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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 is based on the outputs of an *Ecopath* food-web model of the North Sea south of the Skagerrak (ICES area VIb and c), parametrized representing the year 1991. The study also compares the southern to a whole North Sea *Ecopath* model (whole ICES area IV) parametrized for the same year, 1991.

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 in the south, even with a nominally identically gear, to wit, otter trawlers. The largely different fish and catch compositions call for a specific, local management of the shallow southern North Sea's fisheries, which is based on ecosystem boundaries, rather than politically defined areas.

Beyond fished stocks, food-web network indicators suggest that both systems functioned similarly, if compared to a global set of *Ecopath* models. They also deem the 1991 North Sea and its southern sub-part a densely woven, mature and resilient food-web.

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., 2009; Link, 2010; Stäbler et al., 2016). Also, it became evident that fishing can affect inherent properties of marine ecosystems (Jennings et al., 1998; Heymans et al., 2014; Perry et al., 2010). Alike to 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. deeply exploring the structure and functioning of marine food-webs, These aspects need to be considered when deeply exploring the structure and functioning of marine food-webs, 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). EwE is build around a mass-balanced snapshot representation of the

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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 resilience. 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 et al. (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., 2017), 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 ecological 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 (Fig. 1). 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 50 m depth south of the so called '50 m-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 100 m. As such, the 'southern North Sea', as defined for this study, encompasses the largest share of the North Sea with depths < 100 m, with deeper areas only around Devil's Hole (230 m), and a small part of the Norwegian Trench, reaching up to 500 m in the northern Skagerrak. The spatial extend of this area is 345,874 km^2. 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 et al. (2017), 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 divide 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., 2017). The benthos community composition in the North Sea similarly shows a north-south structure, with mobile epibenthos dominating south of the 50 m-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

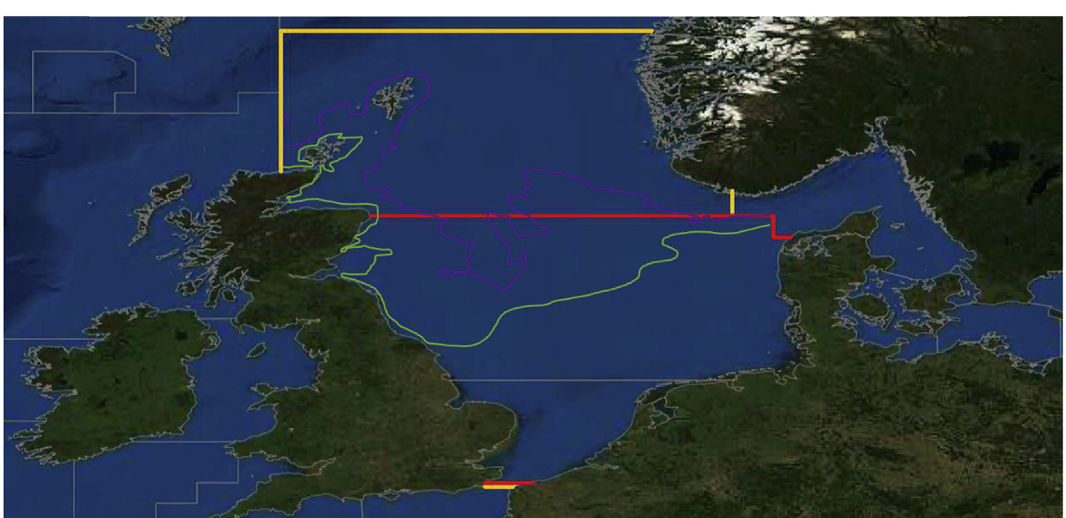

Fig. 1. A map of the study area, statistical areas IVb and c (encircled red), within the total North Sea, statistical areas IVa, b, and c (encircled yellow) of the International Council for the Exploration of the Sea (ICES). 50 m and 100 m isobaths are sketched in light green, and purple, respectively. Adapted from https://geo.ices.dk. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)