Identifying core areas for mobile species in space and time: A case study of the demersal fish community in the North Sea

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Abstract

Identifying well suited sites for spatial conservation measures to protect mobile species is a challenging task. Intra- and interannual movements of individuals due to foraging, reproduction and environmental change make it difficult to identify the best placed locations. This study presents a generic approach for determining a species' consistent core areas in space and time by using point abundance data from annual surveys. For this approach no statistical modelling is required and thereby it is well suited to obtain distribution maps for all surveyed species without knowledge on environmental predictors, thereby ignoring any issues related to data availability, quality and model confidence. Generating distribution maps for a suite of demersal fish species by using data from a scientific fisheries survey allowed to identify consistent core areas for 53 species in winter and summer over a period of 21 years (1998–2018). By overlaying single species' distribution maps, hotspots of fish diversity could be compared to designated sites of marine protected areas (MPA) within the European Natura 2000 network. A majority of the identified diversity hotspots as well as the core areas of threatened and endangered species are currently not overlapping with the designated Natura 2000 MPAs. These MPAs might therefore not contribute sufficiently to the protection of marine demersal fish as an important component of marine ecosystems. Alternative spatial management options and tools implemented through other marine policies are needed to amend the Natura 2000 MPA network for the effective conservation of demersal fish in the North Sea.

1. Introduction

Marine protected areas (MPA) have become an important tool to conserve marine wildlife and manage exploited resources (Edgar et al., 2014; Halpern and Warner, 2003). Locating protected areas for mobile species such as marine fish, however, is a challenging task and it has been debated whether MPAs are the appropriate means to protect such species (Breen et al., 2015; Claudet et al., 2010; Hilborn et al., 2004; Kramer and Chapman, 1999). Intra- and interannual movements of individuals due to foraging, reproduction and environmental changes alter the habitat preferences

of individuals throughout their life cycle (Harden Jones, 1968; Pittman and McAlpine, 2003). It is therefore difficult to assign areas large enough to conserve all life stages of a species (Horwood et al., 1998; Rayfield et al., 2008). Temporary conservation areas in combination with permanent protected areas have been proposed as solution (D'Aloia et al., 2019). However, in many situations political and societal circumstances will not allow for a flexible and adaptive designation of conservation sites (Halpern and Warner, 2003; Kaiser, 2005). Hence these sites should be chosen based on locations with consistently high abundances of threatened or overexploited ecosystem components (i.e. threatened species, habitats or exploited invertebrates or fishes) through space and time. Identifying such locations allows for an efficient allocation of limited spatial resources to conservation objectives.

The implementation of MPAs to manage marine resources has gained impetus at the beginning of the 21st century, as the impacts of intensive fishing during previous decades led to the perception of a crisis in quotabased fisheries management (Beddington et al., 2007; Jacquet, 2007; Worm et al., 2006). At this time, many experts advocated alternative approaches to fisheries management such as the establishment of networks of marine protected areas (MPAs) (Gell and Roberts, 2003; Roberts et al., 2005). While MPAs were demonstrated to be efficient management tools to improve the abundance and size composition of fish associated with structured habitats such as rocky habitats and reefs (Claudet et al., 2008; Claudet et al., 2010; Roberts et al., 2001), similar beneficial effects for fish species inhabiting boreal soft-bottom communities are still being discussed (Breen et al., 2015). Many fish species in temperate and boreal systems undergo wide ranging seasonal migrations between spawning areas, nursery habitats and feeding grounds (Harden Jones, 1968), and were therefore considered to be too mobile and too long-lived to benefit from localised spatial protection (Breen et al., 2015; Hilborn et al., 2004; Kaiser, 2005). However, there is increasing evidence that MPAs may also have positive impacts on demersal fish populations in boreal waters (Kincaid and Rose, 2017; Moland et al., 2013).

In Europe an extensive network of MPAs is established through the Birds and Habitat Directives (BD and HD), requiring European Union (EU) member states to designate MPAs in their coastal seas and exclusive economic zones (Agnesi et al., 2017; Fock, 2011; Mazaris et al., 2019). This network of MPAs is referred to as the Natura 2000 network. Borders of the national Natura 2000 MPAs had to be designated by each member state until 2008, resulting in about 23% of the North Sea being covered by the Natura 2000 network (Agnesi et al., 2017). However, while the BD and HD require the establishment of MPAs to protect sensitive benthic habitats (sandbanks and reefs), marine mammals, and sea birds, neither directive is addressing the conservation of marine fish species apart from a small number of diadromous fish species. As a consequence, very few Natura 2000 MPAs were designated with the aim of protecting marine fish species. In addition, there have been considerable delays to this day to agree upon and implement management measures such as fishing restrictions (Alvarez-Fern´andez´ et al., 2017; Dureuil et al., 2018). Therefore, identifying areas of consistent fish abundance and diversity remains a prerequisite to evaluate the potential conservation effect of the Natura 2000 MPAs on demersal fish.

This study interpolates and condenses point-abundance data in space and time to identify consistent patterns of demersal fish distribution within the North Sea. We used data from an internationally coordinated bi-seasonal scientific fisheries surveys covering a 21-year period to 1) demonstrate the concept of identifying consistent core areas for mobile organisms in space and time, and 2) analyse the potential of the designated Natura 2000 MPA network to protect demersal fish biodiversity in a heavily fished temperate/boreal region.

