Effects of and on the food-web when fishing for maximum sustainable yields in the southern North Sea

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I know the human being and fish can coexist peacefully.

George Walker Bush,

46th Governor of Texas

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Dissertation abstract

A main objective of fisheries management for the southern part of the North Sea under the European Commission's Common Fisheries Policy is the achievement of maximum sustainable yields (MSY) from each stock. However, the stocks are not exploited in isolation, but are linked through biological and technical interactions, and the food-web and ecosystem they are part of. This PhD thesis describes the functioning of the southern North Sea's food-web. It evaluates if, given this functioning, optimum yields of plaice, sole, cod, and brown shrimp can be achieved simultaneously. It also tests if such optimum solutions can be aligned with proxies of good environmental status. Potential changes in the catchabilities of sole and plaice, and their impacts upon MSY fishing are addressed. With the southern North Sea being subject to important ecosystem changes, such as increases in marine mammals and decreased nutrient loads through de-eutrophication measures, this thesis also investigates these processes' consequences for fishing yields and strategies.

Main tool of this thesis is the parametrization and use of a food-web model of ICES areas IVb and c (Figure I on page VII), using the Ecopath with Ecosim approach and software. The time-static Ecopath model represents the structure and functioning of the southern North, which turned out to be a highly connected, mature food-web (Chapter 1). In Chapter 2, the time-dynamic Ecosim model is subjected to a range of different fishing effort regimes to seek solutions leading to concurrent optimum yields of plaice, sole, cod and brown shrimps; and to test for their compliance with proxies of good environmental status. Its results show that direct and indirect trophic interactions between the four species considerably impair these endeavours. Running empirical data analyses, drivers of changes in the catchabilities of sole and plaice were identified, and their consequences upon MSY fishing and bycatch examined using Ecosim in Chapter 3. The results indicate density-dependent changes in catchabilities of sole and plaice. Higher efforts are thus needed to obtain their MSYs in the model, leading to negative effects on bycatch and other species. Chapter 4 uses predictions made by population and ecosystem models to implement likely developments of marine mammal populations and primary productivity in the Ecosim model to explore their effects on MSYs and associated fishing strategies. Its results indicate that, while reduced system productivity severely affects fishing yields and effort strategies, marine mammals are less of a concern, but for cod fisheries.

The studies compiled in this PhD thesis present the development and use of the first model to holistically address trophic and technical interactions between the fisheries for flatfish, cod and brown shrimps in an ecosystem context in the southern North Sea. They stress the importance of considering multispecies interactions and the role of bottom-up control for MSY-infused fisheries management.

Effekte auf und durch das Nahrungsnetz in den auf maximalen Dauerertrag ausgerichteten Fischereien der südlichen Nordsee

Zusammenfassung der Dissertation

Eine der Säulen der Gemeinsamen Fischereipolitik der Europäischen Union ist das Streben danach, allen befischten Beständen die größtmögliche Produktivität abzuschöpfen, sie also nach dem Prinzip des maximalen Dauerertrags (engl.: *Maximum Sustainable Yield, MSY*) zu befischen. Jedoch kann ein einzelner Bestand nie als abgeschlossenes System betrachtet werden, ist er doch durch biologische und fischereitechnische Interaktionen und durch das Nahrungsnetz mit anderen Beständen und Arten verwoben. Diese Dissertation quantifiziert die Funktionsweise des Nahrungsnetzes der südlichen Nordsee. Darauf aufbauend befasst sie sich mit der Frage, ob maximale Dauererträge von Schollen, Seezungen, Kabeljau und Nordseegarnelen (oder *Nordsee-Krabben*) simultan zu vereinbaren sind und wie derartige potentielle, mehrere Arten umfassende Optimal-Lösungen sich gegenüber Indikatoren eines guten Umweltzustandes verhalten. Ändert sich die fischereiliche Fängigkeit von Scholle und Seezunge, so kann sich das auf ein auf MSY ausgerichtetes Fischereimanagement auswirken. Auch diesem Punkt geht diese Dissertation nach. Zudem war und ist die südliche Nordsee im Prozess tiefgreifender Änderungen der Meeresumwelt. So haben etwa die Populationen von Meeressäugern nach Tiefständen in den 70ern beachtlich zugenommen. Am anderen Ende der Nahrungkette wurden seit den 80ern Maßnahmen zur Verringerung der Einfuhr von Nährstoffen durch Abwässer und Landwirtschaft ins Meer umgesetzt. Die vorliegende Dissertation widmet sich daher auch der Frage, wie sich diese Umwälzungen auf die Fischereien auswirken.

Das hauptsächliche Werkzeug dieses Promotionsvorhabens ist ein mathematisches Modell, welches das Nahrungsnetz im Managementbereich IVb und c des Internationaler Rates für Meeresforschung, *ICES*, darstellt (Figure I auf Seite VII). Parametrisiert wurde das Modell gemäß dem *Ecopath with Ecosim* Ansatz unter Verwendung der dazugehörigen Software. Das fertige Ecopath-Modell präsentiert eine Momentaufnahme von Aufbau und Funktionsweise der südlichen Nordsee, welches sich als ein hoch vernetztes und komplexes Nahrungsnetz erweist (Kapitel 1). Im zweiten Kapitel wurde im zeitlich aufgelösten Ecosim-Modell das simulierte Ökosystem einer Reihe verschiedener Szenarien gemischter Fischerei-Aufwände unterworfen um zu sehen, ob und welche Aufwandskombinationen der verschieden Flotten zum gleichzeitigen Erreichen maximaler Dauererträge von Scholle, Seezunge, Kabeljau und Nordseegarnele führen. Es zeigte sich, dass direkte und indirekte Verknüpfungen dieser vier Zielarten durch das Nahrungsnetz dieses Unterfangen behindern. Selbiges gilt für die Vereinbarkeit des maximalen simultanen Dauerertrags der vier Arten mit Indikatoren eines guten Umweltzustandes. In einer Analyse empirischer Daten zeigt sich im dritten Kapitel, dass die Fängigkeiten von Scholle und Seezunge durch Baumkurren in der Vergangenheit bei sinkenden Bestandsdichten zunahm. Implementiert man dies in dem Modell des Nahrungs- und Flottennetzes, so führen nun höhere Fischereiaufwände zu MSY als dies in einem Modell ohne dichteäbhängige Fängigkeiten der Fall wäre. Dies wirkt sich allergrößtenteils negativ auf Beifangarten und andere Komponenten des Nahrungsnetzes aus. Das vierte Kapitel dieser Dissertation stützt sich auf die Ergebnisse externer Populations- und Ökosystemmodelle, um die wahrscheinlichen Entwicklungen

von Meeressäugern und der Produktivität des Phytoplanktons im Nahrungsnetz-Modell zu implementieren. Im so modifizierten Modell werden nun Fischerei-Strategien gesucht, welche zu maximalen kombinierten Dauererträgen von Scholle, Seezunge, Kabeljau und Nordseegarnele führen. Vergleicht man diese Strategien zwischen den verschiedenen Szenarien – *Status quo*, mit vermehrten Meeressäugern und mit verringerter Primärproduktion durch regulierten Nährstoffeinfluss – so zeigt sich ein drastischer Effekt reduzierter Algen-Produktivität, während mehr Robben und Schweinswale vor allem die Kabejau-Fischerei betreffen, sonst aber eher geringe Konsequenzen für die Fischereien verursachen.

Die in dieser Dissertation zusammengefassten Studien beschreiben die Entwicklung und Anwendung des ersten mathematischen Modells, welches die fischereitechnischen und Nahrungsbeziehungen zwischen den verschiedenen Fischereien auf Plattfische, Kabeljau und Nordseegarnele in der südlichen Nordsee im Rahmen eines Ökosystemansatzes in der Fischerei holistisch erfasst. Die Studien belegen, wie wichtig es ist, Mehrarten- und Beute-gesteuerte Interaktionen zu berücksichtigen, wenn maximale Dauererträge angestrebt werden.

Contents

Figure I: A map of the study area, statistical areas IVb and c (encircled red), within the total North Sea, statistical areas IVa, b, and c (encircled yellow) of the International Council for the Exploration of the Sea (ICES). Adapted from https://geo.ices.dk

Dissertation introduction

In the southern North Sea, the different fisheries for flatfish, roundfish, and brown shrimp (*Crangon crangon*) are manifold interlinked through trophic interactions. Both roundfish and flatfish feed on brown shrimp, but also share other prey organisms, which can lead to competition. Young flatfish can become prey for larger roundfish and mature brown shrimp (del Norte-Campos 1995; Oh et al. 2001). Besides their connection through the food-web, the fisheries are also technically entangled (Rätz and Mitrakis 2012; WGNSSK 2016; HAWG 2016; Chapter 1): The beam trawling fleet, towing rigid metal beams with nets attached over the sea floor, primarily targets flatfish (European plaice, *Pleuronectes platessa*; common sole, *Solea solea*; and others), but also catch important amounts of whiting (*Merlangius merlangus*) and cod (*Gadus morhua*). Plaice also make up the major share of otter trawlers' landings, which' nets' openings are not rigid and can be employed on or above the seafloor. Otter trawlers, however, catch a higher proportion of roundfish compared to beam trawlers. The fishery for brown shrimp, despite opting for this high value species exclusively, produce a considerable amount of unintended bycatch, amongst which juvenile plaice are fairly prominent.

1. Assessing the structure and functioning of the southern North Sea and the role that fishing plays in it

The effects of fishing on single species stocks in the North Sea are well studied. Much less investigated are the described links between target stocks through the food- and the fleet-web, and a holistic, ecosystem scale assessment of the structure and functioning of the southern North Sea ecosystem, including an elucidation of the role that fishing plays in it, were yet to be performed. By itself, a holistic understanding of the system bears knowledge to gain, particularly about how it structures and functions, and how it performs compared to other ecosystems and indicators of ecosystem health. It can help point out whether and how the ecosystem is vulnerable to environmental changes – eutrophication, climate change, and changes in key species' dynamics – and, by attempting to include all rather than just selected species interactions, can hint towards indirect, potentially unexpected relationships relevant for management and conservation (Plaganyi 2007; Morissette et al. 2012). The key impetus behind a holistic investigation of exploited ecosystems, however, certainly is to foster our understanding of how fishing affects ecosystem integrity and to gain insights of fishing impacts beyond the assessment of singular phenomena. The all-at-once attitude of such holistic assessments allows the detection of potential indirect effects, mitigated through the food-web, which may not be evident in singular driver-cause examinations. A holistic assessment enables to conclude on the form of impacts of different fishing techniques, and on their importance relative to each other and to environmental forces.

2. Multispecies maximum sustainable yields

Besides the study of the structure and functioning of an ecosystem, its holistic assessment can contribute to actual stock management in an ecosystem context. Fisheries management in the waters of the European Union follows the paradigm of maximum sustainable yields (MSY), under which fishing pressure is opted to be set to the levels which produce maximum long term revenues from the exploited stocks (EU 2013). Grounding in the works of Russel (1931), the MSY concept gained momentum through the development of surplus-production models (Schaefer 1954). Both the fishing mortality respectively fishing effort leading to MSY, as well as the actual extend of that maximum long term catch, could now be estimated with these models. Their application thereby led to the definition of *overfishing* as the execution of fishing pressures beyond those associated with MSY. The

development of more complex and data-intensive yield-per-recruitment models (Beverton and Holt 1957) allowed to take stocks' age- (or length-) structure into consideration when opting to maximize a fisheries' output. The size of fish caught was now balanced against the number of individuals available to the fishery. *Growth overfishing*, here, would happen when fish are taken before they could grow to the size that would provide the maximum yield as a combination of size and abundance. *Underfishing* would be a situation in which fishing pressure is so low that, while fish do grow large, yield opportunities are lost since fishing harder at a lower age or size would produce higher total yields. The maximum sustainable yield, in these models, is thus produced as an ideal combination of fishing pressure and age or size at first capture. Since classic yield-per-recruit models assume a constant recruitment, they run the danger of producing fatal errors when recruitment is actually dependent on the abundance of spawners (c.f. chapter 3; DISS Conclusion). The assessment of stock-recruitment relationships has led to the definition of *recruitment overfishing* as the execution of fishing pressures associated with a reduction of spawners' biomass to a point where total recruitment is compromised.

In its original rationale and application, MSY was and is focussed on the assessment and exploitation of single stocks (Schaefer 1954; Hilborn and Walters 1992; Mace 2001). Besides scepticism that the MSY concept does not safeguard against recruitment failure, ignores economic motivations, and spatial variability (Larkin 1977), a key criticism arises from the fact that MSY has often been demonstrated impossible to achieve for all exploited species in an ecosystem simultaneously, given their connectance through the food-web (e.g. Larkin 1979; Mace 2001; Hilborn 2010; ICES 2013). If, additional to those direct feeding interactions, ecosystem wide indirect effects (mitigated through upper and lower trophic level groups not commercially exploited) are considered as well, the achievement of multispecies MSY becomes even more challenging (Walters et al. 2005; Mackinson et al. 2009b; Chapter 2). Due to substantial criticism upon the MSY concept and its applicability, the *precautionary principle* had long been the prevalent concept in the legal framework of the European Union's fisheries policy. With respects to the aspects outlined above, the application of the precautionary principle in fisheries aims at the avoidance of recruitment overfishing through setting limit and precautionary reference points that safeguard spawners' biomass to stay above levels associated with systematic recruitment decline. Opposed to Larkin's popular 'epitaph for the concept of maximum sustained yield' (1977), however, the MSY concept has not been buried yet. Pivotal for the revivification of the MSY concept for operational policies was the 2002 World Summit on Sustainable Development, which participants agreed to maintain or restore exploited stocks to levels that produce MSY (FAO 2003). By 2006, that objective had found its way into the legislative text of the European Union's Common Fisheries Policy (CFP; EC 2006), as a parallel concept to the precautionary principle. This sparked interest and relevance of research relating to the feasibility and modernization of the MSY concept. In a concerted Europe-wide effort, participants of the MYFISH project (*Maximising yield of fisheries while balancing ecosystem, economic and social concerns*; www.myfishproject.eu) re-evaluated the usability of the MSY approach in the multi-stakeholder, multispecies fisheries of the European seas under the proposition of alternative definitions of MSY. Amongst the systems for which modernized MSY approaches were evaluated was the North Sea, with the southern North Sea included as a sub-regional case study (Kempf et al. 2016).

For the flatfish, roundfish, and brown shrimp fisheries in the southern North Sea, no feasibility study of a multispecies, mixed-fleet MSY had been performed yet. Chapter 2 of this thesis thus engages to explore management options that would deliver good yields from all the discussed key commercial species simultaneously, under consideration of their direct and indirect trophic links as predators, prey and competitors (the food-web), and the mixed-fleet nature of the fishery (the fleet-web). It also seeks to align such a multispecies MSY with a good status of other species and the environment.

3. Sensitivity of multispecies MSY to a) assumptions of how fishing affects the stocks and b) trends in top and bottom trophic levels of the southern North Sea

However holistic such a multispecies MSY with consideration of ecosystem-scale trophic interactions may be, it is still far away from including all details affecting fisheries management in an ecosystem context. In the above described approach to find multispecies MSY, fishing is considered as an external driver, and feeding interactions are provided as the system's internal structure. Besides that, however, two further pivotal assumptions affect MSY considerations: the way that fishing distresses individual stocks, i.e. the shape of the relationship between fishing effort and mortality; and how changes in the dynamics of the very top and bottom of the food-web could cascade through the food-web to affect commercial stocks and their exploitation.

4. A mathematical representation of the southern North Sea food-web

A key tool in answering questions of the kind posed above is the representation of populations and food-web dynamics in mathematical simulation models (e.g. Hilborn and Walters 1992; Jennings et al. 2001). These models have a long history in addressing one of fisheries management's main objectives: To maximize fishing yields while safeguarding the health of populations and the environment. For long, this enterprise has been the realm of single species stock assessments (e.g. Hilborn and Walters 1992). They follow the trajectories of births, deaths, growth and reproduction of single exploited populations, and aim to predict the effects of changes in these factors, e.g. a decrease in mortality through reduced fishing, upon the population. Single species stock assessments have earned a legacy as the workhorse of fisheries management, and are currently the most applied, established, and comprehensible approach to understand and predict the consequences of fishing. However, the above described inherent problems of the single species approach – that stocks are almost never exploited in isolation (Ulrich et al. 2001; Vinther et al. 2004; Miller and Poos 2010; Ulrich et al. 2012), that they are linked through predation (Walters 2005; Mackinson et al. 2009b; Hilborn 2010; Chapter 2), and that fishing affects the physical and biological environment (Jennings and Kaiser 1998; Hiddink et al. 2006, Kuparinen and Merilä 2007; Halpern et al. 2008; Branch 2015) – are now evident for decades, and novel methods were designed to cope with these challenges. Multispecies models link the dynamics of single commercial stocks (and some key predators) with feeding interactions. One of the outputs they provide are estimates of predation mortality of the various stocks and life stages. While in original single species stock assessments, predation mortality was assumed constant, it could now be dynamically estimated through multispecies models and then forwarded to single species assessments (Gislason and Helgason 1985; ICES 1997; WGSAM 2014; WGBFAS 2016; WGNSSK 2016). Cornerstones of the development of multispecies assessment models in the ICES region were the Multi-Species Virtual Population Analysis (Andersen and Ursin 1977; Sparre 1991), and the descended stochastic multispecies model SMS (Lewy and Vinther 2004). Since, the applications of multispecies models have expanded, and they now support the simultaneous exploitation of multiple species through the provision of ranges of sustainable levels of fishing mortalities for the target stocks, given certain conditions of their prey and predators (ICES 2013).

In multispecies models, populations are generally controlled through the abundance and consumption rates of their predators. This sort of trophic control is termed top-down control (Cury et al. 2003). Consumption rates are assumed to be constant in multispecies models such as the MSVPA (Helgason and Gislason 1979; Pope 1979) and SMS (Lewy and Vinther 2004), while in Ecosim, predator diet compositions can change when prey abundances do. The opposite of top-down control, bottom-up control, i.e. the control of predatory stocks through the availability of prey, is less frequently studied with multispecies assessments, notwithstanding its obvious importance. A third pivotal mechanism

controlling ecosystem functioning, the competition by two or more different species or life history stages for a common resource (Volterra 1928; Lotka 1932), is even less often addressed by multispecies models. This point is critical, given that species competition can severely impair the sustainable exploitation of marine living resources (May et al. 1979; Link and Auster 2013). In one of the few cases of the implementation of bottom-up and competitive pathways in a multispecies models, Cormon and colleagues (2016) parametrized the SMS model to hindcast the effect of Norway pout (*Trisopterus esmarkii*) shortage as prey for the declining Saithe (*Pollachius virens*) through food competition with hake (*Merluccius merluccius*) in the North Sea. Aside such incentives to widen the scope of multispecies model through ad-hoc inclusion of relevant upper or lower trophic level dynamics, it were these questions which drove the advent of ecosystem models.

4.1.   Modelling the southern North Sea with Ecopath: Structure and functioning of the ecosystem

The implementation of feeding interactions between species in simulation models is based on records of who eats whom, and how much so. This foundation allows to predict what would happen if one of the eaters changes abundance – be it a fishery or a predator. For multispecies models, that meant that a remarkable sampling effort had to be performed to obtain records of abundances and diets of all species included in the model. It was the demand for this diet data which lead to the internationally concerted North Sea wide stomach sampling efforts known as the 'years of the stomach' (Hislop 1997). An alternative approach to multispecies models, employing basic concepts of ecosystem functioning, was the development of ecosystem models. They embed the dynamics and interactions of target species into a representation of the entire ecosystem, both including top predators, and the foundation of the food-web (phytoplankton, zooplankton, and benthos) that the ecosystem bases upon resulting in the implementation of additional bottom up controls. Compared to multispecies models, this results in the implementation of additional bottom-up controls. The most widely distributed approach to ecosystem modelling follows the Ecopath approach (Christensen et al. 2008), which was derived from the work of Polovina (1984) stating that, when in equilibrium state, trophic flows within an ecosystem should be balanced. For each compartment of the ecosystem, from phytoplankton to whales, the Ecopath concept implies that its energy intake must parallel energy output, which allows to extrapolate unknown properties of any of the groups given known estimates for others. The ecosystem is modelled by a set of linear equations. Each such equation represents one of the groups included in the model, and delivers, once all equations are solved, estimates of biomass, production and consumption for each group. The resulting model quantifies the composition of the food-web in terms of biomass or energy pools (so called 'functional groups'), and the flows between them (Christensen et al. 2008). Classically, these snapshot representations of ecosystems, static in space and time, are used to explore the structure and functioning of food-webs. An Ecopath representation of the southern North Sea and its fisheries, as described in Chapter 1 and 2, thus aids to answer the above mentioned demand (section 1) for an evaluation of the productivity, complexity and connectance of the system, and the role that fishing plays in shaping these factors.

4.2.   Time-dynamic food-web simulations: finding a multispecies MSY

When ecosystem models actually start to complement single species (and multispecies) assessments for policy exploration is when they go beyond the ecosystem snapshot representation and become time-dynamic. In the Ecopath universe, this is the task of Ecosim. Ecosim bases upon the Ecopath representation of the food-web to predict how external drivers (e.g. fishing or climate) change the ecosystem over time. It replaces the linear equations representing groups in the Ecopath model with differential equations, which are then coupled to each other to form the Ecosim model. In Ecosim, consumption by a predator is dependent on the abundance of both predator and prey (analogue to Lotka-Volterra dynamics) and the availability (or vulnerability) of the latter (Christensen et al. 2008).

The development of an Ecosim model of the southern North Sea (Chapter 2 and appendix thereof) empowers policy explorations for the region's multispecies, mixed-fleet fisheries by providing a digital guinea pig ecosystem which can then be subject to a range of different fishing regimes. To do so, the dynamics of the model's compartments were fit to time series of stock abundances and catches, fishing efforts and mortalities to simulate a hindcast of the system during past decades. If the Ecosim model is able to adequately reconstruct the past, it is fair to assume that it would also be able to predict what would happen in the future when the pressures (e.g. fishing efforts) changed shape. The endeavour to identify exploitation levels which lead to good overall yields (multispecies MSY; see section 2) relies on this Ecosim model.

4.3. Testing the effects of underlying assumptions about the relationships between fishing and populations

An outcome of maximum yields in the model is necessarily always a result of the design of the equations utilized in the model, and of the set of variables used to parameterize these equations. Thus, any multispecies MSY simulated by the model is subject to assumptions made about, amongst many, dynamics of the exploited stocks and their interactions with the fishing fleet, or, technically, the setup of equations and parameters chosen. The validity of those assumptions and their consequences in the exploration of multispecies MSY solutions should thus be evaluated (c.f. section 3). One such assumption considers the catchability of the target stocks (here sole and plaice), i.e. how much fish is caught per unit of fishing effort. This factor is assumed constant in stock Ecosim (i.e. catch per unit of effort is dependent on the stocks' abundance only), whereas several studies on these and other species and fisheries reveal that this is by far not a matter of course in the real world (see Chapter 3 for an overview). Chapter 3 thus investigates how fishing affects the flatfish plaice and sole based on empirical data, and implements the emerging relationships between fishing and stock dynamics in the Ecosim model of the southern North Sea.

4.4. How would changes in the top and bottom compartments of the food-web – marine mammals and plankton – affect multispecies MSY solutions?

As outlined above (section 3), the simulation outcomes, which are the foundation upon which explorations of possible multispecies MSY solutions ground, are affected by fishing (and the form of its impact upon stocks, see section 4.3) as an external driver and the food-web's setup and connectance as the internal structure which reacts to it. Anthropogenic or environmental impacts can affect simulation outcomes – here: multispecies MSY solutions – through both channels. Altering external drivers would be the more obvious pathway, but externally induced changes can also affect the food-web's structure and functioning more systematically (one might speak of 'trends' then), such as in the two cases investigated here: predicted negative trends in the productivity of the plankton community through measures to reduce eutrophication in the southern North Sea; and an estimate of how far the ongoing increase in the southern North Sea's marine mammal populations might go. Both scenarios affect the way that the food-web model reacts to fishing pressure, with consequences for the respective target stocks and the fishing strategies leading to MSY. How maximum yields of sole, plaice, cod and brown shrimps are affected through scenarios of changes in the top and bottom compartments of the food-web, and whether and how fishing efforts need to be adopted to provide maximum yields under changed system properties, is explored in Chapter 4.

Chapter 1

Assessing the structure and functioning of the southern North Sea ecosystem with a food-web model

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Abstract

Single species stock assessment models are and will remain the workhorse of fisheries management. However, they are incapable of assessing the structure and functioning of the ecosystem the fisheries operate in. This study describes the trophic structure of the southern North Sea and the flows between the nodes of its food-web. It bases on the outputs of an Ecopath model of ICES area VIb and c, parametrized representing the year 1991. It also compares the southern to a whole North Sea Ecopath model (ICES area IV) for the same year.

The two dominant flows of biomass led from primary producers to detritus, and from there into benthos. The southern North Sea differed from the whole North Sea representation in its fish community composition, primarily attributable to the biogeography of the species. Flatfish were caught more and roundfish less, even with a nominally identically gear, to wit, otter trawlers. Food-web network indicators, however, suggest that both systems functioned similarly, compared to a global set of Ecopath models. They also deem the 1991 North Sea and its southern sub-part a densely woven, mature food-web.

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1. Introduction

For long, fisheries management had been based on the investigation of the dynamics of individual species' populations (Hilborn and Walters 1992). The past decades, however, have seen a growing body of evidence that trade-offs have to be considered when multiple species are exploited simultaneously (Christensen and Walters 2004; Walters et al. 2005; Mackinson et al. 2009b; Link 2010; Chapter 2). Also, it became evident that fishing can affect inherent properties of marine ecosystems (Jennings and Kaiser, 1998; Heymans et al. 2014; Perry et al. 2010). As in other regions of the world, in the North Sea, the need to assess the structure and functioning of (exploited) marine ecosystems has led to assessment and simulation modelling incentives going beyond the single species approach. Multi-species models, such as the pivotal Multi-Species Virtual Population Analysis (Andersen and Ursin 1977; Sparre 1991), the descended stochastic multispecies model SMS (Lewy and Vinther 2004), and others now capture the interdependencies between multiple exploited stocks through predator-prey relationships. Through their focus on commercial species, however, they are unable to address the impact of the dynamics of lower trophic level organisms (phytoplankton, zooplankton, and benthos) upon commercial stocks. In deeply exploring the structure and functioning of marine food-webs, these aspects need to be considered, which led to the development of ecosystem models.

Ecosystem models attempt to embed the interactions between target species and fisheries into a representation of the entire ecosystem. Given the large complexity this implies, and the associated uncertainties, they are less frequently (but increasingly) used for actual management considerations (Payne et al. 2015). The more classic application of ecosystem models is the exploration of the traits and dynamics of ecosystems and the role which fisheries and environmental changes play in these. The probably most commonly applied ecosystem modelling approach follows the Ecopath with Ecosim (EwE) method (Christensen et al. 2008; building upon the work of Polovina 1984), build around a mass-balanced snapshot representation of the food-web (Ecopath), which can then be extended temporally (Ecosim) and spatio-temporally (Ecospace). Assessing the distribution of biomass pools and the flows between them, the quantification of trophic interactions and links in Ecopath models allows ecological network analyses sensu Odum (1971) and taxations based on information theory sensu Ulanowicz (1986). These enable an evaluation of the system's productivity, complexity, connectivity, and ecosystem health. They make different ecosystems numerically comparable and help to address the question of the role that anthropogenic impacts, such as fishing, play in shaping the structure and functioning of the investigated ecosystem.

For the entire North Sea (statistical areas IVa, b, and c of the International Council for the Exploration of the Sea, ICES), an EwE food-web model was parameterized by Mackinson and Daskalov (2007). At the more regionalized scope of the southern North Sea (areas IVb and c), however, no full ecosystem food-web model of comparable standard in data quality and detail in complexity existed, until the development of an EwE model by Stäbler and co-authors (2014; 2016; Kempf et al. 2016). With the southern North Sea being considerably different in bathymetry, oceanography, nutrient loads (ICES 2008), demersal fish communities (Clark and Frid 2001, Frelat et al. under review), and fishing fleets and catch compositions (Rätz and Mitrakis 2012; WGNSSK 2016; HAWG 2016), the structure and functioning of the southern food-web and the impact of fishing on the latter should be expected to differ from a representation of the whole North Sea area. This study describes the composition and trophic flows of the southern North Sea food-web model (sNoSe), and assesses and discusses its properties as expressed in indices of ecosystem network analysis and information theory. It discusses differences to Mackinson and Daskalov's whole North Sea model (MDNS), and derives conclusions about the complexity and maturity of both ecosystems in relation to fishing activities.

2. Methods

2.1.   A north-south gradient in the North Sea

ICES subdivides the North Sea into three sub-divisions, IVa, b and c, of which IVb and c are the middle and southernmost parts. Together, they form the 'southern North Sea' described here. This area is surrounded by the coasts of the UK, France, Belgium, the Netherlands, Germany, and Denmark and lies between 51° and 56° North and 4° West and 9° East. According its bathymetry, the North Sea can broadly be divided into three fairly distinct parts: The southeast is shallow, and does not extend below 50m depth south of the so called '50m-line', which runs from the northern tip of Denmark to the Dogger Bank. The border between areas IVa and b then marks the decline to depths below 100m. As such, the 'southern North Sea', as defined for this study, encompasses the largest share of the North Sea with depths <100m, with deeper areas only around Devil's Hole (230m), and a small part of the Norwegian Trench, reaching up to 500m in the northern Skagerrak. The spatial extend of this area is 345,874 km². Atlantic waters enter the southern North Sea via the Norwegian Trench, the areas off Scotland, and through the Channel. The North Sea's most terrigenous area is its southeast, which is subject to substantial river runoffs. Given its shallow depths, the coastal regions of the southeast are also the area where the water does not stratify in summer, whereas this is the case for the rest of the North Sea.

In accordance with the findings of Clark and Frid (2001), Frelat and colleagues (under review), using tensor decomposition, demonstrated that spatial structure – particularly a north-south gradient – played a by far more important role in shaping the North Sea's demersal fish community 1985 – 2015. The North-South spatial structure of the fish community composition dominated over temporal patterns (correlated with the index of Atlantic Multidecadal Oscillation, AMO). The fish community structure's key property, accordingly, is a split into a southern fraction shaped by high seasonality of bottom temperature and salinity and a productive phytoplankton regime, and a northern fraction subjected to lower primary productivity and variability of temperature and salinity. Typical representatives of southern and south-eastern species are European plaice (*Pleuronectes platessa*) and Common sole (*Solea solea*), European flounder (*Platichthys flesus*), turbot (*Scophthalmus maximus*) and Thornback ray (*Raja clavata*). Characteristic northern and north-eastern species, there against, are gadoids, such as saithe (*Pollachius virens*), pollack (*Pollachius pollachius*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and Norway pout (*Trisopterus esmarkii*), or deeper water species like anglerfish (*Lophius piscatorius*) and halibut (*Hippoglossus hippoglossus*) (Frelat et al. under review). The benthos community composition in the North Sea similarly shows a north-south structure, with mobile epibenthos dominating south of the 50m-line, while epibenthos in the northern North Sea is dominated by sessiles. In the central North Sea, a mixed form prevails (Callaway et al. 2002).

In the North Sea, fisheries directed on benthic invertebrates target brown shrimps (*Crangon crangon*), nephrops (*Nephrops norvegicus*), and Northern prawns (*Pandalus borealis*). Of these, brown shrimp occurrence and extraction is limited to the southern North Sea, whereas fishing for nephrops and Northern prawn concentrates in the north. Differences also occur in the catch composition of demersal trawlers and seiners: While in the north, they primarily target herring (*Clupea harengus*) and gadoids, catches in the southern North Sea contain much higher shares of plaice and dab (*Limanda limanda*) (Mackinson et al. 2009b; Rätz and Mitrakis 2012; WGNSSK 2016; HAWG 2016; this study). Beam trawlers, targeting flatfish, but catching also cod (*Gadus morhua*) and whiting, almost exclusively operate in statistical areas IVb and c, hence in the southern part (Rätz and Mitrakis 2012; WGNSSK 2016).

2.2.   Parameterization of an Ecopath model of the southern North Sea

The parameterization of the Ecopath model for the state of the southern North Sea in 1991 is described in Appendix A and Appendix B. The model was parameterized to cover the whole extend of the food-web, from its lowest trophic levels (phytoplankton, zooplankton, benthos) to the highest (sharks, seals, seabirds, and cetaceans), but with focus on commercial fish and invertebrate species, of which some are represented in *stanza groups*, i.e. split into adults and juveniles. Fishing activities are implemented as eleven fleets, of which the most important ones in terms of tonnage and revenues are beam trawlers, targeting flatfish; demersal pursers and seiners, catching flatfish and gadoids (cod and whiting); and the specialized fishery for brown shrimp.

An overview of the Ecopath with Ecosim (EwE) approach is outlined e.g. in Chapter 2, and the software and modelling approach are fully described in Christensen et al. 2008.

3. Results and discussion

3.1.   Biomass distribution on functional groups and species

Fish groups

Figure 1 shows the biomass densities of the fish groups (plus cephalopods) in the balanced model. Two very different groups stick out: the small sized bentho-pelagic sandeels (Ammodytidae), and the flatfish dab. Sandeels burrow in the sand, and primarily feed on zooplankton, with frequent ingestion of infaunal polychaetes and meiofauna (Chapter 2, Table A5; Mackinson and Daskalov 2007). They are targeted by an industrial fleet. Dab, there against, is a bycatch species of the beam trawl fishery for plaice and sole. Dab primarily consume epifauna (Chapter 2, Table A5; De Clerck and Torreele 1988). After this vastly dominant benthic species, three pelagic fish follow, but none of them reaches even half of the biomass of sandeels or dab. Herring, sprat (*Sprattus sprattus*), and horse mackerel (*Trachurus trachurus*) are all targeted by trawl or seine fisheries, but can also be found as bycatch in small-meshed industrial nets. All feed on zooplankton, while sprat also consume larger amounts of phytoplankton (c.f. Falkenhaug and Dalpadado 2014), and horse mackerels predate macrobenthos and squids (Chapter 2, Table A5). Large flatfish, all of them caught as bycatch in beam trawling, reach the lowest of all fish biomasses in the model: brill (*Scopthalmus rhombus*), halibut, and megrim (*Lepidorhombus whiffiagonis*).
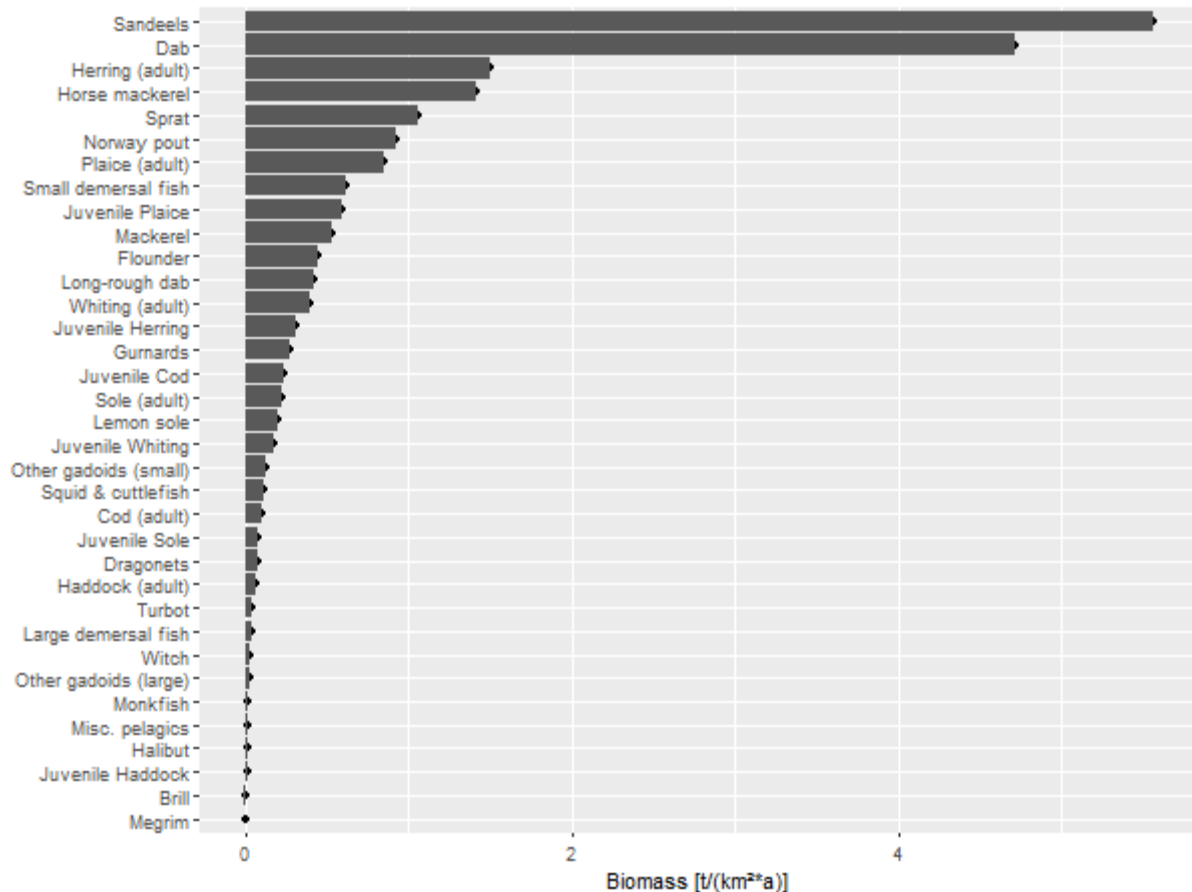
Figure 1: Biomass densities of fish groups in the 1991 southern North Sea model.

Comparison with MDNS

Compared with the Ecopath model of the entire North Sea (MDNS), gurnards (*Eutriglia* sp. and *Triglia* sp.) are 3.5-fold more abundant in the southern North Sea model (sNoSe), thereby representing the largest difference in fish biomass densities between both models (Figure 2). They are followed by large demersals and horse mackerels, both of which are 2.5-fold more abundant in the southern North Sea model. The higher biomass of large demersals is mainly due to the inclusion of saithe into that functional group in the sNoSe model, whereas they formed an individual functional group in the whole North Sea model. In the North Sea, saithe concentrate in area IVa, however, they are not absent from the southern North Sea and dominate the *large demersals* group in its Ecopath representation. Mackerel (*Scomber scombrus*) and the two flatfish megrim and witch (*Glyptocephalus cynoglossus*) are far more abundant in the northern North Sea (ICES area IVa) and thus only have 16% – 35% of their total North Sea biomass in the southern North Sea (ICES areas IVb and c). Referring to the biogeographic origins of the species (Engelhard et al. 2011), it is primarily Atlantic and boreal species (cod, haddock, herring, Norway pout, halibut, and others) which have a lower biomass density in the southern model, whereas Lusitanian species (whiting, gurnards, sprat, flounder, dragonets (*Callionymus* sp.) and others) are more abundant here (Figure 2). A pattern can also be derived from the horizontal habitat association outlined in Engelhard et al. (2011): The coastal flounder and inner shelf associated sandeels are more abundant in the south, whereas outer shelf (Norway pout, megrim) and slope (halibut) species consistently show lower biomasses here. Differences in biomass densities in the numerous shelf associated species are more variable, and no clear pattern can be derived. Besides biogeography and horizontal habitat association, trophic guilds explain much of the patterns in differences between the two models' fish groups (Figure 3). Generally, benthivorous and

planktivorous fish appear to be more abundant in the southern part of the North Sea, whereas piscivores are more dominant in the north.

Figure 2: Differences in biomass densities between common fish groups of the southern and the total North Sea models. Colours indicate horizontal habitat ecotype, and plotting characters show biogeographic ecotype according Engelhard et al. 2011. Mixed species groups do not have ecotypes assigned.
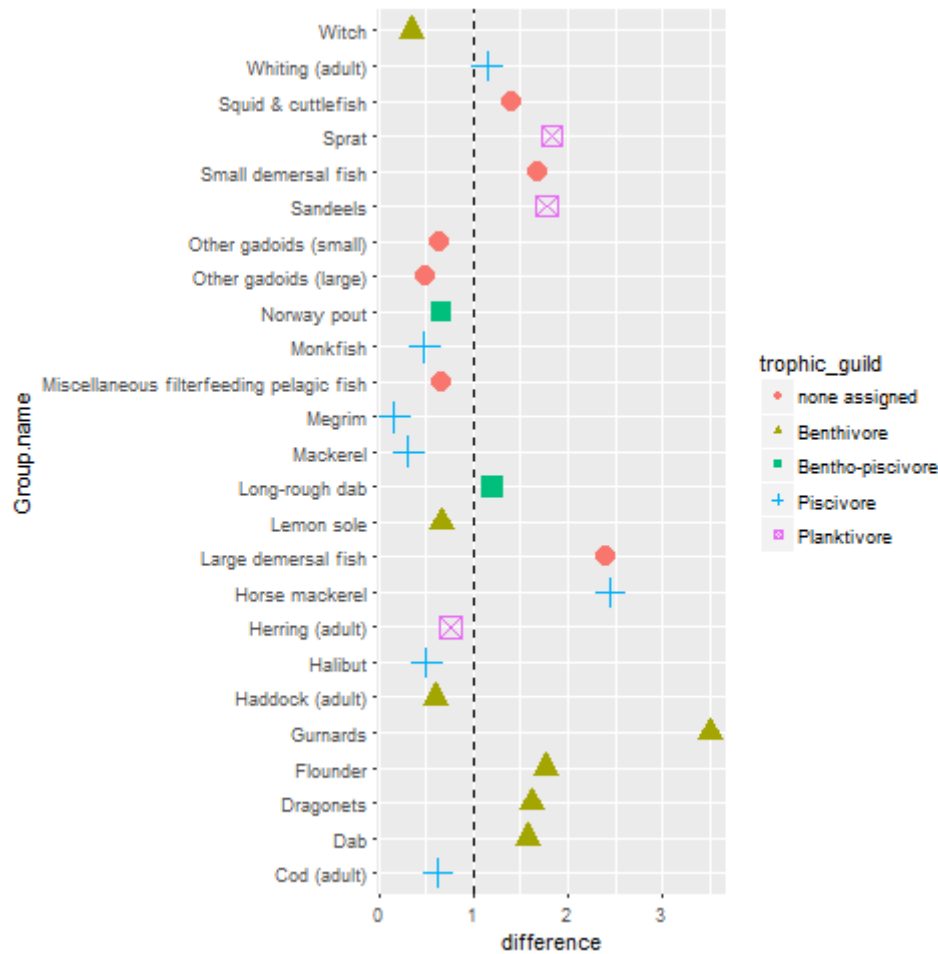
Figure 3: Differences in biomass densities between common fish groups of the southern and the total North Sea models. Colours represent trophic guild according Engelhard et al. 2011. Mixed species groups do not have trophic guilds assigned.

To investigate which of the ecotypological characteristics of the fish groups correlated most with biomass differences between the two models, we ran a classification tree analysis (using the *rpart* package in R; *minsplit* set to 4; N = 25). Biogeography turned out to explain most of the variance in the differences in both models' fish biomass densities, followed by trophic guild and horizontal habitat type, which rank comparably (Figure 4). Vertical habitat, i.e. a more demersal, benthopelagic or fully pelagic lifestyle, played a subordinate role. Given that some species are implemented as finer resolved (turbot and brill) or multi-stanza groups in the southern North Sea model, but not in the whole North Sea one (plaice, sole), while others were neglected in the southern North Sea model (hake, catfish) or shifted to other, coarser groups (saithe), some species that could further validate that pattern are not included here.
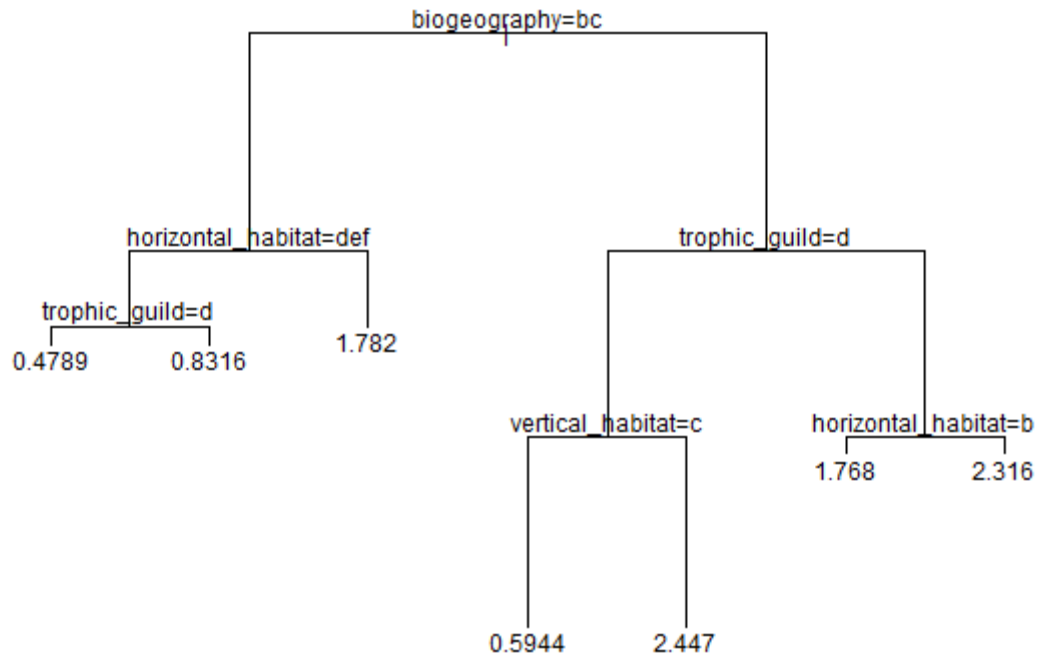
Figure 4: Classification tree model identifying the key ecotypological features (according Engelhard et al. 2011) related to differences in biomass densities between the southern and the total North Sea model. Biogeography 'Atlantic' and 'boreal', trophic guild 'piscivore', and horizontal habitat types 'Outer shelf, 'Shelf', and 'Slope' are the prime features associated with lower biomass densities in the North Sea.

Benthos

Biomass densities of the benthos groups contained in the southern North Sea model are illustrated in Figure 5. Not surprisingly, functional groups that represent a single species (nephrops) or even stanzas of that (brown shrimps) constitute the lower edge of the wide range of benthic biomass densities. Low as well are standing biomasses of benthic bacteria and protozoans, and shrimps in general. Infauna (infaunal polychaetes and other macrobenthos) reach the highest biomasses, followed by sessile and motile epifauna.

Biomass density estimates of some benthic functional groups were adopted from Mackinson and Daskalov (2007) and updates thereof, therefore the two models show no differences for these groups: Small infauna; infaunal macrobenthos; sessile and large and small mobile epifauna; meiofauna; and microflora. The biomass of nephrops in the southern North Sea, there against, was locally rooted through referring to abundance estimates per Functional Unit (WGNSSK 2016). Of these, the larger grounds and stocks are found in ICES area IVa. Also, our approach differs from the method applied by Mackinson and Daskalov (2007). The biomass in the southern North Sea model (0.17 t/km²) is accordingly lower than that in the whole North Sea model (1.10 t/km²). Similarly reduced, however to a lesser extent, are shrimps in the southern model: 0.22 t/km² against 0.50 t/km². Brown shrimps contributed the highest biomass to the pooled shrimps group in MDNS (c.f. Mackinson and Daskalov 2007; Table 11.8). For the sNoSe model, they were isolated from the shrimps functional group. The leftover shrimp species were distributed according their occurrence in IVa or IVb & c, which additionally lowered the shrimp group's biomass density, as another abundant species in the group (*Pandalus borealis*) has a northern distribution. The biomass densities of large crabs (crabs, lobster (*Homarus gammarus*), brown crab (*Cancer pagurus*), and spider crab (*Maja brachydactyla*)), on the other hand, were considerably higher in the southern North Sea model (2.30 t/km² against 1.35 t/km²), again related to the allocation of the different species within the biomass pool onto areas IVa or IVb and c.
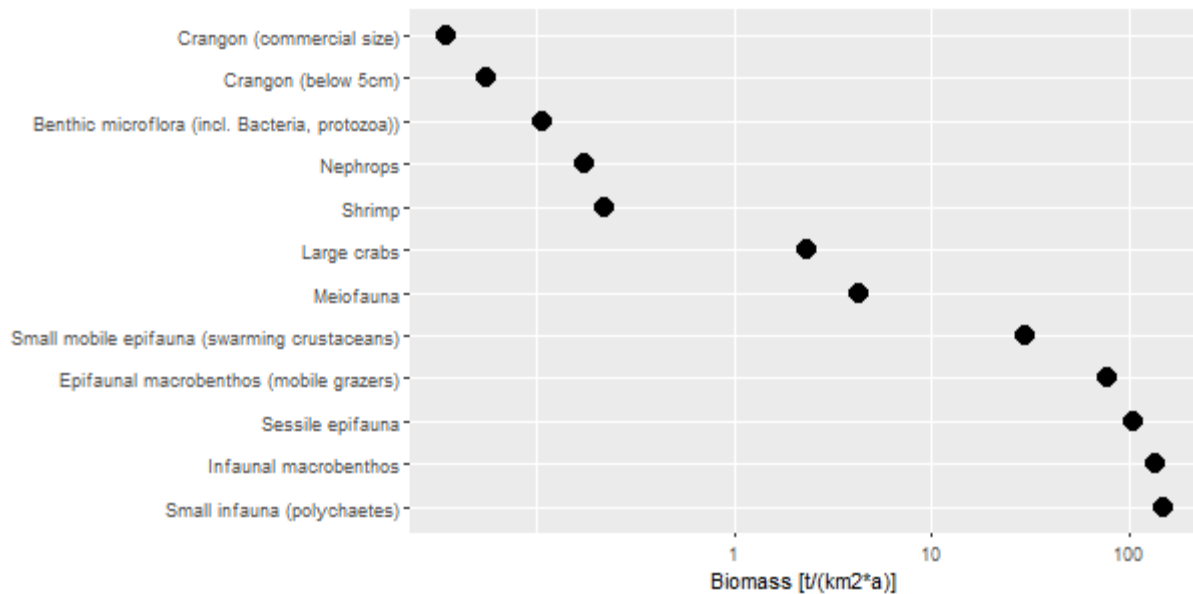
Figure 5: Biomass densities of benthos groups in the southern North Sea model.

3.2.   Consumption

The two dominant flows in the southern North Sea model lead from phytoplankton into detritus and from detritus to benthos (Table 1). Other substantial biomass flows are predation amongst different benthic species, and their flow to detritus, and the uptake of detritus by planktonic microflora. Fish groups primarily consume zooplankton, closely followed by benthos organisms. Of the biomass flowing out of the fish groups, most goes into detritus, dominantly through sandeels, the high production of which is not counteracted by an equivalent predation in the model. While the predation pressure on sandeels during their feeding season in summer is high, they become by far less accessible in winter, which they mostly spend buried in the sand (HAWG 2014). In its importance, the biomass flow of fish to detritus is followed by consumption through cannibalism and other fish groups, of which key commercials make up more than half (amongst those gadoids, clupeids, perciformes, and flatfish).

Key commercials rely on zooplankton even more than fish groups in general. Upper trophic level groups (cetaceans, seals, seabirds and elasmobranchs) chiefly consume fish (primarily key commercials). This consumption constitutes about 13.4% of the total amount of fish predated. The second food source for upper trophic level predators is benthos. Besides fishing and some predation loss of small or juvenile rays and sharks to mature cod or monkfish, and predation by other upper trophic level groups, all their flows lead to detritus and bycatch. This result is in accordance with the whole North Sea model (Mackinson and Daskalov 2007; Table 3.6)

Of all preyed groups, microfloral flagellates, ciliates and bacteria, both benthic and pelagic, are by far the most important ones in tonnes consumed per km² and year (Figure 6). Given that their main food is detritus, this highlights the importance of microbial upcycling of organic matter, which outcompetes primary production as a food source for higher trophic levels. The most consumed fish are sandeels (Figure 6; Figure 7). With only about a third of their value, they are followed by cephalopods (not actually fish, but included here due to their comparable trophic role, c.f. Figure 8). Following in their importance as prey groups are typical forage fish, as sprat, Norway pout, juvenile herring, and small demersals; and dab and juvenile whiting, given their vast abundance. The key commercial species cod, plaice, and sole rank in the lower midfield in their prominence as prey. High trophic level flatfish, which occur at low abundance, form the lower end of the consumption range (Figure 7).

Table 1: Consumption matrix of aggregated groups in the southern North Sea Ecopath model. Indicated are tonnes consumed per km² and year, of prey groups (rows) by predator groups (columns). Colours indicate the importance of consumption flows, from highest (red) to lowest (green).

Prey group	Upper TL	Fish	ZP	Benthos	Detritus & discards	Key commercials	Planktonic microflora	TOTAL
Upper trophic levels	0.0017	0.00073			0.88	0.00070		0.88
Fish	1.32	8.54		0.0025	40.99	4.72		55.60
ZP	0.010	60.79	35.66	0.74	255.11	54.88		407.19
Benthos	0.84	49.96	3.96	1302.70	1132.15	22.06	33.35	2545.04
Detritus & discards	0.11		24.00	2177.58	0.28		1467.24	3669.22
Key commercials	1.01	4.56		0.00056	30.03	2.26		37.85
PP		5.31	461.16	426.98	2423.67	5.19	166.73	3489.04
TOTAL	3.30	129.16	524.81	3908.01	3883.12	89.12	1667.32	10204.82
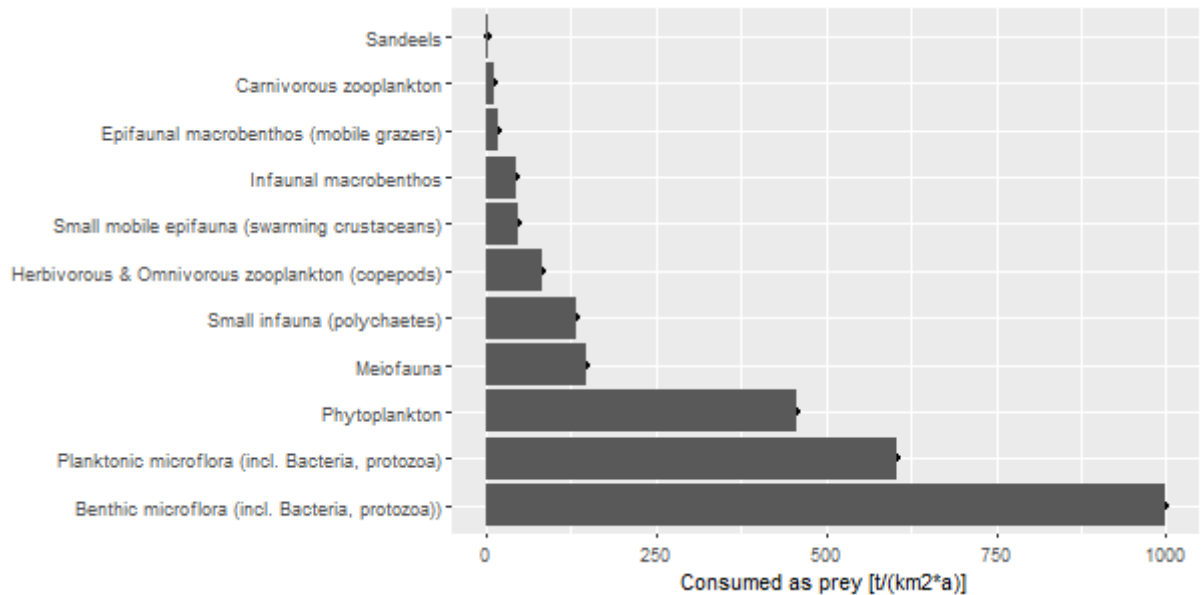
Figure 6: Consumption of top prey groups in the southern North Sea model
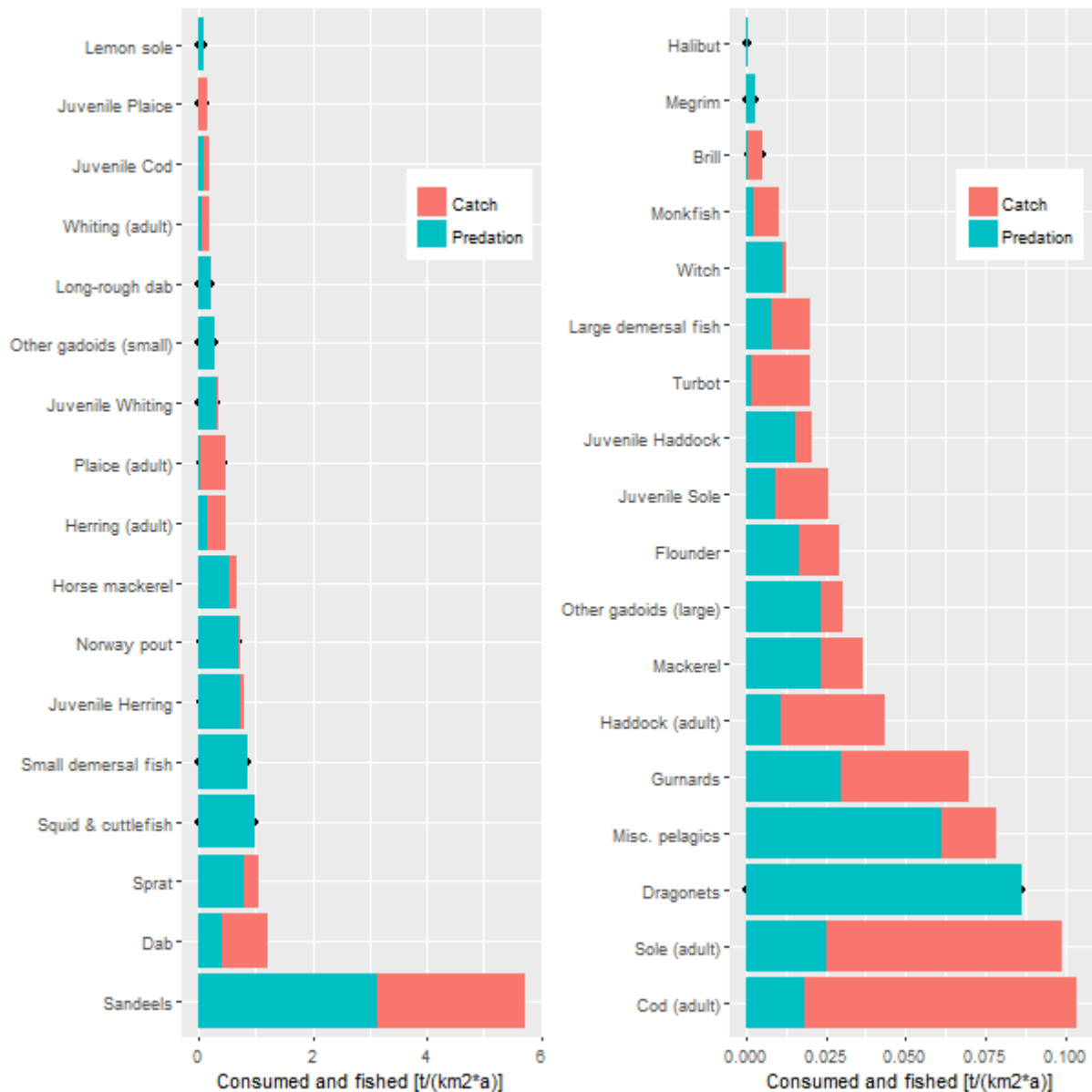
Figure 7: Total consumption and catch of fish prey groups. Note the different scales on the x-axes.

