated total stock biomass (TSB) in 2005 with 44 000 tonnes and the second scenario termed "high" compares to the TSB in 2013 with 163 500 tonnes (HAWG, 2014). Celtic Sea herring has annual migrations from offshore feeding grounds on the Labadie Bank to inshore coastal spawning grounds along the Irish South coast (Molloy, 2006; O'Sullivan et al., 2013; Volkenandt et al., 2014). For each scenario, two herring distributions were constructed: starting offshore herring migrate inshore to coastal spawning grounds, stay inshore for three months and then return to the offshore feeding grounds (Table 6.1). TSB was randomly distributed in patches around the coordinates of the Labadie Bank and the long-term average herring stock centre of gravity (CG) during spawning migration (Volkenandt et al., 2014). Herring invest large amount of energy into reproduction and therefore loss in average approximately 70% of energy content after spawning (Chapter 4). This change in energy value has been integrated into the model with an adjusted average energy density value (kJ per gram biomass) per month (Table 6.1). Energy density values for juvenile, pre- and post-spawning herring have been taken from Chapter 4. Percentage of juvenile and different maturity stages of the adult stock have been estimated based on Chapter 4 and the recruitment - spawning stock biomass ration (HAWG, 2014).

Table 6.1: Characteristic for prey resource implementation into the ecosystem model. The model simulated a period of six months from September to February. CG represents the centre of gravity at the Labadie Bank (offshore) and the long-term mean during spawning migration (Volkenandt et al., 2014). Energy density was calculated according to population composition and energy values presented in Chapter 4. juv. = juvenile herring, prespaw. = adult herring in prespawning state and postspaw. = adult herring in postspawning state.

month	CG	distribution	E in kJg^{-1}	population composition
September	50 / -9.2	offshore	7.98	50% juv., 50% prespaw. adults
October	51.6 / -7.5	inshore	7.98	50% juv., 50% prespaw. adults
November	51.6 / -7.5	inshore	7.98	50% juv., 50% prespaw. adults
December	51.6 / -7.5	inshore	7.09	50% juv., 25% prespaw. and 25% postspaw. adults
January	50 / -9.2	offshore	6.56	50% juv., 16% prespaw. and 34% postspaw. adults
February	50 / -9.2	offshore	5.75	50% juv., 50% postspaw. adults

6.7.3 A first model output

Figure 6.5 presents the first preliminary results of the ecosystem model including the detection of prey, but without forging activity due to technical and conceptual difficulties in coding of the dynamic energy budget. The model shows that only a small proportion of the modelled whales arrive on the Celtic Sea plateau and close to the coast. This observation does not match actual observations during marine mammal surveys in October

(CSHAS, (O'Donnell et al., 2013) and Chapter 3) or landbased sightings of fin, minke and humpback whales from October to December from Irish headlands Figure 6.6. This discrepancy is certainly caused by the model characteristics (e.g. avoidance of waters with low depth), albeit offshore whale distribution observations for comparison are sparse. Including foraging activity and a realistic representation of a prey population by including herring distribution patterns and variability in energy density will further improve the model.

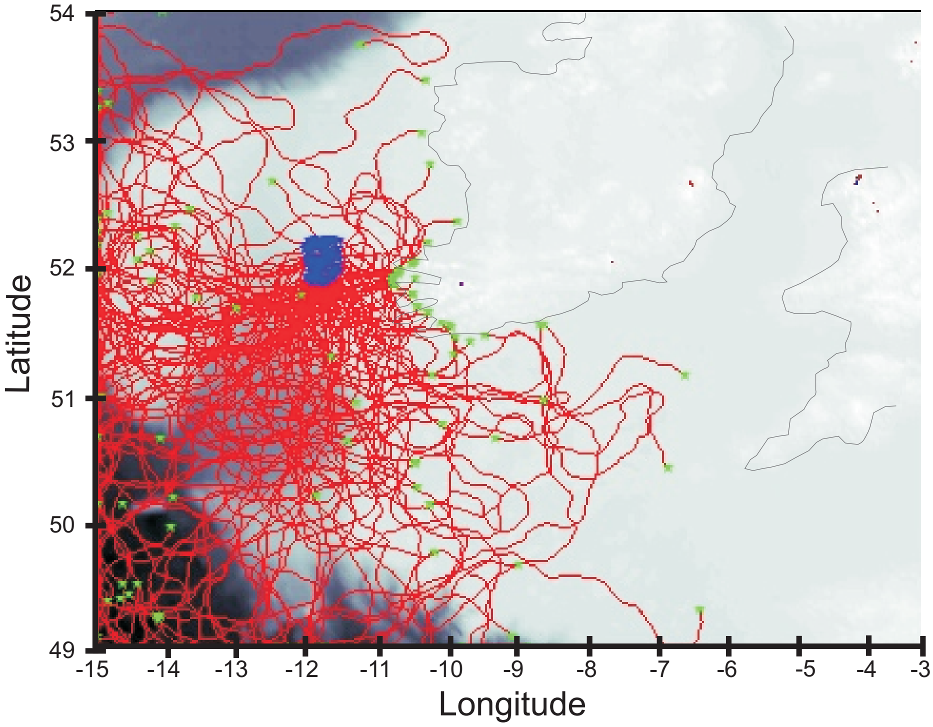

Figure 6.5: The first results of the ecosystem model are shown including a detection of prey and the direct walk towards the prey, however the model does not include foraging activity and a dynamic energy budget due to technical difficulties. Blue points indicate whale start position and green points the end position.

6.7.4 Model challenges and drawbacks

The model contains two major challenges, which could not yet be solved. The first is of technical nature, facing programming difficulties and the second challenge encompass reliable parameter estimation. Further there are several conceptual additions, which could be made to improve the model structure. The model has a multi-level structure, which involves complicated programming to translate a conceptual framework into mathematical processes and to locate and solve errors in the programming code can be time-consuming.

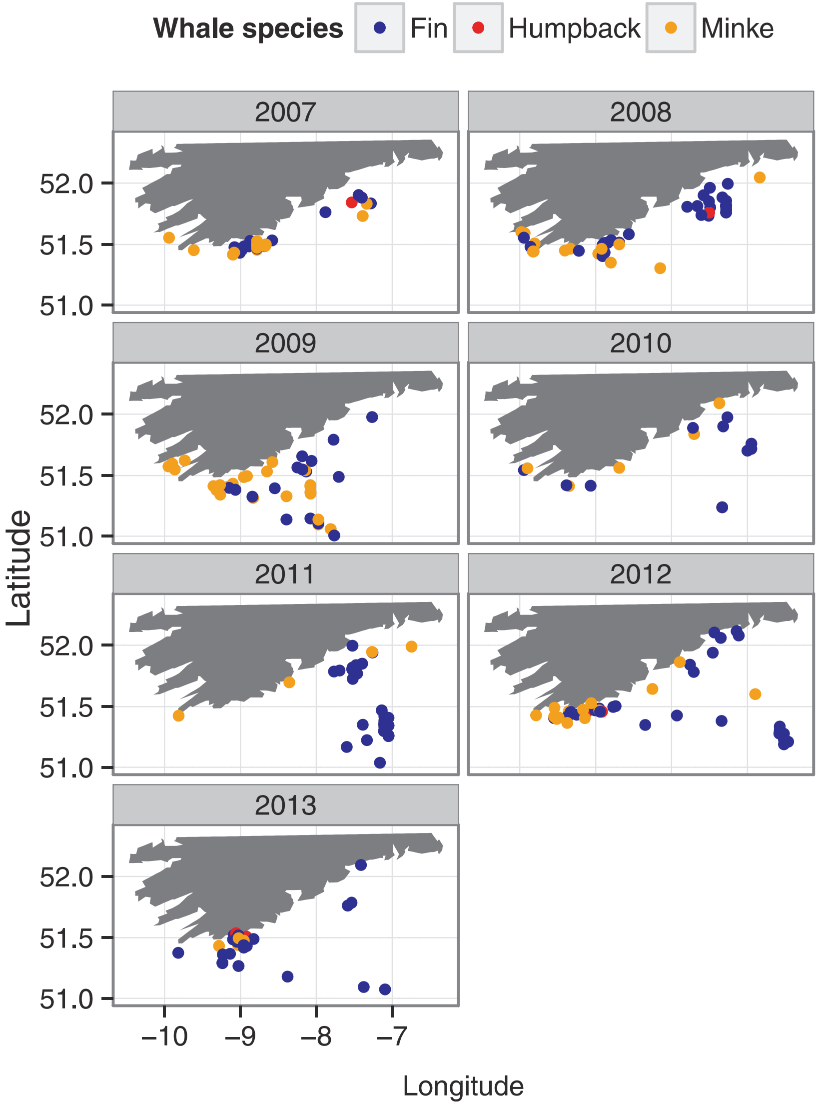

Figure 6.6: Real baleen whale observations recorded during marine mammal surveys in the Celtic Sea in October (CSHAS, O'Donnell et al., 2013 and Chapter 3) and landbased observations from Irish headlands from October to December (all records are validated and available on `http://www.iwdg.ie`

This challenges ecologists and often requires the collaboration with statisticians and programmers (Dickey-Collas et al., 2014).

