ECOLOGICAL IMPACTS OF OFFSHORE WIND FARMS ON FLATFISH

with emphasis on plaice *Pleuronectes platessa*,
a species of commercial interest in the southern North Sea

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Pictures

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To my son Rio
May you discover the world
in all its wonderful facets

SUMMARY

In the near future offshore wind farms (OWFs) will occupy ten percent of the North Sea area while their ecological impact on soft-sediment fish species such as flatfish is not well understood. Therefore, this PhD thesis focuses on filling knowledge gaps regarding the ecological effects of OWFs on plaice *Pleuronectes platessa L.,* an important commercial flatfish species in the southern North Sea. The specific objectives of this work were to investigate whether OWFs affect the spatial distribution, diet, condition and movement of plaice within the context of climate variability and climate change.

The European Union has set itself the goal of becoming climate neutral by 2050. To achieve this goal, Member States are relying on sustainable energy sources for power generation, leading to an exponential increase in OWF installations in European waters. As a result, marine space is lost to other users, such as the fisheries sector, while knowledge about how OWFs affect marine resources is still lacking. OWFs in Europe are often built in soft-bottom environments, introducing hard structures where previously only soft sediments were present. This creates opportunities for fish species associated with hard substrate, but potentially affects typical soft-sediment species such as flatfish in other ways. In addition, the cessation of bottom trawling in most European wind farms may create refuge opportunities for target species, possibly translating into population-level changes, but evidence-based information is still lacking.

Chapter 1 begins with an introduction to the flatfish fishery in the North Sea and how it competes for marine space with the growing offshore wind energy sector. Next, the effects of climate change and climate variability on fish in the North Sea are outlined, followed by an overview of the main ecological effects of OWFs and how they relate to the attraction-production hypothesis. Finally, some general information about the ecology of plaice and the study area is given, as well as an overview of the methods used in this work.

To study the effects of OWFs on fish species, it is crucial to have a good understanding on the environmental variables that are driving its abundances

and distribution on a larger scale. Therefore, Chapter 2 studied long-term trends in fish abundances in the Belgian part of the North Sea (BPNS), which were linked to different climate-related variables using both univariate and multivariate modelling approaches. A community analysis identified three distinctive fish assemblages in the study area, after which common trends in fish abundances were analysed for each assemblage. While the two coastal assemblages were mainly linked to temperature-related drivers, the offshore assemblage had a stronger association with natural climatic oscillations. Further, warm-water preferring species showed a clear positive link with temperature and an exponential increase in abundances during the last decades, while cold-water preferring species showed a weak negative link with temperature and a weak decline in abundances. Finally, fish length over time was studied, but only for plaice a significant decline was observed, while their abundances increased significantly. This is potentially explained by a combination of a fisheries-induced evolution towards individuals that have a smaller size at maturation, and an effect of an increase in water temperature. Overall, the results indicated that within the BPNS, trends in fish assemblages could be linked to climate change and temperature-related variability, but that the importance of certain drivers differed even on a very small spatial scale.

Chapters 3 to 5 aims at better understanding the ecological effects of OWFs on plaice, by investigating potential changes in their spatial distribution (Chapter 3), their diet and condition (Chapter 4) and their movements (Chapter 5) in relation to the presence of OWFs. These field studies were mainly carried out in Belwind, a Belgian OWF consisting of monopiles surrounded by a scour protection layer. Introduced hard substrates in OWFs in the form of turbines and their associated scour protection have been shown to aggregate fish and other megafauna, which is referred to as the 'artificial reef effect'. However, for soft-sediment species, such as flatfish, information about the effects of OWFs on their spatial distribution is largely lacking. In Chapter 3, the aim was to investigate whether plaice distribution was affected by the presence of OWFs on both the turbine and wind farm scale. On the turbine scale, diving transects over the scour protection and surrounding

open sand identified an attraction effect of plaice towards the sandy patches in between the rocks of the scour protection layer. Effects on the wind farm scale were investigated in two different Belgian OWFs using a Before/After-Control/Impact-design. Beam trawl samples were taken before and after the construction of the wind farm both in impacted and control areas. A potential refuge effect, in the form of increased plaice abundances between the turbines, was found for one of the two investigated wind farms. This study showed that a clear artificial reef effect exists for plaice that may be explained by an increase in feeding and shelter opportunities. Refuge effects related to the cessation of fisheries activities, on the other hand, appear to be more site specific.

The observed attraction of plaice towards the sandy patches in between the rocks of the scour protection directly led to follow-up research questions, namely is plaice actively using the hard substrate for foraging, and are wind farms good quality feeding grounds? In Chapter 4, four groups of fish were sampled in and around the Belwind OWF in the BPNS , which represented both impacted and control areas. Stomach content analyses, in combination with stable isotopes and fatty acid analyses, were used to study the trophic ecology of plaice in relation to the OWF. Further, several morphometric and organosomatic condition indices were calculated for each of the four sample groups. Results showed that fish caught on the scour protection mainly fed on typical hard-substrate associated prey, while the diet of the three control sampling groups consisted of characteristic soft-sediment benthic species. In addition, differences in fatty acid composition were observed for the scour protection group, indicating that they fed off the hard substrates for a long period of time. The stable isotope analysis did not pick up this pattern, probably because the soft and hard substrate prey items had overlapping isotopic signatures. Further, condition indices indicated that plaice had access to a higher prey availability near the hard substrate, but this did not result in a clear positive influence on their overall fitness. This study highlights the scour protection as an important feeding habitat for plaice likely due to its increased food availability. Although no clear effects on fish condition and fecundity could be identified, these findings suggest that OWFs might enhance biological fish production of plaice.

In Chapter 5, the small-scale spatial movements of plaice were studied in the vicinity of the turbines and scour protection, together with their long-term presence in the OWF. The objectives were to assess the residency of plaice within and the site fidelity towards the OWF with a particular focus on their yearly spawning migrations, and to determine their habitat association with the hard substrates. Passive acoustic transmitters were attached to 31 fish, which were caught by diving or hook-and-line in the Belwind wind farm. Three different setups of acoustic receivers, that can detect the signals emitted by the transmitters were deployed during different periods of the year. In general, fish had a high residency within the wind farm during the summer months when feeding, and migrated out of the area during the spawning season in winter. Interestingly, one third of the tagged fish returned to the study area the following spring after the spawning season. This indicated that plaice has a very high site fidelity towards the feeding area within the OWF. Further, fish positions of five individuals were calculated from the detections using triangulation to study their habitat association in the vicinity of wind turbines and scour protection. Analysis of the fish positions revealed they mainly stayed relatively close (<100 m) to one particular turbine. Although most estimated positions were located on the soft sediments surrounding the scour protection, a clear diurnal pattern was found in plaice movements, with fish being closer to the hard substrate during day time compared to night time hours. This pattern is most probably linked to their feeding behaviour being regulated by light intensity. Based on these results, we hypothesized that plaice undertakes feeding excursions from the soft sediments to the scour protection layer during daylight hours and swims higher up in the water column at night.

Overall, this thesis shows that OWFs (or larger OWFs zones) can benefit plaice through an artificial reef effect and a refuge effect and, therefore, lead to increased biomass or fish production. However, it is not clear from our findings whether this increase in production can also influence plaice on the

population level through a spillover effect. Therefore, empirical studies are needed that focus on the regional spatial scale and take into account the cumulative effects of OWFs on plaice to determine whether the observed positive effects can benefit flatfish fisheries.

SAMENVATTING

In de nabije toekomst zullen offshore windmolenparken (OWPs) tien procent van de Noordzee in beslag nemen, dat terwijl over hun ecologische impact op zacht-sediment vissoorten zoals platvis nog weinig geweten is. Daarom focust dit proefschrift zich op kennisverwerving over de ecologische effecten van OWPs op schol *Pleuronectes platessa L.*, een belangrijke commerciële platvissoort in de zuidelijke Noordzee. Deze thesis heeft als doel de invloeden van OWPs op de ruimtelijke verspreiding, het dieet, de conditie en de bewegingen van schol te onderzoeken binnen de context van klimaatvariabiliteit en klimaatverandering.

De Europese Unie wil in 2050 klimaatneutraal te zijn. Om dit te bereiken, vertrouwen de lidstaten op duurzame energiebronnen voor stroomopwekking, wat dan weer leidt tot een exponentiële toename van OWP-installaties in Europese wateren. Hierdoor gaat een deel van de mariene ruimte verloren voor andere gebruikers, zoals de visserijsector. Ondertussen ontbreekt nog altijd kennis over de invloed van OWPs op visbestanden. De constructie van OWPs in Europa gebeurt veelal in omgevingen met een zachte bodem, waarbij harde structuren worden geïntroduceerd waar voorheen alleen zand aanwezig was. Dit creëert kansen voor vissoorten die geassocieerd zij met harde substraten, maar kan andere gevolgen hebben voor typische zachtsedimentsoorten zoals platvis. Bovendien kan het verbod op boomkorvisserij die geldt in de meeste Europese windparken schuilmogelijkheden creëren voor beviste soorten. Dit kan zich mogelijks vertalen in veranderingen op populatieniveau, maar empirische kennis hierover ontbreekt nog.

Hoofdstuk 1 begint met een inleiding op de platvisvisserij in de Noordzee en hoe die concurreert voor mariene ruimte met de groeiende offshore windenergiesector. Daarna komen de effecten van klimaatverandering en klimaatvariabiliteit op vissen in de Noordzee aan bod, gevolgd door een overzicht van de belangrijkste ecologische effecten van OWPs en hoe die zich verhouden tot de attractie-productiehypothese. Ten slotte gaat hoofdstuk 1

in op het studiegebied waarin dit onderzoek is uitgevoerd en de ecologie van schol, en volgt daarnaast nog een overzicht van de toegepaste methoden in deze thesis. Het proefschrift bestaat verder uit vijf hoofdstukken: vier onderzoekshoofdstukken, met daarna een algemene discussie.

Om de effecten van een OWP op een vissoort te kunnen bestuderen, is het van cruciaal belang om te weten welke variabelen visdensiteit op grotere schaal bepalen. Daarom bestudeert hoofdstuk 2 lange termijntrends van verschillende vissoorten in het Belgische deel van de Noordzee (BDNZ), gekoppeld aan klimaatgerelateerde variabelen door middel van zowel univariate als multivariate modellering. In het studiegebied volgde de identificatie van drie verschillende visgemeenschappen, samenhangend met een analyse van gemeenschappelijke trends in visdensiteiten voor elke gemeenschap. Terwijl de twee kustgemeenschappen een sterker verband vertoonden met temperatuurgerelateerde factoren, correleerde de offshore-gemeenschap sterker met natuurlijke klimaatoscillaties. Verder vonden we voor warmwatersoorten een duidelijk positief verband met temperatuur en een exponentiële toename in hun aantallen gedurende de laatste decennia. Koudwatersoorten vertoonden daarentegen een zwak negatief verband met temperatuur en een zwakke afname in aantallen. Ten slotte werd ook de lengte van commerciële vissoorten doorheen de tijd bestudeerd. Daarbij liet enkel schol een significante afname in lengte zien, dit terwijl hun aantallen aanzienlijk toenamen. Een mogelijke verklaring hiervoor is een combinatie van een door de visserij veroorzaakte evolutie naar individuen die kleiner zijn bij het bereiken van de volwassenheid, en een effect van een stijging van de watertemperatuur. In het algemeen tonen de resultaten dat trends in vispopulaties binnen het BDNZ verband houden met klimaatverandering en temperatuurgerelateerde variabiliteit, maar dat het belang van bepaalde factoren zelfs op zeer kleine ruimtelijke schaal verschilt.

Hoofdstukken 3 tot en met 5 hebben als doel de ecologische effecten van OWPs op schol te bestuderen door mogelijke veranderingen te onderzoeken in hun ruimtelijke verspreiding (hoofdstuk 3), hun dieet en conditie (hoofdstuk 4) en hun bewegingen (hoofdstuk 5). Deze studies werden hoofdzakelijk uitgevoerd in Belwind, een Belgisch OWP dat bestaat uit monopiles omgeven door een erosiebeschermingslaag. Uit onderzoek blijkt dat geïntroduceerde harde substraten in OWPs, in de vorm van turbines en erosiebescherming, vissen en andere megafauna aantrekken, ook wel "kunstmatig rifeffect" genoemd. Voor zachtsedimentsoorten, zoals platvis, ontbreekt informatie over de effecten van OWPs op hun ruimtelijke verspreiding. In hoofdstuk 3 werd daarom onderzocht of OWPs de verspreiding van schol kunnen beïnvloeden, zowel op turbine- als op windparkschaal. Op turbineschaal stelden duiktransecten over de erosiebescherming en het omliggende open zand een aantrekking van schol vast naar de zandige plekken tussen de rotsen van de erosiebeschermingslaag. Het onderzoek op de schaal van het windmolenpark vond in twee verschillende Belgische OWPs plaats met behulp van een Voor/Na Controle/Impact-analyse. Er werden boomkorstalen genomen voor en na de bouw van het windmolenpark, zowel in impact- als controlegebieden. Voor één van de twee onderzochte windparken is een potentieel refugiumeffect gevonden, in de vorm van verhoogde scholaantallen tussen de turbines. Deze studie toont aan dat er een duidelijk kunstmatig rifeffect voor schol bestaat dat mogelijks toe te schrijven is aan een toename van de voedsel- en/of schuilmogelijkheden. Refugiumeffecten gerelateerd aan het verbod op visserijactiviteiten lijken daarentegen meer plaatsgebonden te zijn.