3.3.   Trophic levels

Being a producer, phytoplankton by definition has a trophic level (TL) of 1 (Lindeman 1942) in the southern North Sea model, thereby ranking lowest (Figure 8). Zooplankton and benthic and pelagic microflora have TLs slightly above 2, indicating that they feed primarily, but not exclusively, on phytoplankton. Most benthos organisms rank between TL 2.5 and 3.5 (yellow group names in Figure 8), but large crabs and brown shrimps reach higher levels. The TL of brown shrimps in the sNoSe model is very different from that of the shrimps functional group in both sNoSe and MDNS, given that their diet composition is parameterized according to a different literature source (del Norte-Campos 1995; Appendix A), which does not report the consumption of detritus (with a TL of 1). In fish, sprat have the lowest TL of just below 3. Other fish groups rank between TLs above 3.25 (sandeels) and 4.75 (cod). Given that they feed on discards, which are assigned the same TL as detritus (TL = 1), surface-feeding seabirds obtain a fairly low TL of 3.2. Elasmobranchs rank between TL 4.25 and 4.75, and large piscivorous sharks and seals, being the top predators in the model, almost reach TL 5.
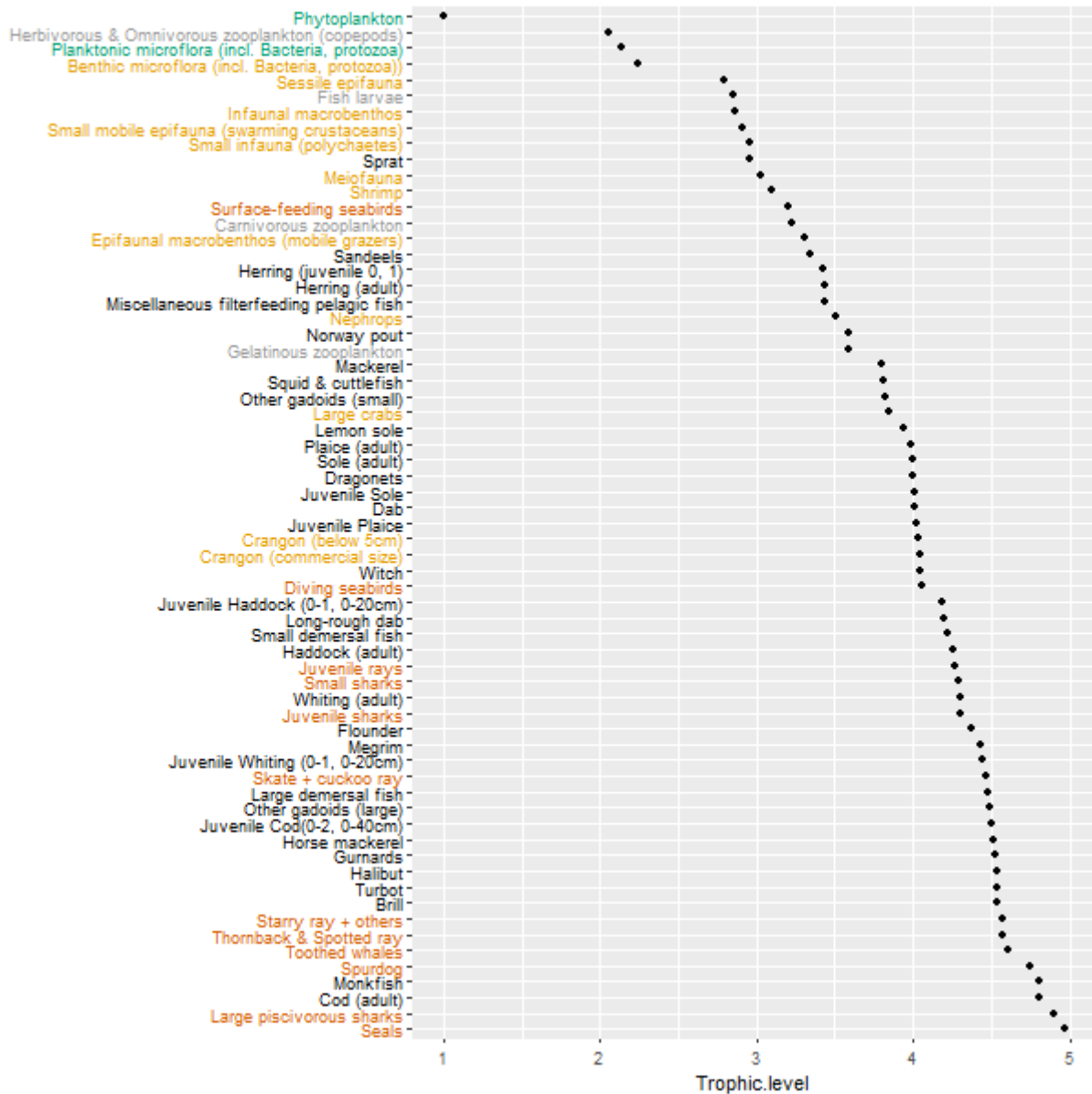
Figure 8: Trophic levels, as output of the southern North Sea model for 1991. Colours represent the association with higher level groups: Upper trophic levels (red), fish (black), benthos (yellow), zooplankton (grey), and phytoplankton (green).

In Figure 9, the trophic levels found for some of the fish groups in the southern North Sea model are plot against trophic levels reported by Engelhard and co-authors (2011) for the same species. For all but sprat and whiting, TLs are lower in the model than they are in Yang (1982), as reported in Engelhard et al. (2011). This particularly counts for fish of mid trophic levels, primarily flatfish, while low and high TL fish groups' estimates lie closer to the values in Engelhard et al. 2011.
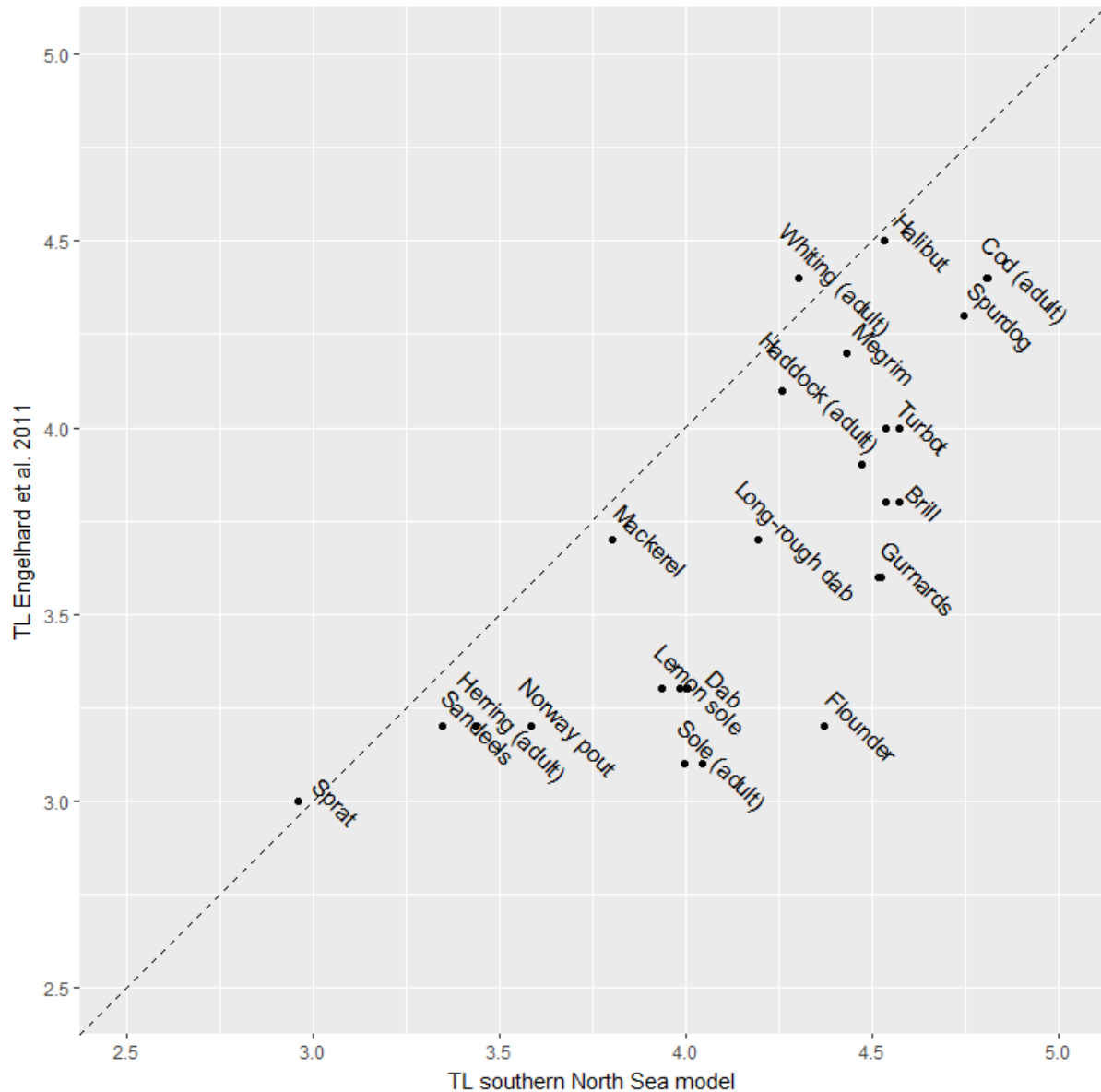
Figure 9: Trophic levels of fish groups in the southern North Sea Ecopath model, compared to trophic levels in Engelhard et al. 2011.

Figure 10, illustrating differences in the trophic levels calculated through the southern and the total North Sea models, respectively, shows that, for most lower trophic level groups, TLs are identical. Given that their diet composition in Chapter 2 is adopted from Mackinson and Daskalov 2007 and updates thereof, this is an expected finding. For fish groups, however, new diet compositions have been calculated for the sNoSe model, mostly based on a regionalized evaluation of ICES' 1991 year of the stomach data (Hislop et al. 1997), but also literature (c.f. Appendix A, section 5.4). Of fish groups for which ecotype information was available from Engelhard et al. 2011, no consistent relationship between trophic guild (colour in Figure 10) and differences between both models' TLs can be found. Neither does association with a specific vertical habitat type lead to systematic differences between both models' TLs; positive and negative differences can be found for any habitat type. The same accounts for horizontal habitat association (not shown). Consistent, however, is the higher TL of juvenile gadoids and the lower TL of their adults in the southern model, which is primarily due to the fact that the juvenile stages extend longer in the parameterization of the sNoSe model (e.g. 33 vs. 24 months for cod), thus consuming larger prey. The TLs of top predators are lower in the sNoSe model, given that large fish species (saithe, cod, other large demersals), and thus potential high TL prey items,

are less abundant in the south. A group of upper mid-level predators (rays, horse mackerel, gurnards), obtains higher TLs in the south, potentially indicating that they take over the niche of the northern large roundfish predators to some extent.
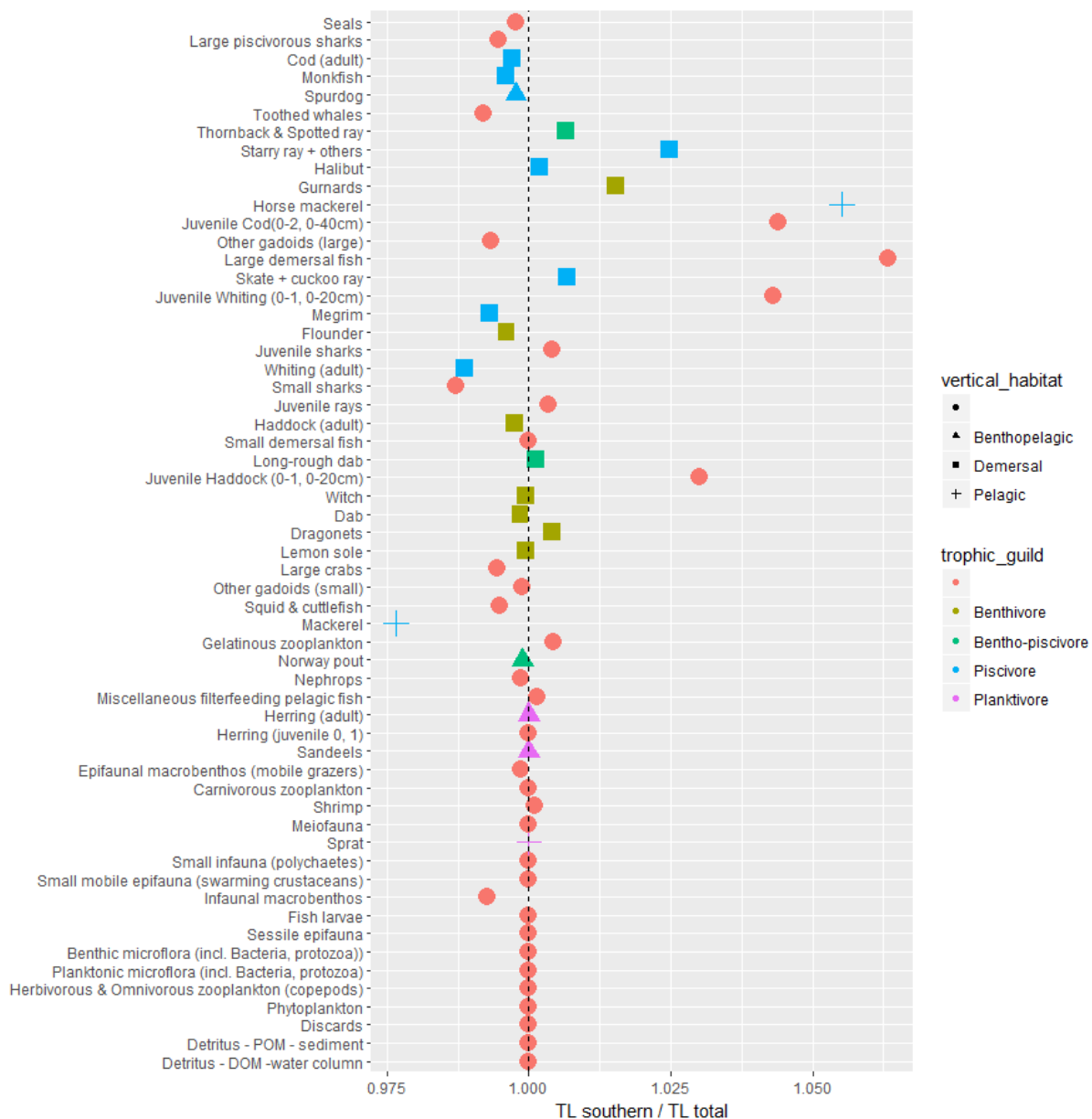
Figure 10: Differences in trophic levels calculated by the southern and the total North Sea model for common functional groups. Groups are ranked by decreasing trophic levels. Plotting characters indicate vertical habitat, and colour trophic guild according Engelhard et al. 2011.

3.4.   Fisheries' catches

Since the sNoSe Ecopath model was primarily set up to serve as the base of an Ecosim model exploring fishing policy options in the 2010s, the catch compositions of the various fleets were parameterized such as to represent the state in 2010. The total tonnage caught, however, represents the state in 1991 in the Ecopath model (see also section 2.2 of Chapter 1; and Appendix B). In terms of total tonnage caught, sandeels were by far the most important species for the fisheries of the southern North Sea in 1991 (Figure 7). With about a third of their catch, they were followed by dab, of which, however, most was discarded. Second to sandeels in terms of landings, and third rank in total catches, were plaice, followed by clupeids (herring and sprat), and then gadoids (whiting and cod). Hereafter followed sole and brown shrimp, with about 20% and 14% of the landings of plaice.

As stated above, the gear-wise catches in the sNoSe model are a mixture of 1991 tonnages and 2010 catch composition. Industrial sandeel trawlers form the by far most important fleet in the southern North Sea model in terms of tonnage caught (Figure 11). Its catches are very selective for sandeel, with a certain amount of sprat and some bycatch of juvenile pelagics and demersal key commercials. Beam trawlers catch about a third of the catch of industrial fleet. They primarily target flatfish, with their main catch being dab, of which most is discarded. Besides plaice, beam trawlers target the more valuable (but less abundant) sole. Minor amounts of medium sized demersal roundfish (cod, whiting, and gurnard) end up in beam trawlers' nets. Just below the beam trawling fleet in terms of total catch in the sNoSe model rank demersal trawlers and seiners, which catch composition is slightly more diverse, but also dominated by the flatfish plaice and dab (Figure 11), given the vast abundance of the species (Figure 1). Dab is almost entirely discarded according the sNoSe model's parameterization, while only 4.5% of adult plaice caught go back overboard. Target species more 'classic' for the northern demersal trawlers (Mackinson et al. 2009b) obtain mid ranges in the importance of the fleet's catches in the south: cod, whiting, and haddock (Figure 11). In the sNoSe model, the pelagic fleet falls short of the above mentioned fleets in terms of total catch and catch diversity. Their catch composition focusses on herring and some horse mackerel. Nephrops trawls and the pot fishery are superior to the shrimp fishery regarding total catch (Appendix B), but the brown shrimp fishery holds particular relevance for the area given its significant landings value (Temming and Hufnagl 2014).
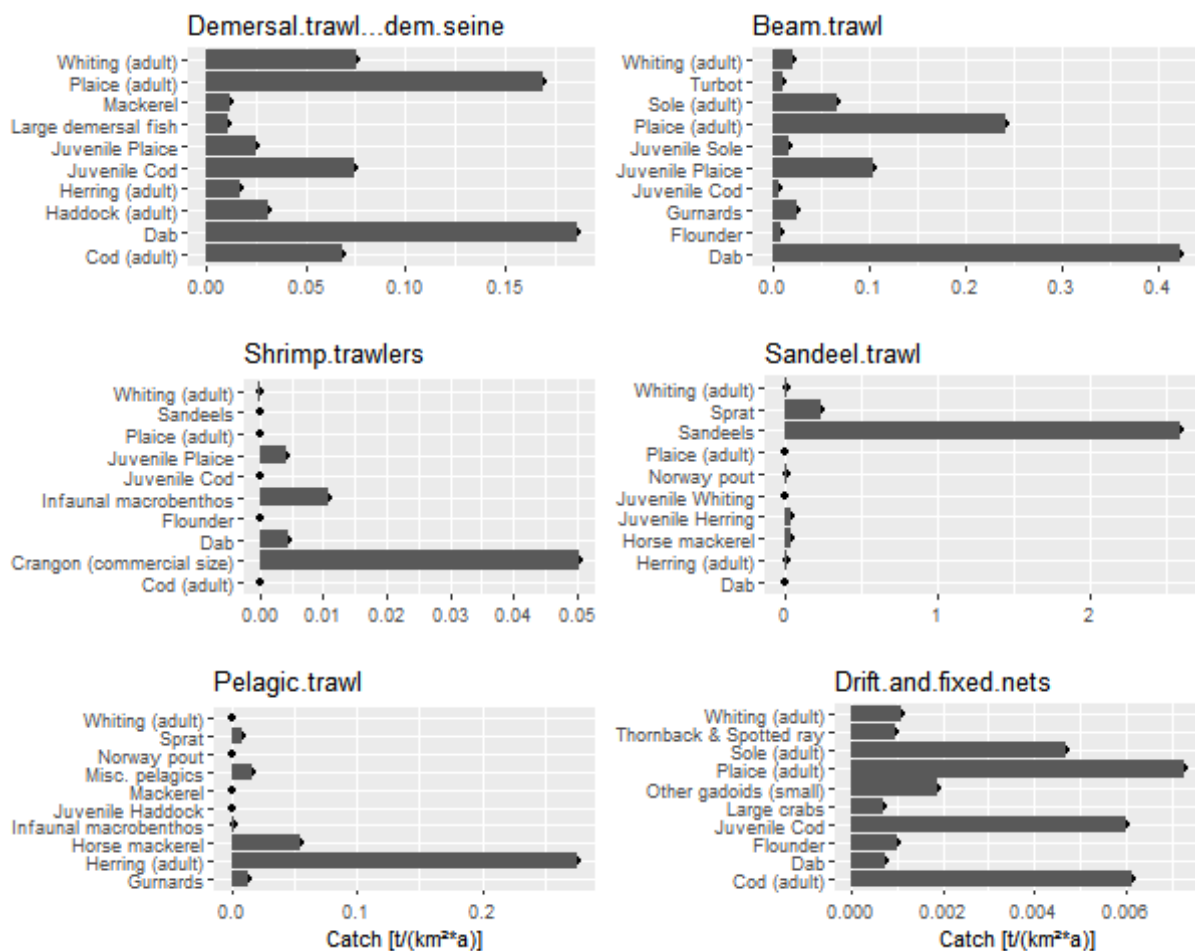
Figure 11: Catch composition of major fleets in the southern North Sea model.

The catch of this specialized fleet is dominated by brown shrimp, but also catches considerable amounts of macrobenthos and juvenile plaice, which are entirely discarded. Besides the brown shrimp

fishery, other artisanal gears are drift and fixed nets. These gears contribute rather few to the total sNoSe model's catch (about 4% of the beam trawlers' catch). Their catch is the most diverse, with key species being plaice, sole and cod, but also whiting, rays, flounder and crabs. Their total discard to catch ratio is amongst the lowest (6%) of all fleets, undergone only by sandeel and pelagic trawlers (1% each). Highest total discard to catch ratios occur in nephrops trawling (80%) and beam trawlers (64%). The by far most discarded species is dab, followed by plaice and whiting.

One of the drivers of the incentive to parameterize an Ecosim model focussing on the southern North Sea particularly rather than using the existing whole North Sea model was the consideration that the catch compositions of seiners, otter and beam trawlers should look very different between both areas. This was thought to compromise the model's ability to support fisheries management explorations for the southern North Sea. Indeed, catch composition of demersal trawlers and seiners in the whole North Sea model differs greatly from the fleet's catches in the sNoSe model (Figure 12). There, roundfish, particularly herring and gadoids, and mackerel dominate the catch. Plaice and dab, as in the southern focussed model, get caught as well, but to a much lower extend. For beam trawlers, plaice are much more dominant in the catch than is the case in the southern subpart, where considerably more dab is caught. Compared to most flatfish species (dab, sole), plaice have a more northern distribution and support (or supported) important fisheries off North England, Scotland, and the Shetland Islands (c.f. e.g. Engelhard et al. 2011 b). Thus, the ratio of plaice to sole catches is higher in the whole North Sea model ($\frac{Cplaice}{Csole} = 5.0$) than it is in the sNoSe model (4.2). As in the southern model, sandeels are the most important species in terms of tonnage caught. Different from the latter, however, it are not flatfish (dab and plaice) and epifauna which follow, but herring and mackerel, illustrating the more pelagic nature of the system and its fisheries.
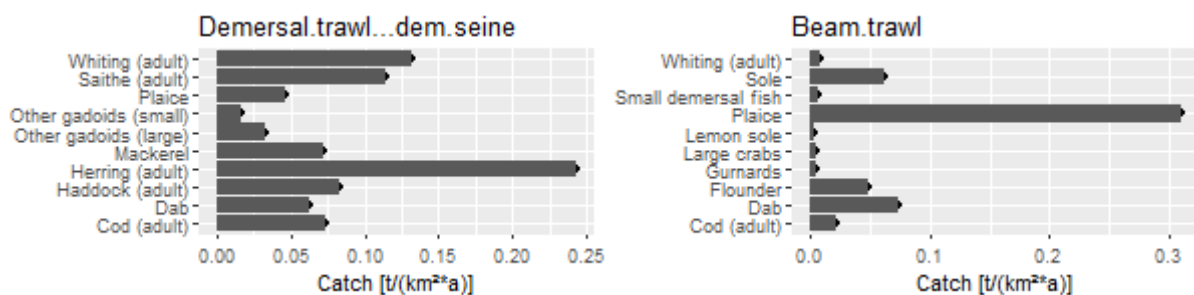
Figure 12: Catch composition of beam trawlers and demersal trawlers and seiners in the whole North Sea model.

3.5.   Predatory niche overlaps

One way of quantifying the subdivision of trophic niches between species in a food web and hence their potential for food competition is the niche overlap index developed by Pianka (1973). In its implementation in the Ecopath software (Christensen et al. 2008), this index describes the overlap of two functional groups' diet compositions. Identical diets would result in predator niche overlap = 1, no relation whatsoever in a value of 0. Table 2 lists the predatory niche overlaps of commercially relevant predator groups. Highest overlaps exist between the two brown shrimp stanzas, between brown shrimp and juvenile sole, and between mature sole and plaice. Of these, the predicted competition between juvenile sole and brown shrimp is partially an artefact of the low taxonomic resolution in the lower trophic levels of the model: juvenile sole feed almost exclusively on small infauna (polychaetes), which also contribute an important part of brown shrimps' diet. *In situ*, however, it would certainly be different polychaete species and stages the two species feed on. Adult plaice, and to a minor extend adult sole, interestingly have a considerable overlap in diet with cod – more so than cod has with the closely related whiting. Based on the diet composition derived from the ICES year of the stomachs data, gurnards, a group of demersal predators with increasing abundance throughout the 1980s and

1990s (Floeter et al. 2005), do have no notable predatory niche overlap with any commercially important group but sandeels and dab. Numerically, that means that their niche overlap index, which can range between 0 and 1, with 1 indicating identical diets, does not exceed 0.11 for any other commercial group than dab and sandeels, for which it reaches values around 0.5.

For the whole North Sea model, Mackinson and Daskalov (2007) do not report important trophic niche overlaps between cod and plaice (Figure 3.14 therein). The difference to our model must thus arise from the more localized diet composition computed for cod and a different literature source for plaice' diet (Schückel et al. 2012; Appendix A) in Chapter 2). In contrast to our findings, Mackinson and Daskalov (2007) found high niche overlaps between whiting and gurnards. Interestingly, they do not report niche overlaps between plaice and sole.

Table 2: Predatory niche overlaps (sensu Pianka 1973) of selected groups in the southern North Sea model.

	Juvenile Cod	Cod (adult)	Juvenile Whiting	Whiting (adult)	Gurnards	Herring (adult)	Sprat	Sandeels	Plaice (adult)	Juvenile Plaice	Dab	Sole (adult)	Juvenile Sole	Crangon (≥ 5cm)
Cod (adult)	0.16													
Juvenile Whiting	0.24	0.03												
Whiting (adult)	0.26	0.49	0.11											
Gurnards	0.04	0.01	0.04	0.05										
Herring (adult)	0.18	0.18	0.13	0.68	0.06									
Sprat	0.17	0.00	0.53	0.05	0.03	0.04								
Sandeels	0.40	0.05	0.27	0.08	0.54	0.11	0.44							
Plaice (adult)	0.53	0.70	0.02	0.35	0.00	0.09	0.04	0.10						
Juvenile Plaice	0.07	0.24	0.10	0.64	0.05	0.64	0.01	0.01	0.08					
Dab	0.17	0.14	0.23	0.39	0.44	0.42	0.09	0.45	0.13	0.35				
Sole (adult)	0.58	0.51	0.01	0.20	0.07	0.01	0.05	0.15	0.95	0.00	0.12			
Juvenile Sole	0.39	0.06	0.24	0.22	0.07	0.33	0.23	0.32	0.02	0.23	0.18	0.00		
Crangon (≥ 5cm)	0.39	0.00	0.26	0.01	0.08	0.11	0.17	0.31	0.04	0.01	0.11	0.05	0.92	
Crangon (< 5cm)	0.39	0.00	0.25	0.01	0.07	0.10	0.19	0.33	0.03	0.01	0.10	0.04	0.93	0.99

3.6. Ecosystem indicators

One of the more classic applications of Ecopath models is the assessment of the entire modelled ecosystem in terms of its productivity, complexity and connectance. Whole system indicators describing these properties are regarded as signals of ecosystem maturity and its stage of development (Odum 1971; Ulanowicz 1986; Christensen 1995), which eventually relate to ecosystem health. Indicators related to biomass and production are the most straight forward of these indicators. Comparing the two modelled systems, they indicate negligible differences in total biomass density and production (Table 3). Both systems hold more community biomass (i.e. the sum of all biomass but that of primary producers and detritus; TB in Table 3) than most shelf systems assessed with Ecopath models (c.f. Heymans et al. 2014, Figure 3b), and considerably more than other systems exploited by fisheries (Figure 9c therein). Total system throughput (TST), an indicator of the size of the ecosystem in terms of trophic flows (Ulanowicz 1986), reaches levels common for shelf systems in both models (c.f. Heymans et al. 2014, Figure 3a; note, however, that the MDNS model forms part of the set of 105 models analysed in that study). Set in relation to TST, total consumption (Q/TST) and respiration (R/TST) are fairly high in both North Sea models compared to other East Atlantic food webs. Heymans

and colleagues (2014) argue that high consumption and respiration rates may relate to comparatively high nutrient inputs, and the North Sea can well be considered nutrient-rich compared to other East Atlantic systems analysed in their study. Both R/TST and flows to detritus, related to TST (FD/TST) are average amongst systems of depth classes <50m and <100m, but the relative flow to detritus is quite low compared to other East Atlantic systems, which is contra-intuitive, given the above mentioned higher nutrient inflow into the North Sea. This is particularly valid for the southern North Sea, and again it comes as a surprise that both the total (FD) and the relative (FD/TST) detritus production are lower in the southern sub-model than in the whole North Sea model. The above mentioned higher nutrient load should lead to opposite expectations. A potential explanation lies in the inclusion of phytoplankton into the diets of groups whose phytoplankton feeding is often not considered (c.f. section 3.1.A). An additional consumption of phytoplankton, compared to other models, leads to a lesser share of primary production going straight into detritus in the southern North Sea model. Relative exports of biomass from the system (Exp/TST) were found to increase with the spatial dimension of the models analysed by Heymans et al. (2014, Figure 5b). Indeed, the opposite is the case for the two models analysed here, where the sNoSe model, being almost half the size of the whole North Sea model, exports almost twice the amount of biomass per km² (Table 1). For both models, relative export is far below what would be expected for models covering comparable surface areas, as well as other East Atlantic models, and values 100 to 200 fold higher should be expected (c.f. Heymans et al. 2014, Figures 5b and 6b).

Given that the parameterization of phytoplankton (biomass and productivity) in the sNoSe model was adopted from MDNS, no differences between their net primary productions (PP) occurred. Differences in PP-related ecosystem indicators are thus dependent on the respective denominator. In both models, net primary production only overshoots total biomass (PP/TB) less than 4-fold, compared to values up to 40 in coastal Mediterranean food-webs (Torres et al. 2013). This indicates that, in the North Sea in general, a large share of the biomass produced through photosynthesis is aggregated in the food-web; an indication of mature networks (Christensen 1995). Ratios of total primary production over the amount of organic matter respired (PP/R) approach values of one in both models, signifying that the energy gained through photosynthesis is almost entirely consumed by organisms' maintenance, again an indication of a mature system sensu Odum (1969). Another gauge for ecosystem maturity would be a high value of the connectance index (CoI), which relates the number of existing trophic links to the number of total theoretically thinkable links (Christensen et al. 2008). It, however, only reaches average levels for both models. Related to CoI is the system omnivory index (SOI), which describes how variable the diets of predators in the system are in terms of the trophic levels fed upon. Here, a high level (as it is for both models, compared to other food webs in the East Atlantic) stands for a non-linear, more web-like structure of trophic flows. To a subtle extend, this is the case for the southern North Sea more than it is for the system as a whole (Table 3), probably due to the dominance of more omnivorous flatfish over more specialized piscivores.

Of the three indices representing the state of fisheries in the system, total catch (TC) sums the landings and discards of all species per km² and year. It is slightly higher for the southern model (Table 3), and, for both models, ranks similar to other assessed European systems, as does gross efficiency (TC/PP). Compared to the global average (0.0002, Christensen et al. 2008), conversion of primary production to fished biomass is an order of magnitude higher ('more efficient') in the North Sea. This is contradictory to the claims made by advocates of the balanced harvesting incentive that well-managed, selective fishing regimes are generally inefficient in the conversion of marine production to fishing yields (Garcia et al. 2012; Kolding et al. 2016). Much rather, it appears that, in the North Sea, a long history of exploitation and management has eventually led to an efficient utilization of aquatic biomass produced, despite its fisheries being quite selective. The mean trophic level of the catch (mTLc) is considerably higher than in other models in the East Atlantic, and in general in temperate

latitudes (Heymans et al. 2014, Figures 9e and f). As expected for a more shallow system (Figure 9d therein), mTLc is lower in the south. Generally, both 1991 North Sea models fulfil indications of the North Sea being a fairly mature system (TB; PP/TB; PP/R; SOI; mTLc), besides its long history of exploitation and high usage of synthesized biomass as fished food (TC/PP). This finding is in line with Mackinson and Daskalov (2007) reporting their North Sea model to show higher stability and maturity than other UK marine ecosystems. Given that system maturity relates to resilience, since in mature systems trophic structure outweighs environmental pressures (Odum 1969), this is good news for the southern and the total North Sea's fisheries and ecosystem managers. This is particularly the case given that fishing efforts of essentially all North Sea fleets, and fishing mortalities of the majority of the assessed stocks have been reduced since 1991 (Appendix of Chapter 2; Mackinson and Daskalov 2007).

Table 3: Summary statistics for the southern North Sea (sNoSe) and whole North Sea (MDNS) ecosystem models.

Parameter	sNoSe	MDNS	Units	Difference
Model characteristics				
Surface area	348874	570000	km²	
Number of functional groups	68	68		
Number of fishing fleets	11	12		
System theory indices				
Total system throughput (TST)	12232.4	12048.7	t/(km² * a)	1.52%
Total biomass (excluding detritus) (TB)	556.5	551.8	t/km²	0.84%
Sum of all production (P)	4717.7	4693.7	t/(km² * a)	0.51%
Sum of all consumption (Q)	6227.0	6150.5	t/(km² * a)	1.24%
Consumption / Tot. system throughput (Q/TST)	0.509	0.510		-0.28%
Sum of all exports (Exp)	190.9	104.6	t/(km² * a)	82.52%
Exports / Tot. system throughput (Exp/TST)	0.016	0.009		79.78%
Sum of all respiratory flows (R)	1960.2	1924.7	t/(km² * a)	1.85%
Respiration / Tot. system throughput (R/TST)	0.1602	0.1597		0.32%
Sum of all flows into detritus (FD)	3854.199	3868.9	t/(km² * a)	-0.38%
Flows to detritus / Tot. system throughput (FD/TST)	0.3151	0.3211		-1.88%
Calculated total net primary production (PP)	2150	2150	t/(km² * a)	0.00%
Tot. primary production/tot. Respiration (PP/R)	1.097	1.117		-1.81%
Net system production (net P)	189.8	225.3	t/(km² * a)	-15.77%
Total biomass/total throughput (TB/TST)	0.0455	0.0458	/year	-0.68%
Total primary production/total biomass (PP/TB)	3.864	3.896		-0.83%
Primary production / total prod. (PP/P)	0.456	0.458		0.51%
Connectance Index (CoI)	0.2330	0.2201		5.83%
System Omnivory Index (SOI)	0.2709	0.2686		0.87%
Fisheries status indices				
Total catch (TC)	5.913	5.668	t/(km² * a)	4.31%
Mean trophic level of the catch (mTLc)	3.580	3.673		-2.54%
Gross efficiency (TC/PP)	0.00275	0.00264		4.31%

4. Conclusion

The 1991 southern North Sea appears to be a comparatively unstressed ecosystem, characterized by the high connectance of a densely woven food-web. Whole ecosystem indicators obtained from the southern North Sea food-web model stand out among systems comparable in location and exploitation

and indicate a mature, resilient ecosystem. In terms of its trophic flows, the southern North Sea is dominated by the lowest trophic levels. The vast majority of organic matter produced through photosynthesis ends up as detritus, and benthic invertebrates play a key role in channelling the energy back into the food-web for consumption of upper-level TL predators.

Compared to a representation of the entire North Sea, the southern sub-part's (particularly fish) community composition considerably differed, which could partially be related systematically to body shape (flatfish over roundfish) and biogeography (Lusitanian over Boreal and Atlantic origin). Also, fisheries' catch patterns and TL of the catch differed, and a nominally identical fleet (demersal trawlers and seiners) had a considerably different catch composition in the south. To a subtle extend, the southern North Sea representation can be considered even more interconnected and mature than its wider scope counterpart, but these differences fade when the ecosystem network indicators were contrasted with a global selection of Ecopath models. Under that perspective, and even under a more confined exploited and East Atlantic comparison context, both models appear as close siblings, if not even twins.

5. Acknowledgements

Author contributions
AT and MS developed the idea of this study. MS parametrized the food-web model, cooperating with AK and advised by AK and AT. MS performed the analyses and wrote the manuscript in close cooperation with AT.

6. Appendix A

This appendix outlines the approaches, data sources and literature references used to parameterize the functional groups (FG) of the southern North Sea (sNoSe) Ecopath model. Three different general approaches were followed to calculate biomasses of functional groups for ICES divisions IVb and IVc, depending on whether analytical assessments of the respective species were available or not and if they were sampled representatively in the ICES International Bottom Trawl Survey (IBTS). An overview of the study area and a graphical representation of the way biomass densities were calculated can be found in Figure A 1.
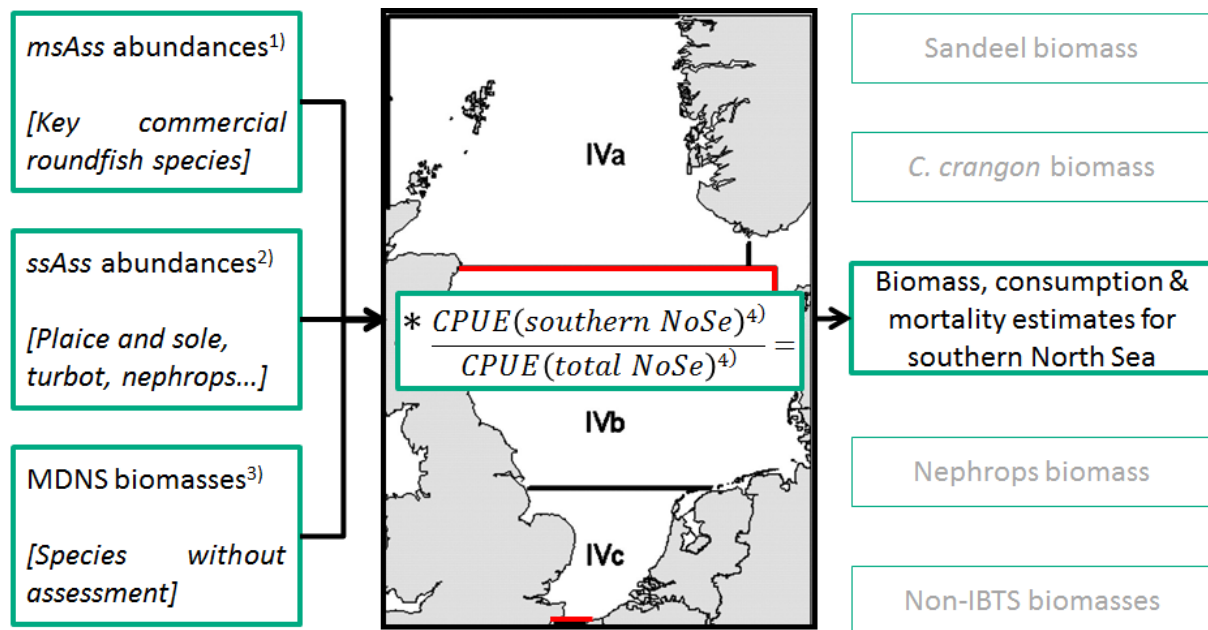
Figure A 1: Schematic representation of how biomasses for the southern North Sea EwE model were calculated. 1) North Sea SMS, the Stochastic Multispecies Model (WGSAM, 2014). 2) XSA, the Extended Survivors Analysis. (WGNSSK, 2013). 3) The North Sea EwE (Mackinson and Daskalov, 2007) 4) IBTS. http://datras.ices.dk/Data_products/Download/Download_Data_public.aspx. Transparent boxes were calculated independent of IBTS data.

6.1. Compiling biomasses of assessed species

The multispecies model SMS (Stochastic Multi Species model; Lewy and Vinther, 2004) delivered abundances of commercial roundfish species – cod (*Gadus morhua*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*), and sprat (*Sprattus sprattus*) – for the entire North Sea (ICES division IV) together with the eastern Channel (area VIId) in the case of cod, herring and whiting and Skagerrak/Kattegat (area IIIa) in the case of cod, herring, whiting and haddock (WGSAM, 2011). To split these total SMS abundance estimates into two fractions, one inside our model area (IVb and c) and one outside (IVa, IIIa and VIId), we used ICES International Bottom Trawl Survey (IBTS) data. For each SMS species at each age and quarter, we identified the contribution of southern North Sea catch per unit effort (CPUE) to the total SMS area abundance in an IBTS "CPUE per age per subarea" dataset downloaded from the ICES Datras web portal (datras.ices.dk, download date 07 August 2014). The *abundance $_{(sNoSe)}$* / *abundance $_{(SMS\ area)}$* ratio was merged with SMS abundances species-, age- and quarter-wise to create corrected abundances for our model area. These corrected abundances were converted into biomass estimates for the 1991 Ecopath model by multiplying them with weight-at-age info in SMS.

During 1991, the IBTS survey did not cover the Channel region. We found that to be of negligible relevance for cod, haddock, mackerel, horse mackerel and sprat. In later years, however, significant amounts of adult whiting and herring could be found in the eastern Channel. We used landings data of 1991 to subtract this share of the total whiting respectively herring population from the SMS-derived biomass. For whiting, we used EUROSTAT (http://info.ices.dk/fish/CATChSTATISTICS.asp, data downloaded 2 December 2012) landings to split the whiting stock into the two proportions in IVb and c and in VIId. We calculated landings$_{(VIId)}$ / landings$_{(VIId+IV)}$ ratios from EUROSTAT landings in 1991 (10.6% on average in 1986 - '96) and subtracted the respective amount from the biomass estimate calculated as described above.

A best estimate for historic distribution of adult herring in the North Sea probably stems from commercial landings (N. Rohlfs, Thünen-Institute of Sea Fisheries, pers. comm.). We referred to the herring stock assessment (HAWG, 1993; Tables 2.1.ff and Figures 2.10.ff), for shares landed in the relevant subareas, and identified the mean annual proportion of adult herring in our study area as 31% of total landings from the SMS area in 1991.

Results of the single species stock assessment model XSA (Extended Survivors Analysis; Shepherd, 1999; WGNSSK, 2013) were referred to for European plaice (*Pleuronectes platessa*). Again, survey abundances from the IBTS were used to identify the respective shares of the whole North Sea stocks in divisions IVb and c, showing that the vast majority of North Sea plaice are located in our study area. Divisions IVb and c are home to the almost entire North Sea stock of European sole (*Solea solea*), and landings are almost exclusively from these two divisions.

Several species and length classes were grouped into stanzas (Christensen et al. 2008) based on their size and age (Table A 1) to represent differences in their life history stages in terms of ontogenetic changes in growth and diet, or because they are subjected to different fishing patterns (as particularly in brown shrimp, *Crangon crangon*).

Table A 1: Age and size margins of transition to adult stanzas. Lenght at maturity for Solea solea and Pleuronectes platessa are from FishBase (Froese and Pauly, 2002). Sole stage is based on (Mollet et al. 2013; Mollet et al. 2007). Plaice stage is based on van Walraven et al. (2010); and C. crangon stages based on recruitment size to fishery.

Defined adult if they exceed size:	… and age	Species
400mm	33 months	*Gadus morhua*
200mm	21 months	*Merlangius merlangus*
200mm	21 months	*Melanogrammus aeglefinus*
200mm	15 months	*Clupea harengus*
300mm	32 months	*Solea solea*
300mm	35 months	*Pleuronectes platessa*
50mm	5 months	*Crangon crangon*

Since the publication of Mackinson and Daskalov (2007), an analytical assessment of turbot (*Psetta maxima*) has become available (WGNSSK, 2013). To make best use of this data and because of the increasing importance of turbot in fisheries management context we included brill (*Scophthalmus rhombus*) and turbot as two separate functional groups, while Mackinson and Daskalov (2007) held a single *turbot and brill* FG. Our 1991 biomass of turbot stems from the total stock biomass (TSB) of the stock assessment (WGNSSK, 2013), after we had verified that the vast majority of North Sea turbot inhabits our model area (http://ices.dk/marine-data/maps/Pages/ICES-FishMap.aspx, accessed 2 March 2015). Brill biomass was calculated relative to the biomass of turbot based on CPUEs from the ICES Beam Trawl Survey (BTS; as cited in Kerby et al. 2013). In 1991, the CPUE of turbot in the BTS was 4.5–fold higher than for brill, suggesting an accordingly lower biomass of brill if one assumes the catchability of the two species to be similar.

Sandeels' (Ammodytidae) estimated TSB is from WGNSSK (2013), section 04. TSBs here are given for each sandeel management area (SA). We summed up the biomasses of SA 1, 2 and 3 for 1991. TSB estimates from SA 4 are not available for 1991, but can be considered to be negligible as landings from this area are substantially lower than those from other areas. The sandeel biomass estimated for the "southern North Sea" in the 1992 ICES Report of the Industrial Fisheries Working Group (Industrial Fisheries Working Group, 1992) served as a comparison. We here multiplied estimated numbers at age from the semi–annual separable VPA for Q1 and Q3 1991 (Table 8.3.4.1) with weight–at–age data from Danish catches (Table 8.3.3.1). The result based on WGNSSK (2012) data, 1924736t, is 20% larger than

the one from the 1992 assessment for the southern component (1609142t). We used the more recent estimate of WGNSSK (2012) for our model.

Nephrops (*Nephrops norvegicus*) biomass for 1991 was estimated based on abundance estimates documented in WGNSSK (2012), Sec. 03. Functional Units (FU) 5, 6, 8, 33 and 34 were chosen to represent our model area (Figure A 2). For FU5, the density of burrows per m² was multiplied with the size of the area, the number of individuals per burrow (we assumed one, as in Mackinson and Daskalov, 2007), and the mean weight of the individuals. This supplied a value for the biomass in 2011. To obtain an estimate for 1991, we referred to the development of the landings per unit of effort (LPUE) in FU5. We then calculated a weighted LPUE for 2000 relative to 2011 and thus 1991, as we assume that to be similar to 2000 based on Figure A 3. The results suggest that the biomass in 1991 was 1.96 fold lower than today.

For FU6, the abundance in 1997 (first year of assessment) was 890 million. This number was multiplied with the assessment's mean weight to obtain a biomass estimate. No mean weight was given for FU6, but we assumed it to be similar to the neighbouring Devil's Hole (FU 34). For this area again, mean weights from FU7 (Fladen Ground) were used for biomass estimates by WGNSSK. We thus used the mean weight for 1997 in Fladen Ground (FU7) to calculate biomass in FU6. The biomass calculated for 1997 was multiplied with the ratios of LPUE of English vessels in 1994 (earliest record) over that in 1997.

Biomass for FU8 in 2011 was obtained by multiplying the current abundance estimate (533 million, see 3.4.4.5 in WGNSSK, 2012; Sec 3) with the mean weight from catches. Assuming a constant mean weight, a biomass value for 1991 could be estimated based on historical abundances (Figure A 4). Abundance in 1991 (first entry) is similar to the one in 2011, thus we assume the same value.

The development of LPUE for FU 33 can be found in WGNSSK (2012; Sec. 03, Figure 3.3.8.1 and Table 3.3.8.1). No biomass, abundance, or even size of the area are given. To estimate the Nephrops biomass in FU 33, the total landings figure from this area in 2011 was multiplied with an average of all other southern areas' biomass-to-total-landings relationships. Biomass in 1993 (the earliest provided LPUE) was then estimated based on this value and Figure 3.3.8.1 and Table 3.3.8.1 in Sec 03.

FU 34's biomass for 1991 is obtained by multiplying abundance (350 million) with mean weight, the latter taken from FU 7 for this exercise, as suggested by WGNSSK (2012; Sec. 03).
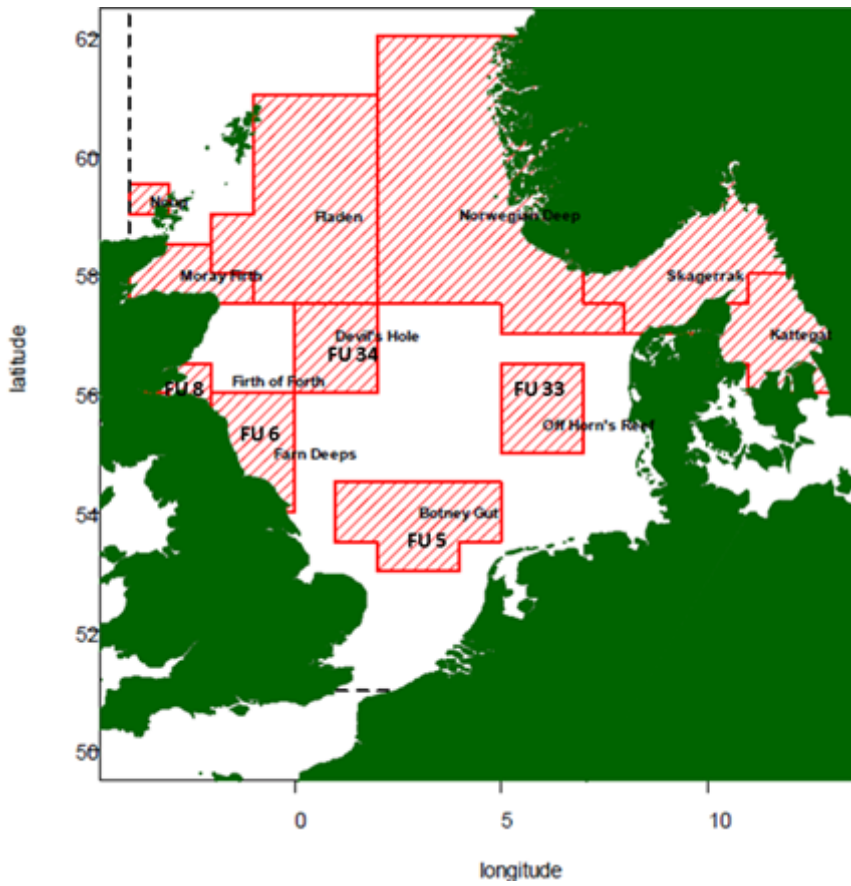
Figure A 2: Nephrops Functional Units in the North Sea and Skagerrak/Kattegat region (WGNSSK, 2012).
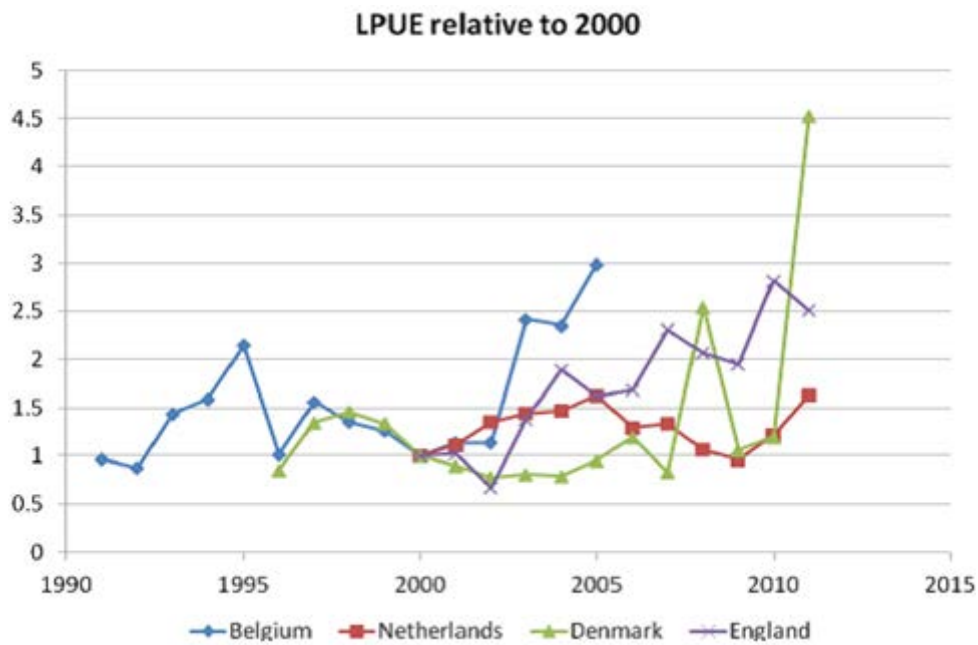
Figure A 3: FU5 Botney Gut/Silver Pit. Long-term trends in nephrops landings per unit of effort (WGNSSK, 2012).
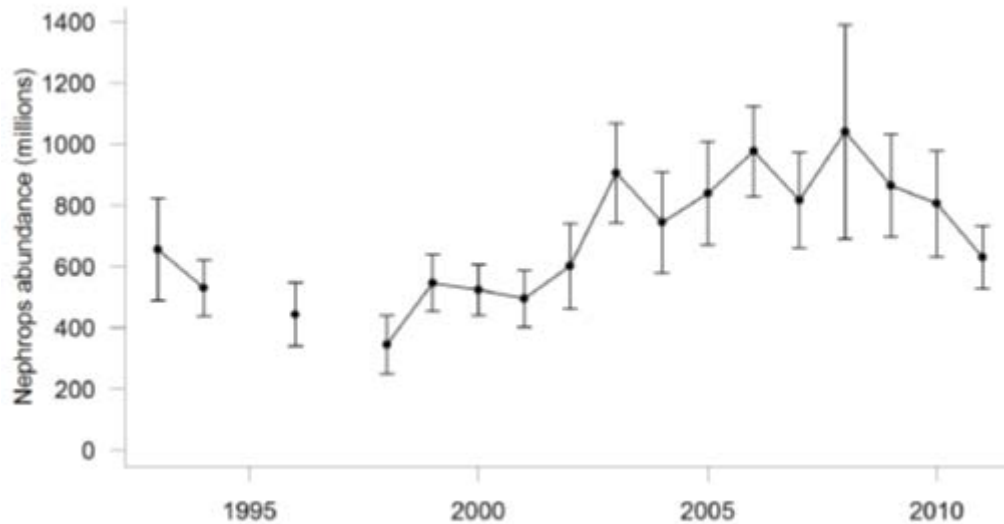
Figure A 4: Nephrops abundance in Firth of Forth, FU8 (WGNSSK, 2012).