Albeit the existence of a conceptual model framework and equations to express the energetic flow in the model, the search for reliable parameter estimation is difficult and concessions on applicability have to be made. An assimilation rate (a) of 84% was presented in Goldbogen et al. (2011) for foraging blue whales. However blue whales have a different diet and metabolism compared to fin, minke and humpback whales, thus energy assimilation rates might not be comparable (Spitz et al., 2012). An estimation of metabolic costs (r) can be obtained via the summation of the basal metabolic rate, metabolic costs for locomotion and foraging expenses. Basal metabolic rate can be considered as a constant; while costs for locomotion depend on swimming speed and foraging expenses depend on the number of dives and lunges during foraging. An extensive literature search and, most importantly a careful consideration of presented parameters for different metabolic processes for baleen whales will be necessary.

The difficulties in obtaining reliable parameter estimates highlight the obstacles in baleen whale research of observing animals in the wild or to collect information on metabolism, energy requirements and other behavioural traits. Increased use of multi-sensor tags can provide valuable in situ measurements, thereby support the development and improvement of ecosystem models (Goldbogen et al., 2013). Albeit the lack of experimental and observational data demonstrate simultaneously the application and usefulness of ecosystem models, especially IBMs, to compare different scenarios involving baleen whales in the ecosystem.

In this conceptual model and its first results, only two players with few behaviour traits in the Celtic Sea ecosystem, baleen whales as predators and herring as prey, were considered. While it is the purpose of models to represent a simplistic view of actual processes (Jackson et al., 2000), more behaviour traits could be added to the model to adjust it to realistic predator-prey interactions. The mechanisms for detecting prey for baleen whales are unknown, but visual and audio cues together with species communication are suggested (Kenney et al., 2001). Foraging dolphins, sea birds and other baleen whales could indicate high density prey patches (Anderwald et al., 2011b; Friedlaender et al., 2014). Baleen whales occur generally solitary, however inter-species feeding aggregations have been observed in nature (e.g. Nøttestad et al., 2014). To the moment, whales in the model search the area with a random walk and when prey is available in neighbouring cells, i.e. a distance of two nautical miles, the whale moves straight to the resources. This behaviour was implemented to represent the ability of baleen whales to detect prey in their close surrounding (Chapter 3). A random walk movement to describe prey search appears to be a suitable method within the optimal foraging theory (Sims et al., 2008), but accounting for inter-species interactions and communications could further improve the ecosystem model. For example an addition to the model could be a joined search and foraging effort of whales and the modelling of whales as individuals and as small groups.

Furthermore, herring was used as single prey species because of availability on distribution, energy density and stock biomass data (Chapters 2 and 4 and HAWG, 2014). However sprat and krill (Euphausiacea) were identified as additional prey for baleen whales in the Celtic Sea (Ryan et al., 2014 and Chapter 3). Including a layer of phytoplankton abundance as approximation for zooplankton and a layer of other forage fish biomass could improve the energy balance of whales in the model and could lead to a more concentrated and directed whale distribution on the Celtic Sea plateau and along the continental shelf, which would correspond to observed baleen whale distribution (Wall et al., 2013).

6.7.5 Concluding remarks to the conceptual model of baleen whales and forage fish in the Celtic Sea

The presented conceptual ecosystem model is in an early development of construction and requires continuous work in programming and parameter estimation; however once advanced, it can provide a suitable platform for exploring predator-prey interactions in the Celtic Sea. The model and its challenges show the application of general ecological characteristics of forage fish and baleen whales as presented in Chapters 2 to 5 and discussed in the previous discussion. It illustrates the strong requirement of a conprehensive understanding of trophic links in an ecosystem before more complex ecosystem models can be created. More advanced ecosystem models, as discussed in Section 6.6, can be used to study ecosystem links within an EBFM framework with consequent management implications. The here presented conceptual model contains a population module, i.e. the in- and offshore migration of herring during spawning and the respective energy density fluctuation, as well an individual based behaviour module, i.e. baleen whale distribution and energy budget. It can be informative for questions as how an increase in prey biomass, comparable to the current Celtic Sea herring stock, could affect baleen whale abundance? Or vice versa, how an increased predator abundance could influence prey dynamics and if this could cause a resource competition with fisheries? This conceptual model allows implementation of additional ecosystem processes and accounts for uncertainty within different processes. Once completed it provides a manageable framework to explore ecosystem interactions.

6.8 Prospects in fisheries management

6.8.1 Setting the scene for EBFM

For an EBFM of forage fish, it is not sufficient to only account for baleen whale predation and possibly modify natural mortality estimates, ideally a stock assessment should include flexible and quickly adjustable processes to incorporate the variability and uncertainty of the system (Rice and Duplisea, 2014). In the case of baleen whale predation, the processes causing uncertainty include distribution, number of individuals and residence time of whales in the ecosystem. The construction of different ecosystem models that test scenarios with different parameters could be used to explore the models' uncertainty and to calculate the probabilities of these scenarios. To prevent uncoordinated construction of scenarios and a parameter search, management fishery targets should be clearly formulised under the participation of stakeholders (Varjopuro et al., 2008). Taking the Celtic Sea herring fishery as a case study, fishery goals could be, for instance: reduce harvest to support higher occurrence of baleen whales in the area to promote ecotourism (as far as this can be influenced by human activities); maintain the apparent stable ecosystem while harvesting below FMSY; increase fishing, which might lead to reduced baleen whale activity or extend fisheries of other forage fish in the Celtic Sea ecosystem (e.g. sprat), which could affect the herring stock. It is important to note and discuss the trade-offs of each target and explore the stakeholders' scope of acceptance on trade-offs (Varjopuro et al., 2008; Levin et al., 2013; Rice and Duplisea, 2014).

Experience has shown that early involvement of stakeholders contributes to successful construction of management plans due to increased transparency and credibility (e.g. Armitage et al., 2008; Röckmann et al., 2012). Stakeholders can be included in the process of model building either as peer-reviewers or via contributing of their own knowledge and experience - a process defined as "participatory modelling" (Röckmann et al., 2012). It is very important for such collaborative work and future support by stakeholders that all participants communicate their targets and that goals are set in agreement (e.g. if models are built out of scientific interest or if they will be used for changes of fisheries policy) (Röckmann et al., 2012). Scientist should present model constructions in a conceptual, yet easy to understand manner to facilitate interaction with stakeholders (e.g.

by organising meetings, giving comprehensible presentations or preparing user manuals) (Röckmann et al., 2012, and citations within). Uncertainties in stock assessment should be openly communicated and address the origin of uncertainty (e.g. in recruitment or natural mortality estimation), the range of uncertainty and its impact, and the nature of uncertainty (e.g. due to missing information about processes or due to natural variability) (Levin et al., 2013; Thorson and Minto, 2014). This will create a common understanding of the processes in stock assessment, its challenges and provides room for collaborative solutions, especially within the extensive field of EBFM.

The Celtic Sea Herring Management Advisory Committee (CSHMAC; Section 1.2; Le Floch et al., 2015) provides an excellent platform for participatory modelling and the development of an EBFM for herring fishery in the Celtic Sea. CHSMAC includes participants from fish producer and processor operations, scientists and non-governmental representatives. This variety could benefit the process of EBFM development and members of the committee appear to be open to new scientific findings on Celtic Sea herring (personal observation); however it has to be remembered that most of the committee is concerned with economic profit, sustainability and more importantly, social security of employees and co-workers (Aanesen et al., 2014). Every stakeholder has a different interpretation about the Celtic Sea herring situation, which could be used to openly discuss targets and ways of implementing baleen whale predation into an EBFM of Celtic Sea herring. With a well-structured plan on participation, an operating schedule and comprehensible and transparent communication, ecosystem models and management scenarios that are supported by the stakeholders could be created for Celtic Sea herring.

6.8.2 Technical pathways for accounting for baleen whale predation in stock assessment

Here, two possibilities are presented on how baleen whale predation can be included in stock assessment: (i) by modifying the rate of natural mortality and (ii) by reducing stock biomass according to whale consumption.
Stock biomass is described as

$$B_{t+1} = B_t + R_t + G_t - M_t - Y_t \tag{6.5}$$

with B_{t+1} as biomass of the next year, B_t actual biomass, R_t recruitment biomass, G_t growth, M_t natural mortality and Y_t harvest (Harvest rule, Russell 1931 in Haddon, 2011).