2. Methods

2.1. Study area and data sources

The Greater North Sea is a semi-enclosed shelf-sea area of the temperate North East Atlantic with a surface area of approximately 570,000 km2 and an average depth of 95 m. The Greater North Sea includes the Kattegat and Skagerrak, connecting the central basin of the North Sea with the Baltic Sea. The North Sea has been affected substantially by anthropogenic impacts (Emeis et al., 2015), but still remains one of the most productive fishing grounds in the world, being the habitat of more than 200 fish species (Daan et al., 1990; FSBI, 2004; Heessen et al., 2015; Muus and Nielsen, 1999).

Data from the internationally coordinated North Sea International Bottom Trawl Survey (NS-IBTS) were analysed to map the annual distributions of demersal fish species in two seasons: winter (January–February) and summer (July–August). The data products analysed were originally derived from the NS-IBTS data set downloaded from the International Council for the Exploration of the Sea (ICES) Database of Trawl Surveys (DATRAS), which were then subjected to a full quality assurance–quality audit procedure (Greenstreet and Moriarty, 2017a, 2017b; Moriarty et al., 2017; Moriarty et al., 2019). These data products provided trawl sample catch data as biomass densities i.e. the weight of each species (of any given species and length category) caught per area of swept seabed (kg km^{-2}). Only hauls meeting the standard IBTS sampling protocol (ICES, 2012), so having 25–35 min tow duration and an average tow depth of less or equal to 250 m were analysed. Only data for the period 1998 to 2018 met the full quality assurance criteria in both seasons, so this defined the period covered in this study.

To prevent the extrapolation of fish abundance to areas outside of the survey area, the study area was clipped by an alpha hull constructed around all NS-IBTS haul locations (see Supplementary material S1). The alpha hull was further used to clip a geographic grid with cell dimensions of 0.2° longitude by 0.1° latitude. Grid cells overlapping with land masses were also clipped from the survey area, as well as grid cells containing less than 19 annual biomass estimates (in either summer or winter). These procedures ensured that each included grid cell had biomass estimates for at least 90% of all 21 years in both seasons.

Data on the geo-location of the network of Natura 2000 MPAs in the North Sea were obtained from the European Environmental Agency website (https://www.eea.europa.eu/data-and-maps/data/natura-8, download on 03.04.2017). These data are based on the national reporting for the BD and HD of the EU member states in 2016.

Table 1 presents an overview on the terminology used to distinguish core areas, consistent core areas and derived metrics.

2.2. Annual distributions of single species in winter and summer

Distributions of 53 of the 56 fish species defined as being members of the "demersal" fish assemblage (Fung et al., 2012; Greenstreet and Hall, 1996, see Supplementary material S2) were mapped on the geographic grid. The remaining three species (conger eel *Conger conger*, sandy ray *Leucoraja circularis* and nurse hound *Scyliorhinus stellaris*) were not analysed since each species was only represented with less than 10 records in each season. Species that were listed as 'threatened or declining' by the Oslo-Paris Convention (OPSAR) or as any other category than 'least concern' or 'data deficient' by the International Union for Conservation of Nature (IUCN) were considered as species of conservation concern (Table 2).

Fish are mobile animals with clustered distributions, so catch-rates at any given sampling location are associated with observation errors. To account for this, the biomass density [kg km^{-2}] in each grid cell was determined as the arithmetic mean of all observed biomass densities within a search radius of 65 km from the centre of the grid cell. This search radius was determined by the relationship between the variance of the mean biomass per km^2 and the number of included hauls (Supplementary material S3). On average, the variance decreased with increasing number of included hauls, with a breakpoint at a search radius of around 50 km. The 50 km search radius resulted in several gaps with many grid cells having no density estimate (NA value). Therefore the search radius was extended to 65 km which resulted in gapless distribution maps. Essentially, averaging the biomass estimates of all hauls within a 65 km radius was a spatial 'cliff-edge' interpolation (SCEI) which gave equal weighting to all hauls within the search radius and zero weighting to all hauls outside (Supplementary material S4). The SCEI interpolation method was chosen for four reasons: 1) The data requirements were minimal, facilitating the production of distribution maps for all species, 2) contrary to habitat models the SCEI requires no data on environmental predictors, 3) SCEI interpolations by species do not result in models of different quality, and 4) SCEI does not produce large amounts of false positives, as the derived data is closely related to the raw data. Multiplying the mean biomass density (kg km^{-2}) for each grid cell by the grid cell area (km^2) provided estimates of biomass (kg) of each species within each grid cell. The mean biomass density had to be based on at least two hauls. Grid cells which did not have at least two hauls within their 65 km search radius were assigned a NA-value. This resulted in the exclusion of grid cells in the north western (west of Shetlands) and south eastern (German Bight) areas of the study area (Supplementary material S1).

2.3. Defining species core areas

For each species in each season and in each year, grid cells were ranked in order of highest to lowest estimated biomass. Grid cells that accounted for 50% of the cumulative population biomass of a species in any given year and season were defined as annual core areas (CA$_W$ in winter and CA$_S$ in summer, see Table 1). Essentially, this was the smallest total seabed area that held 50% of a species' population biomass in the given year and season.