6.2. Compiling biomasses of fish and invertebrate species without analytical assessments

The calculation of 1991 biomasses for functional groups which species are not subject to analytical assessments, but that are representatively sampled by the IBTS, was in essence analogue to the calculation of assessed species' biomasses, but biomass estimates by Mackinson and Daskalov (2007) served as the total North Sea biomass equivalent of SMS or XSA derived biomasses. Here as well, total North Sea biomass (as MDNS (Mackinson and Daskalov 2007) biomass density multiplied by its model area) was split into northern and southern North Sea components by using the IBTS south–to–total–ratio. For functional groups that are not or not representatively sampled by the IBTS, i.e. epifaunal macrobenthos, infaunal macrobenthos, large crabs and sessile epifauna, we kept the biomass densities as used in Mackinson and Daskalov (2007) and updates thereof, assuming uniform distribution of the groups' biomasses throughout the North Sea. Figure A 5 shows a graphical representation of the assignment of invertebrate taxa into functional groups.

According to that standard procedure, squid and cuttlefish biomass would have been based on Mackinson and Daskalov (2007). However, a closer investigation of the south–to–total–ratio from 2003 – 2011 in IBTS catches shows that no ratio during this timeframe is below 0.5 for the respective species in this FG. The same pattern has been found in the ICES FishMap distribution of *Loligo vulgaris* (http://ices.dk/marine-data/maps/Pages/ICES-FishMap.aspx). We thus split the entire MDNS biomass upon northern and southern North Sea according the average IBTS south-to-total-ratio of squid and cuttlefish found in IBTS.

The biomass of brown shrimps (*C. crangon*) was estimated from swept-area based biomass estimates (personal communication Ingrid Tulp, IMARES, Netherlands, publication in preparation; also see the report of the ICES working group on crangon fisheries and life history (WGCRAN 2012). The biomass of *C. crangon* recruits relative to large brown shrimps is based on the population model published in Hufnagl and Temming (2011).

The biomasses for shrimps other than *C. crangon* (including *C. allmannii*) were estimated on individual species level. Each species' best estimate biomasses of Mackinson and Daskalov (2007; Table 11.8) was multiplied with a south–to–total North Sea ratio derived from the Marine Life Encyclopedia (http://www.habitas.org.uk/marinelife, accessed 20 November 2012) and the World Register of

Marine Species (http://marinespecies.org, accessed 20 November 2012): *C. allmanni* (predominantly south), *Eualus pusiolus* (equally distributed south and north), *Pandalus montagui* (south and north), *Spirontocaris lilljeborgi* (south and north), *Processa nouveli* (mainly south), *Pandalus borealis* (north) and *Pandalina* spp. (south and north). *P. nouveli* North Sea biomass was assumed 90% in the south and *P. borealis* was excluded the southern North Sea biomass pool of 'other shrimps'.

6.3.   Production and consumption

For many species, we expected minor differences in production and consumption rates between the southern and in the entire North Sea and thus adopted the parameterization of Mackinson and Daskalov (2007) and updates thereof (Mackinson et al. 2009a; Mackinson et al. 2009b; Heymans et al. 2011; WGSAM, 2011). In specific cases, however, we assumed the differences between both areas to be significant for our study, such as the productivity (P/B = Z) of cod, whiting, haddock and herring. To calculate these specifically for the southern North Sea, we used the 'decay' of abundances from SMS, which we had corrected for the southern North Sea with IBTS south-to-total ratios. We also calculated new consumption rates (C/B) for the above mentioned roundfish as the IBTS-localized SMS abundance multiplied with SMS' food ration.

Further deviating from Mackinson and Daskalov (2007), we introduced a two stanza representation of plaice and sole. Von Bertalanffy growth parameters (VBGF) and total mortalities (Z) therefore had to be found for juvenile flatfish. Flatfish juveniles' P/B = Z was calculated based on SMS abundances at the beginning of age 0 and 3. For this, we performed a designated SMS run with sole and plaice 0-group mortality from literature: Plaice 0-group mortalities came from Iles and Beverton (1991). Daily mortality rates of 0-group plaice in the Wadden Sea and Nordstrander Bay are given therein, which we averaged over years and areas to 0.01056^{-d}, translating to a total mortality of 3.857 per year. Sole 0-group mortality was excerpted from Rijnsdorp et al. (1992); Figure 11 and Table 3, as 3.0. The resulting total mortalities per stanza calculated from the modified SMS runs were then averaged for the years 1988 to '94. The results for the juvenile stanza are 1.119 for plaice and 0.775 for sole. Total mortality (Z) for adult sole and plaice was calculated the same way, based on the same SMS run. Z values here were 0.6238 for sole and 0.6727 for plaice. Detritus fate of juvenile plaice and juvenile sole was set to the standard value used for all fish groups according Mackinson and Daskalov (2007): fate to DOM 0.3 and to POM 0.7.

C. crangon commercial size class' Z was set to 6.5 (Marc Hufnagl, pers. comm.; after Hufnagl et al. 2010b). Z for juveniles was equally estimated to be 12.5. The consumption/biomass ratio for the commercial size stanza was set to 10, while the von Bertalanffy growth function K for *Crangon crangon* was found to be 1.17 by Hufnagl et al. (2010b). The asymptotic length of brown shrimp is 79.32 mm, length at 'maturity' is length at recruitment to the fishery in our case, i.e. 5 cm total length. From both, the corresponding weight can be calculated according Hufnagl et al. (2010a); section 3.1.4. The resulting $W_{maturity}$ / $W_{infinity}$ as basic input to Ecopath is 0.2411.

After the split of the Mackinson and Daskalov (2007) *turbot and brill* FG into two groups, ecological parameters, i.e. production/biomass; consumption/biomass and unassimilated consumption were taken from the whole North Sea model for both, presuming no major ecological differences between the two species. The final biomass, production and consumption estimates are summarized in Table A 2.

Table A 2: Basic estimates for the southern North Sea Ecopath model.

Group name	Biomass in habitat area (t/km²)	Z (/year)	Production / biomass or Z (/year)	Consumption / biomass (/year)	Ecotrophic efficiency	Production / consumption	Unassimil. / consumption	Detritus import (t/km²/year)
Toothed whales	0.017		0.02	17.63			0.2	0
Seals	0.008		0.09	26.842			0.2	0
Surface-feeding seabirds	0.00265		0.102	77.2794			0.22	0
Diving seabirds	0.00489		1.119	86.9717			0.22	0
Juvenile sharks	0.001		0.5	2.5			0.2	0
Spurdog			0.6	2	0.95		0.2	0
Large piscivorous sharks	0.00353543		0.48	1.6			0.2	0
Small sharks	0.00126967		0.51	2.96			0.2	0
Juvenile rays	0.268		0.66	1.7			0.2	0
Starry ray + others	0.1879332		0.66	1.7			0.2	0
Thornback & Spotted ray	0.1157612		0.78	2.3			0.2	0
Skate + cuckoo ray	0.03900189		0.35	1.8			0.2	0
Cod								
Juvenile Cod(0-2, 0-40cm)	0.2402995	1.87		9.96221			0.2	0
Cod (adult)	0.09974	1.05		4.2			0.2	0
Whiting								
Juvenile Whiting (0-1, 0-20cm)	0.1824986	2.17		8.716209			0.2	0
Whiting (adult)	0.40241	0.86		3.49			0.2	0
Haddock								
Juvenile Haddock (0-1, 0-20cm)	0.01583482	2.09		7.849507			0.2	0
Haddock (adult)	0.06307	0.8		2.68			0.2	0
Norway pout	0.9201437		2.2	5.05			0.2	0
Other gadoids (large)			1.27	3.2	0.95		0.2	0
Other gadoids (small)			2.3	6	0.95		0.2	0
Monkfish	0.02006726		0.7	1.9			0.2	0
Gurnards	0.2700875		0.82	3.2			0.2	0
Herring								
Herring (juvenile 0, 1)	0.3101863	2.6		11.69178			0.2	0
Herring (adult)	1.500582	0.94		4.34			0.2	0
Sprat	1.05969		2.28	6			0.2	0
Mackerel	0.5371138		0.6	1.73			0.2	0
Horse mackerel	1.41666		1.2	3.51			0.2	0
Sandeels	5.56484		2.28	10.1			0.2	0
Plaice								
Plaice (adult)	0.8505849	0.6727		3.42			0.2	0
Juvenile Plaice	0.5896387	1.119		7.224079			0.2	0
Dab	4.717529		0.672	3.36			0.2	0
Long-rough dab	0.4214635		0.7	3.4			0.2	0
Flounder	0.441929		1.1	3.2			0.2	0
Sole								
Sole (adult)	0.2256105	0.6238		3.1			0.2	0
Juvenile Sole	0.08317135	0.775		6.134347			0.2	0
Lemon sole	0.2017155		0.864	4.32			0.2	0
Witch	0.02899392		0.9	3			0.2	0
Turbot	0.04441785		0.86	2.3			0.2	0
Brill	0.00987063		0.86	2.3			0.2	0
Megrim	0.00550982		0.72	3.1			0.2	0
Halibut	0.01666703		0.16	3.14			0.2	0
Dragonets	0.07246806		1.6	6			0.2	0
Large demersal fish			0.55	2.54	0.9		0.2	0
Small demersal fish			1.42	3.7	0.98		0.2	0

Miscellaneous filterfeeding pelagic fish			4	10.19	0.98		0.2	0
Squid & cuttlefish	0.1119071		11.025	20			0.2	0
Fish larvae			4	20	0.99		0.2	0
Carnivorous zooplankton			4		0.99	0.32	0.2	0
Herbivorous & Omnivorous zooplankton (copepods)	16		9.2	30			0.38	0
Gelatinous zooplankton	0.09120453		2.858			0.45	0.2	0
Large crabs	2.3018		1.052748			0.2	0.2	0
Nephrops	0.174593		0.6			0.2	0.2	0
Epifaunal macrobenthos (mobile grazers)	78		0.3883938			0.2	0.2	0
Infaunal macrobenthos	136		1			0.3	0.2	0
C. crangon								
Crangon (commercial size)	0.03438	6.5		10		0.3	0.2	0
Crangon (below 5cm)	0.05543824	12.5		25.14523			0.2	0
Shrimp	0.2210504		6.5			0.3	0.2	0
Small mobile epifauna (swarming crustaceans)	30		1.9			0.35	0.2	0
Small infauna (polychaetes)	150		0.9			0.3	0.2	0
Sessile epifauna	105		0.26			0.2	0.2	0
Meiofauna			35	125	0.99		0.2	0
Benthic microflora (incl. Bacteria, protozoa)	0.105		9550			0.5	0.3	0
Planktonic microflora (incl. Bacteria, protozoa)	1.46		571			0.5	0.3	0
Phytoplankton	7.5		286.6667				0	0
Detritus - DOM - water column	25						0.2	0
Detritus - POM - sediment	25						0.2	0
Discards	0.0001				0		0	0

6.4. Diet composition

For many functional groups we did not assume a regional difference to the type and amount of prey consumed in Mackinson and Daskalov (2007) and updates thereof. For cod, whiting, haddock, horse mackerel, gurnards, large demersal fish and starry rays, however, we used the ICES stomach sampling project 1991 database (http://www.ices.dk/marine-data/data-portals/Pages/Fish–stomach.aspx, data downloaded 8 January 2013; see also Hislop et al. 1997) to derive diet compositions specifically for our model area. From these data, we first calculated the mean weight of each prey species in the stomachs of each predator/length class combination. These prey weights were then subsequently averaged over haul; ICES statistical rectangle; the entire southern North Sea (ICES divisions IVb and c) using the CPUE of the predator in each ICES rectangle as weighting factors. We then assigned the prey taxa to functional groups (and stanzas for multi stanza groups) to be implemented in EwE, based on prey species and length classes (a list of more than 600 entries we are willing to share on demand and that is, for invertebrate taxa, graphically represented in Figure A 5). We subsequently averaged prey FG weights in diets over predator FG and finally predator length class. Next, we created annual averages, using the predators' quarterly consumption rates from SMS as weighting factors. Finally, we identified the proportions of each respective prey FGs in each predator FG's diet.

After separating MDNS' single *turbot and brill* functional group into two separate FGs, diet composition as predator was copied, i.e. both species feed on the same prey. The role of both species as prey themselves was estimated by multiplying the respective species' contribution to the original *turbot and brill* biomass (in 1991, the CPUE of turbot in the ICES beam trawl survey was 4.5 times higher than that of brill) with the original share in the diet of each predator, which in this case was seals only. The parameterization of the diets of small and commercial size *C. crangon* relies on data synthesized from del Norte-Campos (1995). Results have been validated through comparison with an assessment of brown shrimps' feeding ecology by Oh et al. (2001) from the Isle of Man, in particular to underpin the role of small *C. crangon* as a predator of plaice recruits. Diet of sole follows Rijnsdorp and Vingerhoed (2001), who investigated the diet of North Sea sole in 1996 by age class. Plaice diet comes from Schückel et al. (2012)**.** The final diet matrix with the proportions of each prey eaten by each predator is shown in Table A 3.
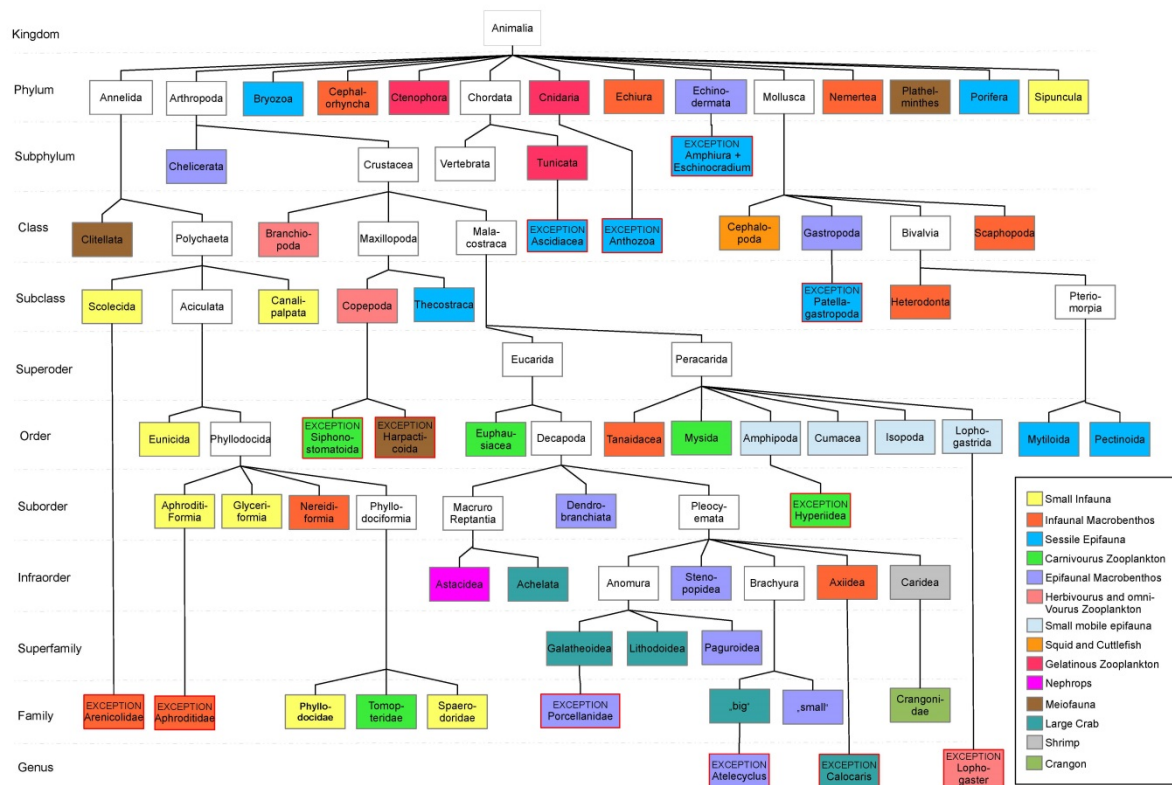
Figure A 5: Taxonomic scheme of assignment of non-vertebrate species to functional groups (adapted from Keth 2014).

Table A 3: Diet matrix with the proportion of each prey (vertical) in each predator's (horizontal) diet.

Prey \ predator	Toothed whales	Seals	Surface-feeding seabirds	Diving seabirds	Juvenile sharks	Spurdog	Large piscivorous sharks	Small sharks	Juvenile rays	Starry ray + others	Thornback & Spotted ray	Skate + cuckoo ray	Juvenile Cod(0-2. 0-40cm)	Cod (adult)
Toothed whales														
Seals														
Surface-feeding seabirds														
Diving seabirds														
Juvenile sharks							0.062288							
Spurdog						0.021511	0.010364							
Large piscivorous sharks														
Small sharks							0.025962							
Juvenile rays							0.062288							
Starry ray + others														0.000030
Thornback & Spotted ray														0.000947
Skate + cuckoo ray														
Juvenile Cod	0.026952	0.033165	0.005230	0.002300					0.002000	0.020591			0.005738	0.008674
Cod (adult)		0.066750												0.008407
Juvenile Whiting	0.022406	0.004513	0.012873	0.017996	0.000401	0.002528		0.000108		0.012439	0.001610	0.001445	0.016187	0.047625
Whiting (adult)	0.068949	0.072313			0.019269	0.121428		0.006372		0.012416				0.076867
Juvenile Haddock	0.001515	0.000315	0.005632	0.000700		0.000260					0.000101	0.000269	0.002182	0.003571
Haddock (adult)	0.004005	0.012384				0.006238								0.008022
Norway pout	0.242243		0.012873	0.000200	0.073364	0.101100	0.103951	0.022789	0.010600	0.065539	0.001408	0.054860	0.057892	0.044879
Other gadoids (large)	0.015695	0.073152	0.002213	0.001200										
Other gadoids (small)	0.051198	0.029177		0.000500	0.002609	0.134657	0.010056	0.011124	0.015000	0.036143	0.032895	0.066960	0.026934	0.023560

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Monkfish		0.010915										0.000940		
Gurnards				0.000100			0.050077	0.000432		0.008550		0.002819	0.000381	0.002984
Herring (juvenile)	0.001191	0.000009			0.000502	0.001807	0.000924			0.005237	0.003219	0.013627	0.004310	0.014897
Herring (adult)	0.003572	0.006402	0.046665	0.058988	0.062826	0.191445	0.104464	0.005832		0.036070			0.002974	0.139689
Sprat	0.113003	0.002939	0.042843	0.054389	0.023183	0.041731		0.014904	0.000100	0.000267	0.019315		0.017227	0.009721
Mackerel	0.021215		0.005833	0.020096	0.013750	0.083676	0.158235	0.005076						0.000044
Horse mackerel	0.013314	0.013014				0.019790							0.000775	0.002638
Sandeels	0.295606	0.316223	0.201945	0.332533	0.014452	0.039472		0.011988	0.395900	0.258164	0.036517	0.391185	0.099143	0.042154
Plaice (adult)		0.064546				0.048507	0.063212	0.002160			0.009255			0.004087
Juvenile Plaice			0.002615	0.000300									0.000016	0.033223
Dab		0.051847		0.000100	0.006724	0.006991	0.063212	0.006372	0.002900	0.031066		0.002937	0.003301	0.191662
Long-rough dab	0.000071	0.011125						0.002268	0.001200	0.072058		0.001880	0.008629	0.058004
Flounder		0.011965												0.002808
Sole (adult)		0.038518						0.002160			0.004527	0.027959		
Juvenile Sole			0.000201							0.003287			0.001731	0.003077
Lemon sole		0.025189												
Witch		0.013119				0.006991				0.003874		0.000940		0.000914
Turbot		0.009102												
Brill		0.002023												
Megrim		0.011545												
Halibut										0.001234				
Dragonets	0.000108	0.011125			0.001004	0.027534	0.055721	0.017929		0.024920		0.080704	0.009941	0.013881
Large demersal fish			0.013879	0.000100								0.001762	0.001609	0.000018
Small demersal fish	0.000325	0.108626	0.002514	0.000800	0.010036	0.010863	0.011083	0.002700	0.000900	0.028554	0.070015	0.012570	0.038908	0.014888
Misc. filterfeeding fish			0.002514		0.003713			0.004428					0.000107	0.000049
Squid & cuttlefish	0.118632		0.003721	0.000100	0.012344	0.023662	0.210570	0.028081	0.000500	0.002384	0.005030	0.009280	0.005667	0.009465
Fish larvae														
Carnivorous zooplankton			0.014080	0.000100	0.019972	0.005700		0.001296	0.008200	0.000058	0.001610	0.003994	0.020847	0.000698

Copepods			0.005129	0.000600						0.000002			0.000006	
Gelatinous zooplankton					0.026997	0.038397							0.001653	0.000884
Large crabs			0.029165	0.010398	0.028202	0.014305		0.123340	0.096000	0.077426	0.384983	0.064023	0.099990	0.090646
Nephrops					0.007427	0.010970		0.020305				0.001762	0.007212	0.001961
Epifaunal macrobenthos			0.000101		0.335307	0.009572	0.007594	0.327573	0.065700	0.161386	0.206827	0.021498	0.182008	0.089075
Infaunal macrobenthos			0.015488	0.359328	0.059916	0.008497		0.196566	0.003200	0.012090	0.002012	0.000705	0.076116	0.033054
Crangon (commercial size)					0.007408	0.001962		0.003777	0.004971	0.004619	0.010532	0.009338	0.036520	0.003040
Crangon (below 5cm)			0.002615		0.019372	0.005130		0.009877	0.013000	0.012078	0.027541	0.024418	0.115985	0.008330
Shrimp			0.009252		0.051601	0.013666		0.026308	0.034628	0.032172	0.073358	0.065040	0.045037	0.004528
Small mobile epifauna					0.069350			0.044605	0.239400	0.010975	0.097076	0.086460	0.004096	0.000022
Small infauna (polychaetes)			0.005029	0.000500	0.121136	0.001613		0.081326	0.101600	0.066402	0.012172	0.052628	0.106738	0.000748
Sessile epifauna			0.023131	0.106579	0.008631			0.009396					0.000137	0.000230
Meiofauna					0.000502			0.010908	0.004200					
Benthic microflora														
Planktonic microflora														
Phytoplankton														
Detritus - DOM -water column														
Detritus - POM - sediment														
Discards			0.469060	0.032094										
Import			0.065400											

Table A3 (continued): Diet matrix with the proportion of each prey (vertical) in each predator's (horizontal) diet.

Prey \ predator	Juvenile Whiting (0-1. 0-20cm)	Whiting (adult)	Juvenile Haddock (0-1. 0-20cm)	Haddock (adult)	Norway pout	Other gadoids (large)	Other gadoids (small)	Monkfish	Gurnards	Herring (juvenile 0. 1)	Herring (adult)	Sprat	Mackerel	Horse mackerel
Toothed whales														
Seals														
Surface-feeding seabirds														
Diving seabirds														
Juvenile sharks														
Spurdog														
Large piscivorous sharks														
Small sharks														
Juvenile rays								0.007686						
Starry ray + others														
Thornback & Spotted ray									0.000030					
Skate + cuckoo ray														
Juvenile Cod	0.002078	0.001006		0.000001		0.029301		0.011630	0.019988				0.001975	
Cod (adult)								0.011630						
Juvenile Whiting	0.000883	0.017474				0.004937	0.000299	0.009911	0.058188				0.000057	0.032996
Whiting (adult)		0.000121						0.118426						
Juvenile Haddock	0.000066	0.000390		0.006136		0.000215		0.002832	0.001489				0.000028	0.000326
Haddock (adult)								0.066646						
Norway pout	0.066537	0.087043		0.126104		0.118708	0.000399	0.133596	0.026781				0.004356	0.002554
Other gadoids (large)						0.028121								

Other gadoids (small)		0.006856		0.002322		0.015563	0.016901		0.058729				0.000394	0.004238
Monkfish								0.003742						
Gurnards	0.000002	0.000213		0.000343					0.000249					0.000127
Herring (juvenile)	0.002245	0.026287		0.000001		0.031877		0.010012	0.001306				0.012691	0.129362
Herring (adult)						0.167543		0.120348						
Sprat	0.013126	0.264368		0.000059			0.003890	0.003742	0.033561				0.029038	0.032249
Mackerel								0.068770	0.001178				0.000008	
Horse mackerel	0.001410	0.008951							0.000154				0.101458	0.083575
Sandeels	0.148481	0.295477	0.139364	0.207233		0.410218	0.000998	0.171926	0.378116				0.119033	0.019858
Plaice (adult)								0.003742						
Juvenile Plaice				0.000845										
Dab	0.000642	0.000108					0.004990	0.030542	0.008826					0.006013
Long-rough dab	0.014634	0.004315	0.001378	0.001816		0.018139		0.045712	0.013631					0.006536
Flounder														
Sole (adult)														
Juvenile Sole	0.001126	0.000483	0.000103	0.000002										
Lemon sole	0.000003							0.011428						
Witch	0.000134							0.003742	0.000074					
Turbot														
Brill														
Megrim								0.003742						
Halibut													0.000001	
Dragonets	0.004777	0.001252	0.000012	0.000021			0.004990	0.003742	0.024533					0.000408
Large demersal fish		0.000320							0.000570				0.000063	
Small demersal fish	0.051138	0.017950	0.000051	0.000091		0.007513	0.013801	0.041970	0.033311				0.001447	0.070340
Misc. filterfeeding fish	0.000453	0.000016						0.003742						
Squid & cuttlefish	0.076864	0.008704	0.000112	0.020022		0.054524	0.000798	0.091626	0.018422				0.008063	0.112658
Fish larvae														

Carnivorous zooplankton	0.121029	0.044069	0.398505	0.170337	0.285700	0.011914	0.100304		0.063621	0.273300	0.309300		0.065703	0.168136
Copepods	0.006020	0.002797	0.019982	0.003219	0.476200	0.021359	0.299611		0.000046	0.674800	0.670100	0.800000	0.482685	0.058322
Gelatinous zooplankton	0.004202	0.003670	0.017255	0.011040									0.084537	0.000084
Large crabs	0.083024	0.022258	0.007652	0.009529		0.012343	0.016401		0.085834				0.021815	0.053445
Nephrops		0.001804	0.000130	0.002008			0.039902	0.007686	0.000477				0.000000	
Epifaunal macrobenthos	0.073272	0.081478	0.189640	0.180073			0.129705	0.011428	0.014434				0.024840	0.171009
Infaunal macrobenthos	0.023884	0.037183	0.060044	0.105625	0.190500		0.169706		0.003706				0.000211	0.000866
Crangon (commercial size)	0.016009	0.002907				0.004311	0.000094		0.000391					0.000949
Crangon (below 5cm)	0.068707	0.013710	0.000367	0.000453		0.011274	0.000247		0.005067				0.000393	0.002215
Shrimp	0.039343	0.017524	0.023346	0.017456		0.030030	0.000657		0.119219				0.000883	0.016873
Small mobile epifauna	0.012429	0.001950	0.019349	0.009104	0.047600	0.009230	0.027501		0.022326	0.051900	0.020600		0.009034	0.019153
Small infauna (polychaetes)	0.166430	0.029199	0.121231	0.108915		0.012880	0.168806		0.005724				0.003340	0.007709
Sessile epifauna	0.000044	0.000091	0.000405	0.015799					0.000018				0.005952	
Meiofauna	0.000003		0.001067	0.001444									0.000001	
Benthic microflora			0.000008	0.000002									0.000008	
Planktonic microflora												0.100000		
Phytoplankton		0.000023										0.100000	0.021989	
DOM -water column														
POM - sediment														
Discards														
Import														

Table A3 (continued): Diet matrix with the proportion of each prey (vertical) in each predator's (horizontal) diet.

Prey \ predator	Sandeels	Plaice (adult)	Juvenile Plaice	Dab	Long-rough dab	Flounder	Sole (adult)	Juvenile Sole	Lemon sole	Witch	Turbot	Brill	Megrim	Halibut
Toothed whales														
Seals														
Surface-feeding seabirds														
Diving seabirds														
Juvenile sharks														
Spurdog														
Large piscivorous sharks														
Small sharks														
Juvenile rays														
Starry ray + others														
Thornback & Spotted ray														
Skate + cuckoo ray														
Juvenile Cod											0.061555	0.061555		0.010500
Cod (adult)														
Juvenile Whiting					0.000400						0.012076	0.012076		0.050954
Whiting (adult)														
Juvenile Haddock														0.010000
Haddock (adult)														
Norway pout					0.005399	0.050120					0.122041	0.122041	0.253277	0.203411
Other gadoids (large)														
Other gadoids (small)					0.026597						0.036334	0.036334	0.240169	0.030248
Monkfish														
Gurnards													0.006554	

Herring (juvenile)		0.000203								0.001496	0.001496		
Herring (adult)													
Sprat										0.182848	0.182848	0.356977	0.101706
Mackerel													
Horse mackerel													
Sandeels		0.007627			0.023298					0.194069	0.194069	0.019450	0.407025
Plaice (adult)													
Juvenile Plaice													
Dab					0.037896	0.069028				0.073738	0.073738		
Long-rough dab						0.050120							
Flounder													
Sole (adult)													
Juvenile Sole													
Lemon sole						0.050120							
Witch													
Turbot													
Brill													
Megrim													
Halibut													
Dragonets										0.007641	0.007641	0.032452	
Large demersal fish													
Small demersal fish					0.037596	0.011505	0.012800	0.006800	0.008200	0.121293	0.121293	0.006554	
Misc. filterfeeding fish												0.025899	
Squid & cuttlefish					0.003000								0.081608
Fish larvae													
Carnivorous zooplankton	0.063100					0.058777							
Copepods	0.610400			0.012500								0.002960	
Gelatinous zooplankton		0.003458				0.081217							

Large crabs		0.016170	0.108299	0.010000	0.042596	0.055701		0.054422					0.029281	0.099676
Nephrops					0.013899									
Epifaunal macrobenthos	0.000800	0.104951	0.021278	0.258200	0.210479	0.255154	0.012800	0.011102	0.041100	0.247300	0.072776	0.072776	0.002960	0.003654
Infaunal macrobenthos	0.005600	0.174715	0.436462	0.239700	0.272073	0.081217	0.115400	0.012708	0.099300	0.034900	0.060593	0.060593		
Crangon (commercial size)		0.000010	0.001518	0.000095	0.003837	0.000711					0.005060	0.005060	0.002078	0.000115
Crangon (below 5cm)		0.000059	0.008604	0.000247	0.010033	0.001858					0.013233	0.013233	0.005434	0.000301
Shrimp		0.000758	0.000556	0.000658	0.026726	0.004949					0.035247	0.035247	0.014475	0.000802
Small mobile epifauna	0.015500	0.196479	0.051271	0.328800	0.003300	0.173824							0.001480	
Small infauna (polychaetes)	0.187500	0.477874	0.361665	0.137900	0.282872		0.423100	0.921769	0.657600	0.685200				
Sessile epifauna		0.014238		0.011000		0.055701			0.195200	0.024400				
Meiofauna	0.047800	0.003458	0.010346	0.000900			0.435900							
Benthic microflora														
Planktonic microflora	0.047600													
Phytoplankton	0.021700													
Detritus - DOM -water column														
Detritus - POM - sediment														
Discards														
Import														

Table A3 (continued): Diet matrix with the proportion of each prey (vertical) in each predator's (horizontal) diet.

Prey \ predator	Dragonets	Large demersal fish	Small demersal fish	Miscellaneous filterfeeding pelagic fish	Squid & cuttlefish	Fish larvae	Carnivorous zooplankton	Herbivorous & Omnivorous zooplankton (copepods)	Gelatinous zooplankton	Large crabs	Nephrops	Epifaunal macrobenthos (mobile grazers)	Infaunal macrobenthos	Crangon (commercial size)
Toothed whales														
Seals														
Surface-feeding seabirds														
Diving seabirds														
Juvenile sharks														
Spurdog														
Large piscivorous sharks														
Small sharks														
Juvenile rays														
Starry ray + others														
Thornback & Spotted ray														
Skate + cuckoo ray														
Juvenile Cod					0.010962									
Cod (adult)														
Juvenile Whiting		0.011944			0.000922									
Whiting (adult)		0.020387												
Juvenile Haddock		0.003588			0.000410									
Haddock (adult)		0.009563												

Norway pout		0.021365			0.010860											
Other gadoids (large)																
Other gadoids (small)		0.033109														
Monkfish																
Gurnards			0.010149													
Herring (juvenile)		0.247965	0.000033		0.000922											
Herring (adult)		0.220117														
Sprat			0.001306		0.010962											
Mackerel																
Horse mackerel					0.010962											
Sandeels		0.011304	0.330298		0.043746											
Plaice (adult)					0.005532											
Juvenile Plaice																0.000452
Dab		0.070273	0.037280		0.005532											
Long-rough dab					0.005532											
Flounder					0.005532											0.001622
Sole (adult)			0.000502		0.005532											
Juvenile Sole																
Lemon sole					0.005532											
Witch					0.002766											
Turbot																
Brill																
Megrim																
Halibut																
Dragonets			0.000533													
Large demersal fish																
Small demersal fish			0.036677		0.005532											0.005073
Misc. filterfeeding fish				0.053100	0.021719											

Squid & cuttlefish		0.001305	0.025624	0.005600	0.054605				0.049800					
Fish larvae					0.010552		0.024500		0.224000					
Carnivorous zooplankton		0.040056	0.000201	0.148900	0.223645		0.050900		0.198900					
Copepods	0.004574		0.091543	0.694900	0.296179	0.800000	0.722300		0.198900					0.002876
Gelatinous zooplankton				0.033200										
Large crabs	0.008131		0.049741							0.001090				0.009901
Nephrops														
Epifaunal macrobenthos	0.094014	0.303068	0.134551	0.026600						0.311547		0.050000		0.003690
Infaunal macrobenthos	0.139750		0.060493							0.318344	0.250000	0.200000		0.000434
Crangon (commercial size)	0.006186	0.000001	0.001909	0.001361	0.002004				0.004707	0.000103				
Crangon (below 5cm)	0.016177	0.000002	0.004992	0.003559	0.005241				0.012308	0.000269				0.041408
Shrimp	0.043090	0.000005	0.013297	0.009480	0.013961				0.032785	0.000717				0.002164
Small mobile epifauna	0.224108	0.005554	0.132039	0.012200	0.164532		0.100500		0.079600	0.021360	0.150000	0.050000	0.020408	0.082893
Small infauna (polychaetes)	0.446184	0.000393	0.039491	0.011100	0.021719					0.112515	0.200000	0.250000	0.112245	0.385550
Sessile epifauna										0.076053	0.100000			0.021914
Meiofauna	0.017786		0.029342										0.051020	0.442024
Benthic microflora										0.053399	0.100000	0.100000	0.306123	
Planktonic microflora							0.101800	0.050000	0.099500	0.053399	0.050000	0.100000	0.102041	
Phytoplankton					0.054605	0.200000		0.900000	0.099500		0.100000	0.050000		
Detritus - DOM -water column									0.050000		0.030000	0.050000	0.102041	
Detritus - POM - sediment											0.020000	0.150000	0.306123	
Discards										0.051205				
Import														

Prey \ predator	Crangon (below 5cm)	Shrimp	Small mobile epifauna (swarming crustaceans)	Small infauna (polychaetes)	Sessile epifauna	Meiofauna	Benthic microflora (incl. Bacteria. protozoa)	Planktonic microflora (incl. Bacteria. protozoa)
Toothed whales								
Seals								
Surface-feeding seabirds								
Diving seabirds								
Juvenile sharks								
Spurdog								
Large piscivorous sharks								
Small sharks								
Juvenile rays								
Starry ray + others								
Thornback & Spotted ray								
Skate + cuckoo ray								
Juvenile Cod								
Cod (adult)								
Juvenile Whiting								
Whiting (adult)								
Juvenile Haddock								
Haddock (adult)								
Norway pout								
Other gadoids (large)								
Other gadoids (small)								
Monkfish								
Gurnards								
Herring (juvenile)								
Herring (adult)								
Sprat								
Mackerel								
Horse mackerel								
Sandeels								
Plaice (adult)								
Juvenile Plaice								
Dab								
Long-rough dab								
Flounder								

Sole (adult)								
Juvenile Sole								
Lemon sole								
Witch								
Turbot								
Brill								
Megrim								
Halibut								
Dragonets								
Large demersal fish								
Small demersal fish								
Misc. filterfeeding fish								
Squid & cuttlefish								
Fish larvae								
Carnivorous zooplankton		0.051578						
Copepods		0.103157						
Gelatinous zooplankton								
Large crabs								
Nephrops								
Epifaunal macrobenthos								
Infaunal macrobenthos								
Crangon (> 5cm)		0.000975						
Crangon (< 5cm)	0.004313	0.002550						
Shrimp		0.006791						
Small mobile epifauna		0.051578	0.100000					
Small infauna (polychaetes)		0.103157		0.050000				
Sessile epifauna								
Meiofauna	0.995687	0.103157	0.150000	0.150000		0.050000		
Benthic microflora		0.154735	0.200000	0.400000		0.750000	0.100000	0.020000
Planktonic microflora		0.123788	0.150000	0.050000	0.700000		0.100000	0.100000
Phytoplankton					0.100000			
Detritus - DOM -water column		0.103157	0.100000	0.150000			0.200000	0.650000
Detritus - POM - sediment		0.175366	0.300000	0.200000	0.200000	0.200000	0.600000	0.230000
Discards		0.020012						
Import								

7. Appendix B

This appendix outlines the parameterization of landings and discards for the Ecopath model.

7.1. Calculation of landings

The standard procedure of landings calculation was to first assign landings recorded by the Scientific, Technical and Economic Committee for Fisheries (STECF; Rätz and Mitrakis, 2012) to our EwE fleets based on gear and mesh size as depicted in Table B 1. We examined how many tonnes (mean 2009–'11) of each species were landed by the fleets of each country; then, country by country, calculated each fleets share of the species' total catches.

We multiplied the EUROSTAT data from divisions IVb and IVc of year 1991, of each species, with the estimated proportions for each fleet. Then, we assigned the landings of species to functional groups and aggregated them over FGs to finally create landings per FG per fleet by aggregating over countries. As outline in materials and methods, Section 2.2, our goal was to achieve a distribution of catches on the fleets that corresponds to the state in 2010, while the total amount of catches is from 1991 in the Ecopath version of our model. *C. crangon* landings come from data supplementing Temming and Hufnagl (2014). The landings of each functional group per fleet are summarized in Table B 2.

Table B 1: How EwE fleets were assigned to gear/mesh size combinations from STECF landings data (Rätz and Mitrakis, 2012).

Gear	Mesh size range	EwE Fleet	Gear	Mesh size range	EwE Fleet
BEAM	<16	Shrimp trawlers	OTTER	>= 105	Demersal trawl + dem seine
BEAM	>=105	Beam trawl	OTTER	>=105	Demersal trawl + dem seine
BEAM	>=120	Beam trawl	OTTER	>=120	Demersal trawl + dem seine
BEAM	100–119	Beam trawl	OTTER	100–104	Demersal trawl + dem seine
BEAM	16–31	Shrimp trawlers	OTTER	100–119	Demersal trawl + dem seine
BEAM	32–54	Beam trawl	OTTER	16–31	Sandeel trawl
BEAM	55–69	Beam trawl	OTTER	32–54	Pelagic trawl
BEAM	70–79	Beam trawl	OTTER	55–69	Pelagic trawl
BEAM	80–89	Beam trawl	OTTER	70–79	Nephrops trawl
BEAM	90–99	Beam trawl	OTTER	80–89	Nephrops trawl
BEAM	NONE	Beam trawl	OTTER	90–99	Nephrops trawl
BEAM	none	Shrimp trawlers	OTTER	NONE	Demersal trawl + dem seine
DEM_SEINE	<16	Demersal trawl + dem seine	OTTER	none	Demersal trawl + dem seine
DEM_SEINE	>=105	Demersal trawl + dem seine	PASSIVE	NONE	Drift and fixed nets
DEM_SEINE	>=120	Demersal trawl + dem seine	PEL_SEINE	<16	Pelagic trawl
DEM_SEINE	100–119	Demersal trawl + dem seine	PEL_SEINE	>=120	Pelagic trawl
DEM_SEINE	16–31	Demersal trawl + dem seine	PEL_SEINE	100–119	Pelagic trawl
DEM_SEINE	32–54	Demersal trawl + dem seine	PEL_SEINE	16–31	Pelagic trawl
DEM_SEINE	55–69	Demersal trawl + dem seine	PEL_SEINE	32–54	Pelagic trawl
DEM_SEINE	70–79	Demersal trawl + dem seine	PEL_SEINE	55–69	Pelagic trawl
DEM_SEINE	80–89	Demersal trawl + dem seine	PEL_SEINE	70–79	Pelagic trawl
DEM_SEINE	90–99	Demersal trawl + dem seine	PEL_SEINE	80–89	Pelagic trawl

DEM_SEINE	NONE	Demersal trawl + dem seine	**PEL_SEINE**	90–99	Pelagic trawl
DEM_SEINE	none	Demersal trawl + dem seine	**PEL_SEINE**	NONE	Pelagic trawl
DREDGE	<16	Dredges	**PEL_SEINE**	none	Pelagic trawl
DREDGE	>=120	Dredges	**PEL_TRAWL**	<16	Sandeel trawl
DREDGE	100–119	Dredges	**PEL_TRAWL**	>= 105	Pelagic trawl
DREDGE	16–31	Dredges	**PEL_TRAWL**	>=105	Pelagic trawl
DREDGE	32–54	Dredges	**PEL_TRAWL**	>=120	Demersal trawl + dem seine
DREDGE	55–69	Dredges	**PEL_TRAWL**	100–119	Demersal trawl + dem seine
DREDGE	70–79	Dredges	**PEL_TRAWL**	16–31	Sandeel trawl
DREDGE	80–89	Dredges	**PEL_TRAWL**	32–54	Pelagic trawl
DREDGE	90–99	Dredges	**PEL_TRAWL**	55–69	Pelagic trawl
DREDGE	NONE	Dredges	**PEL_TRAWL**	70–79	Pelagic trawl
DREDGE	none	Dredges	**PEL_TRAWL**	80–89	Pelagic trawl
GILL	10 –30	Drift and fixed nets	**PEL_TRAWL**	90–99	Sandeel trawl
GILL	>=220	Drift and fixed nets	**PEL_TRAWL**	none	Pelagic trawl
GILL	100–109	Drift and fixed nets	**PEL_TRAWL**	NONE	Pelagic trawl
GILL	110–149	Drift and fixed nets	**POTS**	10 –30	Pots
GILL	110–156	Drift and fixed nets	**POTS**	>=220	Pots
GILL	150–219	Drift and fixed nets	**POTS**	100–109	Pots
GILL	157–219	Drift and fixed nets	**POTS**	110–149	Pots
GILL	31–49	Drift and fixed nets	**POTS**	110–156	Pots
GILL	50–59	Drift and fixed nets	**POTS**	150–219	Pots
GILL	60–69	Drift and fixed nets	**POTS**	157–219	Pots
GILL	70–79	Drift and fixed nets	**POTS**	31–49	Pots
GILL	80–89	Drift and fixed nets	**POTS**	50–59	Pots
GILL	90–99	Drift and fixed nets	**POTS**	60–69	Pots
GILL	NONE	Drift and fixed nets	**POTS**	70–79	Pots
GILL	none	Drift and fixed nets	**POTS**	80–89	Pots
LONGLINE	31–49	Gears using hooks	**POTS**	90–99	Pots
LONGLINE	NONE	Gears using hooks	**POTS**	NONE	Pots
LONGLINE	none	Gears using hooks	**POTS**	none	Pots
LONGLINE		Gears using hooks	**TRAMMEL**	10 –30	Drift and fixed nets
MIS	10–30	Other	**TRAMMEL**	>=220	Drift and fixed nets
MIS	100–109	Other	**TRAMMEL**	100–109	Drift and fixed nets
MIS	110–156	Other	**TRAMMEL**	110–149	Drift and fixed nets
MIS	31–49	Other	**TRAMMEL**	110–156	Drift and fixed nets
MIS	50–59	Other	**TRAMMEL**	150–219	Drift and fixed nets
MIS	60–69	Other	**TRAMMEL**	157–219	Drift and fixed nets
MIS	none	Other	**TRAMMEL**	31–49	Drift and fixed nets
MOBILE	NONE	Other	**TRAMMEL**	50–59	Drift and fixed nets
NONE	110–149	Other	**TRAMMEL**	60–69	Drift and fixed nets
NONE	NONE	Other	**TRAMMEL**	70–79	Drift and fixed nets
None	none	Other	**TRAMMEL**	80–89	Drift and fixed nets
OTTER	<16	Sandeel trawl	**TRAMMEL**	90–99	Drift and fixed nets

*Table B 2: Ecopath landings per functional group and fleet in t/(km² * year)*

Group name	Demersal trawl + dem seine	Beam trawl	Sandeel trawl	Pelagic trawl	Drift and fixed nets
Toothed whales	0	0	0	0	0
Seals	0	0	0	0	0
Surface-feeding seabirds	0	0	0	0	0
Diving seabirds	0	0	0	0	0
Juvenile sharks	0	0	0	0	0
Spurdog	0.00733025	0.00025826	0	1.56E-06	0.00040737
Large piscivorous sharks	0.00018933	1.962E-07	7.60E-05	0	8.80E-05
Small sharks	7.10E-05	0	1.80E-05	0	0.00014831
Juvenile rays	0	0	0	0	0
Starry ray + others	7.66E-05	2.0603E-06	0	3.34E-08	3.98E-07
Thornback & Spotted ray	0.00173921	0.0043136	0	0	0.00096969
Skate + cuckoo ray	1.60E-06	0.00000103	0	5.56E-10	1.40E-07
Cod		0			
Juvenile Cod(0-2, 0-40cm)	0.06078459	0.00532088	0.0001681	2.73E-05	0.00579013
Cod (adult)	0.06353226	0.0055614	0.0001757	2.85E-05	0.00605187
Whiting		0			
Juvenile Whiting (0-1, 0-20cm)	0.00180948	0.00018256	4.60E-05	2.48E-06	2.24E-06
Whiting (adult)	0.03836923	0.00387108	0.00097548	5.27E-05	4.74E-05
Haddock		0			
Juvenile Haddock (0-1, 0-20cm)	0.00434357	1.97E-05	4.90E-05	2.73E-06	3.83E-06
Haddock (adult)	0.02900549	0.0001317	0.0003276	1.82E-05	2.56E-05
Norway pout	0	0	0.02109128	0.00050616	0
Other gadoids (large)	0.00619921	9.9478E-05	2.33E-07	1.60E-05	0.0002138
Other gadoids (small)	8.17E-05	0	0.00013792	7.16E-06	0.00188655
Monkfish	0.00567181	0.00081432	4.13E-07	3.38E-06	0.00014608
Gurnards	0.00243007	0.02280505	0	0.01296818	0.00023519
Herring		0			
Herring (juvenile 0, 1)	0	0	0.03801128	0	0
Herring (adult)	0.01746235	1.0061E-08	0.02147632	0.2747729	0.00011626
Sprat	0.0012109	1.8657E-08	0.2420506	0.00893896	3.28E-05
Mackerel	0.01232881	7.1532E-08	6.95E-06	0.00068235	9.01E-07
Horse mackerel	0.00413948	2.5621E-05	0.04711566	0.05471746	1.80E-06
Sandeels	0	0	2.593822	0	1.50E-08
Plaice		0			
Plaice (adult)	0.1613202	0.1806872	0.00046438	2.47E-05	0.00726869
Juvenile Plaice	0.01456845	0.01631743	4.20E-05	2.23E-06	0.00065642
Dab	0.00877106	0.0045756	0.00090725	6.17E-06	0.0002849
Long-rough dab	1.80E-06	0	2.69E-06	6.45E-08	4.46E-07
Flounder	0.00179868	0.00623135	3.35E-08	6.42E-08	0.00099571
Sole		0			
Sole (adult)	0.0005638	0.06633188	1.98E-06	1.97E-06	0.00468242
Juvenile Sole	4.39E-05	0.0051659	1.54E-07	1.53E-07	0.00036467
Lemon sole	0.00868474	0.00367186	0	2.97E-05	9.99E-05
Witch	0.00109473	1.4103E-06	4.33E-06	1.01E-06	1.85E-06
Turbot	0.00622125	0.01034193	0	0	0
Brill	0.00035675	0.00396737	0	0	0
Megrim	1.00E-04	3.8318E-06	2.90E-10	2.95E-09	4.91E-08
Halibut	0.00012942	3.2614E-07	1.70E-08	3.11E-07	2.23E-06
Dragonets	0	0	0	0	0
Large demersal fish	0.01141893	0.00026332	1.75E-05	4.05E-05	0.00034688
Small demersal fish	0.00171581	0.00217521	5.94E-08	3.79E-06	0.00034929
Miscellaneous filterfeeding pelagic fish	0.00047002	1.1007E-06	0	0.01614474	0
Squid & cuttlefish	0.00095572	9.9139E-06	0	3.15E-06	2.76E-05
Fish larvae	0	0	0	0	0
Carnivorous zooplankton	0	0	0	0	0
Herbivorous & Omnivorous zooplankton (copepods)	0	0	0	0	0
Gelatinous zooplankton	0	0	0	0	0
Large crabs	0.00081221	0.00081995	1.51E-09	2.67E-06	0.00069268
Nephrops	0.00206106	7.5264E-05	2.90E-05	8.83E-06	3.19E-06
Epifaunal macrobenthos (mobile grazers)	0.00057273	7.9375E-05	0	2.04E-07	7.19E-05
Infaunal macrobenthos	6.85E-07	0	0.00033311	0.00296333	0
C. crangon		0			

Group name					
Crangon (commercial size)	0	0	0	0	0
Crangon (below 5cm)	0	0	0	0	0
Shrimp	0	0	0	0	0
Small mobile epifauna (swarming crustaceans)	0	0	0	0	0
Small infauna (polychaetes)	0	0	0	0	0
Sessile epifauna	0	0	0	0	0
Meiofauna	0	0	0	0	0
Benthic microflora (incl. Bacteria, protozoa)	0	0	0	0	0
Planktonic microflora (incl. Bacteria, protozoa)	0	0	0	0	0
Phytoplankton	0	0	0	0	0
Detritus - DOM -water column	0	0	0	0	0
Detritus - POM - sediment	0	0	0	0	0
Discards	0	0	0	0	0
Sum	0.4784389	0.3441273	2.967351	0.3719796	0.03201725

*Table B 2 (continued): Ecopath landings per functional group and fleet in t/(km² * year)*

Group name	Nephrops trawl	Gears using hooks	Shrimp trawlers	Dredges	Pots	Other
Toothed whales	0	0	0	0	0	0
Seals	0	0	0	0	0	0
Surface-feeding seabirds	0	0	0	0	0	0
Diving seabirds	0	0	0	0	0	0
Juvenile sharks	0	0	0	0	0	0
Spurdog	0.00084479	0.00011934	0	0	4.11E-06	0
Large piscivorous sharks	5.57E-06	2.07E-06	0	0	2.23E-07	0
Small sharks	0	0	0	0	6.34E-05	0
Juvenile rays	0	0	0	0	0	0
Starry ray + others	5.32E-06	4.81E-08	7.47E-09	1.93E-09	1.23E-07	0
Thornback & Spotted ray	0	0	0	0	0	0
Skate + cuckoo ray	5.41E-08	5.43E-08	0	6.39E-10	9.29E-10	0
Cod						
Juvenile Cod(0-2, 0-40cm)	0.00219858	0.00038791	4.56E-05	3.45E-06	0.00010388	3.57E-07
Cod (adult)	0.00229796	0.00040545	4.76E-05	3.60E-06	0.00010857	3.73E-07
Whiting						
Juvenile Whiting (0-1, 0-20cm)	0.00020203	5.01E-08	5.37E-06	6.20E-08	3.84E-07	0
Whiting (adult)	0.00428393	1.06E-06	0.00011384	1.31E-06	8.13E-06	0
Haddock						
Juvenile Haddock (0-1, 0-20cm)	0.00017504	3.48E-08	6.00E-11	3.55E-08	1.32E-07	0
Haddock (adult)	0.00116885	2.32E-07	4.01E-10	2.37E-07	8.79E-07	0
Norway pout	0	0	0	0	0	0
Other gadoids (large)	0.00015153	1.13E-05	1.61E-08	3.36E-08	4.46E-06	1.61E-08
Other gadoids (small)	0	0	0	0	0	0
Monkfish	0.00073182	7.56E-08	4.31E-07	7.16E-07	6.80E-07	0
Gurnards	0.00023619	0	0	0	1.81E-06	0.00013682
Herring						
Herring (juvenile 0, 1)	0	0	0	0	0	0
Herring (adult)	1.09E-05	2.38E-06	4.69E-07	1.67E-07	0.00030661	0
Sprat	0	1.54E-07	8.34E-06	6.98E-09	0	0
Mackerel	7.98E-06	2.43E-06	3.87E-07	1.46E-09	8.57E-07	1.32E-09
Horse mackerel	0.00012842	0	2.56E-06	4.14E-12	2.31E-10	0
Sandeels	0	0	4.54E-05	0.00025341	0	0
Plaice						
Plaice (adult)	0.01818714	1.15E-06	9.30E-05	6.53E-06	1.59E-06	5.63E-06
Juvenile Plaice	0.00164244	1.04E-07	8.39E-06	5.90E-07	1.43E-07	5.08E-07
Dab	0.00060631	7.04E-08	8.40E-05	1.17E-07	5.87E-08	1.91E-08
Long-rough dab	6.79E-07	0	0	1.02E-07	0	0
Flounder	0.00165402	1.81E-07	4.49E-05	1.57E-06	3.14E-05	0
Sole						
Sole (adult)	0.00219899	4.78E-06	3.38E-05	4.24E-06	4.24E-06	2.09E-07
Juvenile Sole	0.00017126	3.71E-07	2.63E-06	3.30E-07	3.30E-07	1.63E-08
Lemon sole	0.00281701	3.36E-06	8.04E-06	4.48E-06	5.44E-06	0.0001348

Witch	0.00035092	1.12E-10	0	1.43E-09	2.89E-08	5.61E-10
Turbot	0.00136529	0	0	0	0	0
Brill	0.00048398	0	0	0	0	0
Megrim	6.03E-06	1.05E-10	0	3.53E-10	5.91E-10	0
Halibut	1.22E-05	3.27E-09	0	2.46E-09	5.12E-09	3.13E-10
Dragonets	0	0	0	0	0	0
Large demersal fish	0.00017219	3.00E-05	3.13E-07	1.07E-07	8.37E-07	1.32E-10
Small demersal fish	0.00012672	5.12E-09	0	0	3.92E-07	2.56E-07
Miscellaneous filterfeeding pelagic fish	0	0	0	0	0	0
Squid & cuttlefish	0.00026395	2.65E-08	0	1.69E-06	3.15E-07	1.11E-06
Fish larvae	0	0	0	0	0	0
Carnivorous zooplankton	0	0	0	0	0	0
Herbivorous & Omnivorous zooplankton (copepods)	0	0	0	0	0	0
Gelatinous zooplankton	0	0	0	0	0	0
Large crabs	0.00063956	5.43E-06	2.44E-06	5.51E-07	0.00993083	5.22E-05
Nephrops	0.01111048	1.01E-07	2.86E-09	1.22E-06	2.20E-05	2.59E-09
Epifaunal macrobenthos (mobile grazers)	5.81E-05	0	0	0.00587351	1.70E-05	6.94E-05
Infaunal macrobenthos	0	4.83E-07	0.01064937	0	0.1364515	0
C. crangon						
Crangon (commercial size)	0	0	0.05041	0	0	0
Crangon (below 5cm)	0	0	0	0	0	0
Shrimp	0	0	0	0	0	0
Small mobile epifauna (swarming crustaceans)	0	0	0	0	0	0
Small infauna (polychaetes)	0	0	0	0	0	0
Sessile epifauna	0	0	0	0.3397736	0	0
Meiofauna	0	0	0	0	0	0
Benthic microflora (incl. Bacteria, protozoa)	0	0	0	0	0	0
Planktonic microflora (incl. Bacteria, protozoa)	0	0	0	0	0	0
Phytoplankton	0	0	0	0	0	0
Detritus - DOM -water column	0	0	0	0	0	0
Detritus - POM - sediment	0	0	0	0	0	0
Discards	0	0	0	0	0	0
Sum	0.05431627	0.00097866	0.06160694	0.3459317	0.1470704	0.00040168

7.2. Calculation of discards

Assuming the relationship of discards to landings to be comparable between the entire North Sea and the southern part, we calculated discards for our model as southern discards = southern landings * (North Sea discards/North Sea landings) ; where North Sea refers to values from Mackinson and Daskalov (2007). For plaice, sole, cod, whiting, turbot and brill, however, discard ratios came from Rätz and Mitrakis (2012; Appendix 2). These discard ratios, specific for each species/fleet combination, were combined with our earlier calculated landings to obtain estimates of the total tonnage discarded per species on average 2010-'12. These total amounts were then split on juvenile and adult stanzas of the respective species using mean 2010-'12 discard weights and numbers from Rätz and Mitrakis (2012).

According to ICES WGCRAN (2012), "the mean discard fraction of brown shrimp amounted to 49.9% ±10.6% of the total brown shrimp catch in weight" (p. 51). We used a discard rate of 50% for our model. Discards of other shrimps are set to zero, and we assume no landings of these species.