With sufficient information on fish predators, M could be split into predator proportions:

$$M_t = M_{t1} + M_{t2} + ... + M_{tn} \tag{6.6}$$

Baleen whales represent one proportion of M, and if predation can be estimated, M can be modified accordingly. If predator information is limited, M could be treated as one unit, which would be in- or decreased as one:

$$M_X = M_t + M_{whales} \tag{6.7}$$

or

$$M_X = M_t - M_{whales} \tag{6.8}$$

where predation is treated as additional factor, comparable to fisheries, in population growth. In both cases, M is applied as reducing factor of population growth. It can be included either as a constant

$$N_{t+1} = N_t e^{-(F+M)} \tag{6.9}$$

in the situation of continuous fishing on a stock and constant mortality, or in a pulse fishing scenario, where fishing takes place only in a certain period, i.e. at the beginning of the year

$$N_{t+1} = (N_t - C_t)e^{-M} \tag{6.10}$$

and at the end of the year

$$N_{t+1} = N_t e^{-M} - C_t \tag{6.11}$$

where C_t is fishery catch (Haddon, 2011). The Celtic Sea herring fishery is a pulse fishery with a narrow fishing season open for several weeks. In comparison, baleen whale predation is assumed to be limited to the period of whale migration. Hence, eq. (6.11) should be modified to

$$N_{t+1} = N_t e^{-M_X} - C_t \tag{6.12}$$

where M_X is the modified M including baleen whale predation.

Using consumed biomass instead of a mortality rate could be more operational. Predation would be calculated as lost biomass and taken off the total stock biomass, for instance, as shown in the example in Section 6.3 and Figure 6.1. In the assessment, M would remain unchanged for the total biomass calculation and then whale consumption would be subtracted from the total afterwards. The remaining biomass could be used to calculate reference points e.g. TAC. However this approach would likely overestimate natural mortality.

For both mathematical options, it has to be considered if predation affects the entire population, i.e. all age classes, or if only a certain population proportion is consumed, for example if a prey size selectivity is present. Due to higher uncertainties in the estimation of M, different M-values can be included in population analysis and management strategy evaluations (VPAs and MSEs) to calculate probabilities of the different scenarios (Section 1.3). Energy budget models can help to identify predators on the resources and their predation rate allowing for the incorporation of estimate uncertainty (e.g. Link et al., 2008; Matthiopoulos et al., 2008). Energy budget models, together with general ecosystem models e.g. ECOPATH, ECOSIM, OSMOSE or more applied models as Gadget (Howell and Bogstad, 2010; Andonegi et al., 2011) or a MSVPA model for the Gulf of Maine (Tyrrell et al., 2008), can contribute to an ecosystem understanding and predation estimation on resources with a possible implementation in stock assessment (Pauly et al., 2000; Christensen and Walters, 2004; Shin and Cury, 2004; Travers et al., 2010; Morissette and Brodie, 2014).

6.9 Avenues for EBFM

Data collection and analysis for estimating cetacean predation on forage fish is a step of EFBM. But to follow the principals of EBFM the research scope has to be extended to include additional predators and to account for environmental variability, especially in consideration of pending climate change (Pikitch et al., 2012). Therefore it is important to focus not only on the fish population dynamics itself, but also to include possible distribution shifts due to environmental conditions such as the impact of climate change on forage fish prey (e.g. due to zooplankton dependence on phytoplankton, which are sensitive to environmental conditions) and the consequences for predator populations (Edwards and Richardson, 2004; Durant et al., 2005; Pörtner and Peck, 2010; Peck et al., 2013). As another example, seabird colonies diminished and some whale species showed reduced calving due to low prey availability and prey quality induced by climate change and extreme environmental conditions (e.g. el Niño events) (Leaper et al., 2006; Österblom et al., 2008; Cury et al., 2011; Pikitch et al., 2012).

One possibility for fishery managers to react to variability in the ecosystem is to adapt the harvest rule and account for uncertainty in a long-term management plan that aims for stability and sustainability (Rice and Duplisea, 2014). But EBFM goes beyond optimizing harvesting rules and includes the protection of natural conditions, e.g. the gravel sediment on herring spawning grounds, and the improvement of water quality thus maintaining a suitable habitat for the resource. This demonstrates that EBFM is more than acknowledging the dependence of other predators on the same resource in the ecosystem via modifications of the harvest rules. However determining and understanding the numerous interactions and dependencies around a resource and finding suitable management tools is a big burden for a single-fishery management board. A clear set of targets, reference points and goals of what should be protected, including human well-being and food security, among others, is indispensable (Röckmann et al., 2012). Participation of stakeholders during goal setting and agreements on acceptable trade-offs are necessary (Dankel et al., 2008; Aanesen et al., 2014). This is best summed up in this Pauly and Maclean (2003, p. 93) remark: *"We must expect that healthy ecosystems will produce healthy populations of marine mammals at the top of the trophic pyramid. If we are serious about marine ecosystem management, we must accept the keystone roles played by such predators in the maintenance of marine ecosystems and this presents difficult choices."* Hence, estimating cetacean predation on herring, testing different scenarios of M in the stock assessment and exploring modification of the harvest rules is a crucial step towards EBFM in the Celtic Sea.

The above mentioned considerations can lead to an EBFM increasing the overall understanding of ecosystem interactions benefiting other fisheries in the ecoregion. Together it can lead to an overall ecosystem-based management (EBM) (Link and Browman, 2014). Pauly and Maclean (2003, p. 92) summarises: *"Ecosystem restoration implies ecosystem-based management, which itself implies going beyond the species-by-species, shery-by-shery approach presently used."* Embracing EBM for an ecosystem as for instance, the Celtic Sea, involves stakeholders on multiple levels, i.e. local, regional, national and international. Management plans and targets have to involve national governments. And because of the open and connected marine system, cross-border collaborations with neighbouring countries and international unions (e.g. EU) with interest in the ecosystem have to be created. Data collection for improving ecosystem understanding and management is a joint challenge that requires resources and a network of collaborations.

The CSHAS survey, which provided the data used in this PhD study, opens possibility for studying the Celtic Sea ecosystem by having multi-disciplinary research aims (i.e. oceanographic data collection; marine mammal, seabird and macroplastic observations; O'Donnell et al., 2013). However the survey is planned for herring stock assessment and is limited for some ecological questions and the assessment of other species [4] (Chapter 2). Nevertheless, the CSHAS survey provided a suitable platform for ecological studies (Chapter 3), which was possible due to the jointed effort of the Marine Institute, non-governmental organisations as the Irish Whale and Dolphin Group and BirdWatch Ireland and passionate volunteers. Within an EBFM and EBM, such surveys and observers on fishing vessels should be used as platforms of opportunities to collect more data on ecosystem functioning and depend on secured funding for data collection and analysis. This will require a strong cross-border network of scientists, fishery industry representatives, non-governmental organisations and policy makers, which can work towards management targets for EBFM and EBM in the Celtic Sea.

6.10 Future work

Following the approach of this study, the fields of fish ecology and fisheries, marine mammal ecology and the interactions of the two should be more deeply explored to strengthen knowledge of ecosystem functioning. Future research engaging in the open questions highlighted in this discussion concerning fish population dynamics, baleen whale migration behaviour and abundance estimation will increase the certainty in parameter estimation, which can be integrated into ecosystem modelling. It is very important to build an understanding of sprat ecology and forage fish interactions in the Celtic Sea with explicit sampling plans and surveys adjusted to sprat behaviour. For instance, the CSHAS surveys provide a valuable platform for ecosystem observations and for herring biomass estimation, but reliable and applicable sprat biomass estimations would require a survey later in the year. Continued histological analysis of sprat gonads to define maturation stages, which was started within this project, or alternatively, development of a macroscopic identification method, would advance an understanding of sprat maturation stages.

Within the general framework of an EBFM for the Celtic Sea herring fishery or for an EBM of the Celtic Sea, additional predators aside from baleen whales should be considered and ecosystem links explored. With this doctoral project, simultaneous seabird observations during the CSHAS surveys were started. This formed a cornerstone for building up a seabird observation time series, which can provide ecological insights of the Celtic Sea seabird community and its interactions with cetaceans and fisheries, following the example

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[4] For instance an acoustic survey for sprat assessment should take place later in the year (pers. communication C. O'Donnell)

of over ten years of herring and cetacean observations. Seabirds are known predators of forage fish and therefore should be considered and their impact within the ecosystem has to be assessed within an EBFM framework.

Here, only baleen whales were discussed, however other cetacean species are also foraging on forage fish. Common dolphins occur in high numbers in the Celtic Sea and are observed in feeding aggregations with baleen whales. Directed travelling of dolphins or a feeding pod may act as cues for baleen whales to detect prey. Just recently, a sei whale has been sighted close inshore the Irish coast over several days [5]. These sightings could be exceptional or could have a more important meaning for ecosystem balance. It is important to keep monitoring different cetacean species and their interactions to get a more complete picture on the biodiversity and ecosystem links in the Celtic Sea.

Next to cetaceans and seabirds, other fish species could be foraging on different life stages of herring in the Celtic Sea. Mackerel is a probable predator for juvenile herring. Additionally, in the last two consecutive years, foraging tuna species, especially bluefin tuna (*Thunnus thynnus*), were observed during the CSHAS survey, which could also be targeting herring as forage fish (O'Donnell et al. 2013 and pers. communication C. Nolan). An EBFM should take account of the partitioning of a resource between cetaceans, fisheries and other predators like seabirds and the fish community to encompass the most complete, state-of-the-art, overview of an ecosystem. Future work should aim at increasing the knowledge on single aspects of the ecosystem, but also combine it to an overall cross-linked biodiversity and ecosystem understanding.

