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Exploitation dynamics of the Belgian beam trawl fleet targeting hotspots of flatfish

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Summary

During the last decade, fisheries management increasingly succeeded in rebuilding overfished stocks and preventing overfishing. This is mainly due to the increased availability of data, new scientific insights and better analysis methods that allowed to assess an increasing number of fish stocks. Consequently, fisheries managers could better align the institutional, spatial and temporal scale of fisheries management tools with the biological, socio-economic and political processes that characterize fisheries systems. Nevertheless, fishing systems with greater complexity, such as the mixed-fisheries targeting demersal fish species, have not been associated with similar positive effects. On the contrary, measures such as quota, minimum landing sizes and restrictions on fishing effort (e.g. the number of days the fleet spends at sea) resulted in a number of unintended consequences. For example, the implementation of catch limits through quota often led to higher discards in mixed-fisheries, because fishing activity continued as long as it was profitable to catch fish species for which the quota had not been met.

Europe intends to reduce discarding in mixed-fisheries by installing a landing obligation for a number of commercial fish species. Nevertheless, many fishers fear that such a landing obligation will strongly affect their business. Indeed, depletion of a single quota of a particular species implies an early closure of the fishery in a particular area, and eventually results in a loss of valuable catch opportunities. Besides technical innovations, alternative management systems are considered as an important solution to (partially) circumvent such a scenario. Today, fishing mortality is controlled by regulating the *outputs* of the fishery, being the amount of fish that can be harvested from a specific stock. An alternative system, *effort-based* management, is not based on *output* control but regulates the *inputs* of the fishery, i.e. fishing effort, in order to control fishing mortality.

Although the idea of *effort-based* fisheries management has been circulating for several years, (successful) implementations of such management systems are scarce. This is mainly due to the fact that several questions regarding fleet dynamics, being the response of fishers to such systems, remain unanswered. After all, a prerequisite for *effort-based* management systems is that the link between catch and fishing effort is predictable. Assessing this relationship is not straightforward, because it depends on the spatiotemporal overlap between (i) local abundance of a fish species and (ii) fishing effort, and (iii) the ability of fishers to find and effectively catch the fish.

This PhD thesis provides insights into how fleet dynamics affect the relationship between catch and effort with respect to the three abovementioned factors. Hereto, logbook and location data of commercial Belgian beam trawlers was used to (i) investigate the effect of a change in the temporal distribution of fishing effort on the occurrence of local hotspots of fish, (ii) analyse the tactical decision of fishers regarding the detection of a local hotspot of fish, and (iii) examine the effect of competitive interactions between fishing vessels on the relationship between catch and effort. The obtained insights contribute to (i) a better design of *effort-based* management systems, and (ii) a better understanding and utilization of the available fishery-dependent data sources.

The first aspect of fleet dynamics that was investigated was the relationship between local abundance of fish and the temporal distribution of fishing effort. To do so, we analysed the relationship between a seasonal spawning closure in the Celtic Sea on the daily landing rate of sole (*Solea solea*) of the Belgian beam trawlers. Since 2005, the Trevoise Box, comprising valuable fishing grounds in the Celtic Sea, was closed during February and March. This resulted in a shift of fishing effort from February and March to the first two weeks of April. Analysis of the landing rate of sole demonstrated that this effort reallocation coincided with a twofold increase of the sole landing rate immediately after reopening of the fishery. However, after the fishery reopened, the landing rate of sole immediately declined reaching its reference level after approximately two weeks. This resulted in an annual, short-term race for fish to this area and caused that most of the annual sole quota was depleted during this short period of very intensive fishing. This short-term race for fish was reflected by the spatial distribution of fishing effort. Immediately after the reopening of the fishery, fishing effort was very patchily distributed, but dispersed over the entire area as cumulative fishing effort increased. These observations suggest that sole formed local aggregations during the fishery closure disappearing due to exploitation and/or dispersion as soon as the fishery restarted.

The second aspect that was focused on in this thesis were the tactical decisions of fishers regarding the detection of hotspots of fish. Since no technical equipment exists to detect flatfish species, skippers of beam trawlers need to explore fishing grounds in order to find a good spot to fish. From this perspective, a method was developed to analyse the exploration-exploitation behaviour of Belgian beam trawlers. Data from the satellite-based vessel monitoring system was used to analyse fishing tactics. These tactics were further explored by coupling the landing data as recorded in the electronic logbooks to the different behavioural states. Step lengths and turning angles were calculated from the data and used to model vessel trajectories using Hidden Markov Models, whereupon the identified vessel

activities were linked to the revenue rate and landing rates of sole and plaice (*Pleuronectes platessa*). This method provided a better understanding of the targeting behaviour of the fleet and the spatial distribution of its target species. In this way, the method enabled a better spatial allocation of landing data.

Finally, this thesis investigated how crowding between fishing vessels affected the relationship between catch and effort. Hereto, the effect of increased competition between Belgian and Dutch beam trawlers on the landing rates of the Belgian fleet was analysed. Competition increased due to a reallocation of fishing effort after Dutch beam trawlers switched to pulse trawling. In contrast to Belgian vessels, Dutch vessels did not fish during weekends. This difference in weekly exploitation patterns allowed us to examine the competition through analysis of the catch rates of the target species, being sole and plaice. We found that the sole catch rate of Belgian beam trawlers was remarkably lower during weekdays than during the weekend whereas no such an effect was found in the catch rate of plaice. Because this reversible weekend effect coincided with the introduction of pulse trawling, we suggest the occurrence of interference competition between both fleets. Moreover, the different response observed between the landing rates of sole and plaice suggests that the underlying mechanism of competition is caused by a different anti-predatory behaviour of both species towards fishing gear, and indicates the occurrence of prey-depression.

The insights of this thesis are particularly relevant regarding the design of *effort-based* management systems since these systems are likely to alter the spatiotemporal dynamics of fishing fleets. As demonstrated by this research, this may in turn affect the crucial relationship between catch and effort through feedback loops, interfering with the tactical decisions of fishers and/or direct spatial interactions between fishing vessels. Since most of these processes emerge from the behaviour of fishers, fish, and benthic communities and their interactions, mechanistic understanding of these processes remains limited. Nevertheless, the increased availability of data from commercial fishing vessels at high spatiotemporal resolution and new modelling techniques offer opportunities for observational analyses of fleet dynamics as shown in this research. Although such analyses do not provide direct insights into the mechanisms underlying these processes, they allow to formulate and refine hypotheses that may improve the design of fisheries management systems.

Samenvatting

Gedurende de laatste decennia werd een grote vooruitgang gemaakt in het beheer van visserijsystemen. De toegenomen beschikbaarheid van data, en nieuwe wetenschappelijke inzichten en analyse methodes lieten toe om de institutionele, ruimte- en tijdsschaal van visserijbeheersystemen te verfijnen. Op die manier kon beter ingespeeld worden op de variabiliteit en complexiteit van een aantal biologische, socio-economische en politieke processen wat resulteerde in het herstel van een aantal visbestanden. Echter, dit leidde niet tot de gewenste verbeteringen in visserijsystemen met een grotere complexiteit, zoals de gemene visserij gericht op demersale vissoorten. Integendeel, maatregelen zoals quota, minimum aanlandingsmaten voor bepaalde vissoorten en beperkingen op de visserij-inspanning (bv. het aantal dagen dat de vloot op zee spendeert) hebben in dergelijke visserijen vaak tot een aantal ongewenste neveneffecten geleid. Zo zorgen quota vaak tot teruggooi van vis omdat de visserij doorgaat zolang het rendabel is om vis aan te landen van soorten waarvoor nog quota beschikbaar zijn. Soorten waarvan de quota eerder zijn uitgeput, worden dan teruggeworpen.

Met de gefaseerde invoer van een aanlandplicht voor een aantal commerciële vissoorten, hoopt Europa de teruggooiproblematiek te reduceren. Echter, heel wat studies tonen aan dat een aanlandplicht negatieve socio-economische gevolgen zal hebben voor heel wat visserijsectoren. Immers, wanneer het eerste quotum van een bepaalde soort in een gebied uitgeput is, impliceert dit een vroegtijdige sluiting van de visserij in dat gebied en een reductie van de vangstopportunities. Een aanpassing van het huidige beheersysteem biedt een mogelijkheid om dergelijk scenario (deels) te vermijden. Vandaag worden de meeste visserijen nog steeds beheerd door het controleren van de *outputs*. Dit houdt in dat er een plafond is op de hoeveelheid vis van een specifieke soort en bestand die mag aangeland worden. Een alternatief systeem, *effort-based management*, zou hier van afstappen en de *inputs* in de visserij, zijnde de visserij-inspanning, beheren om op die manier de vissterfte ten gevolge van de visserij te controleren.

Hoewel het idee van deze *effort-based* visserijbeheersystemen reeds een aantal jaar op tafel ligt, zijn er vandaag bijna geen implementaties van dergelijke beheersystemen. Een belangrijke reden hiervoor is dat er nog een aantal vragen onbeantwoord zijn betreffende vlootdynamica, zijnde de respons van vissers ten opzichte van een dergelijk systeem. Een vereiste voor een *effort-based management* systeem is dat de link tussen de vangst van een soort en de visserij-inspanning gekend is. Deze link wordt uitgedrukt door de vangbaarheid (*catchability*) en wordt bepaald door (i) de ruimtelijke en temporele overlap tussen de lokale abundantie van een vissoort en de visserij-inspanning, en (ii) het vermogen

van de visser om de vis te vinden en effectief te vangen. Dus, de betrouwbaarheid waarmee de vangbaarheid wordt ingeschat hangt af van de accuraatheid en precisie waarmee (i) de abundantie van vis, (ii) de visserij-inspanning, en (iii) het vermogen van de visser om de vis te vinden en vangen wordt voorspeld in de ruimte en tijd.

Dit doctoraat analyseert de relatie tussen vloot dynamische mechanismes en de drie bovengenoemde aspecten die de vangbaarheid van een vissoort bepalen. Logboekdata en locatiegegevens van de commerciële Belgische boomkorvloot werden gebruikt om (i) het effect van de temporele distributie van visserij-inspanning en het voorkomen van lokale hotspots van vis te onderzoeken, (ii) een methode te ontwikkelen om de tactiek te analyseren die vissers aanwenden om een lokale hotspot van vis te zoeken, en (iii) de invloed van densiteitseffecten tussen vaartuigen op het lineaire verband tussen visserij-inspanning en vangbaarheid te belichten. De bekomen inzichten dragen bij tot (i) een beter design van deze *effort-based* beheersystemen, en (ii) een betere benutting van de beschikbare data van commerciële vaartuigen met betrekking tot de toepassing van deze beheersystemen.

De link tussen het voorkomen van lokale hotspots van vis en visserij-inspanning was het eerste aspect van vlootdynamica dat onderzocht werd. Immers, bij de boomkorvisserij wordt het vistuig over de zeebodem gesleept, wat het bentische ecosysteem en dus ook de habitat van de belangrijkste doelsoorten van de visserij beïnvloedt. Om de link tussen de ruimtelijke en temporele distributie van de visserij-inspanning en het voorkomen van een lokale aggregatie van vis te onderzoeken werd het effect van een seizoenale sluiting in de Keltische Zee op de vangst van tong geanalyseerd. Sedert 2005 zijn de belangrijkste visgronden in de Keltisch Zee gesloten tijdens de maanden februari en maart waardoor de visserij-inspanning verschoof van deze periode naar de eerste twee weken van april. Ons onderzoek toonde aan dat deze verschuiving verklaard kon worden door de vangst van de doelsoort tong die 1,5 tot 2 keer zo hoog was vlak na de heropening van de visserij. Dit zorgde voor een jaarlijkse wedloop naar dit gebied, met als gevolg dat het grootste deel van het jaarlijkse tongquotum opgevist werd tijdens de eerste twee weken van april. Tijdens deze periode van intensieve visserij zakte de vangst van tong steeds terug naar een normaal niveau. Dit patroon kon gelinkt worden aan de ruimtelijk spreiding van de visserij-inspanning die onmiddellijk na de heropening van de visserij een geaggregeerd patroon vertoonde dat snel weer uitspreidde naarmate de cumulatieve visserij-inspanning toenam. Dit gaf aan dat er vlak na de heropening van het gebied een lokale hotspot van tong is die snel verdween door exploitatie en/of verspreiding eens de visserij terug aanving.

Het tweede aspect van vlootdynamica dat belicht werd met betrekking tot *effort-based* visserijbeheersystemen zijn de tactische beslissingen van vissers tijdens een trip om

visgronden te lokaliseren en exploiteren. Omdat geen technische hulpmiddelen bestaan om platvis, de doelsoort van de boomkorvisserij, te detecteren, moeten vissers voortgaan op hun kennis van visgronden, en deze visgronden verkennen zodoende een lokale hotspot van een doelsoort te detecteren. Vanuit deze vaststelling werd een methode ontwikkeld om dit exploratie-exploitatie gedrag van een visser tijdens een trip te analyseren en te linken aan aanlandingsgegevens op basis van data van commerciële vaartuigen. De locatiegegevens van vaartuigen werden gebruikt om een Hidden Markov Model te fitten waarna de geïdentificeerde vaartuigactiviteiten werden gekoppeld aan de aanlandingsgegevens uit het elektronisch logboek. Deze methode liet toe een beter inzicht te verwerven in (i) de doelsoorten en bijvangsten van de visserij, en (ii) de spatiale en temporele correlaties tussen de vangsten van verschillende vissoorten. Bovendien kon het tactisch gedrag van een visser gebruikt worden om de vangsten uit het elektronisch logboek nauwkeuriger te verdelen over de locatiegegevens van vaartuigen.

Finaal werd onderzocht hoe vlootdynamica de relatie tussen de vangst en de visserij-inspanning beïnvloedt. Vaak wordt verondersteld dat deze relatie lineair is, maar een aantal mechanismes kunnen ervoor zorgen dat de vangst langzamer of sneller afnemen dan de abundantie. In de Belgische visserij gebeurde dit nadat de Nederlandse boomkorvloot omschakelde naar de pulsvisserij in 2012, en hierdoor visgronden exploiteerde die voorheen enkel door Belgische vissers bevestigd werden. Omdat deze Nederlandse vaartuigen, in tegenstelling tot de Belgische, niet tijdens het weekend visten, kon het effect van mogelijke interferentie competitie tijdens wekdagen op de vangsten van de doelsoorten tong en schol onderzocht worden. Hiervoor werden gegevens uit het elektronisch logboek geanalyseerd rekening houdend met de verschillende wekelijkse exploitatiepatronen van de Belgische en Nederlandse vloot. De onderzoeksresultaten toonden aan dat de gestandaardiseerde vangsten van tong opmerkelijk lager waren tijdens wekdagen dan tijdens het weekend nadat de Nederlandse vloot was omgeschakeld op de pulsvisserij. Geen effect werd gevonden op de vangsten van schol. Dit verschil tussen tong en schol kan erop wijzen dat beide soorten een verschillende respons vertonen ten aanzien van de visserij.

De inzichten van dit doctoraat zijn relevant voor het ontwerp van *effort-based* visserijbeheersystemen. Dergelijke beheersystemen beogen een betere, en vaak andere verdeling van de visserij-inspanning in de ruimte en tijd. Echter, dit onderzoek toonde aan dat dergelijke verschuiving van de visserij-inspanning de relatie tussen de visserij-inspanning en vangst kan wijzigen d.m.v. feedback loops, veranderingen in het tactische gedrag van vissers en / of directe ruimtelijke interacties tussen vissersvaartuigen. Omdat de meeste van deze processen afhankelijk zijn van het gedrag van vissers, vissen en het

benthische ecosysteem en de hieruit volgende interacties, blijft de kennis van de onderliggende mechanismes beperkt. Desalniettemin bieden de toegenomen beschikbaarheid van gegevens van commerciële vissersvaartuigen op een hoge spatiele en temporele resolutie en nieuwe modelleringstechnieken nieuwe mogelijkheden om vloot dynamica te onderzoeken a.h.v observationele studies zoals aangetoond in dit onderzoek. Hoewel dergelijke analyses geen direct inzicht verschaffen in de onderliggende mechanismen van deze processen, kan het hypotheses verder verfijnen zodoende het ontwerp van visserijbeheersystemen te verbeteren.

List of abbreviations

ABM	agent-based modelling
AIC	Akaike Information Criterion
AIS	Automatic Identification System
B	stock abundance or standing biomass
C	catch
CFP	Common Fisheries Policy
cpue	catch per unit effort
E	fishing effort
EU	European Union
F	fishing mortality
GAMM	Generalized Additive Mixed Model
GLM	Generalized Linear Model
HMM	Hidden Markov Model
IBM	individual-based modelling
ICES	International Council for the Exploration of the Sea
lpue	landings per unit effort
M	natural mortality
MEY	maximum economic yield
MLS	minimum landing size
MPA	marine protected area
MSE	Management Strategy Evaluation
MSY	maximum sustainable yield
q	catchability
RTC	real-time closures
RTI	real-time incentives
rpue	revenue per unit effort
VMS	vessel monitoring system

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CHAPTER 1

Introduction

Why do fishers fish where they fish? During the last decades, this question has drawn the attention of many fisheries scientists who want to provide scientific advice for fisheries management. It is also the focus of this thesis. This introduction frames the question in the perspective of fisheries management, its theoretical fundamentals and the outline of this thesis. There to, the first section provides a brief overview of the developments in fisheries management to illustrate why this question became so important for the sustainable exploitation of marine resources, and is still relevant in the perspective of today's developments in fisheries management. In the second part of this introduction, I consider the importance of this question from a theoretical perspective and highlight emerging challenges in fisheries science with respect to the current developments in fisheries management. The final part of this introduction provides an outline of this thesis in regard to the research challenges and objectives, and provides the reader the necessary background information regarding the characteristics of the case study used throughout this thesis, the Belgian beam trawl fishery.

1.1. Evolutions in fisheries policies and management

1.1.1 Fish stocks as a common-pool resource

“*On the Dynamics of Exploited Fish Populations*” of Beverton and Holt (1957) is considered the first attempt to propose specific recommendations concerning the exploitation of fish stocks. In this book, recommendations were made to manage the North Sea trawl fisheries targeting plaice (*Pleuronectes platessa*). The authors stressed the need to impose specific management objectives, and were the first to acknowledge the complexity that comes along with such a decision making process by emphasizing the importance of economic and social factors in addition to the obvious biological ones.

Their ideas originated from the population dynamics of the North Sea fish stocks after World War II (WWII). After the outbreak of the war in 1939, commercial fishing activity in the North Sea dropped almost entirely until 1945 as vessel movements were restricted due to the hazard of mines and naval activity, and the most modern fishing vessels were recruited for war services. To date, this was the largest (yet unintended) Marine Protected Area (MPA), because it allowed fish stocks to recover (Beare *et al.*, 2010). Beverton and Holt were triggered to examine the underlying mechanisms which finally resulted in the development of the Beverton-Holt yield-per-recruit model. This model provided a basis for predicting future yields and biomass levels at various levels of fishing mortality. Consequently, it could also be used to calculate the optimal level of fishing effort that maximizes the long term yield, in terms of catches or economic return of a fishery, known as Maximum Sustainable Yield¹ (MSY) and Maximum Economic Yield² (MEY), respectively.

Although many scientists consider the end of WWII as the starting point of the development of modern fisheries management, it is also the point in history where the decline of (most) fish stocks began and resulted in today’s poor state of affairs of most global fish stocks³. Larger vessels with more storage capacity and diesel engines were built that allowed fishers to exploit fishing grounds that were previously either too remote or too deep to be fished. This technological revolution resulted in new fishing gear such as the beam trawl – that had also been introduced in the Belgian fishery around 1960 – which increased the catchability of certain fish species (Rijnsdorp *et al.*, 2008). Finally, the improved transportation network

¹ MSY is defined as the harvest rate that maximizes the long-term yield from a fish stock. Hence, it coincides with the population size at the point of maximum growth rate.

² MEY is the value of the largest positive difference between total revenues and total costs of fishing in the long-term. MEY is typically achieved at a harvest rate that is 10-20% smaller than MSY.

³ According to FAO, 70% of global fish stocks are either fully exploited or overexploited (FAO, 2016)

not only facilitated trade, but also extended the demand for fish because the fish supply could reach inland regions.

Until the early 1960s, fish stocks were common-pool resources to which fishers had unlimited access. The lack of clear boundaries made it impossible for one group to claim the right to manage it. Hence, regulations hardly existed and allowed the Tragedy of the Commons to occur (Hardin, 1968). The revenues from landings were high while operational fishing costs were low. This turned fishing into an attractive business that generated capital and resulted in an instream of more and larger vessels. Consequently, the total number of vessels steeply increased and caused the total annual landings of many fish species to raise to fishing pressure levels far above the level that stocks can sustain.

1.1.2 The establishment of single-species fisheries management

This unsustainable state of affairs in fisheries was soon acknowledged. After president Harry S. Truman extended the rights of the United States to control all the natural resources on its continental shelf in 1945, other nations quickly followed, thereby shaping an institutional framework for fisheries management. In Europe, such a legal framework for fisheries management was created in 1957 through the Treaty of Rome which stated that a Common Fisheries Policy (CFP) should be adopted to regulate fisheries in the Member States. In spite of this, it took 26 years for the first CFP (Regulation (EEC) No 170/83) to come into effect (1983). This was due to the cumbersome process of claiming territorial waters and Exclusive Economic Zones (EEZ) which was marked by two 'Icelandic Cod Wars'⁴, and the instability caused by Regulation (EEC) No 2141/70 that gave all Member States equal access to all fishing waters. The latter happened when last minute changes were made on the morning of 30 June 1970, just before Britain, Ireland, Denmark (including Greenland), and Norway (the countries that control the richest fishing grounds in the world) applied to join the Common Market. This first CFP imposed an increased number of management regulations to the EU fisheries (Daan, 1996). These were based on a single-species approach that aims to maximize the yield of a single fish stock thereby ignoring eventual interactions with other fish stocks or ecosystem components. These included

⁴ The Icelandic Cod Wars (1958 – 1961 and 1972 – 1973) started after Iceland extended its fishery zone (to 12 and 50 nautical miles, respectively), excluding most foreign fishing activities. This led to a (political) dispute between Iceland and the United Kingdom.

output control⁵ management through total allowable catches (TACs), and technical measures such as effort regulations and Minimum Landing Sizes⁶ (MLS).

In many countries, the added regulations did not improve the status of (most) fish stocks and marine resources as expected. For example, when restrictions were set to the total number of fishing licenses, vessel owners simply increased their vessels' engine power (Rijnsdorp *et al.*, 2008). When quota restrictions and MLS were imposed to the fishery, high-grading⁷ of fish occurred (Gillis *et al.*, 1995). In mixed-fisheries⁸, such as the North Sea flatfish fishery, problems were even worse since fishing activity is likely to continue as long as it is profitable to catch up species of non-depleted quota while discarding species of which the quota has been depleted (Daan, 1996; Poos *et al.*, 2010a).

The limitations of designing fisheries management tools that account exclusively for biological component of the system, the fish, were revealed by the pioneering work of Larkin (1978) and Hilborn (1985), among others. They stated that the scope of fisheries management had been defined too narrowly, and as a result, was ineffective at coping with the economic and social aspects of fisheries. Or as Hilborn and Walters (1992) noted, "*it is foolish to study only the prey in the predator-prey system ... it is equally important to monitor and understand basic processes that determine the dynamics of the predator – the fishermen*".

1.1.3 Integrating nominal fishing effort into fisheries management

This new understanding of fisheries systems' altered the course of fisheries management towards input control management tools. These tools control and/or limit the amount of fishing effort that fishers put in their fishing activities thereby indirectly controlling the amount of fish caught. In the European Union, this was done through the implementation of the second CFP (Regulation (EEC) No 3760/92) and the Habitats Directive (Council Directive 92/43/EEC) in 1992. The main objective of this new CFP was to restore the imbalance between the fleet capacity and the catch potential, thereby introducing the concept of fishing effort, while the Habitat Directive imposed the Natura2000 ecological network across land

⁵ Output control rules directly limit the amount of fish that can be harvested from a fish stock.

⁶ The Minimum Landing Size (MLS), now called as Minimum Conservation Reference Size (MCRS), is the minimum length at which fish can be sold for direct human consumption. The MLS is defined as the length at which a specific percentage of a fish stock reaches the maturity stage.

⁷ High-grading is the decision by fishers to discard fish of low value that allows them to land more valuable fish (Batsleer *et al.*, 2015).

⁸ Mixed-fisheries are fisheries where multiple species are caught at the same time during a haul, and/or multiple fleets or métiers catch the same species.

and sea in order to conserve biodiversity in Europe. In this perspective, the capacity of the European fleet was gradually decreased through decommissioning schemes, and an increasing number of Marine Protected Areas (MPAs) with different objectives (e.g. protection of sensitive habitats, spawning areas) were imposed in the early 1990s (Wood *et al.*, 2007).

Although many of these MPAs succeeded in rebuilding fisheries, soon it was clear that MPAs were not a panacea for fisheries management problems, and should rather be considered as a part of the solution than the solution itself (Hilborn *et al.*, 2004; Kaiser, 2005; Halpern *et al.*, 2010). This is particularly the case for complex fisheries systems in which multiple interactions between species and/or fleets might result in feedback loops after an MPA has been introduced. This happened for instance after the “plaice box”⁹ was established in the North Sea in 1989 to reduce discarding of undersized plaice (Pastoors *et al.*, 2000; Beare *et al.*, 2013). In contrast to the expectations, both yield and spawning stock biomass decreased substantially because discards remained high due to the interaction between reallocation of beam trawl effort, food availability and spatial distribution of plaice. Fishing effort dropped in the closed area but increased at its borders. These altered trawling patterns changed the food availability for plaice which subsequently attracted juvenile plaice to this intensively exploited borders of the “plaice box” and resulted in higher discard ratios of undersized plaice than before.

The integration of fishing effort into fisheries management paid off and improved the *environmental status* of an increasing number of fish stocks for which management had put in place (Figure 1.1). In the North Sea for instance, the level of fishing mortality of sole (*Solea solea*) is at a sustainable level since 1997 which resulted in a gradual recovery of the North Sea sole stock (ICES, 2017). Meanwhile, and as illustrated by the abovementioned example, the limitations of the single-species approach underlying the design of management tools were revealed. By the end of the 90s, the need for a more holistic management approach, that does not only protect target species, but also the ecosystems that sustain them, was stressed (Botsford *et al.*, 1997). This resulted in the development of so called ecosystem-based fisheries management (EBFM), or alternatively the ecosystem approach to fisheries (EAF) that aims to avoid the degradation of ecosystems, minimize the risk of irreversible changes, obtain long-term socio-economic

⁹ The Plaice Box is a partially closed area off the Dutch and German coast in the North Sea for beam trawlers (engines > 221 kW). It was established in 1989, aimed to reduce discarding of undersized plaice in the main nursery areas, and consequently, strengthen the recruitment of to the fishery, and enhance the recovery of the plaice stock.

benefits from fishing, and adopt a precautionary approach to uncertainty (Garcia *et al.*, 2003; Pikitch *et al.*, 2004).

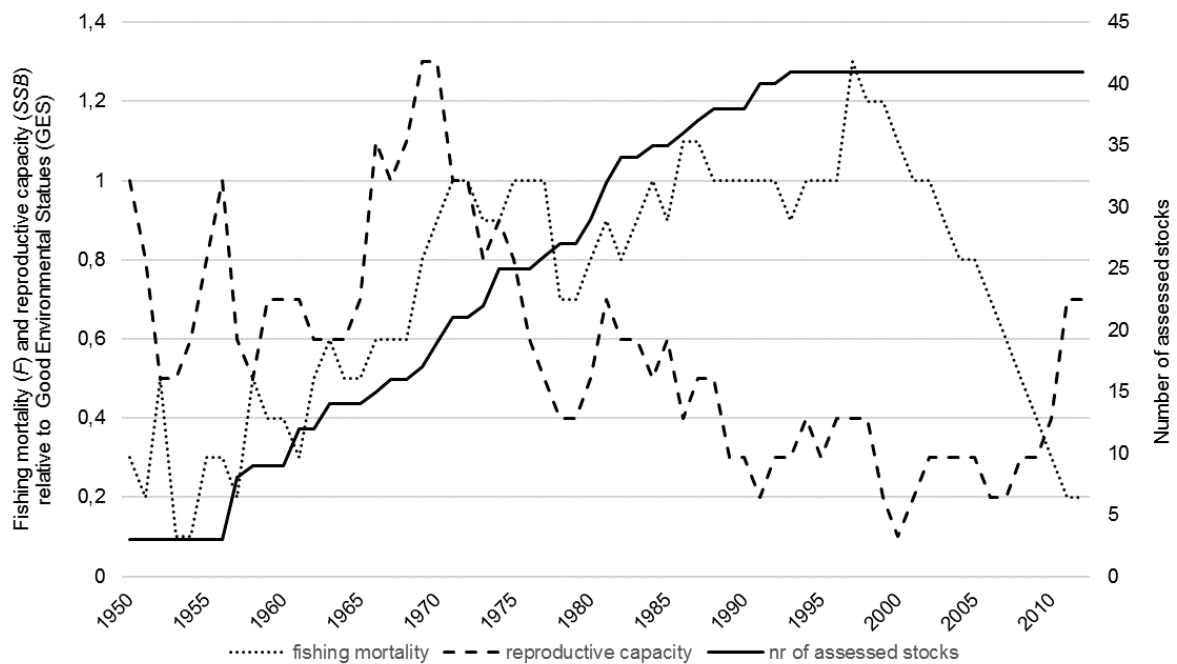


Figure 1.1 Trends in the status of assessed fish stocks in the North-East Atlantic and Baltic Sea with respect to Good Environmental status (GES), being fishing mortality at MSY level (F_{MSY}) and reproductive capacity at MSY level ($MSY B_{trigger}$). For both fishing mortality and reproductive capacity, 0 is the target. Fishing mortality > 0 imply unsustainable harvesting level while $SSB < 0$ indicate that the reproductive capacity is below the precautionary limit and imply that there is a high risk that the reproductive is impaired. (source: ICES and European Environmental Agency)

1.1.4 A quest for new fisheries management tools

The EAF concept resulted in an increased concern regarding the ecosystem effects of fishing such as discarding or the impact on the seabed in trawl fisheries. In the North Sea beam trawl fishery targeting flatfish for example, the estimated discard rate is 71 to 95% (Lindeboom and de Groot, 1998). Besides the economic losses for the trawl fisheries (Cappell, 2001), discards in the North Sea substantially contribute to the overall fishing mortality and are (in)directly related to (i) the loss of biodiversity, (ii) changes in predator-prey interactions and (iii) relative abundance, (iv) serve as prey for several benthic and demersal species, and the growth of seabird populations (Catchpole *et al.*, 2005). In addition, the limited availability of data concerning discard practices increases the uncertainty of fisheries management.

Currently, fisheries policies are slowly adopting the EAF in order to maximize the economic efficiency and limit the ecosystem effects of fishing. In the European Union for example, a new CFP was enrolled in 2014 EAF that explicitly defined EAF as an objective and included the management of discards through the gradual implementation of the landing obligation (Regulation (EEC) No 1380/2013). This ban on discarding obliges fishers to land all

catches, including fish below Minimum Landing Size (MLS), of fish species that are managed through a TAC. For a mixed-fishery, this could result in an early closure of the fishery if the Total Allowable Landings (TALs) for a species are depleted with harmful socio-economic consequences if valuable catch opportunities are underexploited. The fishery would then be *choked* while the species causing the early closure is called the *choke* species. This is likely to endanger the viability of some fisheries such as the Dutch beam trawl fleet (engines > 221kW) targeting flatfish in the North Sea. With respect to this fleet, Batsleer *et al.* (2016) estimate that a discard ban on plaice will result in a reduction of the net-revenue per vessel of 50 to 80% depending on the constraining effect of the annual plaice quota due to strong reductions of fishing opportunities. Moreover, Baarsen *et al.* (2015) estimated that the net-revenue will be further reduced through extra labour costs required to process the discards.

This challenge forces fisheries managers to seek for alternative management tools resulting an increased interest in effort-based management through e.g. Individual Effort Quota (IEQ) (Rijnsdorp *et al.*, 2007). These management tools abandon output controls and rely entirely on controlling the inputs in the fishery, being fishing effort. Compared to fisheries management through TACs, these tools have two major advantages. First, they should increase the ability of managers to deal with the complexity of a fishery as they allow to include the trade-offs between various socio-economic and ecological goals directly into one single effort quota (Rijnsdorp *et al.*, 2007). In the context of the flatfish fishery in the North Sea for instance, managers would be able to set effort quota based on the expected catches of plaice and sole thereby simultaneously optimizing the catch opportunities of both species with respect to the biological safe limits (Rijnsdorp *et al.*, 2007). Second, control and enforcement of effort based management tools would be facilitated since fishing effort can be measured directly in most fisheries through mandatory tracking such as satellite-based vessel monitoring system (VMS).

A key for successful effort-based fisheries management is the accuracy by which the impact of the fishery is converted into effort quota with respect to the spatiotemporal dynamics of the ecosystem (Rijnsdorp *et al.*, 2007). Due to the spatial heterogeneity of many ecosystems, this requires a detailed level of spatial analysis which has been made possible by the advent of VMS and eLogbook data and fully documented fishing (Kindt-Larsen *et al.*, 2011) and resulted in the development of management tools such as real-time closures (RTCs) (Bailey *et al.*, 2010) and real-time incentives (RTIs) (Kraak *et al.*, 2012, 2014, 2015). These rely on the concept of dynamic management or real-time management of marine resources. According to Maxwell *et al.* (2015), this concept is defined as “management that changes rapidly in space and time in response to the shifting nature of the ocean and its

users based on the integration of new biological, oceanographic, social and/or economic data". The idea of such a tool is that management can be adapted by using the latest available data, as such reducing the uncertainty caused by fishery/ecosystem dynamics at high spatiotemporal resolution. One specific proposal is the RTI approach of Kraak et al. (2012) which is based on a nearly real-time transfer of fisheries data (catch and effort data) to a central data platform. This would enable to update tariff maps according to the management objectives, which are subsequently returned to the fishers. This information incentivises and encourages fishers to e.g. leave areas of high catches of a choke species (Little *et al.*, 2015). Although different studies evaluated and demonstrated the potential of real-time fisheries management to deal with e.g. the mixed-fisheries problem, currently few fisheries are managed through such tools. A major reason for this is that a thorough evaluation of the response of the fishery regarding these management systems is needed. This is currently not possible due to the lack of knowledge regarding the various processes that characterize fisheries systems with respect to the spatial and temporal scales of these tools.

To enhance the implementation of effort-based fisheries management tools, this thesis analyses fisheries with respect to the spatiotemporal scales of these tools. After all, this brief historical overview showed that much of the progress made in fisheries management stems from our improved understanding of fisheries systems, in particular fisher behaviour, which allowed to refine, and align, the institutional, spatial and temporal scales of fisheries management with the relevant processes that characterize fisheries

1.2. Fleet dynamics in the context of fisheries management

1.2.1 Integrating fleet dynamics in fisheries management

A prerequisite for a successful implementation of any fisheries management tool is to evaluate how the system will evolve with respect to the predetermined socioeconomic and ecological objectives. Obviously, in the context of fisheries it is not feasible to do this in an empirical way. Fisheries scientists have therefore relied strongly on, where possible, quantitative modelling techniques underpinned by different theoretical concepts to give advice.

Currently, the Management Strategy Evaluation (MSE; Smith, 1993) is considered to be the best framework at hand to provide quantitative, scientific-based advice to fisheries managers (Dankel and Edwards, 2016). MSE integrates various fisheries models into a simulation based framework. As such, it enables to compare alternative fisheries management strategies against a set of performance statistics that are selected with respect to the management objectives. The main advantage of this simulation approach is its ability to deal with the various sources of uncertainty underlying the data and models used in the MSE.

A Management Strategy Evaluation framework consist of two modules representing a *management procedure* and the dynamics of the real world, respectively (Figure 1.2). The management procedure is a feedback-control mechanism in which the state of the resource is perceived and subsequently translated into management measures. During a single loop through the MSE, data of the real world, generated by the *operating model*, is collected and used in a *management procedure* to assess the state of the resource (e.g. by fitting a stock assessment model to the data). The perceived state of the system is then used to formulate a management action. This is mostly done by a decision rule that is typically a simple algorithm known as a *harvest control rule*. Finally, the management action is implemented and new data about the real world is generated through the *operating model*. This can range from a single species population model, to very complex ecosystem

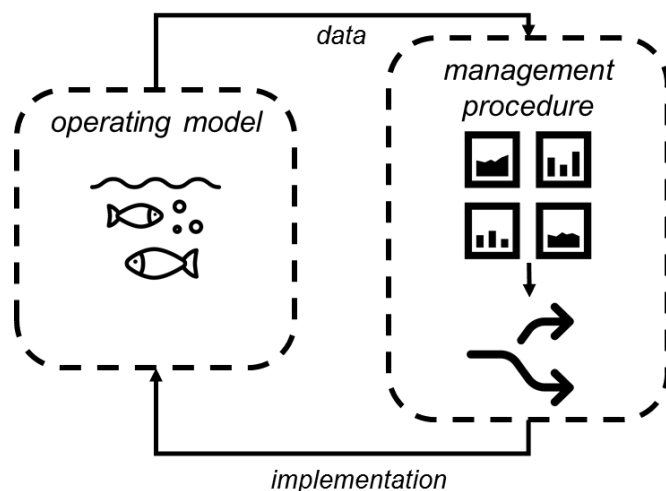


Figure 1.2 Illustration of a single loop through the Management Strategy Evaluation framework.

models at high spatiotemporal resolution, and may include the dynamics of the fishery as well.

Although the importance of fleet dynamics is well recognized since Hilborn's seminal paper in 1985, yet the long and short-term dynamics of a fishery are hardly included in MSEs and thus fisheries management that relies upon this approach (Hamon and Poos, 2016). Fleet dynamics are either the short or long-term developments of a fishery (Hilborn, 1985). The short-term dynamics of the fishery relate to the decisions that fishers make about when and where to fish, what gear to use and whether to discard or not, while the long-term dynamics of fisheries cope with the long-term choices of entrepreneurs such as capital investments and exit-entry decisions in the fishery.

1.2.2 Fundamental concepts of fisheries

Changes in the dynamics of fishing fleets are likely to alter the amount of fishing effort (f) into the fishery and consequently affect fishing mortality (F), being the fraction of the average population taken by fishing. Given that the total catch (C) equals $q \times f \times B$, in which q and B are the catchability coefficient the stock abundance (B) of a species, respectively; fishing mortality (F) and the catch-per-unit-effort ($cpue$) can be deduced and expressed as, $F = C / B = q \times f$ and $cpue = C / f = q \times B$, respectively (Beverton and Holt, 1957). The catchability (q) coefficient of a fish species is a constant that relates the local biomass to fishing mortality and emerges from (i) the spatiotemporal overlap between the distribution of the fish population and fishing effort (Swain and Sinclair, 1994), (ii) and the ability of fishers to find fish and actually catch them (Marchal *et al.*, 2002).

Two of the major hurdles regarding the application of the previous formulas with respect to the design of fisheries management tools are (i) the variability in abundance arising from the mobility of (most) fish species, and (ii) the variation regarding the ability of fishers to actually capture fish resulting from e.g. technological progress (sometimes referred to as technological creep). As a result, the catchability coefficient of fish species, and necessarily fishing effort, are variable in space and time. This implies that the success of effort-based management tools is likely to depend on the capacity to control the overlap between local abundance of fish species and fishing effort with respect to the ability of fishers to find and actually capture the fish.

Nevertheless, for most fish species, such as flatfish, local abundance varies at very fine spatiotemporal scales (100m – 10 km; 1 day – 1 week) due to the interaction between physical processes (e.g. tidal currents and turbulence) and behavioural mechanisms of fish species (e.g. feeding, or bottom fidelity) (Gibson, 1997). Because these mechanisms are often unpredictable, they are a major source of uncertainty regarding the outcomes of

fisheries management (Fulton *et al.*, 2011). Through adjusting the tariffs or impact quota to the local abundance by the use of real-time information of fishers, real-time fisheries management tools aim to neutralize part of this uncertainty arising from such processes acting at high spatiotemporal resolutions.

Although real-time fisheries management tools enable to remove most of the variability caused by some of these practically unpredictable processes, there is still no guarantee that the index of abundance (cpue data), derived from the catch and effort data, used to set the tariffs or impact quota is linearly proportional (*proportionality*) to abundance as is often assumed in the analysis of catch data. The possibility of a nonlinear relationship between cpue and abundance remains (Hilborn and Walters, 1992; Harley *et al.*, 2001). Figure 1.3 illustrates a simplistic form of such a nonlinear relationship ($cpue = qxB^\beta$) in which *hyperstability* ($\beta < 1$) and *hyperdepletion* ($\beta > 1$) imply that the catch-per-unit-effort declines more slowly or steeper than abundance, respectively. Hilborn and Walters (1992) related the occurrence of hyperstability and hyperdepletion, amongst others, to the operational of the fleet and distributional characteristics of the fishery, respectively, and thus fleet dynamics. Nevertheless, evidence that relates fleet dynamics to these phenomena remains weak and is mostly based on simulation experiments. For instance, *hyperstability* may occur through information sharing between fishers as such increasing their ability to find local hotspots of fish as Gaertner and Dreyfus-Leon (2004) demonstrated in a simulation experiment of a tuna (*Thunnus spp.*) purse seine fishery. *Hyperdepletion* occurs less frequently and may arise through localized depletion of fine-scale spatial aggregations (Prince and Hilborn, 1998). Apparent *hyperdepletion* has also been related to interference competition between fishing vessels that exploit a local fishing ground by different authors (Gillis and Peterman, 2008; Walters, 2003; Swain and Wade, 2003) (see Box1 for a more detailed description of interference competition).