We derived estimates of 0-aged plaice tonnage discarded by the German brown shrimp fishery by extrapolating the 516 tonnes of plaice discarded by the German part of the fleet in 2008 (31.67 kg discarded plaice per trip, with a total number of 16279 trips undertaken in 2008 (Ulleweit et al. 2010). To obtain a discard estimate for the entire fleet, we set landings, and in a second approach effort, of

the German part of the fleet relative to landings respectively effort of all countries' vessels together (WGCRAN, 2012): total discards = total catch * (German catch / German discards of plaice); or with effort instead landings in the second approach tested. Extrapolation through both figures delivers comparable amounts, with the more conservative (i.e. 11% higher) extrapolation through landings resulting in a total juvenile plaice discard of 1463 tonnes. All discards per functional group and fleet are summarized in Table B 3.

Table B 3: Ecopath discards per functional group and fleet. Note that only FGs with discards are listed.

Group name	Demersal trawl + dem seine	Beam trawl	Sandeel trawl	Pelagic trawl	Drift and fixed nets	Nephrops trawl
Surface-feeding seabirds	0	0	0	0	6.00E-08	0
Diving seabirds	0	0	0	0	3.15E-05	0
Spurdog	0.0001178	0	0	0	0	0
Juvenile Cod	0.01331854	0.00033709	9.10E-05	1.48E-05	0.00024243	0.00412199
Cod (adult)	0.00506964	0.00012831	9.01E-07	1.46E-07	9.23E-05	0.00156901
Juvenile Whiting	0.00471621	0.00026936	0.0055396	8.10E-06	0.00013035	0.00052657
Whiting (adult)	0.03723673	0.00212673	0.02030818	3.06E-05	0.00102919	0.00415749
Juvenile Haddock	0.00042311	4.16E-07	1.67E-06	0.00023012	4.84E-07	1.10E-05
Haddock (adult)	0.00173739	8.79E-07	0	1.68E-07	1.21E-08	0.00040359
Other gadoids (large)	2.17E-06	2.77E-06	0	0	3.57E-08	0
Monkfish	0	0.00023236	0	0	0	0
Gurnards	0	0.0008781	0	0	0	0
Herring (adult)	0	0	0	0.00165659	0	0
Mackerel	3.32E-05	0	0	4.06E-05	0	0
Plaice (adult)	0.00761114	0.03143566	0	0	5.01E-06	0.00167856
Juvenile Plaice	0.01080497	0.04462686	0	0	7.11E-06	0.00238292
Dab	0.1775357	0.1332025	0	0	0.00045619	0.1933648
Flounder	0.00027575	0.00077549	0	0	0	0
Juvenile Sole	8.58E-07	0.00218433	1.38E-08	1.38E-08	0	0.00011414
Witch	4.28E-08	0	0	0	0	0
Turbot	0	0.00014071	0	0	0	1.38E-05
Brill	0	5.12E-05	0	0	0	0
Megrim	1.14E-06	0	0	0	0	0
Nephrops	0.00023017	7.58E-05	0	0	0	0

Table B3 (continued): Ecopath discards per functional group and fleet. Note that only FGs with discards are listed.

Group name	Gears using hooks	Shrimp trawlers	Dredges	Beam trawl targeting sole	Pots	Other
Surface-feeding seabirds	6.15E-06	0	0	0	0	0
Diving seabirds	1.93E-06	0	0	0	0	0
Spurdog	0	0	0	0	0	0
Juvenile Cod	0.00021001	2.47E-05	1.87E-06	0.00062339	0	1.93E-07
Cod (adult)	2.08E-06	2.44E-07	1.85E-08	0.00023729	0	1.91E-09
Juvenile Whiting	1.63E-07	1.75E-05	2.02E-07	0.00189698	1.25E-06	0
Whiting (adult)	6.18E-07	6.62E-05	7.63E-07	0.0149775	4.72E-06	0
Juvenile Haddock	0	0	0	8.68E-08	0	3.54E-05
Haddock (adult)	0	0	0	1.84E-07	0	0
Other gadoids (large)	0	0	0	1.14E-07	0	0
Monkfish	0	0	0	2.00E-05	0	0
Gurnards	0	0	0	0.0004325	0	0
Herring (adult)	0	0	0	0	0	0
Mackerel	0	0	0	0	0	0
Plaice (adult)	0	0	0	0.03017755	0	0
Juvenile Plaice	0	0.0042286	0	0.04284082	0	0
Dab	0	0.00433401	0	0.284445	0	0
Flounder	0	0	0	0.00068789	0	0
Juvenile Sole	3.34E-08	2.37E-07	2.97E-08	0.00896038	2.97E-08	1.46E-09
Witch	0	0	0	0	0	0
Turbot	0	0	0	0.00021222	0	0
Brill	0	0	0	9.70E-05	0	0
Megrim	0	0	0	0	0	0
Nephrops	0	0	0	4.13E-06	0	0

Chapter 2

Combining efforts to make maximum sustainable yields and good environmental status match in a food-web model of the southern North Sea

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Abstract

The southern North Sea is the stage of conflicting objectives of beam trawlers targeting flatfish; of shrimp trawlers fishing for brown shrimp with bycatch of juvenile flatfish; and of demersal trawlers, the main fishery on cod, a key predator of shrimp and other groups. To expose trade-offs between the fleets' objectives and to explore what a possible variant of a multispecies maximum sustainable yield (MSY) could look like, we parameterized an ecosystem model and subjected it to a range of different fishing effort levels of the three fleets. Long-term projections highlighted multiple fishing regimes that lead to catches of at least 30% of all focal single species MSYs at the same time. Trade-offs between the yields of shrimp fishers and demersal trawlers made higher simultaneous yields impossible. Besides optimizing multispecies catches, we identified effort regimes that satisfied a set of descriptors of good environmental status (GES). We found that GES can only be obtained through low efforts of beam and demersal trawlers, which cannot be aligned with our multispecies MSY variant without accepting trade-offs in fishing yields and/or conservation goals.

1. Introduction

Within the North Sea, the shallow southern part (divisions IVb and IVc of the International Council for Exploration of the Sea, ICES) differs from the north (division IVa) through the importance of flatfish (particularly European plaice, *Pleuronectes platessa* and sole, *Solea solea*) and brown shrimp (*Crangon crangon*) in species and catch compositions. Policies designed to manage fisheries for the two groups face conflicting objectives, as a) fishers barely fish one species alone, but generally extract several species and life stages together (*technical interactions*; Miller and Poos, 2010; Rijnsdorp et al., 2007), b) fished species prey on other target and non-target species or are consumed themselves (*multispecies issues*; Temming and Hufnagl, 2014; Welleman and Daan, 2001) and c) fishing has direct and indirect effects on the marine environment (Gislason, 1994; Jennings and Kaiser, 1998) – and *vice versa* (Hiddink et al., 2011; van Denderen et al., 2013). As such, young flatfish die as bycatch in shrimpers' nets (Berghahn and Purps, 1998); initiatives to recover European cod (*Gadus morhua*) may compromise yields of other species through predation and competition (Temming and Hufnagl, 2014); and other, more vulnerable species like turbot (*Scophthalmus maximus*) and spurdog (*Squalus acanthias*), are affected by extractions through fishing nets (Kerby et al., 2013). All above mentioned points underpin the necessity of ecosystem-based multiannual plans as expressed by the reformed European Union's common fisheries policy (CFP; Article 9, Regulation (EU) No 1380/2013). Science should explore and inform on negotiation spaces in the form of a set of fishing policy options that lead to good results for all sectors (e.g. by providing yields close to the maximum sustainable yield, MSY) while minimizing the probability of bad outcomes for stakeholders and the marine environment. Thus, in this study, we want to:

- Parameterize an ecosystem model of the southern North Sea that is calibrated to historical records of biomasses and landings and plausibly reproduces population dynamics of the species included (Sections 2.1 to 2.3 and Appendix).
- Identify fishing policy options that lead to high yields for the three major fleets of the southern North Sea – beam trawler, brown shrimp trawler and demersal purser and seiner – simultaneously (Section 2.4).
- Examine how these three fleets would have to agitate to reach a good environmental status (GES) of the marine environment (Section 2.5).
- Test if both policy objectives, MSY and GES, are compliable or, if not so, which trade-offs in fishing yield and conservation goals would have to be accepted to bring both in acceptable accordance (Section 2.6).

Identifying and presenting a three-fleet negotiation space, in particular for fisheries on the southern North Sea's main commercial species cod, plaice, sole and brown shrimp, is a problem yet unsolved. ICES multispecies considerations for the North Sea stocks present trade-offs between fishing targets species-wise, as effect of each stock's target fishing mortality (F) on spawning stock biomasses (SSB) and yields (Y) of the very same and other stocks (ICES, 2013). This representation is well suited to comply with the current management maxims of target quotas and Fs. However, it does not consider that Fs may well stem from different fleets, and thus makes it difficult to account for inter-fleet interactions explicitly. Differently so in the work of Mackinson et al. (2009b) who, inspiring the idea presented in this paper, show yields of three demersal North Sea roundfish stocks as a function of the interaction of the two main fleets targeting them. Of any similarly computed or presented three-fleet negotiation space as the one presented here, however, we are unaware. Neither do we know of any multispecies or ecosystem model specifically designed or sufficiently parameterized to address conflicts between local fisheries for brown shrimp and mixed flatfish in an ecosystem context in the southern North Sea (see also Miller and Poos (2010)).

2. Methods

2.1.   A southern North Sea food web model

The 'southern North Sea' as defined for this study, comprises ICES areas IVb and IVc. It is bordered by the coasts of France, Belgium, the Netherlands, Germany, Denmark and the United Kingdom. The study area spans between 51° and 56° North and 4° West and 9° East and covers 345 874 km². The southern North Sea is a shallow sea on the European continental shelf of around 50 m depth, with maximum depths of 125 m, and is characterized by a strong terrigenous influence. It thereby differs from the northern part of the North Sea (IVa) with an average depth below 100 m and maximum depths down to 400 m, where Atlantic influence prevails.

We constructed a food web model of the southern North Sea using the Ecopath with Ecosim (EwE) software version 6.4.11414.0 (Christensen et al., 2008). The EwE software and model framework is designed to quantify the pools and flows of biomass and energy in an ecosystem and equipped to reveal the system's structure and dynamics (Christensen et al., 2008; Christensen and Walters, 2004). In essence, it resembles an accounting system for the food web. Following the assumption of mass-balance – that whatever is in the system must come from the system and stay in the system – it allows closing gaps in knowledge about the biomass, production, consumption and removal of some entities of the ecosystem by predators and fishers through knowledge of these parameters for other organisms. Also, single missing parameters for one group of organisms can be extrapolated if the other parameters for this group are known. All living components of the ecosystem are represented in biomass 'pools' or functional groups (FGs). These groups are linked through feeding relationships and can be composed of a single species or groups thereof that form an ecological guild. The production of each functional group in EwE is expressed by Equation 1, which terms can be split into predation mortality, fisheries removals, net migration, biomass accumulation and other mortality.

$$B_i \cdot \left(\frac{P}{B_i}\right) = \sum_{j=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i + E_i + BA_{i+} \left(\frac{P}{B_i}\right) \cdot B_i \left(1 - EE_i\right)$$

Equation 1

Parameters are B_i = biomass of functional group i; P/B = production per unit of biomass of the functional group i; $(Q/B)_j$ = consumption per unit of biomass of the predator j of biomass B_j; DC_{ij} = proportion of prey i in the diet of predator j; Y_i = exports from the system as fishery catches; E_i = net migration; and EE_i = ecotrophic efficiency of the functional group i. Energetic costs for the respective groups are described by Equation 2:

$$Consumption(Q) = Production\ (P) + respiration\ (R) + unassimilated\ food\ (U)$$

Equation 2

Equations, algorithms and assumptions beyond these two Ecopath master equations can be found in Christensen and Walters (2004) and Christensen et al. (2008).

Our food-web models 68 functional groups rang from planktonic and benthic invertebrates via commercial species targeted by the eleven fleets embraced to sharks, rays, marine mammals and seabirds. Commercially important species were implemented in *stanza groups*, i.e. divided into juveniles and adults with respective ontogenetic growth and diet parameters, to extend the detail of their population dynamics (Table A 1). A list of all functional groups and a taxonomic scheme of assignment of non-vertebrate species to functional groups can be found in Appendix A of chapter 1. The initial static (Ecopath) version of our model represents the southern North Sea ecosystem at the annual average state in 1991, as this is the year for which most information on fish diets is available

(ICES 'year of the stomach'). Figure 1 shows a representation of that food-web, in which the main groups of this study and mass flows between them are highlighted.
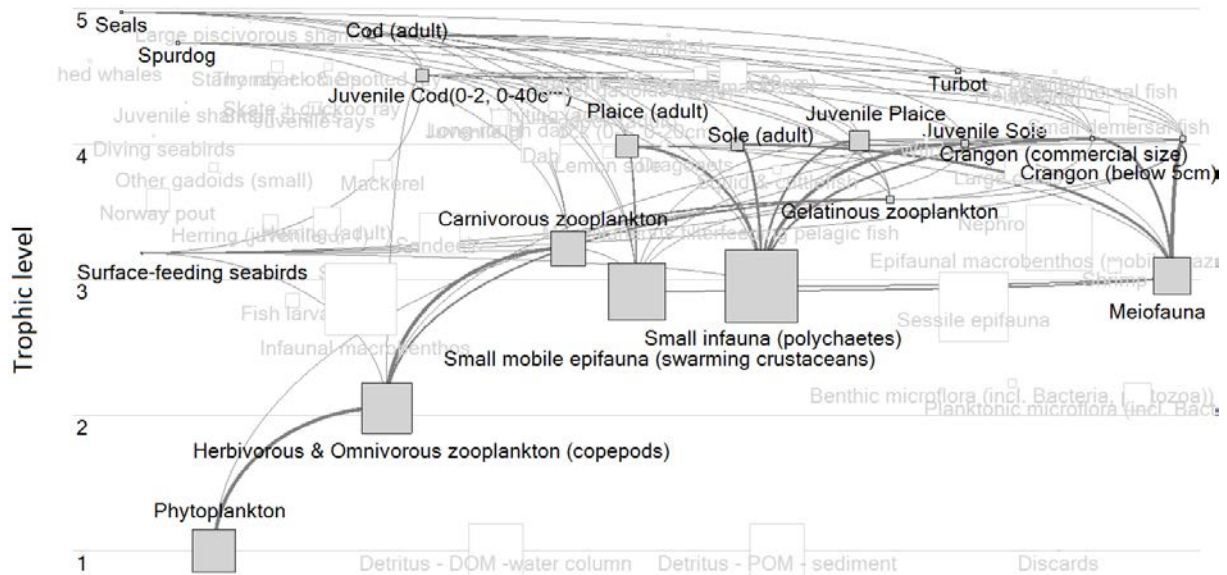
Figure 1: Flow diagram of the southern North Sea food-web. Key species and flows relevant for this study are highlighted. Rectangle size indicates the biomass of the functional group and the thickness of the lines that represent predator-prey relationships is proportional to the importance of each respective flow.

Based on the Ecopath 'snapshot of the food-web' in 1991, we parameterized a time dynamic Ecosim version of the system. Ecosim simulates the effects of fishing and environmental forcing parameters over time, in our case the period 1991-2010. Changes in the biomass of each pool are expressed by

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ij} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i$$

Equation 3

where dB_i is the growth of biomass of functional group i; g_i is its growth's net efficiency, i.e. production / consumption; I_i is immigration rate; while e_i is emigration rate; M_i represents the non-predation natural mortality rate; and F_i is fishing mortality rate.

2.2.   Input data

We collected estimates of biomass, production and consumption rates and information on diet composition from ICES single- and multispecies stock assessments (HAWG, 2013; WGNSSK, 2013; WGSAM, 2014), survey data (ICES International Bottom Trawl Survey, IBTS); ICES working groups (WGCRAN, 2012),, the ICES 'year of the stomach' sampling project (Hislop et al., 1997) and peer-reviewed literature (Figure 2). Where we could not obtain more local data, we referred to the Mackinson and Daskalov (2007) whole North Sea EwE model and updates thereof (Heymans et al., 2011; Mackinson et al., 2009a; WGSAM, 2011); with the underlying assumption that southern North Sea parameters do not differ to a critical extend. See Appendix A of for a detailed overview of data sources and methods used to parameterize the various functional groups.
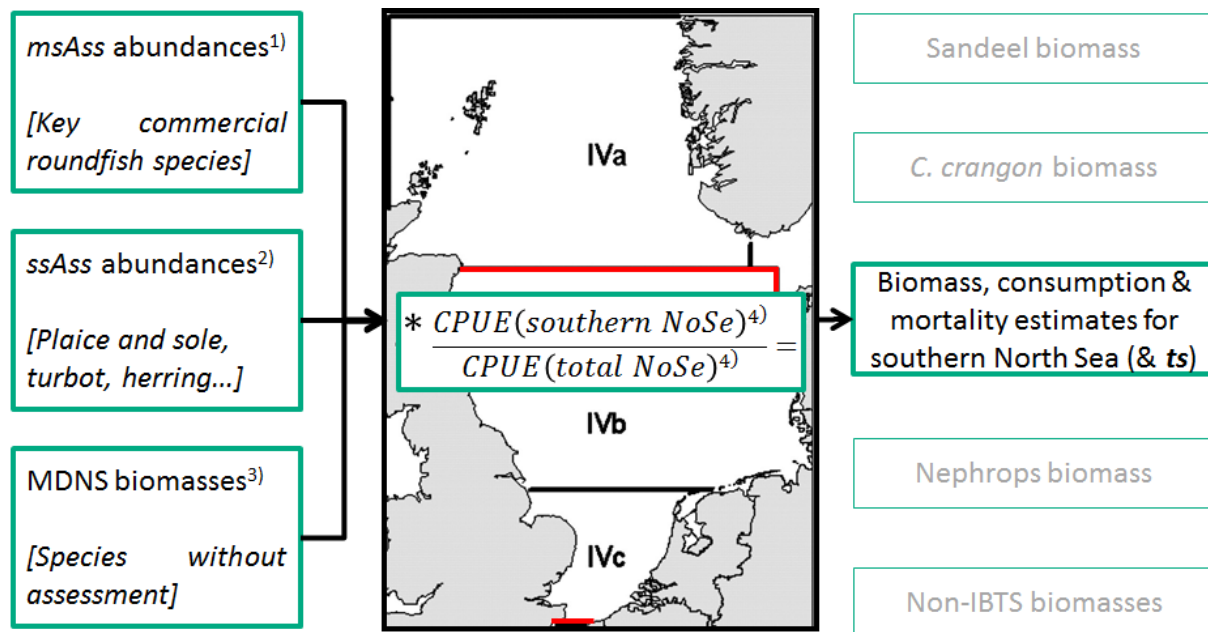
Figure 2: Schematic representation of how biomasses for the southern North Sea EwE model were calculated. msAss: multispecies and ssAss: single species stock assessment. MDNS: Whole North Sea EwE. 1) Stochastic Multispecies Model (SMS). ICES WGSAM 2014 2) XSA, Extended Survivors Analysis. ICES WGNSSK 2013 3) North Sea EwE. Mackinson & Daskalov 2007. CEFAS Sci. Ser. Tech. Rep. No. 142. 4) International Bottom Trawl Survey (IBTS). http://datras.ices.dk/Data_products/Download/Download_Data_public.aspx. Transparent boxes were calculated independent of IBTS data.

Eleven fishing fleets were implemented in our model. Depending on the gear used and the species targeted we separated, in alignment with the European Union data collection framework, between demersal trawl and seine; beam trawl (targeting flatfish); sandeel trawl; pelagic trawl; drift and fixed nets; nephrops trawl; gears using hooks; brown shrimp trawlers; dredges; pots and others. For a gear and fleet classification see Appendix B, Table B 1.

We consulted three different data sources to estimate fisheries' landings: The ICES EUROSTAT catch statistics (http://info.ices.dk/fish/CATChSTATISTICS.asp, data downloaded 2 December 2012) ranging from 1950–2010 and landings data of the European Commissions' Scientific, Technical and Economic Committee (STECF) for Fisheries (Rätz and Mitrakis, 2012; Appendix 08). The reason for using two different data sources was that EUROSTAT holds historic landings back to 1991, but does not inform about the particular gears the catch was taken with, while the STECF landings data is reliable 2009–'11 only, but offers the advantage of holding landings assigned to specific gears and mesh sizes. The catches of the brown shrimp fleet are from the ICES working group on crangon fisheries and life history (WGCRAN, 2012). All landings and computation techniques are given in Appendix B.

Assuming the ratio of discards to landings to be comparable between the entire North Sea and the southern part, we calculated discards for our model based on Mackinson and Daskalov (2007) and our localized landings. For plaice, sole, cod, whiting, turbot and brill, however, discard ratios were adopted from Appendix 2 in Rätz and Mitrakis (2012). We combined our landings calculated as above with discard ratios per species/fleet combination therein. According to WGCRAN (2012), "the mean discard fraction of brown shrimp amounted to 49.9% ±10.6% of the total brown shrimp catch in weight" (p. 51). Discards of non-crangonid shrimp are set to zero as we assume no catches of these species. All discards per functional group and fleet are summarized in Appendix B, Table B 3.

With the goal of this study to assess the effect that the various fleets have on stocks and the ecosystem nowadays, we sought to parameterize the fleets with catch patterns that resemble the situation in 2010, rather than 1991. The implication of that is that in our 1991-2010 hindcast simulation the total

amounts caught correspond to historic time series of that period, but that the distribution of species on the fleets' catches is incorrect prior 2010. A complete description of sources and calculation methods for landings and discards can be found in Appendix B.

2.3.   Fitting and calibrating the Ecosim model

Exploring fishing policy options in the southern North Sea requires the Ecosim model's population dynamics and responses to fishing to be as realistic as possible, where realism can be seen as the ability to reproduce patterns observed in the past. Primal instrument for this was to use Ecosim's non-linear fitting procedure. We fitted model predictions of biomass and landings to time series data across all trophic levels for the period 1991-2010, during which period the model was driven by our time series data of fishing effort and, in some stocks, fishing mortalities. These time series, again, represent our effort to collect and calculate as many, as precise and as locally rooted measures of pressure and state variables as possible.

The Ecosim fitting procedure searches for vulnerabilities (v's) of selected predator groups that lead to the best representation of all groups. In Ecosim, which bases on the *foraging arena* hypothesis (Walters and Christensen, 2007; Walters et al., 1997), each prey pool is split into a fraction accessible to predation of a given predator, whilst the rest of the population remains non-vulnerable. Ecosim's vulnerability parameters determine the flow between these two pools and thus the flow between prey and predator. The default value for vulnerabilities of prey to a predator is two, typifying mixed control of the predator group. Larger values determine the predator to be top-down controlled, while values closer to one represent a bottom-up driven predator pool (Christensen et al., 2008).

Our goal when fitting the Ecosim model was not necessarily an utmost reduction of deviations from observed data. Instead, we followed a parsimonious approach, i.e. we aimed to outbalance better fit (as reduction in the sum of squared deviations (SS) of modelled log biomasses from log predicted biomasses) against the number of parameters estimated when fitting (number of predator groups to search vulnerabilities for; consumption forcing functions and primary production anomaly). Our 'best fit' was thus one with which the Ecosim model describes the data notably better than if any parameter was left out, while adding any further parameter would benefit SS reduction only marginally while leading to a higher risk of over parameterization (as represented by Akaike's information criterion (AIC) that is used in the Ecosim fitting interface to display and sanction against any further parameter added to explain time series data).

Using Ecosim's routine to check the *sensitivity of SS to vulnerabilities*, we identified which predator's vulnerabilities to be changed led to the highest contribution in the overall goodness of fit. This sensitivity check was performed one group after the other, and the resulting overall SS was recorded for each such fitting. Initially, adding any other functional group to the fitting greatly benefited the reduction of total deviation from time series while adding relatively little to the fitting's AIC. With more and more FGs added, however, a point was reached at which adding more groups to the fitting only marginally improved the total deviation from observed data, while ever increasing AIC. For our model, this was the case for a pool of 32 functional groups (Figure 3). These represent our selection of groups to fit vulnerabilities to for the most parsimonious approach. The selected groups ranged across all trophic levels, from marine mammals to copepods (Table D 1 in Appendix D).
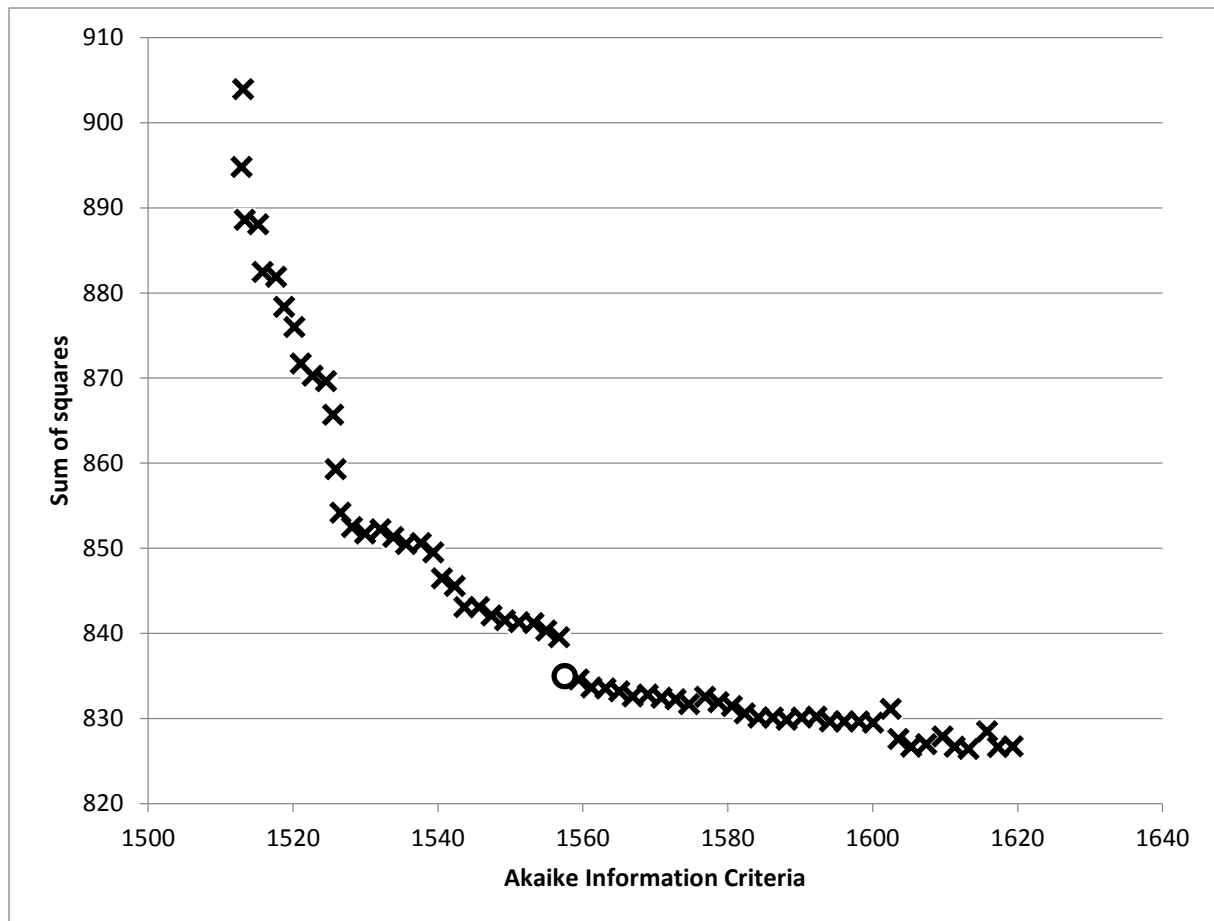
Figure 3: Sensitivity of the sum of squared deviations (SS) and Akaike's information criterion (AIC) to vulnerabilities. Marked with a circle is the selected fitting scenario of 32 groups, after which adding further groups to the fitting increases AIC more than it reduces overall SS.

Up to this point, Ecosim was parameterized to explain historic patterns in biomasses and landings through fishing and trophic relationships alone. We did, however, test for potential environmental parameters to influence these trophic interactions as well. These can either apply to predator-prey interactions or affect primary production (PP).

Screening the literature for trophic interactions impacted by environmental factors in the study area pointed towards cod recruitment being negatively correlated with water temperature in the North Sea (O'Brien et al., 2000), supposedly due to a temperature induced change in plankton dynamics that affects food availability for larval cod (Beaugrand et al., 2003). To identify a suitable forcing function (FF), we sought correlation of cod recruitment with a set of environmental, particularly water temperature related indices: NAO, North Atlantic Oscillation; AMO, Atlantic Multidecadal Oscillation; average sea surface and bottom temperature in the southern North Sea from Nunez-Riboni and Akimova (2015); and HADSST, Hadley Sea Surface Temperature. We used the annual mean AMO index, which is basically mean sea surface temperature in the North Atlantic, as a proxy for North Sea sea surface temperature, as this index, of all tested, showed the strongest correlation with decreases in cod recruits 1991-2010. Note that we did not test for cod recruitment's correlation with plankton indices, as done by Beaugrand and Kirby (2010), because plankton is an intrinsic element of our model.

The Ecosim *fit to time series* routine allows estimating a PP anomaly that, additional to changing vulnerabilities and including consumer forcing functions, minimizes deviation of the model predictions from the observed data. It is based on the *a priori* assumption that changes in the food web, as represented by the time series' biomasses and landings, are importantly related to changes in primary

production. There is reason to assume this to hold relevance for many marine systems (Steinacher et al., 2009), including the North Sea (Mackinson, 2013). We tested different forms of this potential PP anomaly, either annually estimated ones or such generalized as a spline curve.

Both consumption and PP forcing functions' contribution to reducing total SS were tested, solely or in combination. For exploratory reasons, we also recorded SS of adult cod. Searching for a PP anomaly function, smoothed as a curve with three splines, resulted in slightly lower SS than the no FF fitting scenario, while annual PP anomaly estimates substantially increased AICs (filled marks in Figure 4) and raised the number of parameters to be estimated from 32 to 51. Applying annual AMO values (as a North Sea surface temperature proxy) as consumer forcing function to juvenile cod led to no improvement in total SS, however, it did so for the fit of adult cod (open marks in Figure 4). Only when consumer and PP forcing function in the form of a three spline PP anomaly were combined, we found an acceptable balance between decreasing total SS against increasing AIC and the number of parameters (short bar in Figure 4). The resulting PP forcing function describes subtle deviations from the standard value 1 only and is depicted in Figure 5.
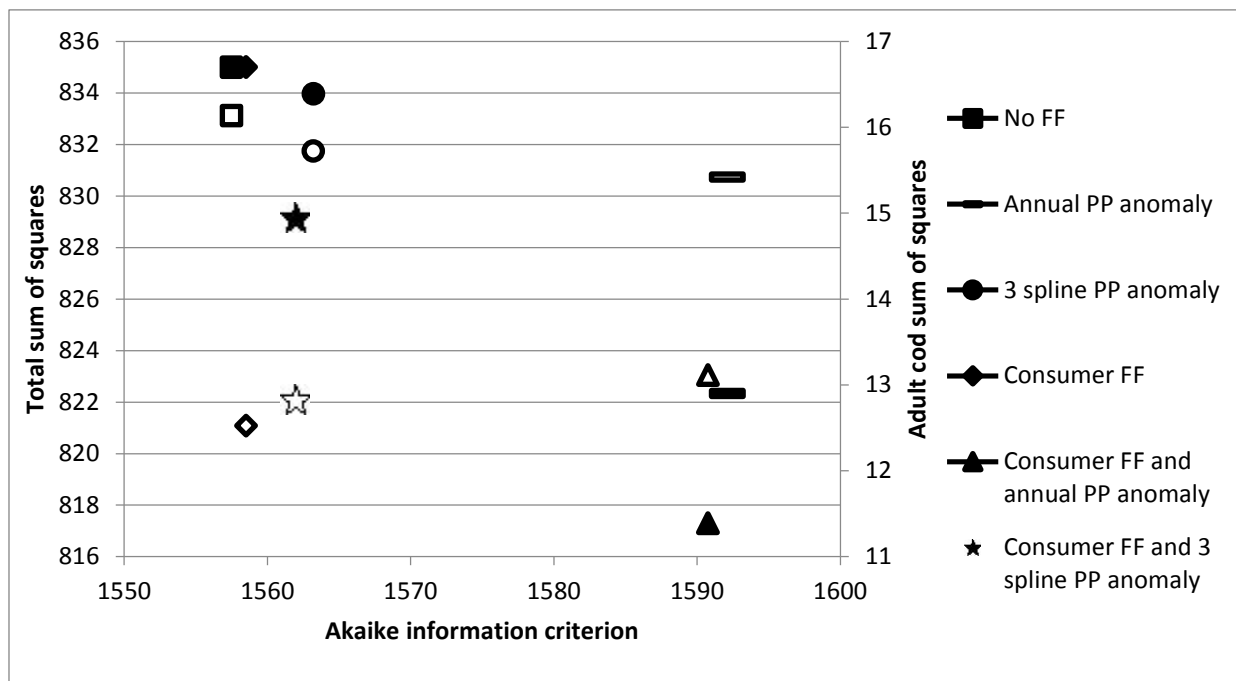
Figure 4: Diagnostics of different strategies of including a primary production (PP) and/or a consumer forcing function (FF), solely or combined, in fitting Ecosim predictions to observations. Respective total system sums of squares are represented by filled, sum of squared deviations for adult cod with open markers.
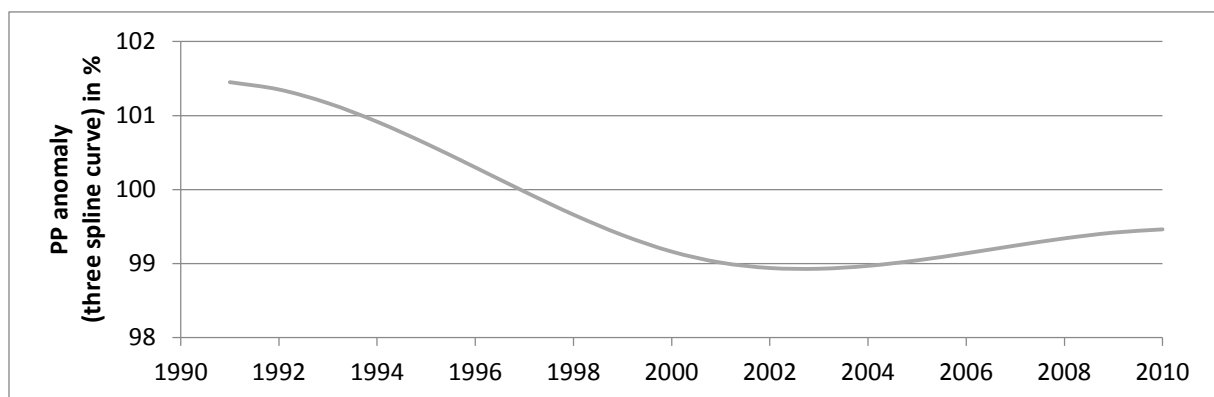
Figure 5: Primary production anomaly estimated by Ecosim for the selected fitting scenario (with annual AMO values (as a North Sea surface temperature proxy) as consumer forcing function).

Once the model was fitted by attempting the closest approximation of observed biomass and catch trajectories throughout the modelled time period, our model was calibrated. Other than fitting, calibration meant that we used information beyond that included in the model database to increase the plausibility of model simulations, even if that additional tuning should impair the fit to observed data points. Particularly, we referred to longer term data on recruitment behaviour from single species assessment (WGNSSK 2013) and multi-species considerations (ICES 2013) to ensure that Ecosim reproduced the stock-recruitment behaviour of the key commercial stocks right. Cod, plaice, sole and brown shrimp make up the most important contributions to fisheries landings and profits in the southern North Sea, and are thus the scope species of this study. Calibrating the Ecosim model ensured that the equilibrium yield of stanza species peaks at a certain fishing mortality rate (F). That peak marked the F associated with this single species' maximum sustainable yield (Fmsy) in our modelled system. We sought for the model to show highest single species yield at levels of F in the range of assessments' or multispecies advices' F_{msy} for the respective multi-stanza species (ICES, 2013; WGNSSK, 2013).
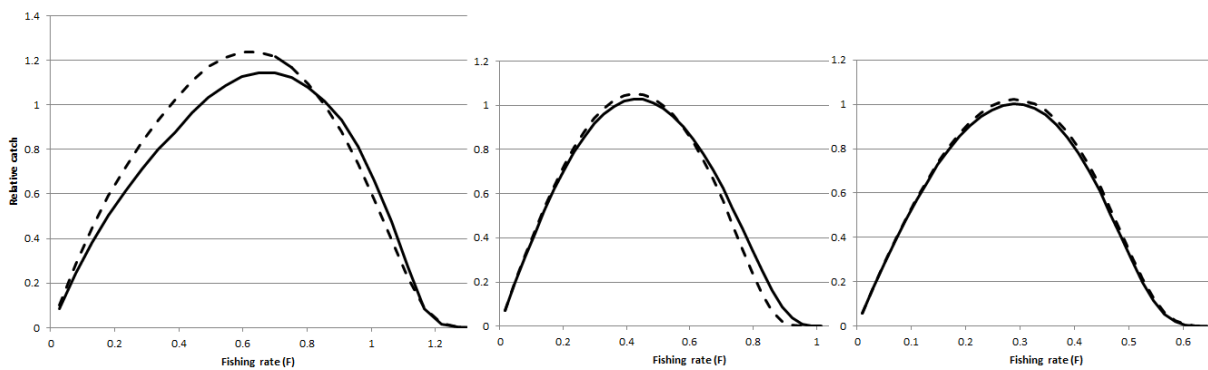
Figure 6: Ecosim equilibrium relationships between fishing mortality and relative catches of cod, plaice and sole. Solid lines represent results when all other groups of the food-web were allowed to vary in biomass as response to the assessed species being fished (full compensatory assessment sensu Walters et al. (2005)). Broken lines represent results when all but the investigated species biomasses' were held constant (stationary system).

Beyond determining single species equilibrium yields, we calibrated the model such that compensatory responses in recruitment would resemble stock-recruitment behaviour in assessments, analogue to the approach outlined in Mackinson et al. (2009b): Based on biomass estimates from WGNSSK (2013), we calculated the ratio of recruits' (R) to spawning stock biomass (SSB) for each year and used these ratios' median across all years to compare the degrees of compensation in recruitment between species. The aim of calibrating our Ecosim models' stock-recruitment was that simulated R / SSB medians for plaice and for sole would relate to simulated R / SSB of cod in a manner similar to how they relate to each other according to stock assessments (Figure 7). While for sole this could be well achieved, plaice in our model remain more productive than according to stock assessments. Any further cuts in plaices' productivity, however, lead to erratic behaviour of Ecosim runs.
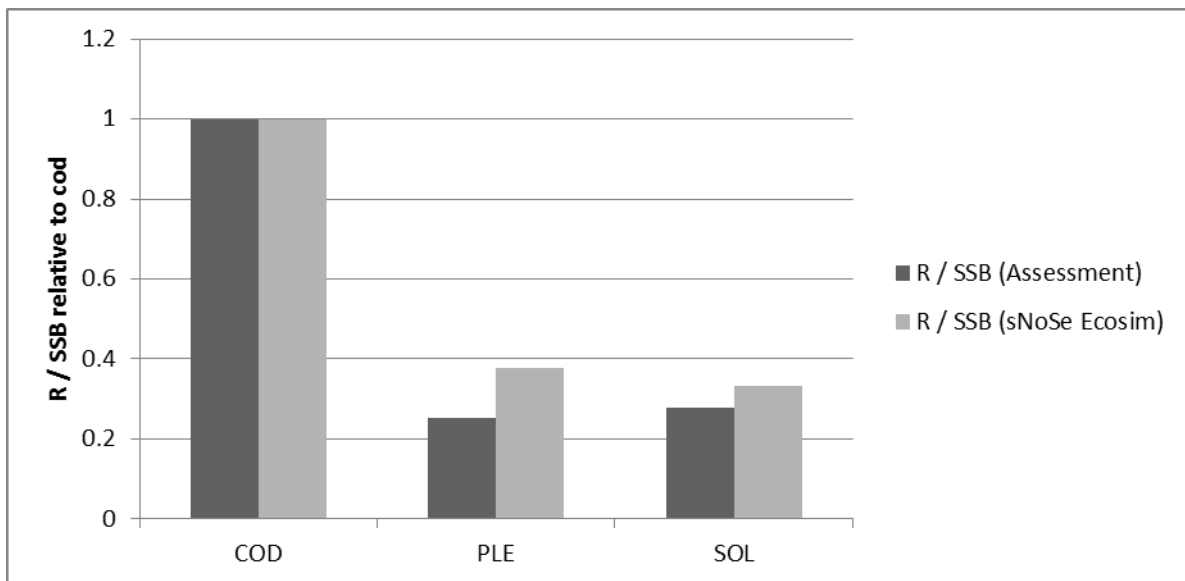
Figure 7: Ratio of median recruits biomass against spawners biomass (R / SSB), relative to that of cod.

Calibrating Ecosim to produce both credible F_{msy} and stock-recruitment behaviour required changes to be made to the model's vulnerabilities fitted as above. These changes are summarized in Table 1. Note that they may lead to historic time series being less well represented by the model than it was the case in the initial fitted version, but that population and exploitation dynamics are better represented in the calibrated model. Our focus on policy explorations lets us decide for the latter variant.

Table 1: Changes to fitted vulnerabilities of stanza groups for model calibration. All other vulnerabilities remained as fitted.

Predator functional group	v fitted	v calibrated
Juvenile cod	1,00	10,00
Adult cod	1,00	3,50
Juvenile whiting	10382,13	10,00
Juvenile haddock	1,00	1,10
Adult haddock	1,00	1,10

2.4.   Evaluating fishing yield optimization scenarios

With the aim of testing the state of the southern North Sea food-web and its exploited stocks as a function of all possible combinations of fishing efforts (and associated fishing mortalities) by demersal, beam and shrimp trawlers, we created time series of varying efforts of the three respective fleets – ranges from zero to three fold 2010er efforts for beam and demersal trawlers, with a step size of 30%; and from zero to six fold for shrimpers, with a 60% step size. All eight other fleets were kept at the 2010 level. As we had used the F of main commercial groups as forcing variables when fitting and calibrating Ecosim, we also did so for the policy evaluation time series. For each effort combination, we computed corresponding Fs based on partial fishing mortalities per fleet exerted on the respective stocks in our calibrated 2010 Ecosim run. In the such composed effort and F time series, each fishing regime sustained 30 years, a period during which we had found the stock dynamics to reach an equilibrium state in prior testings. We ran each time series in Ecosim, with no further forcing functions loaded. As Ecosim simulations can last 500 years at most, we had to split the effort scenarios onto multiple time series to load and run in Ecosim. After each run, we extracted the annual average state variable biomass, catch and fishing mortality of each FG, along with the corresponding forcing variables as beam trawl, shrimper and demersal fleets' efforts, using the CEFAS results extractor plugin. We extracted values of the state variables biomass, F, and catch for all FGs at the equilibrium of each fishing regime.

We defined an 'acceptable outcome for all fleets' and thus a negotiation space for the southern North Sea fisheries as the result of effort regimes that lead to all scope species being extracted at a certain percentage of their respective single species MSYs at the same time. In our particular case, this single species MSY variant was the amount caught of a certain species if all fleets' efforts were optimized for that one goal only. That could include cases in which fleets not targeting the particular species either reduced efforts to allow higher forage species biomasses, or cases where non-targeting fleets increased efforts to cut down predators or competitors of the focal species. This single species MSY variant translates to the maximum of a respective species caught in any of the tested effort combinations.

2.5.   Identifying good environmental state scenarios

Beyond identifying outcomes of high fishing yields, we sought effort regimes that result in a good environmental status of the ecosystem in long term predictions. For our study, rather that testing a complete set of descriptors of GES as demanded by the European Union's Marine Strategy Framework Directive (MSFD), we focused on a smaller selection of descriptors. We deemed our GES proxy as satisfied under the following conditions:

- Biomass of adult plaice and sole should be above the target biomass set as a precautionary approach (B_{pa}) (WGNSSK, 2013). We referred to the entire North Sea B_{pa}, as the vast majority of the two stocks reside in our model area.
- Cod B_{pa} for the entire North Sea is given as 150 000 t (WGNSSK, 2013). Between 1991 and 2010, an average annual 25.9% of the whole SMS biomass of adult cod was in our model area. We thus adopted a localized cod B_{pa} threshold of 38 865 t.
- Turbot F is above precautionary proxy based on $F_{0.1}$, relative to the average of the time series in the 2014 assessment for 2010: F=0.22 (WGNSSK, 2014).
- F of spurdog below the F_{MSY} proxy of 0.029 suggested by the ICES working group on elasmobranch fishes (WGEF, 2014).
- The large fish indicator (LFI), i.e. the biomass contribution of demersal fish with a common length > 40 cm to the total biomass of demersal fish, is larger 30% (Greenstreet et al., 2011).

Note that we used B_{pa} instead of F-related indicators for sole, plaice and cod, as the latter, such as our original threshold candidate $F_{msyUPPER}$ from WKMSYREF3 (2014), stem from single species models. Single species reference F values are hard to align with ecosystem models' F_{msy} estimates (Walters et al., 2005), while this is less of an issue for those biological reference points that are biomass related.

2.6.   Matching GES and optimized yields

With a set of effort regimes that should lead to optimized yields for all fleets simultaneously on the one hand and those that produce GES on the other hand, we sought to identify if there were options that would lead to both objectives' criteria to be satisfied. Those effort regimes would fulfil variants of both the Common Fisheries Reforms' demand for MSY and the MSFD's GES. If no overlap between initial conditions of GES and MSY existed, we would present trade-offs in conservation and fishing targets that have to be accepted to obtain such a match.

3. Results

3.1.   Single species maximum yields

The combination of efforts of beam trawl (BT), demersal (DEM) and shrimpers (SHR) fleet that led to the highest equilibrium catches of cod was, relative to 2010: 300% BT; 90% DEM; 0% SHR. For a maximum equilibrium catch of plaice, this was 210% BT; 240% DEM; and 0% SHR; for sole the combination was 120% BT; 300% DEM; and 540% SHR. Uttermost equilibrium catches of brown shrimp

were obtained at 300% BT; 270% DEM; and 480% SHR. These solutions represent our purposive variant of single species MSYs, and whilst they may occur at the extremes of the effort levels tested (in particular for non-targeting fleets), neighbouring and lower effort levels did well produce yields close to these MSYs. Figure 8 to Figure 11 show combinations of efforts that led, for the four scope species cod, plaice, sole and brown shrimp, respectively, to equilibrium catches of at least 80% of these maximally possible catches.
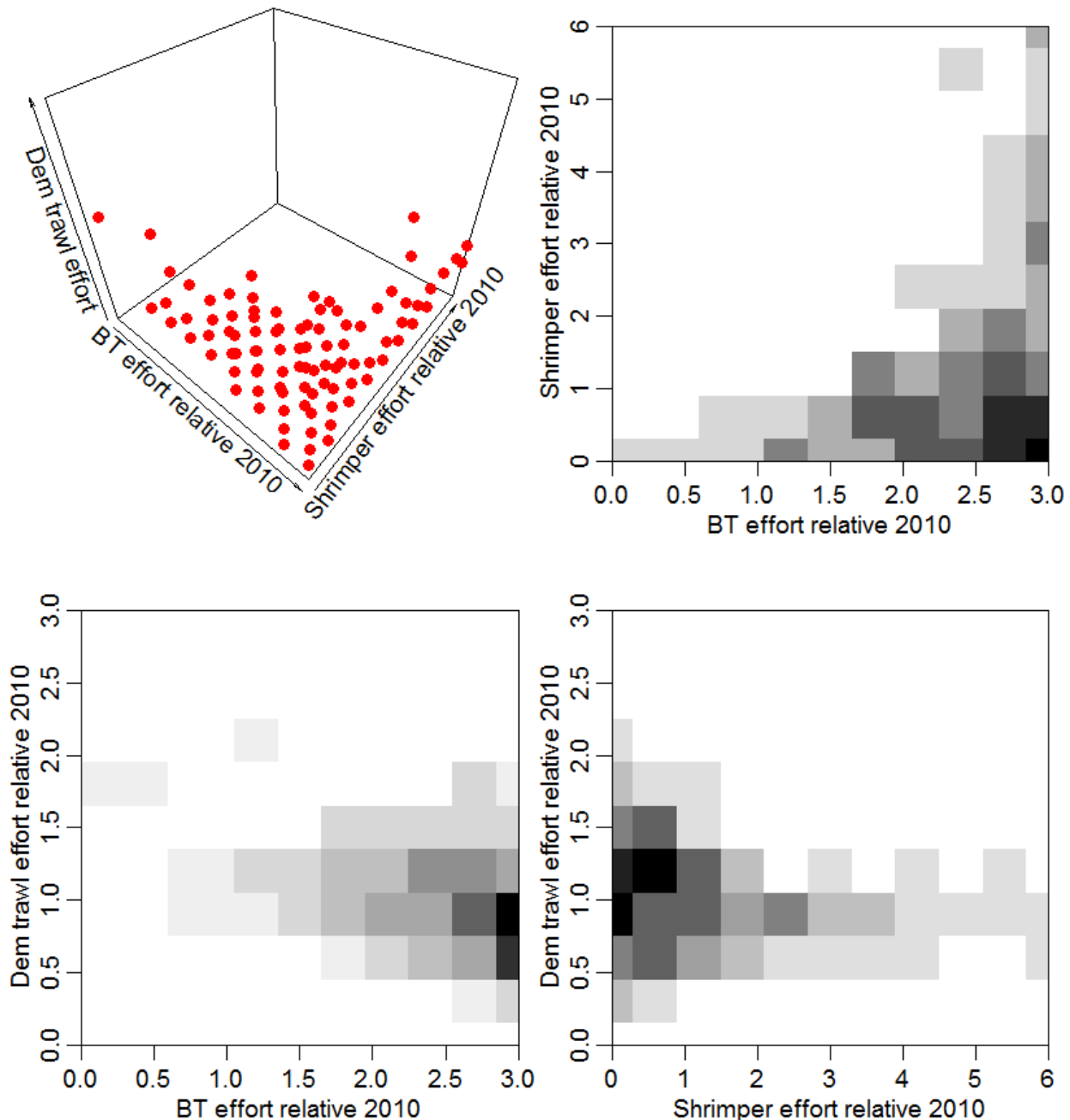
Figure 8: Spheres indicate effort combinations of demersal, shrimp and beam trawlers (BT) that lead to long-term prediction of catches of cod being 80% or more of the maximum possible catch of that species. Shades are projected on the respective planes to assist visual perception. The shades of grey correspond to the amount of overlaying spheres.
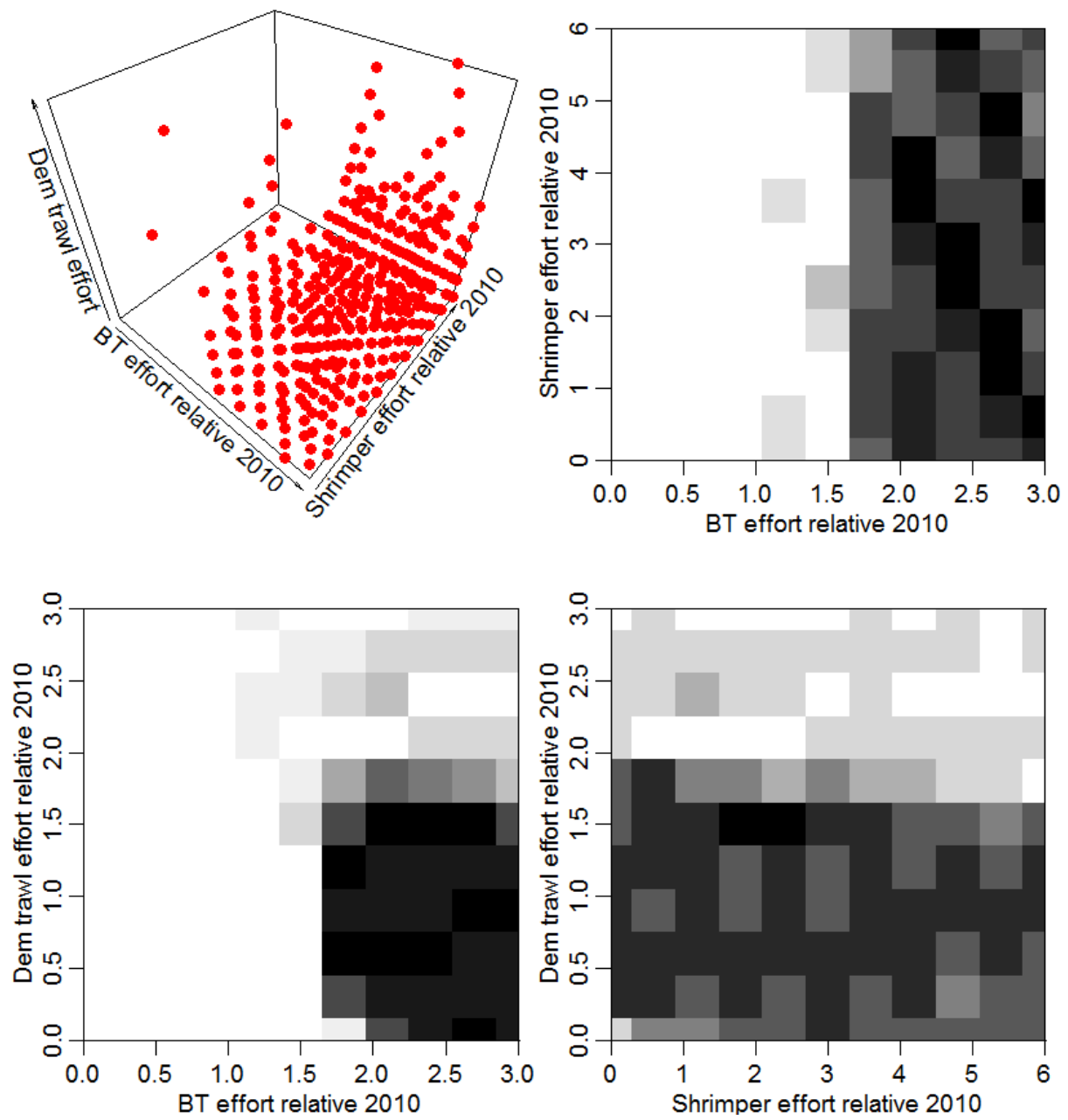
Figure 9: Effort combinations that lead to long-term prediction of plaice catches being 80% or more of the maximum possible catch of that species.
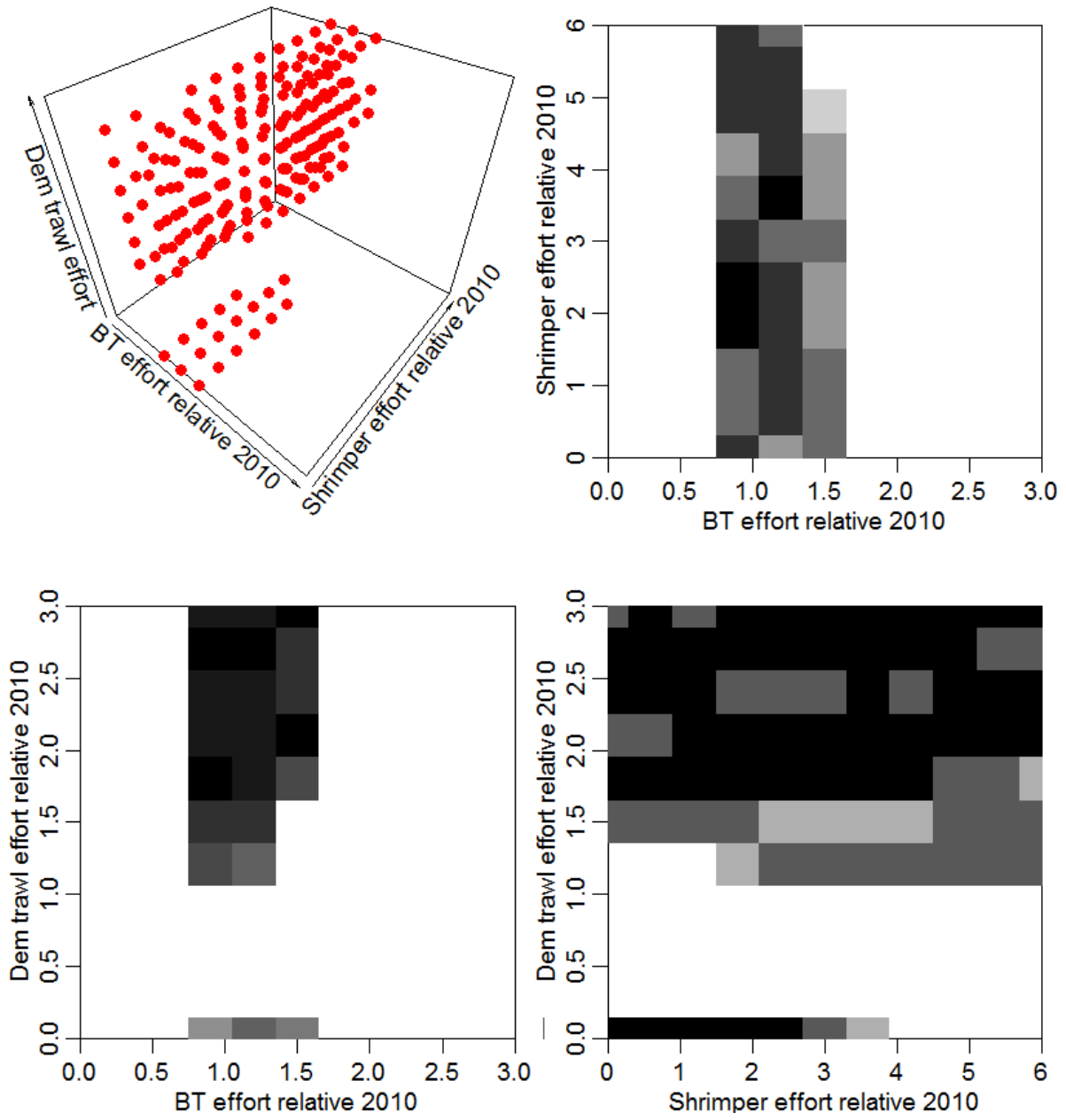
Figure 10: Effort combinations that lead to long-term prediction of sole catches being 80% or more of the maximum possible catch of that species.
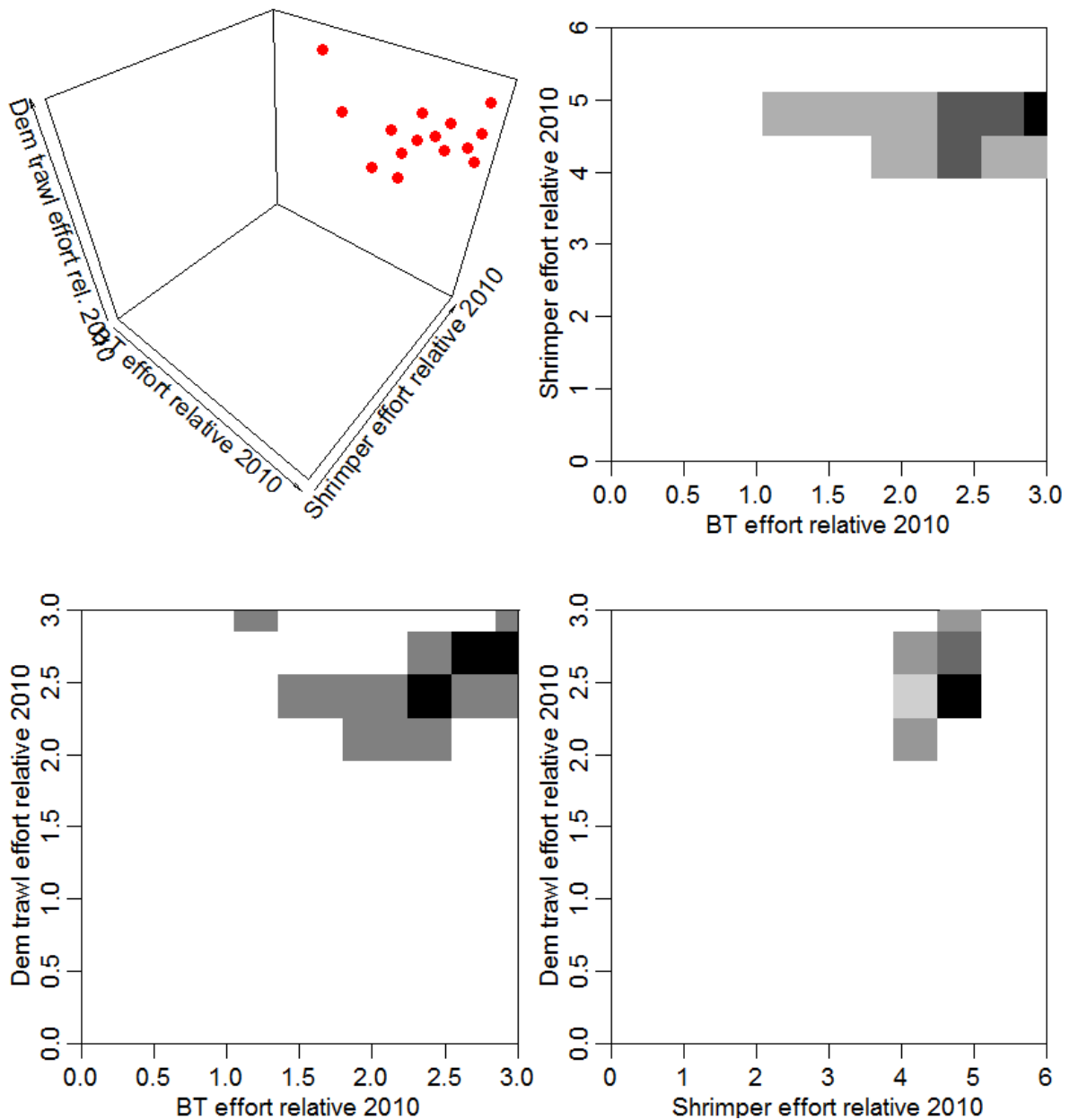
Figure 11: Effort combinations that lead to long-term predictions of brown shrimp catches being 80% or more of the maximum possible catch of that species.