6.11 Conclusion

Encouraged by the recent rebuilding of the Celtic Sea herring stock after years of low biomass and the global movement requesting to manage ecosystems and fisheries within an ecosystem-based management approach, this doctoral study explored the links between baleen whales and forage fish in the Celtic Sea, referring to spatial distribution and energy content as indicators of ecosystem characteristics. Herring distribution was shown to be strongly orientated towards the spawning grounds and its aggregated, random distribution highlights a non-continuous structure. This allows for more accurate prey distribution description within ecosystem modelling. The Celtic Sea has been identified as a prey hot-

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[5] `http://www.iwdg.ie/index.php?option=com_k2&view=item&id=2526:rare-sei-whale-record-off-ventry-co-kerryaccessed15.December2014`

spot for baleen whales, which actively target herring and sprat in the region. Hence baleen whale predation should be assessed within the fishery management of Celtic Sea herring and within a possible future installation of a sprat fishery management. The difficulties of assessing baleen whale predation impacts have been discussed. Energy content and energy assimilation is the link between fish biomass and baleen whale predation. Energy variability of herring, together with sprat and mackerel as other species within the functional group of forage fish, has been linked to maturation stage. Energy content and its variability can influence foraging decisions and can motivate a switch in foraging behaviour which has implementations within ecosystem modelling. The above results were used to define parameters within a conceptual ecosystem model. Such models can help to test different scenarios, as for example a de- or increase in predator and/or prey abundance. Ecosystem modelling is a powerful tool to visualise ecosystem processes. It combines different research areas in an integrative, cross-disciplinary approach and thereby can advocate potentially highly influential decisions within an ecosystem- based approach to fisheries management within the Celtic Sea. Pathways for future research have been shown for the areas of fish population dynamics, cetacean ecology and their interactions. Communication and collaboration between the research sectors is encouraged. Respective progress and results should be communicated in a comprehensible, transparent manner outside of the scientific community to industry representatives and stakeholders with decision power. Closing with the words of Lavigne (1996): *"We do not know how to manage ecosystems and in reality, we don't even try. What we do attempt to manage - and we haven't been very successful at this either - is human activities. The real object of management is not really to regulate wild populations of fish but rather to ensure that catches from them are sustainable into the future."* However, we make the important addition that now, nearly 20 years after Lavigne's statement, we do try to take ecosystem characteristics into account and fisheries management is becoming a more collaborative approach between decision makers, fishery scientists and ecologists.

6.12 References

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Appendices

Appendix A

Reference points and management plan for Celtic Sea herring

Atlantic herring (*Clupea harengus*) Celtic Sea and South of Ireland (Divison VIIa South of 52°30'N and VIIg,h,j,k)

The following information shows the reference points and long-term management plan for Celtic Sea herring. The information was taken from "The Stockbook 2013: Annual Review of Fish Stocks in 2013 with Management Advice for 2014", published by the Marine Institute, Rinville, Oranmore 2013; pages 378 and 384; updated June 2013.

Management plan

In 2011 the Pelagic RAC agreed a new proposed long-term management plan. This plan has a target F of 0.23 and a 30% constraint on TAC change. This TAC constraint prevents sudden changes of the TAC and accounts for uncertainties in the assessment and forecast in the event of strong or low incoming recruitment. This plan would lead to a TAC in 2014 of 22,360 t. In 2012 ICES evaluated this plan and found it to be in accordance with the precautionary approach. It leads to sustainable yield and provides stability in catches over time, at the expense of maximizing yield. The European Commission has communicated to ICES that its preference is that ICES advice follows the ICES MSY transitional framework, while the outcomes from following this plan should be presented in the catch options table. Because F has been below F_{MSY} since 2007, this corresponds to the ICES MSY approach. ICES was not able to simulate the effect of the closed area, but from an operational point of view it seems to have worked to reduce F under the recent recovery plan.

Reference points

	Type	Value	Technical basis
MSY	MSY $B_{trigger}$	61,000 t	Stochastic simulations on segmented regression stock-recruitment relationship
approach	F_{MSY}	0.25	Stochastic simulations on segmented regression stock-recruitment relationship
Management plan	SSB_{MP}	61,000 t	Stochastic simulations on segmented regression stock-recruitment relationship
	F_{MP}	0.23	If SSB in TAC year >61,000 t
Precautionary	B_{lim}	26,000 t	The lowest stock observed
approach	B_{pa}	44,000 t	Low probability of low recruitment
	F_{lim}	not defined	
	F_{pa}	not defined	

Long-term management plan for herring in the Celtic Sea and Division VIIj as agreed by the Pelagic RAC

1. Every effort shall be made to maintain a minimum level of Spawning Stock Biomass (SSB) greater than 41,000 t, the level below which recruitment becomes impaired.
2. Where the SSB, in the year for which the TAC is to be fixed, is estimated to be above 61,000 t ($B_{trigger}$) the TAC will be set consistent with a fishing morality, for appropriate age groups, of 0.23 (F_{target}).
3. Where the SSB is estimated to be below 61,000 t, the TAC will be set consistent with a fishing mortality of: SSB * 0.23 / 61,000
4. Where the rules in paragraphs 2 and 3 would lead to a TAC which deviates by more than 30% from the TAC of the preceding year, the TAC will be fixed such that it is not more than 30% greater or 30% less than the TAC of the preceding year.
5. Where the SSB is estimated to be below 41,000 t, Subdivision VIIaS will be closed until the SSB has recovered to above 41,000 t.

6. Where the SSB is estimated to be below 41,000 t, and Sub-Division VIIaS is closed, a small-scale sentinel fishery will be permitted in the closed area. This fishery will be confined to vessels, of no more than 50 feet in registered length. A maximum catch limitation of 8% of the Irish quota will be exclusively allocated to this sentinel fishery.

7. Notwithstanding paragraphs 2, 3 and 4, if the SSB is estimated to be at or below the level consistent with recruitment impairment (41,000 t), then the TAC will be set at a lower level than that provided for in those paragraphs.

8. No vessels participating in the fishery, if requested, will refuse to take on-board any observer for the purposes of improving the knowledge on the state of the stock. All vessels will, upon request, provide samples of catches for scientific analyses.

9. Every three years from the date of entry into force of this Regulation, the Commission will request ICES and STECF to review and evaluate the plan.

10. This arrangement enters into force on 1st January, 2012.

Appendix B

IUCN Red list status for cetacean species within the Irish EEZ

Table B.1: List of cetacean species recorded within the Irish EEZ and adjacent waters with the status on the IUCN Red List of threatened species. Endangered species are indicated in bold. † = Vagrant; ∗ = Recorded only from stranding

Common name	Species	IUCN Red list of threatened species (Version 2014.2)
Atlantic White-Sided Dolphin	*Lagenorhynchus acutus*	Least concern
Beluga	*Delphinapterus leucas* †	Near threatened
Blue Whale	***Balaenoptera musculus***	**Endangered**
Bottlenose Dolphin	*Tursiops truncatus*	Least concern
Common Dolphin	*Delphinus delphis*	Least concern
Cuvier's Beaked Whale	*Ziphius cavirostris*	Least concern
False Killer Whale	*Pseudorca crassidens*	Data deficient
Fin Whale	***Balaenoptera physalus***	**Endangered**
Gervais' Beaked Whale	*Mesoplodon europaeus* ∗	Data deficient
Harbour Porpoise	*Phocoena phocoena*	Least concern
Humpback Whale	*Megaptera novaeangliae*	Least concern
Killer Whale	*Orcinus orca*	Data deficient
Minke Whale	*Balaenoptera acutorostrata*	Least concern
Northern Bottlenose Whale	*Hyperoodon ampullatus*	Data deficient
Northern Right Whale	***Eubalaena glacialis***	**Endangered**
Pilot Whale (long-finned)	*Globicephala melas*	Data deficient
Pygmy Sperm Whale	*Kogia breviceps*	Data deficient
Risso's Dolphin	*Grampus griseus*	Least concern
Sei Whale	***Balaenoptera borealis***	**Endangered**
Sowerby's Beaked Whale	*Mesplodon bidens*	Data deficient
Sperm Whale	*Physeter macrocephalus*	Vulnerable
Striped Dolphin	*Stenella coeruleoalba*	Least concern
True's Beaked Whale	*Mesplodon mirus*	Data deficient
White-Beaked Dolphin	*Lagenorhynchus albirostris*	Least concern

Appendix C

Software used for this PhD thesis

Analysis

- R (`http://cran.r-project.org`)
- R studio, 2014, Version 0.98.1056 (`http://www.rstudio.com/`)
- Microsoft Excel, 2010, Version 14.0.7128.5000
- GS + Geostatistics for the Environmental Science, Version 5.1.1., Gamma Design Software