De waargenomen aantrekkingskracht van schol tot de zandige plekken tussen de rotsen van de erosiebescherming leidt direct tot vervolgonderzoeksvragen: maakt schol actief gebruik van het harde substraat om te foerageren, en zijn windmolenparken kwalitatief goede voedselgebieden? Hoofdstuk 4 bestudeert vier groepen vissen in en rond het Belwind OWP in het BDNZ, ook hier zowel in impact- als controlegebieden. Analyses van de maag- en darminhoud, in combinatie met stabiele isotopen en vetzuuranalyses, werden gebruikt om de trofische ecologie van schol in relatie tot het OWP te bestuderen. Verder volgde een berekening van verschillende morfometrische en organosomatische conditie-indices voor elk van de vier groepen. De resultaten tonen aan dat vissen gevangen op de erosiebescherming zich hoofdzakelijk voeden met typische hardsubstraatprooien, terwijl het dieet van de drie controlegroepen bestaat uit karakteristieke zachtsubstraatsoorten. De vetzuursamenstelling van de erosiebeschermingsgroep is daarbij anders dan die van de controlegroepen, wat erop wijst dat zij gedurende langere tijd op de harde substraten foerageren. De stabiele isotopenanalyse brengt dit patroon niet aan het licht, waarschijnlijk omdat de isotopische waarden van de harde en zachtesubstraatprooien te veel overlappen. Verder blijkt uit de conditie-indices dat schol in de buurt van het harde substraat toegang heeft tot meer prooien, maar dat dit geen duidelijk positieve invloed heeft op hun conditie. Deze studie wijst erop dat de erosiebescherming een belangrijke voedingshabitat is voor schol, waarschijnlijk door de grotere beschikbaarheid van voedsel. Hoewel er geen duidelijke effecten gevonden werden op de conditie en de vruchtbaarheid van pladijs, suggereren deze bevindingen wel dat OWPs de biologische visproductie van schol kunnen verhogen.

Hoofdstuk 5 onderzoekt de kleinschalige ruimtelijke bewegingen van schol in de buurt van de turbines en de erosiebescherming, samen met hun aanwezigheid op lange termijn in relatie tot een OWP. De doelstellingen waren het nagaan van de residentie in en de sitegetrouwheid aan het OWF, met een focus op hun jaarlijkse paaimigraties, en de bepaling van hun habitatassociatie met de harde substraten. 31 vissen, gevangen in het Belwind OWP door duikers of een lijn, kregen passieve akoestische zenders bevestigd. Drie verschillende opstellingen van akoestische ontvangers, die de door de zenders uitgezonden signalen kunnen detecteren, werden gedurende verschillende periodes van het jaar uitgezet. In het algemeen verbleven de vissen tijdens de zomermaanden bijna ononderbroken in het windmolenpark wanneer ze zich voedden, en trokken ze weg uit het gebied tijdens het paaiseizoen in de winter. Opvallend is dat een derde van de gemerkte vissen het volgende voorjaar na het paaiseizoen terugkeerde naar het studiegebied. Dit wijst erop dat schol een grote sitegetrouwheid vertoont ten opzichte van het foerageergebied binnen het OWP. Verder werden de posities van vijf individuen berekend met behulp van triangulatie om zo hun habitatassociatie in de buurt van de windturbines en erosiebescherming te bestuderen. Uit de analyse van de posities van de vissen bleek dat ze voornamelijk relatief dicht

(< 100 m) bij één bepaalde turbine verbleven. Hoewel de meeste posities zich op de zachte sedimenten rond de erosiebescherming bevonden, vertoonden de bewegingen van de schol een duidelijk diurnaal ritme, waarbij de vissen overdag dichter bij het harde substraat aanwezig waren dan 's nachts. Dit patroon houdt hoogstwaarschijnlijk verband met hun voedingsgedrag gelinkt aan lichtintensiteit. Op basis van deze resultaten formuleert dit onderzoek de hypothese dat schol overdag voedingsexcursies uitvoert van op het zachte sediment naar de erosiebescherming en 's nachts hoger in de waterkolom zwemt.

In het algemeen toont deze thesis aan dat OWPs (of grotere OWP-zones) door een kunstmatig rifeffect en een refugiumeffect gunstig kunnen zijn voor schol en daardoor kunnen leiden tot een hogere biomassa of productie binnen het OWP. Het is niet duidelijk uit onze bevindingen of deze verhoogde productie ook schol op populatieniveau kan beïnvloeden. Daarom zijn empirische studies nodig die zich richten op de regionale ruimtelijke schaal en rekening houden met de cumulatieve effecten van OWPs op schol om te bepalen of de waargenomen positieve effecten de platvisvisserij ten goede kunnen komen.

CONTENTS

PART 1

INTRODUCTION AND BASELINE

1 GENERAL INTRODUCTION

Offshore wind farms (OWFs) are being built across the North Sea in order to support the transition to more sustainable energy sources (WindEurope, 2022). The introduction of hard substrates related to OWFs into sandy sediments can affect the marine environment and the associated fauna in several ways. While some biological communities clearly benefit from such an introduction (Mavraki et al., 2020), others, such as fish, show more variable responses (van Hal et al., 2017). Typical hard-substrate fish have been observed in larger numbers around wind turbine foundations and surrounding scour protection (Reubens et al., 2013a; Stenberg et al., 2015; Krone et al., 2017), what is commonly referred to as the 'artificial reef effect'. This effect is usually explained by an increase in food availability and shelter opportunities offered by the artificial hard substrates (Bohnsack and Sutherland, 1985). On the other hand, typical soft-sediment species such as flatfish may respond differently to the introduction of hard substrates into their natural sandy habitat (Wilber et al., 2018). However, until now there was no in-depth knowledge of the ecological effects of OWFs on flatfish.

Flatfish, especially common sole *Solea solea* (from here on sole) and European plaice *Pleuronectes platessa* (from here on plaice), have been important fishery resources for centuries in the southern North Sea where bottom trawling is very common (Daan, 1997). The development of offshore wind energy, however, claims a lot of marine space which is often no longer available to the fisheries sector, leading to spatial conflicts between the two sectors (Christie et al., 2014). On the other hand, the cessation of bottom trawling within OWFs could benefit target species such as sole and plaice by providing refuge areas, potentially acting in a similar way as marine protected areas (MPAs) (Florin et al., 2013; Halpern, 2003). However, empirical evidence for the existence of such a "fisheries-exclusion effect" in relation to OWFs is currently lacking, complicating the spatial debate between the fisheries and offshore wind energy sector.

Disentangling OWFs effects from other drivers that steer fish distribution and abundances is complex, as all of these processes are acting simultaneously on a very small scale (Lindeboom et al., 2015). Therefore, it is also important to have a good understanding of the most important drivers that influence a species' density, before effects of the presence of an OWF can be interpreted correctly.

This introductory chapter describes the flatfish fishery in the North Sea and outlines the spatial conflict with the growing offshore wind energy sector. Secondly, the effects of climate change and climate variability on fish in the North Sea are discussed. Thirdly, an overview is given of the main ecological effects of OWFs and the link between OWFs and fish production is explained. Finally, the aim and main research questions of the thesis are presented, followed by a description of the study area, some ecological information on the focus species relevant within the framework of this thesis and an overview of the used methods.

1.1 FLATFISH FISHERIES AND OFFSHORE WIND DEVELOPMENT IN THE NORTH SEA

The North Sea region has been an area of vital importance for flatfish fisheries for centuries (Daan, 1997). In the beginning of the 19th century, flatfish were mainly caught by small vessels in inshore waters using drift nets, longlines or handlines (Walsh et al., 2015). In the 1830s, large-scale flatfish fisheries began to develop in the North Sea, which were primarily focused on catching plaice and sole. Fishers mainly used beam trawls mounted on sailing vessels and were mostly active in shallow waters (<100 m) as they needed to haul in the net by hand. The success of this method led to very high catch rates and a rapid expansion of flatfish fisheries in the largely unexploited offshore areas in the southern North Sea. During the following decades, fishing expanded towards the Dogger Bank and from Scotland to the Danish coast. From the 1880s onwards, sailing vessels were gradually replaced by steam-powered trawlers (Walsh et al., 2015). This shift substantially increased the fishing efficiency and landings of plaice in the beginning of the 1900's totalled 50,000 tonnes in the North Sea alone (Rijnsdorp and Millner, 1996). After the Second World War, an intensive beam trawl fishery developed with a concurrent shift towards engine trawlers, and landings of plaice peaked during the late 1980's with an estimate of 169,818 tonnes in 1989 (Walsh et al., 2015; ICES, 2022a). After this, the stock declined fast due to overexploitation, but stabilised again during the late 1990s. The exploitation rate of sole remained low until the end of the 1950s when Dutch fishers started to use double beam trawls with chains to disturb the fish out of the muddy sediments (Rijnsdorp et al., 2008). Landings of sole in the North Sea increased from less than 4,000 tonnes in 1905 to a peak of 33,000 tonnes in 1968 (Walsh et al., 2015). After this, landings declined and only increased again after the 1980s. In 1990, sole landings reached their historical maximum with 35,000 tonnes, after which a steep decline followed until the start of the 2000s (ICES, 2022b).

Nowadays, commercial catches are regulated by the Common Fisheries Policy (CFP, Regulation EU 1380/2013), based on the maximum sustainable yield (MSY) principle. Following this principle, total allowable catches are being determined for each commercially important species so that their stock biomass remains high enough and fishing mortality low enough to ensure maximum sustainable yield in the long term (FAO, 2014). In 2020, sole and plaice landings in the North Sea totalled 8,863 and 32,110 tonnes, respectively, with sole dominating in economic revenue (ICES, 2021a, 2021b).

North Sea sole has been exploited above MSY-level since the start of the stock assessments (ICES, 2022b). Only recently, fishing pressure on sole decreased considerably and its exploitation is now at the level of the MSY. The spawning stock biomass (SSB) has fluctuated around the limit since 2003, thereby compromising overall population growth (Van Bogaert et al., 2020). Although recruitment was estimated to be relatively high in 2019 resulting in an increase in the SSB in the following years, recruitment estimates of the two most recent years are much lower (ICES, 2022b). For plaice in the North Sea and Skagerrak region, fishing pressure has increased since the sixties to far above the sustainable MSY level (ICES, 2022a) (Figure 1.1). After 2001, however, fishing pressure decreased significantly, and currently the species is being exploited below MSY level with high recruitment and SSB estimates for recent years. As such, the two most important flatfish stocks in the North Sea are now sustainably exploited at (sole) or under (plaice) MSY level.

Flatfish in the southern North Sea, and sole and plaice in particular, are usually caught using demersal bottom trawls (beam trawls and, to a lesser extent, otter trawls). Although bottom trawling activities take place over the entire European continental shelf, fishing intensity is highly heterogeneously distributed with 90% of the activity taking place over only 45.4% of the area (Eigaard et al., 2016; van der Reijden et al., 2018) (Figure 1.2). The location of fishing hot spots for bottom trawling activities is thereby highly dependent on the gear type. Beam trawling is due to its depth limitations mainly concentrated in shallow coastal areas in the southern and northeastern North Sea, while demersal otter trawls can be deployed at all depths and have therefore a much wider distribution. On a micro-scale, trawling effort hot spots usually reflect the heterogeneous distribution patterns of the target species and their prey. These patterns can be relatively stable in case they are linked to morphological features, but might also be more transient in nature (Rijnsdorp et al., 1998). Beam trawlers that target sole, for example, concentrate around troughs in shallow waters that are characterised by relatively high bottom temperatures, bed shear stress and low wave action (van der Reijden et al., 2018). Plaice fisheries, on the other hand, seem to concentrate around ridges on top of large scale elevations (e.g. sand banks) that experience high wave action (van der Reijden et al., 2018). However, plaice distribution differs highly between years and even within years, which makes it harder to identify stable fishing hot spots for this species (Eigaard et al., 2016).