3.2.   Multispecies yields

With the goal of presenting a negotiation space that leads to acceptable outcomes for all three fleets, we sought for effort combinations that would result in all four scope species being caught at a certain, ideally high, percentage of the maximum possible catch for the particular species. We did, however, not find any such solutions until we lowered this percentage down to 30%. Responsible for that low outcome are trade-offs between the yields of demersal and shrimp trawlers, as further described in Section 4.3. The resulting negotiation space is shown in Figure 12, which indicates effort regimes that led to catches of every focal species, cod, plaice, sole and brown shrimp, of at least 30% of what would be possible if all three fleets were managed just to obtain maximum yields of that particular species.
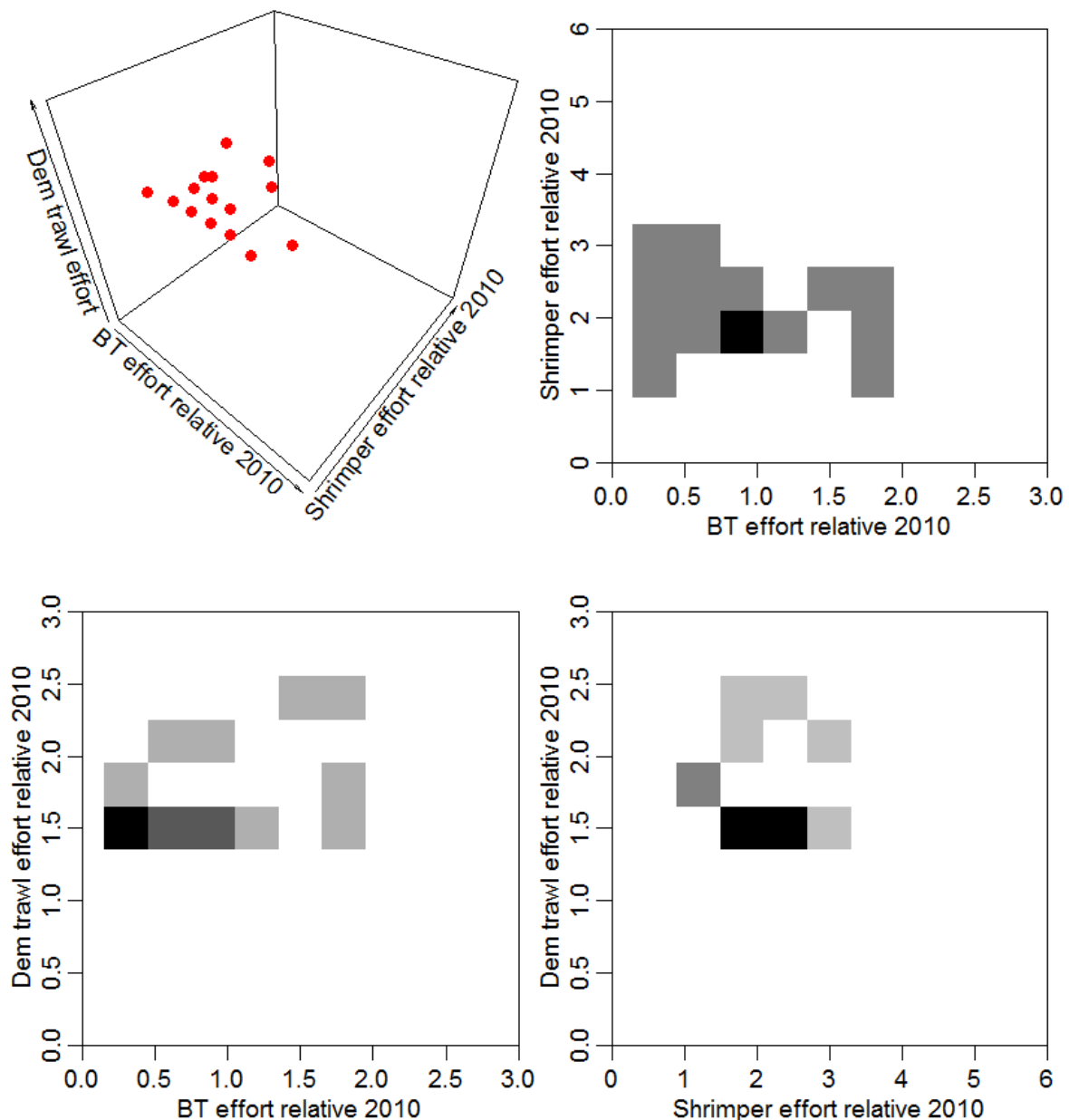
Figure 12: Spheres indicate effort regimes that lead to all four scope species — cod, plaice, sole and brown shrimp – to be simultaneously caught at 30% of their respective maximal possible catches. Shades projected on planes.

3.3.   Good environmental status

No effort regime succeeded to satisfy all indicators that we chose for our proxy of a good environmental status, as the demand for a spurdog F below the F_{MSY} proxy of 0.029 suggested by WGEF (2014) proofed impossible to meet through management of beam, demersal, and shrimp trawlers alone in the southern North Sea. We thus replaced this threshold value and allowed fishing mortality for spurdog to reach up to 0.1, as, according to our model, spurdog can recover to a biomass of around twice the one in 1991 at this F. The resulting effort combinations leading to satisfaction of the updated set of GES indicators are shown in Figure 13. They show strong dependency of GES on beam trawling effort, whilst, based on the set of indicators selected, no effect of shrimpers could be demonstrated. The results suggest that, when aiming to achieve GES, demersal trawling effort should not significantly be increased beyond 2010er levels.
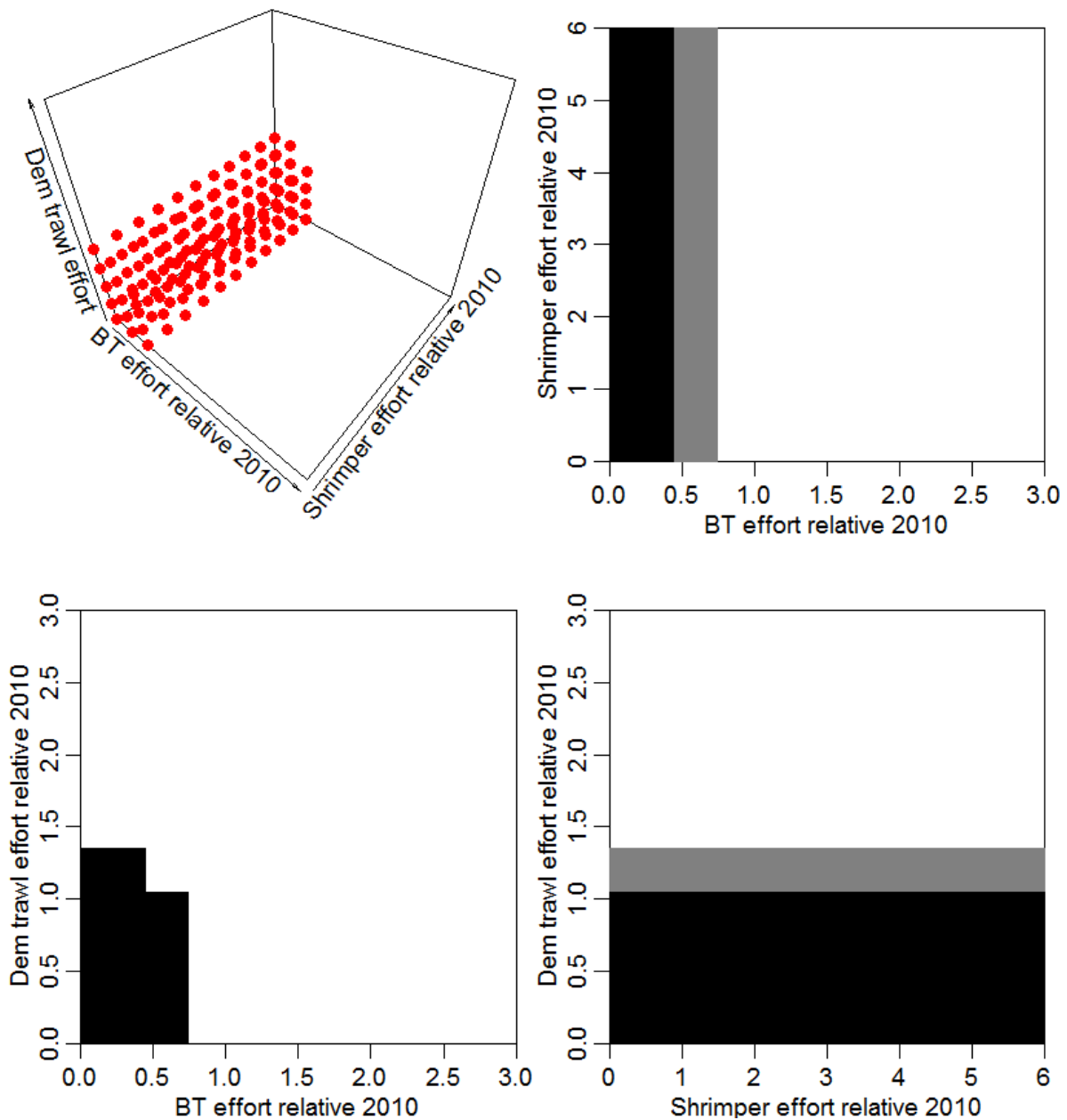
Figure 13: Effort combinations that lead to equilibrium states of the ecosystem deemed to represent a good environmental status.

3.4.   Matching GES and optimized yields

We found no overlap between those fishing regimes that lead to long-term predictions of at least 30% catch of each scope species (Figure 12) and other regimes that produced a long-term GES (Figure 13) without accepting trade-offs in the definition of thresholds. One such alternative threshold for turbot comes from ICES single species assessment for 2013, which suggested F_{max} as a proxy for F_{MSY}, with a range of 0.31 – 0.37. Even the higher of the two, however, does not allow GES and optimized fishing yields to coexist. We thus abandoned an F limit for turbot, and rose the acceptable F limit of spurdog by another 12% to F = 0.12, a value still allowing recovery of the stock according to our model. Figure 14 presents the set of effort regimes that allow all species being fished at least 30% of their maximum possible rate, whilst safeguarding B_{pa} of cod, sole and plaice and with a large fish indicator above the 0.3 threshold. In the three cases indicated, fishing mortality of turbot ranges from 0.42 to 0.65.
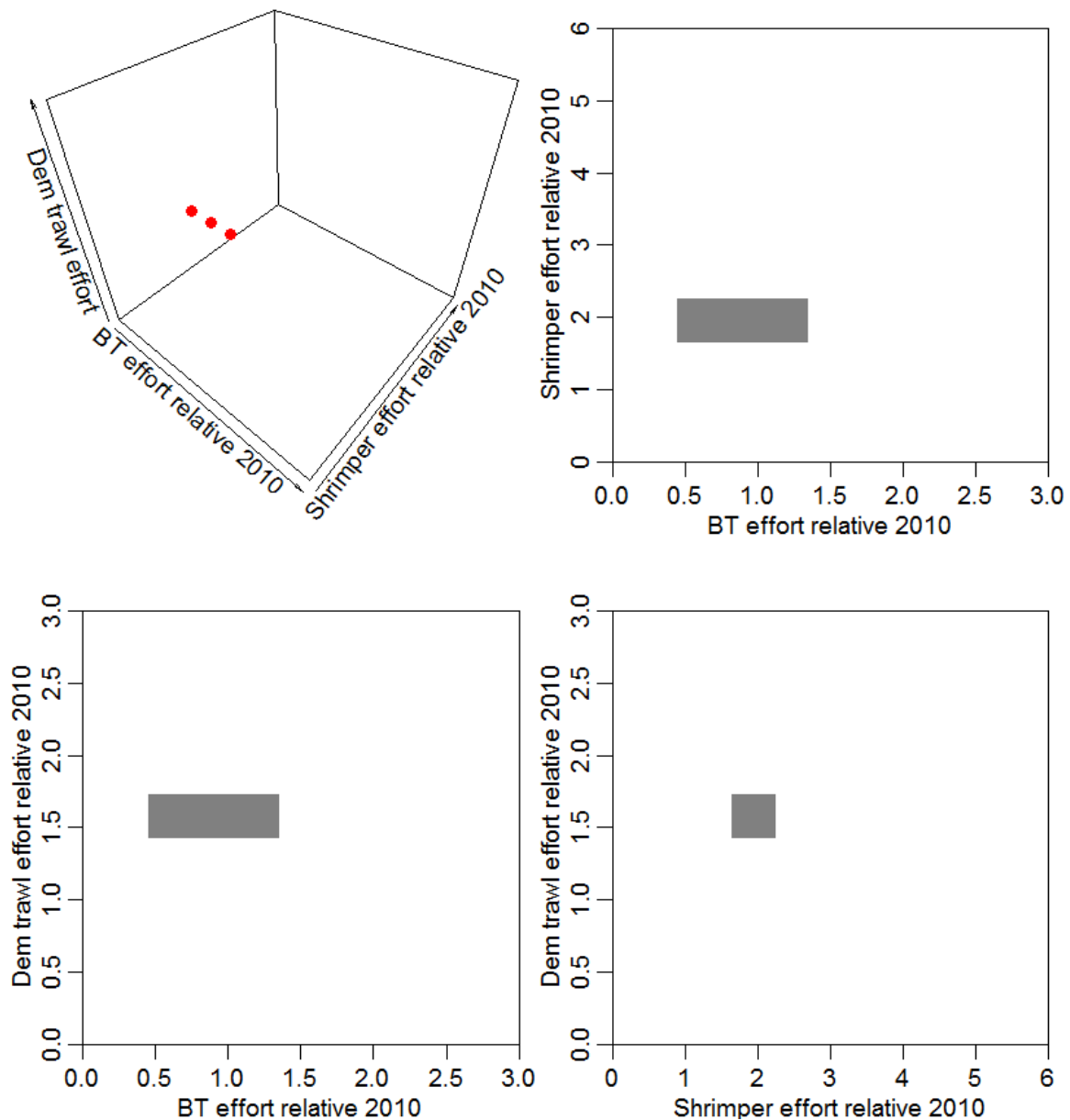
Figure 14: Spheres show fishing effort combinations that safeguard B_{pa} of cod, plaice, and sole, assure LFI larger 0.3 and simultaneously provide at least 30% of the uttermost possible catches of cod, plaice, sole and brown shrimp in long-term predictions.

4. Discussion

4.1.   A southern North Sea food web model

Parametrizing our southern North Sea model for 1991 and driving it to 2010 as a 'hindcast' allowed us to ascertain that the Ecosim model proofed capable of accounting for the interactions between and across fleets and species, as demonstrated through the plausible representations of Fmsy values and stock recruitment relationships (Section 2.3). This approach runs the risk of overlooking changes in fish' and invertebrates' diets that may have occurred since 1991. However, the ICES year of the stomach data still provides the most comprehensive assessment of fish diets in the North Sea, while newer studies are locally restricted. Together with those associated to stomach sampling, our model inherits the uncertainties of the surveys, stock assessments and multispecies model (SMS) data it was

parameterized with and fitted to. As technological development increases the efficiency of fishing vessels (Eigaard et al., 2014), it is questionable in how far STECF effort statistics (Rätz and Mitrakis, 2012) alone deliver a complete picture of the fishing pressure the species were subjected to or whether the so called technological creep may play a role here. Including estimates of technological development in fitting and parameterizing ecosystem models is certainly a promising future exercise.

The fitted and calibrated Ecosim model was able to reproduce trends in most biomass pools estimated for the southern North Sea 1991 – 2010 (Figure D 1 in Appendix D). As outlined in section 2.3, it would have theoretically been possible to acquire an even better fit to the data points by including more groups into the fitting routine or by searching for a primary production function with more than three splines. However, this would have increased the risk of an over parameterization of the model and contradicted the parsimonious approach we followed. Of the scope species of our policy exploration exercise, we achieved a good approximation to the observed biomass time series of plaice and sole, while the model underestimates biomasses of cod in earlier years of the simulation. The upward trend of southern North Sea cod in the later 2000's is, however, well represented. We found the high turnover dynamics of brown shrimp challenging to implement in Ecosim, particularly in an MSY context, as information on their recruits' trophic role and population dynamics are scarce. Generally, our model's most critical uncertainties relate to the quality and implementation of diet data and the fitting and calibration of the vulnerability parameters that designate population and trophic behaviour of the groups. In the latter lay the fundamental challenges posed to ecosystem models for fisheries management: the effect of fishing on marine systems and their fish stocks is often such convoluted with environmental and trophic effects that it is ambitious to impossible to disentangle (Mackinson, 2013; and references therein). Where this endeavour succeeds, the use of ecosystem models for fisheries management traditionally faces debates on the need to incorporate a large set of parameters with associated uncertainties (Essington, 2004; Pikitch et al., 2004). We thus state our findings as being of qualitative rather than quantitative nature. Nevertheless, our approach demonstrates how trade-offs between MSY and GES related policies can lead to serious trade-offs. We propose a way to identify likely trade-offs and to find compromises between different objectives and policies.

4.2.   Single species maximum yields

Our equilibrium simulations of the effect of different fishing effort regimes of demersal, beam, and shrimp trawlers on long term catches of cod indicate that the southern North Sea stock is likely to produce best results at a demersal trawler effort level around the one in 2010 (Figure 8). This is in alignment with what we would expect from the relationships between fishing mortalities and catches we established in the calibration of our Ecosim model (Figure 6): F at highest Ecosim yields is fairly close to adult cods' F in 2010 according to the ICES stock assessment (WGNSSK, 2013). Interestingly, good cod catches are predominantly obtained at high BT efforts. We suspected this effect to relate to competition for food between cod and plaice. We found considerable predator niche overlaps (Christensen et al., 2008) between adult plaice and juvenile (0.5, with 0 meaning no and 1 meaning largest overlap) and adult (0.7) cod for our Ecopath food-web. Similarly, cod on the eastern Scotian Shelf show considerable niche overlap with flatfish, in this case with Long-rough dab, *Hippoglossoides platessoides* (Bundy and Fanning, 2005). In our system, a reduced plaice stock through high beam trawl efforts thus allows eminent cod catches, suggesting that indirect food-web effects counterbalance direct bycatch effects for BT on cod. Cod in the southern North Sea generally benefit from low shrimpers effort, as brown shrimp is one of the main preys consumed by cod juveniles (Table A3 in Appendix A).

High long term catches of plaice (Figure 9) and sole (Figure 10) appear rather subtly dependent on the extend of demersal and shrimp trawling, but scale around beam trawl effort levels that produce F values close to our Ecosim calibrations' F_{msy} for the two species (Figure 6). This is particularly the case

for sole, while plaice shows more interactions with demersal trawls, which contributed around 20% to its fishing mortality. This bycatch surmounts the positive effect of otter trawling on plaice abundance and catch through the above mentioned food-web interaction with cod. A minor impact of shrimp fishing on flatfish catches can be perceived from the precise effort combinations leading to absolute maximum catches of plaice and sole (Section 3.1): While plaice are vulnerable to fishing for shrimp through bycatch of their recruits (around 12% of juvenile plaices' total F was caused by shrimpers in our Ecosim hindcast in 2010), sole appear to indirectly benefit from shrimp trawling: their bycatch in this fishery is negligible, whilst they are in competition for food with plaice when adult, as indicated by a 0.95 predator niche overlap.

Catches of brown shrimp (Figure 11) show a clear benefit from 'culling' of cod through demersal trawling. Cod is crangon's main predator in our model, and its diminution appears to allow the shrimp stock to very well sustain fishing efforts five times higher than the one executed in 2010. Being a low trophic level species with high turnover rates, brown shrimp run a low risk of recruitment overfishing. The suggestion of these high fishing pressure being beneficial must however be interpreted with care; it is sensitive to the parameterization of cods' diet and to the population dynamics of the recruits' stanza of brown shrimp, for which information is scarce. Temming and Hufnagl (2014) found reduced predator stocks to benefit commercial landings of brown shrimp alike. They do, however, warn that, at the current state, the fishery already contributes the major part of brown shrimps' mortality and that a potential growth overfishing of the stock is indicated.

4.3.   Multispecies yields

A first striking insight from the attempt to show effort regimes leading to 'pretty good yields' – not quite *sensu* Hilborn (2010) – from all species simultaneously is that these yields are pretty low. There are regimes that lead to all species being extracted at 30% of their maximum possible rate (Figure 12); however, the fact that no such results exist when 35% are demanded suggests that in the 30% solutions, at least one species produces poor catches. Responsible for that is the interplay between two fleets, but not, as one might expect, a negative one. Much more so, the fishery for brown shrimp such importantly benefits from reduction of its predators cod (and NB also whiting, *Merlangius merlangus*) through the demersal trawlers that yields of at least 30% of the highest possible brown shrimp catch require demersal trawl efforts far beyond those that lead to maximum catches of cod. The resulting negotiation volume is a trade-off between high brown shrimp catches and not entirely ruined cod stocks, which would be substantially overfished at this state. Similarly, Mackinson et al. (2009b) found it impossible to achieve single species MSY of cod, haddock and whiting at the same time in the North Sea. Prior to our study, we thus had not expected yields close to single species MSYs for the much interlinked southern North Sea food-web either. The actual impossibility of achieving even acceptable yields simultaneously, however, is new. The question is in how far that insight represents a failure of our concept of the negotiation space or if rather the approach inherits the problems demonstrated for a variety of systems in which lower trophic species are fished: That considerable increases of fishing pressure are required to produce catches close to maximum sustained yields (Walters et al., 2005), which goes along with significant impacts on predatory species and the ecosystem (Smith et al., 2011).

4.4.   Good environmental status

Effort regimes leading to long-term predictions that satisfied our GES descriptors are depicted in Figure 13. The results are quite direct consequences of the respective effort levels and not marked by unexpected indirect effects. As such, beam trawlers can only fish at the lowest effort rate investigated (30% of 2010), and only so at minimal fishing activities of the demersal fleet, as else turbot fishing mortality overshoots the precautionary proxy F. Demersal trawling effort is limited first by adult cods' biomass falling below B_{pa}, and thus unable to exceed 120% of the effort in 2010. None of the indicators

included so far is sensitive to the effort of shrimp trawlers, which is a factor worthwhile considering in future studies. Candidate indicators for this should certainly include measures of the impact of trawling on seabed integrity. Note that, with such descriptors missing from the current analysis, our conservation scenarios can only be considered as proxies for the GES actually demanded by the MSFD.

4.5.   Matching GES and optimized yields

The initial impossibility of aligning optimized yields and GES in our modelled ecosystem illuminates challenges that may await Europe's fishing grounds. There is a need to localize indices and thresholds, as demonstrated for the limiting spurdog F suggested by the ICES working group on elasmobranch fishes. This threshold proved unfeasible for our model area, potentially as it is derived from assessments on a whole Northeast Atlantic stock. Local population and catch patterns, though, may significantly differ, and for some fisheries, e.g. the southern North Sea's beam trawl fleet, these could well be relevant management entities. Even more importantly, our results caution that the selection of descriptors and thresholds, but also of postulated yields, is critical to allow realistic coexistence of the Common Fisheries Policies' MSY and the MSFD's demand for a GES.

5. Conclusion

With this study, we have suggested one possible interpretation of a multispecies or ecosystem scale variant of MSY for the southern North Sea. We tested the application of the concept and demonstrated that it is impossible to achieve good yields of all species simultaneously. While doing so, we quantified technological and trophic interactions between species and fisheries that lead to trade-offs between policy goals for the respective fleets and marine conservation. The studies' intuitively inconvenient result can be seen as a humble contribution to the question of what we want in fisheries management. In our concrete case, this could mean a discussion about which percentages of the maximum possible single species yields we are willing to accept as 'good outcomes' and in how far these shares can differ between species. Including GES descriptors helps to frame this discourse and shows which conservation thresholds are particularly costly in terms of yields and *vice versa*.

Our study aligns with others questioning the classic MSY approach in multispecies and mixed fisheries concepts (Hilborn, 2010; ICES, 2013; Mackinson et al., 2009b; Walters et al., 2005). In a certain acceptance of that fact, it is now understood in the ICES and also European Commission context that MSY targets should be perceived as ranges, rather than precise values, a notion that lead the development of long term management plans and guided the ICES-MYFISH Workshop to consider the basis for Fmsy ranges for all stocks (WKMSYREF3, 2014). However, as our study indicates, there is a risk that even this range-based approach may not lead to results that are perceived as satisfactory.

6. Acknowledgements

Author contribution

MS and AK developed the idea for this study. MS parametrized the model, in cooperation with AK, SM, and CG; and advised by AK, AT and SM. JJP contributed flatfish data and expertise and the two-

dimensional layouts of figs. 8-12. MS performed the analyses and wrote the text, which all authors revised and discussed. The manuscript has been published in the journal *Ecological Modelling*.

7. Appendix C

This appendix outlines the procedures followed to assemble time series of pressure and state variables to drive and calibrate our Ecosim model of the southern North Sea. An overview of all time series gathered and their respective calculation methods can be found in Table C 1.

7.1.   State variables – biomasses and landings

Analogue to the calculation of biomasses for the Ecopath model, time series for species with an analytical assessment (i.e. commercial round- and flatfish) were calculated based on single or multispecies assessment abundances multiplied with IBTS spring CPUE south-to-total-ratios (Table C 1). Deviating from the calculation for Ecopath, Ecosim time series values were calculated for each year 1991 – 2010 and then transferred to reference biomasses relative to 1991.

As for the Ecopath biomass calculation, sandeel biomass was calculated as the sum of TSB in Sandeel Areas SA1, 2 and 3, for each year from WGNSSK (2012); Tables 4.2.10; 4.3.9 and 4.4.12. Biomass of the years 1991-2010 was then set relative to 1991. Our turbot biomass time series are the change in total stock biomass (TSB) from the stock assessment (WGNSSK, 2013) relative to 1991. For brill, TSB estimates were calculated based on each year's ratio of brill over turbot CPUE in the ICES Beam Trawl Survey (BTS; www.Datras.ices.dk, download date 02 May 2013), multiplied with the respective year's turbot TSB. Biomass indices of nephrops come from different managing areas (FUs). No single time series extends through the entire time span modelled (WGNSSK, 2012). We thus had to create it from data of the various different locations. Using the five time series available for Nephrops in the southern North Sea (Nephrops FU6 TV abundance; Nephrops FU34 (burrows/m²); Nephrops FU34 LPUE; Nephrops FU 33 LPUE and Nephrops FU8 Abundance) we a) converted them into time series relative to the respective maximum value; b) using the total estimated '91 biomass calculated for the respective FU as a weighting , first multiplied each such derived index with the biomass; and c) divided each index value by the total biomass in '91 from those FUs that a value occurred for during the time series year. Note that two different abundance time series were available for FU 34, one burrow- and one LPUE-based index. Both deliver comparable results apart from 2004. At last, d) we created the final unique time series as relative to its 1993 value, as most FUs' time series lacked data prior to 1993. The biomass time series of brown shrimps was estimated from swept-area based biomass estimates mentioned in Annex A.

For functional groups not subject to analytical assessment but included in the IBTS, relative biomass reference time series were created as spring (Q1) CPUE relative to 1991. The benthos time series used in MDNS are from the DOVE marine lab, which is located off Newcastle, i.e. in the centre of our study area. We thus adopted the benthos time series sources Mackinson and Daskalov (2007) and Mackinson (2013) use. The same accounts for abundance time series of the zooplankton groups.

Landings time series were calculated as the total amount of each functional group landed from ICES divisions IVb and IVc according to Eurostat (http://info.ices.dk/fish/CATChSTATISTICS.asp, data downloaded 2 December 2012). There, dab landings apparently have not been reported by the Netherlands between 1990 and 1997 (inclusive). We thus calculated – for each ICES division specifically – the mean contribution of Dutch dab catches to the total amount of this species caught in the respective years, for catch data 1998-2010, and for 1988-'89. For both groups separately (data not pooled), the average was calculated and then multiplied with the total amount of dab caught 1990-'97 by all other nations. This estimate of the catch of Dutch dab by the Netherlands was then entered as Dutch dab landings 1990-'97. Ray landings in Eurostat during the 90's are mostly not resolved up to

species level, but reported as *"Raja rays nei"*. Others were reported as *"Rays; stingrays; mantas nei"*. Between 2008 and '10, resolution of landings to species level increased. We thus calculated the mean ratio of *thornback and spotted rays* versus *skate & cuckoo ray* and *starry ray & others* for this timeframe. These ratios were then applied to the whole time series 1991 – 2010 to split unresolved rays onto the three functional groups: *Skate and cuckoo ray* 1.086%; *Thornback and Spotted ray* 97.745%; and *Starry ray and others* 1.170%. The landings of nephrops from managing areas FU 6,8,33 and 34, as reported in WGNSSK (2012), were summed up annually to create a nephrops landings time series. *C. crangon* landings are from WGCRAN (2012).

7.2.   Pressure variables – fishing efforts and mortalities

We entered time series to force the effort of most fleets over the time period modelled. For *demersal trawl and seine; beam trawl; sandeel trawl; pelagic trawl; brown shrimp trawlers* and *nephrops trawl* time series were used as in Mackinson and Daskalov (2007) and its updates, but from 2003 onwards we relied on relative changes in total effort of the respective fleets in ICES statistical area IVb and c derived from effective effort data per ICES statistical rectangle (Rätz and Mitrakis, 2012; Appendix 05). *Drift and fixed nets'* effort was left on 1991 level until 2004, after which changes relative to 2003 were adopted according Rätz and Mitrakis (2012). Effort time series of the crangon fleet are from WGCRAN (2012). All effort time series relative to 1991 are visualized in Figure C 1 and Figure C 2.

For stocks with an analytical stock assessment available (turbot, sole, cod, herring, plaice, haddock and whiting), assessment F (HAWG, 2013; WGNSSK, 2012; WGNSSK, 2013) was used as forcing F in the model (Figure C 3, Figure C 4 and Figure C 5). Sole Fbar2-6 is from WGNSSK 2013, Table 10.4.1. Whiting Fbar(2-6) is from WGNSSK 2012 Table 12.3.2, as such summary is unavailable in WGNSSK 2013. Plaice Fbar(2-6) comes from WGNSSK 2013, Table 8.4.1. Haddock F(2-4) is from WGNSSK 2013, Table 13.3.5.4. Herring Fbar(2-6) is from HAWG 2013, Table 2.6.3.12. An F time series for commercial size crangon (Figure C 3) comes from Temming and Hufnagl (2014). It was assumed that the Fs from the North Sea wide assessments are representative for the F of the stock component in IVb and c. This is a critical assumption, but no area based F estimates were available during compilation of the time series.
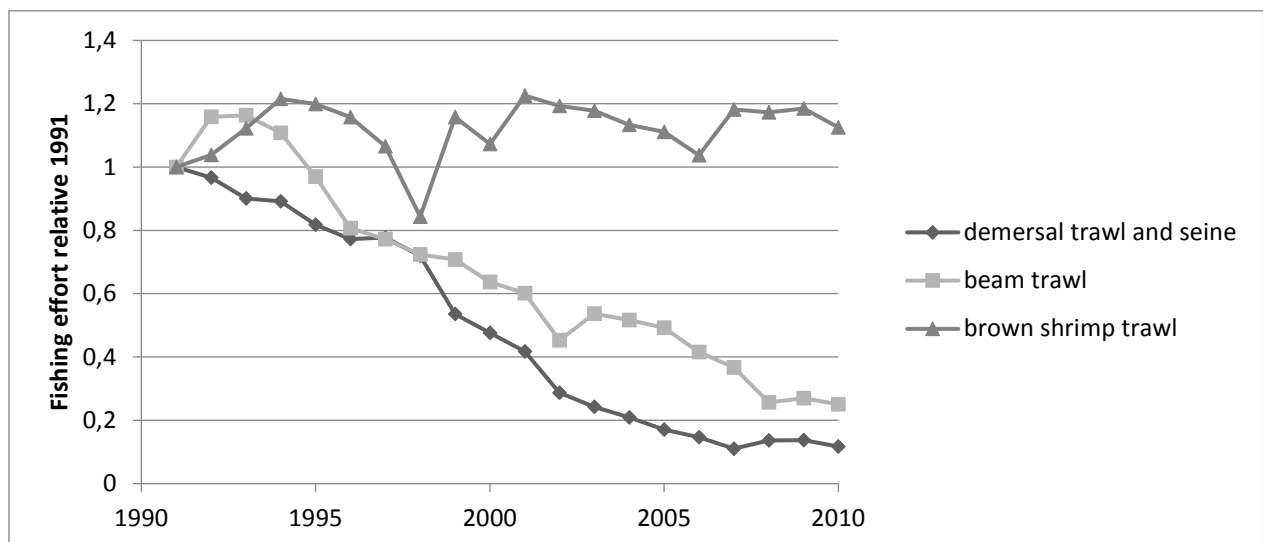
Figure C 1: Fishing effort of demersal trawl and seine, beam trawl and brown shrimp trawl in the southern North Sea relative to 1991.
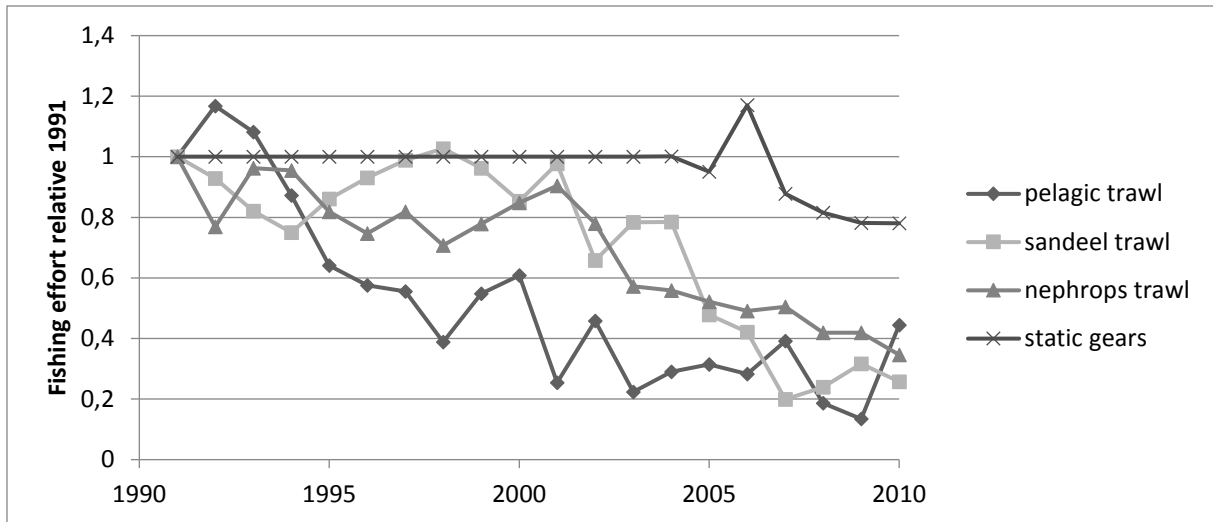
Figure C 2: Fishing effort of pelagic, sandeel and nephrops trawls and static gear in the southern North Sea relative to 1991.
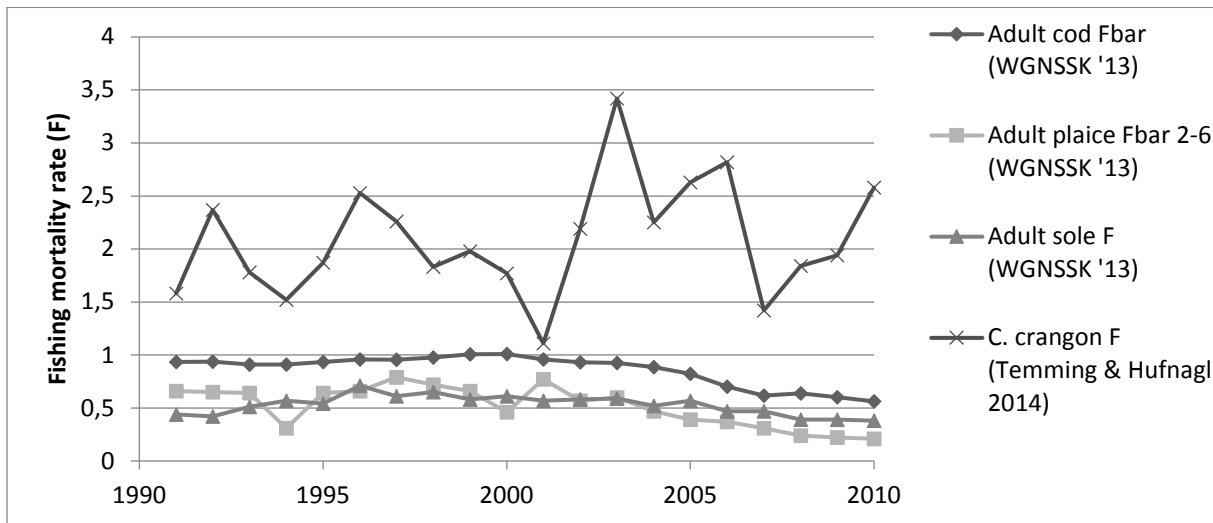
Figure C 3: Fishing mortality rate of cod, plaice, sole and brown shrimp.
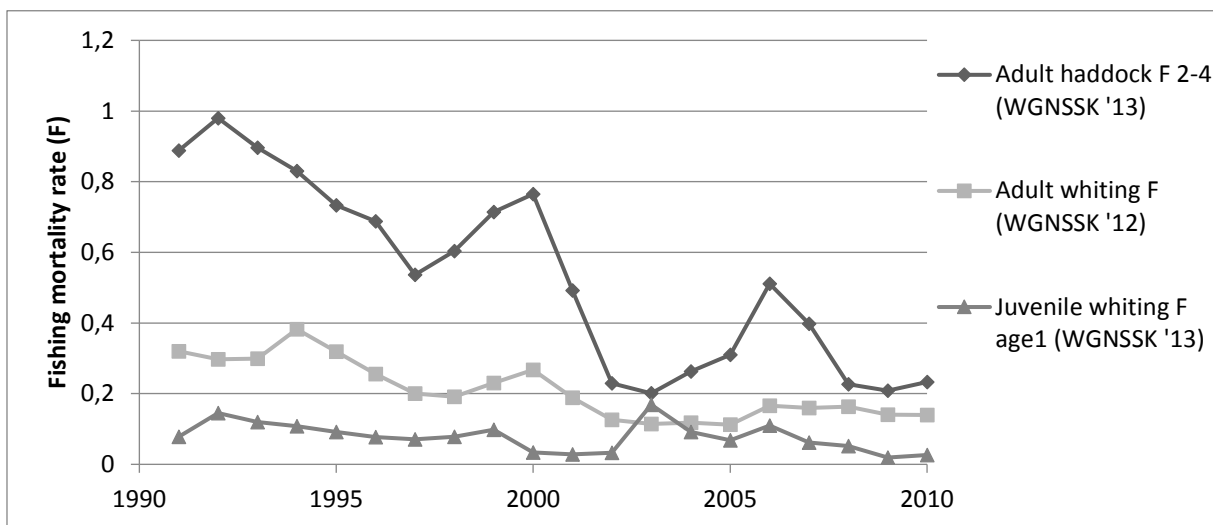
Figure C 4: Fishing mortality rate of haddock and whiting.
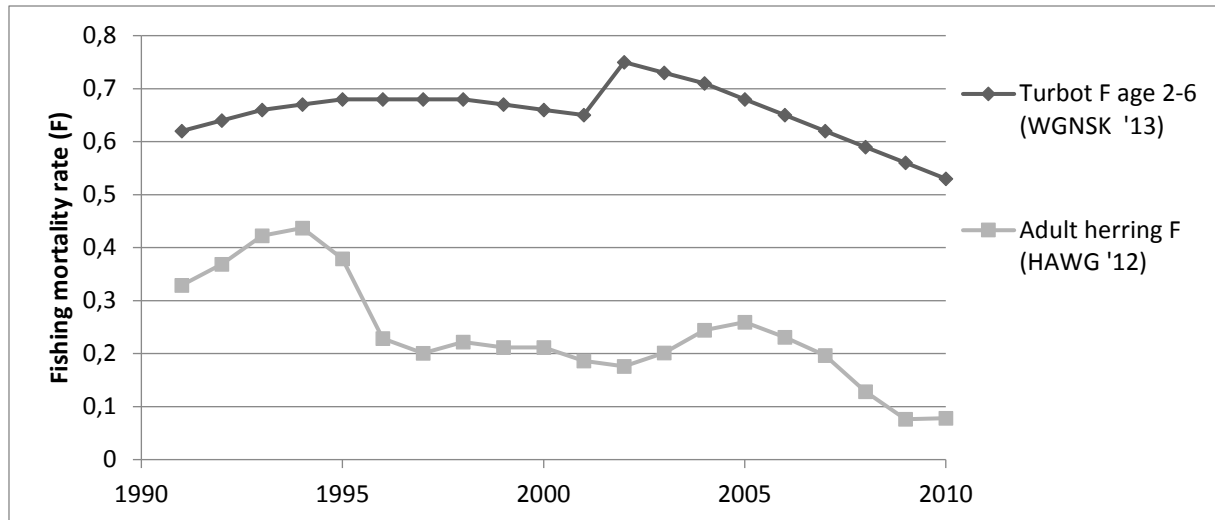
Figure C 5: Fishing mortality rate of turbot and herring.

Table C 1: The Ecosim time series of state and forcing variables and their respective calculation method.

Name of the time series	Type	Calculation method
Spurdog...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Large.piscivorous.sharks...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS autumn (Q3) CPUE*
Small.sharks...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Starry.ray...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Thornback...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Skate...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Juvenile.Cod.0.2..0.40cm...IBTS_corrected_SMS_BIO	Biomass (state)	*IBTS spring (Q1) CPUE*
Cod..adult...IBTS_corrected_SMS_BIO	Biomass (state)	*SMS x IBTS south-to-total*
Juvenile.Whiting..0.1..0.20cm...IBTS_corrected_SMS_BIO	Biomass (state)	*IBTS spring (Q1) CPUE*
Whiting..adult...IBTS_corrected_SMS_BIO	Biomass (state)	*SMS x IBTS south-to-total*
Juvenile.Haddock..0.1..0.20cm...IBTS_corrected_SMS_BIO	Biomass (state)	*IBTS spring (Q1) CPUE*
Haddock..adult...IBTS_corrected_SMS_BIO	Biomass (state)	*SMS x IBTS south-to-total*
Norway.pout...IBTS.Q1.CPUE.kg	Biomass (state)	*SMS x IBTS south-to-total*
Other.gadoids..large...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Other.gadoids..small...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Monkfish...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Gurnards...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Herring..juvenile.0..1....Spring.CPUE	Biomass (state)	*IBTS spring (Q1) CPUE*
Herring..adult....Ass..x.Spring.IBTS	Biomass (state)	*SMS x IBTS south-to-total*
Sprat...SMS.x.Spring.IBTS	Biomass (state)	*SMS x IBTS south-to-total*
Mackerel...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Sandeel.B.WGNSSK12	Biomass (state)	*Sum of TSB in SA 1,2&3 (WGNSSK'12, Tab. 4.2.10; 4.3.9 & 4.4.12)*

Plaice..adult....Ass..x.Spring.IBTS	Biomass (state)	*Assessment (WGNSSK'12) x IBTS south-to-total*
Juvenile.Plaice...Spring.CPUE	Biomass (state)	*IBTS spring (Q1) CPUE*
Dab...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Long.rough.dab...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Flounder...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Sole..adult....Ass..x.Spring.IBTS	Biomass (state)	*Assessment (WGNSSK'12) x IBTS south-to-total*
Juvenile.Sole...Spring.CPUE	Biomass (state)	*IBTS spring (Q1) CPUE*
Lemon.sole...Spring.CPUE	Biomass (state)	*IBTS spring (Q1) CPUE*
Witch...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
rel.TSB.Turbot	Biomass (state)	*Assessment (WGNSSK'13)*
rel.estimated.TSB.Brill	Biomass (state)	*Extrapolated from turbot TSB and BTS CPUEs*
Megrim...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Halibut...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Dragonets...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Large.demersal.fish...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Small.demersal.fish...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
Miscellaneous.filterfeeding.pelagic.fish...IBTS.Q1.CPUE.kg	Biomass (state)	*IBTS spring (Q1) CPUE*
CarnWW	Biomass (state)	*Mackinson and Daskalov (2007) and updates*
HerbOmnWW	Biomass (state)	*Mackinson and Daskalov (2007) and updates*
Nephrops.weighted..Abundance.relative..93	Biomass (state)	*FUs individual biomasses, weighted by FUs biomass in 1991*
StnM1Epifaunalmacrobenthos	Biomass (state)	*Mackinson and Daskalov (2007) and updates*
StnM1Infaunalmacrobenthos	Biomass (state)	*Mackinson and Daskalov (2007) and updates*
comm..Crangon.sNoSe.B	Biomass (state)	*Swept-area based biomass estimates*
StnM1Smallmobileepifauna	Biomass (state)	*Mackinson and Daskalov (2007) and updates*
StnM1Smallinfauna	Biomass (state)	*Mackinson and Daskalov (2007) and updates*
StnM1sessileepifauna	Biomass (state)	*Mackinson and Daskalov (2007) and updates*
DEMERSALTRAWL.DEMERSALSEINEREFF	Fleet effort (forcing)	*Mackinson and Daskalov (2007) and updates' effort time series until 2003, STECF effort past 2003.*
BEAMTRAWLEFF	Fleet effort (forcing)	*Mackinson and Daskalov (2007) and updates' effort time series until 2003, STECF effort past 2003.*
SANDEELTRAWLEFF	Fleet effort (forcing)	*Mackinson and Daskalov (2007) and updates' effort time series until 2003, STECF effort past 2003.*
PELAGICTRAWLS.SEINEEFF	Fleet effort (forcing)	*Mackinson and Daskalov (2007) and updates' effort time series until 2003, STECF effort past 2003.*
FIXED.NET.EFF	Fleet effort (forcing)	*Constant until 2003, STECF effort past 2003*
NEPHROPS.TRAWL.EFF	Fleet effort (forcing)	*Mackinson and Daskalov (2007) and updates' effort time series until 2003, STECF effort past 2003.*
SHRIMP.TRAWL.EFF	Fleet effort (forcing)	*Mackinson and Daskalov (2007) and updates' effort time series until 2003, STECF effort past 2003.*
COD.adu...Fbar.WGNSSK.13	F by pool (forcing)	*Assessment F for entire North Sea (WGNNSK'13)*
WHT.juv...F.age1.sNoSe	F by pool (forcing)	*Assessment F (WGNNSK'13) scaled by EcoPath F*
WHT.adu...F.sNoSe	F by pool (forcing)	*Assessment F (WGNNSK'13) scaled by EcoPath F*

HAD.adu...F.2.4..WGNSSK.13	F by pool (forcing)	*Assessment F for entire North Sea (WGNNSK'13)*
HER.juv...F0.1	F by pool (forcing)	*Assessment F for entire North Sea (HAWG'13)*
HER.adu...F.sNoSe	F by pool (forcing)	*Assessment F for entire North Sea (HAWG'13)*
PLA.adu...Fbar.2.6..WGNSSK.13	F by pool (forcing)	*Assessment F for entire North Sea (WGNNSK'13)*
Sole..adult....F.from.WGNSSK12	F by pool (forcing)	*Assessment F for entire North Sea (WGNNSK'12)*
Turbot.F.age.2.6	F by pool (forcing)	*Assessment F for entire North Sea (WGNNSK'13)*
CRA_F_TEMandHUF2014_rel91	F by pool (forcing)	*Temming and Hufnagl (2014)*
Spurdog...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Large.piscivorous.sharks...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Small.sharks...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Starry.ray...others...extrapol.EUROSTAT.Catch	Catches (rate)	*Eurostat*
Thornback...Spotted.ray...extrapol.EUROSTAT.Catch	Catches (rate)	*Eurostat*
Skate...cuckoo.ray...extrapol.EUROSTAT.Catch	Catches (rate)	*Eurostat*
juvenile.Cod...EUROSTAT.catch	Catches (rate)	*Eurostat*
Cod..adult....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Whiting..adult....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Haddock..adult....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Norway.pout...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Other.gadoids..large....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Other.gadoids..small....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Monkfish...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Gurnards...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Herring..adult....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Sprat...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Mackerel...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Horse.mackerel...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Sandeels...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Plaice..adult....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Dab...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Long.rough.dab...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Flounder...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Sole..adult....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Lemon.sole...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Witch...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Turbot...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Brill...EUROSTAT.Catch	Catches (rate)	*Eurostat*

Megrim...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Halibut...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Large.demersal.fish...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Small.demersal.fish...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Miscellaneous.filterfeeding.pelagic.fish...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Squid...cuttlefish...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Large.crabs...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Nephrops.Landings.FU.6.8.33.34..t.km².	Catches (rate)	*Landings of FU6, 8, 33 & 34 summed (WGNSSK'12)*
Epifaunal.macrobenthos..mobile.grazers....EUROSTAT.Catch	Catches (rate)	*Eurostat*
Infaunal.macrobenthos...EUROSTAT.Catch	Catches (rate)	*Eurostat*
CRA_Landings_TEMandHUFNAGL2014	Catches (rate)	*WGCRAN (2012)*
Shrimp...EUROSTAT.Catch	Catches (rate)	*Eurostat*
Sessile.epifauna...EUROSTAT.Catch	Catches (rate)	*Eurostat*

8. Appendix D

This appendix covers details on the fitting and calibration procedure followed for the Ecosim model underling the analyses.

Table D 1: Final vulnerabilities after fitting and calibration of those functional groups included in the most parsimonious fit. All other predators' vulnerabilities are set to the standard value of 2.

Predator functional group	Vulnerability	Predator functional group	Vulnerability
Toothed whales	1E+10	Horse mackerel	1E+10
Seals	1.0	Sandeels	1.0
Spurdog	1.0	Juvenile Plaice	1E+10
Large piscivorous sharks	1.0	Dab	3.09793
Small sharks	10	Sole (adult)	0.507
Juvenile Cod	10	Juvenile Sole	1E+10
Cod (adult)	3.5	Lemon sole	1E+10
Juvenile Whiting	10	Turbot	1.790493
Juvenile Haddock	1.1	Brill	1.0
Haddock (adult)	1.1	Squid & cuttlefish	1.0
Norway pout	1E+10	Carnivorous zooplankton	1E+10
Other gadoids (large)	1.0	Copepods	868758.3
Other gadoids (small)	0.004791	Large crabs	1.0
Monkfish	1.0	Nephrops	1E+10
Gurnards	1E+10	Crangon (below 5cm)	1.99616
Sprat	1E+10		
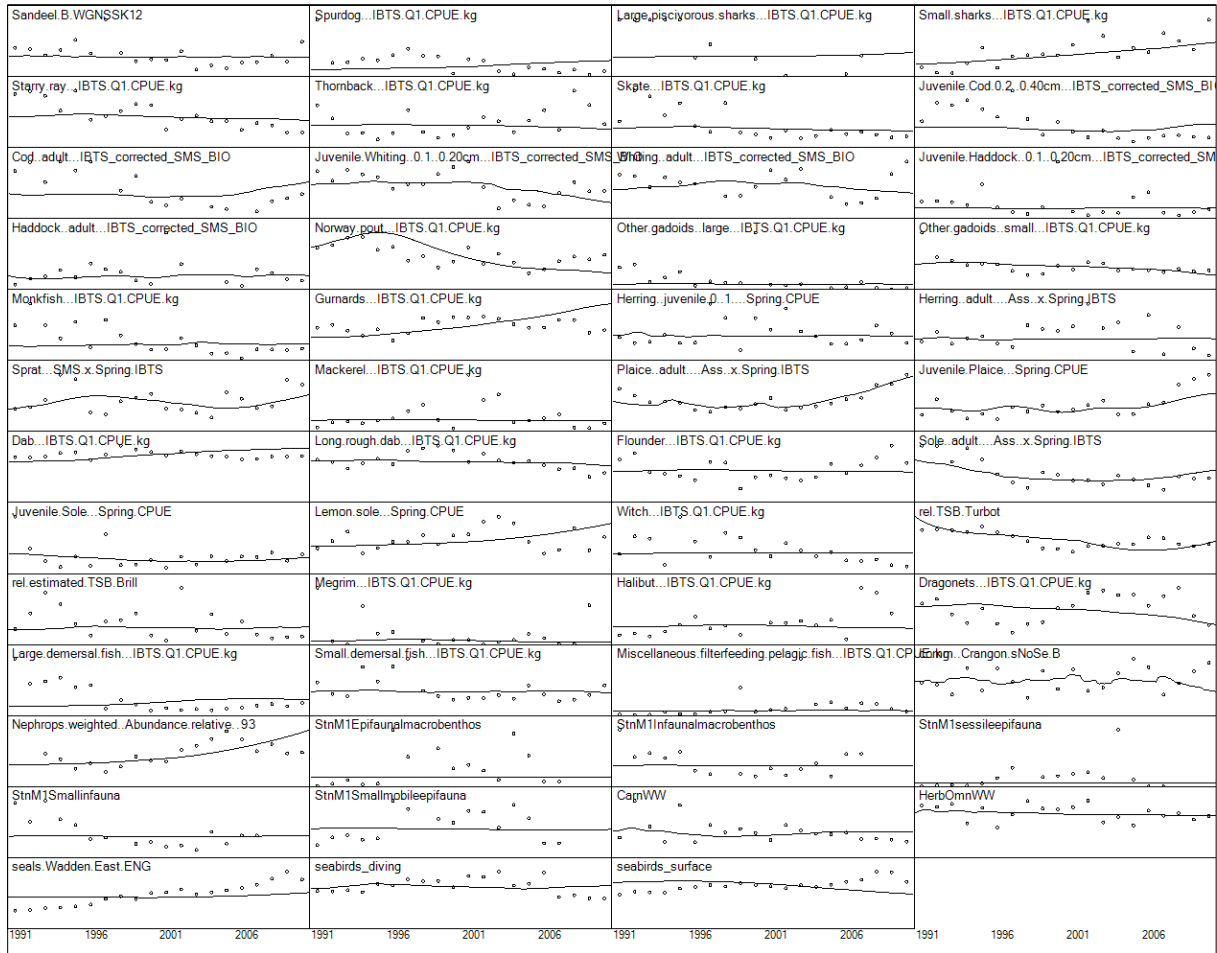
Figure D 1: Biomass estimate time series of the southern North Sea (dots) and biomass simulation results by the Ecosim model (lines).