Plotting

- R package "ggplot2" (`http://ggplot2.org/`)
- CorelDRAW, 2003, Version 12.0.0.458
- Seaturtle (`http://www.seaturtle.org/maptool/`)

Text editor

- Microsoft Word, 2010, Version 14.0.7128.5000
- TexMaker Version 4.3 (`http://www.xm1math.net/texmaker/`)
- MikTex Version 2.9 (`http://miktex.org/`)

Presentations

- Microsoft PowerPoint, 2010, Version 14.0.7128.5000

References

- Qigga, 2014, Version .66s (`http://www.qiqqa.com/`)

Appendix D

Conference contributions

European Marine Biology Symposium (EMBS)

19. - 23. August 2013

Galway, Ireland

Section: 6. Sustainable management of the ocean

Irish Celtic Sea Herring fishery -
a story of a successful stock recovery and its characteristics

Mareike Volkenandt, Ian O'Connor, Simon Berrow

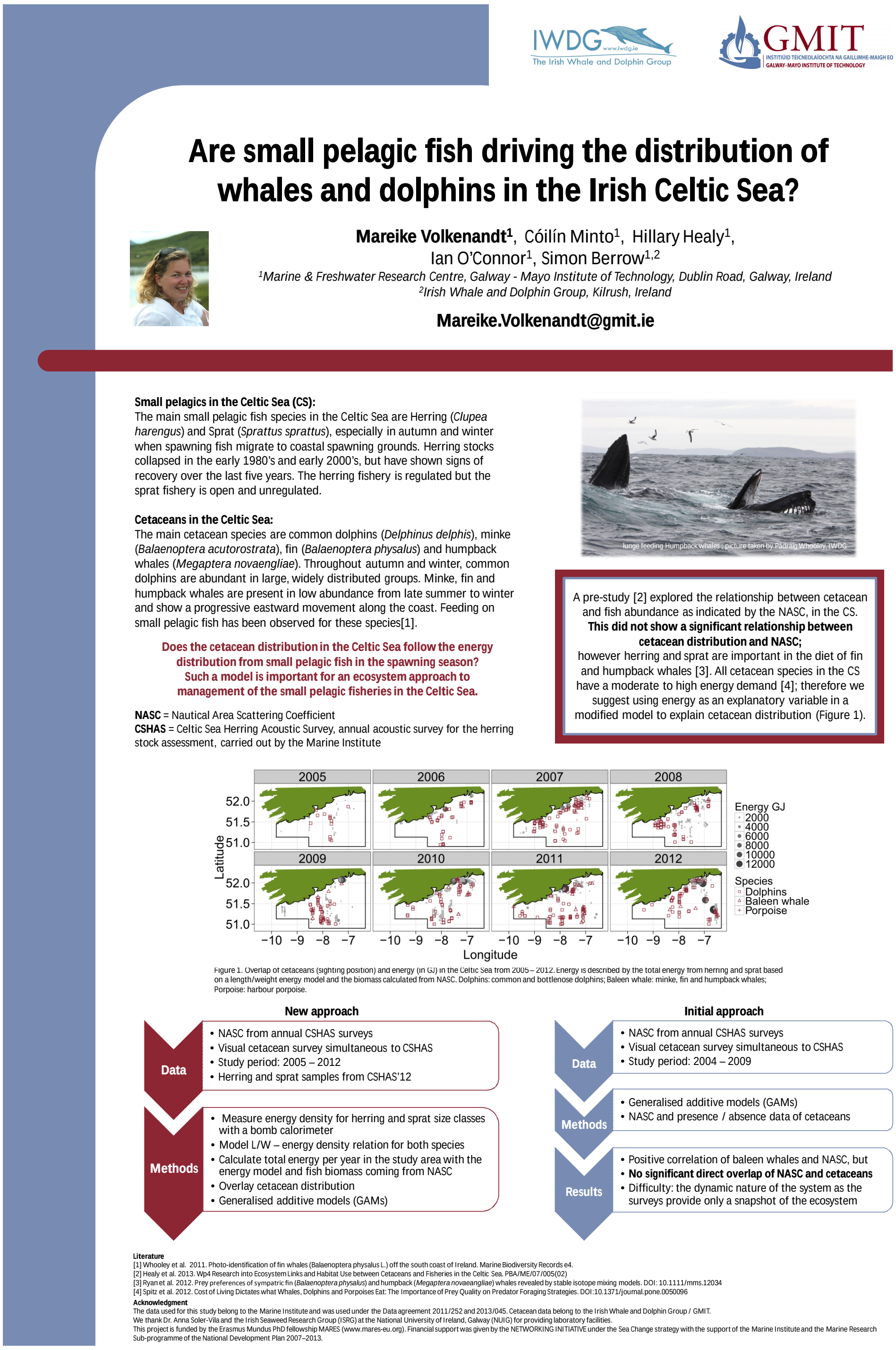
The Celtic Sea (CS) Herring (*Clupea harengus*) is one of the most important fisheries in Ireland but landings declined considerable since the 1970s to a low of 8000 t in the early 1980s. Since 2004 a new management plan including stakeholder involvement is in place, leading to a qualified successful herring fishery with continuously increasing spawning stock biomass (SBB). The fishery management is explained, followed by a presentation of the inter-annual distribution and biological characteristics of the Irish autumn- spawning herring population in the CS for the years 2005 - 2012. We used Center of Gravity and Inertia (CGI) models, together with the SSB, year class strength and length/weight ratios to describe the stock characteristics. Ambient environmental conditions are described by temperature and salinity at the surface and bottom respectively. The precautionary management approach, has led to the doubling of the herring SSB with an estimated 226,505 t in 2012. Strong year classes, contributing to the increasing SSB, were followed over the years (e.g. strong recruitment of 2009). The CGI showed latitudinal variation, while the ambient conditions stayed constant over the study period and were unsuitable to explain the stock distribution. Ambient salinity of the water column (surface and bottom 34.9 ±0.1 PSU and 35.1 ±0.1 PSU respectively) showed less variability compared to temperature (surface and bottom with 14.1 ±0.5° C and 12.8 ±1.1° C respectively). The Irish CS Herring fishery is a successful example of integrating stakeholders into fishery management. A recovering stock provides an opportunity to monitor changes in the ecosystem including the response by seabirds and marine mammals and how the fishing community receive the increasing fishing potential.

ICES Annual Science Conference

23. - 27. September 2013

Reykjavík, Iceland

Session E: Do foodweb dynamics matter in fisheries management?



Are small pelagic fish driving the distribution of whales and dolphins in the Irish Celtic Sea?

Mareike Volkenandt[1], Cóilín Minto[1], Hillary Healy[1],
Ian O'Connor[1], Simon Berrow[1,2]
[1]*Marine & Freshwater Research Centre, Galway - Mayo Institute of Technology, Dublin Road, Galway, Ireland*
[2]*Irish Whale and Dolphin Group, Kilrush, Ireland*

Mareike.Volkenandt@gmit.ie

Small pelagics in the Celtic Sea (CS):
The main small pelagic fish species in the Celtic Sea are Herring (*Clupea harengus*) and Sprat (*Sprattus sprattus*), especially in autumn and winter when spawning fish migrate to coastal spawning grounds. Herring stocks collapsed in the early 1980's and early 2000's, but have shown signs of recovery over the last five years. The herring fishery is regulated but the sprat fishery is open and unregulated.

Cetaceans in the Celtic Sea:
The main cetacean species are common dolphins (*Delphinus delphis*), minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*). Throughout autumn and winter, common dolphins are abundant in large, widely distributed groups. Minke, fin and humpback whales are present in low abundance from late summer to winter and show a progressive eastward movement along the coast. Feeding on small pelagic fish has been observed for these species[1].

Does the cetacean distribution in the Celtic Sea follow the energy distribution from small pelagic fish in the spawning season? Such a model is important for an ecosystem approach to management of the small pelagic fisheries in the Celtic Sea.

NASC = Nautical Area Scattering Coefficient
CSHAS = Celtic Sea Herring Acoustic Survey, annual acoustic survey for the herring stock assessment, carried out by the Marine Institute

lunge feeding Humpback whales , picture taken by Pádraig Whooley, IWDG

A pre-study [2] explored the relationship between cetacean and fish abundance as indicated by the NASC, in the CS. **This did not show a significant relationship between cetacean distribution and NASC;** however herring and sprat are important in the diet of fin and humpback whales [3]. All cetacean species in the CS have a moderate to high energy demand [4]; therefore we suggest using energy as an explanatory variable in a modified model to explain cetacean distribution (Figure 1).

Figure 1. Overlap of cetaceans (sighting position) and energy (in GJ) in the Celtic Sea from 2005 – 2012. Energy is described by the total energy from herring and sprat based on a length/weight energy model and the biomass calculated from NASC. Dolphins: common and bottlenose dolphins; Baleen whale: minke, fin and humpback whales; Porpoise: harbour porpoise.