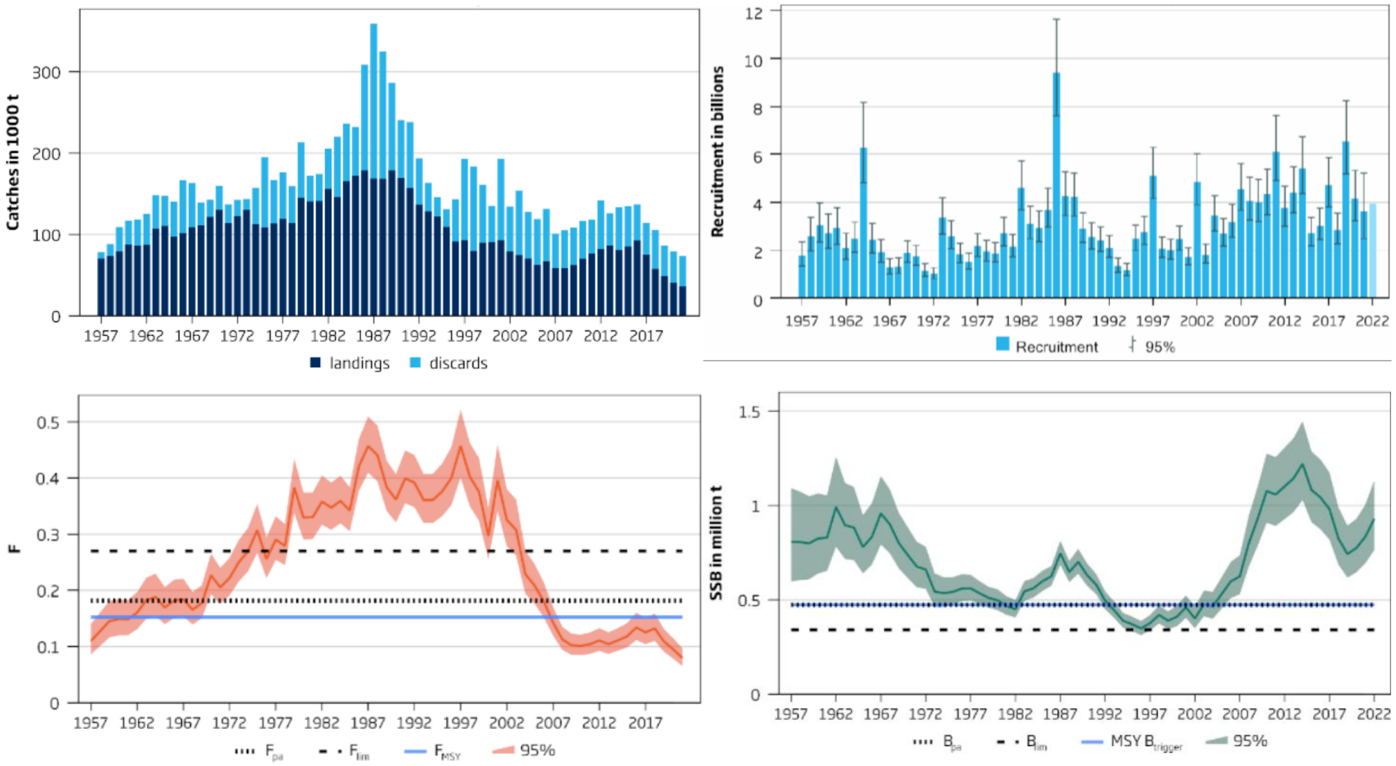

Figure 1.1: Historical catches (upper left), recruitment (upper right) and fishing pressure (lower panel) for plaice *Pleuronectes platessa* in the North Sea and Skagerrak region (source: ICES, 2022).

Apart from the gear type and the distribution of the target species that determine where fishers are most active, there are also regulations (e.g. Common Fisheries Policy, The Habitats Directive) that prevent trawling in certain areas. Unless bilaterally agreed upon, fishing in territorial waters (<12 NM) is reserved for national users and in some nature conservation areas (e.g. Natura 2000), the use of bottom-disturbing fishing techniques is not allowed (European Commission, 2018). Trawling is also forbidden around obstacles, such as oil and gas platforms, in certain areas during military exercises and within OWFs (except in the UK) (Verhalle and Van de Velde, 2020).

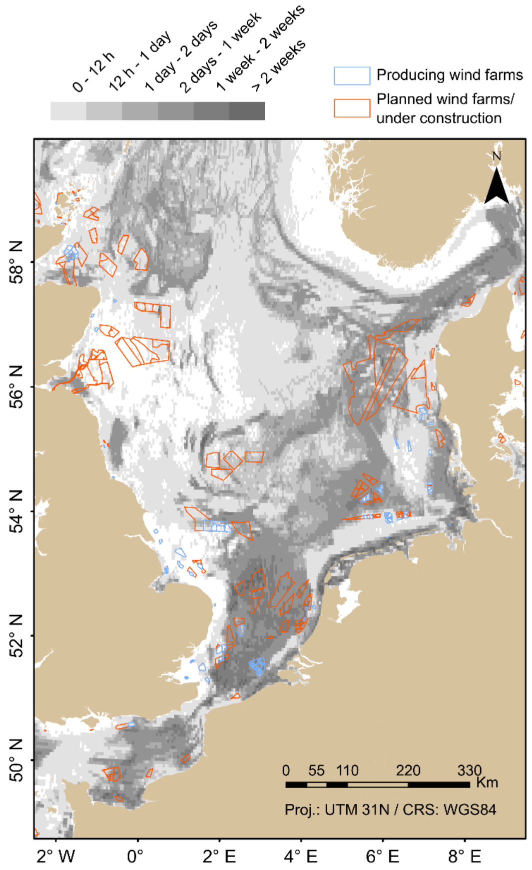

Figure 1.2: Spatial distribution of the summed average annual fishing intensity of the beam and bottom otter trawls in the North Sea region (2009–2017, OSPAR data), together with the location and size of present and future offshore wind farms (EMODnet, Human Activities, Wind Farms, revision 2022-12-19).

OWFs are currently being constructed at a swift rate in North Sea waters. The rapid expansion of offshore wind is coupled to the European Green Deal (Lloret et al., 2022) and the urge to fully exploit green energy production at sea in an attempt to become climate neutral by 2050 (European Commission, 2019). At the end of 2021, a total of 5,785 wind turbines, mainly monopiles, were connected to the European electricity grid resulting in a total power capacity of 28.3 GW (WindEurope, 2022) (Figure 1.3).

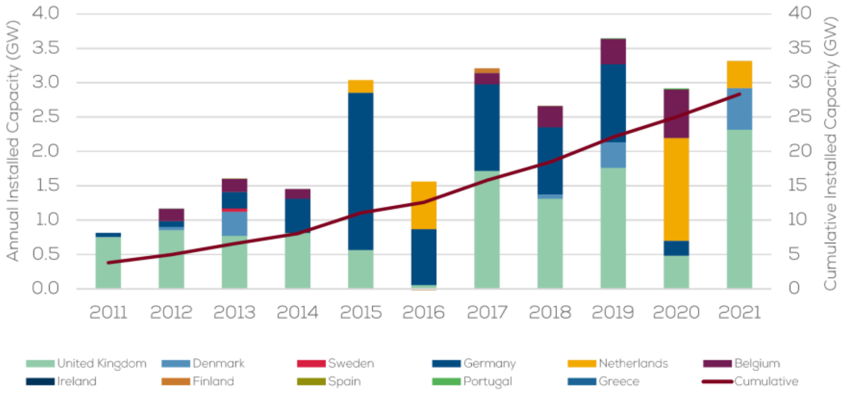

Figure 1.3: Annual offshore wind installed capacity by country (right axis) and total cumulative installed capacity (left axis) in Europe. (source: WindEurope, 2022)

Europe's strategy targets for an installed capacity of 60 GW offshore wind by 2030 and 300 GW by 2050 (European Commission, 2020). And of course, this takes up space. Presently, around 3,775 km^2 of European waters are occupied by wind projects that are in the production phase (EMODnet, 2022). An additional 55,000 km^2 is reserved for projects that are under construction, planned or have been approved for construction during the coming years. If the occupied area of present and planned projects is added up, OWFs will make up approximately 10% of the total surface area of the North Sea (EMODnet, 2022). Many of these projects have been constructed or are planned in historically heavily fished areas, thereby reducing access to traditional fishing grounds (Stelzenmüller et al., 2022) (Figure 1.2). As a consequence, fishers might be forced to relocate to less ideal fishing grounds, which can increase travel duration and, thus, fuel costs. Moreover, relocation or displacement of fishing activities can lead to concentrated efforts and local overfishing, potentially resulting in lower catches and decreasing profits due to competition among fishers (Roach et al., 2018; Dupont et al., 2020). Actually, this conflict on the potential co-existence of fisheries and OWFs is not only ongoing in Europe, but in many other parts of the world as well (Haggett et al., 2020; Zhang et al., 2017).

One way to tackle the problem of limited available marine space is co-location (Stelzenmüller et al., 2021). In the context of OWFs, this refers to the practice of locating other activities within the offshore wind concession area. Such activities can include aquaculture operations, tidal wave energy systems, floating solar panels, nature conservation measures and fishing. The feasibility of co-locating certain activities will depend strongly on the site characteristics, such as its hydrology, ecology and biology, and the management plans that are in place (Christie et al., 2014).

Apart from this 'battle for space', there are also major knowledge gaps on how OWFs might affect fisheries resources, especially where it concerns soft-sediment species such as flatfish. Typical hard-substrate associated fish species (e.g. cod *Gadus morhua*, pouting *Trisopterus luscus* and black sea bass *Centropristis striata)* are found in higher abundances within OWFs and, in general, profit from the introduction of artificial structures into sandy environments as they offer increased food and shelter opportunities (Reubens et al., 2013a; Wilber et al., 2022a).

For flatfish, such as plaice, this relation has not yet been investigated in detail, but may be different as they live in close association with the sea bottom (Wilber et al., 2018). Barbut et al. (2020) modelled that approximately 9.4% of plaice spawning was occurring in present and future OWF areas, a number that will likely further increase within the coming decades with OWF expansion. The scour protection and turbines foundations decrease the available sandy habitat and affect the soft sediments and associated macrobenthos in their immediate vicinity (Lefaible et al., 2018; Coates et al., 2011, 2014), which can deteriorate spawning or nursery grounds for flatfish if they coincide with OWFs (Rochette et al., 2010; Barbut et al., 2020). On the other hand, OWFs might have a positive effect on flatfish through an exclusion of bottom trawling activities, as fish inside the OWF are protected from the impacts of fishing (see Box 1 for the impacts of bottom trawling on flatfish). Moreover, trawling has been shown to decrease the abundance, biomass, production and species richness of benthic invertebrates that serve as food for demersal fish (Hiddink et al., 2011). Cessation of fisheries activities within OWFs could therefore increase prey availability and thus the carrying capacity of the area (Johnson et al., 2015). As such, OWFs can act as refuge areas for flatfish and other demersal species. However, field-based scientific evidence related to OWFs that shows increases in flatfish abundances or changes in catches in adjacent waters (i.e. spillover) is currently still lacking (Gill et al., 2020).

BOX 1 | THE IMPACTS OF BOTTOM TRAWLING ON FLATFISH

Flatfish are usually caught using a demersal beam or otter trawl, a fishing net that is being towed over the sea floor by a vessel (Figure 1.4). In a beam trawl, the net is being held open by a steel beam and is equipped with rows of tickler chains at its opening. These chains penetrate the sea bottom over a depth of several centimetres, thereby stimulating fish to get out of the sediment and into the net. This method not only increases catch efficiency, but it also disturbs the bottom and its associated fauna, leading to high mortality rates (Kaiser and Spencer, 1996; Bergman and van Santbrink, 2000). Frequent bottom disturbances lead to shifts in benthic and epifaunal species composition and size, favouring smaller-sized organisms with high productive rates and short lifespans (Kaiser and Spencer, 1996). However, plaice target these typical opportunistic prey species, which might have led to an increase in their growth rate in the 1960’s and 1970’s, coinciding with an increase in beam trawl effort (Rijnsdorp and Van Leeuwen, 1996). Moreover, by damaging the organisms in their path, beam trawls can locally increase food availability (Bergman and van Santbrink, 1994; Hiddink et al., 2008).

In contrast, more recent meta-analysis studies have shown that, apart from small benthic species, the overall abundance of benthic invertebrates (macrobenthos and epibenthos) decreases in response to bottom trawling (Kaiser et al., 2006; Collie et al., 2017). This was corroborated by a study that was carried out in the North Sea, which showed a decrease in prey biomass in the stomachs of plaice due to the adverse effects of bottom trawling (Eggleton et al., 2018). Furthermore, plaice condition was found to be inversely related to trawling intensity in the Irish Sea. In conclusion, light trawling intensities seem to increase prey availability for plaice, although there is only little support, while high intensive trawling has a clear negative effect on their food availability and condition (Collie et al., 2017).