Chapter 3

Density-dependent changes in the catchabilities of the southern North Sea's mixed flatfish fisheries and their impact upon bycatch species and food-web functioning under MSY objectives

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Keywords: +++ density-dependent changes in catchability +++ technological creep +++ MSY +++ North Sea fisheries +++ multispecies +++ mixed fleets +++ plaice +++ sole +++ food-web modelling +++

Abstract

Systematic causes of variance in a fisheries' catchability include technological development, fishers' behaviour or density-dependent changes in catchability. All three can affect estimations of efforts leading to maximum sustainable yields (MSY), with potentially deteriorating consequences for stocks, bycatch, and ecosystem functioning. This study identifies drivers of variations in catchability in the mixed fishery for sole and plaice in the southern North Sea using a statistical model fit to fishing effort and stock assessment data. It then assesses the spatial overlaps between stocks and efforts and seeks to relate those to density-dependent changes in catchability. Next, it employs a food-web model to seek fishing efforts leading to MSY with and without density-dependent changes in catchability implemented, and assesses the effects upon bycatch and food-web functioning.

Density-dependent changes in catchability significantly affected the catchability of sole and plaice by Dutch and Belgium beam trawlers, with fishers' species-specific targeting additionally playing a role for plaice. Spatial overlap between flatfish and beam trawler distribution at the scale of ICES rectangles did not deliver a conclusive explanation of the observed density-dependent changes in catchability. In our food-web model, efforts leading to MSY were higher, but also closer to efforts associated with stock collapses, when density-dependent changes in catchability were implemented. This caused

considerable effects for bycatch species and indirect effects mitigated through the food-web. In conclusion, density-dependence appears to be a major cause of changes in the catchability of North Sea sole and plaice. This affects the fisheries management of sole and plaice both in single species and ecosystem contexts.

1. Introduction

One critical assumption when using mathematical models for fishing policy explorations is the amount of impact the effort (f) of a fishing fleet has on a fished stock – the so called catchability (q). Many models assume this catchability to be constant, i.e. the proportion of a stock caught, the harvest rate or fishing mortality (F), increases linearly with effort and is independent of stock size. If the proportion of the stock harvested per unit of effort (FPUE) turns out to be dependent on factors other than just fishing effort, these models fail to make reliable predictions of stock stability, for instance because a rising catchability at decreasing abundance would increase the fishing pressure on the stock at a given effort level and raise the probability of a stock collapse. Ignoring density-dependent changes in catchability (ddcq) if they exist would also impair the predictability of effects in relation to effort controlling measures, such as effort levels leading to maximum sustainable yields (MSY) or safeguarding conservation goals. In several fisheries, catchability (q) has been shown to rise with decreasing stock abundance (Rose and Leggett 1991; Hilborn and Walters 1992; Swain et al. 1994; Rose and Kulka 1999). These insights encouraged further analyses on potential abundance related catch rate variabilities (Quirijns et al. 2008; Rindorf and Andersen 2008) and the incorporation of ddcq into mathematical fisheries models (Christensen et al. 2008; Garcia et al. 2012).

In the southern North Sea, as being part of the fishing grounds managed under the European Commission's Common Fisheries Policy (CFP; EC 2013), fisheries management is based on the MSY principle. It thus also applies to the mixed flatfish beam trawl fishery for European plaice (*Pleuronectes platessa*) and common sole (*Solea solea*). Figure 1 and Figure 2, displaying the temporal development of the relationship between F of sole and plaice against f of the Dutch and Belgium beam trawl fleet, shows that the two species' catchabilities in these fisheries appear to be far from constant. If that variability in FPUE could partially be explained by ddcq – and a comparison with biomass estimates (bottom left panels in Figure 1 and Figure 2) suggests so – several consequences for their exploitation in a single- and multispecies MSY context would arise. Primarily, F is no longer a function of effort only, but also of stock size, and efforts leading to the fishing mortality associated with maximum sustainable yields (Fmsy) would be different than under the assumption of abundance-independent catch rates. Note that under ddcq, catches per unit of effort can stay constant while abundance declines, a process referred to as hyperstability (Hilborn and Walters 1992). If, however, efforts leading to MSY differed, the amounts of other species caught in the fishery as bycatch would change as well. That would affect those stocks' management if they are the target of other fisheries (such as for cod, *Gadus morhua*) or a commercially important bycatch in mixed fisheries (e.g. turbot, *Scophthalmus maximus*; and brill, *Scophthalmus rhombus*). Also conservation measures to protect vulnerable species like long-lived elasmobranchs may need adaption. We thus see a need to test for the presence of ddcq in the single species managements of sole and plaice, but even more so in the multispecies MSY context of their mixed fishery with its associated biological and technical interactions.
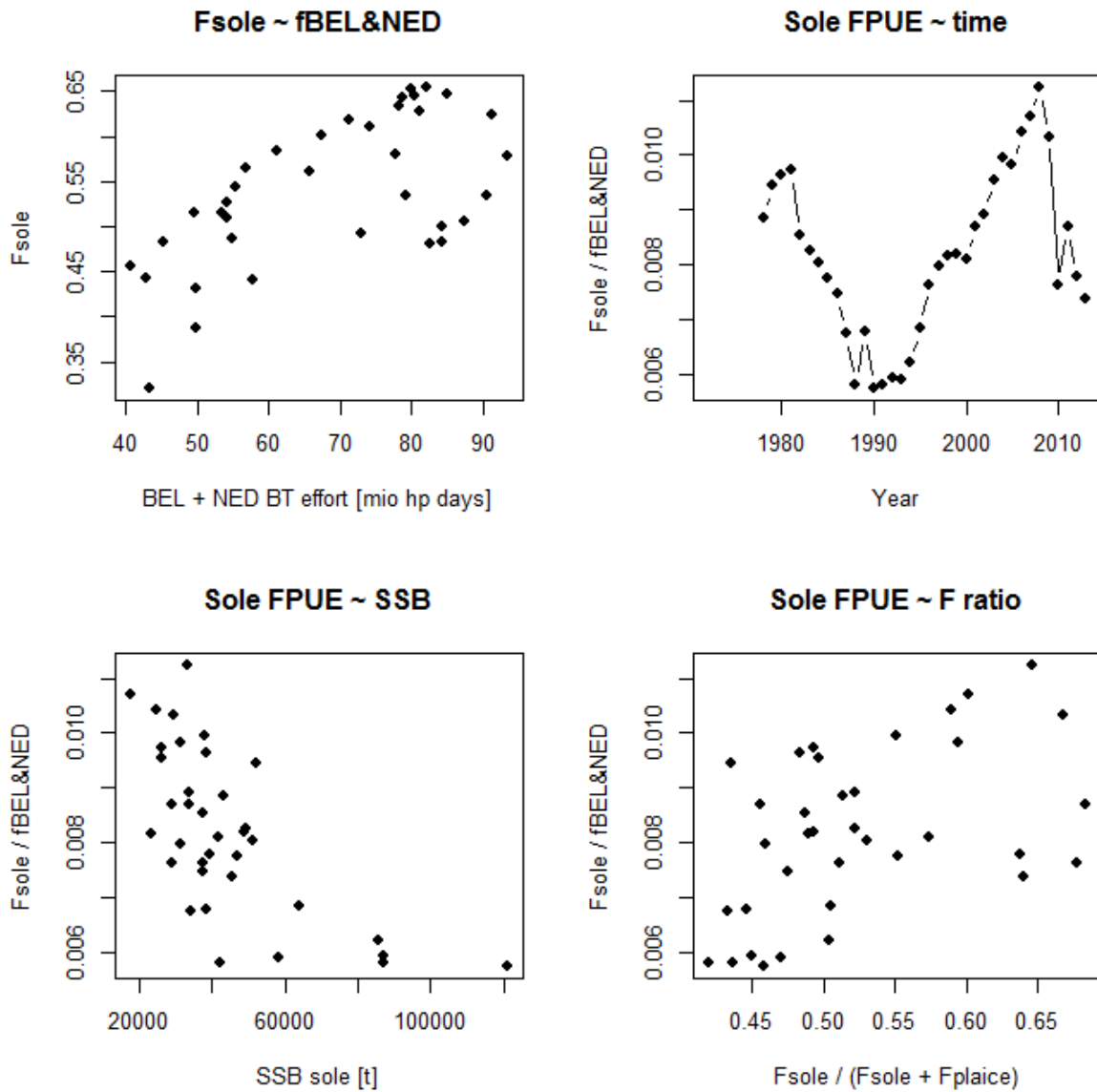
Figure 1: Pairwise comparison with sole fishing mortality and potential driving factors (c.f. section 2): Fishing mortality of sole (Fsole) against combined beam trawling effort of Belgium and the Netherlands 1978 – 2013 (fBEL&NED); the ratio between the latter two and time; sole spawning stock biomass (SSB); and the ratio between sole F and the summed F of sole and plaice (top left to bottom right). For data sources see section 2.1.
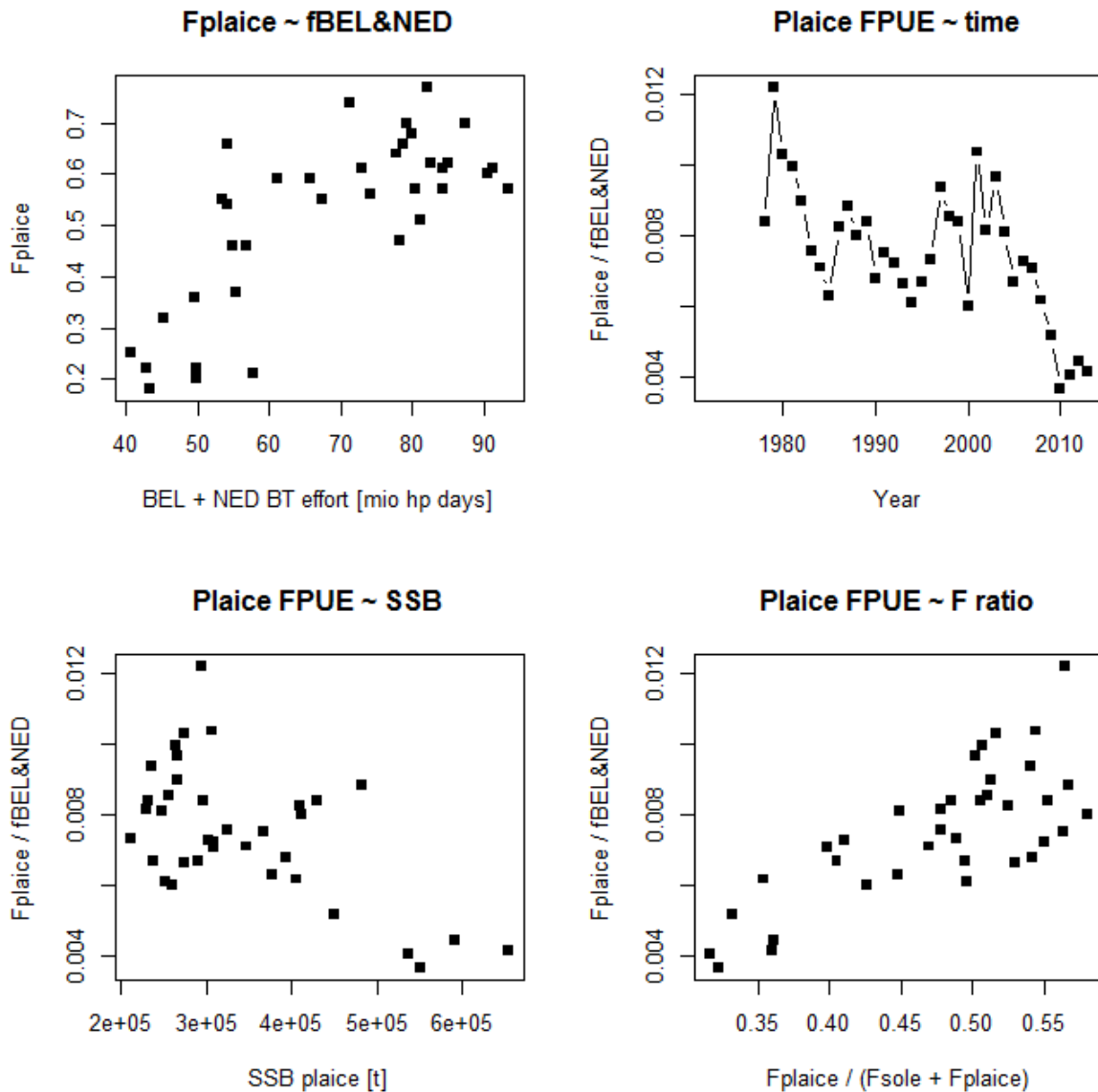
Figure 2: Pairwise comparison with plaice fishing mortality and potential driving factors (c.f. section 2): Fplaice against combined beam trawling effort of Belgium and the Netherlands 1978 – 2013; the ratio between the latter two and time; sole SSB; and the ratio between sole F and the summed F of sole and plaice (top left to bottom right). For data sources see section 2.1.

Ddcq are not the only possible cause of non-constant FPUE. Technological developments in fishing vessels' design, machines and gears, in deck equipment and catch processing facilities can lead to increased capture efficiency over time, a process also referred to as 'technological creep' (Hilborn, 1985; Pascoe and Coglan 2000; Eigaard, Marchal et al. 2014). Additionally, market driven incentives may drive the preference of fishers towards one of the species. As plaice and sole are caught in a mixed fishery by a beam trawling fleet fairly well capable of optimizing their catch composition (Miller and Poos 2010, Engelhard et al. 2011), a unit of effort can be applied to optimise the catch of sole or plaice, depending on economic considerations and quota availability (Quirijns et al. 2008, Poos, Bogaards et al. 2009). In this study, all four factors – fishing effort, stock abundance, technological development and preference of one species over another – were included in a statistical model to identify their effects and significance in driving the species' F.

Here we demonstrate the relevance and potential implications of ddcq of the southern North Sea's sole and plaice stocks in a multispecies, mixed-fisheries MSY context. Our study is broadly divided into a data analysis part (Sections 2.1 and 3.1), a spatial analysis (Sections 2.2 and 3.2) and an ecosystem modelling exercise (Sections 2.3 and 3.3). We tested the variabilities in FPUE (Figure 1 and Figure 2) against three hypothetical explanations, technological development, density-dependent changes in catchability, and focus of effort towards either sole or plaice. Using time series of F, and stock abundances of the flatfish, and fishing efforts of the Dutch and Belgium beam trawl fleet, we sought to understand the respective effects of stock abundance and technological development on variabilities in the response of F to nominal fishing effort. Given positive indications of ddcq through this statistical modelling exercise, we took a look at the spatial distribution of the flatfishes' biomass and beam trawling effort throughout the North Sea and examined whether ddcq could come from an increased spatial overlap of stocks and fleets during periods of lower abundances (Section 2.2).

Having gained estimates of the degree to which stock abundances affected the catchability of sole and plaice in the statistical modelling, we were interested in the consequences this would have on MSY considerations in a multispecies context. We used an ecosystem model of the southern part of the North Sea (divisions IVb and IVc of the International Council for Exploration of the Sea, ICES) to simulate how the ddcq detected in our statistical modelling affect beam trawling efforts leading to MSY (fMSY) and to demonstrate the effects that effort adjustments would have on F and abundances of other target stocks (amongst them cod, which, while being an important bycatch in beam trawling, is mainly caught by otter trawlers) and vulnerable species (Sections 2.3 and 3.3). The ecosystem model utilized for this study was parametrized following the Ecopath with Ecosim approach (Christensen et al. 2008). For a description of the model, see [Chapter 1 and Appendix thereof] or Section 2.3 of this study. Other than single species modelling, the use of an ecosystem model allowed us to also include indirect consequences of changes in fMSY on other species, such as potential positive feedback loops through reduction of a stock's predators or competitors (Mackinson et al. 2009b, Temming and Hufnagl 2014, Chapter 2). We did not investigate potential consequences of technological creep or species selection by fishers in the ecosystem modelling exercise.

2. Methods

2.1.   Statistical modelling

We investigated four factors driving the fishing mortality of sole and plaice stocks in the southern North Sea:

(I)   Beam trawl fishing effort

(II)   Technological development, by which the same nominal effort level can be applied more efficiently (i.e. leads to a higher proportion of the stock being harvested) in more recent times

(III)   Density-dependent changes in catchability, through which F, at a constant level of effort, varies depending on – in the case that mainly adult fish are yielded – spawning stock biomass (SSB) and

(IV)   Preference change of the target species: Directs fishing effort towards a catch composition that optimizes revenue from the fishery and quota uptake.

For the time span 1972 – 2013, we used time series of F and SSB of North Sea sole and plaice from single species assessments (WGNSSK 2015) and fishing efforts of the Dutch and Belgium beam trawl fleets (WGNSSK (2005) prior 2003, STECF (2014; https://stecf.jrc.ec.europa.eu/ewg1413) past 2003; with gear code 'BT2' and vessel sizes larger 15m) and of both combined (cf. Appendix E) to mechanistically model F taking all of the processes mentioned above into consideration. The formula

we used for our statistical model (Equation 2) is an adaptation of the approach used to incorporate ddcq in Ecosim. The original formula, as outlined in chapter 3.19 in Christensen, Walters et al. (2008), reads

Equation 1

$$F = \frac{fscaled * QR0}{1 + (QR0 - 1) * \frac{B}{B0}}$$

where *f scaled* is relative fishing effort, with f0 = F0, i.e. efforts are scaled so base year's q0 = 1; *B* is current biomass and *B0* that of the base year, and *QR0* = qmax / q0, i.e. the maximum possible increase of catchability through changes in stock biomass relative to the catchability in the base year of the analysis. With a QR0 larger 1.0, F at constant f (or FPUE) would increase with decreasing stock biomass (cf. left hand panel in Figure 3).

Basing our model on the Ecosim formulation allowed us to include any identified value of QR0 from our statistical modelling results into the ecosystem model, as Ecosim comes equipped to incorporate that factor in its simulations (Christensen, Walters et al. 2008). The way that catchability can be affected through the biomass of a stock in Ecosim when QR0 is set to values above 1.0 is illustrated in the left hand panel in Figure 3. It illustrates how, at a constant effort level, F can take different values depending on a stock's biomass, if ddcq apply (and QR0 is thus different from 1.0). Beyond the possibility of a non-constancy in F per unit of effort through ddcq, we expanded the equation with a multiplicative term accounting for technological development (or technological creep, *TC*) and an additive term to consider species preference (SP) by the fishers (Equation 2; Figure 3). We chose a linear representation of the effect of technological development through time on F (see mid panel in Figure 3), as a parsimonious representation of the irregular, stepwise changes which we would expect in reality (Eigaard, Marchal et al. 2014). Given that the original Ecosim equation operates on F rather than F per unit of effort (Equation), *f scaled*, i.e. relative fishing effort (c.f. Equation) was always keep on the right hand side of the equation.

Market incentives may cause the fishers to prefer one species over the other, and sole has been shown to be more extensively targeted due to its higher price (Pilling, Kell et al. 2008). We aimed to account for dynamics in this phenomenon through the time series analysed – which is up to 20 years longer than the one of Pilling, Kell et al. (2008). Generally, an increase in F, i.e. raised catches beyond the level supported by an increase of the population, should intrinsically display incentives to catch the species. However, modelling the effect of fishing preference of one flatfish over the other by Fi alone or Fi / Fj is misleading when F of both fleets decrease simultaneously, but due to different reasons, such as in more recent years, when F of sole (Fsol) and plaice (Fple) decreased through stock conservation efforts, but Fple additionally declined through the large increase of the stock. We thus deemed the ratio of F of the investigated species and the summed F of both species to be more appropriate. We chose the ratio Fi / (Fi + Fj), relative to the named ratio in the baseyear (Fi0 / (Fi0 + Fj0)), as an indicator for the catch preference of the species investigated (*i*), where *Fi* denotes F of the latter and *Fj* signifies F of the other of the two flatfishes (Figure 3, right hand panel):

$$Changes\ in\ Fi\ through\ species\ preferences = SP * (\frac{Fi}{Fi + Fj} - \frac{Fi0}{Fi0 + Fj0})$$

SP is the parameter fitted and tested in the statistical models to explain the share of variability in F due to changes in catchability caused by species-specific preferences of the fishers. Our final equation, incorporating representations of the effect of effort, density-dependent changes in catchability, technological creep and species preference by fishers on F of species *i*, reads

Equation 2

$$Fi \sim intercept + q * fx * (1 + TC * t) * \frac{QR0}{1 + (QR0 - 1) * \frac{SSB}{SSB0}} + SP * (\frac{Fi}{Fi + Fj} - \frac{Fi0}{Fi0 + Fj0})$$

where f_x is relative fishing effort of fleet *x*, Dutch or Belgium beam trawlers, or both combined; *intercept* is F if no f of the particular fleet is executed; *q* is the standard, non-density-dependent part of species *i*'s catchability; *QR0* = qmax / q0 with reference to the base year 1991; *t* is years passed since the first year of the analysis; *SSB* is current spawning stock biomass and *SSB0* that in the base year 1991; and *SP* is extend and significance of the species preference by fishers (cf. Figure 3).
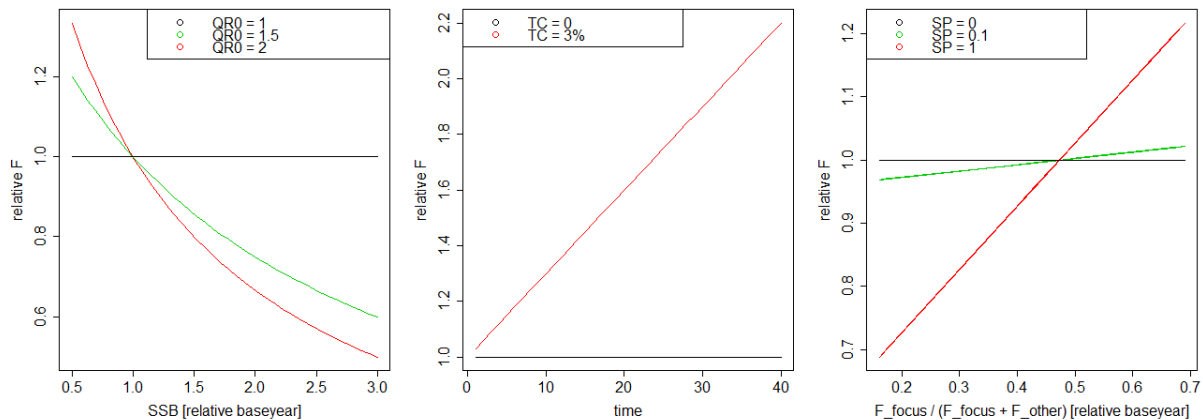
Figure 3: Illustration of the effects of the terms used in Equation 2 on fishing mortality at constant fishing effort (relative F): ddcq (QR0: maximal possible changes in catchability due to changes in biomass), technological development (TC: per annum increase in catchability due to technological development) and fishers' preference for one species over the other (SP: strength of changes in catchability due to species-specific preferences of fishers). Note that in the right hand panel, a value of 0.47 on the x-axis represents the situation of F_focus / (F_focus + F_other) in the baseyear.

Estimation of the parameters *intercept, q, TC*, *QR0* and *SP* was performed using the *nls* fitting routine in the *stats* package of R (version 3.2.4), which determines the nonlinear least-squares estimates of the parameters in the nonlinear model and their significances in explaining the response variable, *Fi*. We chose start values of *q* = 1, *intercept* = 0, *QR0* = 2, *TC* = 0.1 and *SP* = 0, but found the results to be inert to changes in the start values. Six cases were examined: F of sole as a function of beam trawling efforts of the Netherlands and of Belgium, and of both combined, respectively, and F of plaice as related to the Dutch and the Belgium fleets' efforts, and again of both combined, in all cases under consideration of potential ddcq, technological creep and species preference by fishers. Statistical modelling commenced with the full model (including q and intercept, ddcq, technological development and species preference), from which insignificant terms were subsequently removed until the final model would contain significant parameters only. It was then validated that the final, minimal adequate model would not fit the data significantly worse than the full model. Also, its performance was compared to a model representing a simple linear relationship between F and effort, i.e. $F_i \sim$ *intercept* + *q* * *f_x*. In cases where no significant differences in fit and AIC would be detected, and statistical assumptions were equally or better fulfilled by the simpler model (see paragraph below), it was chosen as the final model.

We tested each final model for compliance with statistical assumptions: Normal distributions of the residuals were tested with both Anderson-Darling tests and Cramer-von-Mises tests with a significance threshold of p = 0.1, and reference to QQ-plots and histograms of the residuals (top row in figures of

Appendix F). We verified if there was no trend of the residuals with predicted values through visual inspection of both values plot against each other (right hand side of second row in figures in Appendix F) and their Pearson or Spearman's rank correlation, depending on the nature of the residuals and predicted values. Independence in the stochastic component of the model was confirmed with the runs tests after Wald and Wolfowitz (1940) using the *runs()* function in *R*'s *TSA* package (Maindonald 2009). We further tested for signs of autocorrelation in the residuals, as visualized by the sample autocorrelation function (bottom left in figures of Appendix F) and consistent values below 0.05 in the sequence of Ljung-Box tests' p-values along a sequence of time lags (bottom right in figures of Appendix F; for this test, we considered p-values below 0.05 at five consecutive lags as non-acceptable autocorrelation of the residuals). Autocorrelations in the error terms would suggest that the stochastic component of the model cannot be considered white noise, but that a further process, which we were unable to include in the model, plays a role in driving F. The goodness of fit of the model to the data was expressed with R^2 and by plotting observed against predicted values (left hand side of second row in figures in Appendix F).

2.2.   Spatial overlap between beam trawling effort and flatfish spawning stocks

Where the statistical modelling (Section 2.1) led to significant indications of ddcq for plaice or sole, we investigated the spatial overlap between SSB of the respective species and fishing effort of each of the two fleets, the Dutch and the Belgium beam trawlers, and of both combined. We would use the same fishing effort data set as above (STECF annual effort per ICES statistical rectangle) and add information on the spatial distribution of sole from the ICES Beam Trawl Survey (BTS) and of plaice from the ICES International Bottom Trawl Survey (IBTS; both https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx; downloaded 2016-07-22, 14:00; Quarter 3 data used). As the STECF data covers 2003 – 2013, this was also the temporal extend of our analysis. For each rectangle during each year, we calculated the CPUE in total weight of length classes forming the SSB (>300 mm). As one substep of that, we converted fish length to individual weight using conversion factors from Fishbase (Froese and Pauly 2002), with records from outside the North Sea and Channel excluded (data downloaded 2017-02-16, 13:13). For each rectangle and point in time we then calculated the contribution to total SSB, by dividing its CPUE by the summed CPUE of all rectangles during that year. For fishing effort, we proceeded similarly: effort of large Dutch and Belgium beam trawlers, and of both combined ("BT2" at vessel size over 15m), was summed per rectangle in each year and then divided by the respective total effort throughout the North Sea. We then referred to Schoener's index of partial spatial overlap (Schoener 1970) to quantify the extend of partial overlap of SSB and fishing effort during each year:

Equation 3

$$Schoener\ index = 1 - 0.5 * \sum_{i}^{n} \frac{CPUEi}{CPUE} - \frac{fi}{f}$$

where *i* denotes each rectangle within all rectangles with either effort or SSB records (*n*). This index of spatial overlap for each year was then compared with the SSB from single stock assessment in a Spearman's rank correlation. A significant negative correlation would suggest that, as the stock shrinks, its overlay with fishing effort increases.

2.3.   Ecosystem modelling

2.3.A   An Ecosim food-web model of the southern North Sea

Our ecosystem modelling exercises, i.e. the incorporation of potential ddcq of sole or plaice into simulations of stocks, catches, and the state of the ecosystem, and for comparison of these scenarios with such in which no ddcq were considered, were based on the Ecopath with Ecosim (EwE) model (Christensen et al. 2008) parameterized for the southern North Sea (ICES areas IVb and IVc) in Chapter 1 and 2. The EwE model covers 68 biomass pools, or *functional groups*, ranging from the lowest (phytoplankton, benthic and pelagic microflora and invertebrates) to the highest (marine mammals, sharks and seabirds) trophic levels. Particular focus was given to those species extracted by fisheries, of which some were split into so called *multi-stanza groups*, with separate representation of adults and juveniles, which stock-recruitment dynamics were tuned to stock assessment data. 1991 was chosen as the base year for the model, given the best availability of fish' diets for that year (ICES 'year of the stomach'; Hislop et al. 1997). The time-dynamic Ecosim model was fitted to biomass, abundance, catch, fishing mortality and fishing effort data ranging 1991-2010. For more information about the model and its application, see Chapter 1 and 2, the appendix thereof, and Kempf et al. 2016

2.3.B   Description of the modelling exercise

For cases in which the statistical modelling revealed significant signs of ddcq, we incorporated the estimated QR0 in the Ecosim model (*Ecosim > Input > Group info*) to investigate the consequences on fMSY, and the consequences of a new fMSY on F and biomass of other species. For the traceability of the results, no ddcq of other species was assumed. To seek fMSY, we used Ecosim's dynamic interface and ran a set of different effort time series for 200 years respectively. In these effort time series, we kept all fleets' efforts stable at the level executed in 2010, while only changing the beam trawling fleet's effort by 10% in each consecutive run. After each simulation, we recorded the annual simulated catches of the species investigated, and sought for fMSY, the beam trawling effort that, if steadily applied, would produce the highest total plaice or sole catches at the end of the modelled period.

This search for fMSY was performed twice: Once under the assumption of no ddcq, i.e. with QR0 = 1.0, and once with consideration of the significant QR0 estimated in the statistical modelling. To explore the consequences that an effort adjustment under ddcq would have on other components of the ecosystem, we ran both fMSY scenarios for 200 years and recorded mean biomass (B) and F of all functional groups throughout the last 40 years of the simulations. For comparison and validation of the results with ICES' advice, we displayed the effort of beam trawling leading to fMSY relative to the one that would lead to the Fmsy suggested by ICES (WGNSSK 2015).

3. Results

3.1.   Results of the statistical modelling

We found ddcq (QR0 = 2.00; p < 0.001) to significantly drive the fishing mortality of sole as caused by the Dutch beam trawl fleet, while technological development and species preference by fishers played no significant role (Table 1). The minimal adequate model resulting from the maximal model described in Equation 2 performed significantly better than one of a simple linear relationship model between F and effort, F ~ f (R^2 0.72 vs. 0.53; AIC -118.3 vs -101.0). Residuals of the minimal adequate model were on the edge of normal distribution. They showed minor heteroscedasticity and correlation with the response variable. Some signs of temporal autocorrelation could be found (Figure A 1).

Despite ddcq being a just non-significant contributor to explaining the FPUE of sole caused by Belgium beam trawlers, we maintained the term in the final model, since else the model would perform significantly worse than the maximal model. Besides this effect of ddcq (QR0 = 3.42; p = 0.059; Table 1), TC and species preference played no significant role. The final model derived from Equation 2

outperformed a simple F ~ f relationship (AIC -108.1 vs -99.9; R^2 0.37 vs 0.20). For both models, the residuals were normally distributed. The final model's residuals were further homoscedastic, but correlated positively with the observed F; and were temporally autocorrelated (Figure A 2). The model was associated with a fairly low R^2 (Table 1), presumably indicating that Belgium's beam trawlers are not a key cause of the fishing mortality of sole. Generally, sole catches by the Netherlands are around eight times higher (WGNSSK 2015).

When Dutch and Belgium beam trawling efforts were combined to explain soles' F, a significant indication of ddcq emerged (QR0 = 1.88; p < 0.001; Table 1). Technological development and species preference by fishers did not turn out to be significant drivers of sole F per unit of combined beam trawl effort. The model's intercept of 0.23 suggested that some background fishing mortality would prevail, even if no Dutch or Belgium beam trawling would occur. The minimal adequate model derived from Equation 2 was significantly superior to a simple F ~ f relationship, both in terms of fit (R^2 0.59 vs 0.38) and parsimony (AIC -103.2 vs -90.5). Also, it did not violate more or more severe statistical assumptions than the simpler model did. The final model's residuals were not normally distributed, and correlated significantly with the response variable, showing systematic overestimation at low, and underestimation at high values of observed F. Residuals were homoscedastic against predicted values, but showed signs of temporal autocorrelation (Figure A 3).

We found ddcq (QR0 = 2.08; p < 0.001) and fishers' preference for plaice over sole (SP = 1.60; p < 0.001) to significantly drive the fishing mortality of plaice as caused by the Dutch beam trawl fleet, while technological development played no significant role (Table 1). The minimal adequate model resulting from the maximal model described in Equation 2 performed significantly better than one of a simple linear relationship model between F and effort, F ~ f (R^2 0.96 vs. 0.93; AIC -136.9 vs -63.4). Residuals of the minimal adequate model were on the edge of normal distribution, showed no significant pattern against predicted values or the response variable, and only showed negligible signs of temporal autocorrelation, at longer lags (Figure A 4).

For FPUE of plaice by Belgium beam trawlers, all terms had to be left in the final model, since exclusion of any of them would result in the model being significantly worse than the maximal model. The full model, which here also presented our final model, significantly outperformed the simple F ~ f relationship in fit (R^2 0.91 vs 0.52) and AIC (-126.9 vs -61.8), and produced normally distributed residuals, which the simpler model failed to. By making the maximal model our final model, it does contain non-significant terms, namely ddcq (QR0 = 4.64; p = 0.39) and TC (TC = 7.7%; p = 0.63). Species preference was found significant at that stage (2.02; p < 0.001; Table 1). The model's residuals, besides being normally distributed, were homoscedastic, but displayed some systematic relationship with the response variable (a tendency to systematically underestimate at high values of Fplaice and vice versa). The residuals were considerably temporally autocorrelated at all lags (Figure A 5).

When beam trawling efforts of both, Belgium and the Netherlands, are combined, their effect on plaice' F is driven by ddcq (QR0 = 2.15; p < 0.001) and species preference (SP = 1.75; p < 0.001; Table 1). The minimal adequate model with both these terms included performs significantly better than a simple F ~ f model (R^2 0.92 vs 0.56; AIC -130.9 vs -53.0). The final model's residuals were normally distributed, not correlated with fitted values nor response variable, and not significantly temporally autocorrelated (Figure A 6).

Table 1: Results of the statistical modelling, listing a) estimates for the significants terms of the minimal adequate model, where QR0: density-dependent catchability increase ratio; Tec. creep: technological development; Sp. pref.: targetting of the respective species assumed from, in the case of sole, Fsol / (Fsol + Fple), b) R², N and AIC of the final models and c) model diagnostics stating if the residuals were normally distributed, not correlated with predicted values, independent and not autocorrelated.

Species	Fleet	QR0	Tec. creep	Sp. pref	R^2	N	AIC	Normal	Not corr	Indep	Not autocor
SOL	NLD BT	2.00	/	/	0.73	36	-118.3	Yes	No	No	No
SOL	BEL BT	3.76	/	/	0.37	42	-108.1	Yes	Yes	No	No
SOL	Both	1.88	/	/	0.59	36	-103.2	No	Yes	No	No
PLE	NLD BT	2.08	/	1.60	0.96	36	-136.9	Yes	Yes	No	Yes
PLE	BEL BT	4.64	7.7%	2.02	0.91	42	-126.9	Yes	Yes	No	No
PLE	Both	2.15	/	1.75	0. 96	36	-130.9	Yes	Yes	Yes	Yes

3.2.   Results of the spatial overlap analysis

While statistical modelling suggested that differences exist between the fleet-stock dynamics of Dutch versus Belgium beam trawlers (Section 3.1), our spatial analysis confirmed that both fleets operate in different areas (Figure 4; see also Figure 1 in Sys et al. 2016). The Dutch fleet chiefly fishes off the Wadden Sea and the Dutch and Flemish coast, while Belgium beam trawlers mainly occupy areas further west, off England and the southern Belgium coast. With the two fleets having their core efforts distributed in different areas, they also showed different patterns of spatial overlap with the sole SSB stocks: While for the Dutch fleet, the Schoener index of partial spatial overlap between spawning stock and effort did not show any signs of correlation with sole SSB, this was, to some extend (even though significant at the p = 0.1 level only) the case for Belgium beam trawlers (Figure 5). When efforts of both nations' beam trawlers were combined for the analysis (Figure 4), spatial overlap between stock and effort showed no significant correlation with diminishing stock size (Figure 5).

The spatial overlap between beam trawling efforts and adult plaice was generally lower than the one between BT and sole (Figure 6). For all three cases, Dutch, Belgium, and both fleets combined, the relationship between the spatial overlap of efforts and stock was u-shaped, showing high overlaps during periods with both high and low stock biomasses, with a phase of low overlap at intermediate biomasses 2007-2010. No systematic increase or decrease of the overlap between fleets and stock with SSB could be shown. Using IBTS data from quarter 1 instead of quarter 3 for plaice did not change the result of no correlation between overlaps and stock biomass, but for Belgium (negative correlation (-0.57) at a prevailing u-shape pattern; p = 0.065; results not shown). Generally, all figures and correlation indices indicate that if there was a systematic relationship between overlap and stock biomass it would be a negative one (higher overlap at lower biomass).
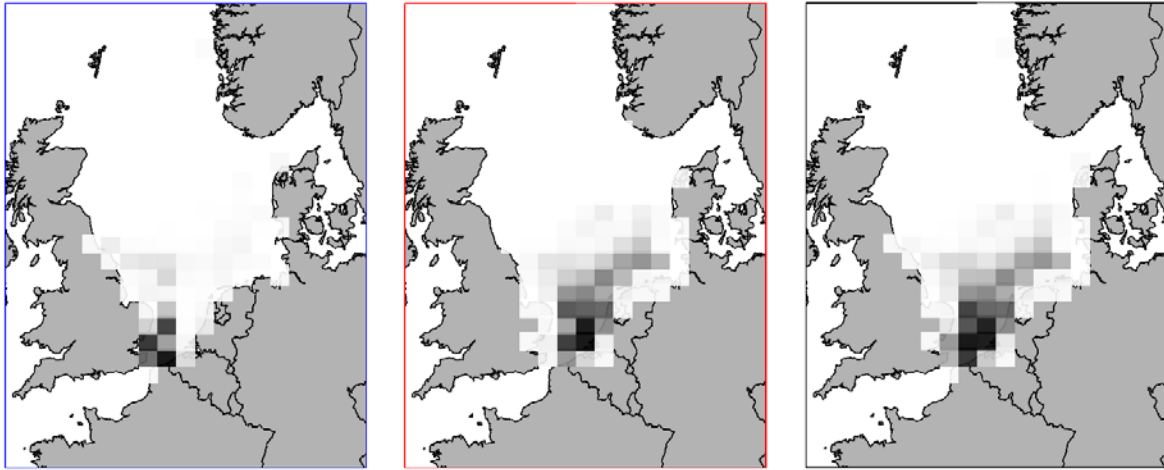
Figure 4: Mean 2003 – 2013 distribution of beam trawling efforts (BT2) by Belgium (left), Dutch (middle) and both nations' (right) vessels larger 15 m in the North Sea.
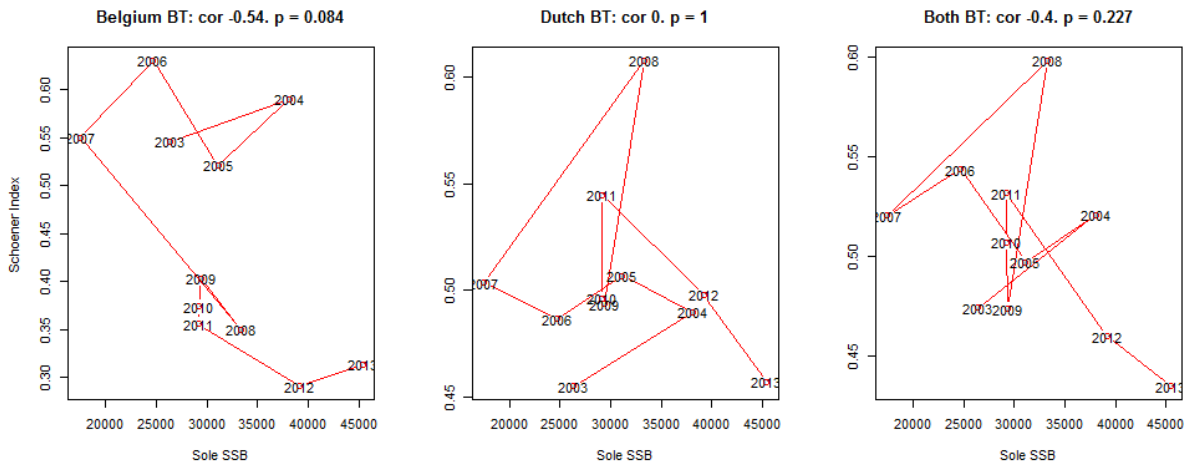
Figure 5: Relationship between sole SSB and Schoener index of partial spatial overlap between sole spawning stock and effort of large (over 15m) beam trawlers of Belgium (left), the Netherlands (middle), and both combined (right). Headers denote Pearson's (Belgium & both) and Spearman's (Netherlands) correlation coefficients and associated p-values.
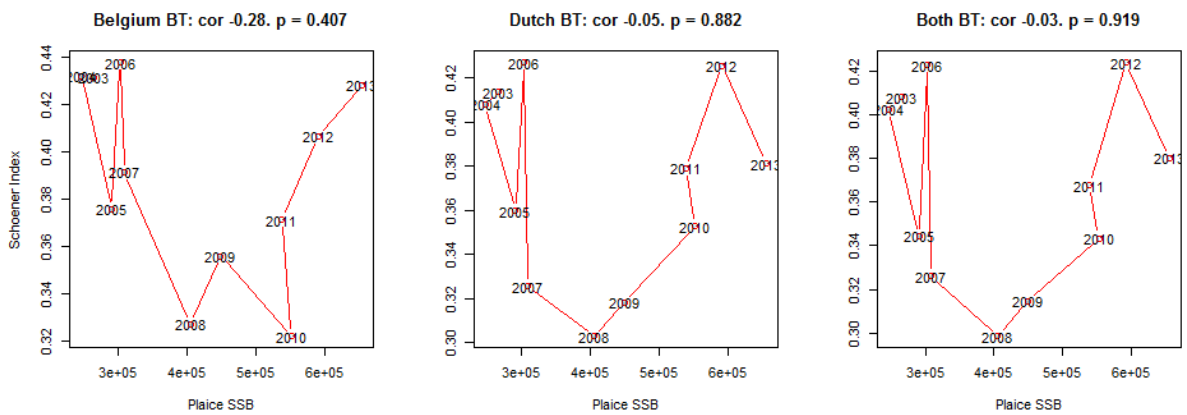
Figure 6: Relationship between plaice SSB and Schoener index of partial spatial overlap between plaice spawning stock and effort of large (over 15m) beam trawlers of Belgium (left), the Netherlands (middle), and both combined (right). Headers denote Pearson's correlation coefficients and associated p-values.

3.3.   Results of the ecosystem modelling

Plausible signs of ddcq were detected for both the North Sea's plaice and sole spawning stocks in the statistical modelling exercise (Section 3.1). Sole showed significant signs of ddcq for the Dutch (QR0 = 2.00) and the Belgium fleet (QR0 = 3.76), and for both nations' fleets combined (QR0 = 1.88; Table 1). Plaice showed similar patterns in ddcq: QR0 = 2.08 for the Dutch and 4.64 for the Belgium fleet, and QR0 = 2.15 for both combined. The implications of the QR0 for both fleets' efforts combined were tested in the ecosystem modelling exercise, since the underlying Ecosim model does not distinguish fleets between countries (Chapter 2). The outcomes of fishing scenarios with these QR0 of 1.88 for sole and 2.15 for plaice considered where compared with those of a baseline run, in which QR0 was set to 1.0 respectively.

3.3.A   Sole

Without consideration of ddcq (and with the fishing efforts of all fleets but those of beam trawlers left at the level executed in 2010), total catches of sole peaked at a beam trawling effort 28% higher than the one that would lead to the Fmsy suggested by ICES ($Fmsy_{ICES}$ = 0.2, (WGNSSK 2015), see Figure 7). Consideration of soles' ddcq for Dutch and Belgium beam trawlers through incorporating QR0 = 1.88 in the Ecosim simulations led to a beam trawl fMSY 39% higher than that leading to ICES Fmsy, and thus 17.4% higher than without ddcq (Figure 7). The F of sole leading to highest yields, however, is literally identical around 0.25 in both the baseline and the ddcq scenarios (Figure 8). The reason why, under ddcq, higher efforts are required to attain a comparable Fmsy is that Fmsy (around 0.25 both with and without ddcq; Figure 8) lies below the model's F as executed in the baseyear 1991 (Fsole = 0.33), thus Bmsy is higher than B in the baseyear (B0). Genuinely, efforts would thus have to be reduced to produce MSY. While that happens throughout the different equilibrium simulations of the model, the respective equilibrium B in each scenario, of course, increases. Now recall that QR0 defines the maximal possible changes in q through changes in B, with catchability (and thus F at constant effort) decreasing if B increases (Figure 3; left hand panel). If now efforts are decreased (relative to the level in 1991) to obtain MSY, the biomass increases relative to that in the baseyear, and with ddcq, the catchability shrinks (the right hand side of Figure 3; left panel). Relative to the non-ddcq runs, that means that F (caused by the same amount of effort) is lower. Now, given that Fmsy is similar in both scenarios (Figure 8) that means that, with ddcq, and under the circumstance of Bmsy > B0, higher efforts are needed to achieve Fmsy under ddcq.

If ddcq apply, the highest achievable catch of sole is 5.3% lower than what would be possible to fish without ddcq (see peaks of the MSY curves in Figure 7). As with intensified fishing, the stock is more and more reduced, ddcq magnifies the effect of effort on F at the right hand side of the yield ~ effort curve and leads to a deviation of the f ~ F relationship from a straight line at efforts higher fMSY, the more drastic the ddcq (left panel in Figure 3). This non-linearity leads to the yield ~ effort curve being positively skewed (Figure 7), which means that, while it requires higher efforts to attain MSY under ddcq compared to the baseline of no ddcq, a stock collapse is then quicker achieved, and that the edge between maximum yields and overfishing is narrower.
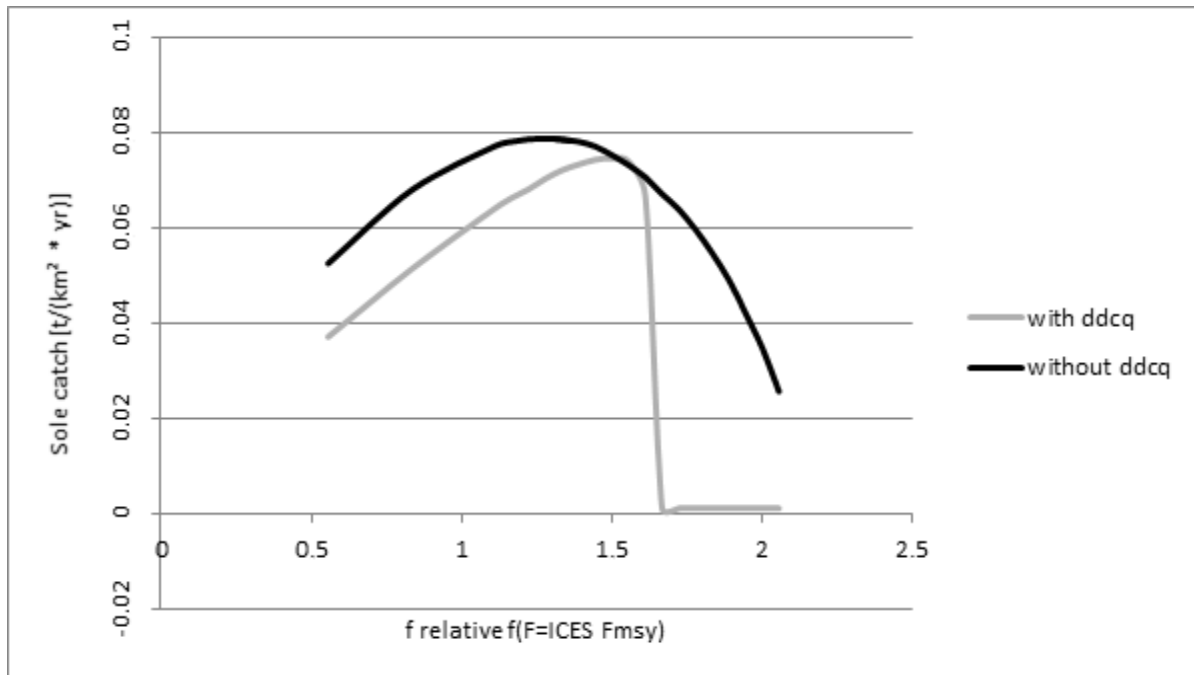
Figure 7: Equilibrium catch of sole > 300 mm as a function of beam trawl fishing effort, where effort is displayed relative to the level that would lead to Fmsy as suggested by ICES. The different curves represent different assumptions made about ddcq in the model (no ddcq (black); ddcq as found for the Dutch and Belgium fleet combined (grey).
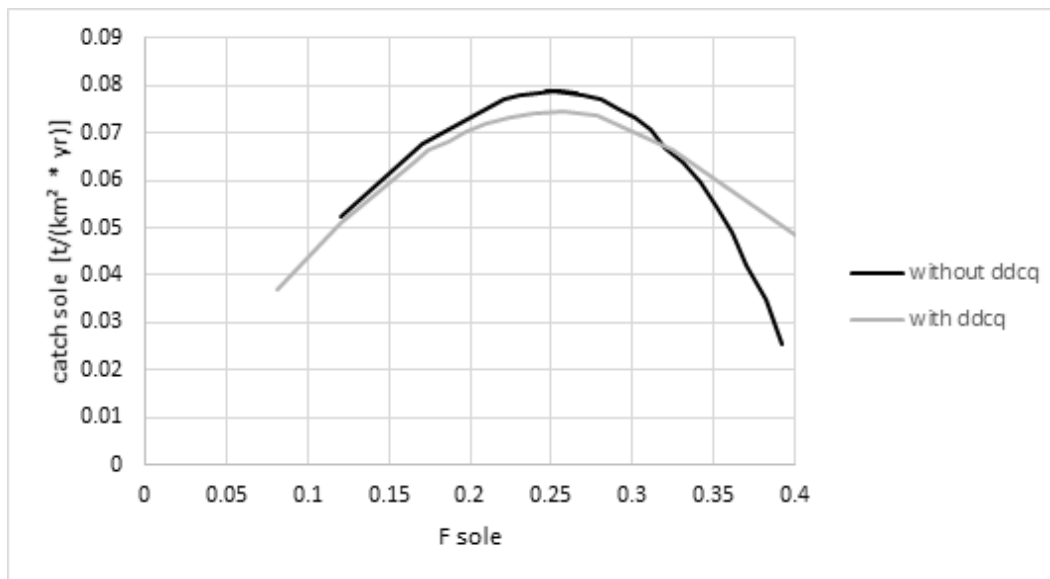
Figure 8: Equilibrium catch of sole > 300 mm as a function of their fishing mortality.
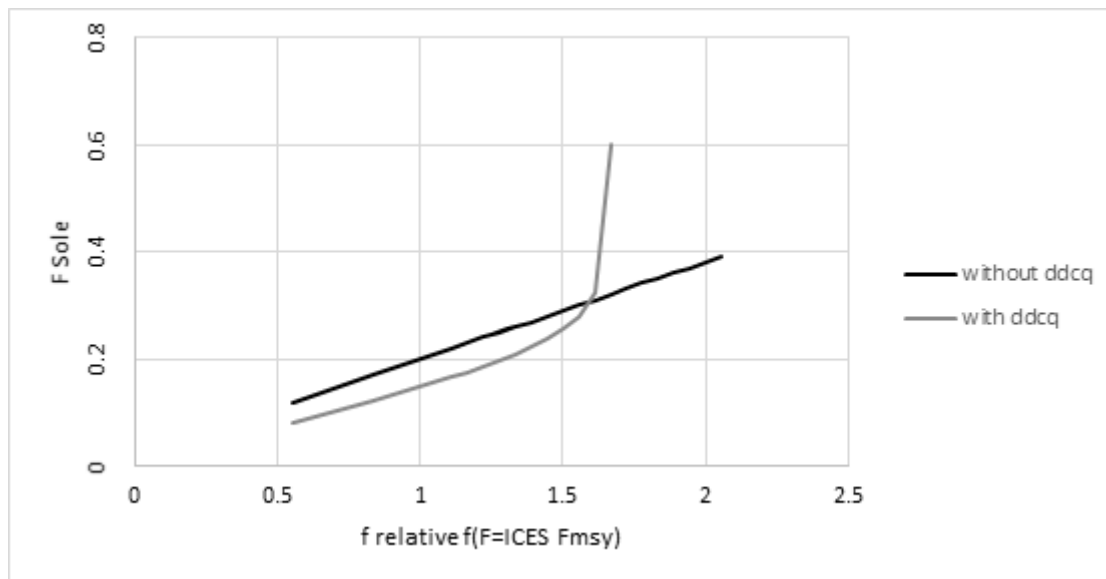
Figure 9: Equilibrium fishing mortality of sole > 300 mm as a function of beam trawl fishing effort, where effort is displayed relative to that level that would lead to Fmsy as suggested by ICES.

As shown above, ddcq in the beam trawl fishery for sole makes an increase of effort necessary if sole MSY is to be achieved. This increase in effort has consequences for the fishing mortalities of other species targeted or bycaught by the beam trawlers (Figure 10). As our fMSY search was based on fishing efforts executed in 2010, with efforts of all other fleets kept stable and only those of beam trawlers altered, the resulting changes in total F of each respective species rank the same as does beam trawlers' contribution (the partial F) to the species' total F in 2010. As an example, the fishing mortality of brill was caused by 86% by beam trawlers in our 2010 state of the model, while beam trawlers contributed by 74% to turbots' and by 68% to plaices' F. The ranking in the left panel of Figure 10 reads accordingly.

Particularly affected through fMSY changes under ddcq of sole were other flatfish targeted by the fleet, such as plaice, turbot and brill. Also elasmobranchs' fishing mortalities increased, but in a heterogeneous manner: while Thornback and Spotted rays (*Raja clavata* and *montagui*) suffered a 13% increase in F when beam trawlers adapted efforts to fish MSY under ddcq, the additional pressure on e.g. starry rays (*Raja radiata*) and spurdog (*Squalus acanthias*) was much lower. Cod, an important bycatch of beam trawlers, which, however, is to the largest part harvested by a fleet of demersal otter trawlers and seiners, was also affected by the changes in beam trawling.
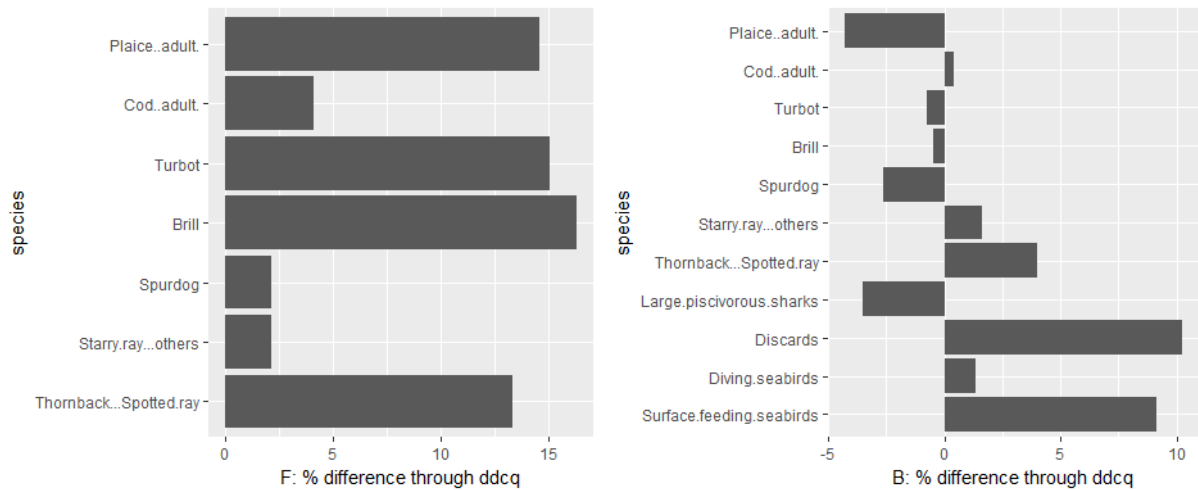
Figure 10: Percentaged changes in equilibrium fishing mortalities and biomasses through simulated fishing efforts' adaption to density dependent changes in catchability – sole.