The threshold of 50% is related to the IUCN criterion of population size reduction (A1–A4), in which 50% of population reduction results in the classification as 'threatened' or 'endangered'. Hence we defined a species' core area as an area which is large enough to prevent a species from becoming listed in a category of conservation concern.

For each species and season, grid cells were designated as seasonally consistent core areas in winter (CCA$_w$) and summer (CCA$_S$) based on the number of years that they were designated as CA$_W$ or CA$_S$ (N$_{CAw}$ or N$_{CAs}$). Grid cells were ranked by N$_{CA}$ in decreasing order and the cumulative sum of N$_{CA}$ in winter and summer was calculated (Supplements material S5). Grid cells within the upper 50%-percentile of this cumulative sum of N$_{CA}$ were designated as CCA$_w$ or CCA$_S$. Further, grid cells identified as CCA in both winter and summer were defined as consistent core areas in both seasons (CCA$_{WS}$).

2.4. Overlap analysis

Maps of individual species' CCA$_S$ and CCA$_W$ were overlaid to identify potential hotspots of consistent core areas among multiple species. In essence this metric is a species richness metric (N$_{CCA}$), as it expresses the number species, which share a given grid cell as consistent core area.

CCA were intersected with polygons of the designated Natura 2000 MPAs. An overlap between single species CCA and the Natura 2000 MPA network of ≥30% was considered as a potentially substantial contribution to the conservation of the species. This threshold was based on political objectives by IUCN and the EU biodiversity strategy 2030 (EU, 2020; IUCN, 2018) as well as O'Leary et al. (2016), because management measures such as fisheries closures and no-take zones are currently not yet implemented in the majority of MPAs (Alvarez-Fern´andez´ et al., 2017; Dureuil et al., 2018).

3. Results

3.1. Patterns of consistent core areas and diversity

Seasonally consistent core areas (CCA_W and CCA_S) were identified for all 53 species, while species inter-seasonal consistent core areas (CCA_{WS}) were identified for 49 species (Table 2). The only species without overlapping CCA_{WS} were tope *Galeorhinus galeus* and topknot *Zeugopterus punctatus*. For five-bearded rockling *Ciliata mustela* and sea scorpion *Taurulus bubalis* catch records were too low to identify consistent CCAS. Therefore CCAWS which are important throughout the year could be identified for the majority of species analysed.

The overlap of multiple species' consistent core areas (N_{CCAw}, N_{CCAS}, N_{CCAws}) was greatest in the northern North Sea around the Shetland and Orkney Islands, the southern fringe of the Norwegian trench, the Skagerrak and Kattegat as well as in several areas along the Scottish and English coast (Fig. 1). These hotspots differed seasonally along the Scottish Coast and the central North Sea, but remained consistent in the northern North Sea, the Skagerrak and Kattegat. The maximum number of overlapping consistent core areas was 14 in winter (N_{CCAw}, Fig. 1A), eleven in summer (N_{CCAs}, Fig. 1B), and eight for both seasons (N_{CCAws}, Fig. 1C).

3.2. Overlap between Natura 2000 MPAs and consistent core areas

The relative overlap between CCA and designated Natura 2000 MPAs ranged from zero for several species in winter, summer or both seasons to a maximum of 51.8% for blond ray Raja brachyura in both seasons (Fig. 2, Table 2, Supplements S6). Averaged across all species, the mean overlap was 9.4% in winter, 9.5% in summer and 8.7% in both seasons. Species with a Natura 2000 MPA – CCA overlap ≥ 30% were: hooknose *Agonus cataphractus*, hagfish *Myxine glutinosa* and thornback ray *Raja clavata* in winter; lesser weever *Echiichthys vipera*, four-bearded rockling *Enchelyopus cimbrius*, grey gurnard *Eutrigla gurnardus*, hagfish and blonde ray in summer; and lump sucker *Cyclopterus lumpus*, hagfish and blond ray in both seasons.

For the species of conservation concern, only thornback ray in winter and lump sucker in both seasons overlapped substantially (≥30%) with the Natura 2000 MPA network. For all other species, the majority of CCAs (≥70%) were outside the Natura 2000 MPA network in winter, summer or all year round (Fig. 3).

4. Discussion

In this study we provide a generic interpolation and aggregation protocol allowing the identification of important core areas for a large suite of mobile fish species. The method presented herein to identify consistent core areas has several advantages: It is modular by species, protocol is flexible and generic, allowing for single species and multispecies applications when species distribution modelling is not possible or feasible. Furthermore, in cases where species distribution models can be generated, the spatial interpolation with the cliff-edge smoother can be used as a baseline to validate and evaluate the performance of the species distribution model.

Consistent core areas could be identified for each species analysed, confirming the common knowledge that each species has preferred areas of occurrence (Heessen et al., 2015). Limiting the access of fisheries to such areas (i.e. consistent core areas) may therefore help to protect populations of sensitive and threatened species, not only in tropical and sub-tropical coral and rocky reefs, but also in temperate waters with soft bottom sediments (Kaiser et al., 2006).