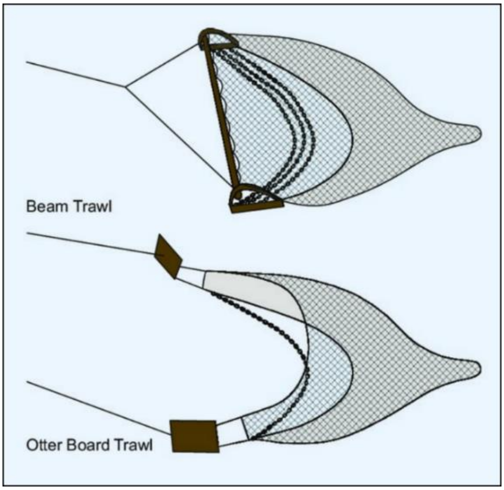

Figure 1.4: Bottom trawling techniques typically used in North Sea flatfish fisheries. Modified from Maarleveld (2020).

Apart from the influences on flatfish trophic ecology, bottom trawling can also affect their life-history characteristics (Gibson et al., 2015). For example, a decrease in length and age at first sexual maturity together with an increase in growth has been observed for plaice and other commercially exploited flatfish in the North Sea, which was most probably caused by fishing (van Walraven et al., 2010). The main hypothesis for explaining this phenomenon is that growth is a density-dependent process with fishing decreasing the overall population density and thus increasing growth rates (Rijnsdorp, 1991). Other hypotheses that were put forward were related to phenotypic plasticity and a change in the age composition of the stock.

1.2 A NORTH SEA UNDER CLIMATE CHANGE AND VARIABILITY

Ever since the industrial revolution, our seas have experienced major changes, induced by extensive human uses. Shipping, fishing, oil and aggregate extraction, and wind farm development are all examples of anthropogenic activities that have altered the marine environment and impacted its associated fauna in various ways (Rijnsdorp and Vingerhoed, 2001; Bergström et al., 2013; Madin et al., 2016; Schutter et al., 2019). These activities often have direct impacts on habitat quality (Eggleton et al., 2018). Monitoring and understanding the effects of such activities is important to allow for a sustainable management of the ecosystem and its resources. However, before we can disentangle the specific impacts of each individual activity on the local environment, it is key to first understand the natural variability that is present within the ecosystem. Increasing our knowledge of this so-called 'baseline' enables us to better frame the potential effects of OWFs or other human activities on the marine resources of interest.

Changes in temperature, both due to natural variability and human-induced climate change, affect fish and other marine organisms (Dulvy et al., 2008; Harris et al., 2014). Large-scale climatic oscillations, such as the North-Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) were found to have strong relationships with certain fish and macrobenthic species abundances in the North Atlantic (Kröncke et al., 1998; Meyer et al., 2016; McLean et al., 2018). Marine biological communities are also affected by the fast increase in temperature due to anthropogenically-induced global warming (Hermant et al., 2010). From 1984-2014, sea surface temperature (SST) in the southern North Sea region has increased with on average 0.45 °C per decade, thereby exceeding the global rate of change or the change in air temperatures on land (UKMMAS, 2019; Bulgin et al., 2020). As temperature is found to be a major driver for changes in the biogeography and abundance of fish, climate change can seriously impact the composition of fish communities (Cheung et al., 2016). Nearly two-thirds of North Sea fish species have shown shifts in depth or latitude during the last 25 years as a response to increasing temperatures (Perry et al., 2005). Most species have shifted northwards or have deepened over time, while southerly warm-water species, such as sole and pouting *Trisopterus luscus*, showed a shallowing response (Dulvy et al., 2008; Cheung et al., 2009). If such geographical shifts do not take place at the same rate for different species, a mismatch might arise in the food web interactions between prey and predators, which could lead to unpredictable effects (Perry et al., 2005).

Interestingly, climate change was also linked to an increase in species richness of marine fish in temperate waters (Hiddink and ter Hofstede, 2008). This increase was mainly explained by a proliferation of small-sized species of southerly origin. Rising water temperatures lead to a decrease in oxygen solubility whilst increasing the anabolic oxygen demand of fish at the same time. Therefore, it is more advantageous to have a smaller body size in warmer water due to the lower surface area to volume ratio, which is commonly referred to as the temperature size rule (Atkinson, 1994). As a result, climate change is predicted to shrink the community-average body size of fish with 14-24% by 2050 (Cheung et al., 2013; Baudron et al., 2014).

All of the abovementioned shifts are thought to have serious consequences for marine resources (Cheung et al., 2016). Commercial species populations might completely move out of previously used fishing grounds, thereby forcing fishers to relocate to deeper and more northern locations. On the other hand, opportunities might also present themselves when southerly species of high commercial value that were not present before move into certain areas (Van Bogaert et al., 2020). However, due to the increase in distributional range of southerly species with high energy demands, competition for food with temperate commercial fish species may occur, thereby decreasing their catch potential if temperatures increase even further (Jennings et al., 2008). It is hypothesized that this is already the case for plaice and sole in the North Sea, which have a dietary overlap with solenette *Buglossidium luteum*, a relatively small and more southerly species (Hiddink and ter Hofstede, 2008; van Hal et al., 2010; Cheung and Oyinlola, 2018). Moreover, species with slow and long life cycles usually have a lower adaptive capacity, which makes them less capable to react to temperature changes, and thus more sensitive to fisheries overexploitation (Perry et al., 2005).

Apart from shifts in biogeography, fish can also react to climate change through phenotypic responses (Crozier and Hutchings, 2014). Changes in traits such as timing of migration and reproduction, age at maturity, age at juvenile migration, growth, survival and fecundity were all found to be driven largely by temperature. In addition, ocean warming increases the metabolic rate in fish, thereby increasing their energy demands (Pörtner and Farrell, 2008; Nagelkerken et al., 2021). Apart from an increase in temperature, climate change also leads to ocean acidification (Denman et al., 2011). CO_2 from human fossil fuel emissions enters the oceans and lowers the pH of the water, which can affect fish physiology and behaviour, but also causes a decline in prey availability (especially those who form shells) (Crozier and Hutchings, 2014). Climate change thus leads to an increase in the energy demands of fish, while the energy availability decreases. This mismatch can affect the energy allocation in individual fish, which might have consequences for populations if less energy is available for reproduction (Nagelkerken et al., 2021).

1.3 ECOLOGICAL EFFECTS OF OFFSHORE WIND FARMS

The construction of offshore wind farms, particularly in Europe, often takes place in soft sediment environments, introducing hard substrate in the form of steel, cables, concrete and rocks into areas where extensive geogenic reef structures are not normally present (Coolen, 2017; Degraer et al., 2020). Such an introduction does not only affect the physical features of the seabed, but also induces changes to the hydrological and wind conditions and introduces noise and electromagnetic fields (EMFs) (Hutchison et al., 2020; Petersen and Malm, 2006; van Berkel et al., 2020). All these changes can have different effects on organisms by directly altering their habitat or their behaviour (Bailey et al., 2014). Such effects can be seen as undesirable, for example when seabirds are colliding with the moving turbine blades (Bailey et al., 2014) or when acoustic calling signals of marine mammals are masked due to the increased underwater sound levels (Sanders et al., 2017), or when species that rely on Earth's magnetic field for foraging or migration get disorientated by EMFs that are emitted through the transport cables (Sanders et al., 2017; Hutchison et al., 2020b).

On the other hand, there are also potentially desirable effects that can be expected, such as a 'refuge' and an 'artificial reef' effect. By prohibiting fishing activities within the wind farm area, refuge opportunities for fish species are created. Furthermore, biomass 'hotspots' might arise where fish and other organisms are attracted to the turbine foundations and the scour protection, as they offer food and shelter opportunities (Krone et al., 2013). However, the way an organism responds to the construction and operation of an OWF will differ greatly among species (Bailey et al., 2014). Flatfish, for example, spend almost their entire life cycle in very close contact with the seabed and might therefore respond differently to the introduction of hard substrate in soft sediment environments compared to pelagic or benthopelagic species (Gibson et al., 2015; Wilber et al., 2018). Increasing our knowledge on how OWFs affect flatfish and if they might offer opportunities to these species forms a major part of the current PhD study.

1.3.1 FISHERIES EXCLUSION AND REFUGE EFFECT

Human activities, such as fisheries, are negatively affecting many marine ecosystems all over Europe. In an attempt to mitigate some of these impacts, the Marine Strategy Framework Directive (MSFD) was issued by the European Commission in 2008 (Directive 2008/56/EC). An important pillar in the implementation of this directive (i.e. to achieve *Good Environmental Status)*, is the establishment of a coherent network of marine protected areas (MPAs). The term MPA was defined by the International Union for Conservation of Nature (IUCN) in 1988 as "*any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part of or the entire enclosed environment*" (IUCN, 1988). Studies on existing

MPAs show that they can have a significant positive influence on various biological variables such as species density, biomass, biodiversity and individual body size (Halpern, 2003; Fenberg et al., 2012). However, important preconditions for their success are the connectivity between similar areas, the measures that are taken and the way they are managed (i.e. so-called paper MPAs vs. effective management).

Marine reserves are defined as no-take zones and are as such a special kind of MPAs that show the largest potential as conservation tools for marine resources (Di Franco et al., 2009). Although such reserves are usually intended to serve various nature conservation goals, their role as fisheries management tools is widely recognized (Pastoors et al., 2000; Miethe et al., 2010). Increases in biomass and density for fished species were shown within marine reserves compared to outside (Di Franco et al., 2009; Florin et al., 2013; Guidetti et al., 2014). This is often referred to as a 'fisheries exclusion' effect. If such an effect also crosses the borders of the reserve, thereby positively influencing fish within adjacent areas, this is called a 'spillover' effect. A sufficient spillover of adult fish could benefit local fisheries or even replenish larger-scale fish stocks, provided that the effect takes place over a large enough area (Halpern et al., 2009).

Although there is a lot of scientific evidence that marine reserves (i.e. no extraction is allowed) can enhance local fisheries, they are relatively scarce within the North Sea region. This is potentially explained by the tradition of separating nature conservation and fisheries management in northern Europe (Sørensen and Thomsen, 2009), together with the strong lobby of the fisheries sector against completely closed areas (Florin et al., 2013). However, due to safety considerations, all commercial fishing activities are currently prohibited within the concession areas of European OWFs (except for the UK), making them no-take zones. Although OWFs generally have no conservation objectives, the existing fisheries exclusion might create opportunities for target species that experience high fishing pressures in adjacent areas (Ashley et al., 2014). Increased fish biodiversity and biomass have already been observed in no-take areas that were not specifically designed for nature conservation purposes, but where providing interaction possibilities between wildlife and the general public was the primary objective (Friedlander et al., 2007). As such, the present and planned OWFs in the North Sea can from a large network of no-take zones that could play an important role in the protection of target species against fishing mortality.

While OWFs might offer refuge to certain target species, they should not be regarded as equivalent alternatives for well-managed MPAs, as they have different objectives. The refuge potential of OWFs will largely depend on their location and size, which is usually based on physical, technical and economic considerations rather than on the natural value of the area in terms of conservation or restoration (Inger et al., 2009; Sanders et al., 2017; Gusatu et al., 2020). Moreover, the introduction of hard structures could lead to habitat degradation of the benthic environment, especially during the construction phase (Sanders et al., 2017). In addition, several non-indigenous epifaunal species have been found on the turbine foundations in an OWF that might compete for resources with the native communities (De Mesel et al., 2015). For plaice, construction of OWFs in nursery areas might negatively affect recruitment if the existing food web is altered or if sediment characteristics undergo large changes (Rabaut et al., 2010; Rochette et al., 2010). Further, it is also unclear how fish are affected by the different types of energy emissions, such as the EMFs emitted from the cables that transport the generated electricity in OWFs (Hutchison et al., 2020b). EMFs might affect fish behaviour, especially in electroreceptive species such as sharks and rays; or in migratory species, such as plaice, which probably use the Earth's magnetic field for orientation during their spawning migrations (Formicki et al., 2019). If the effect of the EMFs is significant, the fitness of organisms can be affected, which can have impacts on the population level (Hutchison et al., 2020b).

Thus far, no or limited species-specific density effects have been detected for soft sediment fish at the wind farm-scale on the short-term (<7 years) in European OWFs (Denmark, Netherlands, Sweden) (Leonhard et al., 2011; Lindeboom et al., 2011; Bergström et al., 2013). A long-term sampling effort is necessary to be able to detect an established refuge effect within an OWF, as this generally takes several years to develop (Babcock et al., 2010). Furthermore, it is also important to have a high sample frequency (not only before and after the construction) as some effects can evolve over time (De Backer et al., 2020). Despite the weak empirical evidence up till now, researchers are still convinced that OWFs can induce refuge effects for different fish species, similar to what is observed in MPAs (Inger et al., 2009; Wilhelmsson and Langhamer, 2014). A recent modelling study even predicted a 7% increase in catch rates in the vicinity of a future OWF-project in the English Channel, suggesting a potential (small) spillover effect (Halouani et al., 2020). If potential spillover effects from OWF areas are sufficiently large, they may (partly) compensate for the loss of fishing grounds due to the development of OWFs (McClanahan and Mangi, 2000; Sale et al., 2005; Inger et al., 2009). However, it is vital to first gather information on the spatial distribution and movements of fish in relation to an OWF, before spillover effects and their potential consequences for local fisheries can be studied.