New approach

Data
- NASC from annual CSHAS surveys
- Visual cetacean survey simultaneous to CSHAS
- Study period: 2005 – 2012
- Herring and sprat samples from CSHAS'12

Methods
- Measure energy density for herring and sprat size classes with a bomb calorimeter
- Model L/W – energy density relation for both species
- Calculate total energy per year in the study area with the energy model and fish biomass coming from NASC
- Overlay cetacean distribution
- Generalised additive models (GAMs)

Initial approach

Data
- NASC from annual CSHAS surveys
- Visual cetacean survey simultaneous to CSHAS
- Study period: 2004 – 2009

Methods
- Generalised additive models (GAMs)
- NASC and presence / absence data of cetaceans

Results
- Positive correlation of baleen whales and NASC, but
- **No significant direct overlap of NASC and cetaceans**
- Difficulty: the dynamic nature of the system as the surveys provide only a snapshot of the ecosystem

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Acknowledgment
The data used for this study belong to the Marine Institute and was used under the Data agreement 2011/252 and 2013/045. Cetacean data belong to the Irish Whale and Dolphin Group / GMIT.
We thank Dr. Anna Soler-Vila and the Irish Seaweed Research Group (ISRG) at the National University of Ireland, Galway (NUIG) for providing laboratory facilities.
This project is funded by the Erasmus Mundus PhD fellowship MARES (www.mares-eu.org). Financial support was given by the NETWORKING INITIATIVE under the Sea Change strategy with the support of the Marine Institute and the Marine Research Sub-programme of the National Development Plan 2007–2013.

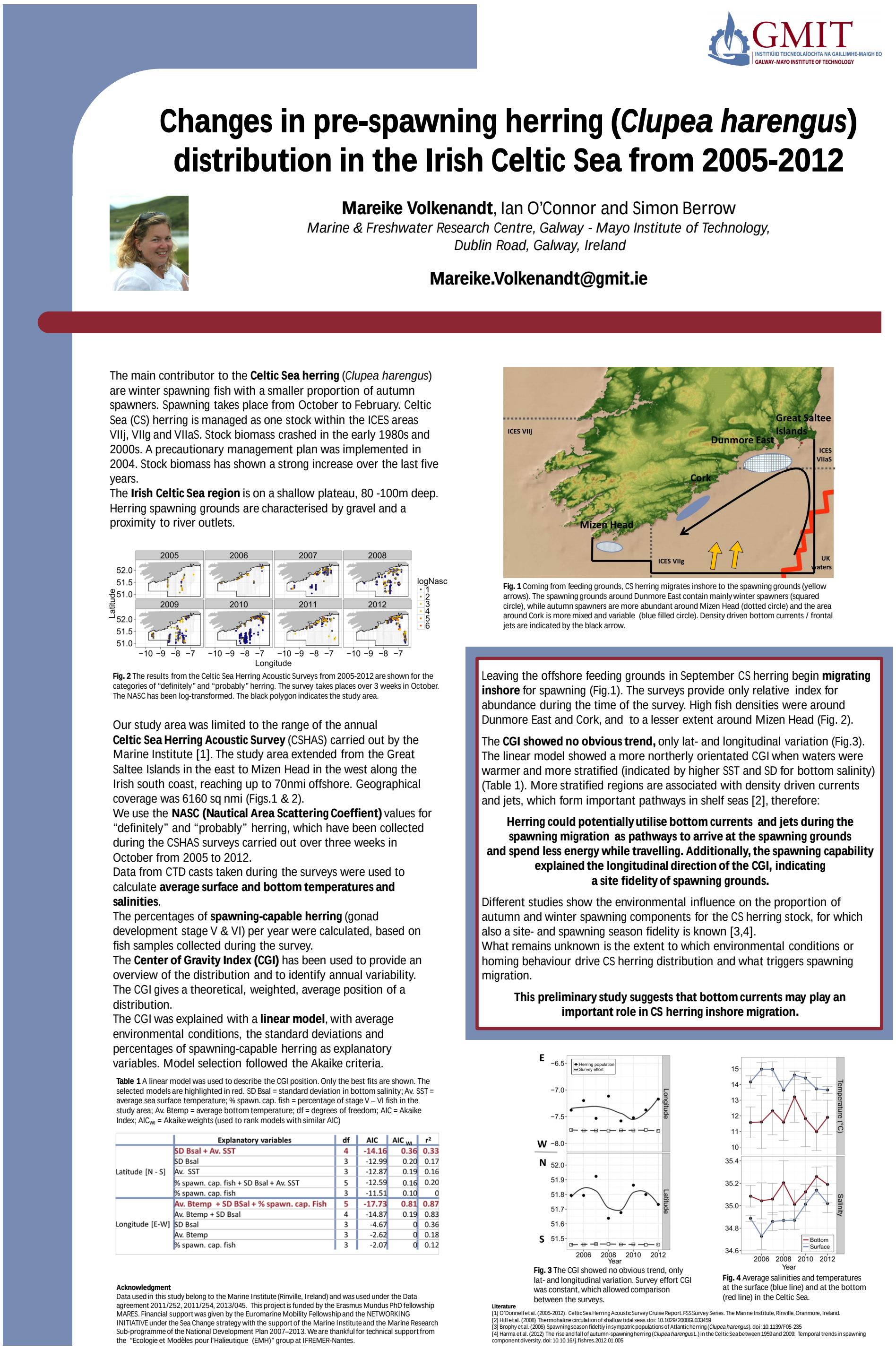
ICES Annual Science Conference

23. - 27. September 2013

Reykjavík, Iceland

Session N: The pelagic fish complexes in the North Atlantic Ocean:

Distribution, productivity, and inter-specific competition during changing climate



Changes in pre-spawning herring (*Clupea harengus*) distribution in the Irish Celtic Sea from 2005-2012

Mareike Volkenandt, Ian O'Connor and Simon Berrow
Marine & Freshwater Research Centre, Galway - Mayo Institute of Technology,
Dublin Road, Galway, Ireland

Mareike.Volkenandt@gmit.ie

The main contributor to the **Celtic Sea herring** (*Clupea harengus*) are winter spawning fish with a smaller proportion of autumn spawners. Spawning takes place from October to February. Celtic Sea (CS) herring is managed as one stock within the ICES areas VIIj, VIIg and VIIaS. Stock biomass crashed in the early 1980s and 2000s. A precautionary management plan was implemented in 2004. Stock biomass has shown a strong increase over the last five years.

The **Irish Celtic Sea region** is on a shallow plateau, 80 -100m deep. Herring spawning grounds are characterised by gravel and a proximity to river outlets.

Fig. 2 The results from the Celtic Sea Herring Acoustic Surveys from 2005-2012 are shown for the categories of "definitely" and "probably" herring. The survey takes places over 3 weeks in October. The NASC has been log-transformed. The black polygon indicates the study area.

Our study area was limited to the range of the annual **Celtic Sea Herring Acoustic Survey** (CSHAS) carried out by the Marine Institute [1]. The study area extended from the Great Saltee Islands in the east to Mizen Head in the west along the Irish south coast, reaching up to 70nmi offshore. Geographical coverage was 6160 sq nmi (Figs.1 & 2).

We use the **NASC (Nautical Area Scattering Coeffient)** values for "definitely" and "probably" herring, which have been collected during the CSHAS surveys carried out over three weeks in October from 2005 to 2012.

Data from CTD casts taken during the surveys were used to calculate **average surface and bottom temperatures and salinities**.

The percentages of **spawning-capable herring** (gonad development stage V & VI) per year were calculated, based on fish samples collected during the survey.

The **Center of Gravity Index (CGI)** has been used to provide an overview of the distribution and to identify annual variability. The CGI gives a theoretical, weighted, average position of a distribution.

The CGI was explained with a **linear model**, with average environmental conditions, the standard deviations and percentages of spawning-capable herring as explanatory variables. Model selection followed the Akaike criteria.

Table 1 A linear model was used to describe the CGI position. Only the best fits are shown. The selected models are highlighted in red. SD Bsal = standard deviation in bottom salinity; Av. SST = average sea surface temperature; % spawn. cap. fish = percentage of stage V – VI fish in the study area; Av. Btemp = average bottom temperature; df = degrees of freedom; AIC = Akaike Index; AIC_{WI} = Akaike weights (used to rank models with similar AIC)

	Explanatory variables	df	AIC	AIC_{WI}	r^2
Latitude [N - S]	**SD Bsal + Av. SST**	**4**	**-14.16**	**0.36**	**0.33**
	SD Bsal	3	-12.99	0.20	0.17
	Av. SST	3	-12.87	0.19	0.16
	% spawn. cap. fish + SD Bsal + Av. SST	5	-12.59	0.16	0.20
	% spawn. cap. fish	3	-11.51	0.10	0
Longitude [E-W]	**Av. Btemp + SD BSal + % spawn. cap. Fish**	**5**	**-17.73**	**0.81**	**0.87**
	Av. Btemp + SD Bsal	4	-14.87	0.19	0.83
	SD Bsal	3	-4.67	0	0.36
	Av. Btemp	3	-2.62	0	0.18
	% spawn. cap. fish	3	-2.07	0	0.12

Acknowledgment
Data used in this study belong to the Marine Institute (Rinville, Ireland) and was used under the Data agreement 2011/252, 2011/254, 2013/045. This project is funded by the Erasmus Mundus PhD fellowship MARES. Financial support was given by the Euromarine Mobility Fellowship and the NETWORKING INITIATIVE under the Sea Change strategy with the support of the Marine Institute and the Marine Research Sub-programme of the National Development Plan 2007–2013. We are thankful for technical support from the "Ecologie et Modèles pour l'Halieutique (EMH)" group at IFREMER-Nantes.