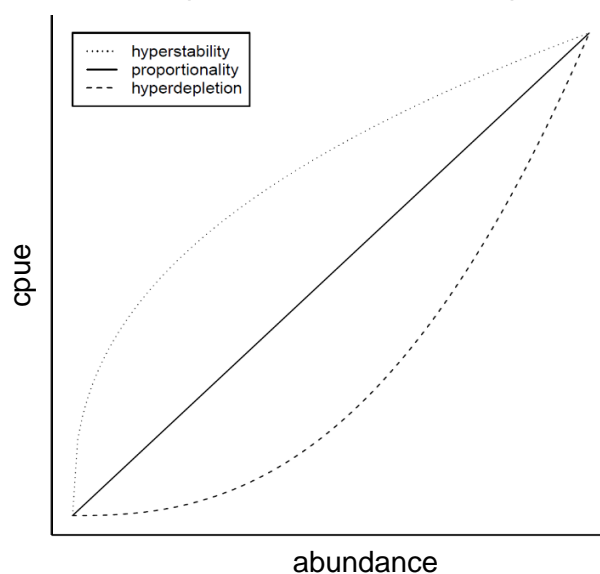


Figure 1.3 Visualisation of the of proportionality, hyperstability and hyperdepletion concepts with respect to the relationship between abundance (B) and catch-per-unit-effort ($cpue$) expressed as: $cpue = qxB^\beta$ (adapted from Hilborn and Walters, 1992).

Box 1: Interference competition

Interference competition, the short-term, reversible decline in intake rate due to the presence of conspecifics in a foragers' proximity (Goss-Custard, 1980; Sutherland, 1983), is supposed to be an important mechanisms underlying the spatial distribution of foraging animals (e.g. Sutherland, 1983; Sutherland and Parker, 1985; Moody and Houston, 1995). As a consequence, the mechanism of interference has also drawn the attention of fisheries scientists to explain the spatial distribution of fishing vessels (e.g. Gillis *et al.*, 1993; Rijnsdorp *et al.*, 2000a; Swain and Wade, 2003; Poos *et al.*, 2010b).

Interference may be caused through mutual interactions between foragers as a consequence of e.g. *kleptoparasitism*. A behavioural mechanism in which foragers steal food items from each other in turn causing an increase of a foragers' average time spend to search food items. In fisheries, stealing of catch has been reported in lobster fisheries where divers or other fishers steal lobsters caught by traps or pots from other fishers (Daw, 2008). Apparent kleptoparasitic behaviour may as well occur through stealing of information between fishers e.g. when a fishing vessel starts to fish in front of another vessel that was already exploiting a fishing ground as has been observed in the beam trawl fishery in the North Sea (personal communication). Other direct interaction mechanisms, such as the time cost of avoidance, between foragers that affect either the searching time for, or handling time of, prey may also cause interference competition. In a fishery, the latter may occur if a vessel has to diverge from the optimal fishing track to avoid collisions with other vessels. Obviously, such a deviations are likely to have a negative effect on the catch rate and occur more frequently at higher vessel densities. The intensity of interference competition through direct interactions between foragers is not only related to the number of competitors, but may also depend on the density of prey items (Dolman, 1995; Cresswell, 1998; Triplet *et al.*, 1999). In most cases, the effect of interference competition tends to increase at low prey-densities as the encounter rate between foragers increases at low densities of prey although the opposite may occur as well (Ruxton and Moody, 1997). In contrast, at high prey-densities, the effect of interference competition is often negligible because both the encounter rate between foragers and the additional time to search a prey item becomes very small.

Another circumstance under which average intake rates decline is if prey items become temporarily less susceptible for foragers, an indirect interaction mechanism between foragers known as *prey-depression* (Selman and Goss-Custard, 1988; Ruxton, 1995; Stillman *et al.*, 2000). This mechanism is induced by a prey-specific response (e.g. increasing state of alertness, retreating down a burrow) whereupon prey become in a less

vulnerable state. Nevertheless, this state is temporary since it comes at a cost for prey, otherwise prey would adopt the less vulnerable state for their entire lives. Since interference through *prey-depression* emerges from behavioural mechanisms of both foragers and prey, it is more complicated to study. As a consequence, the calculation of a foragers' functional response is not straightforward and can take many forms depending on the assumptions underlying the behaviour of foragers and prey (Beddington, 1975; Ruxton, 1995; Stillman *et al.*, 2000).

Even if the index of abundance would provide an accurate estimate of abundance, there might still be a discrepancy between the value of real-time tariff and actual abundance. After all, the value of a real-time tariff remains an estimate of local abundance at the place and time of capture whereupon fish species that were not caught continue with their usual activities of feeding and reproduction. This causes a discrepancy between local abundance and fisheries data which is in most cases mainly predictable through analysis of historic data (Rijnsdorp *et al.*, 2006). Nevertheless, in some fisheries, such as bottom trawl fisheries that target flatfish species, the relationship between fleet dynamics and fish abundance might be strengthened as these fisheries alter both the local abundance of flatfish and their prey (Hiddink *et al.*, 2006). In some cases, this might result in (unexpected) feedback loops between fleet dynamics and abundance where fishing may against all the odds lead to more fish (van Denderen *et al.*, 2013). Thus, the extent to which impact quota and real-time tariffs are able to deal with such feedback loops, directly affects the effectiveness of effort-based and real-time fisheries management tools. Therefore, the degree of correspondence between the spatial and temporal ranges of these feedback loops and the spatiotemporal resolution of the management tool, is a critical aspect regarding the design of effort-based and real-time fisheries management tools.

Finally, changes in fisheries management regimes are known to induce shifts in short and long-term fleet dynamics (Holley and Marchal, 2004). Fishers might for instance explore new fishing grounds or switch between target species, which can alter the relationship between fishing effort and fishing mortality (Holley and Marchal, 2004; Marchal *et al.*, 2006; Poos and Rijnsdorp, 2007a). Depending on their objectives and design, effort-based and real-time fisheries management tools are likely to alter the economic constraints of the fishery which might affect both fishing tactics and strategies. Indeed, the activity during a fishing trip is often characterized by a sequence of processes in order to find and catch fish. Such a behaviour has been demonstrated in the Dutch beam trawl fishery where skippers alternate between exploration and exploitation, in order to find and exploit a local hotspot of

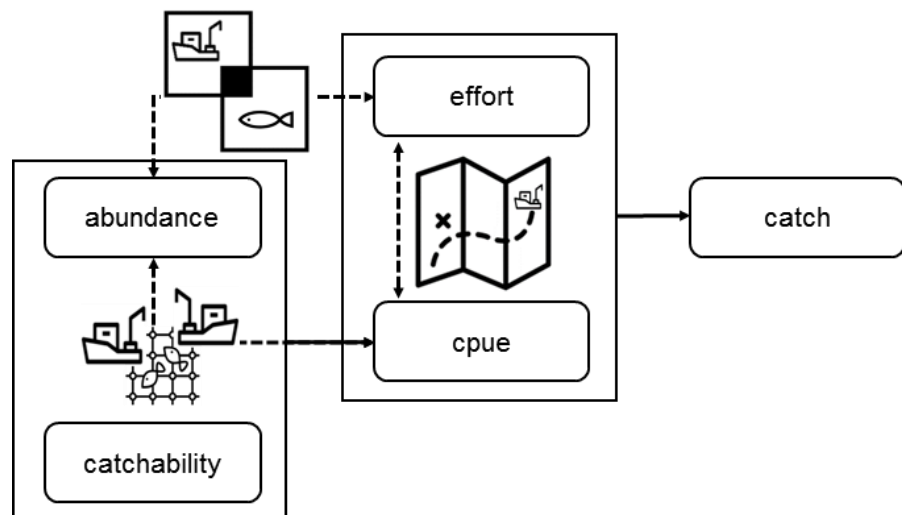
sole, respectively (Rijnsdorp *et al.*, 2000b; 2011). Various design elements of effort-based and real-time management tools such as the spatial resolution, the value and step size of the tariffs, and the way how effort is measured, might interfere with such a process. This might affect the ability of a fisher to find a local aggregation of fish, and creating an incentive to switch between target species. Hence, to prevent such unintended outcomes, a thorough understanding is needed of the mechanisms underlying these fishing tactics with respect to the spatiotemporal resolution of these management tools.

1.3. Outline of the thesis

1.3.1 Research objectives and outline

This thesis addresses the issues, highlighted in section 1.2.2, by analysing the dynamics of the Belgian beam trawl fleet. With this in mind, three general research objectives have been defined: (i) improve the understanding of the effect of fleet dynamic mechanisms at high spatiotemporal resolution on the relationship between fishing effort and fishing mortality, (ii) assess the value of fisheries data and computational modelling techniques with respect to the analysis of fleet dynamics, and (iii) identify implications of fleet dynamics for fisheries management systems. An entirely, desk-based research approach has been followed in which different analytical and modelling methods have been used to analyse fisheries data, being data of the electronic logbook system and the satellite-based vessel monitoring system (VMS) (see Box 2 for a detailed description about the characteristics of this data).

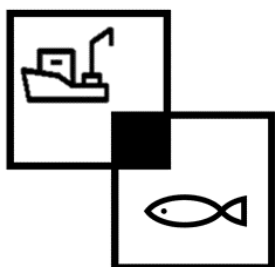
Figure 1.4 Conceptual framework of this thesis based on the relationship between catch (C), fishing effort (f), catch per unit effort ($cpue$), abundance (B) and catchability (q) as highlighted in section 1.2.2.



Chapter 2, 3 and 4 of this thesis provide an in-depth analysis of fleet dynamics with respect to the link between catch and effort. Hereto, this part of this thesis is conceptualized according the different aspects that determine the catch (Figure 1.4). In chapter 2, I analyse the relationship between fishing effort and abundance and how this may interfere with their spatiotemporal overlap. Chapter 3 highlights the tactical decisions of fishers with respect to the detection of a hotspot of fish and analyses these affect the relationship between fishing effort and catch per unit effort. In chapter 4, I look how fishing vessels compete with each other and its result on the ability of a fisher to actually catch fish. As such this thesis will provide insights into how fleet dynamics interact with local abundance, affect fishing effort, and determine the relationship between catch and effort (Figure 1.4). At the end of this thesis (chapter 5), a general discussion section is provided in which this research approach is discussed in the broader theoretical and practical context with respect to the findings of

this thesis. Remark that this thesis does not elaborate on the long term developments of fish stocks with respect to management tools. This limitation stems mainly from the fact that it wouldn't make sense to study the impact of the Belgian fishery on the long term developments of fish stocks as the capacity of the fleet is very limited with respect to the regional context. Hence, such an analysis should be done on a regional scale, or it would require a number of (unrealistic) assumptions about the developments of other fishing fleets.

In Chapter 2, landing and effort data was used to analyse the relationship between the temporal distribution of fishing effort and fishing mortality. To test whether there is a feedback loop between fishing effort and local abundance, the temporal closure of the fishery in the Trevoise Box is used as a natural experiment. Landing data of sole of commercial beam trawlers was standardized to test the hypothesis that the landing rate of



sole increased during the temporal closure of the fishery. Subsequently, these results are coupled with the spatial distribution of fishing effort to examine whether local abundance increased due to the fishery. In chapter 5, the insights of this chapter are further reviewed in the broader theoretical context to formulate a more grounded hypothesis about such a feedback loop.

Chapter 3 addresses the topic of fishing tactics through modelling VMS data of the Belgian beam trawler fleet as a Hidden Markov process. The identified behavioural states of this analysis are coupled with the revenue rate, and landing rates of sole and plaice. As such, inferences can be made regarding the behavioural drivers of Belgian beam trawlers with respect to the landing rate of various fish species. In addition, this chapter illustrated the importance of fisher behaviour with respect to the analysis of effort and landing data.



In Chapter 4, the effect of increased encounter rate between the Belgian beam trawler fleet and the Dutch pulse trawler fleet in the Southern part of the North Sea is analysed with respect to the adoption to pulse trawling of Dutch fishing vessels. To test the hypothesis of the occurrence of interference competition, landing data of sole and plaice as reported in



vessels' electronic logbooks was analysed in a natural experiment based on the different weekly exploitation patterns of both fleets. This topic of competition is further addressed in chapter 5 in which we provide an example for further investigation of such mechanisms with respect to fisheries management tools.

Box 2: logbook and VMS data

In the EU, both electronic logbooks and vessel monitoring systems are mandatory for fishing vessels with length >15 meter. In their electronic logbooks, fishers report the estimated landings (kg) of commercial fish species, and provide information concerning the fishing gear and mesh size used. In the EU, this logbook data is collected at a spatial resolution of an ICES statistical rectangle (1 degree longitude x 0.5 degree latitude ~ 30 x 30 nautical miles), and a temporal resolution of a fishing trip (or daily, as is the case in Belgium). VMS data is collected at intervals of 2 hours from the satellite-based vessel monitoring system, it contains information on vessels' location (longitude; latitude), speed and heading direction.

The primary objectives of logbook and VMS systems are to collect catch/effort statistics, used for stock assessments, and serve as a tool for control and enforcement. Despite (common) inaccuracies in the data, logbook and VMS data are, due to their high spatiotemporal resolution which may eventually be further increased by linking both datasets to each other (Gerritsen and Lordan, 2011; Hintzen *et al.*, 2012; Russo *et al.*, 2014) or through interpolation of VMS data using cubic Hermite splines (Hintzen *et al.*, 2010), particularly well-suited to assess the impact of fishing in space and time (e.g. delineate zones with low and high fishing intensity) (Jennings *et al.*, 1999; van Denderen *et al.*, 2014; Eigaard *et al.*, 2017). In the EU, logbook data is also used to group fishing activities into métiers based on the gear, location, season and target species assemblage as prescribed by the European Data Collection Framework (Deporte *et al.*, 2012). In addition, logbook catch data and effort data are particularly well-suited to model the tactical decisions of fishers. Indeed, revenues and operational costs can be deduced from the landing and effort data, respectively, and used in e.g. *random utility models* to model effort allocation decisions of fishing vessels (e.g. Vermard *et al.*, 2008; Bastardie *et al.*, 2014), or e.g. *optimal foraging models* to model discard and highgrading decisions of fishers (e.g. Poos *et al.*, 2010a; Batsleer *et al.*, 2015).

The reliability and the way how effort is recorded is the major hurdle concerning the correct interpretation and usage of these data. Therefore, a proper standardization of fishing effort is often required before any analysis. This concerns amongst others the selection of an appropriate statistical distribution for the response variable, dealing with zero inflation in the landings, including additive terms, etc. (see Maunder and Punt (2004) for a detailed overview).

1.3.2 The Belgian fishery: fishing grounds, target species and fishing gear

By the end of 2015, the commercial Belgian fishing fleet comprised 76 fishing vessels with a total capacity in terms of engine power and gross tonnage of 45327 kilowatt (kW) and 14072 gross tonnage (GT), respectively (Tessens and Velghe, 2016)(Tessens and Velghe, 2016). Altogether, a volume of 24583 tonnes of fish and shellfish was landed by the fleet with a value of € 93.3 million. Based on their engine capacity, Belgian fishing vessels belong to the *large fleet segment* (> 221 kW; 35 vessels; 80% of the engine capacity of the fleet) or the *small fleet segment* (\leq 221 kW; 41 vessels).

The majority of the vessels that belong to the *small fleet segment* are *coastal fishing vessels* (14 vessels) and *eurocutters* (15 vessels). Coastal fishing vessels make short fishing trips (maximum 48 hours) that start and end in a Belgian harbour. These vessels exploit fishing grounds (mainly <3 miles offshore) off the Belgian coast to target flatfish species, mainly from November to July, and brown shrimp (*Crangon crangon*), mainly from August until October using beam trawls (see below). *Eurocutters* are defined as polyvalent beam trawlers with length \leq 24 meter and gross tonnage \leq 70GT that are constructed since 1981. These vessels make fishing trips with an average duration of 4 days during which they target – depending on the gear, season and fishing ground – flatfish species, nephrops (*Nephrops norvegicus*) or brown shrimp. The main fishing grounds of these vessels are located between 6 and 12 miles off the coastline of the Southern part of the North Sea (ICES subdivision IVc) and the Eastern English Channel (ICES subdivision VIIId). However, when targeting nephrops, *eurocutters* exploit fishing grounds in the Central part of the North Sea (ICES subdivision IVb).

The beam trawlers of the *large vessel segment* constitute the study fleet of this thesis, and were the most important part of the Belgian fleet in terms of landings and revenues during the study period (2006-2014) covered by this thesis. In 2015, 28 vessels belonged to the *large beam trawl* segment, they accounted for 69 % (16864 tonnes) of the total landing volume and 67% (€ 62.4 million) of the total revenues with respect to the entire Belgian commercial fishing fleet (Tessens and Velghe, 2016). These vessels exploit fishing grounds in the Central (IVb) and Southern (IVc) part of the North Sea, the Eastern (VIIId) and Western (VIIe) English Channel, the (Western (VIIh)) Celtic Sea (VIIg), Bristol Channel (VIIf), Irish Sea (VIIa), and Bay of Biscay (VIIIab) (Figure 1.5). As their engines exceed 221 kW, they are not allowed to fish <12 miles off the coastline.

Sole (~14% of the landed volume and ~38% of the revenue) and plaice (~35% of the landed volume and ~15% of the revenue) are the main target species of this segment. However, cod (*Gadus morhua*) (IVb), lemon sole (*Microstomus kitt*) (IVb), turbot (*Psetta maxima*)

(IVc), brill (*Scophthalmus rhombus*) (IVc), cuttlefish (*Sepiidae*) (VIIId), ray species (*Rajidae*) (VIIa,g) and anglerfish (*Lophiidae*) (VIIef, VIIIab) constitute also an important part of the landings, especially in the ICES subdivision mentioned between the brackets.

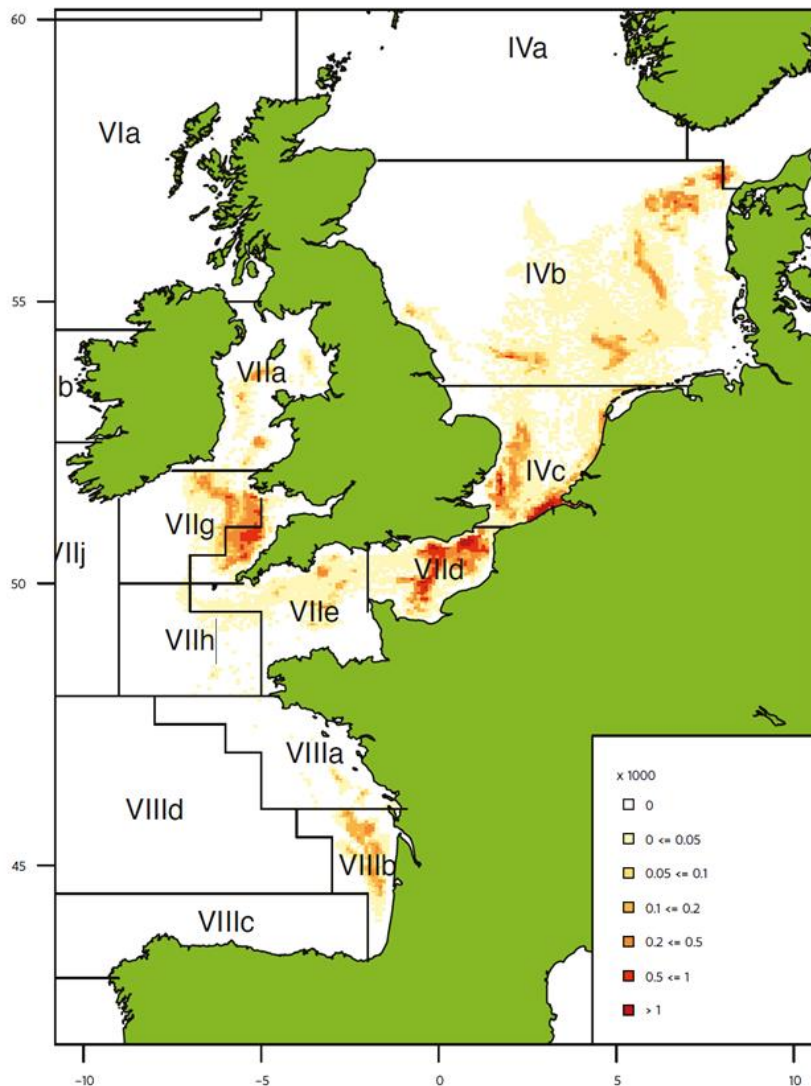


Figure 1.5 Fishing effort distribution (in hours) of the entire Belgian fishing fleet from 2013 until 2015 (source: Platteau *et al.*, 2016). The combination of Roman numeral and letter refer to the ICES subdivision delineated by the black lines.

To target this species, these vessels tow a beam trawl¹⁰ at each side of the vessel over the seafloor (Figure 1.6). A beam trawl consist of a *beam* – eventually replaced by a hydrodynamic wing – trawl *shoes* – eventually replaced by wheels – at each side of the beam, and a cone-shaped *trawl net* ending in a *codend*. Usually, chains are attached between the beam and ground rope to disturb the fish from the seafloor, while a ground rope with rubber bobbins keeps the beam trawl in contact with the bottom (Galbraith *et al.*,

¹⁰ The width of the beam trawl is 12 meter for vessels of the large beam trawl segment and 4 meter for coastal vessels and *eurocutters*.

2004). To target sole, a mesh size of 80 mm is used while a mesh size of 120 mm is used for the directed fishery for plaice (>55 latitude) in the North Sea.

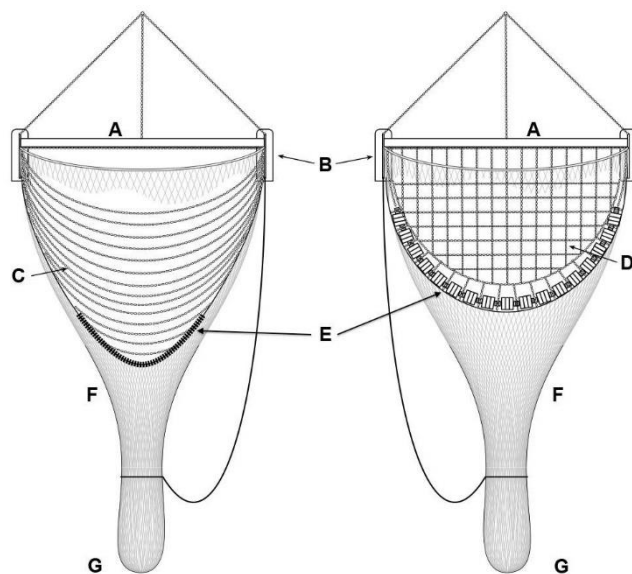
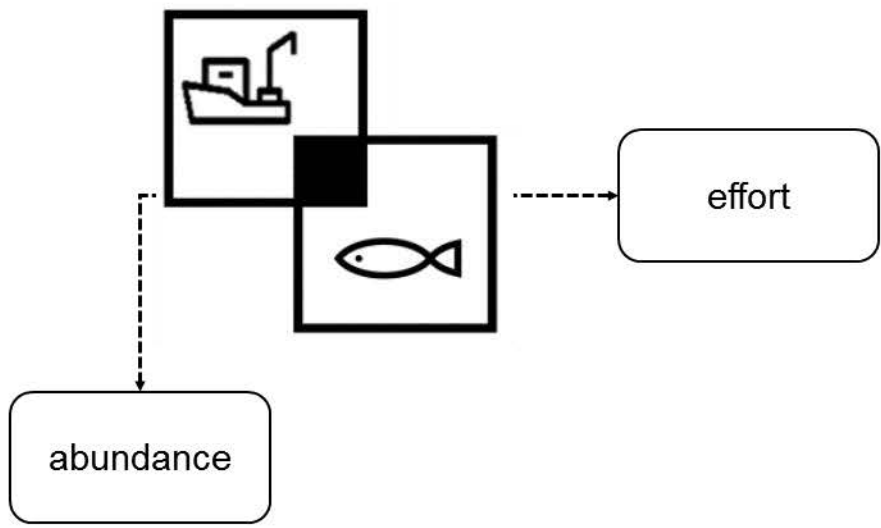


Figure 1.6 Illustration of a beam trawl equipped with V-shaped tickler chains (left) and tickler chains in a matrix design (right). The letters refer to: A: beam; B = shoes; C= tickler chains; D= chain mat; E= ground rope and bobbins; F= trawl net; G= codend. (source: Galbraith *et al.*, 2004)

As the fleet targets sole and plaice, the distribution of fishing effort shows a strong overlap with the preferred habitats of both species, being soft bottom habitats such as sandy or sandy/muddy sediments in shallow coastal waters in which they can bury themselves to avoid predation (Gibson and Robb, 2000). Nevertheless, the majority of the fishing grounds exploited by the large beam trawlers are characterized by an irregular surface scattered with rocks. To exploit these rough fishing grounds, beam trawls with tickler chains in a matrix design are used to prevent rocks from entering the net (Fonteyne and Polet, 1995). As a consequence, fishing speed of Belgian beam trawlers is lower compared to e.g. the Dutch beam trawl fleet that was equipped with V-shaped tickler chains. Notwithstanding this lower fishing speeds, fuel expenses remain a major part (approximately one third) of the operational costs of this fleet segment as a high tractive power is required to drag the gear over the seafloor. Besides the fuel expenses, the wages are constitute a major cost as well. It has been agreed in the Belgian fishery that one third of the revenue of a trip is used to pay the crew.

The management system of the Belgian fishery is rather complex (see Tessens and Velghe (2016) for an overview of the system in 2015). In summary, the national quota of the main target species are managed through an individual non-transferable quota system. Three times per year, large beam trawlers are allocated a share of the quota, often proportional to their engine capacity. Depending on the ICES subdivision, quota of non-target species are managed through daily catch limits or as a common pool system. Besides the quota, the

effort of individual fishing vessels is limited by a maximum number of day-at-sea. In 2015, this limit was set at 275 days-at-sea of which maximum 180 days could be spent in the cod-recovery areas (IVb,c, VIIa,d) for the large beam trawlers. Finally, there are a number of technical measures. For the large beam trawl segment, these are mainly mesh size regulations of which the main measure fixes the minimum mesh size in the directed fishery for sole and plaice at 80 mm and 120 mm, respectively.



CHAPTER 2

A temporal race-for-fish: the interplay between local hotspots of flatfish and exploitation competition between beam trawlers after a seasonal spawning closure

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Abstract

In this paper we examine the response of the Belgian beam trawl fishery after the implementation of a spawning closure in the Celtic Sea. It was observed that fishing effort was mainly reallocated in time, resulting in a short-term “race for fish” immediately after re-opening of the fishery. The rationale of this behaviour was examined by analysing the landing rate of the target species (sole) in a generalized additive mixed model. Results showed that daily sole landings were up to twice as high just after re-opening of the fishery and dropped within 3 weeks to a reference level. This pattern of landing rate per unit (lpue) of sole was strongly related to the spatial distribution of fishing effort in the closed area during the month of re-opening. During the first week, fishing effort was very patchy, with increasing dispersal toward the end of the month. These results give indirect evidence for the occurrence of high local concentration of sole as a result of the closure, and the occurrence of exploitation competition when the fishery restarted.

2.1. Introduction

One of the critical steps towards an effective implementation of an ecosystem based fisheries management (EBFM) is to improve understanding of how ecosystems function, including the interactions between the various subsystems (Crowder & Norse, 2008; Link, 2002; Pikkitch *et al.*, 2004). Therefore, understanding the relationship between a fishery and its resource remains a major research topic of fisheries science (Branch *et al.*, 2006). Improved understanding of the underlying mechanisms and interactions that shape this relationship may reduce the uncertainty of fisher behaviour (Fulton *et al.*, 2011), and consequently increase the effectiveness of fisheries management and enhance the sustainable exploitation of marine resources. This relationship is often expressed as catch-per-unit-effort (cpue), and is known to have a positive linkage with the density of the resource, making it an important parameter in the various models used to design fisheries management (Harley *et al.*, 2001). Nevertheless, cpue is affected by many factors (see Gillis and Peterman (1998) for an overview). Correct interpretation and use of cpue depends largely on both spatial distribution of the fish resource and the allocation of fishing effort (Paloheimo and Dickie, 1964).

Spatiotemporal management tools such as temporary fishery closures are commonly used in fisheries management. The success of these interventions depends strongly on the response of the fishery in terms of spatial and temporal reallocation of fishing effort (Dinmore *et al.*, 2003). Spatial reallocation of fishing effort, often resulting in the strategy called “*fishing the line*” which is characterized by intensive fishing close to the borders of the closed area, has been extensively described (van der Lee *et al.*, 2013; Murawski *et al.*, 2005) and explained through the mechanisms of *spill-over* and *export* of eggs and larvae and juveniles (Gell and Roberts, 2003). In contrast, the underlying mechanisms and effects of a temporal reallocation of fishing effort are not. Trawl fisheries are particularly relevant to this line of inquiry, as this type of fishery has a strong linkage with the flatfish resource due to seafloor disturbance. The heavy trawl gear penetrates the upper layer of the seabed, damaging benthic life and altering the composition of benthic communities (Jennings and Kaiser, 1998). Hiddink *et al.* (2008) and van Denderen *et al.* (2014) proved that both the trawling frequency and the temporal aggregation of fishing effort are important parameters for the impact of bottom trawling on the structure of benthic communities. Ignoring this feedback mechanism in fisheries systems with the trophic interactions between the benthic ecosystem and the target species may result in unforeseen management outcomes. For example, in the Dutch beam trawl fishery, discarding of juvenile plaice (*Pleuronectes platessa*) increased after the Plaice Box was implemented as a protection measure to reduce discarding of juvenile plaice. This was due to the unexpected consequences of fishing effort

reallocation and its knock-on effect on the structure of benthic communities and the abundance of juvenile plaice (Beare *et al.*, 2013).

The objective of this paper is to assess how a reallocation of fishing effort in time influences the relationship between fishers and their resource, and thus affects the link between catch and effort (cpue) and fisher behaviour. Therefore, we use the Belgian beam trawl fishery in the Celtic Sea, in which a remarkable short-term race for fish after re-opening of the fishery in the Trevoise Box in April was observed. First, we explain the rationale of this short term race for fish through analysis of cpue of the target species sole (*Solea solea*). In addition, we explore the underlying mechanisms of this distortion through analysis of the micro distribution of fishing effort, as this may reflect the small scale dynamics of the fish resource (Rijnsdorp *et al.*, 1998). The objective of this paper is to increase knowledge about the interaction and feedback mechanisms between beam trawling and the flatfish resource at a high temporal resolution, with the aim of improving fisheries management outcomes.

2.2. Materials and Methods

2.2.1. The Trevoise Box closure in the Celtic Sea as natural experiment

During the study period (2003-2014), the Celtic Sea (International Council of Exploration of the Sea - ICES divisions VIIg and VIIf) was predominantly exploited by French, Irish, British and Belgian trawlers targeting demersal fish species (Rijnsdorp *et al.*, 1998). Most vessels were French, Irish and British otter trawlers targeting gadoids, with cod (*Gadus morhua*) being the most important species in terms of landed weight and value (ICES, 2007). The remainder of the fleet consisted mainly of Belgian and British beam trawlers targeting flatfish species, with sole being the most important species in terms of landed value (>60%).

This fishery was dominated by Belgian vessels (>60% of the annual Celtic Sea sole landings) with the shallow waters of the Bristol Channel estuary (ICES division VIIf) being the main fishing grounds in terms of annual sole landings as well as fishing effort (Figure 2.1, panel a) (ICES, 2007; ICES, 2015). Belgian beam trawlers were active in the Celtic Sea throughout the year, but effort showed a seasonal pattern. Most effort was concentrated from December to April in the Bristol Channel, with ICES statistical rectangle 30E4 (1° longitude x 0.5° latitude, ca. 30 x 30 nautical miles) being the most frequently exploited. As part of the Celtic Sea cod recovery plan, the Trevoise Box (ICES statistical rectangles 30E4, 31E4 and 32E3), one of the three spawning grounds of the Celtic Sea cod stock, was closed for fishing during January – February 2005, with subsequent annual closures during February – March since 2006. The aim of excluding fishing activities during the spawning season is to reduce fishing mortality of cod, as these fish aggregate during the spawning season and are therefore more vulnerable to fishing. Derogation was given to vessels using

pots and creels, or nets with mesh size < 55mm, and, in March 2005, to beam trawlers as well (ICES, 2007). The Trevoise Box closure caused Belgian beam trawlers to adjust their exploitation patterns in the Celtic Sea.

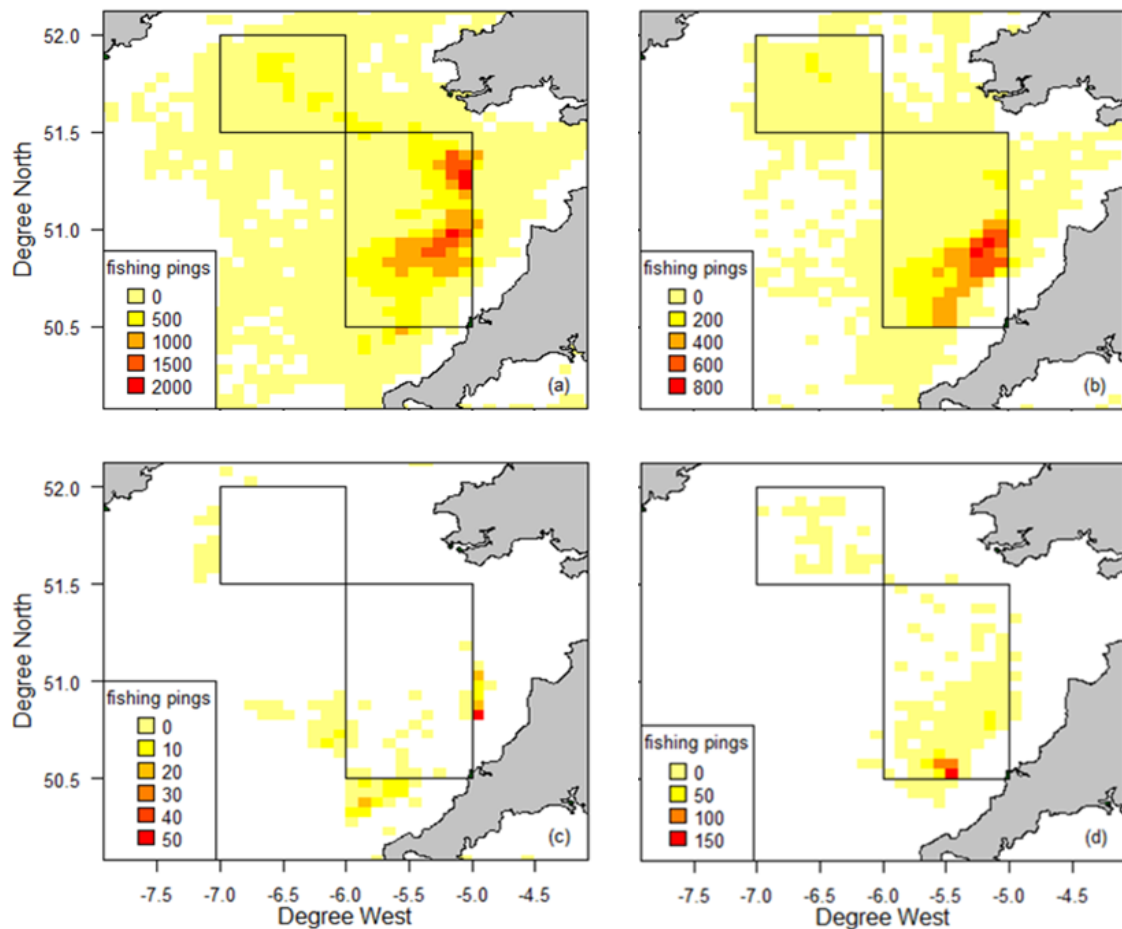


Figure 2.1 Spatial distribution of fishing effort expressed as fishing pings (the VMS data points classified as fishing based on vessels' speed profiles) (grid resolution: $0.05^\circ \times 0.025^\circ$). The Trevoise Box comprising ICES rectangles 30E4 $[-6;-5 \times 50.5;51]$, 31E4 $[-6;-5 \times 51;51.5]$ and 32E3 $[-7;-6 \times 51.5;52]$ is enclosed by the black frame. Panel a-d (bottom right) show the effort distribution during the period 2006-2014 during the entire year (a), during the month April (b), on March 31 (c), on April 1 (d), respectively.

2.2.2. Data

Logbook data from 2003 to 2014 of Belgian beam trawlers with engine powers >221 kW using beam trawls with mesh size 80 mm was used for analysis of the landing rates per unit effort (lpue) of sole (Table 2.1). Along with the daily estimated weights (kg) of the landings of commercial species, logbooks contain daily information about the fishing activity in terms of gear type, mesh size and location (by ICES statistical rectangle). Trip (departure and arrival date and harbour of departure and embarking) and vessel (reference number, length, engine power and gross tonnage) information was added to the logbooks. No information about discards was available, thus the analysis was restricted to the landings per unit effort. Nevertheless, sole discards are considered very small (discard ratio < 5%) causing lpue to

be very close to cpue (ICES, 2015). Due to missing logbook data, 2005 was excluded from the analysis.

Table 2.1 Number of vessels, mean vessel engine power and summary statistics of the sole landings in the Trevoise Box as reported in vessels' electronic logbooks. The ratio of sole landings from the Trevoise Box with respect to the total annual sole landing in the Celtic Sea is given in brackets.

year	Celtic Sea					Trevoise Box				
	no. of vessels	no. of logbook events	Engine power (kW)	annual sole landings (tonnes) by the fleet	mean sole landings (kg) per logbook record	no. of vessels	no. of logbook events	engine power (kW)	annual sole landings (tonnes) by the fleet	mean sole landings (kg) per logbook record
2003	46	2729	887	623	228	46	2410	886	554 (0.89)	230
2004	58	3278	887	633	193	58	2932	888	581 (0.92)	198
2005	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
2006	54	2357	928	477	202	53	2172	928	445 (0.93)	205
2007	58	2143	987	453	211	54	1813	987	373 (0.82)	206
2008	43	1436	1041	377	263	42	1131	1030	303 (0.80)	268
2009	44	1548	1051	385	249	43	1285	1047	328 (0.85)	255
2010	36	1682	1111	512	304	35	1459	1108	433 (0.85)	297
2011	33	1967	1048	631	321	32	1667	1051	545 (0.86)	327
2012	38	2277	1086	691	303	38	1871	1085	578 (0.84)	309
2013	30	2333	1076	680	292	29	1893	1069	562 (0.83)	297
2014	30	1612	1067	592	367	30	1345	1062	479 (0.81)	356

To examine the micro-distribution of fishing effort, data from the satellite-based vessel monitoring system (VMS) was used. This dataset contains the vessel's geographical position (latitude, longitude), heading direction (0 - 360 degrees) and speed (knots) at regular time intervals (approximately every 2 hours; Table 2.2). As vessel monitoring systems are only mandatory for larger vessels (length > 12 m) in the EU since 2006, analysis was restricted to the period 2006 – 2014. Vessels activities were distinguished based on analysis of their speed profiles (Hintzen *et al.*, 2012). Only data representing vessels during the fishing state was retained for analysis of fishing effort. The spatial analysis was restricted to the most heavily exploited ICES statistical rectangle 30E4.