Our results identified a clear mismatch between species' consistent core areas and the Natura 2000 MPA network for the majority of species, pointing towards the obvious gap of the Habitats and Birds Directives neglecting the conservation of marine fish species (Dureuil et al., 2018; EEC, 1992). The North Sea's Natura 2000 MPA sites were designated over a decade ago and the negotiations between the North Sea member states and the European Commission on the management measures, mostly fisheries exclusions, within the MPAs have been extensive and enduring. Hence any future adaptations or extensions to the eventually decided management measures or MPA boundaries will be difficult to achieve (Kaiser et al., 2006). Therefore, the identified weak overlap between consistent core areas and the Natura 2000 MPA network clearly calls for additional spatial management measures to better protect sensitive and threatened demersal fish species as well as hotspots of fish diversity.

The designation of offshore windfarms as conservation sites for demersal fish species could close gaps of the Natura 2000 MPA network. The development of offshore windfarms is ongoing with more than 10.000 km2 surface area reserved for offshore wind farming until 2025 (Stelzenmüller et al., 2020). There is strong evidence that windfarms support the aggregation of demersal fish (Bergstrom ̈ et al., 2013; Reubens et al., 2014; Stelzenmüller et al., 2016; Wilhelmsson et al., 2006). Given the huge amount of surface area designated to offshore wind farms, marine spatial planning could support the conservation of demersal fish by excluding fishing in wind farms, which may provide important habitats for sensitive and threatened fish species e.g. elasmobranchs (Fock et al., 2014) or large gadoids (Reubens et al., 2014). It should be noted, however that offshore wind parks might not cover all relevant consistent core areas as wind parks cluster in the southern North Sea. Through the MSFD and CFP additional spatial measures may need to be introduced to protect important areas for demersal fish. To facilitate their implementation by fostering stakeholders' approval, these measures could be embedded in adaptive management frameworks (Katsanevakis et al., 2011; Stelzenmüller et al., 2013).

One example of such adaptive measures is real time closures (RTC) for juvenile gadoids, which have been implemented in Scottish waters since 2009. The Scottish RCT are short-term (21 days) and small scale (~200 km^2) closures for bottom trawling (Needle and Catarino, 2011). The closures are spontaneously designated when fishermen, observers at-sea or fisheries inspectors report high proportion of juveniles in their catches (EU-COM, 2011). RTC have been also implemented in Iceland, the Faroes, Norway, the United States France, England and Wales (Bailey et al., 2010). The Scottish RTCs are regarded as overall beneficial in reducing the catch of undersized gadoids while being respected by fishermen, but their conservation effect on other species has not been evaluated. Extending the RCT scheme to non-gadoid species may thus foster the conservation of other threatened and sensitive species in the northern North Sea.

A second example of adaptive spatial conservation measures are real time incentives (RTI). RTI have not yet been practically implemented, but have been developed as concept and analysed in a simulation study (Kraak et al., 2015; Kraak et al., 2014; Kraak et al., 2012). RTI are essentially zones in which fishing causes 'costs', which fishermen have to cover from an allocated credit account. Fishing in expensive areas will reduce the credits more quickly than fishing in cheaper areas. The cost of an area is determined by fisheries managers and can be based on the amount of an available resource

or the abundance of a sensitive ecosystem feature. Using the distribution maps of our study, fishing costs could be attributed on the basis of N_{CA} to protect single, sensitive species or N_{CCA} to protect fish diversity. Implementing spatial measures such as RTC or RTI will not exclude fishing per se and may therefore raise less resistance from fishermen, while still achieving a significant degree of protection (Bailey et al., 2010; Kraak et al., 2015; Needle and Catarino, 2011). Furthermore, these measures allow for greater flexibility by having the capacity to adapt to future changes in species distributions (Perry et al., 2005; Rilov et al., 2019; Stelzenmüller et al., 2013).

Our study accounted for temporally flexible management measures by analysing distribution patterns separately in winter and summer and our results can be used to identify relevant areas for spatial conservation measures. However, given the intensive use of the North Sea and the complexity of marine policies in Europe, areas for spatial conservation measures are limited and conflict potential with stakeholders is high (Gimpel et al., 2013; Stelzenmüller et al., 2015). Hence spatial conservation efforts may be forced to focus on the most promising sites which have been most important to species in recent years. The results of our study are also useful for this task by identifying the most consistent core areas for each species, thereby demonstrating the versatility of our approach.

In conclusion, the results of our study demonstrate that mobile species such as marine demersal fish do not distribute evenly, but prefer certain areas throughout space and time. Mobile species therefore can benefit from spatial conservation measures by preserving consistent core areas. Consequently, we see the general potential for spatial conservation measures to facilitate the conservation of demersal fish species within the greater North Sea, but the current Natura 2000 MPA network may need to be extended. Marine offshore wind parks have the potential to partially close this gap, particularly in the southern North Sea. However, alternative adaptive spatial conservation and management tools are needed in the northern North Sea, which respond swiftly to environmental change while being accepted by affected stakeholders.