Fig. 1 Coming from feeding grounds, CS herring migrates inshore to the spawning grounds (yellow arrows). The spawning grounds around Dunmore East contain mainly winter spawners (squared circle), while autumn spawners are more abundant around Mizen Head (dotted circle) and the area around Cork is more mixed and variable (blue filled circle). Density driven bottom currents / frontal jets are indicated by the black arrow.

Leaving the offshore feeding grounds in September CS herring begin **migrating inshore** for spawning (Fig.1). The surveys provide only relative index for abundance during the time of the survey. High fish densities were around Dunmore East and Cork, and to a lesser extent around Mizen Head (Fig. 2).

The **CGI showed no obvious trend,** only lat- and longitudinal variation (Fig.3). The linear model showed a more northerly orientated CGI when waters were warmer and more stratified (indicated by higher SST and SD for bottom salinity) (Table 1). More stratified regions are associated with density driven currents and jets, which form important pathways in shelf seas [2], therefore:

Herring could potentially utilise bottom currents and jets during the spawning migration as pathways to arrive at the spawning grounds and spend less energy while travelling. Additionally, the spawning capability explained the longitudinal direction of the CGI, indicating a site fidelity of spawning grounds.

Different studies show the environmental influence on the proportion of autumn and winter spawning components for the CS herring stock, for which also a site- and spawning season fidelity is known [3,4].

What remains unknown is the extent to which environmental conditions or homing behaviour drive CS herring distribution and what triggers spawning migration.

This preliminary study suggests that bottom currents may play an important role in CS herring inshore migration.

Fig. 3 The CGI showed no obvious trend, only lat- and longitudinal variation. Survey effort CGI was constant, which allowed comparison between the surveys.

Fig. 4 Average salinities and temperatures at the surface (blue line) and at the bottom (red line) in the Celtic Sea.

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Johan Hjort Symposium on Recruitment Dynamics and Stock Variability

7. - 9. October 2014

Bergen, Norway

Session: Spatial aspects and drift

catch me if you can
how whales follow herring

Mareike Volkenandt[1,3]
Ian O'Connor[1], Simon Berrow[1,2], Jean-Marc Guarini[3]
[1] Marine & Freshwater Research Centre, GMIT, Galway, Ireland
[2] Irish Whale and Dolphin Group, Kilrush, Ireland
[3] UPMC, UMR 8222-LECOB, Banyuls sur Mer, France

volkenandt.mareike@gmail.com

Objective

- to gain a better understanding of foraging interactions between baleen whales and small pelagic fish
- to investigate co-occurrence of whales and herring

Method

- using an individual based model for simulating whale movement including:
  1. random oriented random walk
  2. a dynamic energy budget model (optimal foraging theory)
- based on data for fish distribution and whale sightings

\+ non-invasive method - difficult to compute

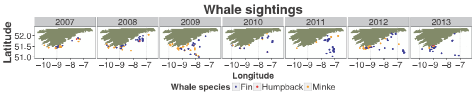
This is not a whale.

Foraging.Biomass.Investigations
FBI
Foto: Nick Massett
THIS CERTIFIES THAT THE SIGNATURE AND PHOTOGRAPH HERON IS AN APPOINTED
Special Agent: *Megaptera novaeangliae* "HBIRL10"
OF THE FORAGING BIOMASS INVESTIGATIONS TASK FORCE "BALEEN WHALE"

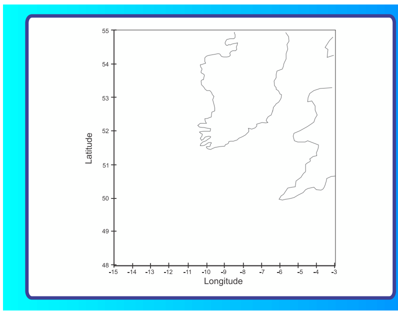
Baleen whales

- Fin whale (*B. physalus*), Humpback whale (*M. novaengliae*) and Minke whale (*B. acutorostrata*)
- Known to forage on pelagic fish shoals [1]
- Oct. - Dec. peak in sightings in the Irish Celtic Sea [2]

Whale sightings



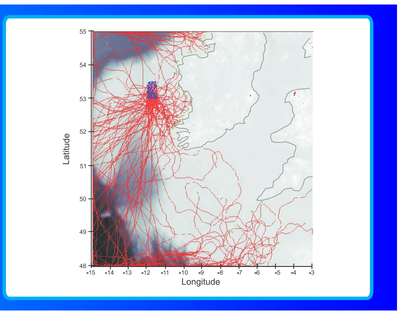
Landbased sightings from October to December and effortbased sightings during the Celtic Sea Herring Acoustic Survey in October.
All records are validated and available on www.iwdg.ie

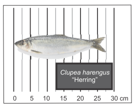


Where would you go?

Compare your random walk with our model output!

Representation of a theoretical distribution of a top predator and its prey, including predation interactions.





Atlantic herring (*Clupea harengus*)

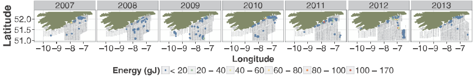
- Celtic Sea herring stock assessment
- Stock shows signs of recovery due to strong year classes
- Estimated spawning stock biomass in 2013: 156 355 tonnes [3]
- Fishing mortality is below F_{MSY}

- Contains autumn- and winter-spawning components with a protracted spawning period from October to January
- Enters inshore areas along the Irish south coast for spawning

- Variograms indicated no continuous structure during prespawning migration [4]
- Shoals were clustered and randomly distributed during spawning migration
- Oceanic factors as temperature and salinity were not limiting herring distribution

- Prespawning adults have high energy contents (e.g. individual of 25 cm contains 1445 kJ)
- During spawning and migration, fish loose up to 70% in energy content (e.g. individual of 25 cm now contains only 444 kJ)

Herring energy distribution



Spatial distribution of energy provided by herring. Acoustic herring data (NASC) has been collected during the Celtic Sea Herring Acoustic Survey by the Irish Marine Institute. CSHAS is an annual survey, taking place in October targeting inshore migrating prespawning herring. A Simrad Ek 60 Echosounder with four frequencies (18, 38, 120 and 200kHz) recorded the backscattered acoustic signal continuously along the ship route. NASC values were converted to fish density using the average fish length of the closest haul to calculate target strength and mean backscattering cross section. Energy per fish was calculated based on a length-energy relationship [5] and multiplied by herring density.

Model parameters

Movement:
- random walk
- if depth too small, change direction
- constantly swimming
- stop for diving / feeding
- slower swimming speed close to the coast

Behaviour:
- perception radius of 6 km
- continue swimming, if energy gain per dive becomes negative
- leave the area when body condition decreases

Dynamic energy budget:
- energy cost of foraging is kept constant
- energy gain is fluctuating depending on prey energy
- energy gain is stored in the blubber
- metabolic costs = basal metabolic costs + energy costs for swimming
- two compartment model:

$$\begin{cases} \dfrac{dE}{dt} = a\,E^{2/3} - (s+r)\,E + kR \\ \dfrac{dR}{dt} = +\,sE - kR \end{cases}$$

a = energy acquisition
r = energy spent for metabolic activities
R = lipid reserve (blubber)
s = stocking process
k = depletion process

Application

- How would an increase in herring biomass affect baleen whale abundance in the Celtic Sea? vice versa: How would an increase in whale abundance affect the Celtic Sea herring stock?
- Can whale presence on the foraging grounds be predicted?

Work in progress

to include:
- a dynamic fish distribution resembling a South-North migration
- a phytoplankton layer as proxy for zooplankton distribution on the shelf
- if whales are within 8 km to some fish, direct movement to the fish source (see poster)
- attract other whales to the same source, if one whale is foraging on large fish shoal (assuming communication between individuals and the formation of feeding concentrations)
- leave area after a certain amount of dives with negative energy gain to guarantee that whales are still in a good condition to migrate to the mating grounds

Acknowledgment

All data used in this study belong to the Marine Institute (DA 2011/252, 2013/045, 2014/118, 2014/161) and the Irish Whale and Dolphin Group. We are grateful for funding from the Marine Institute Networking Initiative under the SeaChange strategy and the Johan Hjort Symposium committee. MARES is a joint doctorate programme selected under Erasmus Mundus (FPA 2011-0016).