1.3.2 ARTIFICIAL REEF EFFECT

Natural reefs are among the most productive and diverse ecosystems in the world (Reaka-Kudla, 1997). They provide substrate for hard substrate colonizing fauna and increase environmental complexity (Coolen, 2017). Reefs can also be introduced into the marine environment by humans, so-called artificial reefs. Whether deliberately or accidentally introduced, e.g. ship wrecks, oil and gas platforms, offshore wind turbines, buoys or coastal defence structures, they can offer similar advantages as their natural counterparts. Organisms associated with artificial reefs are very specific and the majority of those species are normally not found in the surrounding natural soft sediments (Zintzen, 2007). The hard substrate provided by the introduced structures is rapidly colonised by so-called fouling or hard substrate colonizing organisms, which in their turn attract fish and other megafauna such as decapods (Krone et al., 2013). Artificial reefs are usually associated with higher abundances and biomass of fish and colonising species, compared to the surrounding soft sediments (Bohnsack and Sutherland, 1985). It is believed that this 'attraction' effect is primarily caused by an increased food availability and/or easier food accessibility, together with the provision of shelter from predators and currents (Pickering and Whitmarsh, 1997; Claudet and Pelletier, 2004).

OWFs can be considered as artificial reefs, where the turbine foundations and scour protection provide opportunities for various species (Figure 1.5) (see Box 2 for an overview of the most common foundations used in OWFs). They create completely new habitats as the underwater structures occur throughout the entire water column from the sea bottom to the sea surface, where comparable natural hard substrates have never been present before (Degraer et al., 2020). Long-term monitoring of turbine foundations in a Belgian OWF has shown that the structures were quickly inhabited by biofouling assemblages, where the first colonisers are slowly replaced by suspension feeders that are better adapted to the environment, eventually evolving after 10 years to a *Metridium senile/Mytilus edulis*-stage in a process called ecological succession (Kerckhof et al., 2010). Comparable studies in different North Sea OWFs showed a clear vertical zonation pattern along the depth gradient of the turbine foundations with four distinguishable zones from top to bottom: an intertidal zone, the *M. edulis* (blue mussel) zone, a *Jassa herdmani* (an amphipod) zone and a *M. senile* (frilled anemone) zone (Petersen and Malm, 2006; De Mesel et al., 2015; Mavraki et al., 2020). The species composition differs between the turbine foundations and the SPL with a higher diversity found on the latter, probably due to its higher complexity and its resemblance to natural reefs (De Mesel et al., 2013). However, fauna found on the SPL does differ significantly from communities found on natural rocky reefs (Coolen et al., 2020).

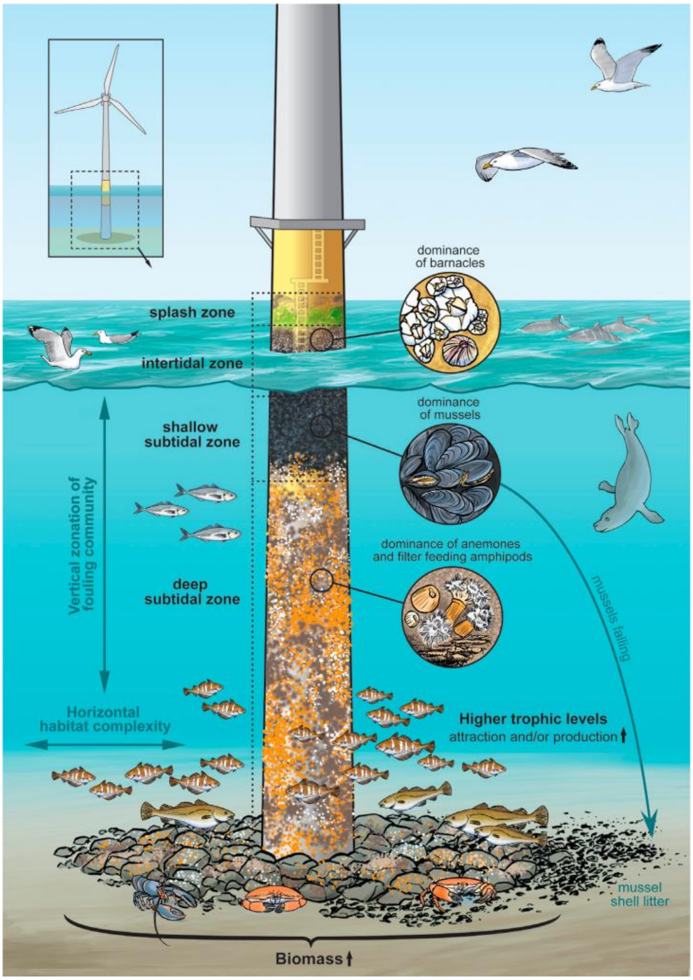

Figure 1.5: Illustration of the artificial reef effect around a monopile foundation with scour protection layer (SPL). Various sessile organisms colonize the turbine foundation and SPL, thereby attracting other megafauna, such as fish, decapods, seabirds and mammals. Source: Degraer et al. (2020). Illustration by Hendrik Gheerardyn.

Apart from the epifauna attached to the hard substrates, mobile megafauna and fish are attracted to the turbine foundations and surrounding SPL as well. Crustaceans such as edible crab *Cancer pagurus*, velvet swimming crab *Necora puber* and European lobster *Homarus gammarus* are observed in high densities on the turbine foundations and rocks of the SPL in different European OWFs (Langhamer et al., 2009; Krone et al., 2013, 2017). Also, different finfish species (e.g. cod *Gadus morhua*, pouting *Trisopterus luscus,* goldsinny wrasse *Ctenolabrus rupestris* and black sea bass *Centropristis striata*) that are often observed in high abundances near other hard substrates (e.g. ship wrecks, oil rigs), were equally found to live in close association with the OWF structures (Bergström et al., 2013; Reubens et al., 2013a; Carey et al., 2020). Indeed, an ecosystem and simulation model, based on the combined input of field sampling studies and existing literature, predicted a substantial increase in benthopelagic fish biomass after the construction of an OWF (Raoux et al., 2017).

Studies on the potential attraction effects towards these OWF hard substrates have, thus far, mainly focused on fish species known to favour such hard-substrate habitats (Reubens et al., 2013a; Langhamer et al., 2018), or the effects were only studied at larger distances from the hard substrates (Lindeboom et al., 2011; Stenberg et al., 2015; Vandendriessche et al., 2015; Wilber et al., 2022a). Up to now, evidence-based information concerning the artificial reef effect for soft-sediment fish species, such as flatfish, is still largely lacking. Generally, no attraction effect or even avoidance behaviour for several flatfish species was observed (Leonhard et al., 2011; van Hal et al., 2017; Wilber et al., 2018). In contrast, a modelling study predicted a significant increase of flatfish biomass after the construction of an OWF in the Bay of Seine (Raoux et al., 2017). Most probably, the spatial and temporal scales at which the abovementioned field studies were performed, were not appropriate to capture the attraction effect for flatfish. First of all, fish redistribution often occurs in the immediate vicinity of the hard substrate (<50 m) whereby the effect gradually decreases with distance (dos Santos et al., 2010; Bergström et al., 2013), so samples taken with bottom trawls in between the turbines at a distance of 100 m or more might not be able to identify small-scale aggregation patterns. Second, the effects of hard substrates and the spatial scale at which they act evolve over time (Dannheim et al., 2020). For example, De Backer et al. (2020) found the first signs of an OWF-effect in the epibentic assemblages between the turbines (±200 m) only seven years post-construction. It is, therefore, important to try and capture the existing gradients in space and their evolution through time in any impact study related to hard substrates in OWFs.

BOX 2 | WIND TURBINE FOUNDATIONS AND SCOUR PROTECTION

Wind turbines can be fixed to the seabed using different methods (Figure 1.6). The choice of the foundation type is mainly based on the depth of the seabed and the prevailing environmental conditions (Sánchez et al., 2019). Within Europe, the most common foundation is the monopile, accounting for 81.5% of all installations, followed by jackets (9.9%) and gravity-based foundations (5%) (WindEurope, 2021). Currently, floating wind systems are on the rise to reduce construction costs in deeper waters (>50 m) where it is not economically feasible to put bottom-fixed structures.

Monopiles are made of steel wind towers that are attached (either directly or through a transition piece) to a steel monopile with a diameter of up to 6 m. Commonly, the monopile pipe is driven into the seabed up to 30 m deep by means of a large impact or vibration hammer (Sánchez et al., 2019).

Jackets exist of four-legged (or more) cylindrical steel tube structures which are driven into the seabed and are interconnected by smaller tubes to provide strength and stability (Malhotra, 2011).

Gravity-based foundations are hollow, concrete structures that are put on the seabed and stay in position solely due to their own weight. Their base width can be adjusted to meet with the prevailing conditions (Sánchez et al., 2019).

Floating wind turbines are attached to a floating platform, which is anchored to the seabed using mooring lines and chains. Such systems have lower environmental impact on the seabed compared to traditional foundations, although scouring of the sediments around the anchors that keep the platform in place may still have a significant impact (Karlsson et al., 2021). Another benefit of floating turbines is that they reduce visual impacts as they can be constructed further away from the coastline.

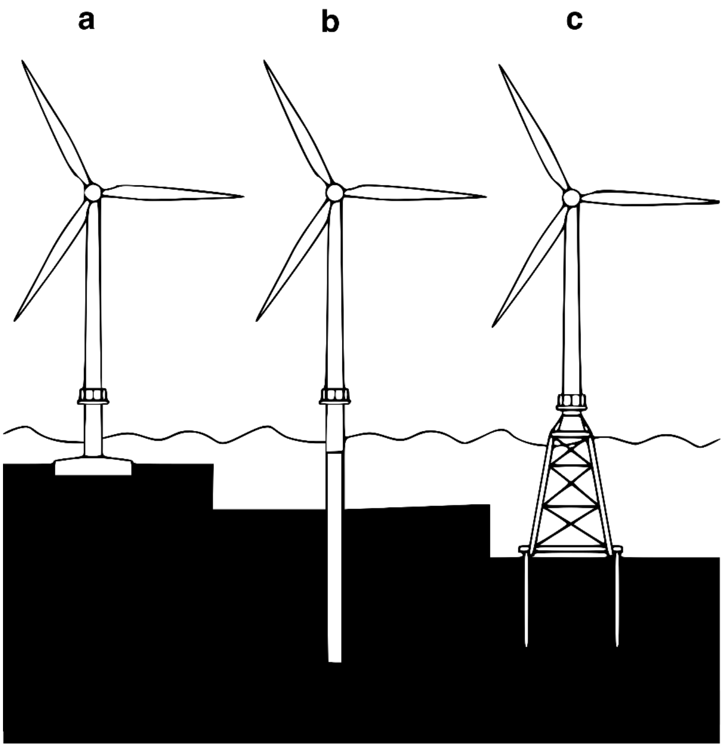

Figure 1.6: Most commonly used types of wind turbine foundations: a: gravity-based foundation, b: monopile foundation, c: jacket foundation. Modified from Kallehave et al. (2015).

Depending on the foundation type and the hydrological conditions, scour protection measures have to be taken to ensure the stability of the sediment around the turbine foundations, which can be removed due to wave or current action (Malhotra, 2011) (Figure 1.7). Usually, such measures consist of adding gravel, quarry run stone or blasted rock around the entire base of the turbine, but the configuration can vary greatly between projects (Whitehouse et al., 2011). For monopile and gravity-based foundations, where water cannot pass freely through the structure, the use of scour protection is often necessary, while this is not the case for jackets.

Figure 1.7: Scour protection layer at the Belwind wind farm (image: Film Johan Devolder).

1.4 THE ATTRACTION-PRODUCTION HYPOTHESIS

An important question related to artificial reef research is whether the observed attraction of organisms to a certain hard structure only induces a relocation (and thus concentration) of those individuals or if the altered habitat can actually support a higher abundance and/or biomass of those organisms (Lindberg, 1997). The latter statement implies an increased carrying capacity of the ecosystem and thus production (Bohnsack and Sutherland, 1985). Artificial reef structures can increase fish production through an increase in their feeding, spawning, nursery or resting habitat (Grossman et al., 1997). This may lead to replenished fish stocks, where both recreational and commercial fisheries receive benefits from the artificial reef in the form of an OWF. On the other hand, if fish individuals are only concentrated around an artificial reef without clear extra production taking place (or too low production rates), the opposite effect might be observed. An increase in fishing effort and increased catches in the vicinity of such an artificial reef or OWF may facilitate overexploitation of already exploited stocks, leading to overall lower standing stock biomass of certain commercial fish species in the area (Grossman et al., 1997). Good management and intensive monitoring of those stocks is in such a case critical.