Table 2.2 Summary statistics of the VMS data from the Belgian beam trawl fleet (> 221 kW). The number of fishing pings in the Celtic Sea, Trevoise Box, and < 5 nautical miles of the border of the Trevoise Box.

	no. of fishing pings (Celtic Sea)	no. of fishing pings (Trevoise Box)	no. of fishing pings (< 5 nm of border)	Average speed (knots)
2006	20778	18823	303	4.97
2007	22733	18544	1757	4.90
2008	15504	12402	1702	4.62
2009	18055	14427	1798	4.76
2010	19175	16481	1059	4.85
2011	19672	15937	1953	4.84
2012	20347	15797	2447	4.72
2013	24900	20441	2551	4.70
2014	16990	13913	1352	4.62

2.2.3. Effect of the Trevoise Box closure on the landing rate of sole

To quantify the effect of re-opening of the Trevoise Box on the landing rates of sole, a generalized additive mixed model (GAMM) was fitted to the daily sole landings as recorded in vessel logbooks. In GAMMs, nonparametric effects and random effects are included. Nonparametric effects allow for inclusion of predictor variables of which the predetermined form is not known; random effects account for sources of specific, individual variation and correct for the bias caused by repeated observations. The effect of re-opening the Trevoise Box on $lpue$ of sole was examined by comparing different models, without and with the effects of interest. Due to the similarity of the fleet, a null model [equation (2.1)], without explanatory variables about the re-opening effect of the Trevoise Box, was specified according to Sys *et al.*, (2016):

$$\log(lpue) = \beta_0 + \beta_{1_i} year + \beta_2 \log(engine) + f(tripday) + f(month)_{rect} + \varepsilon + \mu_v. \quad (2.1)$$

In this model, the inter-annual variation, for example caused by different year-class strengths of sole or technical modifications, is captured by a categorical variable (*year*) with the first year of analysis (2003) included in the intercept β_0 . Hence, the coefficient of β_{1_i} represents the change of every year ($i \in 2004, \dots, 2014$) relative to 2003. The value β_2 is the slope of the log-linear relationship between the landing rates and the beam trawler's engine power ($\log(engine)$) (Rijnsdorp *et al.*, 2000a). Two nonparametric effects were included in the null model; these terms are smoothed to the data using regression splines (Wood, 2006). To capture the intra-annual, spatiotemporal variation caused by migration of adult sole from and to feeding and spawning grounds, a seasonal effect for each ICES statistical

rectangle ($f(month)_{rect}$) of the study area was specified. An extra restriction (cyclic cubic regression splines) was imposed to assure continuity of $lpue$ at the end points (Zuur *et al.*, 2009). An intra-trip effect ($f(tripday)$) was included for the variation caused by the searching and exploitation phases of beam trawlers during a fishing trip (Rijnsdorp *et al.*, 2011). This *tripday* effect was expressed as the number of days before the end of a trip, with a value 0 as the last day of the fishing trip. To account for the occurrence of zero catches and over-dispersion, a negative binomial distribution was specified for the error term (ϵ) by including a logarithmic link function between the linear predictor and the mean. To correct for the variation caused by individual vessel effects for which no data was available (e.g., the skipper effects or physical vessel characteristics), the vessels' reference number (v) was included as random effect (μ_v).

Next, the null model was extended to examine the effect of the re-opening of the Trevoise Box on the landing rates of sole. Therefore, two parametric effects were added to the null model [equation (2.2)]:

$$\log(lpue) = null\ model + \beta_{3_i}opening + \beta_{4_i}opening \times day. \quad (2.2)$$

The categorical *opening* effect was included to capture the response of the sole landing rates in the Trevoise Box after re-opening. This variable was assigned 11 levels: nine for all logbook events during the month of re-opening (April) inside the Trevoise Box since 2006 (*April 2006, ..., April 2014*), one value *else* for logbook events outside the Trevoise Box and/or not during the month of April, and as a last extra reference, logbook events inside the Trevoise Box in April 2004 were coded as *April 2004*. Because no sole landings were reported in April 2003 in the Trevoise Box, this month was not included. Thus the coefficient β_{3_i} shows the increase of the $lpue$ sole with reference to the $lpue$ sole inside the Trevoise Box in April 2004. We hypothesized that immediately after re-opening, availability of sole would be high and would then decrease in the days after the re-opening due to fishing mortality. Therefore, the slope of sole $lpue$ in the Trevoise Box during the month after re-opening was examined using a continuous *day* effect in interaction with the *opening* effect, with the coefficient β_{4_i} , resulting in the slope of $lpue$.

Since local overfishing may lead to nonlinear effects in $cpue$ (Maury and Gascuel, 2001) of which the pattern is not known, we substituted the parametric opening effects of eq. 2.2 with a nonparametric equivalent [equation (2.3)]:

$$\log(lpue) = null\ model + f(day)_{opening}. \quad (2.3)$$

Where $f(\text{day})$ was smoothed to the data for every level of the opening variable and allows visual inspection of the pattern of lpue sole. Over-fitting was avoided by limiting the number of knots used in the smoother to 3.

2.2.4. Micro-scale distribution of fishing effort after re-opening of the Trevoise Box

The micro-distribution of fishing effort inside ICES rectangle 30E4 was examined during the first month after re-opening of the Trevoise Box. To measure the degree of patchiness and how this evolved, the dispersion of fishing effort was calculated for every successive week of the opening month based on the VMS data (Rijnsdorp *et al.*, 1998). Due to the temporal resolution (2-hour interval) of the VMS data and speed of towing (ca. 5 knots, Table 2.2), effort dispersion was calculated at two resolutions, i.e. with grid resolutions of 30 x 30 and 10 x 10 nautical miles.

All grid cells where fishing was allowed were subdivided into a grid of 10 by 10 (100 quadrants). The index of dispersion (ID), expressed as the ratio of variance-to-mean: $ID = \sigma^2/m$, was calculated where the mean density (m), is expressed as the ratio of the total number of fishing pings to the number of quadrants (Q): $m = \sum_Q x_i / Q$ and the variance (σ^2)

is equal to: $\frac{\sum_Q x_i^2 - (\sum_Q x_i)^2 / Q}{Q}$. A dispersion index of 0 corresponds to a perfect uniform distribution and means that each quadrant is fished at the same intensity, while a value of 1 corresponds with a random distribution derived from a homogenous Poisson process. Values > 1 imply stronger clustering, indicating a patchy distribution of fishing effort.

The open-source software platform R (version 3.2; R Core Team, 2016) was used for the analyses. Both logbook and vms data was processed following the procedures of the *vmstools* R-package (Hintzen *et al.*, 2012). Regression and spatial analysis were performed using *mgcv* (Wood, 2004) and *spatstat* (Baddeley and Turner, 2005) R-packages, respectively.

2.3. Results

2.3.1. Patterns in sole landings and spatiotemporal effort allocation

From 2003 to 2014, >80% of the annual Celtic Sea sole landings were caught inside the Trevoise Box (Table 2.1). The Trevoise Box closure resulted only in a small decline of the ratio of sole landings inside the Trevoise Box to the total Celtic Sea landings. In contrast, a major shift occurred in the monthly distribution of Celtic Sea sole landings. Before 2005, most Celtic Sea sole was landed during January – March (Figure 2.2). However, since 2006, a temporal shift was observed: sole landings remained high in January, after which almost no sole were caught in the Celtic Sea during February and March followed by a remarkable peak of the landings in April. Only in 2011, slightly more sole were landed during the month of January. In 2005, when the Trevoise Box was closed during January-February, the most sole were landed during March.

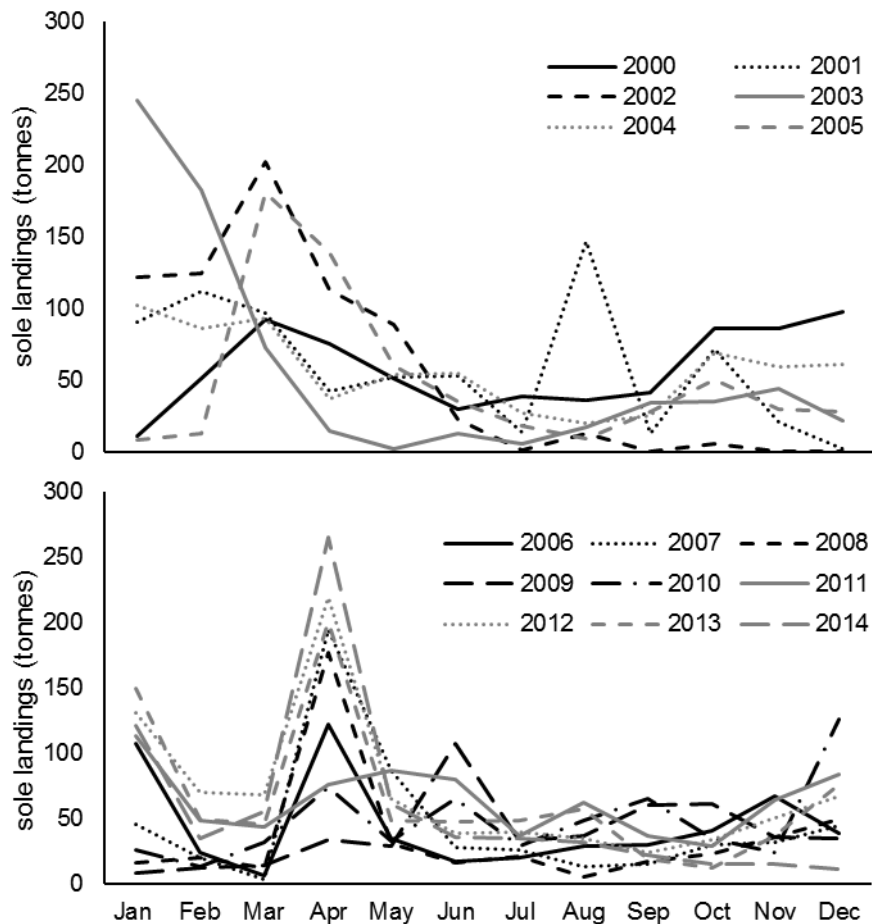


Figure 2.2 Monthly Celtic Sea sole landings of Belgian fishing vessels during from 2000 until 2014. The upper panel represents the situation before the closure of the Trevoise Box in March and April, while the lower panel shows the situation since the implementation of the Trevoise Box closure.

Similar to the pattern of monthly sole landings since 2006, the weekly distribution of fishing effort showed two peaks during the months of January and April (Figure 2.3). With the exception of 2013, fishing effort was always highest in week 14, corresponding with the first week of April and thus the re-opening of the fishery in the Trevoese Box. After week 14, fishing effort remained high, but declined gradually towards the end of the month April (week 17).

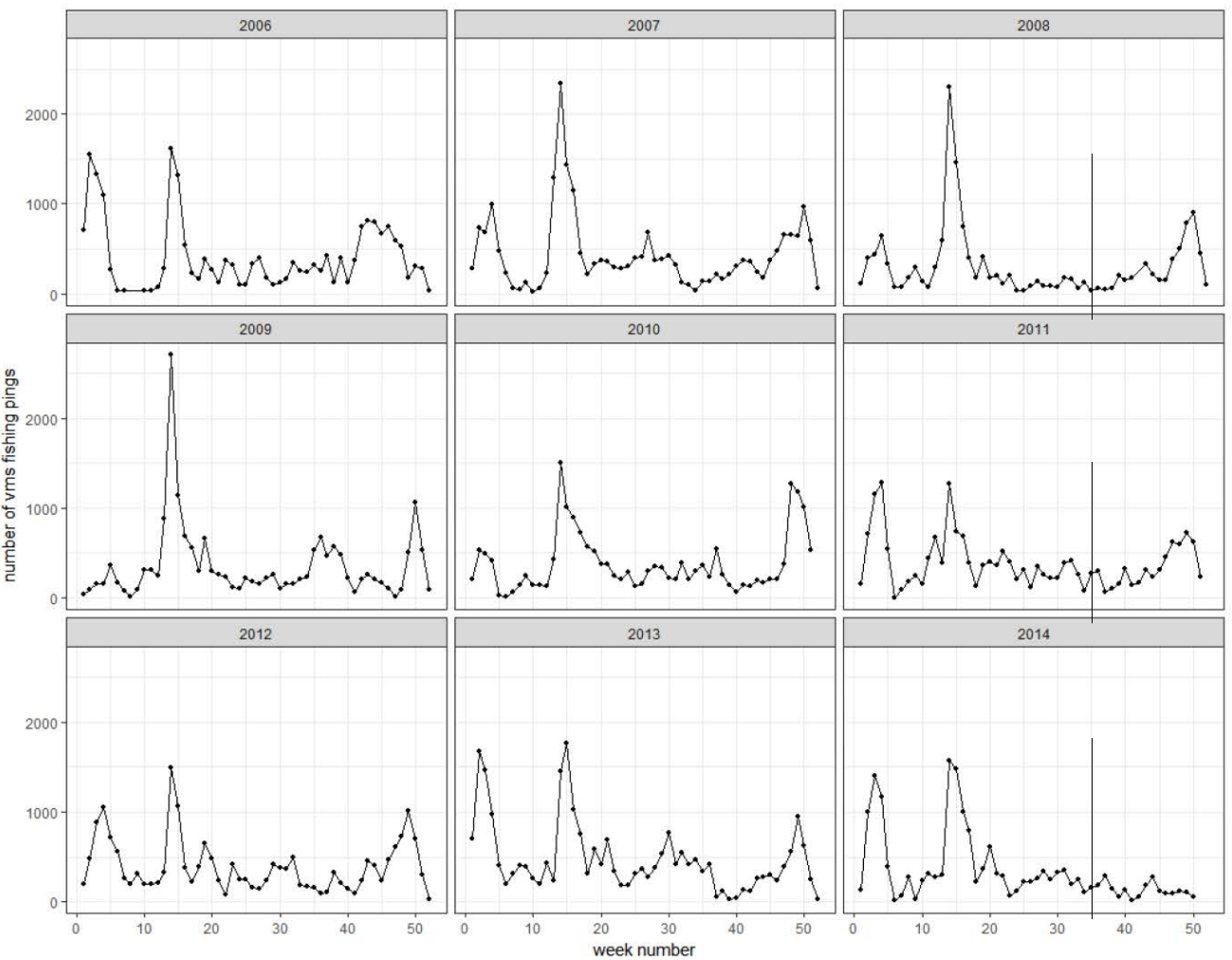


Figure 2.3 Weekly distribution of fishing effort of the Belgian beam trawl fleet (> 221 kW) in the Celtic Sea expressed in number of VMS fishing pings. The Trevoese Box is closed from week 5 until week 13.

These weekly effort patterns are also reflected in the daily effort dynamics around the opening of the fishery. On the day before opening of the Trevoise Box (March 31), Belgian beam trawlers were typically found around the borders of the Trevoise Box and started to fish inside the box immediately after midnight on April 1st (Figure 2.1, panels c and d). During the month of re-opening of the Trevoise Box, >90% of the Celtic Sea fishing pings were concentrated in ICES rectangle 30E4.

During the closure in February and March, some beam trawlers fished near the borders of the closed area. However, the number of fishing pings alongside the border was limited to <10% of the annual fishing effort in the Celtic Sea (Table 2.2). Instead of fishing at the borders of the closed area, most Belgian beam trawlers reallocated fishing effort during the closure to other ICES divisions.

2.3.2. Dynamics of the landings per unit effort of sole

All parametric explanatory variables of the null model were significant at the 5% level (Table 2.3). The landing rate of sole in the Celtic Sea differed considerably among the different years of analysis, showing an increasing trend with the strongest rise during the period 2007 – 2010 (+/- 50%). From 2003 to 2007, the sole landing rate was remarkably lower compared to the period 2010 – 2014, while the highest annual landing rate was found in 2014. The null model revealed a strong positive log-linear relationship between sole $lpue$ and the vessel's engine power, implying that more powerful vessels have higher sole $lpue$. During the trips, the sole landing rate followed a characteristic pattern (Figure 2.4). Landing rates increased at the beginning of a trip and were followed by a plateau phase with high $lpue$ of sole, while at the end of a trip, $lpue$ decreased. Significant seasonal effects were found in most rectangles of the study area. Highest landing rates occurred in winter and early spring, after which a decline occurred resulting in lowest $lpue$ during summer and the start of the autumn; this was in contrast with ICES rectangles 30E3 and 32E2, where an opposite pattern was found. The amplitude of the observed seasonal variation was more pronounced in the ICES rectangles of the Bristol Channel.

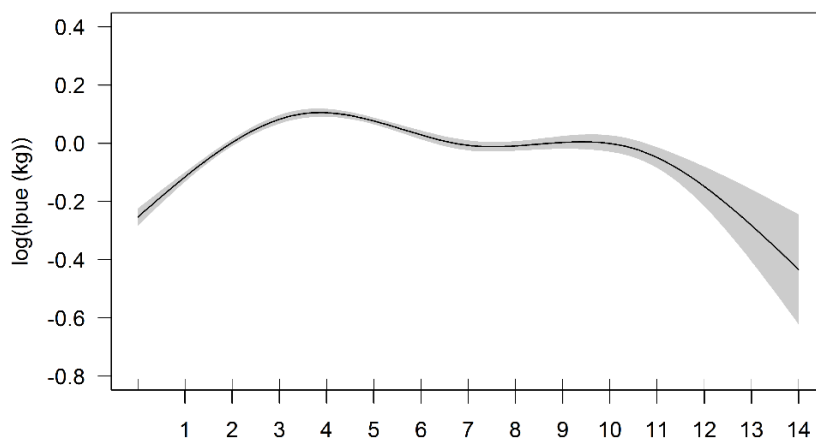


Figure 2.4 Plot of the non-parametric effect [$f(\text{tripday})$] of $lpue$ sole of the null model [equation (2.1)]. The x-axis represents the number of days left before a vessel embarks in the harbour. The 95% confidence interval is represented by the grey shade.

The addition of *opening effects* substantially improved the null model (AIC = 54282) in terms of the Akaike Information Criterion (AIC = 53037). In contrast, the difference between the extended null models with parametric (AIC = 53037) and nonparametric (AIC = 52982) was less pronounced.

Table 2.3 Estimated coefficients, standard errors, and test statistics of the null model [equation (2.1)].

	est. (se)	d.f.	F / t-value	p-value
Intercept	1.80 (0.69)	-	2.60	<0.01
Year	-	10	37.3	<0.01
2004	-0.11 (0.02)		-4.95	<0.01
2006	-0.05 (0.02)		-2.23	0.03
2007	-0.06 (0.03)	-	-2.39	0.02
2008	0.09 (0.03)	-	2.94	<0.01
2009	0.15 (0.03)	-	4.64	<0.01
2010	0.30 (0.03)	-	8.95	<0.01
2011	0.36 (0.03)	-	11.07	<0.01
2012	0.25 (0.04)	-	6.91	0.01
2013	0.21 (0.04)	-	5.81	<0.01
2014	0.40 (0.04)		10.19	<0.01
log(<i>engine</i>)	0.52 (0.10)	1	5.17	<0.01
<i>f(tripday)</i>	-	3.92	90.4	<0.01
<i>f(month)</i> _{29E2}	-	1.41	2.0	0.01
<i>f(month)</i> _{29E3}	-	<0.01	0.0	0.48
<i>f(month)</i> _{29E4}	-	1.98	15.0	<0.01
<i>f(month)</i> _{30E3}	-	2.85	20.1	<0.01
<i>f(month)</i> _{30E4}	-	2.98	323.2	<0.01
<i>f(month)</i> _{30E5}	-	1.72	3.2	<0.01
<i>f(month)</i> _{31E2}	-	<0.01	0.0	0.59
<i>f(month)</i> _{31E3}	-	1.85	3.4	<0.01
<i>f(month)</i> _{31E4}	-	2.92	239.1	<0.01
<i>f(month)</i> _{31E5}	-	2.37	14.0	<0.01
<i>f(month)</i> _{31E6}	-	0.55	1.2	0.13
<i>f(month)</i> _{32E2}	-	2.33	11.4	<0.01
<i>f(month)</i> _{32E3}	-	2.93	131.9	<0.01
<i>f(month)</i> _{32E4}	-	2.72	17.4	<0.01
<i>f(month)</i> _{32E5}	-	<0.01	0.0	0.65

Table 2.4 shows that both the parametric *opening* ($df= 10$; $F\text{-value} = 83.48$; $p\text{-value} < 0.01$) and interaction effect (*opening x day*) ($df= 11$; $F\text{-value} = 62.00$; $p\text{-value} < 0.01$) were found

to be significant in the second model [equation (2.2)] . Immediately after re-opening on April 1, the landing rate of sole was 120 to 200% higher inside the Trevese Box compared to the model without an effect accounting for the re-opening of the Trevese Box. In 2009 (40%) and 2010 (43%) only, the magnitude of this effect was smaller. With the exception of 2010, the interaction (*opening x day*) effect showed that sole landing rates inside the Trevese Box were characterized by a negative slope during the first month after re-opening of the fishery. As a result, l_{pue} of sole returned to a normal, reference level after 1 - 3 weeks. In contrast, during April 2004, when the Trevese Box closure was not yet implemented, l_{pue} of sole was characterized by a small positive slope, indicating that catch rates increased slightly towards the end of the month.

Table 2.4 Estimated coefficients, standard errors, and test statistics of the parametric opening effects [equation (2.2)].

	est. (s.e.)	t-value	p-value
intercept	1.59 (0.68)	2.35	0.02
else	0.14 (0.12)	1.24	0.21
opening 2006	0.83 (0.13)	6.38	<0.01
opening 2007	1.36 (0.13)	10.55	<0.01
opening 2008	1.06 (0.13)	8.16	<0.01
opening 2009	0.37 (0.13)	2.86	<0.01
opening 2010	0.38 (0.14)	2.81	<0.01
opening 2011	0.65 (0.14)	4.69	<0.01
opening 2012	1.29 (0.13)	9.71	<0.01
opening 2013	1.19 (0.13)	9.06	<0.01
opening 2014	1.24 (0.13)	9.28	<0.01
else x day	0.002 (<0.01)	2.48	0.01
April 2004 x day	0.01 (<0.01)	2.37	0.02
opening 2006 x day	-0.03 (<0.01)	-6.29	<0.01
opening 2007 x day	-0.05 (<0.01)	-11.85	<0.01
opening 2008 x day	-0.04 (<0.01)	-8.37	<0.01
opening 2009 x day	-0.02 (<0.01)	-4.42	<0.01
opening 2010 x day	0.004 (<0.01)	0.91	0.36
opening 2011 x day	-0.02 (<0.01)	-4.25	<0.01
opening 2012 x day	-0.04 (<0.01)	-9.35	<0.01
opening 2013 x day	-0.06 (<0.01)	-13.14	<0.01
opening 2014 x day	-0.05 (<0.01)	-11.95	<0.01

Figure 2.5 illustrates the output of the null model extended with nonparametric *opening* effects [equation (2.3)] for each year. Only in 2010, no nonparametric opening effect was found ($p\text{-value} > 0.05$). With the exception of 2009 and 2010, $lpue$ of sole was always highest on the first day after re-opening of the Trevoze Box. After that day, the landing rate of sole gradually returned to the reference level. The declining pattern of the sole landing rate during the month of re-opening differed between the different years of analysis, but visual inspection of the nonparametric effect revealed similar patterns among several years of analysis. In 2006, 2008, 2011, 2012, 2013 and 2014, the strongest decline of $lpue$ of sole occurred just after re-opening and continued for approximately 10 days. After that, the negative slope approached zero and, in some years of analysis, $lpue$ sole increased again towards the end of the month.

2.3.3. Evolution of the micro-scale distribution of fishing effort in ICES rectangle 30E4

During the month of re-opening of the fishery inside the Trevoze Box, fishing effort in ICES rectangle 30E4 shows patchy distribution at the scale of 30 x 30 nautical miles (Table 2.5). With the exception of 2010, the degree of patchiness peaks during the first week of re-opening after which a strong decline was observed in the second week after re-opening. This decline continued in most years of analysis, resulting in lowest ID indexes in the 4th week of April in most years of analysis.

At a grid resolution of 10 x 10 nautical miles, fishing effort was still patchily distributed in most grid cells. Again, the highest values were found in the first week after re-opening and declined towards the end of the month. Nevertheless, in every week of analysis, fishing effort was randomly distributed in some grid cells ($ID_{min} \approx 1$). The strongest decline is found in the ID_{max} value, while ID_{min} is rather stable in the four weeks following re-opening of the fishery. The decline of the ID_{mean} from weeks 1 - 4 is less pronounced compared to the analysis at lower spatial resolution (30 x 30 nautical miles). These results indicate that some grid cells have a very patchy distribution of fishing effort during the first week due to intensive fishing on these patches, while other grid cells have a more equal distribution of fishing effort throughout the month of re-opening.

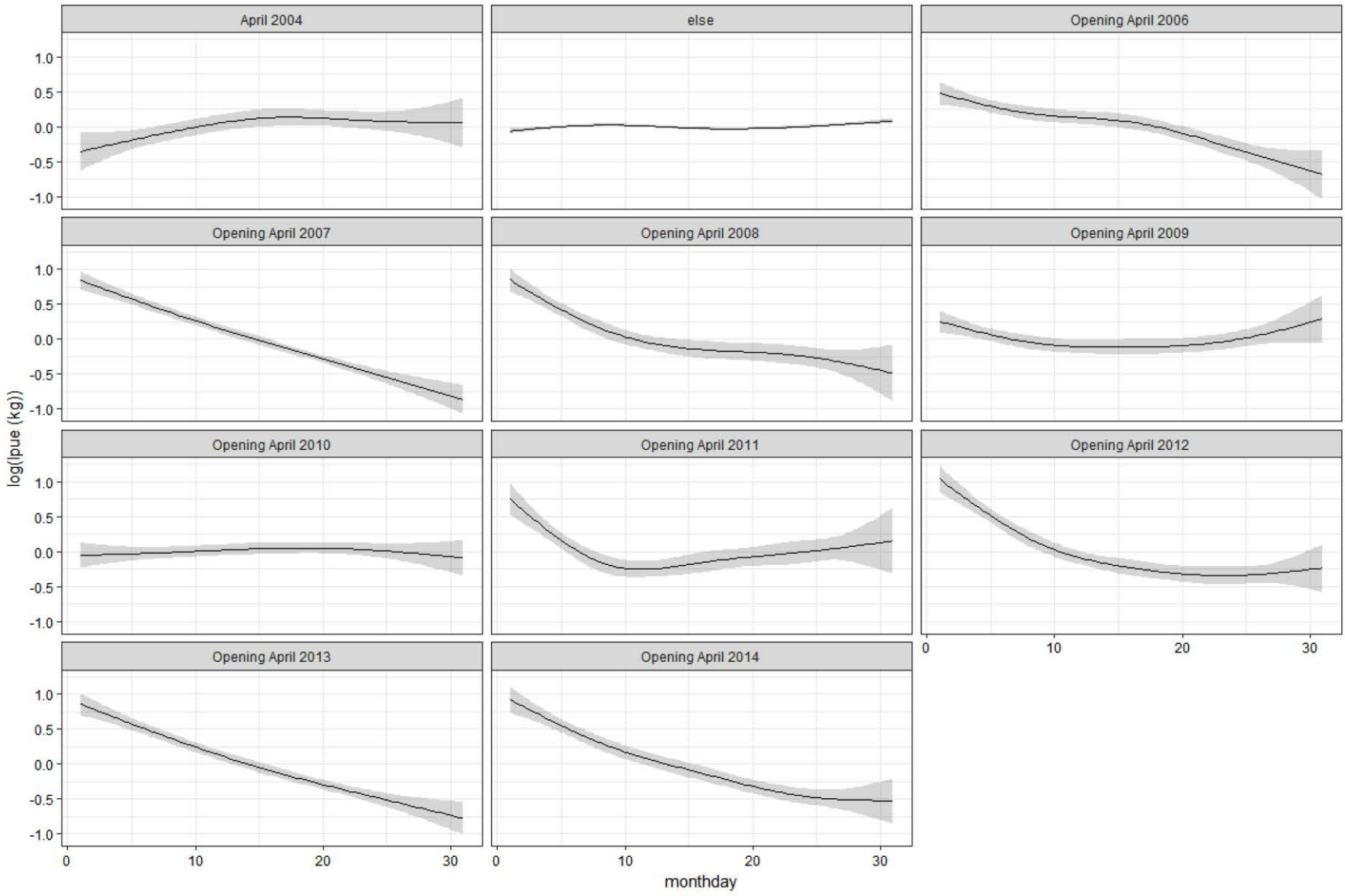


Figure 2.5 Plot of the non-parametric opening effect [$f(\text{day})_{\text{opening}}$] in $\log(\text{pue})$ of sole [equation (2.3)]. The names above the panels refer to the factor levels, and the 95% confidence interval is represented by the grey shade.

Table 2.5 Micro-scale distribution of fishing effort in ICES rectangle 30E4 during the first month after the re-opening of the fishery inside the Trevoze Box. Remark that the fleet could only exploit fishing ground > 12 nm offshore, hence part of the rectangle was not exploited. Grid cells without fishing pings were not considered for the ID calculation (*). During The study period (2006–2014), in 802/900; 97/100 and 9/9 grid cells, ≥ 1 fishing pings were registered. The rows represented by a year provide the number of grid cells trawled during the first 4 weeks of April.

year/	week	no. of grid cells trawled ≥ 1						
		N	(mean nr. of fishing pings grid cell ⁻¹)			dispersion index		
			grid resolution in nautical miles x nautical miles (nr. of grid cells)					
			1 x 1 (900)	3 x 3 (100)	10 x 10 (9)	10 x 10* (9)	30 x 30 (1)	
		N			ID _{mean}	ID _{min max}	ID	
2006			605	87	9			
	1	1328	454 (2.9)	78 (17.0)	9 (147.5)	2.37	1.22 - 3.23	33.27
	2	947	368 (2.6)	76 (12.5)	9 (105.2)	2.21	1.15 - 3.56	15.53
	3	492	252 (2.0)	68 (7.2)	8 (61.5)	1.85	0.97 - 3.03	11.24
	4	97	65 (1.5)	32 (3.0)	6 (16.2)	1.22	0 - 2.67	7.58
2007			588	84	9			
	1	2170	376 (5.8)	64 (33.9)	8 (271.3)	3.3	0.96 - 5.75	45.48
	2	1170	379 (3.1)	72 (16.3)	8 (146.3)	2.47	1.42 - 4.63	19.75
	3	746	338 (2.2)	77 (9.7)	9 (82.9)	1.85	1.19 - 2.78	13.04
	4	297	188 (1.6)	61 (4.9)	9 (33.0)	1.22	0.89 - 1.84	6.37
2008			615	84	9			
	1	1961	406 (4.8)	73 (26.9)	9 (217.9)	3.6	0.96 - 8.57	38.46
	2	1034	363 (2.8)	73 (14.2)	9 (114.9)	2.71	1.29 - 4.25	15.47
	3	495	251 (1.9)	69 (7.2)	9 (55.0)	1.78	1 - 2.55	8.2
	4	325	157 (2.1)	49 (6.6)	8 (40.6)	1.76	0.94 - 4	14.33
2009			645	87	9			
	1	2498	522 (4.8)	82 (30.5)	9 (277.6)	2.88	1.42 - 5.48	28.6
	2	982	398 (2.5)	77 (12.8)	8 (122.8)	1.64	0.94 - 2.23	12.83
	3	308	181 (1.7)	51 (6.0)	7 (44.0)	1.36	0 - 1.98	7.78
	4	149	100 (1.5)	43 (3.5)	8 (18.6)	1.55	0.9 - 3.5	5.6
2010			545	83	9			
	1	990	338 (2.9)	69 (14.3)	9 (110.0)	2.26	1.3 - 3.87	23.95
	2	765	335 (2.3)	67 (11.4)	8 (95.6)	2.4	1.16 - 5.83	11.51
	3	671	209 (3.2)	56 (12.0)	8 (83.8)	2.97	1.5 - 8.07	37.3
	4	531	235 (2.3)	58 (9.2)	8 (66.4)	2.68	1.13 - 5.62	11.97
2011			532	81	9			
	1	1048	287 (3.7)	57 (18.4)	7 (149.7)	1.8	0 - 3.28	27.89
	2	628	323 (1.9)	75 (8.4)	9 (69.8)	1.8	1.32 - 2.41	6.76
	3	422	233 (1.8)	61 (6.9)	8 (52.8)	1.64	1.13 - 3.24	8.84
	4	202	132 (1.5)	53 (3.8)	8 (25.3)	1.62	0.94 - 2.38	4.22

continued on next page

Table 2.5 continued

		no. of grid cells trawled ≥ 1 (mean nr. of fishing pings grid cell ⁻¹)			dispersion index			
		grid resolution in nautical miles x nautical miles (nr. of grid cells)						
year/	week	N	1 x 1 (900)	3 x 3 (100)	10 x 10 (9)	10 x 10* (9)	30 x 30 (1)	
		N				ID _{mean}	ID _{min max}	ID
2012			443	77	9			
	1	1147	256 (4.5)	58 (19.8)	7 (163.9)	2.64	0 - 7.3	47.98
	2	651	267 (2.4)	65 (10.0)	9 (72.3)	2.09	1.13 - 3.42	15.19
	3	225	153 (1.5)	59 (3.8)	8 (28.1)	1.3	0.94 - 1.82	5.76
	4	43	39 (1.1)	29 (1.5)	7 (6.1)	0.91	0 - 1.3	1.64
2013			604	87	9			
	1	1009	304 (3.3)	59 (17.1)	8 (126.1)	2.2	0.99 - 4.14	28.77
	2	1259	384 (3.3)	73 (17.2)	8 (157.4)	2.61	1.46 - 4.69	25.86
	3	632	291 (2.2)	68 (9.3)	9 (70.2)	1.98	0.91 - 3.91	11.64
	4	287	177 (1.6)	55 (5.2)	7 (41.0)	1.35	0 - 2.67	9.59
2014			595	87	9			
	1	1413	313 (4.5)	63 (22.4)	7 (201.9)	2.65	0 - 6.19	33.27
	2	658	254 (2.6)	68 (9.7)	8 (82.3)	2.17	0.93 - 3.67	15.53
	3	657	302 (2.2)	72 (9.1)	9 (73.0)	1.8	0.99 - 2.44	11.25
		380	214 (1.8)	64 (5.9)	9 (42.2)	1.66	0.98 - 2.3	7.58

At the scale of 10 x 10 nautical miles, no pattern is visible in the number of grid cells where trawling occurred. In most cases, trawling occurred in every grid cell, even at very low fishing intensity. During the first week after re-opening, when fishing levels were highest, not all grid cells were trawled in some years (2007, 2011, 2012, 2013 and 2014). This coincides with the high indices of dispersion found at the 30x30 resolution during the first weeks of April: the mean trawling intensity per grid cell declined sharply from week 1 to week 4. At a spatial resolution of 3 x 3 nautical miles, in most years of analysis, more cells were trawled during the second week than during the first week after re-opening, despite the higher amount of fishing effort in the first week (with the exception of 2013). This implies that fishing effort is more aggregated during the first week and tends to disperse as cumulative fishing effort increases. At the highest spatial resolution (1x1), the same trends are visible in the number of grid cells trawled where trawling occurred. Although the number of fishing pings recorded declined dramatically in the second and third week as compared to the first week, there was no corresponding decline in the number of grid cells where trawling occurred. The decline in mean trawling intensity is also less pronounced compared to the analysis at lower temporal resolution, which may indicate that fishing effort becomes increasingly randomly distributed at higher temporal resolutions. In all analyses, the patterns in 2010

differ from the other years: in that year the weekly effort, number of grid cells where trawling occurred and mean intensity are much more stable in comparison to the other years.

2.4. Discussion

2.4.1. Effect of the Trevoise Box closure on the spatiotemporal allocation of fishing effort

The Trevoise Box closure altered the temporal fishing effort allocation patterns of Belgian beam trawlers. Before the closure was implemented, fishing effort peaked during the months of February and March coinciding with the spawning season of sole in the Celtic Sea and the seasonal migration of sole into the shallow waters of the Trevoise Box (Horwood, 1993). Since the closure, effort was displaced partly to January and particularly to April. Vessels redistributed fishing effort in order to fill their individual quota for sole, the most financially valuable target species. This observed reallocation of fishing effort can be explained by the high sole landing rate in April and corroborates with the assumption that commercial fishers act rationally in terms of maximizing their profit (van Putten *et al.*, 2011). Nevertheless, this response of Belgian beam trawlers differs from other studies. In many cases, fishers often reallocated effort to other spatial areas in response to fishery closures, either to the borders of the closed area (van der Lee *et al.*, 2013; Murawski *et al.*, 2005) or to other fishing grounds (Beare *et al.*, 2013; Poos and Rijnsdorp, 2007a; Tidd *et al.*, 2012). Based on our analysis, this is related to three factors: the fishing opportunities of Belgian beam trawlers, the seasonal dynamics of the target species (sole) and the economic incentive created by the fishery closure. During the study period, Belgian beam trawlers (>221 kW) had fishing rights in different ICES divisions. Hence, Belgian fishers had the opportunity to fish in other ICES divisions during the period of the closure and were not constrained to reallocate their fishing effort to other fishing grounds within the Celtic Sea. As a result, the phenomenon of “*fishing the line*” as observed around the borders of the seasonal haddock (*Melanogrammus aeglefinus*) spawning closure on the Scotian shelf (van der Lee *et al.*, 2013) was barely observed. Instead, many beam trawlers exploited fishing grounds in the eastern English Channel (ICES division VIIId) during the closure of the Trevoise Box. Second, the seasonal closure during February and March does not fully cover the spawning period (February-April) of sole in the Trevoise Box. In April, as most adult sole have not yet returned to their offshore feeding grounds, many adult fish is left inside the Trevoise Box. Third, our analysis shows that Ipue of the target species sole was very high after re-opening of the fishery inside the Trevoise Box. Such high catch rates create a strong economic incentive to allocate fishing effort to April.

2.4.2. Analysis of the sole landing rate in the Celtic Sea

Sole landing rates of the Belgian beam trawler fleet in the Celtic Sea showed a positive log-linear relationship with the vessel's engine power. This relationship was also found in the Dutch beam trawler fleet (Rijnsdorp *et al.*, 2000a). Poos *et al.* (2010b) demonstrated that Dutch beam trawlers increased engine power (*i*) to fish at higher speeds, increasing the swept-area-per-unit-effort, and (*ii*) to use more chains in front of the net-opening to increase the penetration depth of the gear, resulting in higher landing rates of more deeply buried flatfish.

Lpue of sole rose during the study period and was characterized by a remarkable increase since 2010. We hypothesize that this is related to both the dynamics of the Celtic Sea sole stock and the dynamics of the beam trawler fleet. High recruitment in 2008 may have resulted in strong year-classes since 2010, and thus higher catchability of adult sole (ICES, 2015). Despite the lack of a clear positive trend in the spawning stock biomass of sole in the Celtic Sea, we believe that the changes of the Belgian beam trawler fleet had a more substantial effect on the increase in the sole landing rate. As a result of rising energy prices and a decommissioning round within the Belgian fisheries sector in 2009, the Belgian beam trawler fleet now has fewer vessels. Because mainly older and less efficient vessels are likely to have been withdrawn from the fleet (Tidd *et al.*, 2011), the remaining vessels are expected to have higher technical efficiency. Moreover, the sharp rise in fuel prices in 2008 was an important trigger for the remaining vessel owners to invest in energy-saving technologies. From 2008 to 2010, many vessels replaced their old engines and traditional beam trawl gears were modified (Platteau *et al.*, 2016) to reduce the towing resistance of the gear by replacing the traditional shoes with wheels, using hydrodynamic wing profiles, lighter nets, etc. We argue that both the withdrawal of less efficient vessels and the wave of technological development may have resulted in a technological creep in the Belgian beam trawl fishery, and are as such important drivers of the increase in lpue of sole of the Belgian beam trawler fleet.

The typical exploitation dynamics of beam trawlers during a fishing trip is reflected by the pattern of the nonparametric intra-trip effect. Since flatfish concentrations cannot be detected through equipment such as echo sounders, fishers search for good fishing spots using trial and error: they perform a series of short hauls over a large surface area (Rijnsdorp *et al.*, 2011). This explains the lower sole landing rates at the start of a fishing trip. Once a good fishing spot is detected, an exploitation phase follows, during which landing rates are stable and high. The decrease of the sole landing rate at the end of a trip may be due to either depletion of the fishing ground or continued fishing on the return trip, including less abundant fishing grounds.

Since 2006, the landing rates of sole in the Trevoise Box were characterized by a strong re-opening effect. Immediately after re-opening, the landing rates of sole were much higher inside the Trevoise Box followed by a sudden decline in the first days after re-opening. Landing rates had returned to the reference level within 1 - 3 weeks. Although the decline in l_{pue} of sole differed among the analysed years, several years showed a similar pattern characterized by an exponential decline in the first weeks of April. Such a declining trend in l_{pue} of sole on fishing grounds where intensive trawling occurred during consecutive weeks was also found in studies of Rijnsdorp *et al.*, (2000b) and Maury and Gascuel (2001). This opening effect and decline of l_{pue} of sole corresponds with the observed temporal allocation of fishing effort after reopening of the Trevoise Box. The high sole landing rates results in temporary high revenues for fishers, but they rapidly return to a normal level. Hence, assuming rational profit maximization behaviour, the best strategy is to fish as much as possible as soon as possible. As a result, after re-opening of the Trevoise, this results in a temporal *race for fish*.