The altered fishing mortalities through changed fMSY under ddcq presented in Figure 10 and those of many other species not shown here have consequences for the affected stocks, but may also cascade through the ecosystem as indirect effects of e.g. altered food availability or abundances of predators and competitors (right hand panel in Figure 10). As an example of the latter, the biomass of large piscivorous sharks decreases by 3.5% through intensified beam trawling of their prey stocks, namely plaice and gurnards, while their own F is only raised by two per mill. The probably strongest indirect effect, however, applies to Thornback and Spotted rays, for which, despite a 13% increase in fishing mortality (Figure 10), biomass increases by about four percent through stronger beam trawling. Similarly, B of Starry rays increases despite risen F. The reason why rays draw benefit from increasing beam trawling at that particular effort range in the simulations is that the enlarged F is outbalanced by an improved availability of benthic food organisms as flatfish stocks decline. Namely the enhanced catches of plaice, dab and gurnards and the associated ease in the predation pressure they execute upon the model's benthic compartments enables particularly large crabs, shrimps and other mobile epifauna to reach higher biomasses. This additional benthic production benefits the rays in the model, such that the reduced food competition with plaice, dab and gurnards allows a higher total biomass consumption by Thornback and Spotted rays. According the Ecosim base equation (Equation 4; Christensen, Walters et al. (2008)), this additionally consumed biomass is added to the rays' own biomass pools:

Equation 4

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ij} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i$$

where dB_i is the growth of the biomass pool i; g_i is its growth's net efficiency, i.e. production / consumption; $\sum Q_{ij}$ is biomass of all prey species j consumed by group i; $\sum Q_{ji}$ is biomass of group i consumed through all its predators j; I_i is immigration rate; while e_i is emigration rate; M_i represents the non-predation natural mortality rate; and F_i is fishing mortality rate. As long as considerably more biomass of their competitors than biomass of the rays themselves is removed, they may take profit from beam trawling through the increased availability and consumption of prey resources.

Other effects of the higher fMSY under ddcq are consistent reductions of B with raised Fs, such as for plaice, turbot, brill and spurdog. Here as well though, a comparable increase in F can accompany considerably different responses in biomass. Plaice, turbot and brill experience F alterations of similar magnitudes, but the reaction of plaice is more pronounced (Figure 10). Both bottom-up and top-down

effects, as indirect causes of the increased beam trawling effort mitigated through the food-web, cause this differential response: Intensified trawling leads to a drop of the simulated predation mortalities of brill, turbot and mature plaice, e.g. through a decrease in seal biomass (Tollit and Thompson 1996) caused by their increased competition for food with the fisheries in the model. However, this does not apply for juvenile plaice. Their predation mortality stays fairly constant under higher beam trawl efforts, chiefly because the biomass of their main predator, cod, also does so (Figure 10). Indeed, cod, also, are caught by beam trawlers in the southern North Sea. However, at 2010 efforts levels, beam trawlers only cause 12% of adult and 11% of juvenile cods' fishing mortality, whereas otter trawlers are the by far most important drivers of cods' fishing mortality, causing 50% of it for adults and 49% for juveniles (c.f. also [Chapter 1] for 1991) . In this respect, the differential response of plaice versus other flatfish can be considered a model artefact, as will be discussed below. A second difference between plaice and the two larger flatfish species lies in the changes in consumed prey biomass: as beam trawling rises, both adults' and juvenile plaice' consumption of their main food, small infauna, drops through enhanced competition by macrobenthic grazers, which again benefit from reduced predation by fished flatfish. Meanwhile, the total consumption of turbot and brill stays unaffected, as their main prey items – small fish species like sprat, sandeels and macrobenthic grazers – are left aside by large mesh beam trawling.

3.3.B   Plaice

Maximal equilibrium plaice catches were obtained at fishing efforts considerably larger than those that would lead to the Fmsy proposed by ICES for the stock (Fmsy$_{ICES}$ = 0.19; WGNSSK 2015). Primarily, that is for the fact that, in the Ecosim model, and in both scenarios, plaice catches peak at F = 0.39 (Figure 12), which is larger than Fmsy$_{ICES}$, the fishing mortality associated with MSY according ICES single species assessment based advice (WGNSSK 2015). Without ddcq, equilibrium catches should peak at twice that effort, and for the case with ddcq, that would be the case at 2.375-fold fMSY$_{ICES}$; and thus at a level 19% higher than without ddcq (Figure 11). Total achievable catches would be 6% lower under ddcq. Again, the catch-effort curve is considerable negatively skewed under ddcq, pointing out that catches and stocks can rapidly collapse if fMSY is only slightly overshot.

As for the case of sole, it is primarily other flatfish, and Thornback and Spotted rays, which are tackled harder if beam trawling efforts are adjusted to fish MSY of plaice under ddcq (Figure 13; left hand panel). The ranking of the changes in fishing mortalities directly correlates to what was reported for the sole case, but total changes in F are higher, given the higher effort under plaice ddcq. The changes in biomasses caused by ddcq, however, differ. Unlike the effort adaptation for sole, the effort modification for plaice causes no single positive effect, but for Starry and other rays (Figure 13). The disproportionately higher increase in fishing efforts leads to the detrimental effects of increased fishing mortalities to dominate over potential indirect positive effects. Sole even collapses as a cause of a fishing mortality unbearable for the stock (F = 0.5). But also for the other species shown, a such high beam trawling effort lies beyond what the populations can sustain. Potential indirect positive feedbacks through decreased competition are more than outbalanced by fishing mortality, and important food organisms, such as sprat (*Sprattus sprattus*), nephrops (*Nephrops norvegicus*), gurnards (*Trigla* sp, *Eutrigla* sp., and *Aspitrigla*), dab (*Limanda limanda*), and the obvious sole and plaice, are severely reduced.
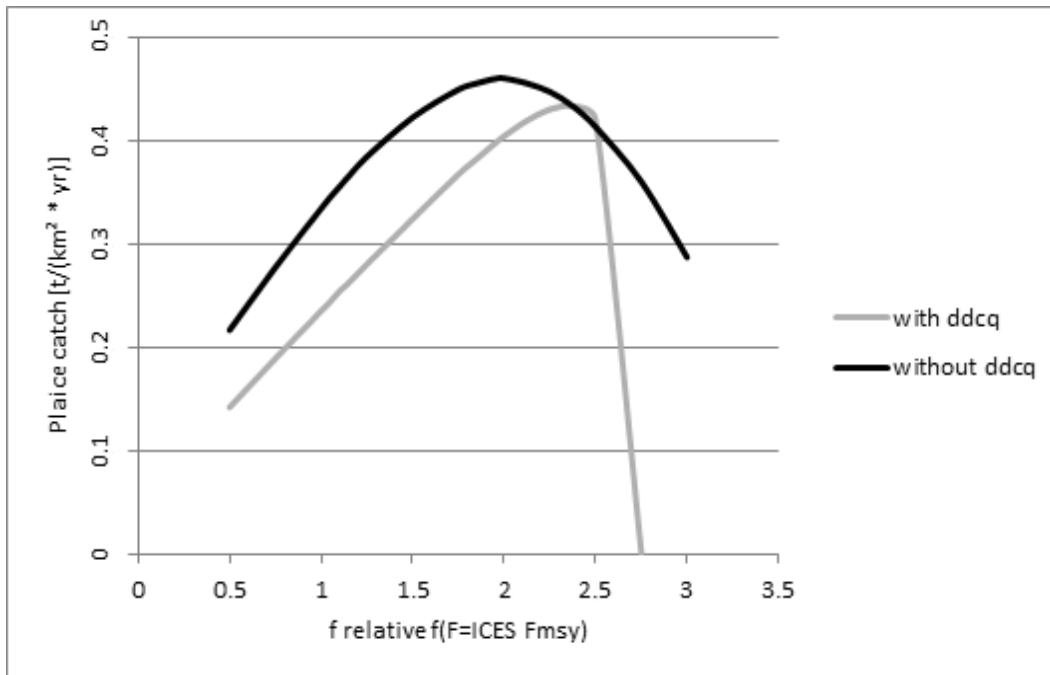
Figure 11: Equilibrium catch of plaice > 300 mm as a function of beam trawl fishing effort, where effort is displayed relative to that level that would lead to Fmsy as suggested by ICES. The different curves represent different assumptions made about ddcq in the model (no ddcq (black); ddcq as found for the Dutch and Belgium fleet combined (grey).
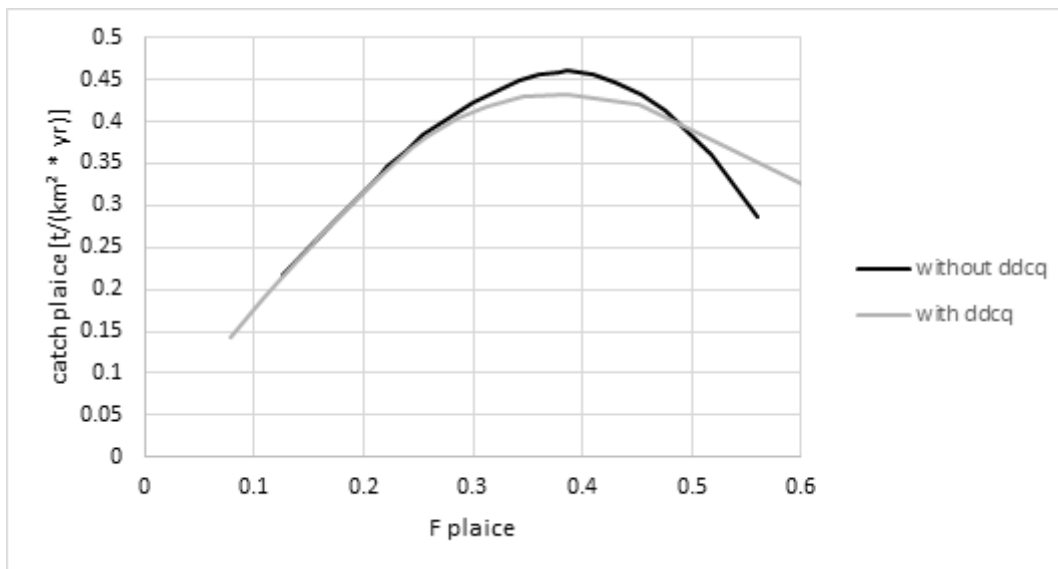

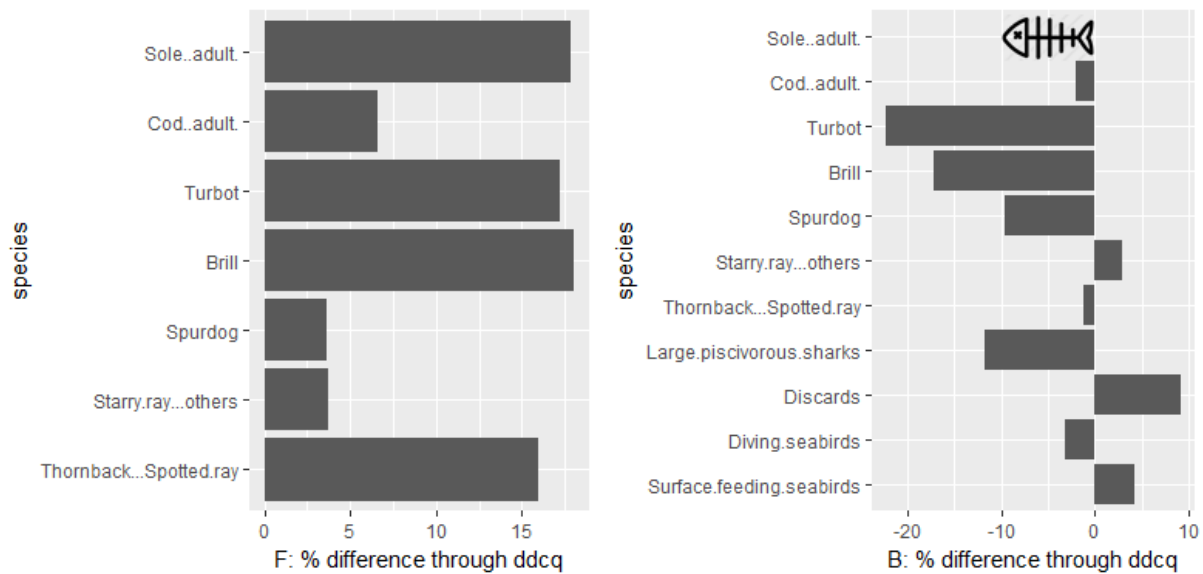*Figure 12: Equilibrium catch of plaice > 300 mm as a function of their fishing mortality, with and without ddcq.*

Figure 13: Percentage changes in equilibrium F and B through simulated fishing efforts' adaption to density dependent changes in catchability of plaice. The simulated sole stock collapsed in the ddcq scenario.

4. Discussion

4.1.   Relevance

North Sea sole and plaice are primarily managed through output control (total allowable catches; European Commission 2013), assisted by some input control measures (fishing effort restrictions; c.f. EC Council Regulation No. 41/2007, but also No. 2056/2001, No. 51/2006 and No. 40/2008, annex IIa). Both measures are affected by the underlying assumptions about the fishing mortality caused per unit of fishing effort, which we here referred to as catchability (see next paragraph). Testing for variability in these catchabilities and attempting to identify these variabilities' possible drivers thus holds relevance. We found significant signs of ddcq for both sole and plaice, and our modelling results suggest that their consequences for the stocks' management and the ecosystem context in which the fishery operates can be considerable.

4.2.   Ddcq

The simulated 17% to 19% increase in beam trawling effort required to match Fmsy of sole and plaice under ddcq, compared to a scenarios without ddcq (Section 3.3), are well within the range of variation that occurred in the past decade, sometimes even between two consecutive years (Rätz and Mitrakis 2012). However, those 'real-world' variabilities (chiefly a constant effort reduction since the beginning of the nineties) occurred in a dynamic system, whereas the ecosystem modelling exercise performed here refers to equilibrium assumptions, in which subtle differences weight more. Though we found that ddcq very likely are happening, and that, theoretically, higher efforts are required for MSY fishing, our findings cannot be read as a suggestion to management to incentivise an increase in beam trawling efforts. Total allowable catches (TACs) are currently the main management measure in the North Sea to achieve Fmsy (https://ec.europa.eu/fisheries/cfp/fishing_rules/tacs_en) while, e.g. for cod, effort control has been implemented to some degree via the cod management plan (EC Council Regulation No 1342/2008). Its effectiveness, however, has been questioned (Kraak et al. 2013). Besides TACs and effort control, technical measures (minimum conservation reference sizes and mesh size restrictions) and area restrictions (e.g. Natura 2000 sites; plaice box) additionally aim at conserving habitats and increasing the selectivity in fisheries. Thus, while TACs are provided by the European Commission, the individual effort strategy leading to their actual achievement is left to fishers. The management of

North Sea fisheries based on effort control alone is so far refrained from, and effort control is not used as a main lever to achieve MSY. The question arising through this study is thus not whether fishers should increase their efforts to fish Fmsy. Under output control, this is assumed to be the case anyways, as fishers would keep fishing until they have reached their quota (or until fishing is no more profitable). As our modelling exercise cautions, with ddcq, this effort would be higher, which, due to its consequences on other species and the ecosystem, must be considered by quota setting managers following Fmsy approaches, e.g. in multiannual plans or multispecies considerations. But not only through bycatch effects can our rationales be read as supporting those cautioning that Fmsy should be regarded as a threshold, rather than a target (Mace 2001). Evidence for this comes from single species considerations made here as well. As such, Figure 7 and Figure 11 suggest that, with ddcq, overshooting the effort leading to MSY can have drastically more detrimental effects on stocks and catches than without ddcq, due to the negative skewness of the yield curve under ddcq (c.f. section 3.3, 3rd paragraph).

A brief exploration of FPUE against SSB (data from WGNSSK 2016; WGCRAN 2014; Rätz and Mitrakis 2012) of other North Sea stocks than sole and plaice would suggest that for numerous other fisheries, ddcq could potentially play a role. Here, we focussed on the flatfish fishery and thus only derived estimates of ddcq (and technological creep and species targeting) for these two. However, many other species would be promising candidates for a (re-)inspection of factors driving catchability, e.g. since they school at low densities or, following line with the ideal free distribution theory (Fretwell and Lucas 1970), tend to aggregate in optimal habitats (Myers and Stokes 1989; MacCall 1990). In a more realistic ecosystem simulation, estimates of ddcq would be provided for all fished stocks, and most likely, complex and unexpected cross-over effects could be observed. In this study, however, our aim was primarily to comprehensibly point out the phenomenon and effects of ddcq when fishing selected target species at Fmsy in a multispecies fishery context, and we thus forwent the endeavour of mixing the ddcq effects of multiple species in the mixed fishery.

4.3.   Technological creep

As a sort of by-product, our study estimates the significance of technological development in the sole and plaice fisheries in the southern North Sea, ranked against ddcq. While we included multiple potential drivers of changes in fishing power into our statistical models, other studies often investigate them separately (TC: Pascoe and Coglan 2000; Eigaard et al. 2014. SP: Quirijns et al. 2008; Pilling et al. 2008; Poos et al. 2009. Ddcq: Rose and Leggett 1991; Swain et al. 1994; Rose and Kulka 1999; Rindorf and Andersen 2008; Quirijns et al. 2008). That bears the risk of e.g. overlooking ddcq as a cause of changes in catchability and exclusively assigning the effect to TC while stocks decline over time. Apart from a remarkable 7.7% annual increase in Fplaice per unit of Belgium effort through technological development (which, however, was an insignificant term in a flawed final statistical model; c.f. section 3.1), we generally found no indication of TC for beam trawlers fishing plaice or sole (Table 1). This result contradicts the findings of other studies, using different methods, which report an average 2% technology related annual change in the efficiency of North Sea beam trawlers (for an overview, see Eigaard et al. 2014). We are thus careful with the proclamation of that finding. Given the comparatively high amount of parameters in the model, it is possible that one of the other factors (ddcq, species targeting) masks the effect of technological development on catchability if that has a uniform temporal component. As such, sole experienced a broadly declining (albeit very variable) abundance trend throughout most of the time period analysed, which makes ddcq and technological creep hard to disentangle, until abundance rises towards the very end of the time series. Plaice abundance, there against, showed no consistent trend, but rather a peak in the late 1980s, after which SSB declined again before it started ascending to its current all-time high (WGNSSK 2016). Thus, if the role of TC in the development of plaice' catchability was masked, it is probably so for the species preference through fishers, indicated by the strong correlation between catchability and Fsole/Fple (Figure 2, bottom right)

and the significance of this factor in the statistical modelling (section 3.1). That technological development and growing fishing experience should have an effect on fishing power is common sense. However, as a matter of fact, our results indicate that other processes can rank at least similarly in importance, and encourage, if not necessitate, that they be equally considered when technological creep is investigated. Not including fishers' targeting behaviour and density-dependent changes in catchability into analyses of variances in catchabilities can lead to the false association of too large proportions of those variations to technological development, whereas they might actually stem from other systematic causes.

With the ongoing introduction of pulse trawls into the North Sea flatfish fishery, our results with regard to technological creep may become obsolete. The temporal extend of our data analysis (1972 – 2013) does only cover the very beginning of the rise of pulse trawls in the Dutch beam trawl fleet. A first 30 licenses were given out in 2011, followed by another 42 licenses in 2012 (WGNSSK 2015). With the takeover of these gear types, which were designed to minimize the fisheries' bottom disturbance, catchabilities can be expected to change abruptly (van Marlen et al. 2014).

4.4.   Species preference

Changes in the FPUE of plaice were significantly related to our indicator of species targeting behaviour (Table 1), the increase in F of the species investigated relative to the total change of both species' F combined (c.f. Equation 2, section 2.1). According our rationale, this would indicate that the respective years' efforts were directed towards a catch composition optimizing revenue and quota uptake. Our findings of changes in fishers' targeting behaviour are backed by Poos and Verkempynck (2015), who describe a shift of beam trawling efforts to the more southern waters since the start of the millennium, where sole are more abundant, while plaice found there are chiefly juveniles. Also Quirijns and co-authors (2008) found targeting behaviour to be a significant driver of CPUE of the Dutch beam trawl fleet. While our findings suggest preferential targeting to play a role for plaice only, Quirijns and colleagues report it for both plaice and sole in their results.

4.5.   Spatial overlap analysis

We found no consistent significant relationships between the fleet-stock overlaps and stock biomasses (Section 3.2). The Schoener's index of spatial overlap did not change systematically with SSB of neither plaice nor sole (with the exception of the interaction between Belgium beam trawlers and sole; and with plaice when IBTS data of Q1 was used). This is contradictory to what could be expect under ddcq, where the stock is assumed to contract at lower biomass and the overlap with fishing effort increased. We hypothesize that rather than large scale processes observable at the scale of ICES rectangles (in which STECF reports efforts), it are micro scale movements of fleets and stocks which drive the ddcq that section 3.1 uncovers. Rijnsdorp et al. (1998) showed that Dutch beam trawlers concentrate their efforts at fine scale patches of 10x10 nautical miles, while this patchiness is lost at the coarser resolution of the 30x30 miles of ICES rectangles. Later, Poos and Rijnsdorp (2007) found both sole and plaice to be patchily distributed at small scale, based on Dutch beam trawlers' catch rates. A second potential cause of why we may fail to demonstrate an increase in spatial overlap when stock sizes are low are changes of both distributions through the seasons. As our analysis bases on the only annually available STECF effort reports, we may miss out the role of the seasonality of sole', and even more so, plaice' seasonal migration patterns (Poos and Rijnsdorp 2007).

4.6.   EwE fMSY vs ICES Fmsy

As shown in Figure 7 and Figure 11, efforts leading to Fmsy in our model are higher than those leading to the Fmsy suggested by ICES. That relates to Fmsy itself being higher in the underlying Ecosim model (sole $Fmsy_{EwE}$ = 0.29; plaice $Fmsy_{EwE}$ = 0.43; (c.f. Figure 6 in Chapter 2) than those provided by the single species stock assessments (sole $Fmsy_{ICES}$ = 0.2; plaice $Fmsy_{ICES}$ = 0.19 (WGNSSK 2015). Often, it is argued

that Fmsy proxies in multispecies models, or ecosystem models like Ecosim, can be higher than those of single species models, given that multispecies models incorporate predation mortalities of all stages of a stock as a function of dynamic species interactions including density dependent effects (Walters et al. 2005; Mackinson et al. 2009b). In addition, Fmsy discrepancies were driven by the model's calibration, as described in Chapter 2: When tuning the multi-stanza dynamics to observed stock-recruitment relationships, sole and plaice were calibrated following the approach first described by Mackinson et al. 2009b, which ascertains that the median of the ratio of modelled biomasses of spawners and their respective recruits would relate between the key species similar to how it does for single species stock assessments (c.f. section 2.3 and Figure 7 in Chapter 2). While this safeguarded that the different stocks' productivities were plausible in relation to each other, it does not necessarily lead to a realistic reproduction of the stocks' inherent stock-recruitment dynamics themselves. In particular, the described approach does not necessarily lead to the multi-stanza groups showing compensatory recruitment, i.e. a relatively constant production of recruits over a wide range of spawning biomasses, with juvenile survival rate compensatory increasing when SSB falls below a certain level. Competition or cannibalism can be causes of compensatory recruitment. In its absence, the juvenile survival rate would be constant, and the resulting relationship between SSB and recruits' biomass linear. In our Ecosim model, this is what we see for sole and (to a lesser extend) plaice (Figure 14). The results are Lotka-Volterra like stock production dynamics, in which functional groups can grow (almost) linearly, without any saturation effect. It is evident that this affects Fmsy considerations, which are based upon the assumption that not maximal stock sizes, but intermediate ones are maximally productive. The weak curvature of the modelled stock-recruitment relationships shown in Figure 14 counteracts this to some extent. With that point made, however, it can be questioned whether compensatory recruitment would be a parsimonious explanation of sole and plaice SSBs and recruits' biomasses as taken from single species stock assessments for the years 1957 – 2012 (WGNSSK 2015; Figure 14). Less recent studies, however, suggest a density-dependent variability in sole recruitment success through increasing competition for nursery areas at high abundance (Rijnsdorp et al. 1992); with hints of a similar phenomenon applying for plaice (Berghahn 1987; Karakiri et al. 1991). In any case, comparisons between both model types and derived implications of that for actual management should thus be taken with care, as results are caused by different mathematical parametrizations in the simulations.
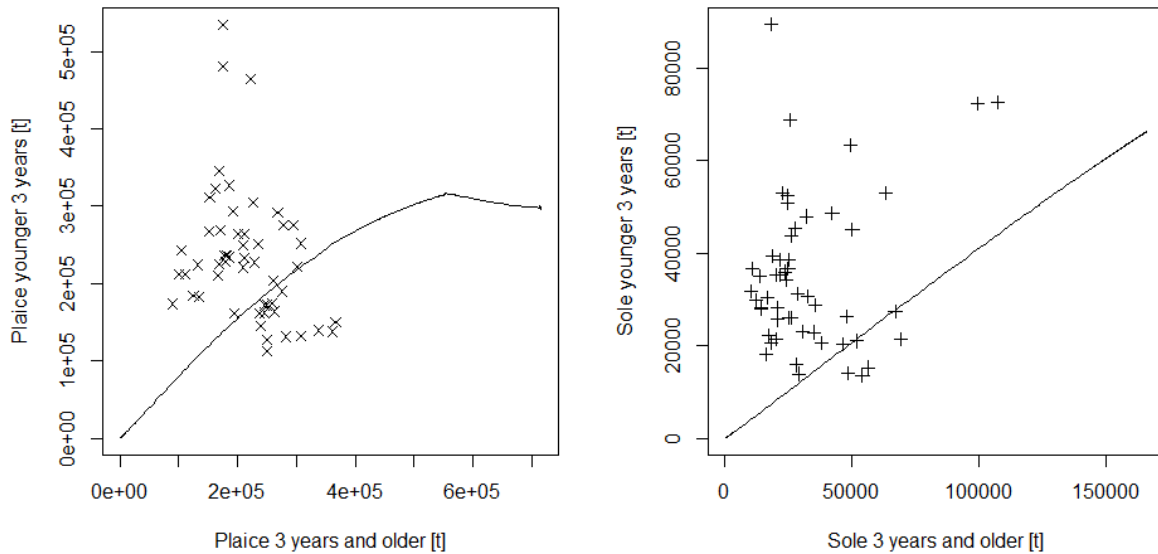
Figure 14: Biomasses of plaice (left) and sole (right) spawners and recruits as modelled by ICES' single species stock assessment (crosses) and the southern North Sea Ecosim model (lines).

In conclusion, our study demonstrates that a considerable share of the variability in FPUE of sole and plaice, as shown in Figure 1 and Figure 2, can be explained through the effects of ddcq, and, in the case of plaice, fishers' targeting behaviour. Assuming a linear relationship between soles' fishing mortality and beam trawling effort in the southern North Sea can thus lead to systematic errors in predictions.

5. Acknowledgements

Author contributions
MS developed the idea of this study, based on discussions with AK and AT. MS performed the analyses and modelling, advised by AK and AT. MS wrote the manuscript in close collaboration with AK and AT.

6. Appendix E

To make Dutch and Belgium beam trawling efforts comparable, we had to translate the HP hours in which Belgium effort is noted in (WGNSSK 2005) into HP days. A simple multiplication with assumed hours fishing per day was not feasible, as the Belgium effort was 'corrected for fishing power' in an unreported manner. We referred to reports of Belgium fisheries landings and returns (De Belgische zeevisserij: aanvoer en besomming; (VLIZ 2003, 2001, 1986) from the Flanders Marine Institute to obtain annual records of the Belgium fleet's days at sea in the North Sea, of the proportion of beam trawlers in the total fleet and of the average engine power of its beam trawlers. We could obtain

complete records for the years 1985 and 1986 and for years 2000 – 2003. We then established the relationship between Belgium beam trawl HP days in the North Sea from VLIZ data and corrected HP days from (WGNSSK 2005) through linear regression and used the coefficients to obtain extrapolated annual HP days from the effort time series provided in (WGNSSK 2005).

Table 2: Reported Belgium fishing efforts in hp days (VLIZ 1986, 2001 and 2003) and hp hours (WGNSSK 2005) and extrapolated hp days based upon linear regression thereof.

year	VLIZ HP days	WGNSSK 2005 corrected HP hours	Extrapolated HP days
1972		29.8	7.631845
1973		29.4	7.572976
1974		32.2	7.985059
1975		39.2	9.015266
1976		44.7	9.824715
1977		47.6	10.25152
1978		50.3	10.64888
1979		40	9.133004
1980		35.2	8.426576
1981		31.1	7.823169
1982		34.9	8.382424
1983		35.4	8.456011
1984		42.8	9.545087
1985	9194142	51.4	10.81077
1986	8299156	42.5	9.500935
1987		50.7	10.70775
1988		53	11.04625
1989		54.3	11.23757
1990		64.7	12.76817
1991		74.3	14.18102
1992		67.7	13.20968
1993		71.1	13.71007
1994		60	12.07645
1995		46.5	10.08963
1996		64.9	12.7976
1997		47.2	10.19265
1998		43.6	9.662825
1999		55.7	11.44361
2000	12246556	49.3	10.50171
2001	11301332	45.5	9.942453
2002	10670752	51.6	10.84021
2003	9399787	42.6	9.515653

8. Appendix F
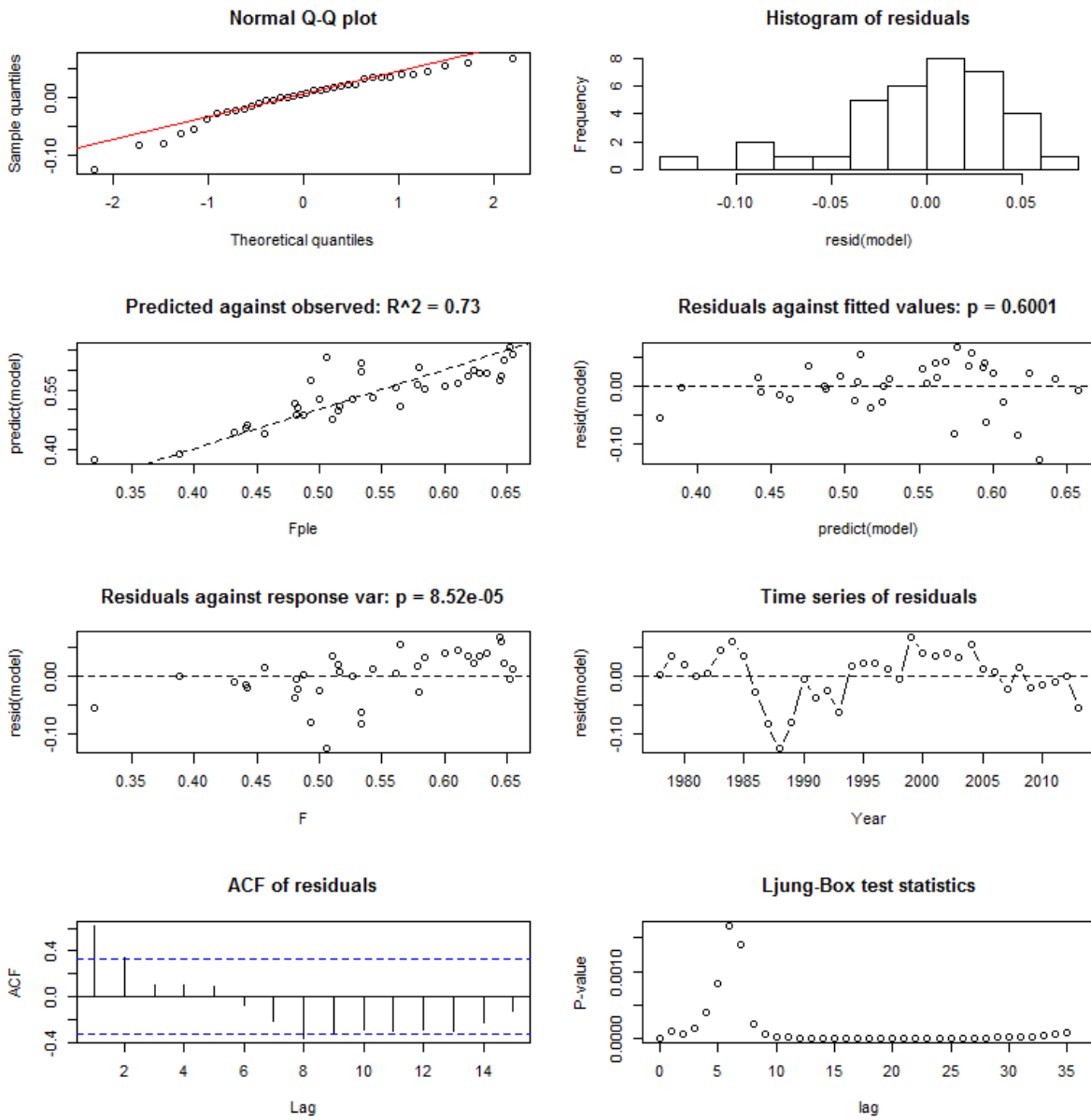
Figure A 1: Residual diagnostics of the final statistic model on Fsol by Dutch beam trawlers.
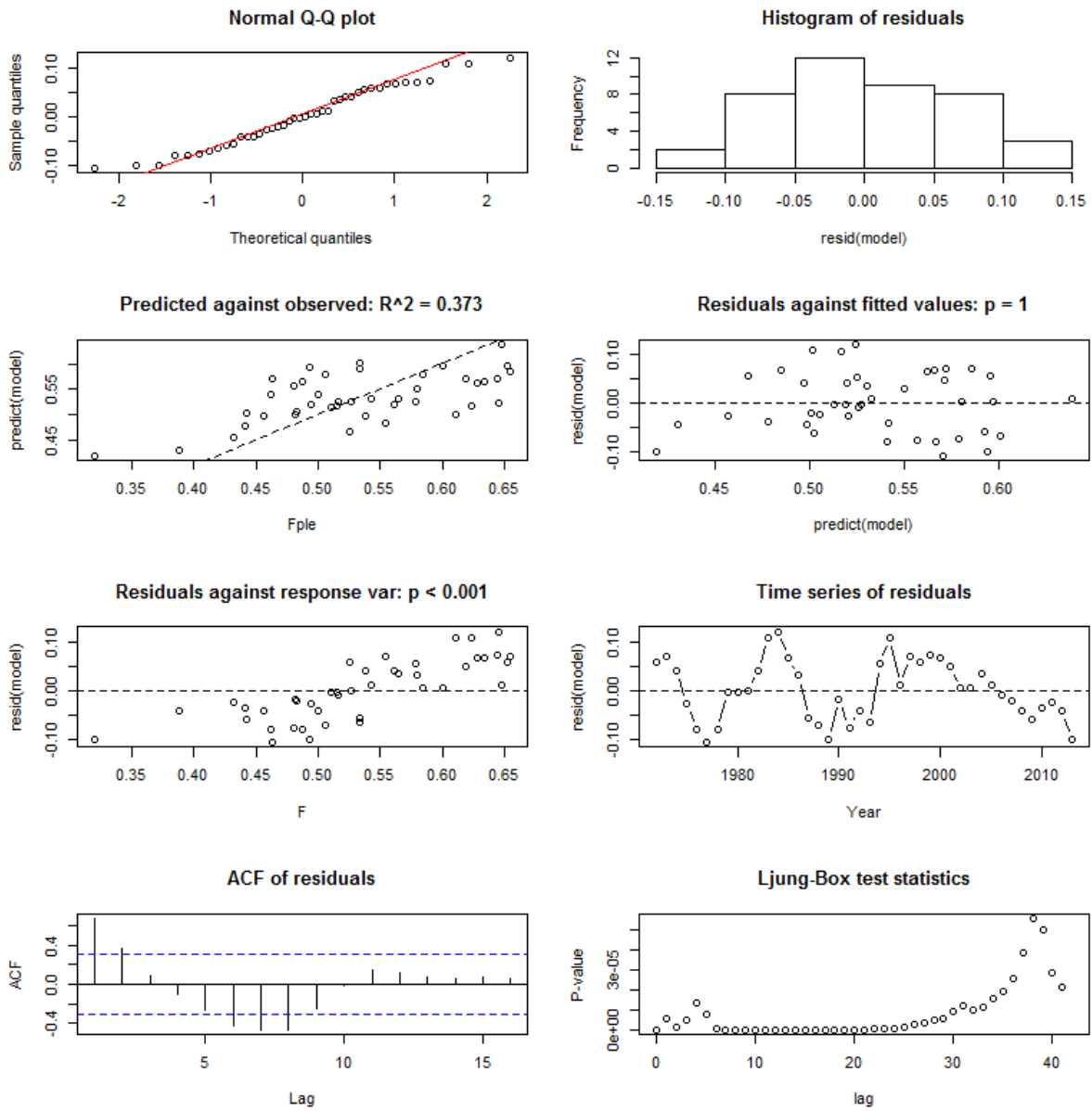
Figure A 2: Residual diagnostics of the final statistic model on Fsol by Belgium beam trawlers.
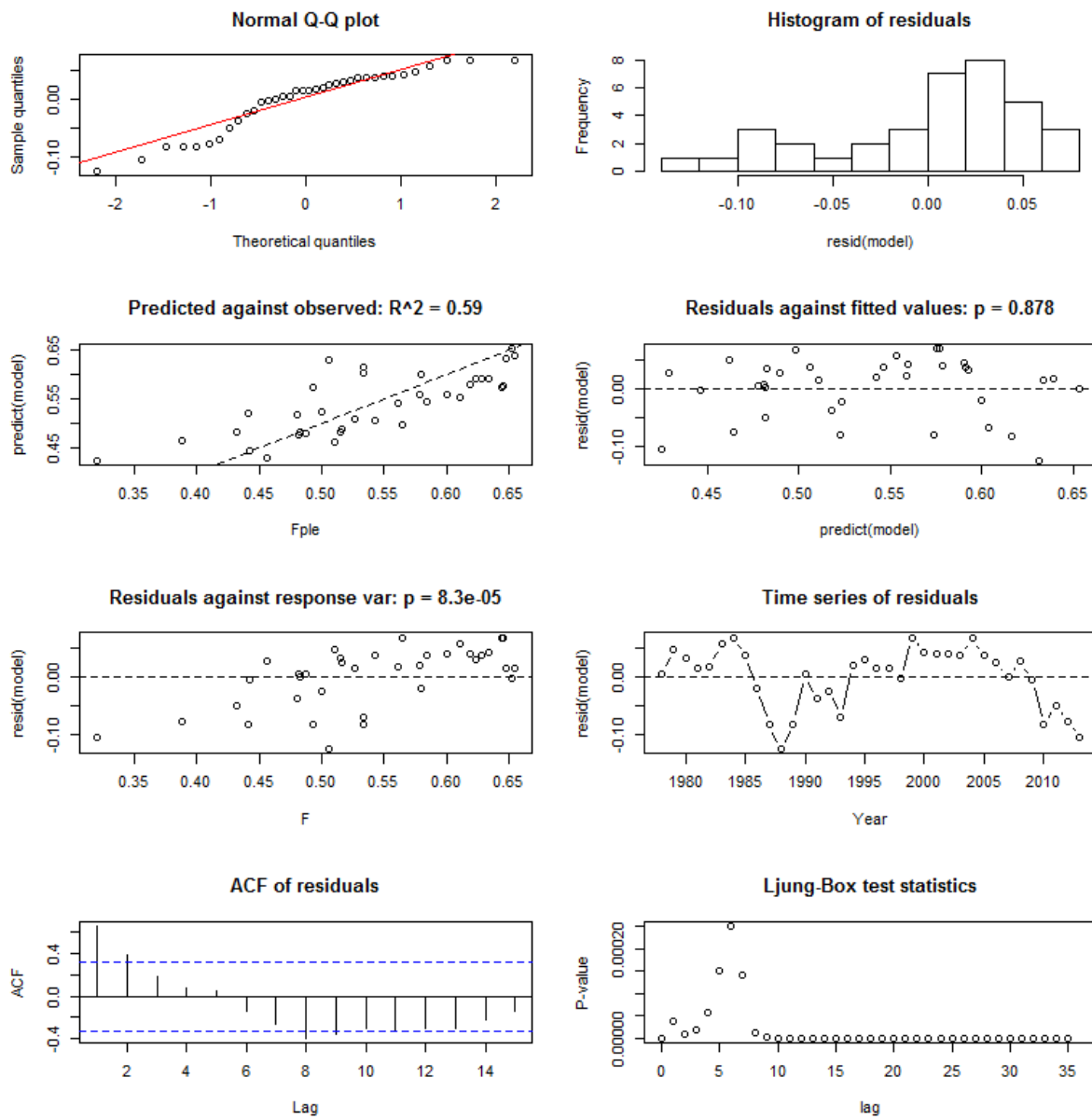
Figure A 3: Residual diagnostics of the final statistic model on Fsol by combined beam trawling efforts.
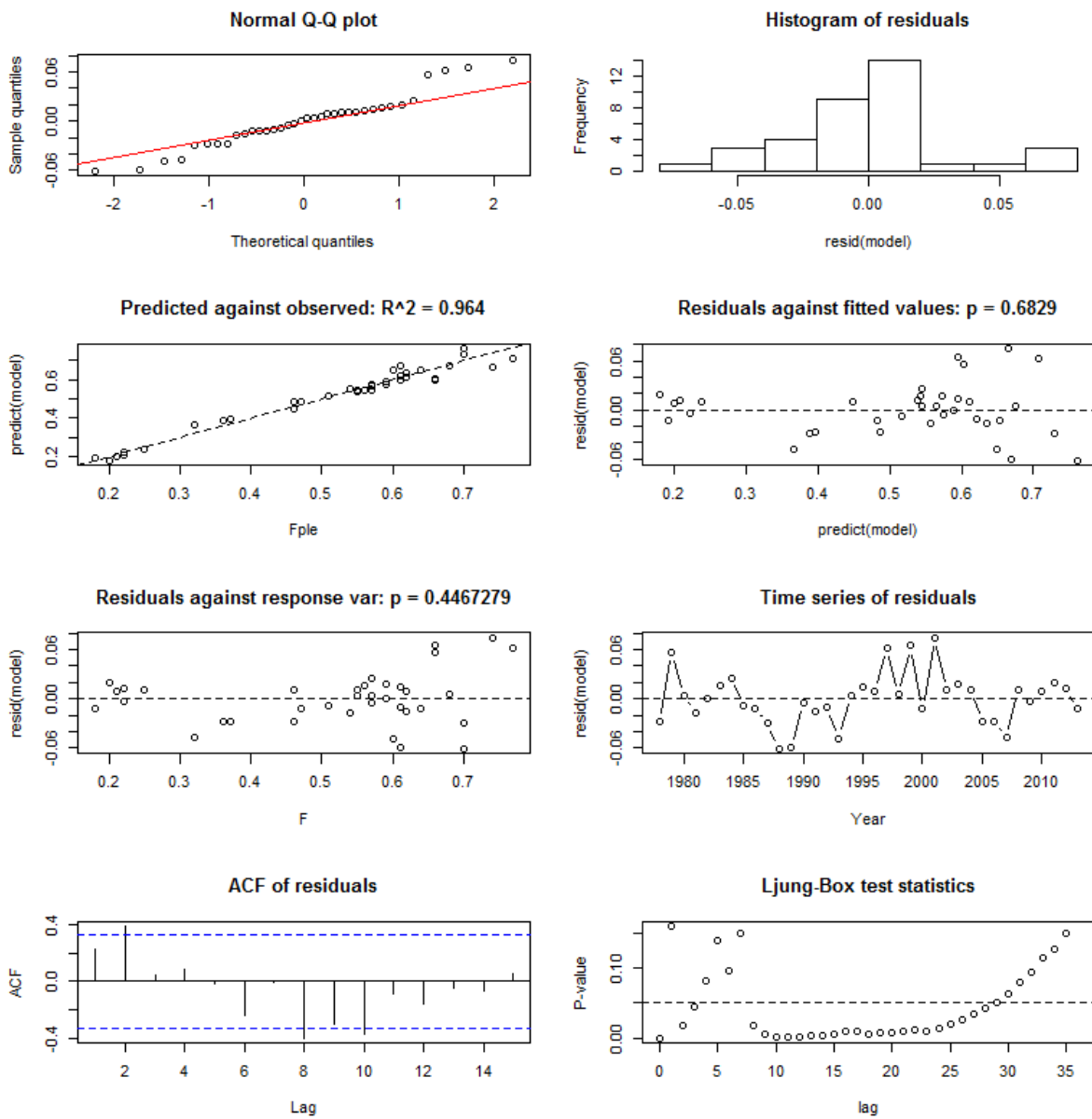
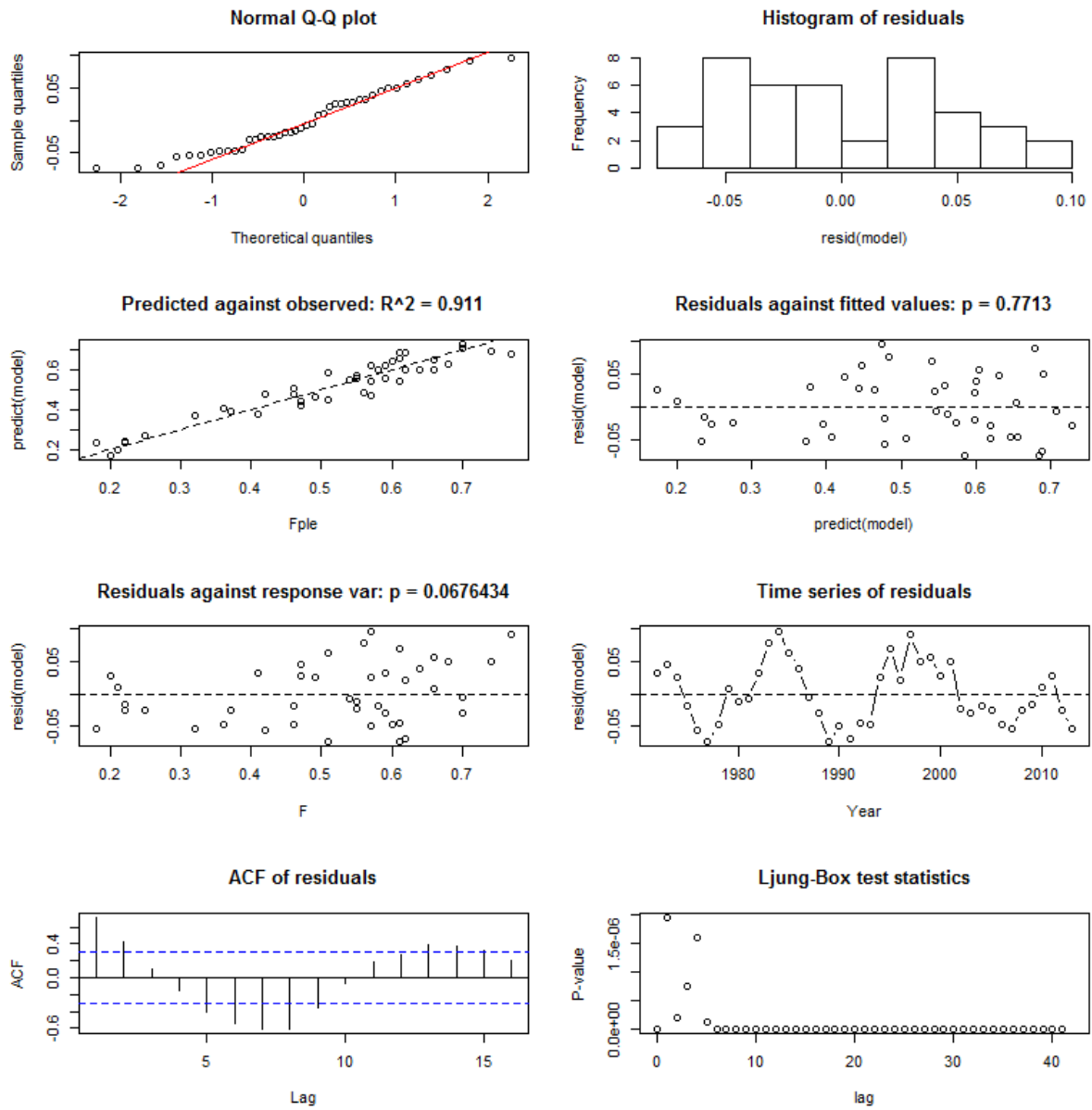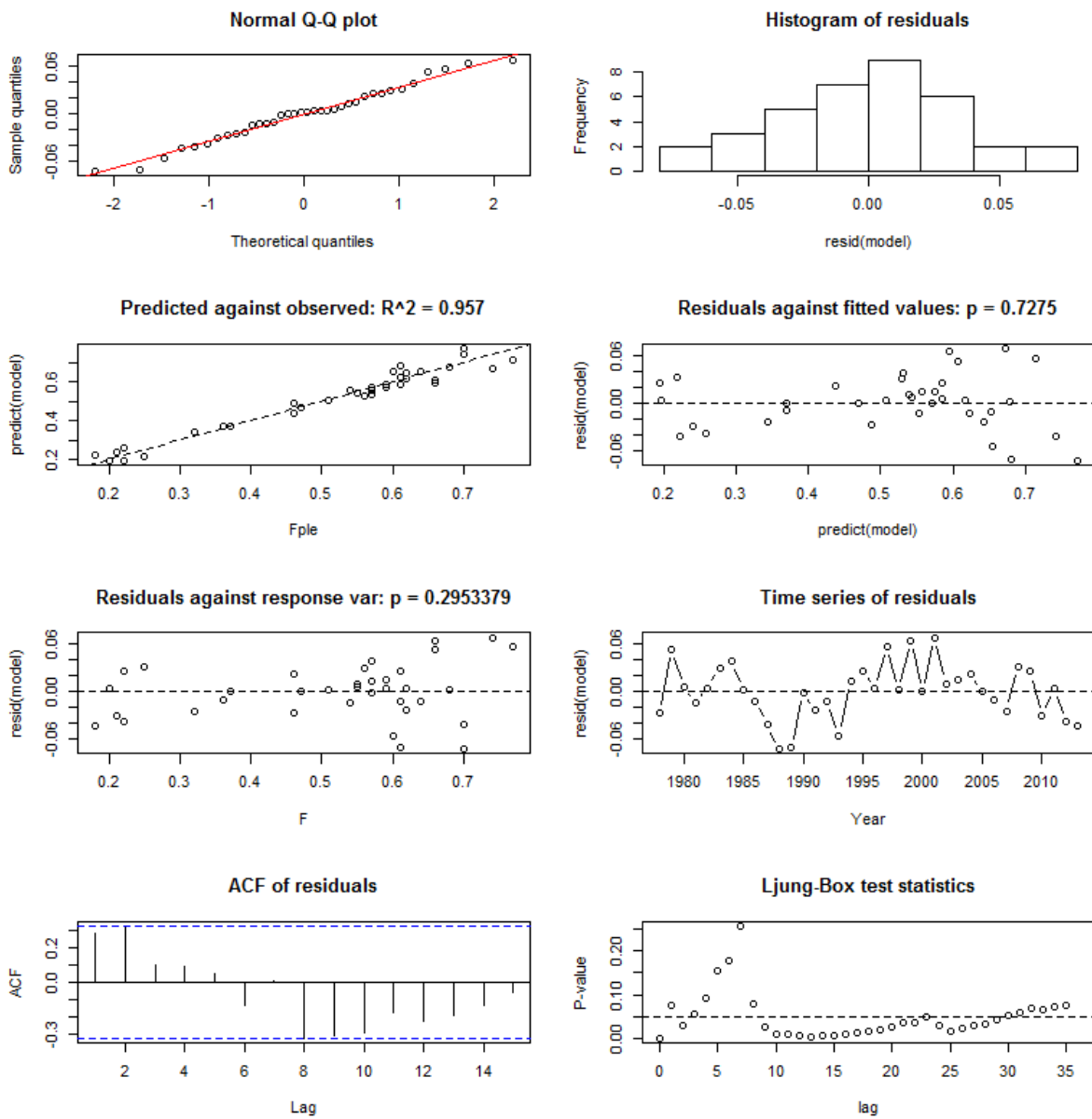*Figure A 4: Residual diagnostics of the final statistic model on Fple by Dutch beam trawlers.*

Figure A 5: Residual diagnostics of the final statistic model on Fple by Belgium beam trawlers.

Figure A 6: Residual diagnostics of the final statistic model on Fple by Dutch and Belgium beam trawling efforts combined.

Chapter 4

Sensitivity of multispecies MSY to trends in the top (marine mammals) and bottom (primary production) compartments of a food-web model of the southern North Sea

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Abstract

In an ecosystem approach to fisheries, maximum sustainable yield considerations are affected by changes in the top and bottom compartments of the food-web. This study addresses changes in the southern North Sea food-web through increases in marine mammals and a reduced primary productivity, and explores how fisheries may need to adjust their efforts to maintain optimum yields of sole, plaice, cod and brown shrimp. We construct probable scenarios of ongoing food-web changes using Bayesian age-structured population models to derive carrying capacities of harbour porpoises (*Phocoena phocoena*) and grey seals (*Halichoerus grypus*); and of losses in primary productivity predicted by lower trophic level ecosystem models. These scenarios are implemented in a food-web model of the southern North Sea. For each scenario, we sought mixed-fleet fishing efforts that would deliver maximum yields of sole, plaice, cod and brown shrimp combined. We also did so for a baseline run and compared the differences in optimal fishing strategies, predicted yields, and states of the stocks between the scenarios.

We found the predicted decline in primary productivity to be more decisive for stocks and yields. Increased marine mammal predation predominantly affected cod, which even benefitted brown shrimps compared to the baseline run. Under reduced primary productivity, fishing efforts had to be reduced by 50% to still provide maximum yields, whereas the marine mammal scenario induced no need to adjust the fishing regime. This draws attention to the potential gains of incorporating bottom-up processes into long-term management considerations, while marine mammal predation may be less of a concern for particularly flatfish fisheries in the North Sea, and may even benefit shrimp trawlers.

1. Introduction

Managing fisheries for cod (*Gadus morhua*), plaice (*Pleuronectes platessa*), sole (*Solea solea*) and brown shrimp (*Crangon crangon*) in the southern North Sea (divisions IVb and IVc of the International Council for Exploration of the Sea, ICES) is a challenging enterprise, as the various target species are linked to each other through a complex food-web (Temming and Hufnagl 2014, Chapter 2, Kempf et al. 2016). Also, one and the same species can be extracted by different gears with different consequences for other stocks and life stages and the environment (Ulrich et al. 2001; Vinther et al. 2004; Miller and Poos 2010; Ulrich et al. 2012). Both multispecies and mixed-fleet effects have consequences when considering maximum sustainable yield (MSY) options for the area, questioning whether maximum yields of all single stocks can be achieved simultaneously here (Mackinson et al. 2009b; Miller and Poos 2010; Chapter 2). Rather than singles species MSYs, the goal in such cases should be the achievement of a multispecies MSY (msMSY), in which the trade-offs of fishing trophically or technically interlinked species are balanced such as to generate optimum aggregated outcomes to fishers and society (Mackinson et al. 2009b; Kempf et al. 2016; Chapter 2).

But management of the southern North Sea's living resources is not only confronted by trophic and technical interactions between fished stocks. The ecosystem is also subject to changes and trends in its system properties. Since the beginning of the 1980s, de-eutrophication measures led to reduced riverine discharges of inorganic phosphorous (Claussen, Zevenboom et al. 2009). This decrease of nutrient availability can affect primary and secondary production (Colijn et al. 2002; Lenhart, Mills et al. 2010), a change in system productivity which bears the potential of cascading through the food-chain to affect exploited populations and fishing yields (Colijn et al. 2002).

At the other end of the southern North Sea's trophic spectrum, populations of marine mammals, namely harbour porpoise (*Phocoena phocoena*) and grey seals (*Halichoerus grypus*) have recovered from low densities in previous decades and can be suspected to grow even further (TMAP 2013; Camphuysen 2004; Appendix G: Grey seal projections and Appendix H: Harbour Porpoise Model). This can have direct negative effects on commercial species, if they contribute to the mammals' diets (Temming and Hufnagl 2014). However, this competition between fishers and marine mammals is by far not self-evident (Alexander et al. 2015; Trites et al. 1999). For those stocks that have their predators removed by mammals, the effect can even be indirectly positive (Temming and Hufnagl 2014).