Author statement

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Declaration of competing interest

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Figures and Tables

Table 1 Overview on terminology and metrics used in this paper. Possible maximum values are provided for N_{CA} and N_{CCA} based on the number of years and species analysed. Capitalised AND/OR indicate logical operands.

Term	Abbreviation	Description	Temporal aspects	Seasonal aspects	Single/ multi-species	Unit
Core area within a season and year	CA_W CA_S	Grid cells containing 50% of cumulative population biomass in any given year and season	Annual	Winter OR summer	Single species	km^2
No. of CA across all years (only in Supplements S5 & S6)	N_{CAw} N_{CAs}	No. of CA per grid cell by species. Can be considered as metric of consistency.	Multi-annual	Winter OR summer	Single-species	Number of years (max. = 21)
Consistent core area in winter or summer	CCA_W CCA_S	Grid cells containing at least 50% of all CA_W or CA_S cumulatively summed across all years	Multi-annual	Winter OR summer	Single species	km^2
CCA in both seasons	CCA_{WS}	Grid cells which are CCA_W AND CCA_S	Multi-annual	Both seasons	Single species	km^2
No. of overlapping CCA	N_{CCAw} N_{CCAs} N_{CCAws}	No. of species' CCA per grid cell. Can be considered as metric of species richness.	Multi-annual	Winter, summer or both seasons	Multi-species	Number of species (max. = 53)

Table 2 List of mapped species, their conservation status according to the red lists of the Oslo Paris Convention (OSPAR) and the International Union for Conservation of Nature (IUCN), the extent of their consistent core areas in winter, summer and both seasons (CCAW, CCAS, CCAWS), and their overlap with Natura 2000 marine protected areas (N2K). Codes for IUCN red list Europe are DD=data deficient, LC=least concern, NT=near threatened, VU=vulnerable, EN=endangered, CR=critically endangered, EW=extinct in the wild, EX=extinct. Species of conservation concern are highlighted in bold font.