There are three anomalies in the results: no race for fish in the first week of April 2013, a slight increase of l_{pue} sole during April 2004, and anomalies in the data for April 2010. All three can be explained by other factors not included in the analysis. First, the absence of a race for fish during the first week of April in 2013 does not correspond with the high l_{pue} of sole during that week. This can be explained from the meteorological conditions. The low temperatures during that first week (ca. 0°C) made the conditions for beam trawling less favourable. After the temperature returned to a normal level in the second week, a sharp increase in fishing activity was observed. Second, only a slight increase of l_{pue} sole during April 2004 was noted, which contrasts with the migration of sole away from the spawning grounds in the Trevoise Box. However, we believe that the increase might be due to the intensive fishing inside the Trevoise Box during February-March of that same year. The fishing effort may have resulted in a local depletion of the fish stock (exploitation competition) after which replenishment occurred at lower fishing intensities. Such a replenishment of the local stock could also explain why l_{pue} of sole increased during April 2009, 2011 and 2012 again at the end of the month (Figure 2.5). Third, both the dynamics of l_{pue} of sole and the exploitation patterns of Belgian beam trawlers differ in April 2010 from the expected pattern. There is no clear reason why l_{pue} of sole during April 2010 did not show either a declining pattern or a race for fish. A possible explanation can be found in the dynamics of the Celtic Sea sole stock. The number of age 1 recruitments of sole in the Celtic Sea in 2010 was very low compared to the other years of our analysis (ICES, 2015), which may indicate that spawning conditions were different during that year.

2.4.3. *Microscale distribution of fishing effort*

Our study revealed that the spatial distribution of fishing effort in the Trevoze box during the month of re-opening of the fishery showed a characteristic pattern. With the exception of 2010, distribution of fishing effort was always very patchy immediately after re-opening of the fishery, as indicated by the high ID indices during the first week. Afterwards, ID indices declined, with the strongest decline occurring between week 1 and 2 at the lowest spatial resolution (30 x30 nautical miles). This implies that fishing effort tends to spread during the month of re-opening of the fishery. ID indices are always highest at the lowest spatial resolution. At a grid resolution of 3x3 nm, ID indices of some grid cells are ~ 1 , especially when fishing intensity decreases towards the end of the month, indicating that fishing effort is normally distributed. This is in agreement with Rijnsdorp *et al.* (1998) who found that beam trawl effort is patchily distributed in grid cells of 3x3 nautical miles at lower fishing intensities.

Furthermore, our results showed that there is a strong relationship between both the temporal pattern of fishing effort distribution and the sole landing rate in the Trevoze Box during the month of re-opening. Both patterns show a similar decline that is steepest between week 1 and 2, after which fishing effort dispersion and l_{pue} of sole return to a stable reference level. The corresponding patterns of the micro-distribution of fishing effort and the high landing rates immediately after re-opening give indirect evidence of the occurrence of high densities of sole just after re-opening of the closed area. Nevertheless, we did not take into account other factors such as fish behaviour, environmental conditions and competitive interactions, which may also affect this relationship.

Our study does not provide insights into the underlying mechanisms that cause the peak in l_{pue} of sole just after re-opening and the strong decrease of l_{pue} sole when the fishery starts. Therefore, more specific studies such as tagging experiments that allow constant monitoring of fish species, analysis of stomach contents and laboratory experiments, are required. Nevertheless, we propose a different mechanism to explain our results.

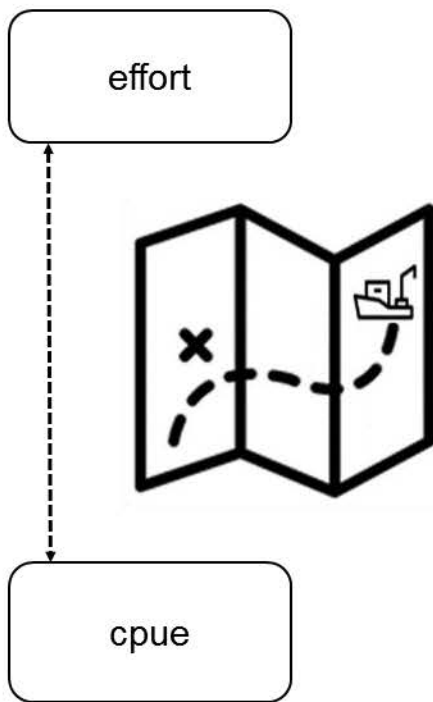
The diet of sole primarily consists of benthic organisms, such as bivalves or polychaetes (Rijnsdorp and Vingerhoed, 2001). The temporal aggregation of fishing effort is an important factor determining the impact of beam trawling on these benthic communities (van Denderen *et al.*, 2014). We assume that a temporal effort reallocation during which the benthic communities are not disturbed will have a positive effect on the growth of benthos biomass, will increase the availability of food for the target species sole, and will in turn increase sole abundance.

Our study showed that lpue of sole returned to its reference level after 1 - 3 weeks after re-opening. This is reflected by the dispersion of fishing effort and suggests that local concentrations of fish are depleted after 1 - 3 weeks. This is in agreement with Poos and Rijnsdorp (2007b) who showed that local patches of sole and plaice persist up to 2 - 3 weeks on the scale of 20 - 30 nautical miles. In this study, two hypotheses, namely a food web interaction (assuming that flatfish species require 2 - 3 weeks to deplete a local concentration of prey) and a fishery dependent interaction (exploitation competition leading to resource depletion by the fishery) were proposed to explain the persistence of flatfish concentrations up to 2 – 3 weeks. The results of our study, in which a strong relationship between fishing effort and lpue of sole was found, support the mechanism of exploitation competition. This is also supported by the deviating pattern in 2010, during which fishing intensity was lower but more stable and the spatial distribution of fishing effort was more stable. In that year, lpue did not decline during re-opening.

A second mechanism to explain the decline in lpue may be found in fish response to the passage of beam trawl gear. The noise and vibrations created during towing of the beam trawl gear over the seafloor may induce evasive behaviour such as digging deeper into the sediment (Poos *et al.*, 2010b).

Despite the grounded theoretical basis that justifies the implementation of spawning closures (van Overzee and Rijnsdorp, 2015), barriers hamper the successful implementation of such spatial management tools. This is especially the case for trawl fisheries that target flatfish species owing to their high degree of complexity. Rijnsdorp *et al.* (2012) demonstrated that a spawning closure for plaice (*Pleuronectes platessa*) in the North Sea beam trawl fishery would be desirable for the plaice stock but would have adverse ecological effects as well. The spawning stock biomass of sole would decrease and an increase would occur in the trawling impact on benthos. This complexity gives rise to different ecological and economic trade-offs which are differently valued by various stakeholders and may as such hamper the design of fisheries management tools. In addition, our study showed that the interaction between a beam trawl fishery and its flatfish resource has a high degree complexity which can result in local overfishing and nonlinear trends in cpue. This corroborates with the findings of Maury and Gascuel (2001) who demonstrated a similar nonlinear relationship in cpue when local overfishing occurred by non-cooperative vessels with a high capacity to detect fish. Such nonlinear relationships obstruct fisheries managers to make accurate predictions about fishing effort allocation, hence, ecological effects may be not as foreseen due to e.g. changes in spatiotemporal trawling frequency of the seafloor, and also social effects may be unforeseen due to e.g. increased competition between beam trawlers in the remaining open areas (Poos and

Rijnsdorp, 2007a). These challenges can be addressed through consulting various stakeholders while defining management objectives and by real-time management tools that cope with the dynamics of the fishery.



CHAPTER 3

Fishing tactics of commercial beam trawlers, the missing link between effort and landing data

Abstract

In this chapter, the effect of the tactical decision of Belgian beam trawlers on the revenue and landing rates of sole and plaice is analysed. Location data of the commercial Belgian beam trawl fleet (engine power > 221 kW) available through the VMS data was transformed into information on vessel's step lengths and turning angles which was subsequently used to fit Hidden Markov Models. This analysis demonstrated that fishing trips of beam trawlers are characterized by 3 different states: exploration, exploitation and steaming. In few trips, a fourth state was detected which represented no movement. The covariates demonstrated that if a grid cell has been trawled during a fishing trip, a vessel is more likely to change to the exploitation state. To test the validity of the identified behavioural states, the exploration and exploitation fishing pings were coupled to logbook data. Analysis of the revenue rate demonstrated a stronger positive relationship associated with the exploitation behaviour compared to the exploration behaviour. Similar relationships were found in the landing rates of the target species plaice and sole with respect to the ICES subdivisions. The results of this chapter demonstrate that fishing tactics are strongly related to the target behaviour of the fleet and, as a result, may improve both the standardization of fishing effort and the coupling between VMS and logbook data at high spatiotemporal resolutions.

3.1. Introduction

Management through total allowable catches (TACs) based on single-species advice, has often failed in fisheries where multiple species are caught simultaneously (mixed fisheries; Daan, 1996; Vinther *et al.*, 2004; Rijnsdorp *et al.*, 2007). Fishing activity is likely to continue as long as it is profitable to catch fish species for which the quota have not been met. This practice results in discarding and possible misreporting of species for which the quota has been met (Gillis *et al.*, 1995; Poos *et al.*, 2010a; Batsleer *et al.*, 2016), and leads to a discrepancy between policy and practice, where fishing effort and related fishing mortality in mixed fisheries are not aligned with the individual species quota. To overcome this problem, alternative management approaches that focus on input controls (e.g., fleet-based measures) have been proposed. Examples of such a tools are Total Allowable Effort (TAE) eventually combined with Individual Effort Quota (IEQ) (Rijnsdorp *et al.*, 2007) or dynamic fisheries management tools such as Real-Time Closures (Needle and Catarino, 2011) or Real-Time Incentives (RTIs) (Kraak *et al.*, 2012; Little *et al.*, 2015).

A key element in the design of effort-based management systems is insight into the relationship between fishing effort and fishing mortality. If this relationship is inadequately incorporated into effort-based management systems, such management systems are not likely to perform better than management approaches that rely on TACs regarding mixed-fisheries management (Baudron *et al.*, 2010). This happened for instance in the demersal fishery in the Faroe Islands where an effort-based management system failed to reduce fishing mortality of cod (*Gadus morhua*) due to the fact that the targeting behaviour of the fleet was insufficiently integrated in the effort-based management system (Jákupsstovu *et al.*, 2007). Indeed, the target behaviour of a fleet is strongly related to the strategies and tactics of fishers, which has in turn implications for the standardization of fishing effort and thus fishing mortality (Marchal *et al.*, 2006). While fishing strategies are often incorporated into management of mixed-fisheries through the *métier* concept (Ullrich *et al.*, 2012), fishing tactics received little attention with respect to the design of fisheries management. Now the mandatory vessel monitoring system (VMS) offers an increased availability of data at high spatiotemporal resolution to address this gap. These data allows to reconstruct fine scale movement and dispersion patterns of fishing fleets, analyse these patterns, and eventually couple them to catch or landing data to make inferences about fishing tactics and/or the dynamics of the fish stocks.

The location data available through VMS can be used to describe vessel trajectories, and to extract turning angles and step lengths in these trajectories. Based on this information, Hidden Markov Models (HMMs) can be used to detect different behavioural states of

individuals (Patterson *et al.*, 2008). Vermard *et al.* (2010) tested the applicability of this method in a fisheries context, different HMMs - with a vessel's speed and turning angle as model parameters - were used to simulate data under various conditions. These simulated data was compared to HMMs that were fitted to the VMS data of pelagic trawlers in the Bay of Biscay. The different behavioural states of the simulated data could be related to the observed states. This demonstrated the applicability of the method to identify the relevant behavioural states (steaming, fishing, stopping) of fishing vessels if the temporal interval (*i*) between the majority of the data points is constant, and (*ii*) is adequately defined to capture the different behavioural modes.

Several authors have used the HMM approach to analyse vessel trajectories with respect to different behavioural states of fishing vessels since (e.g. Bez *et al.*, 2011; Peel and Good, 2011; Joo *et al.*, 2013; Gloaguen *et al.*, 2015; De Souza *et al.*, 2016) To our knowledge, only one study has linked landing data with the different behavioural states identified in a HMM model: Charles *et al.* (2014) demonstrated the potential of using HMM derived movement variables to improve catch standardization in the static snow crab (*Chionoecetes opilio*) fishery. In that fishery the patterns in the landing rates per unit effort were related to the different behavioural modes of fishing vessels.

If different behavioural modes exist in a mixed fishery and could be related to the landing rates of the different species caught, this could provide insight into (*i*) the classification of target and bycatch species, (*ii*) the spatiotemporal correlation structures between the abundance of different species, (*iii*) data anomalies, (*iv*) the accuracy of dispatching landing data in space and time, and (*v*) the standardization of catch-per-unit-effort.

In the present study, we analyse the targeting behaviour of the Belgian beam trawler fleet, a mixed fishery targeting several demersal fish species. Various Hidden Markov Models were fitted to vessels' step lengths and turning angles – derived from the VMS data – to identify the unobserved activities of beam trawlers. Based on the results of this analysis, fishing activity is linked with the landings of sole (*Solea solea*) and plaice (*Pleuronectes platessa*) as registered in the electronic logbooks. This allowed us to analyse the relationship between the behavioural states of a beam trawler and the landing rate of various species and to examine the correlation structures between the landing rates of different species with respect to fisher behaviour.

3.2. Materials and Methods

3.2.1. *The Belgian beam trawl fishery*

The study fleet comprised all Belgian fishing vessels with engine powers ranging from 662 kW to 1200 kW that tow heavy beam trawls over the seafloor. These vessels have fishing rights in different International Council for the Exploration of the Sea (ICES) subdivisions where they target a wide range of demersal flatfish and roundfish species. Sole and plaice are the most important species in terms of landed weight and value, but depending on the season, location and available quota, other species such as anglerfish (*Lophiidae spp*), cod (*Gadus morhua*), lemon sole (*Microstomus kitt*), turbot (*Psetta maxima*), and brill (*Scophthalmus rhombus*) are also targeted.

These beam trawlers make fishing trips with an average duration of nine days that consist of a series of hauls with an average duration of 2 h haul⁻¹. When fishing in distant areas, they often stop in foreign harbours and load the landings into refrigerated trucks for transport to a Belgian harbour, thus saving time and steaming costs. Consequently, the exploitation pattern of this fleet segment is characterized by so-called “campaigns”: periodic cycles during which the fleet goes to a (distant) ICES subdivision to catch the quota of the most valuable species. As a consequence, the course of a fishing trip is variable, e.g. fishing trips on distant fishing grounds that start or end in Belgian harbour may begin or end with 2 or 3 days of steaming, respectively, while other trips have fishing records in multiple ICES subdivisions alternated with longer periods of steaming.

3.2.2. *Data*

In the present study, vessel monitoring system (VMS) data from 2006 until 2015 was used to analyse vessel trajectories. This includes a vessel's position (geographical coordinates expressed as latitude and longitude), speed (in knots), heading direction (degrees), time stamp (year-month-day-hours-minutes) and reference number. This dataset was matched with vessel logbooks to assign a trip reference number to each VMS record. The step lengths (km) were obtained by calculating the distance between two consecutive fishing points using the Haversine formula that accounts for the curvature of the earth, while the angle formed by three consecutive VMS points was used as turning angle (radians). For analysis, fishing trips were extracted where the time interval between consecutive VMS records was approximately 2 h and maximum one missing record (time interval of 4h between 2 points). In summary, 95267 VMS records of 1186 different trips were retained for analysis. In 95% and 5% of all VMS points, the time interval between 2 consecutive points was between 114 to 122 minutes and from 230 to 248 minutes, respectively. An example of the pre-processed data of a single trip is provided in Figure 3.1.

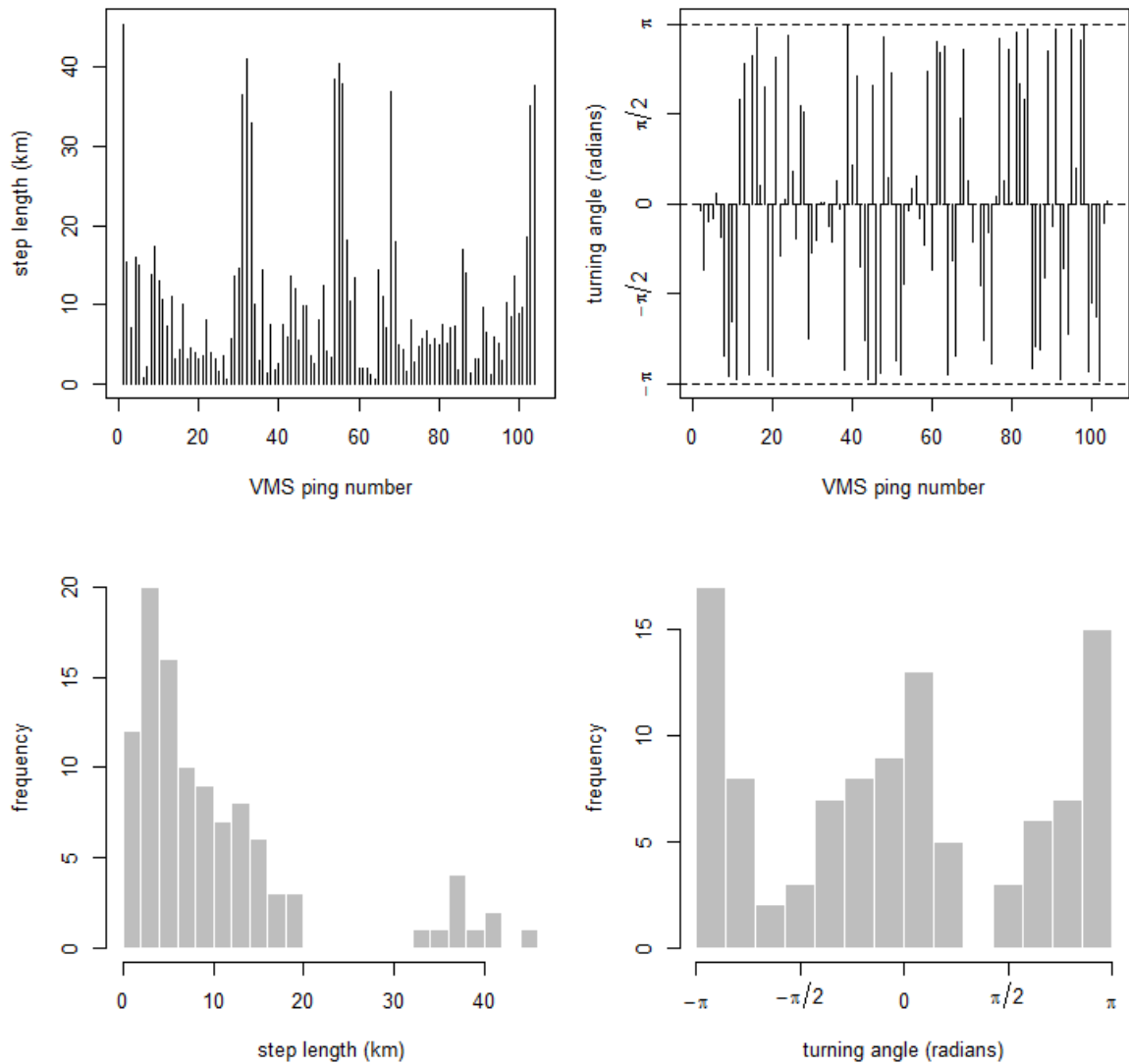


Figure 3.1 Plot of the step lengths (left panels) and turning angles (right panels) as obtained from the VMS data of a single fishing trip. The upper panel illustrate the chronological sequence while the lower panels show the frequency distributions.

Based on this dataset, two additional variables were created and used as covariates in the HMMs. An *id_nr* variable with a triangular distribution taking a value of 0 in the middle of a fishing trip and linearly increasing to a value of 1 at the first and last VMS record of a fishing trip. These variables were used to account for the different behavioural modes (such as steaming) which is more likely to occur at the start and end of a fishing trip when leaving or returning to the harbour. To account for a memory effect, we included a variable *previously_trawled*. For each grid cell (10 x 10 nm) where a vessel is fishing, the variable takes either a values of 1 (if the cell has been visited before within the trip), or a value of 0 (if not).

To analyse the revenue rate and landing rates of plaice and sole, data from the electronic logbooks was used. The logbooks contain the daily landings (kg) and ex-vessel prices (€)

of all commercial species and include a vessel and trip reference number. Logbook records were only used if they met two criteria: they could be matched to the VMS data used for the vessel trajectory analysis and they contained VMS fishing points within a single ICES subdivision.

Table 3.1 Summary statistics (n= number of logbook records; sd= standard deviation, zero= frequency of logbook records in which no landings were recorded) of the revenue and landings of plaice and sole per ICES subdivision for the logbook records that could be linked to the VMS data used for analysis.

	n	revenue (€)		sole landings (kg)			plaice landings (kg)		
		mean	sd	mean	sd	zero	mean	sd	zero
IVb	474	6978	3178	191	175	15	1427	1017	1
IVc	1667	4628	2823	284	224	85	344	456	135
VIIa	810	6057	3582	280	250	32	225	257	62
VIIId	2643	6714	3387	359	235	48	440	490	94
VIIe	534	4745	2584	64	128	145	237	283	73
VIIIfg	2464	6615	3458	281	217	77	63	101	717
VIIh	3	6428	4920	423	454	0	0	0	3
VIII	609	6332	3040	464	248	0	1	10	575

3.2.3. Hidden Markov Model

Vessel trajectories were analysed through fitting different Hidden Markov Models to the VMS data. The key idea of this approach is that a vessel trajectory is a result of processes driven by different behavioural modes of a fishing vessel during a single trip. Such a sequence of states is assumed to be generated by a Markov chain in which each state has an initial probability, i.e., the probability that the system starts in a specific state, and a transition probability of going from one state to another. In the case of VMS data, these states cannot be observed directly from the data, and are thus hidden. Therefore, the corresponding initial and state transition probabilities of the Markov model are parameters that cannot be calculated directly from the data and need to be estimated; this is done by maximizing the likelihood function. Once the models have been fitted to the data, the state sequence with the highest probability of occurrence is assigned to the data using a recursive dynamic programming algorithm.

The step length and turning angle between consecutive VMS points during a fishing trip are used to describe the different behavioural movement modes. A Gamma and Wrapped-Cauchy distribution were selected to model the step lengths and turning angles, respectively (Vermard *et al.*, 2010). Similar to the transition probabilities, the parameters that characterize these state-dependent distributions are not known *a priori* and should thus be

estimated using a set of starting parameters. For each HMM, 5 sets of values were given to the starting parameters to increase the probability that the estimation algorithm will find the model parameters associated with the global optimum (Michelot *et al.*, 2016). The parameters for the step lengths were sampled from three normal distributions that reflect fishing, steaming and no movement with mean 10, 30 and 1, and variance 5, 15 and 0.5, respectively. The mean and concentration parameters for the wrapped Cauchy distribution were sampled from two uniform distributions within the interval $]-\pi; \pi[$ and $]0;1[$, respectively.

For a beam trawler, we suggest that the number of behavioural modes is assumed to range from 2 to 4. Obviously, a *steaming* and *fishing* mode are included in each HMM. Steaming occurs when fishing vessels need to travel either from a harbour to a fishing ground and vice versa, or between fishing grounds. *Fishing* represents the process of deploying, towing and retrieving the gear to catch fish. We assume that fishing can be represented by one or two behavioral modes: exploration or exploitation. Because hot-spots of flatfish cannot be detected through electronic equipment such as vessel finders or echo sounders due to absence of a swim bladder, beam trawlers find local hotspots of flatfish through a trial-and-error method, which results in *exploration* and *exploitation* phases during a fishing trip (Rijnsdorp, 2000b; Rijnsdorp *et al.*, 2011). A fourth state was included that represents *no movement*, which may occasionally happen for various reasons such as making repairs to the nets or equipment. Based on these states, four different HMM scenarios were tested: *steaming and fishing* (HMM1); *steaming, fishing and no movement* (HMM2); *steaming, exploration and exploitation* (HMM3); *steaming, exploration, exploitation and no movement* (HMM4).

These models were compared based on the Akaike Information Criterion (AIC) and normality of the pseudo-residuals (Patterson *et al.*, 2009). The AIC is a measure based on a models' likelihood but includes a penalty for the number of estimated parameters to discourage overfitting. Plotting the quantiles of the pseudo-residuals against the theoretical quantiles of the normal distribution indicates how well the model reflects the true data-generating process.

3.2.4. *The effect of fishing tactics on landing rates*

To examine the relationship between a vessel's activity and landing rates, the states detected by the HMMs were coupled to the logbook data. First, each VMS record was linked to a logbook record based on the vessel's reference number and date, which are included in both datasets. Next, additional columns were added to the logbook data that contained the frequency of the different states that could be linked to each logbook record. Finally, an

additional columns was added that included the frequency of fishing pings in each ICES subdivision linked to a particular logbook record.

The relationship between the exploitation and exploration strategies of beam trawlers and the landing rates of various species were analysed in Generalized Linear Models (GLMs). Hereto, the landings and revenues were standardized to one VMS fishing ping by dividing the landings and revenues by the number of VMS points assigned to the fishing state. A null model was specified in which the $rpue$ and $lpue$ of sole and plaice were modelled in function of an intercept [equation (3.1)]. This null model was compared with a model that accounted for the amount of exploration and exploitation behaviour with respect to one fishing ping [equation (3.2)]. Hereto the exploration and exploitation fishing pings were divided by the total number of fishing pings. Hence, the values of the *exploration* and *exploitation* variables ranged from 0 to 1. To reduce noise from logbook events with fishing activity in different ICES subdivision, the GLMs were fitted to subsets of the data per ICES subdivision. Due to the limited number of logbook records that had fishing activity exclusively in the Western Celtic Sea (VIIh), this ICES subdivision was excluded from the analysis. A negative binomial distribution and logarithmic link function were specified for the distribution of the error term and the relationship between the linear predictor and mean of the distribution function, respectively. Likelihood ratio test were used to compare the following GLMs :

$$\log(lpue) \text{ or } \log(rpue) = \beta_0 + \varepsilon, \quad (3.1)$$

$$\log(lpue) \text{ or } \log(rpue) = \beta_1 x \text{ exploration} + \beta_2 x \text{ exploitation pings} + \varepsilon. \quad (3.2)$$

3.2.5. Linking the landings with VMS data

The landings from the logbook records were distributed across the VMS fishing pings in two ways. An equal distribution of a species' landings as recorded in the logbooks across the fishing pings that have been matched to that logbook record (Hintzen *et al.*, 2012), and a distribution accounting for the different behavioural modes related to fishing activities (state 1 and 3) linked to a particular logbook record. In this way, the GLMs are used to predict the landings of a species given the observed frequencies of the different fishing states of a logbook record. Based on this prediction, the ratio of landings to be assigned to the exploration and exploitation fishing pings was calculated. Finally, these ratios were used to distribute the observed landings across the various fishing pings, with the difference between the real value and the predicted value equally distributed over all landings. This was done for the landings of sole in the Southern Part of the North Sea (IVc) and the Irish Sea (VIIa). To analyse the effect of fishing activity on the spatial distribution of landings,

sole landings were distributed over a grid with resolutions ranging from 1 cell per ICES statistical rectangle (30 x 30 nm ~ 55 x 55 km) to 200 x 200 cells per ICES statistical rectangle (0.15 x 0.15 nm ~ 300 x 300 m).

All analyses were performed with the open source software 'R' (version 3.4.1) (R Core Team, 2016). The vessel trajectories were analysed using the *moveHMM* package (Michelot *et al.*, 2016), and regression analysis was performed using the *MASS* package (Venables and Ripley, 2002).

3.3. Results

3.3.1. Vessel trajectory analysis

The values of the starting parameters supplied to the maximum likelihood estimation algorithm did not affect the outcome of the optimization routine. As a result, equal values were found for the step length, turning angle, initial state and transition probability parameters for all fitted Hidden Markov Models with respect to their number of hidden states. This implied that the two HMM scenarios with three hidden states (*steaming, fishing and no-movement* and *steaming, exploitation and exploration*) converged to one single model with the 3 states being *steaming, exploitation and exploration*.

Based on the Akaike Information Criterion, the model with 4 (973274) and 3 (989222) hidden states performed best, while the model with 2 hidden states had the highest AIC (1021613). Plotting the pseudo-residuals against the theoretical quantiles of a normal distribution confirms that the HMMs with 3 and 4 hidden states fit the data better, especially with respect to the turning angles (Figure 3.2). Based on the results of the AIC and the normality of the pseudo residuals, it is more likely that the true data generating process is represented by the HMMs with 3 or 4 hidden states. Therefore, the rest of the results section focuses on the HMMs with 3 and 4 hidden states.

These models have identical parameters for the step lengths and turning angles for 3 states (Figure 3.3). This implies that the HMM with 4 hidden states is similar to the HMM with 3 states, except that it includes an additional state which had been assigned to less than 1% of all VMS points. This fourth state (state 4 = *no-movement*) has a zero mass parameter of 0.99, implying that the step length was 0 in 99% of the VMS records that were assigned this state, and a uniform distributed turning angle which indicates the occurrence of a stationary phase in a vessel trajectory. The 3 other states include a movement mode characterized by straight motion with larger step lengths (state 2 = *steaming*), a movement mode with short step lengths and sharp tuning angles around π indicating local movement (state 1 = *exploitation*), and a movement mode with intermediate step lengths and turning angles

ranging between $-\pi/2$ and $\pi/2$ (state 3 = *exploration*). These movement modes are referred to below as steaming (state 2), exploitation (state 1) and exploration (state 3), respectively.

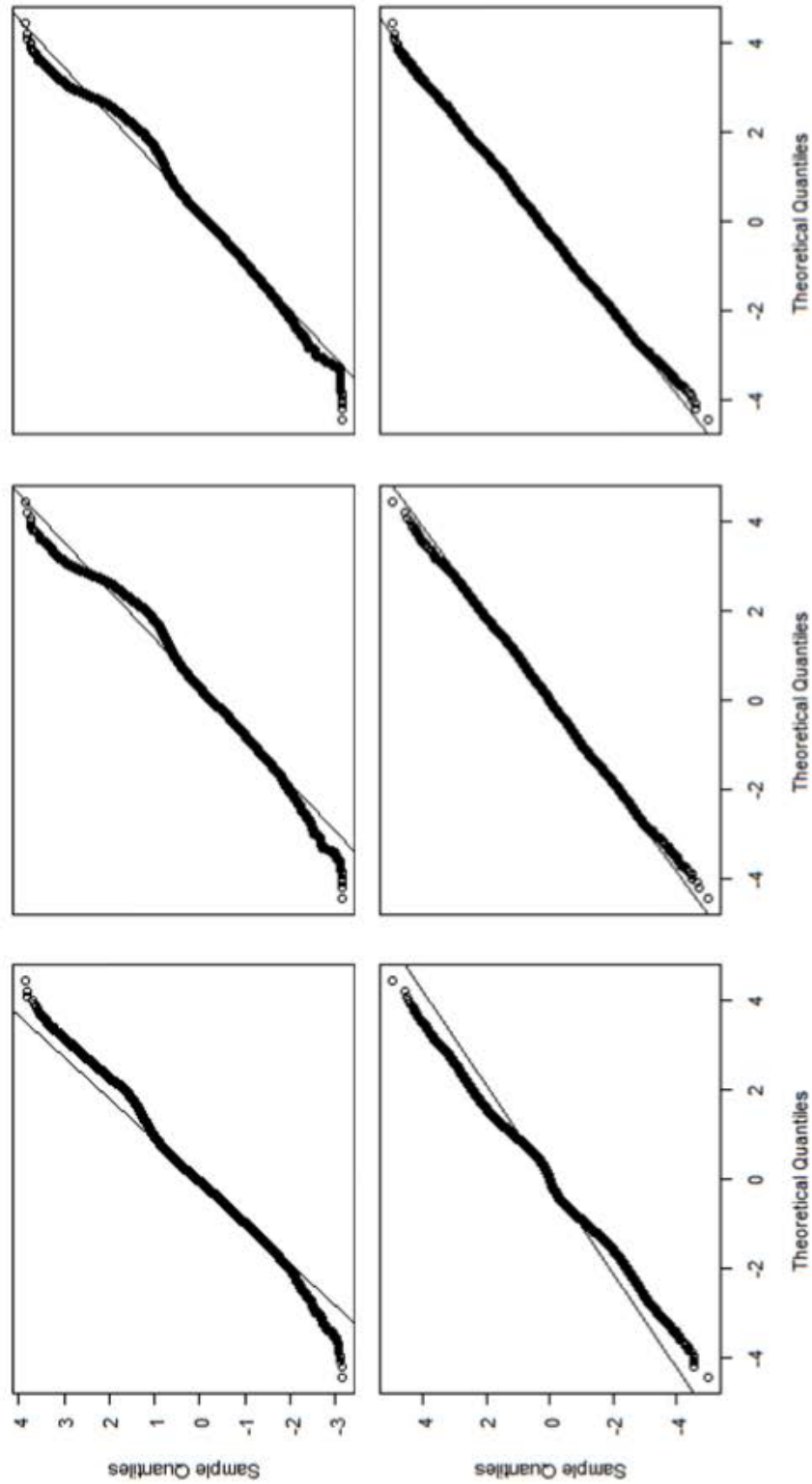


Figure 3.2 Quantile-quantile plots of the step length (upper row) and turning angle (lower row) pseudo-residuals of the estimated Hidden Markov Models with 2 (left panels), 3 (middle panels), and 4 (right panels) hidden states.

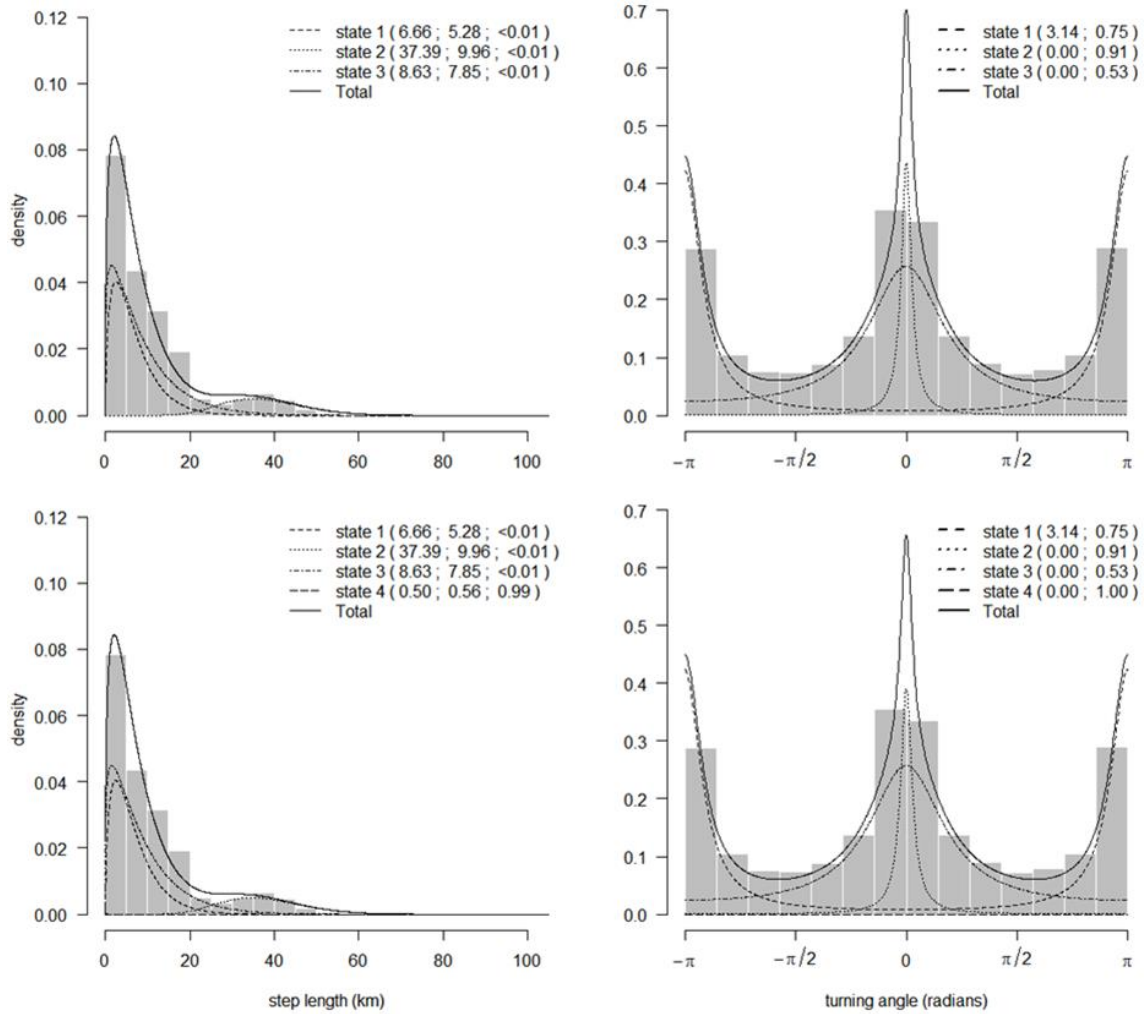


Figure 3.3 Histograms of the step lengths and turning angles of the VMS data overlaid with the densities of the fitted model parameters per state (state 1 = exploitation; state 2 = steaming; state 3 = exploration; state 4 = floating). The values between brackets are the mean, standard deviation, and zero-mass parameters of the Gamma distribution and the mean, standard deviation, and zero-mass parameters of the Wrapped Cauchy distribution with respect to the step lengths (km) and turning angle's (radians), respectively.

According to the initial state probabilities, 83% of the vessel trajectories started in the steaming phase and 13% in the exploration phase. When a vessel is in the steaming state, the coefficient of the intercept shows that vessels are 100 times much more likely to enter the exploration (est. coef. = -1) phase than the exploitation (est. coef. = -100) phase. The probability to return from the fishing state to the steaming phase is also highest for a vessel in the exploration state, especially at the beginning or ending of a fishing trip. The probabilities associated with transitions from state 1 (exploitation) to 3 (exploration) and vice versa were less pronounced but are affected by the coefficients associated with the covariates of the HMM. The stronger negative value of the *id_nr* covariate on the transition probability (-0.57) from the exploration to the exploitation state compared to the transition from state 1 to 3 (-0.03) implies that it is more likely for a vessel to go to the exploitation state in the middle of a fishing trip. In addition, the effect of the *previously_trawled* covariate

is more pronounced on the transition probability to go from exploration to exploitation (1.05) compared to the opposite transition (0.36). This indicates vessels are more likely to stay on a fishing ground if that grid cell has already been trawled during the trip. All transition probabilities related with state 4 (no movement) are negative. This implies that it is not likely for a vessel to go to this state, nor for it to transition from state 4 to another state. This indicates that this behavioural mode is a data artefact that occurs at the last point of a fishing trip.

3.3.2. *Linking fishing activity to the revenue and landing rates of sole and plaice*

For each ICES subdivision, a significant positive relationship was found between the number of fishing pings and the revenue per unit effort (rpue). Including the different fishing activities as explanatory variables in the GLMs improved the models in terms of likelihood ratio (Table 3.2). Except for the Western English Channel (VIle), the difference of the effect on rpue between exploration and exploitation behaviour was less pronounced. The fishing pings associated with exploitation behaviour had a stronger positive value compared to the exploration fishing pings, indicating a stronger increase of revenue during the exploitation phase compared to the exploration phase. This difference was most pronounced in the Irish Sea (VIIa).

The GLMs of the revenue rate are reflected by those of the landing rate per unit effort (lpue) of the most valuable species, sole (Table 3.2). Including the exploration and exploitation behavioral states improved the GLMs for the Southern Part of the North Sea (IVc), the Irish Sea, the Eastern English Channel (VIId), the Celtic Sea (VIIf,g) and the Bay of Biscay (VIIIa,b). In each of these ICES subdivisions, the exploitation behaviour showed a stronger positive slope than the exploration behaviour, which confirms the expectation that sole is targeted in these ICES subdivisions (Table 3.1). Similar to the rpue, the strongest difference between the slopes associated with exploitation and exploration behaviours was found in the Irish Sea. In the Central Part of the North Sea (IVb), a positive effect was found between the number of fishing pings and the sole landing rate; however, differentiating between both fishing activity modes did not improve the model. In the Western Celtic Sea, no relationship between fishing activity and lpue of sole was found, implying that more fishing did not affect the daily landing rate for sole.

A positive effect of fishing activity on the daily landing rates of plaice was found in ICES subdivisions IVb, IVc, VIIa, VIId, VIIe and VIIfg, while a negative effect was found in VIII. However, this can be explained by the fact that in approximately 95% of the logbook records in the Bay of Biscay no plaice had been caught (Table 3.1). Including the type of fishing activity could only improve the GLMs of lpue plaice in the Central Part of the North Sea and

the Eastern English Channel. In the Central Part of the North Sea, where plaice is expected to be targeted by the fleet (Table 3.1), a stronger positive slope is associated with exploitation behaviour compared to exploration behaviour. In contrast, the GLM of the lpue of plaice in the Eastern English Channel revealed a counterintuitive result being a stronger positive relationship associated with the fishing pings related to exploration behaviour compared to the exploitation behaviour.

Table 3.2 Estimated coefficients (coef), standard errors (se) and *p-values* (*p*) of the GLMs (eq. 3.1 and 3.2) with revenue per unit effort (rpue), and landings per unit effort (lpue) of sole and plaice in each ICES subdivision as response variable. The last column gives the *p-value* of the model comparison (log likelihood ratio test).