Trying to unravel the attraction-production hypothesis within OWFs is vital to ensure the sustainable management of fisheries resources, which might be affected by the development of offshore wind (Cresson et al., 2014; Mavraki et al., 2021). It is often difficult to provide sufficient evidence to state that potential increased production around a local artificial reef also positively affects fish populations on a larger scale (Pickering and Whitmarsh, 1997). The majority of research up till now has focused on abundances of different species to detect a potential attraction effect around the hard substrates in OWFs (Leonhard et al., 2011; Lindeboom et al., 2011; Reubens et al., 2011a; Bergström et al., 2013; Krone et al., 2017; Wilber et al., 2018). Despite most sampling methods for determining fish abundances being relatively straightforward, challenges arise when they are applied in OWFs. Strict safety restrictions make it difficult to apply traditional methods such as beam trawling in the vicinity of cables, turbines and scour protection. Alternative methods are labour intensive (e.g. visual diving censuses) or have not been fully validated yet in the field (e.g. eDNA).

Generally, fish individuals that are attracted to an artificial reef, even if no extra production takes place, do benefit from their relocation due to a higher food availability and/or increased shelter opportunities (Smith et al., 2016). However, when environments experience rapid changes (e.g. when artificial structures are introduced), animals can mistakenly prefer a lower quality habitat due to a mismatch in attractiveness and suitability of that habitat (Robertson and Hutto, 2006; Hale and Swearer, 2016). This is commonly referred to as the 'ecological trap' hypothesis and may lead to deleterious effects on the animal's fitness, and by extension the fitness of an entire population (Hale and Swearer, 2016). Therefore, monitoring surveys should not only focus on abundances to determine whether a new habitat has a positive effect on a species, but also on the individual fitness and condition levels. By combining abundance data with knowledge on the trophic and behavioural ecology of a species, a number of studies have already suggested that production could be taking place for certain fish species in a Belgian OWF (Mavraki et al., 2021; Reubens et al., 2013c).

To gain more insight whether production of soft-sediment fish species, such as flatfish, might be occurring within OWFs, this thesis investigated the effects of the presence of OWFs on several aspects of plaice ecology in the Belgian part of the North Sea.

1.5 CASE STUDY: PLAICE IN THE BELGIAN OWF ZONE

1.5.1 AIMS AND OBJECTIVES OF THE PHD STUDY

During the last decades, OWFs are built at an exponential rate in European waters to mitigate the effects of climate change. The development of these OWFs takes up large amounts of already scarce marine space, which often cannot be used anymore by other or previous users, such as the fishing industry. Furthermore, the construction and operation of OWFs might also affect the ecology of important target species. Artificial structures, such as turbines foundations and scour protection, that are placed in a soft-bottom environment can offer opportunities to some fish species, but might also alter the sandy habitat in such a way that the natural biological communities are negatively affected. If these changes are substantial, this can then indirectly affect local or even regional fisheries. However, it is often difficult to disentangle the direct impacts of human activities, such as OWFs, from climate change or the natural variability present in the ecosystem. Therefore, the overall aim of this PhD study was **to investigate how OWFs affect the ecology of plaice *Pleuronectes platessa*, a typical soft-bottom species and important fisheries resource in Belgian waters and beyond, against a background of an ever changing North Sea environment.**

Therefore, the main research questions were the following:

1 | Can long-term trends within the different fish assemblages in the Belgian part of the North Sea be explained by climate change and/or variability?

2 | What are the effects of offshore wind farms on the spatial distribution patterns of plaice at the turbine and wind farm scale?

3 | What are the effects of offshore wind farms on the diet and condition of plaice?

4 | How can the small- and large scale movements of plaice in relation to an offshore wind farm be described?

5 | Is plaice production likely in offshore wind farms and what could be the effects for flatfish fisheries?

1.5.2 STUDY AREA: THE BELGIAN PART OF THE NORTH SEA

The Belgian part of the North Sea (BPNS) is situated at the most southern tip of the North Sea and covers 0.5% (3,454 km^2) of the total North Sea surface. It is a shallow sea with an average water depth of 20 m and a maximum depth of 46 m, characterized by numerous sand bank systems that lie more or less parallel to the coastline (Figure 1.8). The sea bottom exists mainly of medium sand with fine sand along the coastline and a high mud content near the mouth of the Scheldt estuary in the eastern part of the BPNS. Grain size increases gradually with distance from the coast and some gravel beds are present in the outmost north-western corner as well as on the Hinder Banks (Verfaillie et al., 2006; Van Lancker et al., 2007). This highly variable sedimentology and topography is associated with five diverse macrobenthic assemblages (*Abra alba, Macoma balthica, Magelona-Ensis leei, Nephtys cirrosa* and *Hesionura elongata*), each characterized by the above described grainsize characteristics and some typical dominant macrobenthos species (Breine et al., 2018). This also corresponds with more or less similar distribution maps for the epibenthos and demersal fish assemblages (De Backer et al., 2023, in press).

Despite its small size, the BPNS is one of the most intensively used areas in the world, including: shipping, dredging, sand extraction, nature conservation, wind farm development, tourism and of course both commercial and recreational fisheries (Maes et al., 2005). To better regulate all these activities and to minimise their impact on the marine environment, the Belgian authorities undersigned a marine spatial plan (MSP) in 2014, which is revised every 6 years (Verhalle and Van de Velde, 2020). Within this plan, a large zone for renewable energy production (238 km^2) was designated in the northeastern part of the BPNS. Currently, this zone is completely operational with nine concessions, consisting of 399 turbines with a total capacity of 2,262 MW. A second zone for renewable energy of 285 km^2, the Princess Elisabeth Zone, has been delineated within the MSP of 2020-2026 (Rumes and Brabant, 2021).

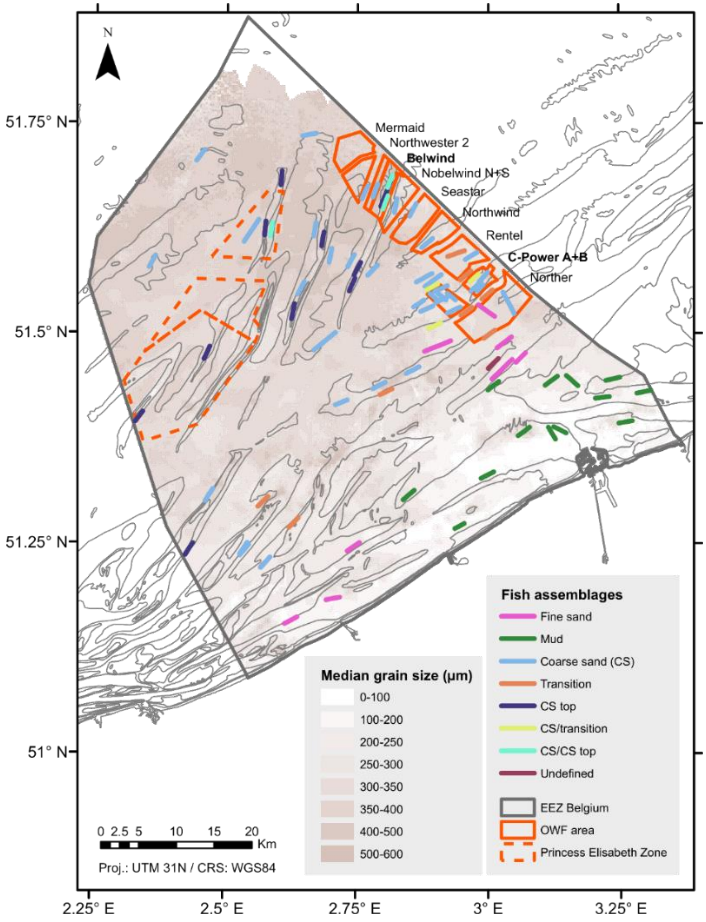

Figure 1.8: Overview map of the BPNS showing the locations of the different wind farms and the fish assemblages (fish assemblages from De Backer et al., 2022, in prep.). The wind farms where samples were taking for this thesis are shown in bold.

This PhD study is framed within the WinMon.BE monitoring programme (a cooperation between different Belgian institutes led by the Royal Belgian Institute of Natural Sciences (RBINS)) that aims at studying the environmental impacts of OWFs on the marine environment. This thesis focuses on the two oldest wind farm concessions, Belwind and to a lesser extent C-Power.

C-Power is located on the Thorntonbank at a distance of 27 km from the shore and with a depth between 14-28 m. Its construction started in 2007 with a pilot phase that existed of the installation of six gravity-based wind turbines (GBFs) surrounded by scour protection with a width of 44-58 m (finished in 2008). The scour protection consists of a filter layer made up by pebble (2.5-75 mm) with an armour layer on top, which is composed of a protective stone mattress with rocks (250-750 mm) (Reubens et al., 2011b). During the second and third phase of the C-Power construction (2010-2013), 48 turbines were installed on jacket foundations without scour protection (Rumes et al., 2013).

The construction of Belwind on the Bligh Bank started in 2009 and was completed in 2010. A total of 55 turbines on monopile foundations were installed at a water depth between 15-37 m. All turbines were provided with a scour protection layer of 38 m diameter, existing of a filter layer of smaller rocks with a layer of larger rocks on top (median rock size = 370 mm, solid rock density = 2.65 ton/m^3). In most locations (especially further away from the turbine foundations), sandy patches are present in between the rocks of the armour layer due to sedimentation and the relatively low density of rocks. In 2013, a larger turbine was added in the northern part of the wind farm as a test. The turbine was attached to the seabed with a jacket foundation and provided with scour protection in the form of a square plane.

Due to safety considerations, no shipping or fishing activities were allowed in and around the construction zones (500 m safety perimeter) from approximately three months before the actual works started. No fishing activities except for monitoring purposes were allowed after construction and during the operational phase. The choice for Belwind and C-Power in this study was primarily based on the large amount of knowledge and data that were already available for these areas, together with their high maturity, as some OWF-effects may take several years before they become apparent.

1.5.3 FOCUS SPECIES: EUROPEAN PLAICE

This study focuses on plaice (*Pleuronectes platessa* L., 1758), a right-sided flatfish species common in the North-East Atlantic Ocean. It is most abundant on sandy bottoms in water depths from 10-50 m, but has been found in waters up to 200 m (Maitland and Herdson, 1972). Plaice becomes sexually mature around 2-3 years for males and around 4-5 years for females. In autumn, mature adults undertake large migrations between feeding and spawning areas using selective tidal stream transport (Arnold and Holford, 1995). They leave the sea bottom during slack water and swim with the direction of the tide. When the tide reverses, they return to the bottom where they bury themselves into the sand until the conditions are favourable again (Hunter et al., 2004). During the migrations and spawning (from late autumn to the beginning of spring), plaice almost completely ceases to feed (De Groot, 1971). After spawning, plaice returns to their feeding areas where they remain until the next spawning season. Site fidelity to spawning and feeding areas is very high, with individuals recaptured at a scale of kilometres or even hundreds of meters from their release location (Burrows et al., 2004; Solmundsson et al., 2005). Genetic population structure analysis of plaice in the North Sea revealed that Icelandic plaice differentiated from plaice on the continental shelf, potentially shaped by bathymetry (Hoarau et al., 2002).

Spawning itself occurs between December and March with a peak in January (Figure 1.9). For the Southern Bight, this peak is around 19 January with a standard deviation of seven days (Simpson, 1959). The onset and end of spawning is negatively correlated with the water temperature at the start of and during the spawning period, so plaice in the northern part of the North Sea tend to spawn later compared to plaice in the Southern Bight and English Channel (Rijnsdorp, 1989). Plaice produces pelagic eggs, as most flatfish species, and the timing of spawning is synchronized with the production of the pelagic system, so that eggs hatch when the productivity is at its highest during spring (Cushing, 1969). Plaice' spawning grounds are widespread in the North Sea and include the Southern and German Bight, the Dogger Bank, Moray Firth, Firth of Forth and Flamborough Head (Poxton and Nasir, 1985; Coombs et al., 1990; Ellis et al., 2012). In addition, there are also important areas identified in the eastern part of the English Channel and the Irish Sea (Figure 1.10). It is thought that spawning areas have evolved in such a way that released eggs have the greatest chance of reaching the nursery areas, so their location is determined by the hydrography that links spawning and nursery areas (Gibson, 1999). The pelagic eggs hatch after 9-25 days, depending on the temperature, with colder waters resulting in longer development times (Bolle et al., 2009). The pelagic eggs and larvae are transported passively to the nursery areas by residual currents or, at later larval stages, by selective tidal transport (Bolle et al., 2009). After metamorphosis, the larvae settle in coastal waters or estuaries and enter the demersal juvenile stage of development (Gibson et al., 2015). Juveniles remain in these shallow waters (<10 m) during the first years of their life. As the juvenile fish mature, they gradually move further offshore towards deeper water (Gibson, 1997).