Species	OSPAR red list	IUCN status	Area CCA$_W$ [km^2]	Area CCA$_S$ [km^2]	Area CCA$_{WS}$ [km^2]	Overlap N2K & CCA$_W$ [km^2 (%)]	Overlap N2K & CCA$_S$ [km^2 (%)]	Overlap N2K & CCA$_{WS}$ [km^2 (%)]
Agonus cataphractus	–	LC	8864.8	19,881.2	2965.9	3268.8 (36.87)	2385.3 (12.00)	717.0 (24.17)
Amblyraja radiata	–	VU	36,606.7	27,267.5	16,891.4	900.5 (2.46)	0.0 (0.00)	0.0 (0.00)
Anarhichas lupus	–	DD	21,719.7	24,905.0	13,547.7	0.0 (0.00)	4.6 (0.02)	0.0 (0.00)
Brosme brosme	–	LC	15,452.6	9421.9	7877.9	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Callionymus lyra	–	LC	52,352.1	61,011.8	13,482.3	3429.8 (6.55)	13,245.8 (21.71)	61.6 (0.46)
Callionymus maculatus	–	LC	13,294.8	36,702.5	13,294.8	2340.7 (17.61)	4004.3 (10.91)	3171.4 (23.85)
Capros aper	–	LC	5017.2	6485.7	3946.5	0.0 (0.00)	25.4 (0.39)	0.0 (0.00)
Ciliata mustela		LC	9.682.4	–	–	2872.6 (29.67)	–	–
Cyclopterus lumpus	–	**NT**	**23,307.9**	**17,377.3**	**5963.4**	**4822.2 (20.69)**	**3512.5 (20.21)**	**1882.2 (31.56)**
Echiichthys vipera	–	LC	11,745.9	10,549.8	1641.1	296.5 (2.52)	4085.2 (38.72)	296.5 (18.07)
Enchelyopus cimbrius	–	LC	26,428.2	19,067.9	9733.7	6435.7 (24.35)	6138.9 (32.19)	2662.1 (27.35)
Eutrigla gurnardus	–	LC	35,440.1	30,870.3	2245.1	15.1 (0.04)	13,331.3 (43.18)	15.1 (0.67)
Gadus morhua	X	**LC**	**58,665**	**46,628.5**	**21,767.0**	**6927.1 (11.81)**	**4625.9 (9.92)**	**3149.2 (14.47)**
Gaidropsarus vulgaris	–	LC	27,578.0	13,288.0	2977.8	1759.9 (6.38)	813.7 (6.12)	213.1 (7.16)
Galeorhinus galeus	–	VU	**20,995.0**	**10,466.5**	**0.0**	**978.1 (4.66)**	**21.8 (0.21)**	**0.0 (0.00)**
Glyptocephalus cynoglossus	–	LC	28,936.0	44,758.0	20,009.3	4034.0 (13.94)	4042.6 (9.03)	3914.8 (19.56)
Helicolenus dactylopterus	–	LC	11,583.5	12,647.3	6402.5	450.6 (3.89)	850.6 (6.73)	216 (3.37)
Hippoglossoides platessoides	–	LC	59,369.0	60,313	30,019.8	6845.4 (11.53)	5382.6 (8.92)	6213.3 (20.7)
Hippoglossus hippoglossus	–	VU	**43,717.9**	**44,918.6**	**16,936.0**	**102.7 (0.23)**	**103.8 (0.23)**	**4.6 (0.03)**
Lepidorhombus whiffiagonis	–	LC	10,308.1	8097.9	5474.2	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Leucoraja naevus	–	LC	24,766.1	19,653.5	12,079.9	132.0 (0.53)	84.0 (0.43)	71.8 (0.59)
Limanda limanda	–	LC	59,516	52,468.5	21,994.8	13,500.1 (22.68)	10,708.9 (20.41)	2874.8 (13.07)
Lophius budegassa	–	LC	27,824.6	40,499.6	13,182.4	113.8 (0.41)	153 (0.38)	25.5 (0.19)
Lophius piscatorius	–	LC	30,805.6	42,754.7	25,504.1	20.8 (0.07)	107.8 (0.25)	20.8 (0.08)
Melanogrammus aeglefinus	–	LC	33,365.3	40,417.8	28,054.8	77.1 (0.23)	79.1 (0.20)	96.1 (0.34)
Merlangius merlangus	–	LC	47,381.4	50,710.2	27,593.2	4297.2 (9.07)	4332.8 (8.54)	1721.3 (6.24)
Merluccius merluccius	–	LC	25,028.5	31,549.7	21,356.5	0.0 (0.00)	357.2 (1.13)	0.0 (0.00)
Microstomus kitt	–	LC	60,083.5	55,380.4	31,922.3	151.5 (0.25)	2098.5 (3.79)	132.9 (0.42)
Molva molva	–	LC	14,733.9	11,945.2	9790.2	25.4 (0.17)	0.0 (0.00)	0.0 (0.00)
Myoxocephalus scorpius	–	LC	26,459.8	24,907.7	9491.3	7055.0 (26.66)	3293.6 (13.22)	1070.8 (11.28)
Myxine glutinosa	–	LC	6291.9	6268.1	4705.0	2550.8 (40.54)	2178.1 (34.75)	1780.1 (37.83)
Pholis gunnellus	–	LC	17,523.2	7434.6	6615.3	3235.7 (18.47)	809.9 (10.89)	1297.0 (19.61)
Phrynorhombus norvegicus	–	LC	28,274.9	13,846.4	3597.0	436.7 (1.54)	1191.3 (8.60)	2.0 (0.06)
Phycis blennoides	–	DD	19,771.3	15,207.5	6480.5	113.5 (0.57)	325.7 (2.14)	12.3 (0.19)
Platichthys flesus	–	LC	3711.1	12,023.2	3711.1	319.9 (8.62)	2024.9 (16.84)	319.9 (8.62)
Pleuronectes platessa	–	LC	44,254.2	56,674.8	23,877.3	3611.5 (8.16)	8072.3 (14.24)	1839.7 (7.7)
Pollachius pollachius	–	LC	20,236.0	12,036.9	8162.7	669 (3.31)	0.0 (0.00)	0.0 (0.00)
Pollachius virens	–	LC	18,199.2	25,100.7	14,118	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Raja brachyura	–	NT	13,337.3	7371.9	1099.6	3917.0 (29.37)	2337.0 (31.7)	569.0 (51.75)
Raja clavata	X	**NT**	**16,447.9**	**3392.3**	**3392.3**	**5073.9 (30.85)**	**944.5 (27.84)**	**944.5 (27.84)**
Raja montagui	X	LC	13,926.2	5955.5	3526.4	1627.6 (11.69)	53.6 (0.90)	46.7 (1.32)
Scophthalmus maximus	–	VU	**67,616.5**	**57,415.2**	**20,400.3**	**5320.1 (7.87)**	**9894.3 (17.23)**	**1818.6 (8.91)**
Scophthalmus rhombus	–	VU	**11,446.7**	**20,663.0**	**10,899.9**	**1774.4 (15.5)**	**3723.4 (18.02)**	**1879.2 (17.24)**
Scyliorhinus canicula	–	LC	19,005.4	14,428.8	5768.6	1809.2 (9.52)	620 (4.03)	480.6 (8.33)
Sebastes viviparus	–	LC	13,730.8	17,914.7	2794.7	0.0 (0.00)	82.4 (0.46)	0.0 (0.00)
Squalus acanthias	X	**EN**	**51,408.9**	**33,331.4**	**6081.7**	**2017.4 (3.92)**	**7885.8 (23.66)**	**1452.7 (23.89)**
Taurulus bubalis		LC	3267.5	–	–	628.3 (19.23)	–	–
Triglops murrayi	–	LC	13,996.6	6911.0	2762.7	12.7 (0.09)	2.0 (0.03)	10.3 (0.37)
Trisopterus esmarkii	–	LC	38,863.4	30,176.4	12,393.8	181.4 (0.47)	83.6 (0.28)	17.6 (0.14)
Trisopterus luscus	–	LC	6631.2	5842.3	2155.5	1811.7 (27.32)	1010.1 (17.29)	516.0 (23.94)
Trisopterus minutus	–	LC	20,459.6	27,305.2	12,925.1	209.8 (1.03)	1384.4 (5.07)	183.8 (1.42)
Zeugopterus punctatus	–	LC	25,713.1	27,726.9	0	1571 (6.11)	576.6 (2.08)	0.0 (0.00)
Zeus faber	–	DD	33,052.1	14,869.8	8585.2	179.2 (0.54)	57.5 (0.39)	72.7 (0.85)

Fig. 1. Number of species' core areas in A) winter [N$_{CCA}$w], B) summer [N$_{CCAS}$] and C) both seasons [N$_{CCAWS}$].