In a food-web model of the southern North Sea (Chapter 1 and 2 their Appendices), we sought fishing effort levels for the three primal fleets of the area, demersal purser and seiners (DEM), beam trawlers (BT) and brown shrimp trawlers (SHR), that would lead to a msMSY of cod, plaice, sole and brown shrimp. This effort regime and model setup would form the baseline scenario. We then subjected the modelled ecosystem to alternative scenarios and repeated the search for fishing efforts leading to msMSY. With the new msMSY found, we documented differences in biomass (B), catches (C), fishing mortality (F, where F = C/B) and revenue from landings per species. We compared each scenarios'

msMSY outcomes with the baseline scenario to quantify the sensitivity of msMSY to changes in modelled system properties and assumptions. The tested scenarios were:

1. Decrease in system productivity (e.g. through de-eutrophication measures)
2. Increase in the abundance of marine mammals, under
   a. Ongoing southwards drift of the porpoise population
   b. Halt of the southward migration of porpoises' centre of distribution

For each such potential change of the modelled system, we investigated if it would lead to a need to adopt new fishing strategies (as expressed by fishing effort and mortalities) to achieve msMSY and the consequences it would cause to yields (in weight and revenues from landings) and stock biomasses.

2. Methods

2.1. A multispecies MSY for the southern North Sea flatfish, brown shrimp and cod fisheries

To establish estimates of fishing effort regimes which would lead to msMSY of cod, plaice, sole and brown shrimp, we used a time-dynamic food-web model of ICES divisions IVb and IVc (Chapter 2 and Appendix thereof). The model follows the Ecopath with Ecosim (EwE) approach and utilizes the dedicated software, version 6.4.11414.0 (Christensen et al. 2008). Parametrizing an EwE model typically starts with setting up of an Ecopath model, the time-static snapshot representation of the ecosystem's average state throughout a year. A set of linear equations covers the exchange of mass between the different biomass pools (or 'functional groups') of the model, where the flows into and out of any single group are characterized by the equation

Equation 1

$$\text{B}_i \cdot \left(\frac{\text{P}}{\text{B}_i}\right) = \sum_{j=1}^{n} \text{B}_j \cdot \left(\frac{\text{Q}}{\text{B}}\right)_j \cdot \text{DC}_{ij} + \text{Y}_i + \text{E}_i + \text{BA}_{i+} \left(\frac{\text{P}}{\text{B}_i}\right) \cdot \text{B}_i \left(1 - \text{EE}_i\right)$$

, where B_i = biomass of functional group i; P/B = production per unit of biomass of the functional group i; $(\text{Q/B})_j$ = consumption per unit of biomass of the predator j of biomass B_j; DC_{ij} = proportion of prey i in the diet of predator j; Y_i = exports from the system as fishery catches; E_i = net migration; and EE_i = ecotrophic efficiency of the functional group i. Energetic costs for the respective groups are described by Equation 2:

Equation 2

$$Consumption\,(Q) = Production\,(P) + respiration\,(R) + unassimilated\,food\,(U)$$

Based on that snapshot representation of the ecosystem, Ecosim adds the dimension of time to the dynamics of the functional groups of the food-web. It simulates the development of the biomass of each functional groups as response to internal system structure (the underlying Ecopath) and external drivers, e.g. fishing or environmental changes, according

Equation 3

$$\frac{dBi}{dt} = gi \sum_j Qij - \sum_j Qij + Ii - (Mi + Fi + ei)Bi$$

; where dB_i is the growth of biomass of functional group i; g_i is its growth's net efficiency, i.e. production/consumption; I_i is immigration rate; while e_i is emigration rate; M_i represents the non-predation natural mortality rate; and F_i is fishing mortality rate. Christensen and Walters (2004) and

Christensen et al. (2008) expand further upon EwE's compartments and assumptions beyond these base equations. The EwE model designed for the southern North Sea covers 68 functional groups. As a characteristic of a food-web, or ecosystem model, these span from the very bottom (phytoplankton, benthic and pelagic microflora and invertebrates) to the top (marine mammals, sharks and seabirds) compartments of the represented ecosystem rather than commercial species (like multispecies models) or commercials with some top predators (minimum realistic models, see Plaganyi 2007; Dissertation introduction; Dissertation conclusion) only. However, in the southern North Sea Ecopath model as well, fisheries' target species were implemented in particular detail, including the representation in so called multi-stanza groups, with adults and juveniles modelled separately. Wherever possible, single species dynamics, including stock-recruitment dynamics, were tuned to single or multispecies stock assessment data (Chapter 2). The Ecopath model, and thus baseyear of the Ecosim simulations, is 1991, since the ICES 'year of the stomach' (Hislop et al. 1997) provides uncompeted availability of fish diet data for that year. Fitting the Ecosim model to biomass, abundance, catch, fishing mortality and fishing effort data ranging 1991-2010 ascertained the best achievable plausibility of the model and its anticipated ability to predict future developments under changing external pressures. Chapter 1 and 2 and Kempf et al. (2016) provide further details about the model and its applications. In a set of equilibrium simulations from 2010 onwards, we altered the fishing efforts of the major fleets, DEM, BT and SHR, while keeping the effort ratios between the fleets stable, which means that if the effort of fleet a was increased by a factor x, the same factor was applied to efforts of the other fleets. The rationale behind this procedure was the assumption that each major fleet has to contribute equally to reach Fmsy for the main target species in the southern North Sea. Efforts were adjusted until we found a level that would produce maximum total equilibrium yields from the four scope species combined. We differentiated between yield in tonnes caught (msMSYt) and revenues from landings in Euros (msMSY€), for which we multiplied tonnes caught with 2014 off-vessel prices (German landings declarations, collected according to REGULATION (EC) 1224/2009 ON FISHERIES CONTROL http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:32009R1224). In our search for maximum yields, only catches of the scope fleets were considered, while other fishing activities, such as gill netters or pelagic fleets, were left aside. We recorded B, F and catch in tonnes and revenues from landings (€) for cod, plaice, sole and brown shrimp at msMSY as outcome of our baseline scenarios. We sought msMSYt and msMSY€ for the baseline scenario with both a search grid of 0.1-fold the respective fishing efforts executed in 2010 to compare msMSYt and msMSY€, and with a 0.5-fold grid for comparison among the scenarios.

Having established the baseline msMSY, we repeated the search for msMSY as described above, but prior to that changed the properties of the modelled ecosystem. Our search grid for this was 0.5-fold the respective fleets' fishing efforts in 2010. In total, three alternative scenarios were tested:

2.2.   Decrease in system productivity

To overcome eutrophication phenomena, such as local anoxia (Dethlefsen and Von Westernhagen 1983) and changes in plankton species composition (Colijn et al. 2002; Beaugrand et al. 2003), measures to reduce the nutrient loads into the catchment area of the southern North Sea were and are being applied (Claussen et al. 2009). The respective PARCOM 1988 convention foresaw a reduction of nutrient loads to 50% of the 1985 level until 2010 (de Jong 2006). Besides their intended effect of counteracting phytoplankton blooms and associated processes like hypoxia and shifts in phyto- and zooplankton species composition that may cascade through the food-web (Beaugrand et al. 2003; Niiranen et al. 2013), cuts of the nutrient loads have the potential to affect fisheries' yields and policies: By reducing the productivity and biomass of algae, which again serve as the basis of the marine food-web and eventually feed into exploited stocks, efforts to overcome eutrophication may lead to reduced stock productivities, and for brown shrimp (Boddeke 1996), sole (Rijnsdorp et al. 2004) and plaice

(Rijnsdorp and Leeuwen 1996), positive relationships between somatic growth or recruitment success and nutrient loads were found.

We evaluated how a decrease in net primary production (NPP, i.e. gross primary production (photosynthesis) minus respiration) of the maximum -30% projected by Lenhart et al. (2010) would cascade through the food-web and affect fishing yields under msMSY considerations. We therefore reduced primary productivity to 70% of its original value in our food-web model to create a scenario representing the decreased system productivity predicted by their study. To some extent, this approach is an example of an offline, one way model coupling exercise: Lenhart and colleagues (2010) used an ensemble run of six different lower trophic level models (nutrients to zooplankton, with a physical model compartment) to generate predictions of primary production in the North Sea under a standard run and a 50% nutrient reduction scenarios. The across-model average maximum difference in NPP between the standard runs and the reduction scenarios (-30%, see section 4.2 therein) is their output we then build upon for the construction of our de-eutrophication scenario.

2.3.   Increase in the abundance of marine mammals

Both the populations of grey seals and harbour porpoises in the southern North Sea have increased through the last three decades. In the case of grey seals, this population growth is related to a recovery since the 1970s, when hunting and diseases had severely reduced the population (ICES 2008). We conducted a population modelling exercise (see Appendix G: Grey seal projections) which suggests that the current population is still far from its carrying capacity, but may grow to almost six fold its 1991 biomass. For our scenarios representing an increase in marine mammal abundance we therefore forced the biomass of the respective functional group 'seals' in our model to a level of 5.76 times its 1991 value.

In the original fitted Ecosim model (Chapter 2), the 'vulnerability', i.e. the availability of prey pools to seal predators (cf. Christensen et al. 2008), was estimated 1.0. This implies that the trophic flow from prey pools into the seal predator pool would be entirely bottom-up controlled, increases in the predator biomass would thus not result in increased consumption of its prey. For our analysis, we thus set the vulnerability (v) of prey to seals to two, which is the default value suggested by Christensen, et al. (2008) and typifies mixed control, i.e. neither bottom-up nor top-down processes (Cury et al. 2003) dominantly control the populations' dynamics.

Harbour porpoises form the most abundant cetacean species of the southern North Sea. Since the 1990s, their centre of distribution has moved here from the northern part of the North Sea (ICES 2008). It is uncertain whether or not this southwards shift of the porpoise population will continue in the future. We thus implemented two different scenarios for our msMSY analysis, one in which the southward shift of porpoises would continue and one in which the distribution shift was assumed to end. For both versions, we estimated the southern North Sea's population's carrying capacity using a designated population model that considers, amongst other factors, current bycatch rates of porpoises in fishing gears (cf. Appendix H: Harbour Porpoise Model). In the case of ongoing southward migration of the population, carrying capacity would reach 2.09-fold its 1991 biomass, whilst at a stopped drift this figure would be 1.46. Such numbers can be considered plausible, given that Camphuysen (2004) reported an average annual 41% increase in the number of sightings of harbour porpoises between 1989 and 2004, corresponding with a comparable increase in the number of reported strandings. The respective values were applied to the Ecosim functional group 'toothed whales' in our model and multiplied with 1991 abundance. Combined with the above described increase in seal biomass, they formed our two marine mammals scenarios to test the sensitivity of msMSY to changes in these species: one in which grey seals and harbour porpoises would reach their anticipated carrying

capacities, and one in which this would be the case, but porpoises would additionally keep up their southward migration.

3. Results

In the baseline scenarios, efforts and fishing mortalities leading to msMSYt were around 10% higher than those leading to msMSY€. This is for the contradictory biological and ecological dynamics of plaice and sole: While plaice is the more solid of the two stocks in the southern North Sea, it also reaches only about 16% of the market price of sole. A fishing strategy opting for maximum yields in tonnes combined will thus plea for higher efforts, resulting in higher catches of plaice but overfishing of sole, while the opposite will be the case for strategies aiming for high revenues from landings. When applying a more coarse msMSY effort search grid, in which, in the endeavour to find msMSY, fishing efforts were changed in steps of 0.5-fold those efforts executed in 2010 (c.f. section 2), the difference between msMSYt and msMSY€ became indistinct and both fishing strategies now were alike. For the further analysis and comparison of the baseline with other scenarios, this will be the msMSY version used.

Comparing this baseline msMSY with the scenario of projected future marine mammal populations, our results suggest that increases in the abundance of marine mammals do not lead to a need to reconsider the fishing strategy leading to msMSY. At a 0.5-fold search grid (c.f. section 2), there are no differences in effort and F levels between the two marine mammals scenarios and the baseline (Table 1). Increases in the populations of harbour porpoises and grey seals considerably affect cod catches and biomasses (and more so, as expected, for the scenario with pertained southwards drift of the porpoise population), while they have a much more limited effect on flatfish (Table 2 and Table 3). As suggested by Temming and Hufnagl (2014), our study also shows that seal predation on cod relieves brown shrimp from their key predator, leading to higher stock biomasses and catches of the shrimp (Table 3). The only subtle differences between the scenario with and the one without ongoing southward shift of harbour porpoises illustrates the dominant impact of seals on fished stocks compared to the cetaceans.

A cut in system productivity, as modelled through the 30% decreased primary productivity, has severe consequences on the food-web and its fisheries. Efforts and thus Fs (given that the relationship between F and effort is assumed linear, c.f. Chapter 3) have to be reduced to half the levels they would be at msMSY with a primary production as is (Table). This counts for both msMSYt, i.e. the fishery optimized to catch a maximum total tonnage of the four scope species combined, as well as msMSY€, the strategy leading to the largest overall revenue from landings of the four species. Brown shrimps are struck the hardest, having their biomass reduced to less than a fourth of the baseline msMSY value (Table 2). With brown shrimp being a prime prey organism of cod in the model, it comes as no surprise that the latter suffers severely from reduced system productivity cascading through the modelled food-web. Its biomass collapses below half of what was found at the baseline msMSY (Table 2), despite considerably lower fishing pressures (Table 1). Flatfish SSB are the least affected by a reduced primary productivity, but still lose a fourth of their biomass compared to the baseline scenario (Table 2). Their catches and revenues from landings are more affected and drop to around 40% (Table 3 and Table 4). Catches of cod are depleted to a fourth, and shrimp fishery is affected the strongest with its yields down to a tenth of what was produced as the baseline msMSY.

Table 1: Fishing mortalities (F) of mature cod, plaice, sole, and brown shrimp, and effort at multispecies MSY for maximum catch in biomass (t) or revenue from landings (€) under different scenarios

Scenario	msMSY	Effort relative baseline	F Cod	F Plaice	F Sole	F C. crangon
Baseline	t	/	0.45	0.40	0.33	2.46
Baseline	€	/	0.45	0.40	0.33	2.46
PP 70%	t	0.5	0.26	0.21	0.18	1.23
PP 70%	€	0.5	0.26	0.21	0.18	1.23
Mammals with drift	t	1	0.45	0.40	0.33	2.46
Mammals with drift	€	1	0.45	0.40	0.33	2.46
Mammals without drift	t	1	0.45	0.40	0.33	2.46
Mammals without drift	€	1	0.45	0.40	0.33	2.46

Table 2 : Equilibrium spawning stock biomasses at multispecies MSY under different scenarios relative baseline multispecies MSY

Scenario	msMSY	SSB Cod	SSB Plaice	SSB Sole	B C. crangon
PP 70%	t	44%	77%	75%	23%
PP 70%	€	44%	77%	75%	23%
Mammals with drift	t	78%	95%	98%	134%
Mammals with drift	€	78%	95%	98%	134%
Mammals without drift	t	79%	96%	98%	133%
Mammals without drift	€	79%	96%	98%	133%

Table 3: Catch in tonnes at respective values of multispecies MSY relative baseline scenario's multispecies MSY

Scenario	msMSY	C_t Cod	C_t Plaice	C_t Sole	C_t C. crangon
PP 70%	t	25%	40%	40%	12%
PP 70%	€	25%	40%	40%	12%
Mammals with drift	t	78%	95%	98%	134%
Mammals with drift	€	78%	95%	98%	134%
Mammals without drift	t	79%	96%	98%	133%
Mammals without drift	€	79%	96%	98%	133%

Table 4: Revenues from landings at respective values of multispecies MSY relative baseline scenario's multispecies MSY

Scenario	msMSY	$C_€$ Cod	$C_€$ Plaice	$C_€$ Sole	$C_€$ C. crangon
PP 70%	t	22%	39%	38%	12%
PP 70%	€	22%	39%	38%	12%
Mammals with drift	t	78%	95%	98%	133%
Mammals with drift	€	78%	95%	98%	133%
Mammals without drift	t	79%	96%	98%	133%
Mammals without drift	€	79%	96%	98%	133%

4. Discussion

This study explores the sensitivity of msMSY fishing strategies and yields to ecological changes in a food-web model of the southern North Sea. It shows in which cases fishing pressures have to be adopted in response to potential future ecosystem regimes to produce maximum catches and revenues, and how yields and spawning stock biomasses may react. All potential environmental changes tested here have negative effects on the yields of the three fish species sole, plaice, and cod. Generally, plaice catches are most robust, followed by sole. Brown shrimp catches suffer from cuts in system productivity, but benefit from cod stock reductions through marine mammals. Of the scenarios tested, losses in primary productivity pose the most severe challenges to all three fisheries, beam, otter and brown shrimp trawlers, while the predicted increases in marine mammals consistently raise the least concerns.

It came as an expected result that fished stocks' productivity would decline with primary productivity (representing nutrient reduction) in the model. As such, Rijnsdorp and Leeuwen (1996) found hints that juvenile plaice in nearshore areas of the North Sea may grow better under increased nutrient loads, alike to findings for sole (Rijnsdorp et al. 2004) and brown shrimps (Boddeke 1996). The result of stock and yield decline under the de-eutrophication scenario was also expectable since we did not implement the negative processes through which high nutrient loads can harm resource productivity. Positive effects of de-eutrophication measures on fished stocks can arise though a lower likelihood of bottom oxygen deficiencies. These oxygen depletions can occur if excess production of phytoplankton organisms leads to them sinking to the sea floor before they can get grazed in the water column. On the bottom, this excess organic matter is consumed through oxygen intensive microbial processes, which can lead to local oxygen depletion. Hypoxia, also termed oxygen deficiency, which regularly occurs in the southern North Sea (Große et al. 2016), makes brown shrimp metabolism less efficient (Hagerman and Vismann 1995), and impairs the egg development (MacKenzie et al. 2012) and year class strength (Plikshs et al. 1993) of cod in the Baltic Sea. Besides a decreasing likelihood of hypoxia, further effects of de-eutrophication are rather complex to predict. This refers to nutrient-induced changes in the species composition of phyto- and zooplanktonic communities and those species' respective attractiveness and availabilities (or *vulnerabilities*) to predators (e.g. Colijn et al. 2002; Beaugrand et al. 2003). The plankton groups are only very coarsely represented in our Ecosim model. Zooplankton is constituted of just three functional groups in the model, of which copepods form a single one. Even just with regard to copepods, the transfer of changes in primary productivity (in our case derived from external models; Lenhart et al. 2010) to higher trophic levels via zooplankton must thus be considered as oversimplified and potentially flawed in our model. Copepod species composition , rather than pure abundance, has been shown to play a pivotal role in driving cod stock productivity (Beaugrand et al. 2003; Beaugrand and Kirby 2010), and such a phenomenon would not be resolved by our model. Neither resolved were species- respectively size-specific preferences or even non-edibility of phytoplankton by zooplankton. Higher nutrient availability leads to higher phytoplankton cell sizes, which can, given that zooplankton larval stages may be incapable to ingest them, lead to a decoupling of zooplankton from phytoplankton growth (Falkowski et al. 1998). Their longer generation cycles compared to phytoplankton may make copepods incapable of skimming of boosted primary production in the North Sea (Colebrook 1979). Larger, heavier cells growing during high-nutrient phases can be better armoured with a calcifereous or silicate shell, and tend to sink faster, thereby adding up to the inavailability of the additional phytoplankton biomass to zooplankton in enhanced nutrient conditions (Falkowski et al. 1998), and microzooplankton (heterotrophic protozoans), amongst the most important consumers in pelagic food-webs, prefer small celled dinoflagellates; cryptophytes and green algae over the often dominant diatoms (Burkill et al. 1987).

While a lack of detail in the pelagic lower trophic level compartment chiefly questions the credibility of our simulated results with regard to cod, it is a matter of slightly less concern for flatfish, or brown shrimps. The positive trophic effect of high nutrient loads on the productivity of sole and plaice (Rijnsdorp and Leeuwen 1996; Rijnsdorp et al. 2004) primarily arise from an enhanced benthic production under eutrophication (Reise 1982, Beukema and Cadée 1986 Beukema et al. 2002). Total benthos production can, even alongside a change of species composition, be fueled through both phytoplankton edible or non-edible by intermediate trophic levels, given that the latter would end up as detritus and feed into the benthos compartment that way (Chapter 1). For freshwater lakes, de-eutrophication measures have been demonstrated to impair fisheries production for some cases (Gerdeaux et al 2006; Stockner et al. 2011), but also to leave them unaffected in other studies (Ludsin et al. 2001).

As stated, with the potential positive effects of de-eutrophication and the complexity implied by the diverse phyto- and zooplankton communities and their feeding interactions not included in the simulation modelling of this study, and given the ultimate dependence of all other production in the model upon primary production, it was unsurprising to see phytoplankton decline affecting predicted stock productivities and yields solely negatively in the model. That being said, it is still noteworthy that the resulting loss in biomasses, yields and revenues is generally overproportional relative to the implemented algae reduction, and that it would cascade through the entire food-web to affect e.g. cod pretty much undamped. Interesting in this context is the less severe response of flatfish, which probably relates to their more flexible diet (Chapter 1; Chapter 2). The plausibility of these modelled results is disputable, and could be underpinned by studying the past correlations of stock productivity and nutrient loads. In a study which, however, relates coastal nutrient loads with spatial distribution rather than stock productivity, Støttrup and colleagues (2017) found indications that declines in coastal nitrogen loads have driven juvenile plaice away from the shore into deeper waters of the North Sea since the early 1990s. Colijn and co-authors (2002) reviewed trends in the biomasses and productivities of plankton, benthos, fish and shrimps, and related these changes to nutrient enrichment. However, given the multitude of drivers affecting stock biomass and productivity and those drivers' likely multicollinearities, they found the causes hard to disentangle. Until this has been successfully performed, our study presents a meaningful what-if simulation.

Considering the predicted consequences of marine mammal upsurge, the remarkable extend (an almost sixfold increase of seal biomass) lead to underproportional responses of biomasses and yields, in contrast to the amplified, overproportional effect of the 30% reduced primary production. Should this appear unexpected at first, that anticipation gets entirely reversed when looking at absolute changes in biomass or production in tonnes per annum: The standing stock of phytoplankton alone is 300 times higher than that of all marine mammals combined, whereas the annual total primary production (P/B*B = P) is six orders of magnitude higher than that of marine mammals in the Ecopath 1991 base model (Chapter 1). That being said, a 30% reduction in primary production would of course be expected to overrule the effect of a sixfold increase in predation through marine mammals. From this perspective, it is rather surprising that the two phenomenas' effects are even broadly comparable. That, again, arises from the fact that the fish target species investigated here belong to that particular group of species for which seals cause a considerable (flatfish) to pivotal (cod) share of their total predation pressure (Chapters 1 and 2]).

To launch our marine mammal scenarios, we set the vulnerability (v) of seals to 2.0 instead of the originally fitted 1.0. Christensen, Walters et al. (2008) caution that the decision for the default value 2.0 is as valid as the decision for any other value, and the extent to which an increase of seal biomass affects its prey is a directly predictable function of that input parameter v. However, whether we choose v = 1.0 or v = 2.0 does not affect FmsMSY, but only BmsMSY and CmsMSY (results not shown).

In our attempt to predict a carrying capacity of seals (section 2.3), we only included grey seals in the analysis, but left harbour seals (*Phoca vitulina*) aside. This flaw is primarily due to the unavailability of an appropriate population model, and we consider it to be of minor importance in estimating potential future seal predation, as both populations appear to grow (ICES 2008) and since grey seals contribute the major share of total seals' biomass (Mackinson and Daskalov 2007). A more severe shortcoming is the fact that seal predation is a local phenomenon (Temming and Hufnagl 2014), with both species bound to coastal waters to raise and feed their pups (ICES 2008). However, while harbour seals are quite bound to the shore, grey seals can be seen much further offshore (ICES 2008), and harbour porpoises are sighted in high densities up to 300km off the nearest coast (SCANS I and SCANS II surveys). We thus argue that marine mammal predation is, if not spatially uniform, at least an omnipresent phenomenon in the southern North Sea.

For the management of sole and plaice in the North Sea, seal and porpoise predation does not play a role in ICES' stock assessments and management considerations (WGNSSK 2015). Very different so for cod, for which updated seal abundance and diet data are plead to be included into estimating predation mortality (WGNSSK 2015), e.g. through the stochastic multispecies model SMS (WGNSSK 2015, WGSAM 2016). Since currently no input nor output management scheme applies for brown shrimp in the North Sea, the issue of potential indirect effects between shrimps and mammal populations is not addressed on an ICES advisory level, but it was described by Temming and Hufnagl (2014). Effects of nutrient loads upon stock productivities are generally not referred to in the stock assessments reports of plaice and cod (WGNSSK 2014; WGNSSK 2015), but the potential positive relationship between riverine phosphate discharge and the growth of sole (Rijnsdorp et al. 2004) was mentioned under 'ecosystem aspects' in the 2014 assessment (WGNSSK 2014). That is no surprise, given that, while impacts of selected upper trophic level predators on target stocks can be addressed by some multispecies models (e.g. SMS; see WGSAM 2016), explicit implementations of lower trophic level dynamics and their direct and indirect interactions with target species are the unique feature of food-web models (or designated minimum realistic models; c.f. Plaganyi 2007) and cannot be included into the single species assessment models which dominantly produce ICES' advice. The larger set of explanatory parameters in food-web models, of course, comes for the price of walking the tightrope between overparametrization and boundless uncertainties (Plaganyi 2007; Chapter 2; Dissertation conclusion). Thus, as any model, particularly data intensive ones like our Ecosim model, which is rich in input parameters and biomass pools, it inherits the uncertainties of its data sources (Mackinson et al. 2009b; Chapter 1 and 2) and can be biased through the potentially flawed assumption of stable patterns in any of the input parameters, such as e.g. dietary preferences. Additional limitations arise through the application of the different scenarios. As such, our primary productivity setup is tangled with issues in any of the lower trophic level model runs synthesized by Lenhart and co-authors (c.f. section 2.2). Also, the -30% primary productivity there applies for certain areas only, while we interpreted it as a whole area average in the case of de-eutrophication. Many of the de-eutrophication measures mentioned in Lenhart, Mills et al. (2010) have already been undertaken, such that it cannot be taken for granted that the decrease in primary productivity we hypothesize would prevail.

Our results indicate that exploitation intensities, i.e. fishing mortalities and efforts, leading to msMSY may only be robust to changes in marine mammal predation. Decreases in system productivity, there against, lead to a need to reconsider fishing strategies when opting for maximized yields in weight and revenue. In essence, the level of exploitation had to be reduced in all respective cases. These results advocate the benefits of fishing at the lower edge of MSY ranges, i.e. with fishing pressures that, while still providing acceptable yields, lie below those associated with absolute maximum yields (Hilborn 2010; ICES 2015; Kempf et al. 2016; Chapter 3; Dissertation conclusion). Regarding fishing intensities that theoretically provide absolute optimum yields as a limit that is to be avoided, rather than a target may provide not only conservation safeguards, but also increase the robustness of aspired yields.

5. Acknowledgements

Author contributions

MS, AK, SM and AT developed the idea of this study. SM contributed the marine mammal population models and their documentation (Appendix G and H). MS performed the analyses, advised by AK. MS wrote the manuscript in close collaboration with AK and AT.

6. Appendix G: Grey seal projections

As composed by Sophie Smout and colleagues at the Scottish Oceans Institute, East Sands, St Andrews

6.1. Introduction

This document describes the approach used to predict grey seal numbers and biomass in the southern part of the North Sea for use in the MYFISH project. The model structure and parameters are based on a Bayesian age-structured population model described by Thomas (2013). The model divides the UK grey seal breeding population into several areas of which the whole-North-Sea, excluding Orkney, is one. Model selection suggests that these breeding populations are separate, and the model assumes each of them is internally well-mixed without further spatial structure. We focus on the model outputs representing the grey seal population which breeds in the main part of the North Sea, which is considered a reasonable approximation to the population using the southern region of ICES area IV.

Future scenarios may involve different assumptions about the levels of fishing in fisheries that may result in seal bycatch, and/or the nature of density dependence in the seal population.

6.2. Methods

- The population model was fitted to aerial survey pup count data, and summer count data for adult grey seals (Thomas 2013). Pup count data are available for all years in the time series, but only one count survey for adults was completed. The model was fitted using informative priors (for survival and fecundity) based on long-term observational studies and on the analysis of historical shot samples. (Lonergan 2012). Density dependence in this model acts though first-year pup survival, with low survival rates currently predicted for some UK populations (though not that in the North Sea which does not yet appear to be approaching carrying capacity).
- In order to interpolate/extrapolate the NS population, a simulation is provided using EXCEL based on the age-structured population model fitted for the North Sea area. To initialise the model, following the method of Thomas (2013), the initial population structure is assumed. It is derived from a Leslie matrix model with values of survival and fecundity corresponding to a low-density population (i.e. showing very little effect of density dependence).
- To convert from numbers-at-age to biomass, I assumed the following masses–at-age in kg (Sparling 2003)

Table G.1: Mass-at-age conversion to convert numbers-at-age to biomasses.

	pups	1	2	3	4	5	Adults
females	34.5	46.25	61.25	76	89.5	101.5	154
males	34.5	49	64	80	95.75	110.75	214
weighted mean	34.50	47.38	62.38	77.65	92.07	105.31	178.71

6.2.A   Running the model to generate predictions

The baseline model has been run forward in time for 50 years from the present. Different scenarios that might be explored could include:

Adjust carrying capacity

Because the North Sea grey seal population does not currently appear to be close to carrying capacity, estimates of its carrying capacity based on current time series data sets are subject to considerable uncertainty. The effects of this uncertainty on the population projections can be investigated by altering the parameter chi, currently set at 14400. Plausible values to try, based on the posterior distribution of the parameter χ would be 12000, 16000(Thomas 2013).

Include bycatch explicitly where future fishing effort intensifies

Currently, the grey seal population model does not explicitly include grey seal bycatch, because this is not thought to be an important driver for grey seal populations in the North Sea. Bycatch mortality that has been operating over the time represented in the data set will have been 'absorbed' into natural mortality during the model fitting process.

The effect of additional removals due to alternative, more intensive bycatch scenarios could be included using a simple subtraction representing 'additional' annual bycatch (see sheet 2 "remove adult females" for one example, in which 'extra' bycatch has been implemented from 2013 onwards).

The effect of bycatch on the population trajectory will depend on the impact on different age classes: removals of adult females will cause the greatest change in the population trajectory, while removals of juveniles will have less effect. In general with marine mammals, it is often the case that it is the naïve younger animals that experience greater mortality in interactions with fishing gear. For the sake of developing a speculative scenario it might be reasonable to allocate most of the bycatch to juvenile animals but we must be cautious in interpreting results. Because of low sample sizes in records of bycatch, very little data is available indicating the true relative vulnerability of different grey seal age classes to bycatch.

If a future scenario with increased effort in midwater trawling or in set net fishing is to be explored, the rates in the following table may be of use. Conservatively, it might be appropriate to assume the impact of all seal bycatch focussed on grey seals (for this assessment). Note that rates are not (within the range of available data) significantly affected by the grey seal population size.

Table G.2: Fisheries catch rates.

	General gear type	Observations			Catch rate per 1000 days at sea	
		No of hauls observed	No of bycaught individuals	Expected No of hauls per day	Mean	95% UCL
Seal (2 spp).	All midwater trawl	205	50	1.2	292.68	[370.31]
	All set nets	6099	84	3.2	44.07	54.48

6.3. Caveats

1. The numbers of observed bycaught animals are low and therefore this is noisy data, resulting in uncertain catch rate estimates. It is not possible to estimate the age-structure of by-caught animals and thus difficult to estimate any difference in vulnerability between age classes. It is possible that the overall calculated bycatch rates are biased low (Northridge pers com).
2. The population model assumes that UK populations of grey seals using the Orkneys, North Sea, and West coast are entirely separate. For breeding, this may be approximately true. However in practice during the foraging season there can be substantial movements between areas, and it is very likely that the impact of high levels of bycatch in one area would be "shared" by animals that breed outside this area. In the case of the North Sea, large numbers of animals breeding in Orkney are known to use the North Sea for foraging.

7. Appendix H: Harbour Porpoise Model

As composed by Sophie Smout and colleagues at the Scottish Oceans Institute, East Sands, St Andrews

7.1. Introduction

This document describes the approach used to predict harbour porpoise numbers and biomass in the southern part of the North Sea for use in the MYFISH project. The methodology is based on a Bayesian age-structured population model developed by Winship (2009) which includes bycatch as a source of mortality for the animals in addition to natural background mortality. The model used has the whole-North-Sea as one mixed population. Therefore to allocate numbers/biomass to the appropriate area, distribution maps from the SCANS project have been used.

Future scenarios may involve different assumptions about the allocation of animals to the Southern North Sea, and about future levels of gillnetting effort.

7.2. Methods

*   Harbour porpoise summer distribution and abundance in the North Sea (NS) were estimated from the SCANS1 and SCANS2 surveys (1994 and 2005). These estimates do not include calves i.e. they represent numbers of 1+ animals.
*   To interpolate between these surveys and to extrapolate the population forward in time, a simple production-type model could have been used. However, the age structure of the population may be important not only in estimating biomass, but also in reflecting the time-lags likely to be important in a population of long-lived animals that reproduce at a relatively slow rate (relative to teleost fish).

- In order to interpolate/extrapolate the NS population, to include calves, and estimate changes in overall biomass, a simulation has been coded in R based on the age-structured population model developed by Winship (2009). This model was originally fitted using Bayesian methods to the 2 SCANS estimates, and also made use of substantial prior information based on life-history data from stranded and bycaught animals. The model is initialised with an age structure based on that estimated by Winship during the original model-fitting.

- To convert from numbers-at-age to biomass, a Gompertz growth model was fitted to data described in Van Utrecht 1978 using a non-linear least squares routine in order to estimate mass-at-age for both male and female porpoises (females are larger in this species). The age-to-mass calculation is carried out within the simulation so that time series of numbers (calves and 1+ animals) and also of total biomass are produced.

- Bycatch in gillnet fisheries in UK and Danish waters was included in the original population model. The impact of bycatch acts like a fishery, removing individuals from the population. Bycatch effort data available at the time of the modelling exercise were rather complicated.
    - 10 different gillnet fisheries were identified in UK and Danish waters: these were the main source of bycatch for porpoises and other fisheries had relatively little impact.
    - Bycatch rates were recorded as number of bycaught porpoises per unit effort in each fishery.
    - Effort was recorded in two different forms: for UK waters, the number of hauls was used. For Danish waters, catch of target species of the fishery was used. The modelling was possible using this method because bycatch rates could be associated with these measures of effort for each fishery, but the effort data are not easily comparable with one another or with other data.
    - However, extrapolation should be possible. "Inside" the simulation there are 10 fisheries, each with associated effort for each year. If we assume that the distribution of effort between these static fisheries remains fixed, then it is possible to predict the impact of "general" changes in effort in gillnetting. For example, if gillnetting effort in general doubles from 2005 to 2010, a factor 2 can be applied in the simulation to the effort invested in each of the 10 fisheries. This should act to simulate overall changes in static fishing effort and their effects on harbour porpoises. This method is implemented in the R simulation.

- Spatial distribution. Porpoise distribution has changed substantially between the 2 SCANS surveys (Hammond et al 2013). The population model predicts number and biomass for the whole North Sea area, but estimates are needed for the southern area. Therefore, we allocate numbers/biomass based on the distribution maps (density surfaces or layers) predicted from the SCANS survey data. Based on these maps, abundance is summed over the grid cells lying in ICES Areas IVb and IVc , and compared with total North Sea abundance. The corresponding proportions of the total population are then allocated to the southern area in 1994 and 2005.

- To estimate the proportion that should be allocated to the south area in other years, between 1994 and 2005 and in future years, a simple linear trend was fitted based on those two years. This was then used to predict changes in the proportion in the south. The linear function was truncated at 1 and 0 so that no negative predictions could be produced and so that the population in the south could not exceed the total population. This is a crude model (a logistic curve might be more aesthetically pleasing) but the trend is relatively gradual so it may suffice.

7.3. Running the model to generate predictions

R code is included here as an appendix. All the code needed to run a simulation is included, along with the relevant data e.g. the parameters of the growth model, historical levels of gillnetting effort etc.

The user can decide how many years into the future the simulation will run, what levels of gillnetting effort will be applied (relative to those in 2005).

The user can choose either to keep the 2005 spatial distribution of porpoises in the North Sea or else to continue the 'southward drift' of the population using a simple linear trend.

Therefore the user can apply different scenarios of gillnetting effort and spatial change in order to explore the overall impact on the southern part of the harbour porpoise population in the North Sea.

7.4.   Caveats

1.   The simulation represents one of several different models that Winship fitted to the SCANS data. It was chosen because density dependence is included and it seems important to include this possibility when dealing with 'future scenarios'. However, if substantial increases in population size are predicted, these should be regarded with some scepticism . The original model was fitted using data from years when the harbour porpoise population was pretty steady around 250000 in the North Sea. Estimates of density dependence were therefore difficult and uncertain, and the value assumed in the simulation is one of many possible ones.

2.   Alloction of gillnetting effort between UK and Denmark, and between gears/target species, might change. Bycatch rates do vary between gears so this might be problematical.

3.   The 'linear model' used to predict re-distribution is very naïve. Unfortunately we do not yet know what is driving the re-distribution of porpoises (and perhaps seals) towards the southern part of the North Sea. It is therefore difficult to be predictive about it. It seems likely that this is resource-based and would be very interesting to investigate further.

Dissertation conclusion

Approaches and implications of maximizing multispecies yields in the southern North Sea in an ecosystem context

This Ph.D. thesis revolves around the question of what happens when yields of the southern North Sea's demersal fishing fleets are sought to be optimized under the consideration of the direct and indirect trophic and technical interactions amongst the species they target (Chapters 2, 3, and 4). It further explores how such multispecies maximum yield options would align with the state and health of populations that are not of primary or any commercial interest (Chapters 2 and 3). Once identified, fishing regimes predicted to produce optimum yields are tested for their sensitivity to assumptions about the relationships between fishing effort and mortality (Chapter 3) and long-term, large-scale trends in the dynamics of the top (marine mammals) and bottom (plankton productivity) compartments of the southern North Sea food-web's (Chapter 4). Apart from maximum yield considerations, the general state and functioning of the past food-web and the effect of fisheries as a whole are assessed (Chapter 1).

How does the southern North Sea's food-web function and what is the role that fishing plays in that?

Our holistic assessment of the southern North Sea ecosystem in 1991 points out that its different compartments are trophically highly connected and that the food-web is densely woven (Chapter 1). Ecological theory (Odum 1971; Ulanowicz 1986; Christensen 1995) suggests that these properties correlate with a system's resilience to external pressures (including fishing) and that they are indicative of ecosystem health. Finding that for the southern North Sea came comparatively unexpected, given the narrative of the North Sea bearing a long history of heavy exploitation, with associated consequences for species and ecosystem (Jennings and Kaiser 1998; Rogers and Ellis 2000; Thurstan et al. 2010). From today's perspective, one might argue that considerable conservation efforts had been undertaken, including stock rebuilding (e.g. the 'cod recovery plan'; EC Council Regulation No 423/2004) and fishing effort restriction (c.f. EC Council Regulation No. 41/2007; No. 2056/2001; No. 51/2006; and No. 40/2008, annex IIa). However, these efforts have largely only started to show effects throughout the 1990s (Jennings et al. 1999; Rätz and Mitrakis 2012), and fishing efforts were on a high level still in our model's base year, 1991. It was actually only during the second half of the 1980s that beam trawling effort started to emerge, reaching its peak in 1992 (Jennings et al. 1999). The possible explanation of finding a comparatively healthy and resilient southern North Sea (and total North Sea in general; c.f. Mackinson and Daskalov 2007) as the result of successful fisheries conservation efforts does that not appear to hold. Rather, one could hypothesize that the system had, by 1991, adopted to the anthropogenic pressure (which, by then, had at least been a fairly constant factor throughout decades) in a system-wide evolutionary process to such an extent that it could cope with the (constant) stressors and still be resilient to potential additional (pulsed) impacts. This, of course, is a risky assumption and would have to be verified by e.g. analyses of empirical data about how the existing system reacted to any novel, pulsed events in the past. Another thinkable hypothesis of why the southern North Sea was found to be highly complex is a more disillusioning one: Is it not natural to assume that the more thorough and holistic the attempt to model an ecosystem, and the more effort put into establishing all possible compartments and their interactions, i.e. the 'bigger' the model, the more complex it will become – to some extend independent of how complex it actually is, compared to other systems? If that was the case, the southern North Sea would appear to be a mature, healthy system (as expressed through total biomass density; a high system omnivory index; large share of the biomass produced through photosynthesis being aggregated in the food-web; or respired; c.f. Odum 1969; and Christensen 1995) simply because it is a big model. As such, our model ranges at the upper edge of global Ecopath models in terms of the number of functional groups (68; compared to an average 26 and maximum 68 in an assessment of 105 global Ecopath models by Heymans et al. 2014)

and the data richness of the modelled system (with e.g. the 'year of the stomach' data providing an exceptional dataset allowing a fine-scaled parametrization of diets, which could e.g. boost the extend of omnivory compared to systems for which diet information is more scarce). The question of how sampling and parametrization efforts affect the characteristics of the resulting food-web model was thoroughly debated in the past with the conclusion that, while food-web models are generally not scale-free (Dunne et al. 2002), e.g. the connectance index (which scored average compared to other models for ours; c.f. Chapter 1) is indeed a property constant across a range of sampling and parameterization efforts (Martinez 1993; Havens 1993; Martinez et al. 1999). Alike has total biomass density – which indicates high system maturity for the southern North Sea model – been shown to be robust against generic model properties like numbers of nodes and links (Heymans et al. 2014). The independence of other indices associated with ecosystem maturity, however, is not necessarily substantiated, and e.g. system omnivory co-varies with model construction (Heymans et al. 2014). The finding that the southern North Sea (and the entire North Sea, c.f. Mackinson and Daskalov 2007) can be considered a mature food-web should thus be carefully weighed against the role which sampling and parametrization effort can play in systematically affecting the relevant indices.

Can good yields of flatfish, cod, and brown shrimp be achieved simultaneously in the southern North Sea?

The endeavour to find fishing regimes which would lead to the synchronous fulfilment of single species specific management goals, i.e. high yields of plaice, sole, cod and brown shrimp simultaneously, was impaired to incapacitated by biological and technical interactions between the target species. In particular, the direct predator/prey relationship between cod and brown shrimp leads to mechanisms similar to the then ground-breaking findings of first multispecies models (Pope 1991) that higher fishing efforts can produce higher multispecies yields if the reduction of a predatory stock releases its prey from predation mortality, which can then be replaced by fishing mortality to increase yields from the prey stock (Pope 1991). For the southern North Sea Ecosim model, maximum brown shrimp yields were thus obtained when cod was overfished, i.e. its stock size reduced below a level which produces single species maximum sustainable yield (MSY). Using brown shrimp catch data and estimates of predation through cod and whiting, this phenomenon was also described by Temming and Hufnagl (2014). To a more subtle extend, the achievement of good yields of all key commercial species simultaneously was hindered by predatory competition between cod and flatfish, which share a significant extend of common prey resources in the southern North Sea (Chapter 1 and 2) and thus benefit from low stock sizes of the respective competitor. Both these phenomena, predator/prey dynamics of a 'standard' and a low trophic level target species, and prey resource competition between two target species, would not have shown in classic multispecies assessment models, since they require an explicit representation of the population dynamics of the lower parts of the food-chain.

The apparent impossibility to achieve good yields of multiple trophically interlinked species simultaneously came as no surprise. It aligns with similar findings for the roundfish fishery of the entire North Sea (Mackinson et al. 2009b) and with the detrimental effects demonstrated for a multitude of ecosystem models when all single species are fished simultaneously at Fmsy, i.e. the fishing mortality associated with single species MSY (Walters et al. 2005). In conclusion it must thus be questioned, for the southern North Sea's demersal fishery, and in concert with comparable findings on a globally scale, if the promotion of maximizing fishing yields should be considered wise in the multispecies respectively ecosystem reality in which literally every fishery operates. As Chapter 2 and comparable studies suggest (Mackinson et al. 2009b; Ulrich et al. 2017), optimal solutions (respectively simulations thereof) for the North Sea's multispecies fisheries do exist. Such optima, however, are often 'multispecies best possible yields' rather than actual 'good yields'. It is questionable in how far such mathematical solutions are socially, economically and environmentally acceptable; and I would regard it as certain that the plead for maximizing single species catches without considering multispecies

trade-offs is a dangerous endeavour. While this insight in its computed explicitness can be considered novel (though not surprising) for the southern North Sea's four key demersal stocks, it is luckily neither new nor ignored on a global scale(Larkin 1977; Mace 2001 ; Walters et al. 2005; Mackinson et al. 2009b; Hilborn 2010; ICES 2013). Here, in a conclusion on a set of studies exploring the feasibility of "Maximising yield of fisheries while balancing ecosystem, economic and social concerns" (www.myfishproject.eu), however, it is worthwhile being echoed.

Do multispecies MSY scenarios hold up to testing the assumptions made by the ecosystem model?
Density-dependent changes in catchability
As described above and in chapter 2 there were indeed fishing scenarios which lead to simulated outcomes of 'multispecies best possible yields', meaning that they provided the maximum possible catches of the four key commercial species combined, under the restrictions posed by technical and biological interferences. These restrictions, however, were considerable and lead to catches in the multispecies MSY variant not exceeding 35% of some hypothetical maximum single species catches (Chapter 2). Leaving the social and ecological acceptability of such solutions aside, another pondering question concerns the appropriateness and implications of the assumptions made when arriving to them. These assumptions are implemented though the underlying equations in Ecosim, and their parameterizations, and concern e.g. the relationship between fishing effort and mortality. Is the catchability of sole and plaice – i.e. the proportion of the stock caught per unit of fishing effort – really constant, as the standard parametrization of Ecosim (and numerous other single and multispecies stock assessment models) assumes?

Given the remarkable and apparently systematic variability in the flatfish stocks' fishing mortality per unit of effort in the beam trawl fishery (Chapter 3), finding constant catchability would have been surprising. And indeed, based on fishing effort and single species stock assessment data, we found that the assumption of a constant catchability does not hold true for (at least) sole and plaice. Their catchability, i.e. the proportion of the stock harvested per unit of effort, changes with the abundance of the stock. This is a relevant finding per se, however, we pushed the thinking a bit further by using the Ecosim model to explore whether fishing efforts producing maximum catches of the two flatfish would be the same under assumptions of constant catchability and under density-dependent changes in catchability. The finding that fishing efforts leading to simulated MSY significantly vary with modelling assumptions, and that one of these many assumptions (constant catchability) would have been falsely made if Ecosim was parameterized the way it very often is (literally no other study does include density-dependent changes in catchability into its Ecosim fishing policy explorations) warrants caution as to whether even very holistic modelling approaches such as Ecopath with Ecosim can actually cover, beware handle, the complexity associated with fisheries management in an ecosystem context.

Importantly, the point of how detailed we can go, and whether that makes sense (c.f. also Plaganyi 2007), is ultimately a question of parsimony: Would we even have sufficient data points to adequately fit all the parameters it takes to additionally implement density-dependent changes in catchability in the model (to name just one of the many examples where detail can be added)? And would that significantly improve the realism of the model, i.e. its ability to predict the observed data. Or are we running the risk of overparametrization? And if we were so, and not consider density-dependent changes in catchability (to only name one of the limitless examples): What would be the respective uncertainty added to the predicted policy exploration outcomes, such as, in this case, fishing efforts leading to maximum catches? It is answering these questions upon which, I feel, the ongoing development of ecosystem models 'from toys to tools' in fisheries management will critically depend. One step forward on that path could be a 'power analysis' of Ecosim models, i.e. an assessment of how many data points it would take to fit the model statistically sound, given the number of parameters

which are estimated (primarily the 'vulnerabilites' determining the strength of trophic flows, c.f. Christensen et al. 2008). Along that path a significance threshold should emerge as suitable, similar to the t-statistics (with associated p-value) for individual parameters in multiple regression, which indicates whether or not the estimation of any additional parameter (predator-specific 'vulnerability' (Chapter 2), but also primary production anomaly (Chapter 2) or the above mentioned density-dependent changes in catchability; see Chapter 3) significantly adds to the explanatory power of the Ecosim model. Also, an equivalent of the multiple regression's model-embracing F-statistic, which associated p-value indicates the significance (or non-significance) of the entire statistical model, and the mentioned confidence intervals of predicted outcomes should be attemptable.

Trends in marine mammals populations and phytoplankton productivity
A second set of assumptions we tested with respect to their potential implications upon maximum yields of sole, plaice, cod and brown shrimp, and the fishing strategies predicted to produce such maximized yields, were expectable or apparent changes in the dynamics of the highest and lowest trophic levels of the food-web. Both decreasing nutrient loads into the southern North Sea (Lenhart et al. 2010) and increases in the population of harbour porpoises (*Phocoena phocoena*) and grey seals (*Halichoerus grypus*) were ongoing trends in the time scale covered by the Ecosim model (1991-2010), and Chapter 4 thus raises the question as to how far these phenomena bear the potential to affect multispecies MSY fishing for the southern North Sea's key demersal stocks. It finds that the examined drop in primary productivity would have dramatic consequences upon maximum yields. Also, the modelled 'worst case' reduction scenario of loss in primary productivity (Lenhart et al. 2010) lead to considerable cuts to be made to fishing efforts to produce the then possible MSYs. The increases of marine mammals predicted by ad-hoc population modelling (Appendix of Chapter 4) would have an expectable negative impact upon cod, whereas flatfish are barely and brown shrimp even positively affected. For conservation reasons, stocks of marine mammals in the North Sea are 'unmanageable' in the sense that they cannot purposefully be negatively affected. The predicted possibility of interferences with fishing yields must thus be accepted as a given, for which one can only be prepared. Despite the nature of the predictions being fairly coarse in both scenarios, with two very different types of modelled coupled to each other in an off-line, one-way manner respectively, the findings of Chapter 4 indicate that baselines upon which management considerations are based are changing. To foster our understanding about how likely and to what extend these changes will probably apply is, particularly with regard to the different, but interlinked responses of cod vs. brown shrimp, an area of research well invested in.

Trophic entire-food-web interactions are the main actors in this study, which thereby demonstrates one of the applications of ecosystem models for fisheries management which multispecies assessment models would partially be incapable of, as the latter fall short of explicit representations of the population dynamics of (often) top and (always) bottom compartments of the food-web, and their links with target stocks. However, just because such properties are included in the southern North Sea Ecosim model, it does not warrant them with the same credibility in their dynamics that key target stocks herein are equipped with (c.f. chapter 2). Their most truthful implementation would require a detail of the data of marine mammals' or plankton's diet compositions comparable to that for fish, as provided by the year of the stomachs (Hislop et al. 1997). Such detailed and representative stomach content studies are far from reality for marine mammals and probably far from even possibility for zooplankton. The core issue compromising the realism of the simulations outlined in Chapter 4 with regard to the conversion of enhanced nutrient loads into productivity and biomasses of higher trophic levels (fish and shrimps) through the phyto- and zooplankton compartments lies in the variety of species and size groups in these groups and their exact interactions (c.f. Chapter 4). It are these critical processes of eutrophication processes which our Ecosim model is incapable of accurately capturing, given that it lacks detail in the resolution of the phyto- and zooplankton compartment. Work-arounds

to overcome such shortcomings of the Ecosim models could be model coupling exercises with designated lower trophic level models, such as ECOHAM (Lorkowski et al. 2012; Pätsch and Kühn 2008). Such couplings were discussed during the course of this PhD project, but not undertaken, given that both models would have to have at least one trophic level represented in comparable detail, either fish and benthos in the lower trophic level model, or zooplankton in the Ecosim model. As such, the study presented in Chapter 4 is certainly more a what-if scenario modelling exercise rather than a realistic prediction, beware advice, on what to expect and do in the future. What it is, however, is yet another indication that fishing at the lower edge of the MSY curve can help safeguard 'pretty good yields' (Hilborn 2010) under uncertain conditions (which they always are when fishing in an ecosystem context), and that it can strengthen the resilience of not only the ecosystem itself, but also of the MSY fishing strategy. Further, the study aids to emphasize that whole ecosystem models can at times present the suitable model choice for fisheries management questions.

So what?

The concluding question must be: What are the merits of constructing and using a food-web model to investigate MSY-related fisheries management issues for the southern North Sea, rather than solely relying on existing single species assessment models (WGNSSK 2016) or (not yet existing) multispecies assessment or minimum realistic models (c.f. Plaganyi 2007; Miller and Poos 2010)? The studies compiled in this thesis show that there are processes critical to a MSY-motivated management of the trophically (and, more of a side-effect here, but nonetheless significant and addressable in our model: technically) interlinked key demersal stocks of the southern North Sea which are specific to ecosystem models, and would be left aside in models with a more narrow scope. A direct predator-prey relationship between two target species, one of which is a low trophic level organism, and indirect trophic links through the explicitly modelled lower compartments of the food-web play pivotal roles for the target species' population dynamics and their exploitation. That being said, critical thinking and the considerations outlined in Chapters 3 and 4 demonstrate that the detail of both the predictions of the food-web's structure and the shape of the (fishing) impacts it is subjected to can still be enhanced. Still, the resulting model would only represent a fraction of the detail thinkable if a round of experts of different fields was envisioning all possible factors driving the ecosystem's response to fishing and *vice versa* (c.f. Atlantis; Fulton et al. 2004; Fulton et al. 2011). For the southern North Sea case, even at the end of this thesis, it remains unclear as to where detail should be purposefully added, and where it might even be reduced, depending on the questions addressed. The danger of overfitting is always lurking around the corner, and despite the efforts to circumvent it here (Chapter 2), we might have fallen prey to it as well.

Despite that critical reflection, the processes outlined here certainly deserve to be drawn attention to: the trophic entanglement of the key demersal commercials; the apparent impossibility of achieving their MSYs (and a good environmental status) simultaneously; that density-dependent changes in catchability seem to apply for sole and plaice and that associated consequences for bycatch species may emerge under MSY fishing incentives; and that expectable changes in the dynamics of species outside the scope of classic single and multispecies assessment models can have considerable effects upon fishing under the MSY directive. Concluding on a more generic level, the message of all questions addressed in this thesis, the ones about food-web structure (Chapter 1), multispecies maximum yield options (Chapter 2), and those addressing the sensitivity of MSY-fishing to underlying model assumptions (Chapters 3 and 4), surprisingly consistently was: It is more complex than one would have genuinely presumed.

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Declaration on oath

I hereby declare, on oath, that I have written the present dissertation by my own and have not used any other than the acknowledged resources and aids.

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, 2017 / 07 / 06

Effects of and on the food-web when fishing for maximum sustainable yields in the southern North Sea

A main objective of fisheries management for the southern part of the North Sea under the European Commission's Common Fisheries Policy is the achievement of maximum sustainable yields (MSY) from each stock. However, the stocks are not exploited in isolation, but are linked through biological and technical interactions, and the food-web and ecosystem they are part of. This PhD thesis describes the functioning of the southern North Sea's food-web. It evaluates if, given this functioning, optimum yields of plaice, sole, cod, and brown shrimp can be achieved simultaneously. It also tests if such optimum solutions can be aligned with proxies of good environmental status. Potential changes in the catchabilities of sole and plaice, and their impacts upon MSY fishing are addressed. With the southern North Sea being subject to important ecosystem changes, such as increases in marine mammals and decreased nutrient loads through de-eutrophication measures, this thesis also investigates these processes' consequences for fishing yields and strategies.

Main tool of this thesis is the parametrization and use of a food-web model of ICES areas IVb and c (Figure I on page VII), using the Ecopath with Ecosim approach and software. The time-static Ecopath model represents the structure and functioning of the southern North, which turned out to be a highly connected, mature food-web (Chapter 1). In Chapter 2, the time-dynamic Ecosim model is subjected to a range of different fishing effort regimes to seek solutions leading to concurrent optimum yields of plaice, sole, cod and brown shrimps; and to test for their compliance with proxies of good environmental status. Its results show that direct and indirect trophic interactions between the four species considerably impair these endeavours. Running empirical data analyses, drivers of changes in the catchabilities of sole and plaice were identified, and their consequences upon MSY fishing and bycatch examined using Ecosim in Chapter 3. The results indicate density-dependent changes in catchabilities of sole and plaice. Higher efforts are thus needed to obtain their MSYs in the model, leading to negative effects on bycatch and other species. Chapter 4 uses predictions made by population and ecosystem models to implement likely developments of marine mammal populations and primary productivity in the Ecosim model to explore their effects on MSYs and associated fishing strategies. Its results indicate that, while reduced system productivity severely affects fishing yields and effort strategies, marine mammals are less of a concern, but for cod fisheries.

The studies compiled in this PhD thesis present the development and use of the first model to holistically address trophic and technical interactions between the fisheries for flatfish, cod and brown shrimps in an ecosystem context in the southern North Sea. They stress the importance of considering multispecies interactions and the role of bottom-up control for MSY-infused fisheries management.