	β_0			β_1			β_2			ANOVA
	coef	se	<i>p</i>	coef	se	<i>p</i>	coef	se	<i>p</i>	<i>p</i>
	revenue (eq. 4.1)			revenue (eq. 4.2)						
IVb	6.54	0.02	<0.01	6.70	0.06	<0.01	6.39	0.05	<0.01	<0.01
IVc	6.21	0.01	<0.01	6.41	0.05	<0.01	6.09	0.03	<0.01	<0.01
VIIa	6.38	0.02	<0.01	6.79	0.06	<0.01	6.02	0.05	<0.01	<0.01
VIIId	6.51	0.01	<0.01	6.60	0.03	<0.01	6.43	0.02	<0.01	<0.01
VIIe	6.15	0.02	<0.01	6.28	0.07	<0.01	6.05	0.06	<0.01	0.072
VIIIfg	6.48	0.01	<0.01	6.71	0.03	<0.01	6.28	0.03	<0.01	<0.01
VIII	6.43	0.02	<0.01	6.56	0.05	<0.01	6.30	0.05	<0.01	<0.01
	sole (eq. 4.1)			sole (eq. 4.2)						
IVb	2.93	0.05	0.015	2.82	0.12	0.038	3.03	0.11	<0.01	0.305
IVc	3.43	0.02	<0.01	3.79	0.08	<0.01	3.19	0.05	<0.01	<0.01
VIIa	3.31	0.03	<0.01	3.87	0.09	<0.01	2.82	0.08	<0.01	<0.01
VIIId	3.58	0.01	<0.01	3.80	0.04	<0.01	3.42	0.03	<0.01	<0.01
VIIe	1.74	0.07	<0.01	1.69	0.21	0.017	1.78	0.17	<0.01	0.796
VIIIfg	3.32	0.02	<0.01	3.50	0.05	<0.01	3.16	0.04	<0.01	<0.01
VIII	3.81	0.02	<0.01	3.94	0.06	<0.01	3.69	0.06	<0.01	0.025
	plaice (eq. 4.1)			plaice (eq. 4.2)						
IVb	4.94	0.03	<0.01	5.13	0.09	<0.01	4.77	0.07	<0.01	0.021
IVc	3.57	0.03	<0.01	3.48	0.12	<0.01	3.62	0.08	<0.01	0.407
VIIa	3.09	0.04	<0.01	3.00	0.13	<0.01	3.17	0.10	<0.01	0.415
VIIId	3.72	0.02	<0.01	3.43	0.07	<0.01	3.94	0.05	<0.01	<0.01
VIIe	3.15	0.06	<0.01	3.28	0.18	<0.01	3.05	0.15	<0.01	0.499
VIIIfg	1.77	0.03	<0.01	1.86	0.09	<0.01	1.70	0.08	<0.01	0.309
VIII	-2.21	0.26	<0.01	-2.28	0.76	<0.01	-2.17	0.71	<0.01	0.828

3.3.3. *Coupling fishing activity, VMS and logbook data*

Figure 3.4 illustrates the effect of including fishing activity in the distribution of landings over VMS fishing pings. The position of the peak of the explorative and exploitation curve is rather similar: around approximately 3 to 5 kg, respectively. In contrast, the distribution of both density curves differs remarkably. The curve related with exploration has a more dense distribution around the maximum density, while the exploitation curve is more flattened and dispersed. As a consequence, almost all landings at the right tail of the curve (>10 kg with respect to the intercept) are attributed to the exploitation fishing pings.

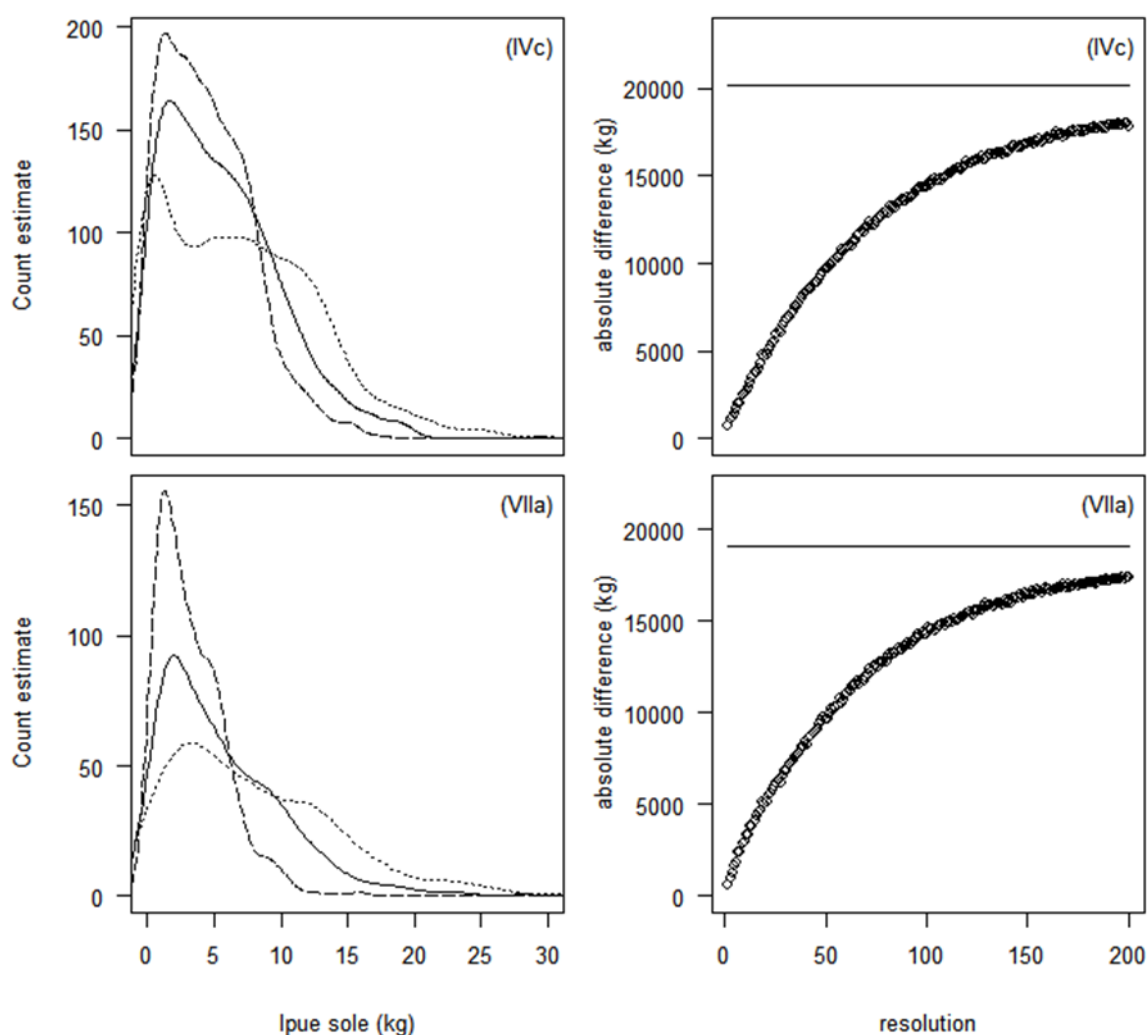


Figure 3.4 Effect of fishing tactics on the allocation of landing data to VMS data with respect to the results of the GLMs of sole in the Southern part of the North Sea and Irish Sea. The left panels give the density plots of the North Sea (Southern Part) and Irish Sea sole landings spread over VMS fishing points according the two distribution modes (minus the intercept). The solid line represent the density of the sole landing according an distribution model without fishing tactics. The dashed and dotted lines show the density of the fishing pings related to the exploration and exploitation states, respectively. The right panels show the absolute difference in sole landing allocations between the two distribution methods with respect to different resolutions of the grid. The solid line represents the absolute difference between both distribution models.

In terms of absolute difference between fishing pings, approximately 4% (20 out of 454 tonnes) and 8% (19 out of 217 tonnes) of all sole landings differed between the two distributions in the Southern Part of the North Sea and Irish Sea, respectively (Figure 3.4). When allocating the landings on a grid, the absolute difference between both methods of landing allocations obviously increased with a higher resolution of the grid, and reaches the maximum difference if each cell contains one VMS point. At a resolution of 54x54 and 50x50 cells per ICES rectangle, corresponding with cells of approximately 1 x 1 km, 50% of the total difference had allocated in the Southern Part of the North Sea and Irish Sea, respectively. Increasing the resolution from 100 to 200 resulted in both ICES subdivision (17%) in a limited increase of the difference in landing allocations.

3.4. Discussion

3.4.1. State-switching behaviour of beam trawlers

In contrast to the studies of Vermard *et al.* (2010), Gloaguen *et al.* (2015) and de Souza *et al.* (2016) that used a vessel's speed at a given time as state variable to fit HMMs, we used the distance between subsequent VMS records to model fishing behaviour. Although a vessel's speed might give a more accurate description of its actual state, it is also more likely to emit the wrong signal. Speed might be affected by a short steaming phase time between hauls, or by turning or retrieving the gear. As a consequence of the larger time intervals between the VMS points in our study, we opted to use the distance between two VMS points. The distance between two points is approximately equivalent to the average speed, and is therefore more robust with respect to short variations in a vessel's speed.

The state-dependent behaviour found by the HMMs can be explained by the typical modes of movement of beam trawlers during a fishing trip as illustrated in Figure 3.5. All models clearly showed the occurrence of a straight movement mode characterized by long step lengths. Both the initial state probabilities and the *VMS_id* covariate showed that this state has a higher probability of occurring at the beginning or ending of a fishing trip. It is clear that this mode represents steaming which, obviously, is most likely to occur at the beginning and/or end of a trip when either arriving at or leaving the harbour, respectively, or when changing between fishing grounds (Figure 3.5). To save on fuel costs, fishers follow the shortest path when steaming to a fishing ground or harbour, a straight line with minimal turning if no obstacles are encountered. The larger step lengths found in this state can be explained by the fact that steaming occurs at higher speeds (~12 knots, or ~22 km h⁻¹) compared to fishing (~5 knots) (Poos *et al.*, 2012). In the ICES subdivision IVc, VIId, VIIe and VIIh, the steaming state has a higher frequency compared to the other subdivisions (Table 3.3). This can be explained by the fact that these ICES subdivisions have to be

crossed when steaming from a Belgian harbour to a fishing ground located in the Central Part of the North Sea, the Celtic Sea or Bay of Biscay, or vice versa.

The model with 4 hidden states included a behavioural mode during which no movement occurred. Such a behaviour is not common (>0.6% of the VMS points) and could be caused by an interruption of the usual activities. In our analysis, the VMS points that were assigned this *no movement* state were detected either close to or in a harbour. This might indicate that a vessel had to wait at a lock before leaving, or emitted a GPS signal although the vessel had already started steaming.

Table 3.3 Frequencies of the states per ICES subdivision. State 1 – 4 represent exploration, steaming, exploitation and no-movement, respectively.

	HMM (3 states)			HMM (4 states)			
	1	2	3	1	2	3	4
IVb	2296	400	2897	2316	387	2857	33
IVc	5975	4126	10363	5956	4126	10369	13
VIIa	3836	818	4761	3817	760	4784	54
VIIId	10997	3568	15427	11017	3593	15378	4
VIIe	2527	1907	3454	2526	1908	3442	12
VIIIf,g	11347	1658	13751	11369	1617	13768	2
VIIh	40	79	76	40	81	74	0
VIIIa,b	2822	367	2989	2818	377	2982	1

The HMMs with 3 and 4 hidden states outperformed the HMM with 2 hidden states in terms of AIC and normality of the pseudo-residuals. In the 2-state HMM, fishing activity was related to a single behavioural mode, while the 3- and 4-state HMM assigned 2 behavioural modes to the fishing activity. All these fishing states are comparable in terms of the step length distribution in which the mean step length corresponds to the length of a trawl. However, these behavioural modes differ considerably in terms of distributions of the turning angle. In the 2-state HMM, the distribution of the turning angle has a more uniform shape, while the 3- and 4-state HMM include a state with a very narrow distribution of the turning angle around π , resulting in U-turns, and a state where the turning angle shows a rather normal distribution around 0 (Figure 3.3). The covariate *previously_trawled* showed a positive relationship with the transition probability of going from the state with random turning angles around 0 to the state with U-turn turning angles. In other words, if a vessel returns to a grid cell that has been visited before during that trip, vessels are more likely to stay there. This confirms our expectations and indicates that a vessel makes a number of hauls to explore a fishing ground, after which the best local fishing ground is exploited.

A limitation of our approach is that the probability of going from one state to another is only dependent on the current state. Obviously, this assumption is not valid in the real world, as fishers use information about previous tows as indicated by the covariate *previously_trawled* in our study. This might have implications regarding differentiating between exploration and exploitation behaviour. For instance, during the exploitation phase, some fishers alter two hauls in one direction with two hauls in the opposite direction, resulting in a lower frequency of U-turns (Rijnsdorp *et al.* 2000b). Obviously, if previous states could be included in the model, it is likely that it would differentiate better between these states.

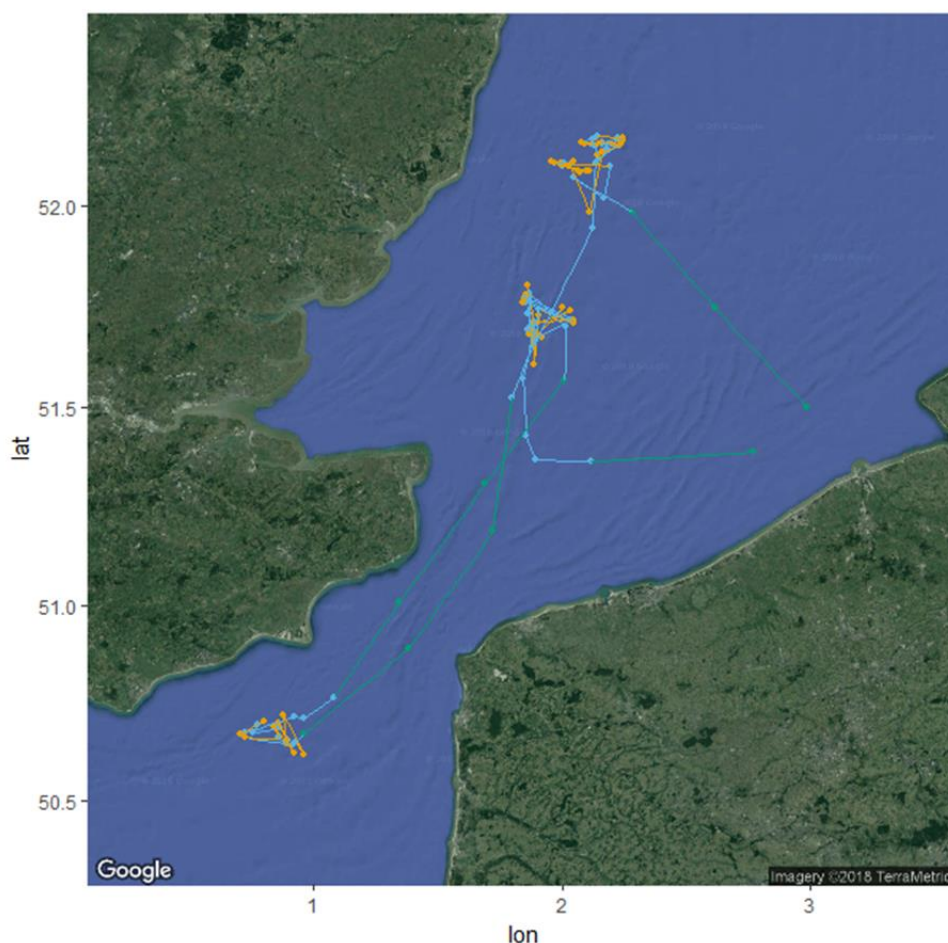


Figure 3.5 Reconstruction of a vessel trajectory based on VMS data (the same as in Figure 3.1). The states are based on the decoded HMM with 4 states using the Viterbi algorithm. The colours refer to as: green = *steaming*; blue = *exploration*, orange = *exploitation*; no VMS points were associated with state 4 (*steaming*) in this trip.

No observer data was available to validate the fitted HMMs with real information about the fishing activity. Nevertheless, evidence for exploration and exploitation behaviour was found in studies of Rijnsdorp *et al.* (2000b, 2011) in which the framework of the Marginal Value Theorem was used to analyse fishing tactics of Dutch beam trawlers in the North Sea targeting sole (*Solea solea*) and plaice (*Pleuronectes platessa*). This theory predicts how

long foraging animals should exploit a local patch of food, assuming net energy intake rate maximization behaviour (Charnov, 1976). The authors found that beam trawlers deploy fishing strategies that maximize trip revenues, thus alternating between two phases: an exploration phase during which fishers search for a good fishing ground, and an exploitation phase during which a local hotspot of flatfish is depleted. After exploiting the hotspot, the vessels search for a new flatfish hotspot. These phases are reflected in the vessel trajectories (Figure 3.5). Exploration is usually characterized by a series of hauls with larger inter distance and more dispersed turning angles, thus covering a larger area. In contrast, during the exploitation phase, hauls are clustered in space, and vessel trajectories are characterized by hauls with short inter distance and a higher frequency of sharp turning angles.

3.4.2. Linking fishing tactics with landing rates

Exploration-exploitation behaviour can only occur if the spatial distribution of the target species is patchy, and local hotspots of fish species cannot be detected using equipment such as fish finders or echo sounders. Plaice and sole are known to form local aggregations that persist up to 3 weeks (Poos and Rijnsdorp, 2007b). Hence, fishers need to deploy a trial-and-error method to detect local hotspots of these species by coupling the revenue and landing rates of sole and plaice to the different behavioural modes of fishing activity, which suggests that the HMMs with exploration and exploitation behaviour might reflect the true data generation process. Revenue rates were higher during the state with sharp turns and shorter step lengths compared to the phase with directional movement and longer step lengths which verifies the hypothesis that this behavioural mode reflects the exploitation of a local hotspot of fish. In all ICES subdivisions of our study, except the Western English Channel, this exploration-exploitation behaviour could be related to the landing rates of sole (IVc, VIIa, VIId, VIIfg, VIII) or plaice (IVb) which confirms our expectations that these species are targeted in these ICES subdivisions (Table 3.2; Table 3.4).

Table 3.4 shows that there are some remarkable results with respect to the exploration and exploitation landing rates which cannot be explained by the target behavior of the fleet. In the Eastern English Channel, the higher exploration landing rate of plaice with respect to the exploitation landing rate is counterintuitive. This would imply that fishers avoid hotspots of plaice which is not straightforward as such a tactic comes at a cost and fishers are allowed to discard plaice. Therefore, we suggest that this may be due to misreporting's caused by an imbalance between the catch rate of plaice in this area and the daily catch limit of plaice (personal communication). It is likely to assume that this imbalance has created an incentive for fishers to report plaice caught in the Eastern English Channel to

the Southern part of the North Sea if fishing occurred in both ICES subdivision during a trip (Figure 3.5).

Table 3.4 The natural exponent of the coefficients as reported in Table 3.2.

	revenue (€)		sole (kg)		plaice (kg)	
	exploitation	exploration	exploitation	exploration	exploitation	exploration
IVb	814	595	17	21	169	118
IVc	607	440	44	25	32	38
VIIa	890	412	48	17	20	24
VIIId	737	623	45	30	31	51
VIIe	531	424	5	6	27	21
VIIIfg	823	534	33	24	6	5
VIII	705	544	51	40	0.1	0.1

With respect to the landing rate of sole, the largest difference between exploitation and exploration is found in the Irish Sea. This result can be related to the discrepancy between the observations of the scientific survey – stating that the Irish Sea sole stock is at risk –, and the fishing industry – stating that the catch rate is high – regarding the stock assessment of the Irish Sea sole stock. The strong difference between the exploitation and exploration landing rate of sole may be caused by the fact that there are a number of local hotspots of sole in the Irish Sea while the abundance in the background is very low. Such a strong aggregations of sole may have resulted in a nonlinear relationship between cpue and abundance which would in this case cause hyperstability.

To our knowledge, evidence for such a relationship between the exploration-exploitation tactics of trawl fisheries and its landing rates was only found through cluster analysis of haul-by-haul data (Branch *et al.*, 2005; Rijnsdorp *et al.*, 2011 see above). To detect fishing opportunities, Branch *et al.* (2005) developed a method in which trawls were clustered based on the Euclidean distance between the starting and ending positions of two trawls. This method has been applied in the Patagonian scallop fishery which revealed that 30% of the trawls were classified as explore and 70% as exploit fishing trawls. The first group represented trawls that could not be related to other trawls, while the latter represented locations with high trawling activity with catch-per-unit-effort being 4 times that of the exploratory trawls.

Similar to the approach of Branch *et al.* (2005), tow-by-tow data was used to cluster individual tows of Dutch beam trawlers (Rijnsdorp *et al.*, 2011). Based on the relationship between the nearest neighbor distance, the occurrence of tows in group, the time spent fishing at a local fishing ground and the revenue-per-unit-effort of the tows, patterns were

detected as predicted by the MVT. They found that tows clustered within a radius of 1-2 nm represent a local hotspot in which the revenue-per-unit-effort (rpue) is 36% higher compared to the rpue in the background (>6 nm from the centre). Beam trawlers exploited these local hotspots as long as the rpue was above a certain threshold to maximize trip revenues.

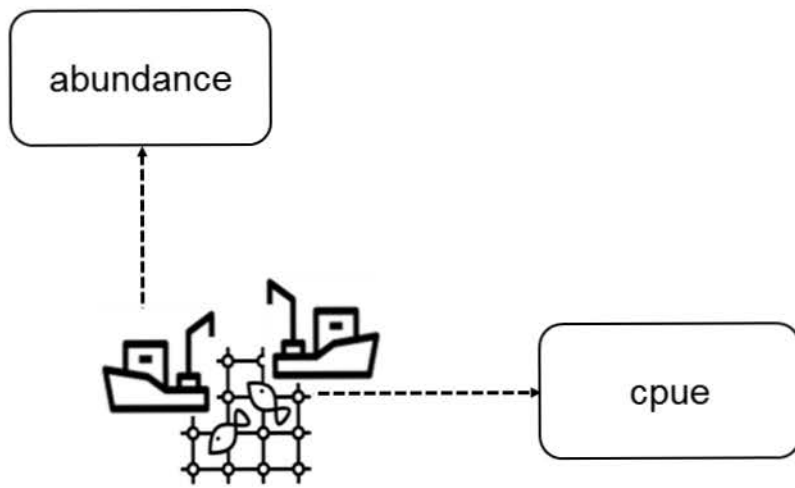
An alternative approach that has been used to relate fishing tactics to landing rates is the Lévy flight foraging hypothesis. This theory states that animals looking for sparsely and randomly distributed targets should adopt a strategy where turning angles and step lengths are generated by a Lévy walk process. This is a random walk process of which the turning angle (α) and the step size (li) are derived from a uniform distribution ($\alpha \in [0^\circ, 360^\circ]$) and a power-tail distribution ($P(li)=li^{-\mu}$, with the foraging parameter $\mu \in [1, 3]$), respectively (Viswanathan *et al.*, 1996). Bertrand *et al.* (2005) and Marchal *et al.* (2007) found evidence for the occurrence of Lévy flight patterns in the trajectories of fishing vessels. In their analysis, they demonstrated that the distances between consecutive fishing points of Peruvian purse-seiners and French and Dutch otter and beam trawlers were described by a power-tail distribution with a μ value of approximately 1.8 for Peruvian trawlers and 1.6 and 1.2-1.4 for French and Dutch otter and beam trawlers, respectively. Marchal *et al.* (2007) related the values of the foraging parameter, μ , to revenue-per-unit-of-effort of the Dutch and French fleets and found evidence that vessels adopt their fishing tactics so that the revenue rate is maximized with respect to abundance.

However, the evidence for the occurrence of Lévy flights in vessel (and foraging) trajectories has been increasingly criticized because alternative step length distributions give a better fit to observed foraging trajectories and omit directionality between successive steps (Edwards, 2011; Pyke, 2015). This criticism may be explained with the result of our study in which was showed that directionality between successive VMS points is an important feature underlying the different behavioural states that represent fishing tactics. This may be caused by the fact that fishing grounds have an elongated shape (Rijnsdorp *et al.*, 2011), and because it may be assumed that course of a fishing vessel during a haul is rather straight. In addition, our study showed that fishers are likely to enter the exploitation state if a grid cell has already been trawled during a fishing trips. This indicates that fishing tactics are affected through a memory effect which violates the assumption of a featureless environment underlying the Lévy flight foraging hypothesis. Finally, the Lévy flight foraging hypothesis does not allow to differentiate between fishing and steaming which limits the ability of the Levy flight foraging hypothesis to allocate landings to VMS points.

3.4.3. Implications for the spatial distribution of landing data

Accounting for fishing activity in the spatial distribution of sole landings had only a minor effect in the southern part of the North Sea and Irish Sea. This might be caused by our use of two models (HMM and GLM) to distribute landing data, both of which have limitations in terms of accuracy. As a result of these limited differences, we were unable to detect any spatial patterns in fishing activity with respect to the spatial distribution of landings. However, Figure 3.4 shows that increasing the resolution of the grid from 1 to 50 can explain the largest part of the difference between both distributions models which corroborates with the results of Rijnsdorp *et al.* (2011) who found that fishing effort is concentrated within a radius of 2 nm from the centre of a fishing ground.

Although the main results of our study are specific for the Belgian beam trawl fishery, the aim of this study was to demonstrate how the increased availability of data at high spatiotemporal resolutions of commercial fishing vessels could be used to gain insights into the fishery. Because this data is currently underexploited, they are underused in fisheries management advice. Better use of such data could not only improve our understanding of fisheries, but the minimal cost of this type of data collection could also improve the cost-efficiency of fisheries science.



CHAPTER 4

Competitive interactions between two fishing fleets in the North Sea

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Abstract

We examine whether the landing rates of Belgian beam trawlers in the Southern Bight of the North Sea were affected through competitive interactions with the Dutch beam trawler fleet and whether the development of a pulse trawler fleet has altered competitive interactions between both fleets. Effects of competition were investigated through a natural experiment based on the different weekly exploitation patterns of both fleets. Logbook data was used to fit a generalized additive mixed model (GAMM) for the daily landing rates of the target species sole (*Solea solea*) and plaice (*Pleuronectes platessa*). Results showed that landing rates of sole by the Belgian beam trawlers (>221 kW) from 2006 to 2013 were lower during weekdays than during weekends when the Dutch trawler fleet is in harbour, while no such an effect was found for plaice. After the development of a pulse trawler fleet in 2011, the negative weekday effect in the sole landing rates was much more pronounced in 2012 and 2013. This increased loss of efficiency during weekdays, as a result of increased competition with the Dutch trawler fleet, coincided with a reallocation of fishing effort by the Belgian beam trawler fleet.

4.1. Introduction

Commercial fishers constantly innovate to remain economically competitive and to increase the value of their catch, reduce operational costs, aid navigation, and improve safety at sea (Valdemarsen, 2001; Eigaard *et al.*, 2014). Such innovations may occur suddenly, as was observed when beam trawls were introduced in the Dutch flatfish fishery in the early 1960s. In less than 10 years, the demersal fishery changed from an otter trawl fishery to a beam trawl fishery (Rijnsdorp *et al.*, 2008). The innovations often cause an increase in the catchabilities of fish species and could arguably be one of the main reasons that many of the world's fisheries are suffering from declining resources (Eigaard *et al.*, 2014).

The social and economic dynamics of uptake of new technologies are complex (Eigaard, 2009) and we often observe that the speed of uptake is heterogeneous in fisheries. In the transition period, where some parts of fishing fleets adopt new technologies while others remain unchanged, the competitive dynamics among fleets change. This change can cause knock-on effects in the fishery, such as changes in fishing effort allocation.

In the North Sea, we have observed a sudden change in fishing technology in one of the major demersal fisheries: the Dutch demersal flatfish fishery. As a result of the increased pressure on the beam trawler fishery (Soetaert *et al.*, 2015), the EU in 2009 allowed the use of the pulse trawl gear for a part of the beam trawlers active in the North Sea (EU, 2009). The major difference is that heavy tickler chains are substituted by electrodes producing electric stimuli. This results in a weight reduction and decline in fuel usage of ca. 50% compared to beam trawling (van Marlen *et al.*, 2014). Until 2013, the transition to pulse trawling occurred mainly in the Dutch beam trawler fleet. The development of a pulse trawler fleet is expected to alter fishing tactics in the Dutch trawler fleet (Batsleer *et al.*, 2016), potentially resulting in increased spatial overlap with the beam trawler fleet of neighbouring Belgium. In this paper, we examine the occurrence of competition between both fleets and whether this changed since the development of the Dutch pulse trawler fleet. We also study how the change in competitive interactions has altered fishing behaviour in the Belgium fleet as a knock-on effect of the changes in the Dutch fleet.

Competitive interactions affect the relationship between fish abundance and catch per unit effort (cpue) and thus the allocation of fishing effort (Gillis and Peterman, 1998; Gillis, 2003; Poos and Rijnsdorp, 2007a; Girardin *et al.*, 2015). Competition among fishing vessels is a result of (i) direct interactions among fishing vessels (interference competition), e.g. through increased risk of net-loss or inducing a change in fish behaviour and/or (ii) through local depletion of the resource (exploitation competition). Knowledge about the mechanistic processes causing interference competition and about the fine-scale dynamics in fish

abundance is required to distinguish interference competition from exploitation competition. However, interference competition results typically in a direct and negative response in catch rates towards an increase in vessel density, while we expect exploitation competition to result in a gradual response in catch rates to changes in vessel density. Empirical research to quantify the effects of competition on catch rates is difficult because of practical constraints. First, biotic factors affecting the distribution of fish species are difficult to control when carrying out field experiments (Abrahams and Healey, 1993). Second, setting up experiments with fishing vessels is hampered by high financial costs. To our knowledge, only one experiment was conducted in which vessel density was directly manipulated (Abrahams and Healey, 1993). In this study, increased vessel density of the British Columbia salmon troll fleet had negative, positive, and no effect on catch rates, depending on the fish species. In studies by Rijnsdorp *et al.* (2000a) and Poos and Rijnsdorp (2007a), competitive interactions between Dutch beam trawlers caused by a weekly decrease and monthly increase in vessel density were quantified, respectively. In the first study, the effect of a week of “prayer”, during which the Urk fleet stays in the harbour and vessel density per ICES rectangle was reduced by 75% resulted in a 10% increase in revenue per unit effort. In the second study, it was found that an increase in vessel density with 28% due to the implementation of an area closure forced part of the fleet to reallocate fishing effort to the fishing grounds that remained open, resulted in a decline of the revenue per unit effort of 14%. To study the competitive interactions between the Belgium and Dutch fleets, we use a cultural difference between the fleets as a natural experiment. While Dutch vessels tend to stay in port over the weekend, Belgium vessels fish irrespective of the weekday. This weekly, cyclic change of vessel density puts us in a unique position to analyse the effects of competition between both fleets.

By assessing the effects of competitive interactions among fishing fleets as a result of different uptake speed of fisheries technologies and the adaptive response of fishermen, this paper aims to gain more insights in the underlying mechanisms of fleet dynamics. This may reduce the uncertainty generated through unintended behaviour of fishermen, and increase the effectiveness of fisheries management in achieving its ecologic and socio-economic goals.

4.2. Material and Methods

4.2.1. *Development of the flatfish fishery in the Southern Bight*

During the study period (2006–2013), the flatfish fishery in the Southern Bight targeted a wide range of demersal fish species, with sole (*Solea solea*) and plaice (*Pleuronectes platessa*) being the dominant species landed (Rijnsdorp *et al.*, 1998). The fishery is

dominated by beam trawlers fishing under the Belgian or Dutch flag. From 2006 until 2013, the nominal value of sole (*mean*= €10.53 kg⁻¹; *standard deviation*= €1.54 kg⁻¹) was ca. 7-fold higher than the nominal value of plaice (*mean*= €1.52 kg⁻¹; *standard deviation*= €0.36 kg⁻¹), due to its high price, sole accounted for > 60% of the landed value of the Belgian beam trawl fishery in the Southern Bight. Before 2011, Dutch beam trawlers were generally equipped with chains in the net opening penetrating the seabed (Creutzberg *et al.*, 1987; Eigaard *et al.*, 2015). Depending on seabed characteristics, two configurations of chains were used: (i) V-shaped tickler chains or (ii) chain mats (Fonteyne and Polet, 1995). V-shaped tickler chains are used on fishing grounds with smooth surfaces, such as sandy sediments (Rijnsdorp *et al.*, 2008). On rough fishing grounds, characterized by an irregular surface scattered with rocks, a matrix design of the tickler chains called chain mats is used. While most Dutch beam trawlers traditionally used the V-shaped tickler chain configuration, the Belgian beam trawlers typically used chain mats (Fonteyne and Polet, 1995; Rijnsdorp *et al.*, 2008). Hence, rocky fishing grounds were mainly exploited by Belgian beam trawlers, whereas smooth fishing grounds were mainly trawled by Dutch vessels. Consequently, Belgian and Dutch beam trawl fleets were spatially segregated (Figure 4.1). Vessels from other countries were less numerous and mainly exploited other fishing grounds; therefore, they are not taken into account in this study.

In pulse trawls, the mechanic stimulus of fish by chains is replaced by electric stimuli of electrodes rigged in the net opening (Soetaert *et al.*, 2015). These electrodes cause muscle contractions in fish, decreasing their ability to swim away or dive under the net opening. The relatively light design of the pulse trawl allows operation on a wider range of sediments (Rasenbergh *et al.*, 2013). Additionally, catch composition of pulse trawlers differs compared to beam trawling (van Marlen *et al.*, 2014). The change in catch composition affects the relative profitability of the various fishing grounds because of the mixed nature of the flatfish fishery where different fish species are caught simultaneously. As a result, the development of the commercial Dutch pulse trawler fleet caused a reallocation of fishing effort (Batsleer *et al.*, 2016).

4.2.2. Data

In this study, we focus on the Belgian beam trawler segment with engine powers > 221 kW. These vessels are obliged to fish outside the 12-mile coastal zone. More than 80% of the fishing effort by the Belgian study fleet in the Southern Bight was concentrated in four ICES statistical rectangles (1° longitude x 0.5) latitude, ca. 30 x 30 nautical miles): 32F1, 32F2, 33F2, 34F2 (Figure 4.1). Other statistical rectangles were incidentally fished, but not retained for analysis.

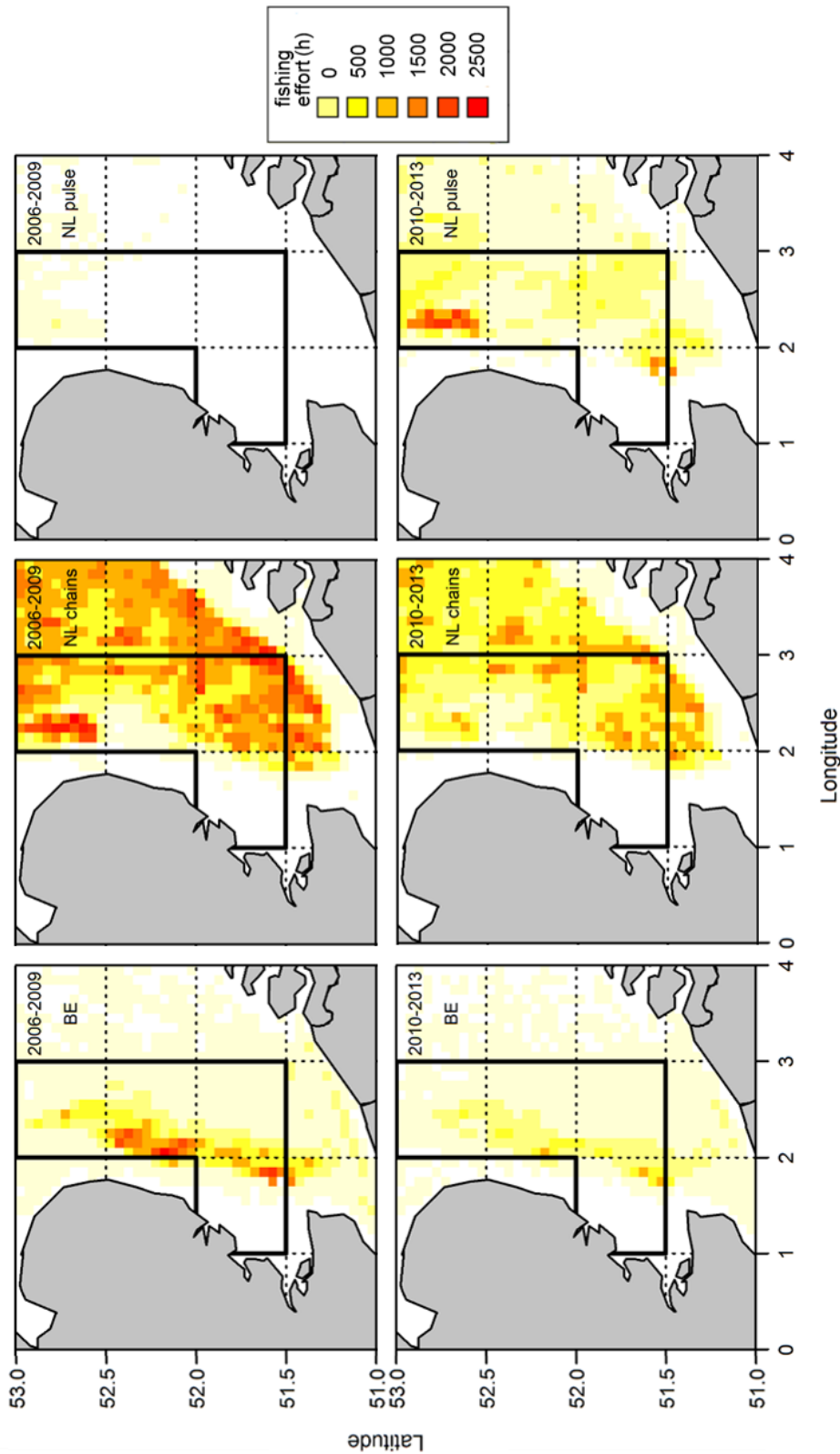


Figure 4.1 Spatial distribution of fishing effort (hours fished) of the Belgian beam trawlers (>221 kW) (left panels), Dutch beam trawlers with tickler chains (middle panels), and Dutch pulse trawlers (right panels) in the Southern Bight during the period 2006–2009 and 2010–2013, as recorded by satellite-based vessel monitoring systems (VMS) (resolution: 0.1 x 0.05 degrees) . The four ICES statistical rectangles comprising the study area are enclosed by the black frame.

Mandatory logbook data for 2006 – 2013 was used for statistical analysis. In these logbooks, fishers report fishing activities on a daily basis by specifying fishing location (by ICES statistical rectangle), fishing gear, mesh size and estimated weight of landings by species. In addition, vessel information (reference number, length, motor engine and gross tonnage) was available for analysis. No data on discarding was available. Hence, the analysis is restricted to the landings per unit effort (lpue), which is the portion of the daily catch commercialized. Logbook records for the Belgium fleet (>221 kW) fishing in the study area are summarized in Table 4.1. Fine-scale spatial distribution of the Dutch and Belgium fleet is obtained using the VMS data (Hintzen *et al.*, 2012).

Table 4.1 Summary statistics, grouped by year and weekday or weekend, of the logbook data of the Belgian beam trawl fleet (>221 kW) in the study area used for analysis. The number of logbook events and different vessels that were active in the study area, the average engine power (kW), and daily landings (kg day⁻¹) of sole and plaice. In total, there are 5063 logbook events recorded during weekdays and 3767 recorded during weekends.

Year	no. of vessels	no. of trips	weekdays (n=5063)				weekends (n=3767)			
			no. of logbook events	engine power (kW)	sole landings (kg day ⁻¹)	plaice landings (kg day ⁻¹)	no. of logbook events	engine power (kW)	sole landings (kg day ⁻¹)	plaice landings
2006	48	341	880	810	247	220	688	806	266	229
2007	42	236	566	775	302	264	437	774	315	246
2008	46	335	966	877	363	249	741	878	395	268
2009	41	370	1056	910	335	311	773	907	335	269
2010	30	280	801	899	358	523	519	885	363	481
2011	27	150	352	868	390	484	248	858	373	587
2012	23	91	181	859	300	450	131	824	349	485
2013	21	101	261	780	427	650	230	779	503	621

4.2.3. Analysis of competition in a natural experiment

Competition was analysed using the different weekly exploitation patterns of Belgian and Dutch fishers. Dutch fishers typically make fishing trips of 4 days starting on Monday morning and ending on Thursday (Rijnsdorp *et al.*, 2000a). Consequently, fishing activity by the Dutch beam trawlers is much lower from Friday until Sunday (Table 4.2). In contrast, the Belgian beam trawlers have no fixed weekly exploitation patterns. Most fishing trips have a duration of 8–10 days, and fishing effort is spread equally throughout the week. As a result of these different weekly fishing patterns, the probability of a Belgian fishing vessel encountering other vessels is much higher Monday–Thursday than Friday–Sunday. Consequently, effects of competition should be higher during weekdays than weekends.