A) CAW

B) CAS

C) CAWS

Latitude [°]

Longitude [°]

EEZ
N2K
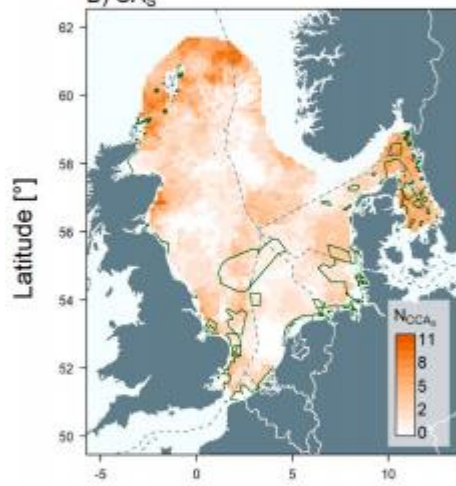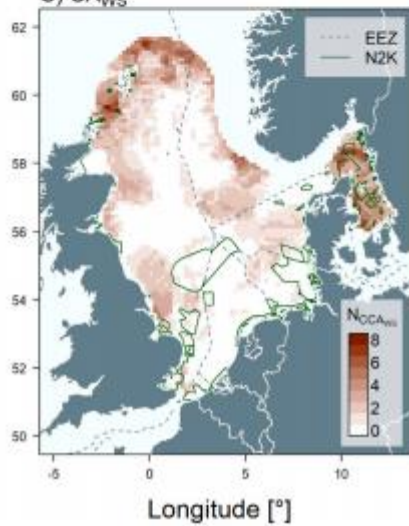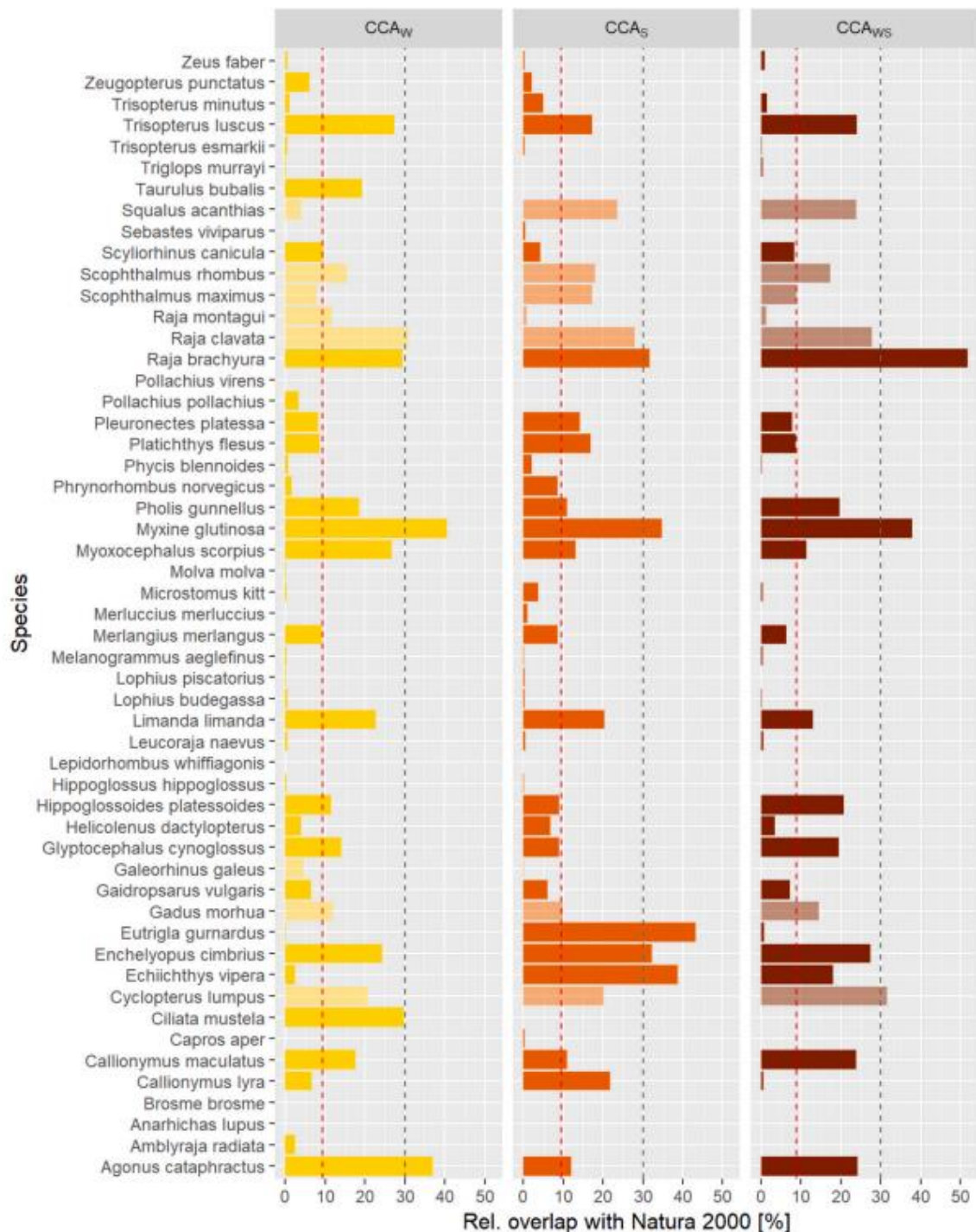
Fig. 2. Relative overlap between marine protected areas of the Natura 2000 network and species consistent core areas in A) winter [CCA$_W$], B) summer [CCA$_S$] and C) both seasons [CCA$_{WS}$]. Grey dashed line indicates 30% overlap between Natura 2000 network and CCA, red dashed line indicates the mean relative overlap across all species. Transparent