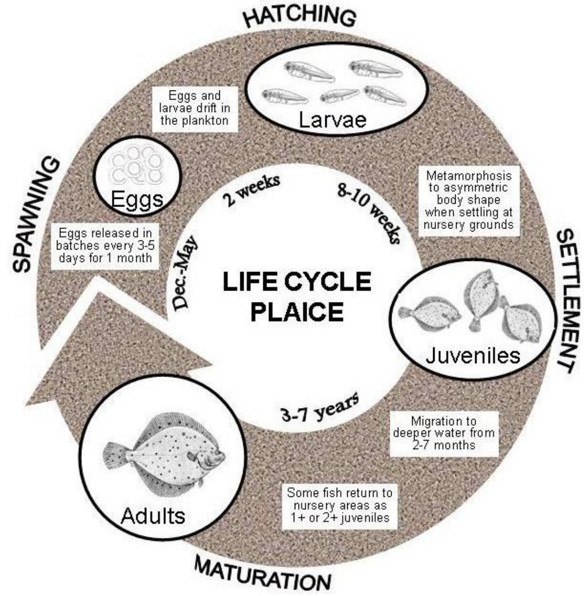

Figure 1.9: General features of the life cycle of plaice, *Pleuronectes platessa*. Source: Raedemaecker et al. (2011)

Plaice is an opportunistic feeder and its diet typically exists of small benthic organisms such as polychaetes, bivalves, echinoderms and crustaceans (Rijnsdorp and Vingerhoed, 2001; Gibson et al., 2015). Juveniles also prey on bivalve siphon tips that are protruding from the seabed, which can make up 80% of their diet if present in the environment (Ansell and Gibson, 1990). Plaice is a daytime feeder and has a clear diurnal feeding periodicity that is linked to the prevailing light conditions (De Groot, 1971). During the day plaice, swim close to the bottom in search of prey, while they move higher up in the water column during the night. When the light intensity is at its maximum however, they stop moving and bury themselves into the sand to avoid predation (Gibson et al., 2015).

There are several reasons why we chose plaice as a focus species for this study. First of all, it is one of the most important target species of the Belgian fishing fleet, especially in terms of volumes (Polet et al., 2022). In 2020, the landings in both Belgian and foreign ports totalled 3.683 tonnes, good for 20% of the total catch volume of the entire Belgian fleet and 17% of the total revenue. Second, the species is widespread over the BPNS (and is thus also present in the wind farm area), in contrast to sole, which is spatially restricted to the coastal area. Third, there is already a lot of ecological knowledge available on plaice within and outside the study area, which can facilitate the interpretation of own findings. Lastly, occasional sightings of plaice individuals on the scour protection layer in Belwind (Jan Reubens, personal communication) and the observations of higher abundances of plaice within the C-Power wind farm (De Backer and Hostens, 2017) in the framework of the WinMon.BE programme, led to the main hypothesis of this PhD study, namely that not only hard substrate-associated fish species are attracted to the OWFs, but soft-sediment fish species as well. We further hypothesized that these effects could be explained by an artificial reef effect, a fisheries exclusion refuge effect or a combination of both.

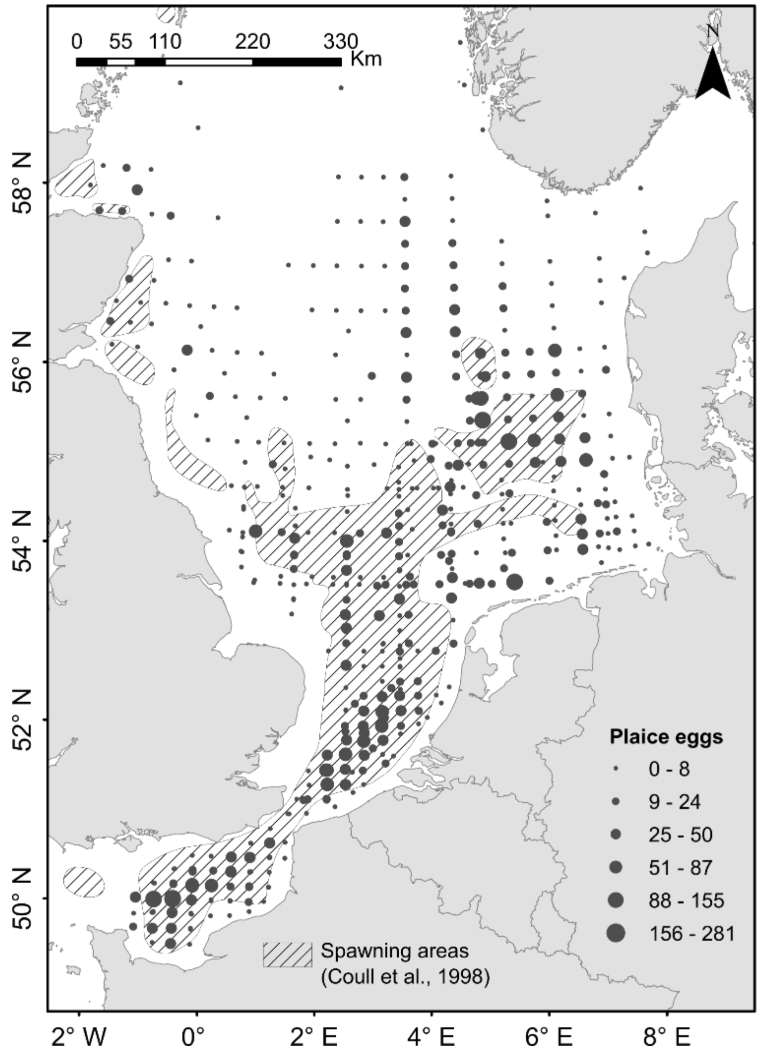

Figure 1.10: Spawning grounds of plaice (Coull et al., 1998) and egg data based on ichthyoplankton surveys (Ellis et al., 2012).

1.5.4 SAMPLING METHODS TO STUDY FLATFISH ECOLOGY IN OWFS

The choice of a certain sampling method or analysis technique depends largely on the objective or the specific research question that needs to be answered. Often, a combination of methods is needed to capture different temporal and spatial scales or to account for the limitations of certain techniques. Apart from the research question, aspects such as technical and logistical feasibility, safety regulations and ethical considerations (e.g. invasive vs. non-invasive methods) may also play a role in the choice of method. Below, an overview of the methods used in this thesis to address the different objectives is given. In addition, the advantages and limitations of each method are explained in the context of studying flatfish ecology in OWFs.

Objective 1: Studying spatial distribution patterns of flatfish on turbine and OWF scale

- *Beam trawl sampling*

Beam trawling is a traditional and widely-used method for collecting flatfish in relatively shallow areas (<100 m) (Amara et al., 2007; Tulp et al., 2008). The beam keeps the net open, while the tickler chains disturb the fish so they swim up from the sea bottom and into the net. This type of sampling is very effective and so a lot of specimens can be collected in a short period of time (Gibson et al., 2015) (Table 1.1). This method has been applied in combination with a Before/After Control/impact study design to investigate the effects of OWFs on the spatial distribution and composition of benthopelagic and demersal fish communities (Lindeboom et al., 2011; Vandendriessche et al., 2015). In such a study design, samples are taken in impacted and reference areas and this before and after the impact takes place. Reference areas are typically chosen based on their similarity in physical characteristics to the impacted areas (Wilber et al., 2022a). Although it is a very efficient method, it is destructive, has a high bycatch rate when sampling a specific species and has limited applicability in the vicinity of hard structures (e.g. cables, turbines) due to safety restrictions.

Table 1.1: Advantages and limitations of beam trawl sampling.

Advantages/limitations		References
+	Effective for catching flatfish	Gibson et al. (2015)
+	Standardized method	Gibson et al. (2015)
-	Destructive for habitats and associated fauna	Kaiser et al. (2006)
-	Invasive method: 75% of plaice survives a 20 min tow for at least 14 days	Uhlmann et al. (2016)
-	Bycatch of other species	Catchpole et al. (2008)
-	Not applicable in areas with difficult access or near hard structures	Gibson et al. (2015)

- *Visual diving census*

Visual diving censuses are often applied to estimate densities of reef-associated fish in shallow areas (Edgar et al., 2004). Although they are very time consuming, it is sometimes the only feasible method to determine fish abundances in areas that are difficult to access and where no fishing gear can be deployed due to safety reasons (e.g. scour protection layer around wind turbine foundations) (Reubens et al., 2011a) (Table 1.2). Moreover, it allows for in-situ observations of the organism and its habitat (e.g. on a rock/on the sand/in a crevice), which is especially interesting for bottom-associated fish in an area that is very heterogeneous. If a measuring tape is used while doing the census, the distance of the fish to the hard substrate can be determined, which also tells something about the level of association and thus the importance of the hard substrate for the fish. However, in areas such as the North Sea where currents are very strong, diving is often restricted to narrow time windows and in specific directions. This can cause biases in the results when fish abundances are influenced by tides or currents. Moreover, unless the same diver conducts all of the sampling within a study, an observer bias might exist with some divers being more efficient in observing and identifying fish specimens than others (Dickens et al., 2011). In addition, visual diving censuses are also dependent on the water visibility. Especially in more turbid waters this can seriously hamper the applicability of the method. Finally, diving is restricted by water depth.

Table 1.2: Advantages and limitations of visual diving census sampling.

Advantages/limitations		References
+	Applicable in areas with difficult access (e.g. SPL)	Edgar et al. (2004)
+	Direct observation of the organism and its surrounding habitat	Edgar et al. (2004)
+	Non-invasive (unless extraction is occurring)	Edgar et al. (2004)
-	Observer bias	Dickens et al. (2011)
-	Dependent on water visibility and currents	Edgar et al. (2004)
-	Restricted to shallower areas	Boavida et al. (2016)
-	Time consuming	Boavida et al. (2016)

Objective 2: Studying the trophic ecology of plaice within an OWF

- *Stomach content analysis*

Stomach content analysis (SCA) is one of the most widely used methods for studying fish diet and the trophic interactions between species in general (Hyslop, 1980). It offers a highly detailed taxonomic overview of the ingested food items of a species over a short time frame (<10 h) and is relatively easy to conduct (Table 1.3). Moreover, it is one of the only methods that allow for a direct observation of feeding behaviour and prey selection (Amundsen and Sánchez-Hernández, 2019). SCA has already been applied to study the diet of different fish species in relation to OWFs (Reubens et al., 2011a; Derweduwen et al., 2012, 2016a; Mavraki et al., 2021; Wilber et al., 2022b). However, it does have some limitations compared to other methods. An intrinsic problem with this method is that it overestimates the diet contribution of slowly digested prey taxa, thereby causing a detection bias (Jobling, 1980). Further, it also requires large sample sizes with a high frequency to obtain a space and time-integrated overview of a species' dietary habits (Davis et al., 2012). In addition, SCA offers only a 'snapshot' of ingested food items and does not give any information on their degree of assimilation in the consumer tissues (Parkyn et al., 2001). Finally, fish often have empty stomachs, causing gaps in the data (Nolan and Britton, 2018).

Table 1.3: Advantages and limitations of stomach content analysis.

Advantages/limitations		References
+	High taxonomic resolution	Amundsen and Sánchez-Hernández (2019)
+	No need for specialized lab equipment and/or trained personnel	Amundsen and Sánchez-Hernández (2019)
-	Large sample sizes are needed	Davis et al. (2012)
-	Snapshot of diet at time of sampling	Amundsen and Sánchez-Hernández (2019)
-	Invasive method: need to remove stomach	da Silveira et al. (2020)
-	Contribution of slowly digested prey taxa can be overrated	Amundsen and Sánchez-Hernández (2019)
-	Time consuming and labour intensive	Amundsen and Sánchez-Hernández (2019)

- *Stable isotope analysis*

An alternative method that is used for studying trophic interactions between species is stable isotope analysis (SIA). This method is based on the determination of the ratio of stable isotopes in consumer tissues, from which information about its diet can be deduced (Post, 2002). The two most commonly used isotopes in trophic ecology studies are ^{13}C and ^{15}N. The ratio of nitrogen isotopes (expressed as δ^{15}N) can be used to estimate the trophic position of a species, because its value increases by approximately 3-4‰ with a trophic transfer from prey to consumer. The ratio of carbon isotopes, on the other hand, only changes little (approx. 1‰) when it moves through the food web. Therefore, this ratio can be used to determine the dietary sources of carbon of an organism (Deniro and Epstein, 1981; Peterson and Fry, 1987). Apart from its traditional use in food web studies, SIA has also been increasingly used to trace ontogenetic dietary shifts in fish (Davis et al., 2012). A major advantage of this method, compared to SCA, is that it offers dietary information on a much longer time scale of weeks up to months (Table 1.4). It also requires much smaller samples sizes as the variability in isotopic signatures is lower than for stomach contents. Furthermore, it also reflects how food items are assimilated by the consumer (Post, 2002). Due to the inherent limitations and benefits of both methods, SCA and SIA are often combined to obtain a more complete overview of the feeding ecology of fish species (Parkyn et al., 2001; Nithirojpakdee et al., 2014; Mavraki et al., 2021).