Table 4.2 Daily distribution of the effort (time present) in the study area (expressed as percentages) based on the logbooks of the Belgian and Dutch beam trawler fleet (engine power >221 kW).

year	Belgium							The Netherlands						
	Mon	Tue	Wed	Thu	Fri	Sat	Sun	Mon	Tue	Wed	Thu	Fri	Sat	Sun
2006	14	14	13	14	15	16	15	19	24	24	23	7	1	1
2007	13	15	14	14	14	16	14	19	25	25	23	6	1	1
2008	14	14	14	14	14	16	15	20	24	25	23	6	1	1
2009	15	15	15	14	13	15	14	20	25	24	23	5	1	1
2010	14	16	16	14	13	13	13	20	25	24	22	6	1	1
2011	14	14	15	15	15	15	12	21	24	24	22	6	2	1
2012	16	16	13	11	13	17	14	22	25	24	19	6	2	2
2013	12	11	12	14	16	19	16	21	24	24	20	7	3	2

Competition was examined by analysing the daily landing rates (*lpue*) of the target species sole and plaice. To investigate both linear and non-linear relationships between the landing rates per unit effort (kg day^{-1}) and the explanatory variables, a generalized additive mixed model (GAMM) was fitted. The vessel reference number was included as random effect (μ) to correct for vessel effects. Such vessel effects include skipper effects and physical characteristics of vessels that are not recorded in the data. The temporal patterns of the dependent variables were compared in different regression models. The null model [equation (4.1)] includes the annual and seasonal temporal trends, a vessels' engine power, and an intra-trip effect:

$$\log(lpue) = \beta_0 + \beta_{1_i} \text{year} + \beta_2 \log(\text{engine power}) + f(\text{month})_{rect} + f(\text{tripday}) + \varepsilon + \mu \quad (4.1)$$

The model is fitted to both species separately. In the null model, β_0 represents the intercept. A categorical variable (*year*) was used to capture the annual variation in landing rates. The first year of the analysis, 2006, was the reference year and is included in the intercept. Therefore, β_{1_i} represents the year effect of each year i ($i \in 2007, \dots, 2013$) relative to 2006. The coefficient β_2 is the slope of the log-linear relationship between engine power ($\log(\text{engine power})$) of a vessel and landing rates (Rijnsdorp *et al.*, 2000a). The intra-annual variation caused by seasonal migration of adult sole and plaice (Rijnsdorp *et al.*, 1998) was captured by a seasonal term of the catch month for each ICES statistical rectangle ($f(\text{month})_{rect}$). This term is smoothed to the data using regression splines (Wood, 2004). Because a seasonal trend is assumed, cyclic cubic splines were used to avoid discontinuity at the end points (Wood, 2006). To examine intra-trip variation in the landing rates, a tripday

effect was included. This variable represents the number of days left before the end of the trip; hence, the day of arrival in a harbour is 0. Since there is no *a priori* knowledge about the underlying pattern, the intra-trip variation was included as a non-parametric effect and smoothed to the data. To allow overdispersion and 0 catches, a logarithmic link function between the linear predictor and the mean was specified with a negative binomial distribution of the error term (ε).

To investigate the reduction of landings during weekdays resulting from competition, the null model was extended to include a weekday effect without [equation (4.2)] and with [equation (4.3)] interaction with the annual effect:

$$\log(lpue) = \text{null model} + \beta_4 \text{ weekday}, \quad (4.2)$$

$$\log(lpue) = \text{null model} + \beta_{4_i} \text{ weekday} \times \text{year}. \quad (4.3)$$

In the first model [equation (4.2)], a categorical weekday effect (*weekday*) was added to the null model. The weekday variable was assigned a value of 0 for weekdays (Monday–Thursday) and a value of 1 for weekends (Friday – Sunday). Therefore, β_4 represents the effect of the weekend compared to weekdays. In the second model [equation (4.3)], the categorical weekday effect is included as an interaction term with the categorical year variable (*weekday* \times *year*). Hence, β_{4_i} represents the change of the dependent variable in weekends relative to weekdays for each year i ($i \in 2007, \dots, 2013$) of the study period.

Finally, to gain insight in the type of competition, we analysed whether the landing rates during weekdays and weekends showed a negative or positive slope, which could indicate the occurrence of competition through local depletion of fish stocks (exploitation competition).

$$\log(lpue) = \text{null model} + \beta_{5_j} \text{ day} \times \text{weekday} \quad (4.4)$$

Therefore the null model was extended with an interaction term between the numeric day effect (*day*) (Monday = 1, ..., Sunday = 7) and the categorical weekday effect (*weekday*) [equation (4.4)]. Hence, the coefficient of β_{5_j} represents the slope of the landing rates during weekdays and weekends.

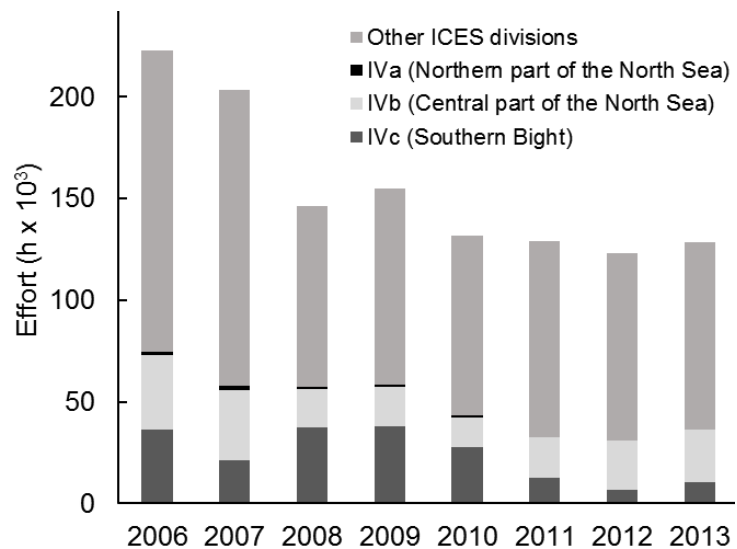
The open-source software platform R (version 3.1.3; R Development Core Team, 2013) was used for analyses. Logbook data was used and processed following the workflow as described in the *vmstools* R-package (Hintzen *et al.*, 2012) and time-date conversions were carried out with the *lubridate* R-package (Grolemund and Wickham, 2011). The R-package *mgcv* was used to fit the GAMM models (Wood, 2004).

4.3. Results

4.3.1. Changes in the spatiotemporal allocation of fishing effort

During the study period, the number of Belgian beam trawlers participating in the flatfish fishery in the Southern Bight declined, and the fishery reallocated fishing effort. This resulted in a decline of fishing effort in the Southern Bight (Figure 4.2). The number of vessels showed a decline during the study period (Table 4.1). Fishing effort allocation was characterized by a more complex pattern. After an increase in 2008 and 2009, fishing effort in the Southern Bight strongly decreased. The steepest decline occurred from 2010 to 2012, when a reduction of 76% was observed. In 2013, fishing effort increased again. Nevertheless, fishing effort allocation in the Southern Bight in 2013 was still more than 50% lower than in 2006–2010.

Figure 4.2 Fishing effort allocation per ICES division of the Belgian beam trawl fleet (>221 kW).



Apart from spatial effort reallocation, a shift occurred in the weekly exploitation patterns of the Belgian beam trawlers fishing in the Southern Bight. Most vessels land their fish in a Belgian harbour the day before the auction to sell their landings. Auctions occur weekly on Monday, Wednesday and Friday; hence, most fishing trips end on Sunday, Tuesday and Thursday (Table 4.3). During 2011–2013, >50% of the fishing trips of the study fleet ended on Tuesday or Thursday, while less trips ended on Sunday, except in 2007. In contrast, a shift occurred in 2012 and 2013, with a higher proportion of trips ending at the end of the weekend on Sunday or just after the weekend on Monday.

Year	Mon	Tue	Wed	Thu	Fri	Sat	Sun
2006	6	29	5	24	6	10	20
2007	3	28	6	25	1	7	30
2008	3	32	3	27	4	7	24
2009	3	30	4	24	7	8	25
2010	2	28	3	31	7	8	21
2011	3	31	2	30	7	7	21
2012	5	21	7	25	4	4	33
2013	15	19	5	25	4	4	29

Table 4.3 Weekly distribution of Belgian beam trawlers (<221 kW) (expressed as percentages) embarking in a Belgian harbour after a fishing trip in the Southern Bight (source: logbook data).

4.3.2. Statistical analysis of the sole and plaice landing rate

All parametric effects of the null model were significant at the 0.05 level for both sole and plaice (Table 4.4). There was a positive log-linear relationship with vessel engine power, indicating that more powerful vessels have higher landings rates. Similar intra-trip patterns were found in the landing rates of both species (Figure 4.3). At the start of a trip, lpue values for both species show increasing trends with wide confidence interval bounds. Between 10 and 3 d before the end of a trip, landing rates are rather stable and decline again towards the end of the trip. The slopes of the increase and decrease at, respectively, the start and the end of a trip are steeper for sole lpue than for plaice lpue. Seasonal variation in sole lpue differed between ICES statistical rectangle 32F1 and the other ICES statistical rectangles of the study area (Figure 4.4). The seasonal pattern in rectangle 32F1 was characterized by two peaks, one in spring and one in autumn, while sole lpue in the other rectangles had a single peak in autumn. In contrast, the seasonal variation in plaice lpue showed similar patterns in each of the four ICES statistical rectangles of analysis, with low values in spring and a strong increase in summer, after which the landing rate of plaice remained equal until the end of the year (Figure 4.5).

The null models were extended with a weekday effect with (*weekday x year*) and without (*weekday*) interaction with the year effect. A weekday effect was found significant (*t-value* = 2.33; *p-value* = 0.02) in sole lpue during 2006–2013. Landing rates of sole ($\beta = 0.036$; *s.e.* = 0.016) were 4% higher from Friday to Sunday compared to weekdays (Monday–Thursday). In contrast, no overall weekday effect was found at the 0.05 level in the landing rates of plaice.

Table 4.4 Estimated coefficients (β) and standard error (s.e.), and t-value (right side of F/t -value columns) of the parametric effects and ANOVA output, with the degrees of freedom (d.f.) and F -value (left side of F/t -value columns) per variable of the null model of sole and plaice lpue.

	lpue sole				lpue plaice			
	β (s.e.)	d.f.	F/t -value	p-value	β (s.e.)	d.f.	F/t -value	p-value
intercept	2.09 (0.82)	-	2.55	0.01	0.16 (1.32)	-	0.13	0.90
Year	-	7	20.7	<0.01	-	7	55.2	<0.01
2006	-	-	-	-	-	-	-	-
2007	0.17 (0.03)	-	5.70	<0.01	0.17 (0.05)	-	3.22	<0.01
2008	0.20 (0.03)	-	7.34	<0.01	0.08 (0.05)	-	1.81	0.07
2009	0.13 (0.03)	-	4.85	<0.01	0.21 (0.04)	-	4.70	<0.01
2010	0.19 (0.03)	-	6.43	<0.01	0.61 (0.05)	-	12.61	<0.01
2011	0.24 (0.04)	-	6.63	<0.01	0.77 (0.06)	-	13.17	<0.01
2012	0.12 (0.05)	-	2.57	0.01	0.60 (0.08)	-	7.91	<0.01
2013	0.46 (0.05)	-	10.95	<0.01	0.84 (0.07)	-	12.34	<0.01
$\log(\text{engine power})$	0.48 (0.12)	1	4.03	<0.01	0.77 (0.19)	1	3.94	<0.01
$f(\text{tripday})$	-	3.92	97.9	<0.01	-	3.58	22.1	<0.01
$f(\text{month})_{32F1}$	-	2.90	11.2	<0.01	-	2.96	153.6	<0.01
$f(\text{month})_{32F2}$	-	0.76	0.4	0.22	-	2.96	113.3	<0.01
$f(\text{month})_{33F2}$	-	2.63	26.0	<0.01	-	2.98	115.8	<0.01
$f(\text{month})_{34F2}$	-	2.41	16.7	<0.01	-	2.90	28.2	<0.01

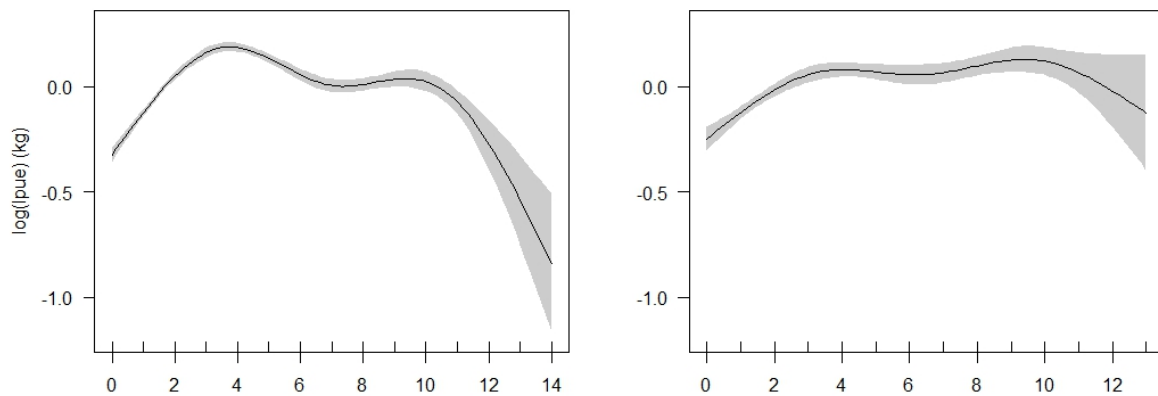


Figure 4.3 Plot of the non-parametric intra-trip effect [$f(\text{tripday})$] of the null model. The x-axis represents the number of days before the end of the trip, while the y-axis is the marginal response in sole lpue (left panel) and plaice lpue (right panel). The grey shade represents the 95% confidence interval.

Chapter 4

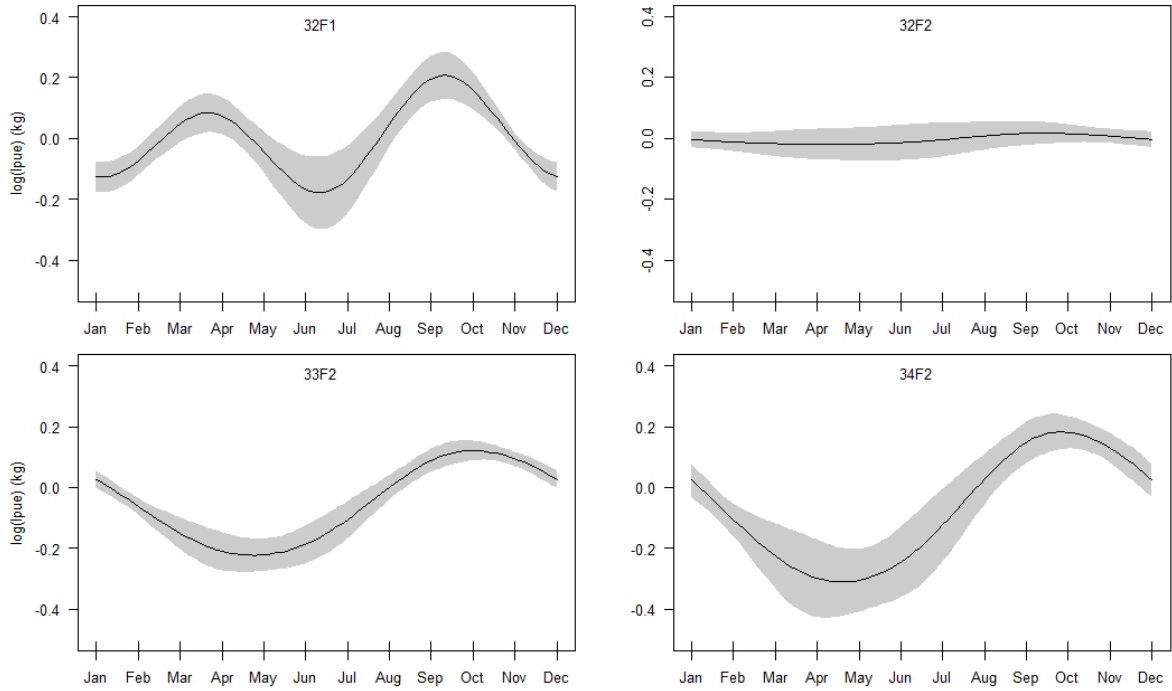


Figure 4.4 Plot of the non-parametric seasonal effect $[f(month)_{rect}]$ of the null model of sole lpue. The different panels show the seasonal effect in each ICES rectangle of the study area while the grey shade represents the 95% confidence interval.

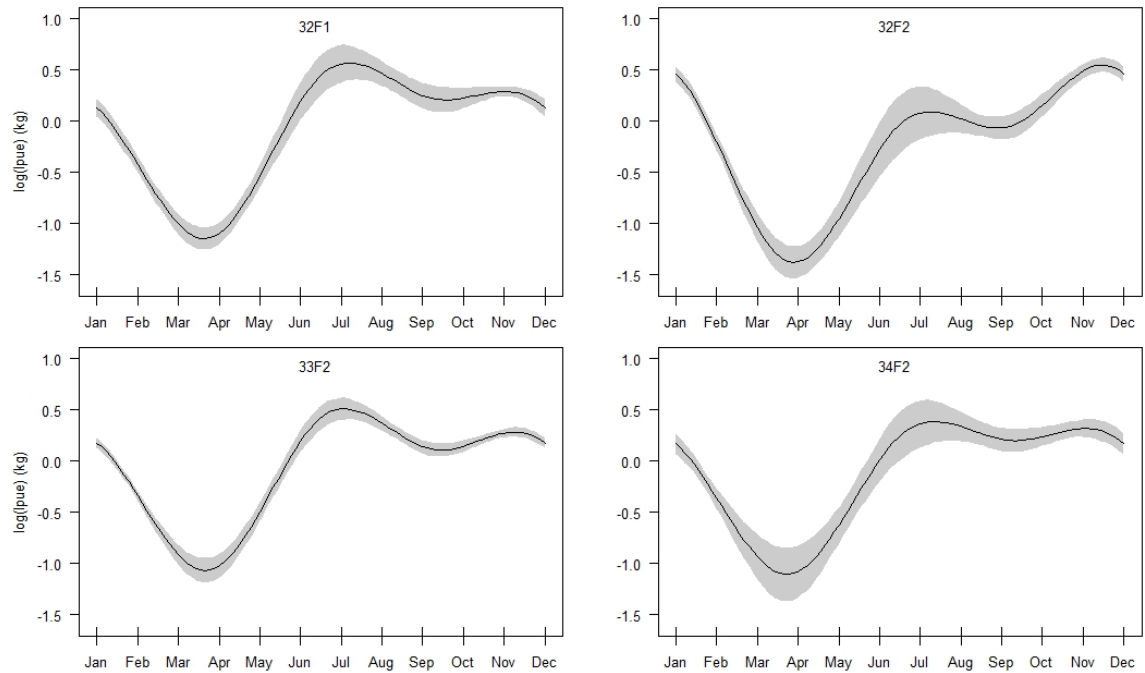


Figure 4.5 Plot of the non-parametric seasonal effect $[f(month)_{rect}]$ of the null model of plaice lpue. The different panels show the seasonal effect in each ICES rectangle of the study area while the grey shade represents the 95% confidence interval.

Including the weekday effect as interaction effect with the year effect resulted in significant (p -value < 0.05) weekday effects in the landing rates of sole in 2008 and 2013 (Figure 4.6). In 2006 (t -value = 1.85; p -value = 0.07) and 2012 (t -value = 1.84; p -value = 0.07), weekday effects showed a similar trend. In all of these years, the effect was positive, indicating that sole landings were depressed during weekdays. In 2006 and 2008, daily sole landings were, respectively, 7% (β = 0.068; $s.e.$ = 0.037) and 9% (β = 0.085; $s.e.$ = 0.036) lower during weekdays compared to weekends, whereas in 2012 (16%) (β = 0.149; $s.e.$ = 0.081) and 2013 (13%) (β = 0.125; $s.e.$ = 0.063), the magnitude of the weekday effect was considerably higher. The landing rates of plaice were only characterized by a positive weekend effect in 2011 (t -value = 1.803; p -value = 0.07) during which plaice landings were ca. 19% higher in weekends (Friday–Sunday).

Analysis of landing rates during weekdays and weekends showed a negative trend in l_{pue} for sole during weekdays, whereas no pattern was found in the landing rates of plaice during weekdays. During Monday–Thursday, landing rates of sole declined with 4% (β = -0.014; $s.e.$ = 0.006; t -value = -2.345; p -value = 0.02). The landing rates of both species during weekends did not show a decreasing or increasing trend.

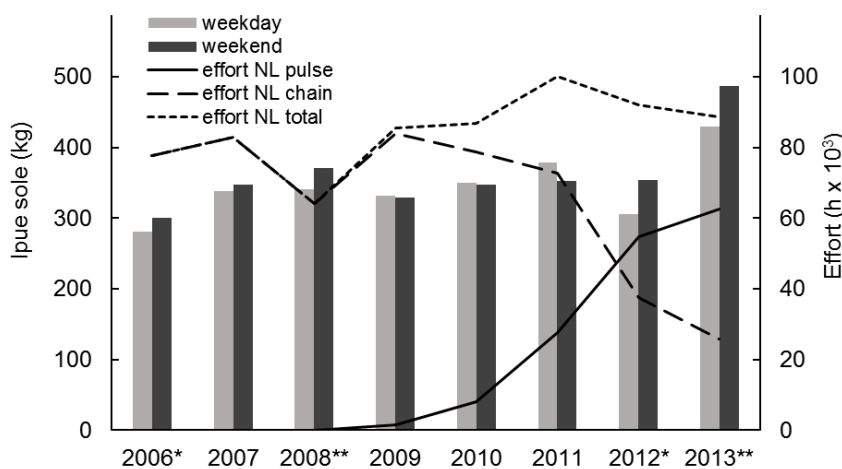


Figure 4.6 Bar plot of the fitted values (eq. 4.3) of sole l_{pue} in weekdays and weekends (engine = 900 kW; month = January; ICES rectangle = 32F1; tripday = 3). Years with a difference between landing rates in weekdays and weekends are indicated with * (p -value < 0.1) and ** (p -value < 0.05). The lines illustrate the annual effort trends of the Dutch beam pulse and beam trawl fleets.

4.4. Discussion

4.4.1. Patterns in landings per unit effort of sole and plaice

The landing rates of the target species sole and plaice of Belgian beam trawlers using chain mats is positively related to a vessel's engine power, similar to other trawl fisheries (Rijnsdorp *et al.*, 2000a; Eigaard and Munch-petersen, 2010). More powerful vessels are able to tow faster and use heavier fishing gear with more chains in the net-opening, and the increased penetration depth of the fishing gear, results in higher catchability.

The null model reveals a strong effect of tripday on catch rate showing similar patterns with the exploitation dynamics found in the Dutch beam trawler fishery (Rijnsdorp *et al.*, 2000b; Rijnsdorp *et al.*, 2011). Following Rijnsdorp *et al.*, 2000b, we hypothesize that at the beginning of a trip, skippers search for local high densities of fish, which explains the increasing trend in $lpue$. Once skippers have located local hotspots of fish, an exploitation phase follows during which $lpue$ is high. At the end of a trip, $lpue$ tends to decrease again, which may be a consequence of a local depletion of the resources. Seasonal patterns in sole and plaice $lpue$ are related to the spawning–feeding migrations of both species. Sole migrate in spring to spawning grounds in shallow coastal waters (Rijnsdorp *et al.*, 1992). One of these spawning grounds, the Thames estuary, is partially located within our study area (ICES rectangle 32F1), which explains the occurrence of a peak in sole $lpue$ in April in this ICES rectangle. In autumn, sole leaves the coastal areas and migrates to warmer, offshore waters, coinciding with a peak in sole landing rates in October. Compared to sole, the migration of plaice to and from spawning areas occurs over longer distances, resulting in stronger seasonal variation in landing rates (Poos and Rijnsdorp, 2007b). Mature plaice migrate between spawning grounds in the south in winter and feeding grounds in the north in summer and autumn (Houghton and Harding, 1976). This migratory behaviour of plaice does not correspond with the high landing rates of plaice observed in summer. A possible explanation for the strong increase in plaice $lpue$ in July is the allocation of the national quota which is distributed several times a year to individual vessels. Until June, Belgian beam trawlers have a limited plaice quota in the North Sea. In July, quota is redistributed, whereby the individual plaice quota strongly increases. We hypothesize that this affects the targeting and discard behaviour, in turn affecting the observed seasonal $lpue$ levels.

4.4.2. Competition

The weekday effect found in sole $lpue$ suggests that competition is related to the fishing activity of the Dutch trawler fleet. When Dutch trawlers fish from Monday to Thursday, sole landings of Belgian beam trawlers are lower, while the opposite occurs when the Dutch beam trawler activity drops from Friday to Sunday. Since we did not examine the underlying mechanisms, there is no unequivocal explanation for the occurrence of this weekday effect. Nevertheless, the direct and reversible response of landing rates to a change in fishing activity of the Dutch beam trawlers suggests the occurrence of interference competition. However, the decreasing trend from Monday to Thursday in the landing rates of sole, which was also found in the Dutch beam trawler fleet (Rijnsdorp *et al.*, 2000b), suggests that local depletion of the sole fishing grounds occurs as well (exploitative competition).

Inspection of the interaction effect of weekday and year did not suggest a clear relationship between the development of the Dutch pulse fleet and the reduction of *Ipue* during weekdays in the Belgian fleet. This could be the result of several confounding effects that were not tested. Inter-annual variation in the distribution of sole and plaice may alter the exploitation dynamics of both fleets and their spatial overlap and thus competitive interactions between the different years of analysis. Additionally, changes of external factors such as fuel prices may affect fishing tactics and spatial interactions between fishing vessels. Poos *et al.*, (2012) showed that Dutch beam trawlers fished closer to harbours in response to high fuel prices in 2008. Additionally, the number of vessels participating in the fishery may have affected the level of competition between both fleets. Despite the development of the pulse trawl fleet starting in 2009, no weekday effects were observed in 2009–2011. During this years, nominal fishing effort of the pulse trawler fleet was much smaller (Figure 4.6); moreover, fishers learned about the optimal use of fishing gear and characteristics of new fishing grounds, which may explain the absence of the weekday effect (Rasenberg *et al.*, 2013).

The landing rates of plaice were not characterized by a weekday effect over the entire study period. This suggests no clear relationship between the landing rates of plaice and exploitation patterns of the Dutch beam trawlers nor with the development of the pulse trawler fleet.

Differences in the response of catchability of different fish species to vessel density was also found in the experiment of Abrahams and Healey (1993). Additional research about the underlying mechanistic processes of interference competition, e.g. through experiments with tagged fish species, potentially provides insights about the observed differences in the response of sole and plaice catchability to vessel density. Since sole is the most important species, in terms of revenue in this fishery, the absence of a weekday effect in plaice *Ipue* may be related to the fleet's targeting behaviour for sole. Another possible suggestion is that pulse trawlers catch less plaice than beam trawlers (van Marlen *et al.*, 2014), owing to a different response to the pulses (Breen *et al.*, 2011). This different response of both species might induce a different level of interference competition and might explain why plaice *Ipue* is not affected by a change in vessel density.

The design of our study did not allow us to quantify the relationship between vessel density and interference competition. Despite this limitation, the relative decline of revenue per unit effort (*rpue*) towards an increase in fishing effort during weekdays measured in our study, is similar to the decline in *rpue* found in studies of Rijnsdorp *et al.* (2000b) and Poos and Rijnsdorp (2007a). In those studies, *rpue*, based on landings of the target species sole and plaice, for a vessel with engine power of 2000 HP (ca. 1491 kW) dropped by, respectively,

10% and 14% when vessel density increased. In our study, in which sole counts for 67% of the total landed value, *rpue* declined by 11 (2012) and 9% (2013) for a vessel of 1200 kW. Despite the different setup of the vessel density experiment in all of these studies, a similar response in revenue rates in response to a change of vessel density was measured.

4.4.3. *Spatio-temporal effort allocation of the Belgian beam trawlers*

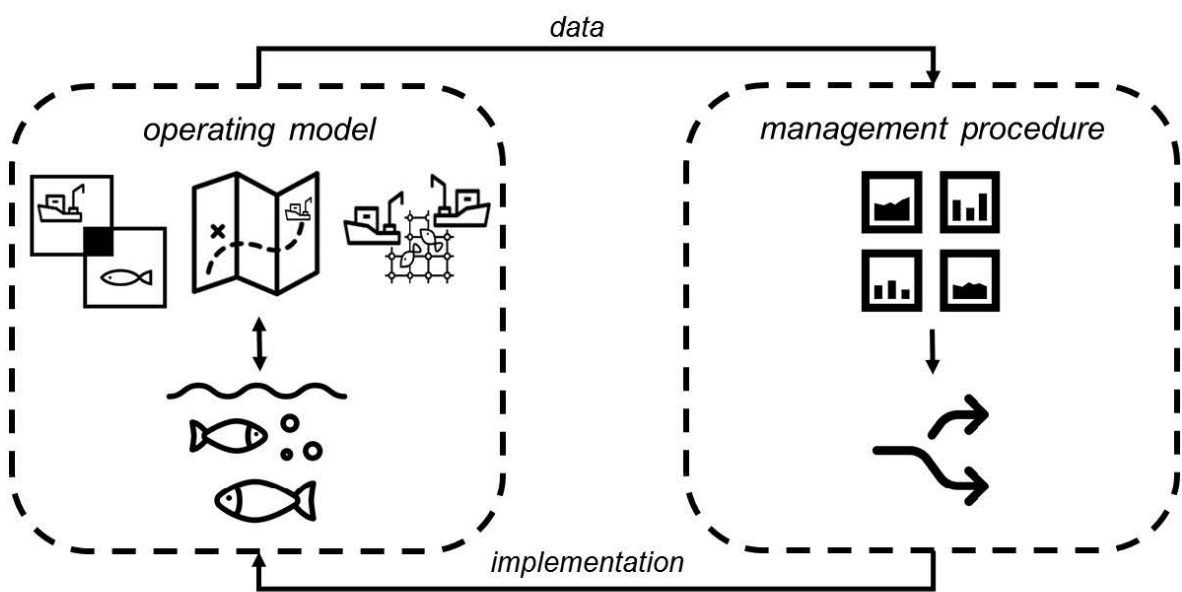
Fishing effort allocation in the Belgian beam trawler fleet (>221kW) in the Southern Bight showed strong variation during the study period. The high effort allocation in the Southern Bight in 2008 and 2009 is strongly related to the fuel price crisis at the end of 2008. Fishers adapted their fishing strategies by reallocating fishing effort closer to harbours to reduce steaming costs (Poos *et al.*, 2012; Bastardie *et al.*, 2013). After the fuel price crisis, fishing effort in the Southern Bight declined again. The Belgian beam trawlers reallocated fishing effort to grounds outside the North Sea and in the central part of the North Sea (ICES Division IVb). Effort reduction in the Southern Bight occurred simultaneously with the development of the Dutch pulse trawlers in 2011. We hypothesize that increased competition between both fleets was an important driver of this effort reallocation.

Apart from spatial effort reallocation, a shift occurred in the weekly exploitation patterns of the Belgian beam trawlers. Since sole *lpue* was reduced during weekdays in 2012 and 2013, a higher proportion of the fishing trips in the Southern Bight ended on Sunday and Monday, while the share of fishing trips ending on Friday and Saturday decreased. This shift can be understood from the viewpoint of increased competition: the drop of sole *lpue* through increased interference competition on Monday would force more fishers to leave fishing grounds in the Southern Bight and return to the harbour on Monday, while ending fishing trips on Friday or Saturday would be less likely due to the higher landing rates of sole on weekends, creating an incentive to continue fishing.

4.4.4. *Management implications*

Competitive differences may have important consequences for both the short- and long-term dynamics of the beam trawler fleet in the North Sea. The occurrence of spatial segregation as a result of different competitive abilities of fishing vessels was observed in the Dutch beam trawler fleet and the French demersal fleet. In studies by Rijnsdorp *et al.* (2000a); Poos *et al.* (2010b) and Girardin *et al.* (2015), the occurrence of segregation among vessels was shown, with higher prevalence of more powerful vessels on the best fishing grounds. In contrast, less powerful vessels lost efficiency in presence of stronger vessels and were more prevalent on poorer fishing grounds (Rijnsdorp *et al.* 2000a). Because no Belgian trawlers used the pulse trawl during the study period, we could not analyse competitive differences between beam and pulse trawlers.

In addition, interference competition may breakdown the correlation structure between fishing effort and abundance (Gillis and Peterman, 1998). Hence, if this mechanism is ignored during the standardization of cpue, stock assessment models are likely to provide an underestimation of stock abundance whereupon managers may define too conservative harvest rates. Finally, competitive interactions between fishing vessels are an important aspect regarding the use of marine space. Obviously, the reduction of fishing grounds through the increased use of marine space for other activities such as dredging or conservation areas, may have important implications for the fishery through a direct loss of fishing grounds, but also through increased competition on the remaining fishing grounds.



CHAPTER 5

General discussion

This final chapter provides a general reflection on fleet dynamics with respect to the objectives as highlighted in the introductory chapter of this thesis. In section 5.1, I summarize the main findings of chapters 2, 3 and 4 to highlight the identified effects of fleet dynamics on the relationship between fishing effort and fishing mortality. In the second part of this chapter, I consider the findings of this research within the broader theoretical context of fleet dynamics. From this theoretical perspective, I discuss the value of fisheries data and computational modelling techniques regarding the identified implications for future research. In the final section of this general discussion, I review the insights of this research with respect to the implication for fisheries management.

5.1. Summary of the main findings

This thesis analysed the effect of fleet dynamics on the relationship between fishing effort and catches. Given the growing interest in spatial based fisheries management tools, the focus was on spatial based mechanisms underlying fleet dynamics. To this end, a quantitative approach based on different modelling techniques was used to analyse landing and effort data of commercial beam trawlers which enabled to identify mechanisms regarding the spatiotemporal effort allocation dynamics and harvesting efficiency of the Belgian beam trawl fleet. Remark that the results of this thesis are discussed with respect to the dynamics of the Belgian beam trawl fleet and that the effect of other anthropogenic activities and fleets has been ignored. Obviously, it is very likely that these other activities have affected the results of this thesis as well. However, the experiments were chosen so that the effect of these other activities was minimized, and consequently, it may be assumed that these do not alter the interpretation of the results.

The thesis focused on the effect fleet dynamic mechanisms regarding ecological feedback loops, fishing tactics, and spatial interactions between fishing vessels. In chapter 2 and 4 of the dissertation, the effect of fishing effort reallocation was analysed with respect to the relationship between the temporal distribution of fishing effort on the harvest efficiency of the fleet, and spatial interaction mechanisms between fishing vessels. Chapter 3 used a state-switching model to identify the tactical decision of fishers from VMS data.

The observed relationship between the landing rate of sole and the exploitation patterns of the fleet, as demonstrated in chapter 2 of this thesis, provided evidence to highlight the mechanism of exploitation competition. In this particular case, the entire fleet was attracted to a fishing ground with high catchability of sole after a temporal closure. Nevertheless, as soon as the fishery re-opened, the catchability dropped quickly to its reference level which suggests an irreversible effect on the local abundance of sole probably resulting from local depletion through the fishery and spatial dispersal of sole.

Chapter 4 revealed a relationship between the weekly patterns in the daily landing rate of sole, and the weekly exploitation patterns of the Dutch pulse trawl fleet which suggested the occurrence of interference competition between both fleets. Due to the absence of this relationship in the landing rate of plaice, which is caught simultaneously with sole, it is plausible to assume that interference competition is induced by a species specific response towards pulse trawling, prey-depression, and not through direct interactions between fishing vessels.

In both cases, the changes in catchability induced a response in the spatiotemporal effort allocation patterns of the fleet which corroborated with the effort dynamics that were

expected assuming profit maximization. Interference competition caused Belgian beam trawlers to reallocate fishing effort in space and time to avoid interference competition with the Dutch pulse trawl fleet, while exploitation competition of a local aggregation of the most valuable species, sole, forced fishers to participate in a short-term race for fish.

Chapter 2 illustrated the emergence of an ecological feedback loop after a seasonal spawning closure was imposed to the fishery in 2005. Following the closure of the Trevoise Box in the Celtic Sea during the months February and March, the catchability of sole increased to a level that was approximately twice as high with respect to the reference catchability. Assuming that the harvest efficiency of the fleet did not change during this period, this suggests that the seasonal closure of the fishery induced an increase of local abundance of sole. Neither the research approach, neither other scientific literature did allow us to explain the underlying mechanisms of this phenomenon. Nevertheless, given the direct relationship between beam trawling and the state of benthic ecosystem, it is plausible to believe – from an ecosystem-based perspective – that the exclusion of fishing effort during the closure might have increased the availability of prey to sustain a higher local abundance of sole.

In chapter 3, effort and landing data was coupled to analyse the fishing tactics of the Belgian beam trawl fleet at high spatiotemporal resolution. The identified fishing tactics corroborated with both the expected behaviour of the fleet, and the landing data, although the identified behavioural modes could not be validated with data of real observations. Two fishing states were identified that demonstrate how beam trawlers detect and exploit local hot spots of fish during a fishing trip. The different movement modes associated with the exploration and exploitation of the fleet provide a starting point regarding the targeting behaviour of the fleet, a more accurate description of the relationship between catch and effort, and the spatial distribution of the resource.

This research demonstrated how short-term fleet dynamics emerge from the interactions (*i*) between fishers and their resource, and (*ii*) amongst fishers. While the majority of the underlying mechanisms cannot be observed directly, this thesis illustrates how various modelling approaches based on fisheries data can be used to identify, refine or reject hypotheses concerning the dynamics of fishing vessels. Such an approach provides a cheap and fast way to explore fisheries systems, and identify relevant challenges and knowledge gaps with respect to fisheries management.

5.2. Theoretical considerations of fleet dynamics

5.2.1. *Feedback loops between fishing effort and local fish abundance*

The strong relationship between the temporal distribution of fishing effort and the fluctuations in the catch rate of sole as demonstrated in chapter 2, suggests the occurrence of a short-term feedback loop between fish abundance and beam trawling. Although such feedback loops are an omnipresent feature of fisheries systems, limited attention has been paid to the occurrence of ecological feedback loops amplified by anthropogenic processes on shorter time horizons. Hereunder, I gather theoretical models with empirical observations to formulate a hypothesis that may explain the observed feedback loop in chapter 2.

It is reasonable to assume that the high landing rate of sole was caused by an increase in local abundance, and not by an increased efficiency of the fleet, or change in fisher behaviour, given the short time period (approximately 2 weeks) of this phenomenon. Such an increase of local abundance has to be caused by somatic growth of individuals and/or a net movement of fish into the closed area as the period of the spawning closure was too short with respect to the reproduction process of sole. Nevertheless, the effect of somatic growth is expected to be minimal. First, somatic growth of juvenile flatfish is characterized by a high interspecies variability (Van Der Veer *et al.*, 1994), hence it is not likely that an entire year-class of a juvenile flatfish reached the length expected at the age of maturity. In addition, due to the low temperature of the sea water during the month of April, it may be expected that the growth rate was rather slow during the period of closure. Moreover, as the density of fish increased during the period of closure, the growth rate is likely to have decreased as a result of competition for food unless the availability of food increased.

Therefore, it is plausible to believe that a net-movement of sole into the closed area occurred. Such a movement process of fish can be described through a diffusion process in which fish species disperse in a random direction and at a rate proportional to the number of fish in a given area (Beverton and Holt, 1957). Hence, a net diffusion into the closed area implies that (i) the concentration of fish was higher outside the closed area, and/or (ii) the direction of dispersal was not random, and/or (iii) the rate of dispersal was not proportional to the abundance. In chapter 2, it was shown that the sole landing rate was not higher outside the closed area compared to the same period of the year before the closure had been implemented in 2005. Therefore, it is unlikely to assume that the abundance was higher outside the closed area, which implies that at least one of the other diffusion statements occurred.

Beverton and Holt (1957) provided multiple extensions of their theoretical model that can be used with respect to the findings of chapter 2. I discuss the two most relevant extensions,

being directed migration, and food availability. Directed migration states that diffusion is not random, but dominated by dispersal in one direction. This corroborates with the migratory behaviour of most fish species, and is the most plausible explanation regarding the increased local abundance inside the Trevoise Box. After all, the Trevoise Box comprises an important spawning ground of the Celtic Sea sole stock from February until April. Hence, the combination of the directed migration to this spawning ground and the reduction of fishing mortality are likely to have resulted in an increase of local abundance of sole.