bars represent species which are considered to be of conservation concern according to the Oslo-Paris Convention or the International Union for Conservation of Nature. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
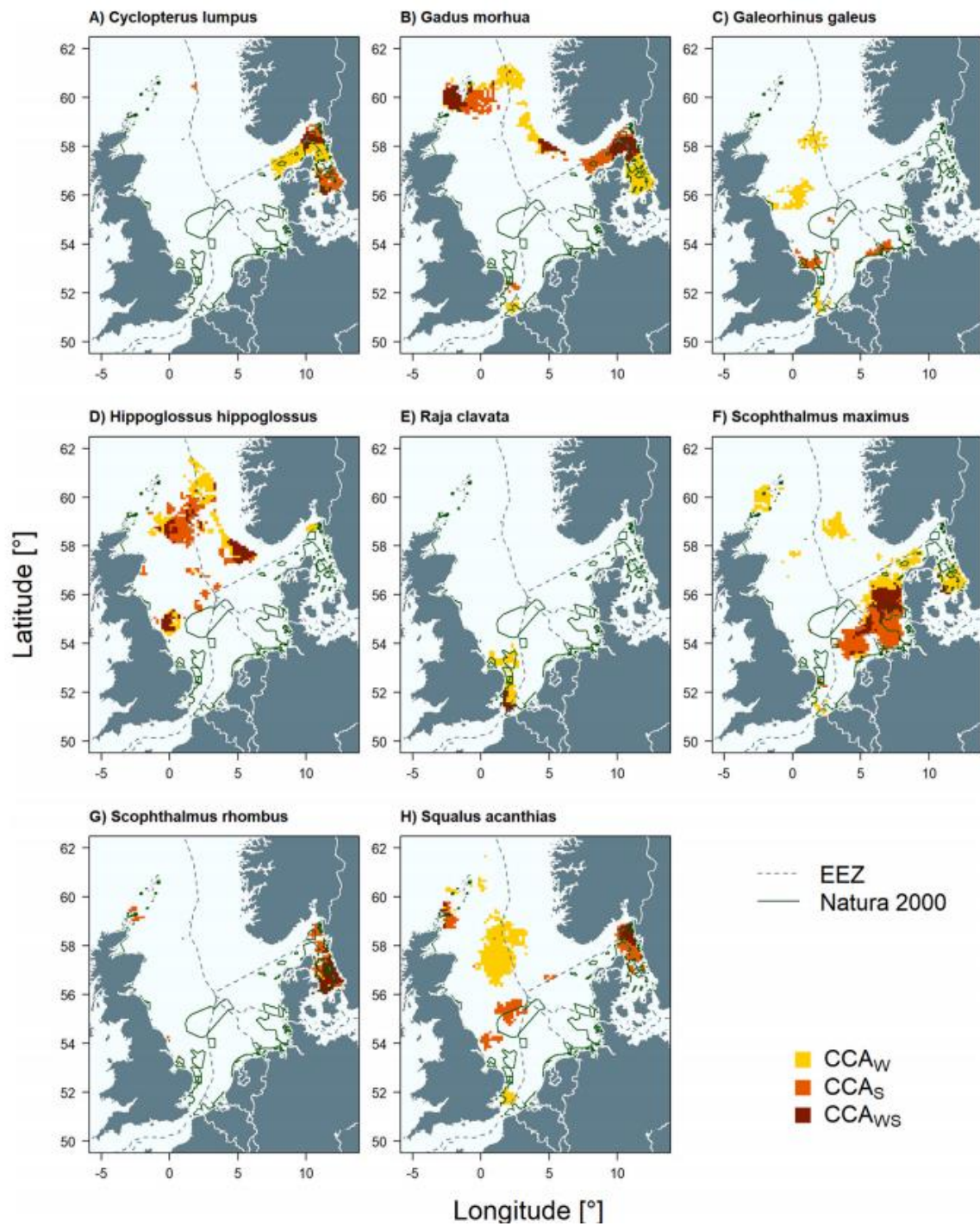
Fig. 3. Consistent core areas in winter, summer and both seasons for the eight demersal fish species that are listed by the Oslo-Paris convention or the International Union for the Conservation of Nature as threatened species or species of conservation concern.