Download this poster as pdf here:

References

[1] Ryan et al. 2014; doi:10.1111/mms.120343
[2] Berrow et al. 2010, Irish Cetacean Review (2000-2009), IWDG
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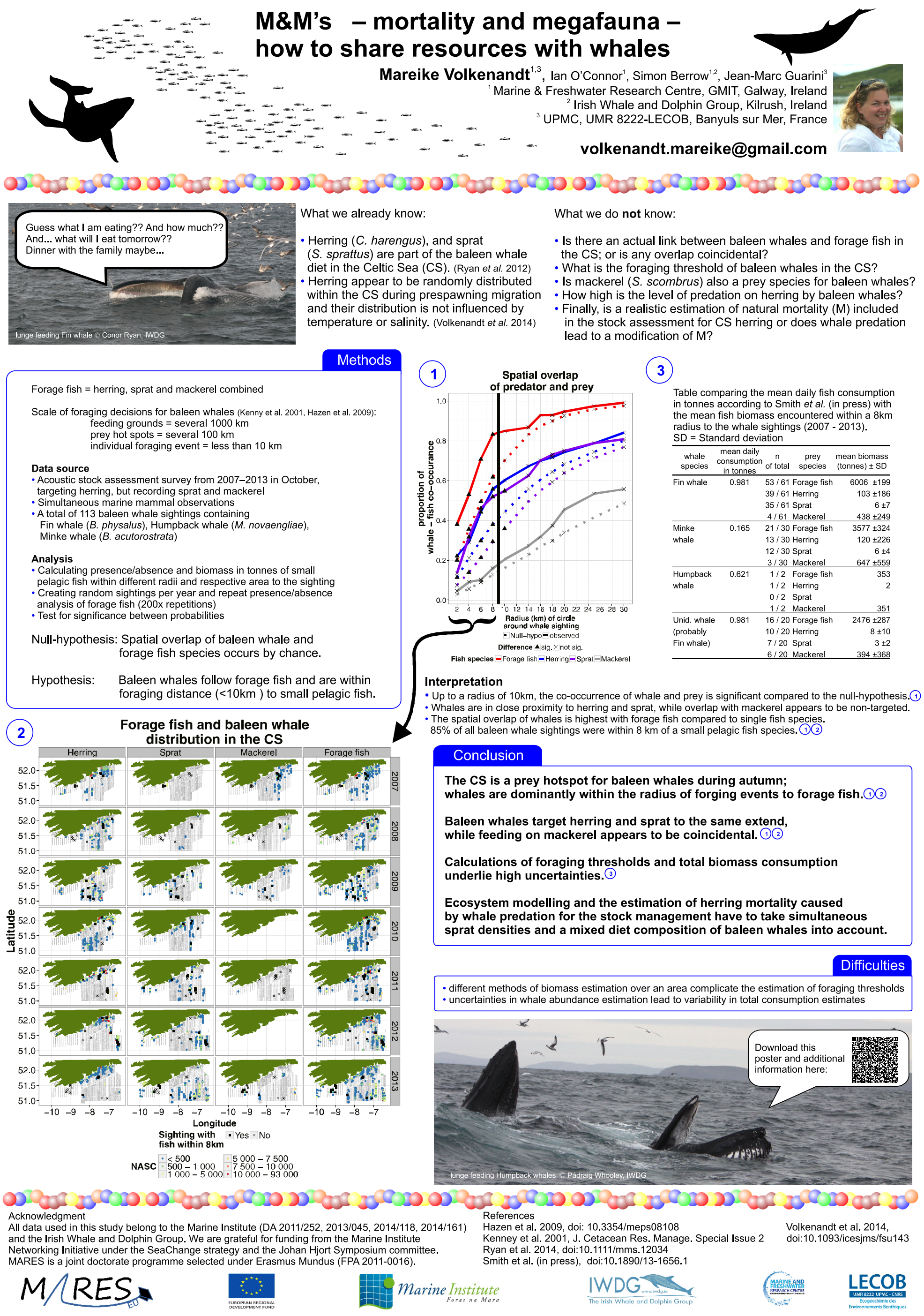
[4] Volkenandt et al. 2014; doi:10.1093/icesjms/fsu143
[5] Volkenandt et al. in preparation

Johan Hjort Symposium on Recruitment Dynamics and Stock Variability

7. - 9. October 2014

Bergen, Norway

Session: Environmental drivers fluctuations and change



M&M's – mortality and megafauna – how to share resources with whales

Mareike Volkenandt[1,3], Ian O'Connor[1], Simon Berrow[1,2], Jean-Marc Guarini[3]
[1] Marine & Freshwater Research Centre, GMIT, Galway, Ireland
[2] Irish Whale and Dolphin Group, Kilrush, Ireland
[3] UPMC, UMR 8222-LECOB, Banyuls sur Mer, France
volkenandt.mareike@gmail.com

lunge feeding Fin whale © Conor Ryan, IWDG

What we already know:

- Herring (*C. harengus*), and sprat (*S. sprattus*) are part of the baleen whale diet in the Celtic Sea (CS). (Ryan *et al.* 2012)
- Herring appear to be randomly distributed within the CS during prespawning migration and their distribution is not influenced by temperature or salinity. (Volkenandt *et al.* 2014)

What we do **not** know:

- Is there an actual link between baleen whales and forage fish in the CS; or is any overlap coincidental?
- What is the foraging threshold of baleen whales in the CS?
- Is mackerel (*S. scombrus*) also a prey species for baleen whales?
- How high is the level of predation on herring by baleen whales?
- Finally, is a realistic estimation of natural mortality (M) included in the stock assessment for CS herring or does whale predation lead to a modification of M?

Methods

Forage fish = herring, sprat and mackerel combined

Scale of foraging decisions for baleen whales (Kenny et al. 2001, Hazen et al. 2009):
feeding grounds = several 1000 km
prey hot spots = several 100 km
individual foraging event = less than 10 km

Data source

- Acoustic stock assessment survey from 2007–2013 in October, targeting herring, but recording sprat and mackerel
- Simultaneous marine mammal observations
- A total of 113 baleen whale sightings containing Fin whale (*B. physalus*), Humpback whale (*M. novaengliae*), Minke whale (*B. acutorostrata*)

Analysis

- Calculating presence/absence and biomass in tonnes of small pelagic fish within different radii and respective area to the sighting
- Creating random sightings per year and repeat presence/absence analysis of forage fish (200x repetitions)
- Test for significance between probabilities

Null-hypothesis: Spatial overlap of baleen whale and forage fish species occurs by chance.

Hypothesis: Baleen whales follow forage fish and are within foraging distance (<10km) to small pelagic fish.

① Spatial overlap of predator and prey

② Forage fish and baleen whale distribution in the CS

③

Table comparing the mean daily fish consumption in tonnes according to Smith *et al.* (in press) with the mean fish biomass encountered within a 8km radius to the whale sightings (2007 - 2013).
SD = Standard deviation

whale species	mean daily consumption in tonnes	n of total	prey species	mean biomass (tonnes) ± SD
Fin whale	0.981	53 / 61	Forage fish	6006 ±199
		39 / 61	Herring	103 ±186
		35 / 61	Sprat	6 ±7
		4 / 61	Mackerel	438 ±249
Minke whale	0.165	21 / 30	Forage fish	3577 ±324
		13 / 30	Herring	120 ±226
		12 / 30	Sprat	6 ±4
		3 / 30	Mackerel	647 ±559
Humpback whale	0.621	1 / 2	Forage fish	353
		1 / 2	Herring	2
		0 / 2	Sprat	
		1 / 2	Mackerel	351
Unid. whale (probably Fin whale)	0.981	16 / 20	Forage fish	2476 ±287
		10 / 20	Herring	8 ±10
		7 / 20	Sprat	3 ±2
		6 / 20	Mackerel	394 ±368

Interpretation

- Up to a radius of 10km, the co-occurrence of whale and prey is significant compared to the null-hypothesis.①
- Whales are in close proximity to herring and sprat, while overlap with mackerel appears to be non-targeted.
- The spatial overlap of whales is highest with forage fish compared to single fish species. 85% of all baleen whale sightings were within 8 km of a small pelagic fish species.①②

Conclusion

The CS is a prey hotspot for baleen whales during autumn; whales are dominantly within the radius of forging events to forage fish.①②

Baleen whales target herring and sprat to the same extend, while feeding on mackerel appears to be coincidental.①②

Calculations of foraging thresholds and total biomass consumption underlie high uncertainties.③

Ecosystem modelling and the estimation of herring mortality caused by whale predation for the stock management have to take simultaneous sprat densities and a mixed diet composition of baleen whales into account.

Difficulties

- different methods of biomass estimation over an area complicate the estimation of foraging thresholds
- uncertainties in whale abundance estimation lead to variability in total consumption estimates

lunge feeding Humpback whales © Pádraig Whooley, IWDG

Acknowledgment
All data used in this study belong to the Marine Institute (DA 2011/252, 2013/045, 2014/118, 2014/161) and the Irish Whale and Dolphin Group. We are grateful for funding from the Marine Institute Networking Initiative under the SeaChange strategy and the Johan Hjort Symposium committee. MARES is a joint doctorate programme selected under Erasmus Mundus (FPA 2011-0016).

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