In addition, movement of fish is mainly driven by the search for prey. As a consequence, an increase of local abundance can only be maintained if the density of prey does not restrict the intake rate of prey by the fish. Consequently, the rate of dispersal and availability of prey are closely related, wherewith in theory, an increase of prey availability should result in a reduction of the dispersal rate (Bertignac *et al.*, 1998). Therefore, it can be hypothesized that the availability of prey for sole increased during the closure of the fishery in the Trevoise Box, leading to a decline in the dispersion rate of sole, resulting in an increase of local abundance inside the Trevoise Box. Such a reduction of the dispersion rate could also explain why the phenomenon of *fishing the line*, being intensive fishing at the borders of a closed area, was hardly observed in our study which contrasts with many other studies where (seasonal) closures have been imposed to the fishery (Kellner *et al.*, 2007; Lee *et al.*, 2013).

A prerequisite for the abovementioned hypothesis, is that there exists a direct relationship between fishing effort and the density of prey. Such a relationship has been found in bottom trawl fisheries due to the physical impact of the gear on the seabed. This might alter the functioning of the benthic ecosystem which provides food for the targeted demersal fish species (Jennings *et al.*, 2001; Hiddink *et al.*, 2008). In such fisheries, both the trawling intensity (Tillin *et al.*, 2006) and its temporal distribution (van Denderen *et al.*, 2014) determine the impact of the fishery on the benthic ecosystem. Depending whether the regulation of the benthic ecosystem is bottom-up or top-down, trawling may feedback into the fishery system, altering the production and/or biodiversity of benthic communities through changes in competitive interactions and cause that more fishing increases or decreases the yields of the fishery, respectively (van Denderen *et al.*, 2013). A mechanism that resembles to the intermediate disturbance hypothesis (Connell, 1978) which is a non-equilibrium model relying on the trade-off between species richness and competitive exclusion. Since the temporal distribution of fishing effort in the Trevoise Box altered after a seasonal spawning closure was imposed to the fishery, this may be a plausible mechanism to explain the increase of local abundance of sole inside the Trevoise Box.

However, this relationship depends on various other biotic factors such as benthic food web interactions (van Denderen *et al.*, 2016), natural disturbance (Hiddink *et al.*, 2006) and sediment type (Shephard *et al.*, 2010) that hamper the quantification of these mechanisms. This stresses the need for further data collection concerning the impact of fishing gears on the benthic ecosystem, and theoretical modelling exercises for further exploration of this hypothesis.

The latter could be done using a pattern-oriented modelling approach in which patterns generated by an IBM are compared with observed patterns in the real world to make inference about the underlying mechanistic processes (Grimm *et al.*, 2005). In this case, an IBM could be developed with models of the fish diffusion process, the benthic ecosystem dynamics, and fishing effort allocation, that would enable to explore different interaction mechanisms between these subsystems. The generated patterns (e.g. fish abundance and fishing effort) could then be compared with observed catchability and effort patterns of fisheries data to make inferences about the mechanisms underlying such a feedback loop.

5.2.2. *Tactical decision of fishers*

Despite the fact that the assumption of profit-maximization was not directly addressed, the observations throughout this thesis show that profit-maximization behaviour can be considered an important driver of the short-term dynamics of Belgian beam trawlers. Profit maximization behaviour is likely to explain the gradual reduction of fishing effort by the fleet between 2012 and 2014 after the landing rate of the target species decreased due to competition (chapter 4). Support for this assumption was also provided by the observation of a short-term race for fish of individual fishing vessels in the Trevoise Box during the month April (chapter 2). Finally, the stronger positive relationship of the revenue per unit effort associated with the exploitation phase of beam trawlers compared to the exploration phase identified in chapter 3, corroborates with optimal foraging theory, and consequently, the profit maximization concept.

This profit-maximization behaviour is in line with findings from the Dutch beam trawl fleet, that has strong similarities with the fleet studied in this thesis. In this fleet, the discard and high grading behaviour of the fleet could be explained by a contingency model¹¹ from optimal foraging theory, in this case profit maximization (Poos *et al.*, 2010a; Batsleer *et al.*, 2016), and the changed exploitation pattern of the fleet in response to changing fuel prices

¹¹ The contingency model, also known as the prey choice model or optimal diet model is a model of optimal foraging theory. It models the decisions of foragers to consume a prey item, with a given cost to handle this item, or continue the search for a more profitable prey item. As such it can be used in fisheries to analyse the decisions of fishers to keep the catch or discard (part of) it.

(Poos *et al.*, 2012). These observations support the suggestion of Salas and Gaertner (2004) that the profit maximization concept is typically applicable for specialised and industrialised fishing vessels owned by private entrepreneurs.

The insights regarding fishing tactics are based on the analysis of fisheries data. Nevertheless, fishing tactics are the outcome of the complex decision making process of humans with different cognitive abilities, risk perceptions, emotions, social norms, habits, etc. (Salas and Gaertner, 2004). Therefore, conclusions concerning fishing tactics can only be made if direct observations are available which can be done through interviews, surveys, role-playing games or participatory modelling.

Nevertheless, fishers are known to be rather reluctant to share information about fishing tactics and strategies, as they have favourite fishing spots which they want to keep secret. Therefore, the willingness of fishers to participate in such data collection projects may be limited. This is one of the reasons why the majority of analyses regarding fishing tactics is based on modelling approaches. Such modelling approaches typically test observed fisher behaviour against a theoretical framework of fishing tactics, an approach which has been followed in chapter 3 of this thesis. Nevertheless, different theoretical and modelling frameworks can be used to analyse fisher behaviour (van Putten *et al.*, 2012). Hence, a deliberate choice of theoretical framework should be made to reduce the uncertainty generated by the human component regarding fleet dynamic models used for scientific advice in fisheries management (Fulton *et al.*, 2011).

Despite the aforementioned issue, rational decision making driven by profit maximization remains the dominant framework with respect to the analysis of the dynamics of beam trawlers. Nevertheless, in the Belgian fishery, the wages of the crew and skipper are directly related to the total trip revenue. This creates an incentive to maximize the revenues of the landings rather than profits. In this perspective, it might be interesting to test whether this affects the fishing patterns of the fleet. This could be done by comparing the outcomes of optimization models with different objective functions to observed fisheries data.

In addition, Holland (2008) suggested that the maximization concept may be more suited to describe the decisions of fishers on an aggregated level than on an individual level. The latter may be an important aspect as the actions of individual fishers may become increasingly important given the tendency to increase the spatiotemporal resolution of fisheries management. This stressed the need to explore the applicability of alternative theoretical frameworks of human decision making that ideally enable to include aspects such as traditions, risk attitudes, morals and norms or personality type in simulation models of fleet dynamics. The *consumat* approach is an example of a theoretical framework that

enables to integrate more complex and realistic human-decision making into ecological-economic models. (Jager *et al.*, 2000) In this approach, agents engage in a cognitive processes through repetition, deliberation, social comparison and imitation which can significantly affect the exploitation of natural resources as demonstrated in a theoretical fisheries model of Jager *et al.* (2000).

5.2.3. Competition between fishing vessels

Chapter 2 and 4 of this thesis demonstrated how exploitation and interference competition induced a remarkable response in the fishing effort allocation patterns of the Belgian beam trawler fleet. Nevertheless, these mechanisms received little attention in the scientific literature and the design of fisheries management. I suggest that this may be due to two reasons: the lack of empirical evidence concerning these mechanisms and the difficulty to include these mechanisms in fleet dynamic models. Hereunder, based on our findings and literature information, I elaborate on these issues and look how fisheries data and modelling techniques could be used to address these challenges.

The lack of empirical evidence regarding competitive interactions in fisheries stems from the difficulty to observe the underlying mechanisms. Most of the underlying processes occur under water which makes direct observation complicated. Operational decisions of skippers are also not registered. This is the reason why no unequivocal conclusions could be made regarding the type of competition involved in chapter 2 and 4, and is also the major limitation of other studies that used fisheries data to make inferences about competition (Gillis *et al.*, 1993; Rijnsdorp *et al.*, 2000a; Poos and Rijnsdorp, 2007a).

The mechanisms underlying interference competition in fisheries are currently not well understood. However, several hypotheses comprising direct interactions between fishing vessels (e.g. if a skipper needs to deviate from the optimal fishing track to avoid a collision) and prey-depression mechanisms (e.g. anti-predator behaviour of fish species) have been formulated to explain the causes of interference competition between fishing vessels. In chapter 4, interference competition had a different effect on the landing rate of sole and plaice, hence, it is likely to assume that this was induced by a species specific response. This suggests the occurrence of interference competition through prey-depression which is also hypothesized in other studies of the beam trawl fishery (Poos and Rijnsdorp, 2007a; Poos *et al.*, 2010b). This hypothesis corroborates refugee behaviour in another flatfish species, Greenland halibut (*Reinhardtius hippoglossoides*), in response to fishing gear stimuli which Albert *et al.* (2003) observed through underwater video recording.

Insights into the underlying mechanisms may also provide support for the hypothesis that interference competition may cause hyperdepletion in fisheries as has been suggested by

a number of authors (e.g. Walters, 2003; Swain and Wade, 2003). In the case that interference is caused by mutual interactions between fishing vessels (e.g. avoidance), the encounter rate between fishing vessels is disproportional to the density of the resource. Logically, at an increasing resource density, the average searching time decreases which implies that the likelihood of entering in interference interaction with another searching forager decreases (Moody and Ruxton, 1996). In case interference competition is caused through the mechanism of prey-depression, Ruxton (1995) showed that there is a breakdown of the linear relationship between the functional response and the density of prey for a given level of competitors if handling time > 0 . On the scale of a fishing trip, beam trawlers deploy an exploration-exploitation strategy to find and exploit local hotspots of flatfish as illustrated in chapter 3 of this thesis. Hence, if the time needed to exploit a local hotspot of flatfish is considered as the handling time, a nonlinear relationship arises between cpue and abundance.

Nevertheless, Gillis *et al.* (1995) state that handling time of fishing vessels can be ignored which implies that Ruxton's (1995) model can be approximated by the model of Beddington (1975) which results in a linear relationship between a foragers' intake rate (I) and the density of prey (n) given by $I = \frac{an}{1 + qp}$, in which p , q and a represent the number of foragers, the competition and search efficiency coefficients, respectively.

In addition, it is likely that the form of the functional response in the case of interference competition through prey-depression depends from the assumptions made about the behavioural mechanisms of both foragers (e.g. searching behaviour) and prey (e.g. migration between vulnerable and invulnerable state) and eventually cause that the strength of interference is in function of the density of prey (Stillman *et al.*, 2000). Based on the literature, I discuss three assumptions underlying the model of Ruxton (1995) with respect to the strength of interference competition in fisheries.

To derive a mathematical expression for the functional response, Ruxton (1995) assumes that there is homogeneous mixing between vulnerable prey and searching foragers so that the coefficient governing the forager-prey encounter rate is constant. Nevertheless, this is not likely to be the case for beam trawlers targeting flatfish species because the distribution of flatfish is known to be patchy which implies that the predator-prey encounter rate is in function of both the density and distribution of prey. This was demonstrated by Higginson and Ruxton (2015) using an optimal foraging model. They predicted that foragers alter both searching strategies and searching time with respect to the density and distribution of prey items so that the reward of encounter and consuming prey minus the cost associated with foraging is maximized. In general, and similar to the finding of Stillman *et al.* (2000), lower densities of prey cause that foragers spend more searching time and vice versa, which

implies that at lower densities of prey, relative more prey will be depressed. Assuming that fishers are driven through profit-maximization, this implies that skippers should adopt fishing tactics wherewith the time spend steaming, exploring (searching) and exploiting maximizes the economic return. Evidence for such an optimal searching behaviour has been found in the Dutch beam trawl using the Marginal Valuem Theorem (Rijnsdorp *et al.*, 2011) and the Lévy fight foraging hypothesis (Marchal *et al.*, 2007).

Another assumption underlying the model of Ruxton (1995) is that the average time prey spend in the invulnerable state is constant. Nevertheless, prey-depression mechanisms are known to come at a cost for prey, in most cases this is due to a reduction of the food intake-rate during the invulnerable state which is also assumed to be the case for adult flatfish species that burry into the sediment in response to the presence of a predator (Burrows, 1994; Burrows and Gibson, 1995). Given the trade-off between the risk of starvation, determined by the food intake-rate, and the risk of predation, optimality theory can be used to predict the time spend in both states (Gabriel and Thomas, 1988; Burrows, 1994). As has been observed in juvenile plaice, lower food intake-rates may increase the risk of starvation and cause fish species to spend more time in the vulnerable state at an equal predation risk, while the opposite happens if the risk of predation increases (Burrows, 1994). Hence, since the growth-rate of flatfish species and thus the food intake-rate is density dependent as assumed by Beverton and Holt (1957), it may be hypothesized that prey-hiding is not constant. Nevertheless, evidence for density-dependent growth rates of flatfish species is weak, probably because this effect is absent in exploited flatfish populations (Rijnsdorp, 1994).

Since there is evidence that habitat selection of flatfish species is density-dependent (Laurel *et al.*, 2007), it is likely to assume that the prey-hiding coefficient of flatfish species is related to the habitat characteristics as well. Laurel *et al.* (2007) showed that flatfish have a preference for habitats with fine sediment (sand) that offer sufficient protection to predators. Nevertheless, at increasing population densities, the good refugee spots (sandy sediment) become occupied and part of the flatfish species will occupy poorer refugee spots (coarser sediments). Therefore, it would be interesting to investigate the hypothesis that the quality of the refugee spots affects the hiding capacity of flatfish which may in turn affect the time that flatfish spend in the invulnerable state.

The final assumption underlying Ruxtons' (1995) model is that the response time, being the propensity of prey to use the invulnerable state is constant. However, it may be hypothesized that the response time, being the time needed to switch to the invulnerable state after encountering a fishing vessel, is also likely to be density-dependent as Godø *et al.* (1999) observed that the swimming behaviour of American plaice (*Hippoglossoides*

platessoides) in the mouth of bottom trawls differed with respect to the density. At higher densities of fish, there was less zigzag movement which resulted in lower escape rates compared to individual fish. Hence, it may be expected that lower densities of flatfish result in lower response times as such increasing the ratio of fish that turn to the invulnerable state and strengthening the effect of interference competition.

Evidence regarding the underlying mechanism of the observations in chapter 2 and 4 can only be obtained through analysis of the direct interactions between fishing vessels or direct observation of fish species. This might be done through e.g. interviewing skippers, lab experiments in which the response of fish species towards fishery dependent stimuli (e.g. noise, vibrations, turbulence) could be observed, or through the use of emerging technologies such as underwater cameras on trawls with automatic visual content analysis (Rosen *et al.*, 2013).

Desk-based studies, as shown in this thesis, offer an alternative approach that may be more appropriate given the time and budget constraints of most research projects. The increased availability of landing and effort data of commercial fishing vessels at high spatiotemporal resolution (Gerritsen and Lordan, 2011), the improvements made regarding complex modelling techniques such as interpolation of VMS data (Hintzen *et al.*, 2010) or analysis of foraging trajectories (Patterson *et al.*, 2008) and the increased access to (cheap) computational power offer new opportunities to make inferences about competitive interactions between fishing vessels. In spite of the abovementioned limitations, these might enable to quantify the effect of competition between fishing vessels, which may allow researchers to refine and test existing, or formulate new hypotheses.

Finally, competitive mechanisms are difficult to include in the majority of the fleet dynamic simulation models that are mainly based on discrete choice or mathematical programming approaches (van Putten *et al.*, 2012). Discrete choice models often rely on random utility theory, and require a statistical relationship between the decision and explanatory variables. Girardin *et al.* (2017) demonstrated that in most discrete choice models, vessel density effects were associated with attraction, and thus a higher utility. The effect of repulsion, which is expected through competition between vessels was hardly observed. This can be explained by the fact that density dependent mechanisms can be flattened out through opposite effects. This can occur if e.g. catch rates increase through information sharing between fishers (Little *et al.*, 2004) while a simultaneous decrease of the catch rates can occur through competition. Obviously, this limits the ability of statistical models to detect all the underlying mechanisms. Such an opposite, attraction effect may have occurred in our study, causing an underestimation of the effect of interference competition in chapter 4 of this thesis.

With respect to mathematical programming approaches (e.g. models based on optimal foraging theory), density dependent interaction mechanisms increase model complexity and result in an exponential increase of the solution space. This is a substantial challenge for optimization algorithms (e.g. dynamic programming) regarding computational performance and ability to find an optimum (Clark and Mangel, 2000). Therefore, these models are rather applied at the level of an individual vessel thereby assuming that vessel interactions are negligible. Population-based metaheuristic optimization algorithms, e.g. genetic algorithms or particle swarm optimization, applied in an individual or agent-based modelling framework offer an approach to circumvent this. The IBM enables to include interactions between fishing vessels (as demonstrated in section 5.3. where the prey-depression model of Ruxton (1995) is used) while an *evolutionary process* enables to optimize vessel behaviour after each model iteration. This makes it possible to obtain optimal foraging strategies for individual vessels while accounting for interactions between individuals (Giske *et al.*, 1998). None of the two latter approaches guarantee to provide a global optimal solution which is in itself also an advantage because observed strategies emerge from individual optimisations and do also not result in global optima.

5.3. Implications for fisheries management

5.3.1. Feedback loops

In contrast to the well-established Management Strategy Evaluation (MSE) approach to control the annual feedback loop between fishing effort and fishing mortality (Smith., 1993), such management strategies do hardly exist at higher temporal resolutions. Similar to competitive interactions, I suggest that this is due to the fact that such short-term feedback loops do not directly affect the outcomes of fisheries management through TACs since they do not alter the amount of fish that can be harvested from the resource.

Consequently, in some cases where short-term feedback mechanisms occurred and resulted in unexpected outcomes, e.g. through spillover and export of fish to adjacent areas of MPAs, ex-post evaluation was performed whereupon the management tool was eventually adopted as happened with the Plaice Box (Beare *et al.*, 2013). In other cases, the effects of feedback loops are ignored and as a consequence, their effects are not known. This is for instance the case with the spawning closure of the Trevoze Box where the effect of the temporal race for sole has not been evaluated with respect to the Celtic Sea sole stock. Moreover, it is currently not known whether other species such as plaice exhibit similar feedback mechanisms between fishing effort and local abundance. However, due to the similarities between both species, it can be hypothesized that the local abundance of plaice increased during the closure, and resulted in more discards of plaice after re-opening

of the fishery in April. Nevertheless, since plaice landings of beam trawlers in the Celtic Sea were managed through a daily catch limit, that was reached almost every day of the study period, it was impossible to analyze whether the landing rate of plaice was characterized by a similar pattern as identified in the sole landing rate.

Besides the potential direct effects, it is likely that the limited knowledge of these short-term feedback loops may have indirect effects on fisheries management as they may create a diverging perception of resource dynamics. In turn, this is likely to hamper participatory processes in fisheries management which is seen as a key to increase the support for management measures (Gray and Hatchard, 2003). For instance, the observations in chapter 2 of this thesis may support the hypothesis of fishers that alternating periods of disturbance through beam trawling with recovery periods increases the availability of prey for flatfish species, and consequently sustain higher levels of fishing mortality. A mechanism to which fishers often refer to as ploughing due to the similarities of tillage in agriculture (Verweij and van Densen, 2010). Obviously, if such a phenomena cannot be explained, they are likely to be counterproductive for management measures that seek to reduce the impact of trawl fisheries on the benthic ecosystem.

5.3.2. *Fishing tactics*

Fishing tactics and strategies can be considered as the main reason of many failures in fisheries management due to the unexpected or unintended responses of fishers regarding changes in fisheries management or other environmental constraints.

This thesis did not provide an example of such an unintended management outcome through changes in fisher behaviour. Nevertheless, the short-term race for fish as highlighted in chapter 2 of this thesis may have some consequences for local fishers as demonstrated by a number of local newspapers¹² reporting about the race for fish behaviour of the Belgian beam trawl fleet. In these articles, local fishers complained that the Belgian beam trawlers fished too intensive during this short period which destructed the fishery for the rest of the year. However, these complaints have not been thoroughly addressed yet.

Another example of how changes in fisher behaviour may interfere with the objectives of fisheries management was given in chapter 4 of this thesis. It was observed that Belgian fishers increased fishing effort during the weekend after competition increased. Again, the effects of this change have not been quantified, although it can be expected that such a

¹² <https://www.fishupdate.com/trevose-box-beamer-invasion-is-appalling-fishupdate-com/>

<http://www.boatstories.co.uk/news/inside-the-box>

shift has a negative effect on a fishers' social life. Moreover, it may hamper the succession in the fishery, currently one of the major problems in the Belgian fishery.

5.3.3. *Competitive interactions*

Competitive interactions between vessels affect neither the amount of fish that can be harvested from a fish stock nor the minimum landing size of fish species. Consequently, they do not directly alter the outcome of most management tools that rely on output controls or technical measures, respectively. I suggest that this is a major reason why competitive interactions have hardly been considered with respect to the design of fisheries management.

Moreover, policy makers and fisheries managers may even be unaware of these mechanisms which might prevent fisheries management from achieving its objectives. This happened for instance in the beam trawl fishery in the North Sea, as illustrated in chapter 4 of this thesis. After the Dutch beam trawl fleet switched to the pulse trawl, Belgian beam trawlers experienced a reduction of the sole landing rate due to increased competition with the Dutch pulse trawl fleet. As a result, the Belgian beam trawl fleet reallocated fishing effort to ICES subdivisions outside the Southern part of the North Sea. This effort reallocation caused that important catch opportunities of sole nearby the Belgian coastline were underexploited (Tessens and Velghe, 2015). Further, it fed a scepticism regarding electric fishing among Belgian vessel owners which is considered an important burden regarding the adoption of pulse trawling in the fishery (Hamon *et al.*, n.d.).

Besides the abovementioned indirect effects on fisheries management, competitive interactions are also known to hamper management through TACs. As demonstrated in chapter 4 of this thesis, interference competition is known to alter the slope of the linear relationship between fishing effort and cpue and affect the correlation structure between abundance and cpue (Gillis and Peterman, 1998). This is a major burden with respect to the standardization of fishing effort and thus for the accuracy wherewith the catch-per-unit-effort is determined (Hilborn and Walters, 1992; Maunder and Punt, 2004). Standardization of catch rates is an important aspect regarding stock assessments as it aims to remove the variance in the catch rates that is not attributed to changes in abundance. Hence, such a standardization of catch rates is also an important issue if fisheries data is used to make inferences about fleet dynamics as demonstrated in this thesis. Therefore, poor standardization of catch rates may prevent managers to define an appropriate annual harvest amount of a fish stock with respect to the management objectives which is considered one of the main reasons of the collapse of the northern cod stock off Newfoundland and Labrador (Rose and Kulka, 1999). Nevertheless, as interference

competition negatively affect the catch rates, it is likely to result in an underestimation of the stock status. This may cause that managers set annual harvest amounts too low thereby eventually undermining the economic opportunities of the fishery. In line with the difficulties regarding the definition of harvest amounts, interference competition may also hamper the accuracy of decommissioning schemes through vessel-buyback programs (Dowling *et al.*, 2017) (Dowling *et al.*, 2017). After all, following a reduction of the number of vessels, it is likely that cpue will increase as happened in the flathead (*Neoplatycephalus richardsoni*) fishery in Australia. Obviously, such an unexpected increase of cpue may cause that the expected reduction of fishing mortality due to a vessel-buyback program is not achieved.

The species specific character of interference competition, as illustrated in chapter 4 of this thesis, may also affect discarding behaviour and technical interactions in a mixed-fishery. For instance, if interference competition causes a decline in the landing rate of a target species, while the landing rate of the bycatch species is not affected, this is likely to increase discarding of the bycatch species assuming that the quota of the bycatch species constrains the fishery. It is also suggested that increased vessel density on a fishing ground could induce a size specific response in fishes (Poos *et al.*, 2010b). Assuming that larger fish exhibit a stronger response than smaller fish species towards interference competition (e.g. because they burry deeper into the sediment after passage of a trawl gear), the size distribution of fish in the landings may change. This could increase the practice of high grading of smaller sized fish species if the quota are too restrictive to land all catches of commercial fish, and the larger sized fish species have a higher value as is the case for e.g. plaice in the Dutch beam trawl fishery (Batsleer *et al.*, 2016).

Finally, this difference in burying depth between species could alter technical interactions in a mixed-fishery. This was observed in the Dutch beam trawl fishery where a segregation between the small and large beam trawl segment was observed and related to their different capacity to capture species according their burying depth (Poos *et al.*, 2010b). If such a segregation through competitive differences forces smaller fishing vessels to less valuable fishing grounds, this may have negative socio-economic consequences for certain fleet segments and lead to unsatisfied fishers.

5.3.4. Implications for effort-based management systems

The success of effort-based fisheries management systems is directly determined by the stability or predictability of the relationship between fishing effort and fishing mortality (Rijnsdorp *et al.*, 2007). Hence, the fleet dynamic mechanisms highlighted in this thesis reveal a number of interesting mechanisms which are hereunder explored with respect to effort-based management systems.

Given that interference competition breaks down this relationship, it is worthwhile to test how this affects the performance of effort-based management systems. Poos and Rijnsdorp (2007a) used the model of Beddington (1975) to quantify the effect of interference competition through prey-depression on the catch rate of fishing vessels. Assuming that the handling time can be ignored, the relationship between the intake rate (I) and the vessel density (p) is described by $I = \frac{an}{1 + qp}$. In this equation, q and a represent the competition and search efficiency parameters, respectively. I applied this equation in the individual-based model of Kraak *et al.* (2015) to explore how interference competition affects the performance of real-time fisheries management for a hypothetical mixed-fishery that targets two cod like species, one with high and one with low catchability, that move in the opposite direction. A detailed description of this IBM can be found in Kraak *et al.* (2005) and Appendix A, respectively.

Figure 5.1 and Figure 5.2 show that, for most of the simulation runs, the annual harvest rate of species 1 and 2, respectively, was less than 10% above the target harvest rate (0.33) at the end of the simulation (year 20). This indicates that real-time management may offer sufficient protection regarding overshooting of the harvest rate in case of interference competition. The target harvest rate of both species was only overshooted in some simulation runs during the first and/or second year, but the annual feedback loop caused that the tariff setting became more stringent resulting in a reduction of the harvest rates.

If interference competition depressed the catch rate of the choke species (species 1), the harvest rate of species 1 was below the target harvest rate from year 1 until 8 because the protection for the choke species was too strong (Figure 5.1). This is due to the fact that fishery for the choke species is restricted to a limited number of fishing grounds causing a higher level of interference competition. Managers should be aware of this, since undershooting of the harvest rate may lead to misreporting (Kraak *et al.*, 2014), or eventually force fishers out of the fishery or switch between métiers. Nevertheless, the annual feedback loop caused that the harvest rate reached the objective harvest rate at the end of the simulation. Obviously, interference competition for species 2 did not affect the harvest rate of the choke species (species 1).

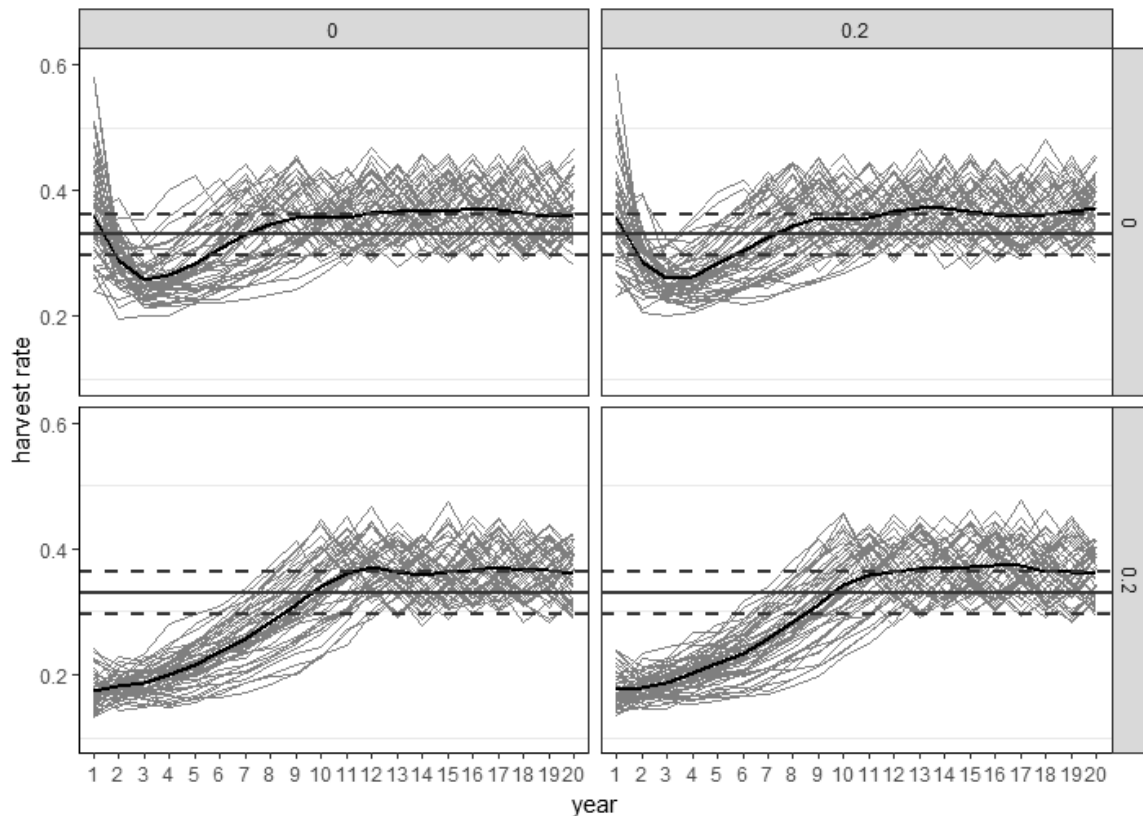


Figure 5.1 The evolution of the annual harvest rate (annual catch divided by the total biomass) of species 1 (the choke species with high catchability) in a hypothetical real-time management system. The panels on the left represent the situation with no competition for species 2, the two upper panels represent the scenarios without competition for species 1. The panels on the right and lower panels demonstrate the scenarios with competition for species 2 and species 1, respectively. The horizontal line represents the target harvest rate (0.33), while the dotted lines represent the +10% and -10% deviation of the target harvest rate. The black line is the mean harvest rate of all simulation runs ($n=50$).

The target harvest rate of species 2 could only be achieved if there was interference competition for the choke species and not for the non-choke species (Figure 5.2). Obviously, if the catch rate of the choke species is depressed through interference competition, while not for the other species, the probability of an early closure of the fishery decreases. Logically, in the opposite situation the target harvest rate for species 2 cannot be achieved as the choke pressure of species 1 increases.

In this basic simulation model, the spatial distribution of fishing vessels between subsequent weeks was characterized by small changes. Hence, it can be expected that the effect of interference competition on the weekly update mechanism of the tariffs was rather limited. Nevertheless, in the unlikely case of strong fluctuation of the spatial distribution of the fishing fleet between subsequent weeks, it may be expected that interference completion could reduce the effectiveness of real-time fisheries management tools. For instance, if fishers would develop a strategy wherewith the distribution of fishing effort is aggregated during one week, and dispersed in the next week and vice versa, fishers would have partly control

of the weekly update mechanism of the cell tariffs if interference competition occurs. As such, it may happen that the target harvest rate is not achieved. Nevertheless, if this leads to overshooting of the harvest rate, it can be expected that the annual feedback control mechanism would result in more stringent tariff quota in the next year as is for instance the case if fishers misreport their landings (Kraak *et al.*, 2014).

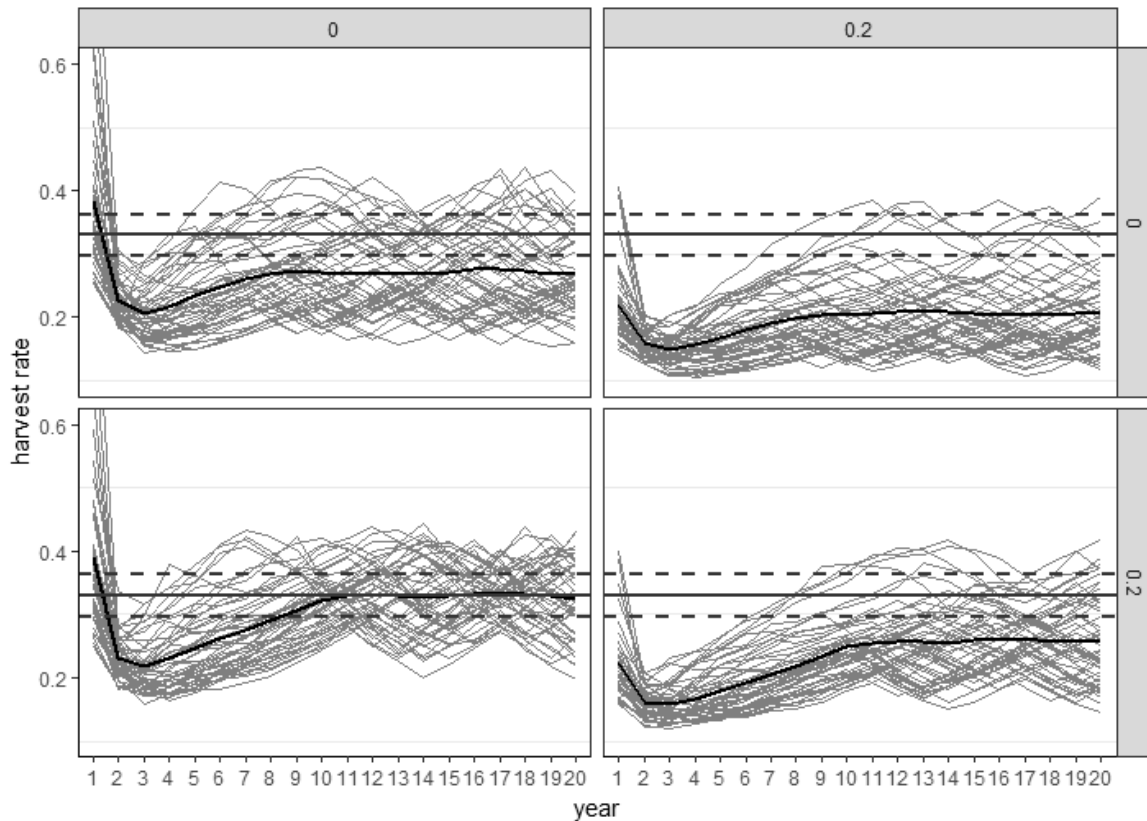


Figure 5.2 The evolution of the annual harvest rate (annual catch divided by the total biomass) of species 2 (species with low catchability) in a hypothetical real-time management system. The panels on the left represent the situation with no competition for species 2, the two upper panels represent the scenarios without competition for species 1. The panels on the right and lower panels demonstrate the scenarios with competition for species 2 and species 1, respectively. The horizontal line represents the target harvest rate (0.33), while the dotted lines represent the +10% and -10% deviation of the target harvest rate. The black line is the mean harvest rate of all simulation runs ($n=50$).

The results of the exercise described above provide an indication of the robustness of effort-based management systems, such as real-time fisheries management, with respect to interference competition. While some interesting patterns were revealed, no inferences can be made as the underlying models did not capture all relevant processes of fleet and population dynamics. Therefore, a further exploration of such systems with fleet and population dynamic models adopted to specific cases is needed.

Besides its effect on the relationship between catch and effort, competition between fishing vessels may also affect the willingness of fishers to share information with each other which

is a key element underlying real-time management tools. As argued by Maurstad (2002), knowledge of fishing grounds is an asset of fishers, especially in fisheries where effort is shifted in space and time. Finding a good fishing spot, it is important not to distribute the news immediately as it would draw other fishers to the place. Instead, fishers try to keep their new “asset” secret as long as possible. Obviously, the strength of interference competition determines the value of these intangible assets and is therefore likely to affect the information flow from the fishery to the management system. Hence, compliance of fishers with respect to real-time management tools is likely to be a function of the trade-off between the gains resulting from information sharing e.g. to avoid bycatches of choke species, and the losses experienced from increased competition on valuable fishing ground through attraction of competing vessels.

With respect to short-term feedback loops between fishing effort and fishing mortality, it can be expected that effort-based management systems do not perform as intended. For example, in the RTI management system proposed by Kraak *et al.* (2014; 2015), cells with the highest tariff would be closed for the fishery and re-open after 3 weeks. If such a temporal closure would result in an increase of local abundance of a certain species, this may result in a short-term discrepancy between a cells’ local abundance and tariff and eventually result in an unexpected high fishing pressure. Obviously, if such feedback loops occur, much attention should be paid to the temporal resolution of the management tool. A higher temporal resolution may increase the ability of the management system to deal with feedback loops but reduce the number of data (catch and effort) entries from the fishery which may affect the accuracy of the tariff update mechanism. In contrast, when the temporal resolution is too low, it may increase the probability that a local hotspot is formed, eventually resulting in unintended high fishing mortality of a species.

Finally, I use the exploration-exploitation strategy of fishers to formulate an example of how effort-based management systems could change fisher behaviour. As demonstrated in chapter 3, beam trawlers use an exploration-exploitation strategy to locate hotspots of their target species. Such a strategy implies that fishers explore a larger area whereupon they exploit a smaller surface of a fishing ground. Since effort-based management systems aim to capture part of the spatial heterogeneity regarding the impact of fisheries on the marine ecosystem, fishing areas will be divided in different spatial units with an impact credit or quota according their vulnerability (Batsleer *et al.*, 2018). Obviously, the spatial resolution at which the units are defined will be an important aspect regarding the accuracy of the management tool, but may interfere with the exploration-exploitation tactics of fishers. It can be expected that a too coarse spatial resolution of the management tool will reduce the capacity of the system to cope with the spatial heterogeneity of the ecosystem, while the

opposite, a too high spatial resolution may interfere with fishing tactics and hinder fishers to detect local hotspots of a target species, in turn reducing the catchability of fish species, and jeopardize the profitability of the fishery. In addition, if the spatial distribution of fishing vessels changes, the relationship between catch and effort may also change through interference competition. Moreover, if such changes in cpue differ among species, fishers may start to target other species which may have a number of negative consequences across the fisheries sector.

Although most insights of this PhD dissertation specifically apply to the Belgian beam trawl fishery, the insights of this research highlight that fleet dynamics are a key element of the design of effort-based management systems in bottom trawl fisheries. Interaction mechanisms between fishing vessels, tactical behaviour of fishers, and the temporal distribution of fishing effort were revealed as important mechanisms underlying the socioeconomic performance of the fishery and its impact on the marine ecosystem. These received little attention with respect to the design of traditional fisheries management systems because they were not known or their effect was flattened out at coarser management scales. However, on a higher temporal and spatial resolution, as considered for effort-based management systems, their effects may add up and eventually affect management outcomes. Nevertheless, since these fleet dynamic processes emerge from the interactions between biological processes, affected by fish behaviour and the dynamics of benthic communities, and human processes (e.g. fisher behaviour) that are often not well understood, it remains a major challenge to include these processes into the design of fisheries management tools. In developed fisheries, where data of fishing vessels is increasingly available, new modelling techniques offer an opportunity to address this challenge. As demonstrated in this thesis, this data enables to analyse fleet dynamic processes, formulate hypotheses and specify uncertainty. Hence, integrating these processes into a Management Strategy Evaluation framework, as shown by the illustration at the start of this chapter (p 86), would allow to compare alternative implementations of effort-based management systems given the uncertainty of fleet dynamics processes.

References

- Abrahams, M. V., and Healey, M. C. 1993. Some consequences of variation in vessel density: a manipulative field experiment. *Fisheries Research*, 15: 315–322.
- Albert, O. T., Harbitz, A., and Høines, Å. S. 2003. Greenland halibut observed by video in front of survey trawl: Behaviour, escapement, and spatial pattern. *Journal of Sea Research*, 50: 117–127.
- Baddeley, A., and Turner, R. 2005. spatstat: An R package for Analyzing Spatial Point Patterns. *Journal of Statistical Software*, 12: 1–42.
- Bailey, N., Campbell, N., Holmes, S., Needle, C., and Wright, P. 2010. Real time closures of fisheries. IP/B/PECH/IC/2009-091, 56 pp..
- Bastardie, F., Nielsen, J. R., Andersen, B. S., and Eigaard, O. R. 2013. Integrating individual trip planning in energy efficiency – Building decision tree models for Danish fisheries. *Fisheries Research*, 143: 119–130.
- Bastardie, F., Nielsen, J. R., and Miethé, T. 2014. DISPLACE : a dynamic , individual-based model for spatial fishing planning and effort displacement — integrating underlying fish population models. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(3): 366-386.
- Batsleer, J., Hamon, K. G., van Overzee, H. M. J., Rijnsdorp, A. D., and Poos, J. J. 2015. High-grading and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries*, 25: 715–736.
- Batsleer, J., Rijnsdorp, A. D., Hamon, K. G., van Overzee, H. M. J., and Poos, J. J. 2016. Mixed fisheries management: Is the ban on discarding likely to promote more selective and fuel efficient fishing in the Dutch flatfish fishery? *Fisheries Research*, 174: 118–128.
- Batsleer, J., Marchal, P., Vaz, S., Vermard, V., Rijnsdorp, A. D., and Poos, J. J. 2018. Exploring habitat credits to manage the benthic impact in a mixed fishery. *Marine Ecology Progress Series*, 586: 167–179.
- Baudron, A., Ulrich, C., Nielsen, J. R., and Boje, J. 2010. Comparative evaluation of a mixed-fisheries effort-management system based on the Faroe Islands example. *ICES Journal of Marine Science*, 67: 1036–1050.

References

- Beare, D., Hölker, F., Engelhard, G. H., McKenzie, E., and Reid, D. G. 2010. An unintended experiment in fisheries science: A marine area protected by war results in Mexican waves in fish numbers-at-age. *Naturwissenschaften*, 97: 797–808.
- Beare, D., Rijnsdorp, A. D., Blaesberg, M., Damm, U., Egekvist, J., Fock, H., Kloppmann, M., et al. 2013. Evaluating the effect of fishery closures: Lessons learnt from the Plaice Box. *Journal of Sea Research*, 84: 49–60.
- Beddington, J. R. 1975. Mutual Interference Between Parasites or Predators and its Effect on Searching Efficiency. *Journal of Animal Ecology*, 44: 331–340.
- Bertignac, M., Lehodey, P., and Hampton, J. 1998. A spatial population dynamics simulation model of tropical tunas using a habitat index based on environmental parameters. *Fisheries Oceanography*, 7: 326–334.
- Bertrand, S., Burgos, J. M., Gerlotto, F., and Atiquipa, J. 2005. Lévy trajectories of Peruvian purse-seiners as an indicator of the spatial distribution of anchovy (*Engraulis ringens*). *ICES Journal of Marine Science*, 62: 477–482 .
- Beverton, R. J. H., and Holt, S. J. 1957. On the Dynamics of Exploited Fish Populations. Vol 19. Her Majesty's Stationery Office, London, UK, 533 pp.
- Bez, N., Walker, E., Gaertner, D., Rivoirard, J., Gaspar, P., and Walters, C. J. 2011. Fishing activity of tuna purse seiners estimated from vessel monitoring system (VMS) data. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 1998–2010.
- Botsford, L. W., Castilla, J. C., and Peterson, C. H. 1997. The management of fisheries and marine ecosystems. *Science*, 277: 509–515.
- Branch, T. A., Hilborn, R., and Bogazzi, E. 2005. Escaping the tyranny of the grid: a more realistic way of defining fishing opportunities. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 631–642.
- Branch, T. A., Hilborn, R., Haynie, A. C., Fay, G., Flynn, L., Griffiths, J., Marshall, K. N., et al. 2006. Fleet dynamics and fishermen behavior: lessons for fisheries managers. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 1647–1668.
- Breen, M., Howell, T., and Copland, P. 2011. A report on electrical fishing for razor clams (*Ensis sp.*) and its likely effects on the marine environment. 120 pp.
- Burrows, M. T. 1994. An optimal foraging and migration model for juvenile plaice. *Evolutionary Ecology*, 8: 125–149.

- Burrows, M. T., and Gibson, R. N. 1995. The effects of food, predation risk and endogenous rhythmicity on the behaviour of juvenile plaice, *Pleuronectes platessa* L. *Animal Behaviour*, 50: 41–52.
- Cappell, R. 2001. Economic Aspects of Discarding UK Case Study: Discarding by North Sea Whitefish Trawlers. Nautilus Consultants. 104 pp.
- Catchpole, T. L., Frid, C. L. J., and Gray, T. S. 2005. Discards in North Sea fisheries: Causes, consequences and solutions. *Marine Policy*, 29: 421–430.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9: 129–136.
- Clark, C. W., and Mangel, M. 2000. Dynamic State Variable Models in Ecology: Methods and Applications. Oxford University Press, Oxford, UK, 289 pp.
- Connell, J. H. 1978. Diversity in Tropical Rain Forests and Coral Reefs. *Science*, 199: 1302–1310.
- Council Regulation (EEC) No 2141/70 of 20 October 1970 laying down a common structural policy for the fishing industry. *Official Journal of the European Communities*, 13: 703–706.
- Council Regulation (EEC) No 92/43 on the conservation of natural habitat and of wild fauna and flora. *Official Journal of the European Communities*, L269: 1–15.
- Council Regulation (EEC) No 3760/92 of 20 December 1992 establishing a Community system for fisheries and aquaculture. *Official Journal of the European Communities*, 26: 1–13.
- Council Regulation (EEC) No 170/83 of 25 January 1983 establishing a Community system for the conservation and management of fishery resources. *Official Journal of the European Communities*, 4: 1–14.
- Council Regulation (EEC) No 1380/2013 of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC. *Official Journal of the European Union*, L354: 22–61.
- Cresswell, W. 1998. Variation in the strength of interference competition with resource density in blackbirds, *Turdus merula*. *Oikos*, 81: 152–160.
- Creutzberg, F., Duinveveld, G. C. A., and van Noort, G. J. 1987. The effect of different numbers of tickler chains on beam-trawl catches. *ICES Journal of Marine Science*, 43: 159–168.

References

- Crowder, L., and Norse, E. 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Marine Policy*, 32: 772–778.
- Daan, N. 1996. TAC management in North Sea flatfish fisheries. *Journal of Sea Research*, 37: 321–341.
- Dankel, D.J., and Edwards, C. T. T. 2016. Fishery systems and the role of management science. In *Management science in fisheries: an introduction to simulation based methods*. Edited by C.T.T. Edwards and D.J. Dankel. Routledge, New York. pp. 3–15.
- Daw, T. M. 2008. Spatial distribution of effort by artisanal fishers: Exploring economic factors affecting the lobster fisheries of the Corn Islands, Nicaragua. *Fisheries Research*, 90: 17–25.
- De Souza, E. N., Boerder, K., Matwin, S., and Worm, B. 2016. Improving fishing pattern detection from satellite AIS using data mining and machine learning. *PLoS ONE*, 11(7).
- Deporte, N., Ulrich, C., and Bastardie, F. 2012. Regional métier definition: a comparative investigation of statistical methods using a workflow applied to international otter trawl fleets in the North Sea. *ICES Journal of Marine Science*, 69: 331–342.
- Dolman, P. M. 1995. The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrophenax nivalis*. *Oecologia*, 102: 511–514.
- Dowling, N. A., Mangel, M., and Haddon, M. 2017. Quantifying the effect of vessel interference on catch rates: A theoretical approach. *Ecological Modelling*, 359: 293–300.
- Edwards, A. M. 2011. Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. *Ecology*, 92(6): 1247–1257.
- Eigaard, O. R. 2009. A bottom-up approach to technological development and its management implications in a commercial fishery. *ICES Journal of Marine Science*, 66: 916–927.
- Eigaard, O. R., and Munch-petersen, S. 2010. Influence of fleet renewal and trawl development on landings per unit effort of the Danish northern shrimp (*Pandalus borealis*) fishery. *ICES Journal of Marine Science*, 68: 26–31.
- Eigaard, O. R., Marchal, P., Gislason, H., and Rijnsdorp, A. D. 2014. Technological Development and Fisheries Management. *Reviews in Fisheries Science & Aquaculture*, 22: 156–174.

- Eigaard, O. R., Bastardie, F., Breen, M., Dinesen, G. E., Hintzen, N. T., Laffargue, P., Mortensen, L. O., et al. 2015. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES Journal of Marine Science*, 73: i27–i43. .
- Eigaard, O. R., Bastardie, F., Hintzen, N. T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G. E., et al. 2017. The footprint of bottom trawling in European waters: Distribution, intensity, and seabed integrity. *ICES Journal of Marine Science*, 74: 847–865.
- FAO. 2016. The State of World Fisheries and Aquaculture 2016 (SOFIA): Contributing to food security and nutrition for all. Rome: Food and Agriculture Organization, 200 pp.
- Fonteyne, R., and Polet, H. 1995. Ontwikkeling van een species selectieve boomkor. Ontwikkeling van een species selectieve boomkor. Mededeling van het Rijkstation voor Zeevisserij (CLO Gent), Publikatie nr. 236, 49 pp.
- Fulton, E. a, Smith, A. D. M., Smith, D. C., and van Putten, I. E. 2011. Human behaviour: the key source of uncertainty in fisheries management. *Fish and Fisheries*, 12: 2–17.
- Gabriel, W., and Thomas, B. 1988. Vertical Migration of Zooplankton as an Evolutionarily Stable Strategy. *The American Naturalist*, 132: 199–216.
- Gaertner, D., and Dreyfus-Leon, M. 2004. Analysis of non-linear relationships between catch per unit effort and abundance in a tuna purse-seine fishery simulated with artificial neural networks. *ICES Journal of Marine Science*, 61: 812–820.
- Galbraith, R. D., Rice, A., and Strange, E. S. 2004. An Introduction to Commercial Fishing Gear and Methods Used in Scotland. Scottish Fisheries Information Pamphlet, No. 25, 43 pp.
- Garcia, S. M., Zerbi, A., Aliaume, C., Do Chi, T., and Lasserre, G. 2003. The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. FAO Fisheries Technical Paper. No. 443. Rome, FAO, 71 pp.
- Gell, F. R., and Roberts, C. M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution*, 18: 448–455.
- Gerritsen, H., and Lordan, C. 2011. Integrating vessel monitoring systems (VMS) data with daily catch data from logbooks to explore the spatial distribution of catch and effort at high resolution. *ICES Journal of Marine Science*, 68: 245–252.

References

- Gibson, R. N. 1997. Behaviour and the distribution of flatfishes. *Journal of Sea Research*, 37: 241–256.
- Gibson, R. N., and Robb, L. 2000. Sediment selection in juvenile plaice and its behavioural basis. *Journal of Fish Biology*, 56: 1258–1275.
- Gillis, D. M., Peterman, R. M., and Tyler, A. V. 1993. Movement Dynamics in a Fishery: Application of the Ideal Free Distribution to Spatial Allocation of Effort. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 323–333.
- Gillis, D. M., Pikitch, E. K., and Peterman, R. M. 1995. Dynamic discarding decisions: Foraging theory for high-grading in a trawl fishery. *Behavioral Ecology*, 6: 146–154.
- Gillis, D. M., and Peterman, R. M. 1998. Implications of interference among fishing vessels and the ideal free distribution to the interpretation of CPUE. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 37–46.
- Gillis, D. M. 2003. Ideal free distributions in fleet dynamics : A behavioral perspective on vessel movement in fisheries analysis. *Canadian Journal of Zoology*, 81: 177–187.
- Girardin, R., Vermard, Y., Thébaud, O., Tidd, A., and Marchal, P. 2015. Predicting fisher response to competition for space and resources in a mixed demersal fishery. *Ocean and Coastal Management*, 106: 124–135.
- Girardin, R., Hamon, K. G., Pinnegar, J., Poos, J. J., Thébaud, O., Tidd, A., Vermard, Y., et al. 2017. Thirty years of fleet dynamics modelling using discrete-choice models: What have we learned? *Fish and Fisheries*, 18: 638–655.
- Giske, J., Huse, G., and Fiksen, O. 1998. Modelling spatial dynamics of fish. *Reviews in Fish Biology and Fisheries*, 8: 57–91.
- Gloaguen, P., Mahévas, S., Rivot, E., Woillez, M., Guitton, J., Vermard, Y., and Etienne, M. P. 2015. An autoregressive model to describe fishing vessel movement and activity. *Environmetrics*, 26(1): 17–28.
- Godø, O. R., Engås, A., and Walsh, S. J. 1999. Investigating density-dependent catchability in bottom-trawl surveys. *ICES Journal of Marine Science*, 56: 292–298.
- Goss-Custard, J. 1980. Competition for food and interference among waders. *Ardea*, 68: 31–52.
- Gray, T., and Hatchard, J. 2003. The 2002 Reform of the Common Fisheries Policy's system of governance - Rhetoric or reality? *Marine Policy*, 27: 545–554.

- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Steven, F., Thulke, H., et al. 2005. Pattern-Oriented Modeling of Agent Based Complex Systems: Lessons from Ecology. *Science*, 310: 987–991.
- Grolemund, G., and Wickham, H. 2011. Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, 40: 1–25.
- Halpern, B. S., Lester, S. E., and McLeod, K. L. 2010. Placing marine protected areas onto the ecosystem-based management seascape. *Proceedings of the National Academy of Sciences*, 107: 18312–18317.
- Hamon, K. G., and Poos, J. J., 2016. The practical evaluation of feedback control strategies. In *Management science in fisheries: an introduction to simulation based methods*. Edited by C.T.T. Edwards and D.J. Dankel. Routledge, New York. pp. 39–63.
- Hamon, K. G., Kinds, A., Polet, H., Poos, J. J., Verlé, K., Vos, B. de, and Rijnsdorp, A. D. (n.d.). manuscript in draft. unpublished manuscript.
- Hardin, G. 1968. The Tragedy of the Commons. *Science*, 162: 1243–1248.
- Harley, S. J., Myers, R. a., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1760–1772.
- Hiddink, J. G., Jennings, S., Kaiser, M. J., Queirós, A. M., Duplisea, D. E., and Piet, G. J. 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 721–736.
- Hiddink, J. G., Rijnsdorp, A. D., and Piet, G. 2008. Can bottom trawling disturbance increase food production for a commercial fish species? *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 1393–1401.
- Higginson, A. D., and Ruxton, G. D. 2015. Foraging mode switching: The importance of prey distribution and foraging currency. *Animal Behaviour*, 105: 121–137.
- Hilborn, R. 1985. Fleet Dynamics and Individual Variation: Why Some People Catch More Fish than Others. *Canadian Journal of Fisheries and Aquatic Sciences*, 42: 2–13.
- Hilborn, R., and Walters, C. J. 1992. *Managing Fisheries. Quantitative fisheries stock assessment: choice, dynamics and uncertainty*, Chapman & Hall, New York, 570 pp.
- Hilborn, R., Stokes, K., Maguire, J. J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., et al. 2004. When can marine reserves improve fisheries management? *Ocean and Coastal Management*, 47: 197–205.

References

- Hintzen, N. T., Piet, G. J., and Brunel, T. 2010. Improved estimation of trawling tracks using cubic Hermite spline interpolation of position registration data. *Fisheries Research*, 101: 108–115.
- Hintzen, N. T., Bastardie, F., Beare, D., Piet, G. J., Ulrich, C., Deporte, N., Egekvist, J., et al. 2012. VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. *Fisheries Research*, 115–116: 31–43.
- Holland, D. S. 2008. Are Fishermen Rational? A Fishing Expedition. *Marine Resource Economics*, 23: 325–344.
- Holley, J. F., and Marchal, P. 2004. Fishing strategy development under changing conditions: Examples from the French offshore fleet fishing in the North Atlantic. *ICES Journal of Marine Science*, 61: 1410–1431.
- Horwood, J. 1993. The Bristol Channel Sole (*Solea solea* (L.)): A Fisheries Case Study. *Advances in Marine Biology*, 29: 215–367.
- Houghton, R. G., and Harding, D. 1976. The plaice of the English Channel: spawning and migration. *ICES Journal of Marine Science*, 36: 229–239.
- ICES. 2007. Report on the ICES Advisory Committee on Fisheries Management. ICES Advice. Book 5, 241 pp.
- ICES. 2015. Sole (*Solea solea*) in Divisions VII,f (Bristol Channel, Celtic Sea). In ICES Advice on fishing opportunities, catch, and effort. Celtic Seas ecoregion.
- ICES. 2017. Sole (*Solea solea*) in subarea 4 (North Sea Sea). In ICES Advice on fishing opportunities, catch, and effort. Greater North Sea ecoregion.
- Jager, W., Janssen, M. A., De Vries, H. J. M., De Greef, J., and Vlek, C. A. J. 2000. Behaviour in commons dilemmas: Homo economicus and Homo psychologicus in an ecological-economic model. *Ecological Economics*, 35: 357–379.
- Jákupsstovu, S. H.í, Cruz, L. R., Maguire, J-J., and Reinert, J. 2007. Effort regulation of the demersal fisheries at the Faroe Islands: a 10-year appraisal. *ICES Journal of Marine Science*, 64: 730–737.
- Jennings, S., and Kaiser, M. J. 1998. The Effects of Fishing on Marine Ecosystems. In *Advances in Marine Biology*, pp. 201–352. Ed. by J. H. S. Blaxter, A. J. Southward, and P. A. Tyler. Academic Press, London, UK, pp 201–352.

- Jennings, S., Alvsvåg, J., Cotter, A. J. R., Ehrich, S., Greenstreet, S. P. R., Jarre-Teichmann, A., Mergardt, N., et al. 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International trawling effort in the North Sea: An analysis of spatial and temporal trends. *Fisheries Research*, 40: 125–134.
- Jennings, S., Pinnegar, J. K., Polunin, N. V. C., and Warr, K. J. 2001. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series*, 213: 127–142.
- Joo, R., Bertrand, S., Tam, J., and Fablet, R. 2013. Hidden Markov Models: The Best Model for Forager Movements? *PlosONE*, 8(8): e71246.
- Kaiser, M. J. 2005. Are marine protected areas a red herring or a panacea? *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 1194–1199.
- Kellner, J. B., Tetreault, I., Gaines, S. D., and Nisbet, R. M. 2007. Fishing the line near marine reserves in single and multispecies fisheries. *Ecological Applications*, 14(4): 1039–1054.
- Kindt-Larsen, L., Kirkegaard, E., and Dalskov, J. 2011. Fully documented fishery: A tool to support a catch quota management system. *ICES Journal of Marine Science*, 68: 1606–1610.
- Kraak, S. B. M., Reid, D. G., Gerritsen, H. D., Kelly, C. J., Fitzpatrick, M., Codling, E. A., and Rogan, E. 2012. 21st century fisheries management: A spatio-temporally explicit tariff-based approach combining multiple drivers and incentivising responsible fishing. *ICES Journal of Marine Science*, 69(4): 590–601.
- Kraak, S. B. M., Reid, D. G., and Codling, E. A. 2014. Exploring the RTI (real-time incentive) tariff-based approach to single-species fisheries management. *Fisheries Research*, 155: 90–102.
- Kraak, S. B. M., Reid, D. G., Bal, G., Barkai, A., Codling, E. A., Kelly, C. J., and Rogan, E. 2015. RTI ('Real-Time Incentives') outperforms traditional management in a simulated mixed fishery and cases incorporating protection of vulnerable species and areas. *Fisheries Research*, 172: 209–224.
- Larkin, P. A. 1978. Fisheries Management- An Essay for Ecologists. *Annual Review of Ecology and Systematics*, 9: 57–73.
- Laurel, B. J., Stoner, A. W., and Hurst, T. P. 2007. Density-dependent habitat selection in marine flatfish: The dynamic role of ontogeny and temperature. *Marine Ecology Progress Series*, 338: 183–192.

References

- Lindeboom, H. J., and de Groot, S. J. 1998. Impact-II: The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. NIOZ-rapport, 1998(1). Netherlands Institute for Sea Research: Den Burg. 1-404 pp. Part of: NIOZ-rapport. Netherlands Institute for Sea Research (NIOZ): Den Burg. ISSN 0923-3210.
- Link, J. S. 2002. What Does Ecosystem-Based Fisheries Management Mean? *Fisheries*, 27: 18–21.
- Little, A. S., Needle, C. L., Hilborn, R., Holland, D. S., and Marshall, C. T. 2015. Real-time spatial management approaches to reduce bycatch and discards: Experiences from Europe and the United States. *Fish and Fisheries*, 16(4): 576–602..
- Little, L., Kuikka, S., Punt, A., Pantus, F., Davies, C., and Mapstone, B. 2004. Information flow among fishing vessels modelled using a Bayesian network. *Environmental Modelling & Software*, 19: 27–34.
- Marchal, P., Ulrich, C., and Pastoors, M. 2002. Area-based management and fishing efficiency. *Aquatic Living Resources*, 15: 73–85.
- Marchal, P., Andersen, B., Caillart, B., Eigaard, O., Guyader, O., Hovgaard, H., Iriondo, A., et al. 2006. Impact of technological creep on fishing effort and fishing mortality , for a selection of European fleets. *ICES Journal of Marine Science*, 64: 192–209.
- Marchal, P., Poos, J. J., and Quirijns, F. 2007. Linkage between fishers' foraging, market and fish stocks density: Examples from some North Sea fisheries. *Fisheries Research*, 83: 33–43.
- Maunder, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*, 70: 141–159.
- Maurstad, A. 2002. Fishing in murky waters-ethics and politics of research on fisher knowledge. *Marine Policy*, 26: 159–166.
- Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., Briscoe, D. K., et al. 2015. Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. *Marine Policy*, 48: 42–50.
- Michélot, T., Langrock, R., and Patterson, T. A. 2016. moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, 7(11): 1308–1315.
- Moody, A. L., and Houston, A. I. 1995. Interference and the Ideal Free Distribution. *Animal Behaviour*, 49: 1065–1072.

- Moody, A. L., and Ruxton, G. D. 1996. The intensity of interference varies with food density: support for behaviour-based models of interference. *Oecologia*, 108: 446–449.
- Murawski, S., Wigley, S., Fogarty, M., Rago, P., and Mountain, D. 2005. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES Journal of Marine Science*, 1167: 1150–1167.
- Needle, C. L., and Catarino, R. 2011. Evaluating the effect of real-time closures on cod targeting. *ICES Journal of Marine Science*, 68(8): 1647–1655.
- Pastors, M., Rijnsdorp, A. D., and Van Beek, F. A. 2000. Effects of a partially closed area in the North Sea ('plaice box') on stock development of plaice. *ICES Journal of Marine Science*, 57: 1014–1022.
- Patterson, T. A., Basson, M., Bravington, M. V., and Gunn, J. S. 2009. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology*, 78: 1113–1123.
- Peel, D., and Good, N. 2011. A Hidden Markov Model Approach for determining vessel activity from Vessel Monitoring System data. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(7): 1–37.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., et al. 2004. Ecosystem-Based Fishery Management. *Science*, 305: 346–347.
- Platteau, J., Van Gijsegem, D., Van Bogaert, T., and Vuylsteke, A. 2016. Voedsel om over na te denken. Landbouw- en Visserijrapport 2016. Departement Landbouw en Visserij. Brussel.
- Poos, J. J., and Rijnsdorp, A. D. 2007a. An ' experiment ' on effort allocation of fishing vessels : the role of interference competition and area specialization. *Canadian Journal of Fisheries and Aquatic Sciences*, 64: 304–313.
- Poos, J. J., and Rijnsdorp, A. D. 2007b. The dynamics of small-scale patchiness of plaice and sole as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the fleet dynamics. *Journal of Sea Research*, 58: 100–112.
- Poos, J. J., Bogaards, J. A., Quirijns, F. J., Gillis, D. M., and Rijnsdorp, A. D. 2010a. Individual quotas, fishing effort allocation, and over-quota discarding in mixed fisheries. *ICES Journal of Marine Science*, 67: 323–333.
- Poos, J. J., Quirijns, F. J., and Rijnsdorp, A. D. 2010b. Spatial segregation among fishing vessels in a multispecies fishery. *ICES Journal of Marine Science*, 67: 155–164.

References

- Poos, J. J., Turenhout, M. N. J., Oostenbrugge, H. A. E. Van, and Rijnsdorp, A. D. 2012. Adaptive response of beam trawl fishers to rising fuel cost. *ICES Journal of Marine Science*, 70: 675–684.
- Pyke, G. H. 2015. Understanding movements of organisms: It's time to abandon the Lévy foraging hypothesis. *Methods in Ecology and Evolution*, 6: 1–16.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>.
- Rasenberg, M., van Overzee, H., Quirijns, F., Warmerdam, M., van Os, B., Rink, G., and IM, R. number C. 2013. Monitoring catches in the pulse fishery. IMARES – Institute for Marine Resources & Ecosystem Studies. Report number C122/13, 59 pp.. 59 pp.
- Rijnsdorp, A. D., van Beek, F. A., Flatman, S., Millner, R. M., Riley, J. D., Giret, M., and De Clerck, R. 1992. Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic. *Journal of Sea Research*, 29: 173–192.
- Rijnsdorp, A. D. 1994. Population-regulating processes during the adult phase in flatfish. *Journal of Sea Research*, 32: 207–223.
- Rijnsdorp, A. D., Buys, A. M., Storbeck, F., and Visser, E. G. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES Journal of Marine Science*, 55: 403–419.
- Rijnsdorp, A. D., Dol, W., Hoyer, M., and Pastoors, M. A. 2000a. Effects of fishing power and competitive interactions among vessels on the effort allocation on the trip level of the Dutch beam trawl fleet. *ICES Journal of Marine Science*, 57: 927–937.
- Rijnsdorp, A. D., van Mourik Broekman, P. L., and Visser, E. G. 2000b. Competitive interactions among beam trawlers exploiting local patches of flatfish in the North Sea. *ICES Journal of Marine Science*, 57: 894–902.
- Rijnsdorp, A. D., and Vingerhoed, B. 2001. Feeding of plaice *Pleuronectes platessa* (L.) and sole *Solea solea* (L.) in relation to the effects of bottom trawling. *Journal of Sea Research*, 45: 219–229.
- Rijnsdorp, A. D., Daan, N., and Dekker, W. 2006. Partial fishing mortality per fishing trip : a useful indicator of effective fishing effort in mixed demersal fisheries. *ICES Journal of Marine Science*, 566: 556–566.

- Rijnsdorp, A. D., Daan, N., Dekker, W., Poos, J. J., and Van Densen, W. L. T. 2007. Sustainable use of flatfish resources: Addressing the credibility crisis in mixed fisheries management. *Journal of Sea Research*, 57: 114–125.
- Rijnsdorp, A. D., Poos, J. J., Quirijns, F. J., HilleRisLambers, R., De Wilde, J. W., and Den Heijer, W. M. 2008. The arms race between fishers. *Journal of Sea Research*, 60: 126–138.
- Rijnsdorp, A. D., Poos, J. J., and Quirijns, F. J. 2011. Spatial dimension and exploitation dynamics of local fishing grounds by fishers targeting several flatfish species. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 1064–1076.
- Rose, G., and Kulka, D. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 118–127.
- Rosen, S., Jörgensen, T., Hammersland-White, D., and Holst, J. C. 2013. DeepVision: a stereo camera system provides highly accurate counts and lengths of fish passing inside a trawl. *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 1456–1467.
- Russo, T., D'Andrea, L., Parisi, A., and Cataudella, S. 2014. VMSbase: An R-Package for VMS and logbook data management and analysis in fisheries ecology. *PLoS ONE*, 9(6): e100195.
- Ruxton, G. D. 1995. Short term refuge use and stability of predator-prey models. *theoretical Population Biology* 47(1):1–17.
- Ruxton, G. D. G., and Moody, A. L. AL. 1997. The ideal free distribution with kleptoparasitism. *Journal of Theoretical Biology*, 186: 449–458.
- Salas, S., and Gaertner, D. 2004. The behavioural dynamics of fishers: Management implications. *Fish and Fisheries*, 5: 153–167.
- Selman, J., and Goss-Custard, J. D. 1988. Interference between foraging redshank *Tringa totanus*. *Animal Behaviour*, 36: 1542–1544.
- Shephard, S., Brophy, D., and Reid, D. G. 2010. Can bottom trawling indirectly diminish carrying capacity in a marine ecosystem? *Marine Biology*, 157: 2375–2381.
- Smith, A. D. M. 1993. Risk assessment or management strategy evaluation: What do manager need and want? *ICES CM*, D: 18: 1–6.
- Soetaert, M., Decostere, A., Polet, H., Verschueren, B., and Chiers, K. 2015. Electrotrawling: a promising alternative fishing technique warranting further exploration. *Fish and Fisheries*, 16: 104–124.

References

- Stillman, R. A., Goss-Custard, J. D., and Alexander, M. J. 2000. Predator search pattern and the strength of interference through prey depression. *Behavioral Ecology*, 11: 597–605.
- Sutherland, W. J. 1983. Aggregation and the ideal free distribution. *Journal of Animal Ecology*, 52: 821–828.
- Sutherland, W. J., and Parker, G. A. 1985. Distribution of unequal competitors. s. - In: Sibly, R. M. and Smith, R. H. (eds), *Behavioural ecology - ecological consequences of adaptive behaviour*. Blackwell, Oxford, pp. 255-274.
- Swain, D. P., and Sinclair, A. F. 1994. Fish Distribution and Catchability: What Is the Appropriate Measure of Distribution? *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 1046–1054.
- Swain, D. P., and Wade, E. J. 2003. Spatial distribution of catch and effort in a fishery for snow crab (*Chionoecetes opilio*): tests of predictions of the ideal free distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 897–909.
- Sys, K., Poos, J. J., Meensel, J. Van, Polet, H., and Buysse, J. 2016. Competitive interactions between two fishing fleets in the North Sea. *ICES Journal of Marine Science*, 73: 1485–1493.
- Tessens, E., and Velghe, M. 2014. De Belgische zeevisserij 2013: Aanvoer en besomming: Vloot, quota, vangsten, visserijmethoden en activiteit. Departement Landbouw en Visserij, 114 pp.
- Tessens, E., and Velghe, M. 2016. De Belgische zeevisserij 2015: Aanvoer en besomming: Vloot, quota, vangsten, visserijmethoden en activiteit. Departement Landbouw en Visserij, 127 pp.
- Tidd, A. N., Hutton, T., Kell, L. T., and Padda, G. 2011. Exit and entry of fishing vessels : an evaluation of factors affecting investment decisions in the North Sea English beam trawl fleet. *ICES Journal of Marine Science*, 68: 961–971.
- Tidd, A. N., Hutton, T., Kell, L. T., and Blanchard, J. L. 2012. Dynamic prediction of effort reallocation in mixed fisheries. *Fisheries Research*, 125–126: 243–253.
- Tillin, H. M., Hiddink, J. G., Jennings, S., and Kaiser, M. J. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, 318: 31–45.
- Triplet, P., Stillman, R. A., and Goss-Custard, J. D. 1999. Prey abundance and the strength of interference in a foraging shorebird. *Journal of Animal Ecology*, 68: 254–265.

- Valdemarsen, J. W. 2001. Technological trends in capture fisheries. *Ocean & Coastal Management*, 44: 635–651.
- van Denderen, P. D., van Kooten, T., and Rijnsdorp, A. D. 2013. When does fishing lead to more fish? Community consequences of bottom trawl fisheries in demersal food webs. *Proceedings of the Royal Society B: Biological Sciences*, 280: 2013.1883.
- van Denderen, D. P., Hintzen, N. T., Kooten, T. Van, and Rijnsdorp, A. D. 2014. Temporal aggregation of bottom trawling and its implication for the impact on the benthic ecosystem. *ICES Journal of Marine Science*, 72(3): 952–961.
- van Denderen, P. D., Rijnsdorp, A. D., and van Kooten, T. 2016. Using marine reserves to manage bottom trawl fisheries requires consideration of benthic food web interactions. *Ecological Applications*, 26: 2302–2310.
- Van Der Lee, A. Van Der, Gillis, D. M., Comeau, P., and Hurley, P. 2013. Fishing the line : catch and effort distribution around the seasonal haddock (*Melanogrammus aeglefinus*) spawning closure on the Scotian Shelf. *Canadian Journal of Fisheries & Aquatic Sciences*, 981: 973–981.
- Van Der Veer, H. W., Berghahn, R., and Rijnsdorp, A. D. 1994. Impact of juvenile growth on recruitment in flatfish. *Journal of Sea Research*, 32: 153–173.
- van Marlen, B., Wiegerinck, J. A. M., van Os-Koomen, E., and van Barneveld, E. 2014. Catch comparison of flatfish pulse trawls and a tickler chain beam trawl. *Fisheries Research*, 151: 57–69.
- Van Overzee, H. M. and Rijnsdorp, A. D. 2014. Effects of fishing during the spawning period: Implications for sustainable management. *Reviews in Fish Biology and Fisheries*, 25: 1–19.
- van Putten, I. E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K. G., Hutton, T., and Pascoe, S. 2012. Theories and behavioural drivers underlying fleet dynamics models. *Fish and Fisheries*, 13: 216–235.
- Venables, W. N., and Ripley, B. D. 2002. MASS: modern applied statistics with S. Fourth Edition. Springer. New York, 504 pp.
- Vermard, Y., Marchal, P., Mahévas, S., and Thébaud, O. 2008. A dynamic model of the Bay of Biscay pelagic fleet simulating fishing trip choice: the response to the closure of the European anchovy (*Engraulis encrasicolus*) fishery in 2005. *Canadian Journal of Fisheries & Aquatic Sciences*, 65: 2444–2453.

References

- Vermard, Y., Rivot, E., Mahévas, S., Marchal, P., and Gascuel, D. 2010. Identifying fishing trip behaviour and estimating fishing effort from VMS data using Bayesian Hidden Markov Models. *Ecological Modelling*, 221(15): 1757–1769.
- Verweij, M. C., and van Densen, W. L. T. 2010. Differences in causal reasoning about resource dynamics and consequences for the participatory debate on North Sea fisheries. *Marine Policy*, 34: 1144–1155.
- Vinther, M., Reeves, S. A., and Patterson, K. R. 2004. From single-species advice to mixed-species management: Taking the next step. *ICES Journal of Marine Science*, 61(8): 1398–1409.
- Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A., and Stanley, H. E. 1996. Lévy flight search patterns of wandering albatrosses. *Nature*, 381: 413–415.
- Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association*, 99: 673–686.
- Wood, S. N. 2006. *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC Press. Boca Raton, FL, USA, 410 pp.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Savelieve, A. A., and Smith, G. M. 2009. *Mixed effect models and extensions in ecology in R*. Springer. New York. 574 pp.

Appendix A

Description of the individual-based simulation model based on the RTI as proposed by Kraak et al. (2012)

To include the fleet dynamic mechanisms highlighted in this thesis, a simplified version of the model of Ruxton (1975) is used similar to Poos and Rijnsdorp (2007a). This model describes the intake rate of fish (I) in function of the vessel density (p) in a cell, including the vessel itself, in situations of prey depression: $I = \frac{an}{1 + qp}$. In this equation, the fish density (n) is set to 1 unit, while the competition (q) and search efficiency (a) parameters vary according the different scenarios for both species (0 or 2). Hence, the intake rate is expressed with respect to 1 catch unit, and used as a multiplier in the models' catch equation.

The model as described hereunder is developed based on the IBM of Kraak *et al.* (2014; 2015). In the simulation model, 100 fishers fish exploit a sea that contains two cod like species. The sea is modelled as a ring of 100 individual cells so that each cell has two neighbouring cells. At the start of each simulation, the cells of the sea are populated with both fish species assuming a spatial correlation structure between neighbouring cells. Thereto, the 2 species are distributed over 20 cells (cell 1, 6, 11, 16,..., 96) by sampling 20 random numbers from the following lognormal distribution with $E(\ln(a)) = \mu = \ln(100)$ and $Var(\ln(a)) = \sigma^2 = (\ln(4))^2$. Subsequently, both species are spread over the neighbouring cells through a diffusion process with diffusion coefficient (D) 1. The probability, $p(x)$, that a biomass unit is distributed over a distance x ($-50 \geq x \leq 50$) to a neighbouring cell is given by

$p(x) = \frac{e^{-x^2/4D}}{\sqrt{4\pi D}}$. Finally, the biomass of both species is rescaled so that the total biomass of

each species is 10000 units at the start of each simulation. At the start of each week, the species biomass (B) grows according a standard surplus model based on a logistic growth model: $g(B) = rB(1 - B/K)$. For both species, the growth rate (r) is set to 1 and the carrying capacity (K) is 15000. Similar as in Kraak *et al.* (2015), the objective is to maintain the biomass at 10000 units, hence the annual harvest rate is set at 1/3 corresponding to an equilibrium yield of 3333.

This additional weekly biomass is allocated to the cells proportional to the initial cell biomass. Nevertheless, during the first 25 weeks, the growth biomass is added to the cells in one direction, thereby shifting one cell per week in a particular direction. From week 26 to 50, the opposite happens, and the biomass growth returns gradually to the initial cell. This simple migration process happens for both species in the opposite direction.

The initial tariffs (0.1; 0.5; 1; 2; 5 or 10, with rank 1 to 6, respectively) of each individual cell are determined by the highest of both species specific tariff which are calculated based on the initial cell biomass of both species (Kraak *et al.*, 2015). Nevertheless, the species specific biomass in each cell is converted into the catch-per-unit-effort assuming a linear relationship. This allows to use the cpue data of fishers for the weekly update algorithm of the tariffs but does not affect the initial value of the tariffs. The cpue boundaries to set the tariffs of species 1 are 4 times more restrictive than those of species 2.

Every simulation run covers a period of 20 years. A year comprises 50 weeks, while a week consist of 6 days. At the start of each year, each fisher receives a total effort quota of 200 tariff units. Half of the fishers target species 1, and half of the fishers target species 2. The targeting behaviour causes fishers to select a cell amongst those cells with a higher biomass of the target species than the average cell biomass of the target species. Cells with the highest tariff (10) are closed and thus not exploited. If a fishers individual tariff quota drops below the tariffs of the potential fishing cells, the fisher will not fish.

Fishers harvest a proportion ($q \in [0;1]$) of a cells' current biomass. This is determined by a species catchability (Q) taking a value of 1/300 and 1/600 for species 1 and 2, respectively, and a random number (k) from the lognormal distribution with mean: $E(\ln(a)) = \mu = \ln(0)$, and variance: $var(\ln(a)) = \sigma^2 = (\ln(0.5))^2$. If a species is targeted, k is adjusted so that $k \geq 1$.

After every week, the tariffs of cells where fishing occurred are updated. Therefore, the mean weekly cpue of each cell that has been fished is divided by the mean cpue of all cells that have been fished and assigned a rank. If the current species specific rank is higher than a cells' species specific rank during the previous week, the species specific tariff is incremented with one level, if the rank is lower, the tariff is decremented, whereas the tariff doesn't change if both ranks are equal. Again, the final tariff is determined by the highest species specific rank. Cells with the highest rank (tariff= 10; rank = 6) and thus closed for the fishery, re-open after 3 weeks. The tariff of these cells is set to 5.

After each year, the harvest rate is calculated assuming that the catches and biomass are known. If the harvest rate is more than 10% above the target harvest rate, the species specific multiplier which determines the bin size of tariff ranks (initially set to 1 at the start of each simulation run) is multiplied with 0.9. In contrast, if the harvest rate is 10% below the target harvest rate, the multiplier is set to 1.1. As such the tariff ranks become more or less stringent, respectively.

Curriculum Vitae

Personal information

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Education

2014-2018: PhD in Bioscience Engineering (ILVO / Ghent University)
Supervisors: Prof. dr. ir. Jeroen Buysse (Ghent University), dr. ir. Jef Van Meensel (ILVO),
dr. ir. Hans Polet (ILVO)

2007-2011: Master of Bioscience Engineering, Agriculture (Ghent University)
2004-2007: Bachelor of Bioscience Engineering, Agriculture (Ghent University)

Scientific publications in journals/ book with peer review

Sys, K., Poos, J. J., Meensel, J. Van, Polet, H., and Buysse, J. 2016. Competitive interactions between two fishing fleets in the North Sea. *ICES Journal of Marine Science*, 73: 1485–1493.

Sys, K., Meensel, J. Van, Polet, H., and Buysse, J. 2017. A temporal race-for-fish : the interplay between local hotspots of flatfish and exploitation competition between beam trawlers after a seasonal spawning closure. *Fisheries Research*, 193: 21–32.

Verlé, K., Sys, K., Verleye, T., van Winsen, F. & Lescrauwaet, A.K. (2018). Factors leading to re-emerging small-scale fisheries in Belgium. In Pascual-Fernandez, J.; Pita, C. & Bavinck, M. (Eds.). *Small-Scale Fisheries in Europe: Status, resilience and governance*. Springer, MARE Publication Series (in press).

Conferences and symposia

International conferences with oral presentation

2017: ICES Annual Science Symposium, Fort Lauderdale, United States of America

2017: EAFE (European Association of Fisheries Economists), Dublin, Ireland

2016: ESSA (European Social Simulation Association), Rome, Italy

2015: EAFE (European Association of Fisheries Economists), Salerno, Italy

2015: ESSA (European Social Simulation Association), Groningen, The Netherlands

2015: ICES Annual Science Symposium, Copenhagen, Denmark

National symposia with oral presentation

2015: VLIZ Young Scientist Day, Bruges, Belgium

2015: NSABS, Louvain-la-Neuve, Belgium

Peer reviewing

Peer reviewing for 'North American Journal of Fisheries Management' (1) and 'Marine Ecology Progress Series' (1)

Specialist courses

2017: Applications of quantitative methods in fishery management (ICES/NOAA)

2017: Postacademische opleiding Big Data (Ugain - UGent)

2017: Introduction to Categorical Data Analysis with R (FLAMES)

2014: Applied Rural Economic Research Methods (UGent)

2014: CSI -ABM Summer School (UGent)

Other courses

2016: Advanced Academic English: Conference Skills - Presentation Skills in English (UGent)

2015: Summer School Wetenschapcommunicatie 'Zeg 't eens' (KU Leuven)

2015: Schrijven voor niet-vakgenoten en pers (UGent)

2015: Personal Effectiveness (UGent)