Table 1.4: Advantages and limitations of stable isotope analysis.

Advantages/limitations		References
+	Time-integrated analysis of diet	Post (2002)
+	Limited amount of samples are needed	Jackson et al. (2011)
+	Gives information about what is assimilated, not only on what is ingested	Parkyn et al. (2001)
-	Invasive method: need tissue samples	Post (2002)
-	Low taxonomic resolution	Post (2002)

- *Fatty acid analysis*

During the last decades, fatty acids (FAs) have been increasingly used as trophic markers in aquatic ecology (Dalsgaard et al., 2003). FAs are typically conserved when they are passed from a prey to a consumer, making them interesting to use in dietary studies. As the FA composition of an organism is not only determined by its diet, but also by biotic and environmental factors, it can give information on the physiological condition and habitat type of that organism (Meyer et al., 2019). Compared to stable isotopes, FAs, and especially polyunsaturated FAs, better reflect specific primary producers as they are stored in their original state in the tissues of the consumer (Sargent et al., 1999; Iverson et al., 2004; Plumlee et al., 2021) (Table 1.5). FA analysis thereby offers a much finer resolution of prey items than a bulk isotopic analysis, especially because with SIA it is sometimes difficult to discriminate between primary producers and secondary consumers due to their overlapping isotopic niches. Therefore, both methods are often being used together to study food web structure (Rooker et al., 2006). FA analysis has already been used to study the trophic ecology of fish around artificial reef structures and within OWFs (De Troch et al., 2013; Plumlee et al., 2021).

Table 1.5: Advantages and limitations of fatty acid analysis.

Advantages/limitations		References
+	Time-integrated analysis of diet	Iverson et al. (2004)
+	Gives information about what is assimilated, not only on what is ingested	Dalsgaard et al. (2003)
+	Conservatively built into tissues	Dalsgaard et al. (2003)
+	Limited amount of samples are needed	Dalsgaard et al. (2003)
+	Better reflects specific primary producers than SIA	Sargent et al. (1999)
-	Low taxonomic resolution	da Silveira et al. (2020)
-	Invasive method: need tissue samples	da Silveira et al. (2020)
-	Requires specialized equipment, expensive	da Silveira et al. (2020)

Objective 3: Studying the spatial movements of plaice within and in relation to an OWF

- *Acoustic telemetry using ID-tags*

A complete different approach for gathering information on the behavioural ecology of a species in relation to an artificial reef consists of studying its movements on and around the artificial reef through time (Mitamura et al., 2021). Information on movements allows for the quantification of home ranges and site fidelity, which tells something about the importance of the artificial reef for that particular species (dos Santos et al., 2010). Further, the identification of temporal patterns in spatial movements can help to link species activity to environmental cues (Hunter et al., 2003). A widely used method that can track individual animals in the marine environment is acoustic telemetry. An organism is provided with a small transmitter that emits an acoustic signal with a specified time interval (Thorstad et al., 2013). Such an acoustic signal is logged by an acoustic receiver when the organism moves within its detection range. Each transmitter has a unique ID, which is stored on the receiver together with the date and exact time of the detection. These detections can then be used to calculate different metrics (e.g. presence/absence within a certain time frame) or to determine the fish positions at the time of the detection using triangulation analysis (Espinoza et al., 2011; Baktoft et al., 2017). This method has already been widely applied to study fish movements and behaviour around artificial reef structures and in OWFs (Winter et al., 2010; Reubens et al., 2011b; Bacheler et al., 2019). However, an important limitation when using ID-tags in telemetry studies is that no data is available when the fish moves outside the study area (Goossens et al., 2023). Further, no information is available on where the fish is situated in the water column and the detection probability of the receivers is dependent on various environmental factors such as current speed, background noise and the focus species (Goossens et al., 2022). Lastly, the cost of purchasing tags is high and their attachment to the fish requires invasive surgery techniques, which may have an effect on the behaviour of the animal (Moser et al., 2005).

Table 1.6: Advantages and limitations of acoustic telemetry using ID-tags.

Advantages/limitations		References
+	Data on individual fish movements	Matley et al. (2022)
+	Can be used to track animals over long time periods (> 1 year)	Matley et al. (2022)
-	Invasive method	Moser et al. (2005)
-	Only information on 2D-movements with ID-tags	Espinoza et al., (2011)
-	Detection probability depends on species and environmental conditions	Goossens et al. (2022)
-	No data if fish is present outside study area	Goossens et al. (2023)
-	Tags are costly	Jepsen et al. (2015)

1.6 OVERVIEW OF THE PHD THESIS

The current PhD thesis is subdivided in three large parts. Part 1 includes a general introduction (Chapter 1), in which the most important concepts related to this thesis are explained, together with a long-term baseline study describing the effects of climate variability on the fish assemblages in the Belgian part of the North Sea (Chapter 2). Part 2 consists of three chapters that present the results of field-based studies in two offshore wind farms in the BPNS, related to different ecological effects of offshore wind farms on plaice (Chapter 3, 4 and 5). Part 3 concludes this thesis with an overall discussion in which the findings of this thesis are integrated and put into a wider context (Chapter 6). Apart from chapter 1 and 6, each chapter is written as a stand-alone research article, which is either published, in review or in preparation.

Chapter 2 - Long-term series demonstrate small-scale differences in trends within fish assemblages explained by climate variability

Disentangling the ecological effects of human activities (e.g. offshore wind farms) from each other and from impacts due to climate change requires good knowledge of the natural variability in the ecosystem. Therefore, this chapter describes a study of long-term trends in fish abundances within the BPNS, which were linked to climate-related variables such as climatic oscillations (i.e. AMO and NAO) and sea surface temperature. These relationships can then be used to frame the results from other field studies and to better substantiate certain hypotheses about the combined effects of climate change and offshore wind farms on fish abundances.

Chapter 3 - Offshore wind farms affect the spatial distribution patterns of plaice *Pleuronectes platessa* at both the turbine and wind farm scale

In addressing the attraction-production hypothesis related to offshore wind farms for a certain species, the first question that needs to be answered is whether that species is attracted to the introduced structures (i.e. turbines, cables and scour protection) and to the wind farm area as a whole. To do so, the distribution of plaice was studied on two different spatial scales (the smaller turbine scale and the larger wind farm scale) in two different Belgian offshore wind farms. The results of this study were then used to hypothesize if an artificial reef and/or refuge effect might be present for plaice within the studied wind farms.

Chapter 4 - Increased food availability at offshore wind farms affects trophic ecology of plaice *Pleuronectes platessa*.

To investigate whether an offshore wind farm could enhance plaice production, a study was carried out that thoroughly analysed the trophic ecology of the species within and outside the Belwind wind farm. To do so, the digestive system of four sample groups of fish was dissected and their diet was compared on a short and longer time frame using several methods. Further, various condition indicators were calculated to check if a potential difference in diet or food availability might have affected fish condition.

Chapter 5 - Hard substrates in offshore wind farms influence spatial movements of plaice *Pleuronectes platessa*

To further explore the significance of an offshore wind farm for plaice, their spatial movements related to that wind farm were analysed over the period of a year using acoustic tagging. Information on the small-scale movements around the turbine foundations give more insight in how much time they spend in close association to the hard substrate, while larger scale movements in relation to the wind farm reflects its importance as a feeding ground.

Chapter 6 - Flatfish in offshore wind farms: are there opportunities for fisheries?

This final chapter reviews the results of all the different chapters and discusses the main ecological effects of offshore wind farms on plaice against a background of climate change and variability. The importance of offshore wind farms as artificial reefs and refuge areas is considered, together with their interaction with climate change, and hypotheses are formulated on how these effects might influence flatfish fisheries as a whole. This is followed by a discussion on what is needed to upscale OWF effects on individuals to populations. Finally, recommendations, considerations and ideas for further research are presented based on our findings.

2 LONG-TERM SERIES DEMONSTRATE SMALL-SCALE DIFFERENCES IN TRENDS WITHIN FISH ASSEMBLAGES EXPLAINED BY CLIMATE VARIABILITY

This chapter is a modified version of the paper published as Buyse, J., Hostens, K., Degraer, S., De Backer, A., 2022. Long-term series demonstrate small-scale differences in trends within fish assemblages explained by climate variability. Estuar. Coast. Shelf Sci. 264, 107663.

Abstract

Over 30 years (1985-2018) of environmental monitoring data in the Belgian part of the North Sea allowed us to study common and individual species trends within three spatially distinct demersal and benthopelagic fish assemblages in relation to climate related variability. A combination of multivariate (dynamic factor analysis) and univariate modelling techniques (Trendspotter and Spearman rank correlations) showed that the observed trends in fish densities in two coastal (mud and fine sand) assemblages were best explained by sea surface temperature (SST)-related variables and the Atlantic multidecadal oscillation winter index (AMO_{winter}). Higher fish densities seem to be linked with extreme cold winters in the year before (e.g. 1985, 1996, 2010), while warmer years may be linked to lower fish densities (fine sand assemblage) a few years later. Trends for the more offshore coarse sand fish assemblage were rather related to the North-Atlantic Oscillation index (NAO) (next to AMO_{winter}), coupled to the circulation and inflow of warmer saline waters through the English channel. The temporal decrease in densities in this assemblage may partially reflect climate and subsequent biological regime shifts, as described for the broader North Sea region.

At the species level, both positive, negative and varying trends in densities were noted, dependent on the fish assemblage. Overall, densities of most Lusitanean (warm water) species increased over the last decade, positively correlated with most SST-related variables and $\text{AMO}_{\text{winter}}$-values, indicating a northward expansion of their habitat range, which corroborates the findings of other studies. On the contrary, several Boreal (cold water) species were negatively correlated with SST and $\text{AMO}_{\text{winter}}$, with more or less stable trends in density between 1985 and 2000 followed by a decrease in the last decade, potentially explained by a relocation to deeper waters to cope with increasing seawater temperatures. For plaice *Pleuronectes platessa*, a commercially important species, a linear and significant decrease in length was observed over the 34-year period, most probably related to a combination of climatic influences and fishing induced selection. The current study shows that environmental, climate related drivers are important to explain part of the biological variability, and should be taken into account when investigating the direct impact of human activities on the marine, demersal and benthopelagic ecosystem.

Key words

North Sea, demersal fish, benthopelagic fish, climate variability, DFA (dynamic factor analysis), time-series analysis, trends

2.1 INTRODUCTION

Marine ecosystems have undergone extensive changes in diversity and species composition due to the combined effects of human activities and climate change (Roessig et al., 2004; Dulvy et al., 2008; van Hal et al., 2010; McLean et al., 2018; Pauly and Cheung, 2018). Studying the effects of human activities on marine communities is challenging, because they often act in combination and simultaneously with environmental variability, including climate induced effects. To untangle these different processes, it is important to have a profound understanding of the important environmental drivers and how they affect different species, before focussing on direct effects of human impacts (Cannaby and Hüsrevolu, 2009; Kröncke et al., 2019). To get insight in the ecosystem variability, standardized long-term biological and climatic time series are essential, however, rarely available for larger areas.

Temperature is an important climate-related environmental driver in marine species ecology. Seawater temperature in the North Sea is affected by natural variability together with a warming trend caused by human-induced climate change (Garcia-Soto and Pingree, 2012; Harris et al., 2014). This warming is found to be happening faster in some areas, like the southern North Sea and the English Channel (Garcia-Soto and Pingree, 2012), probably because of the proximity to land masses and the limited depth of the water masses, as such making these areas more vulnerable to the consequences of climate change (Harris et al., 2014). Several studies linked temperature changes in the North Sea to various biological responses. Almost two thirds of the fish species in the North Sea have shifted in latitude or depth over a period of 25 years as a response to increasing temperatures (Perry et al., 2005), while an overall increase in fish species richness has been observed due to a range expansion of small southerly fish species (Hiddink and ter Hofstede, 2008). Tulp et al. (2008) found different trends in density for warm water (Lusitanean) species, with more species showing increased densities compared to cold water (Boreal) species. Moreover, it is suggested that an increase in temperature, and a coupled decrease in oxygen content, will cause a general shrinking of the mean body size within marine fish communities and even of individual species (Cheung et al., 2013). This demonstrates that several marine fish species have a high dispersal ability and phenological plasticity to cope with changes in their environment, depending on the life characteristics of the species and the connectivity between suitable habitats. Species with long reproductive cycles or that depend on patchy reef structures will have a harder time to adjust to a changing environment than fast reproducing organisms that live in homogenous sandy habitats (Menéndez et al., 2006; Hiddink et al., 2016).

Next to the above-mentioned linear warming trend, also climatic modes, such as the North-Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) introduce variability to the environment (Garcia-Soto and Pingree, 2012; Harris et al., 2014; McLean et al., 2018). Although their importance seems to differ at regional scale, a clear correlation with species density for different taxonomic groups has been shown. The NAO climatic index represents the normalized difference in sea pressure level between Iceland and the Azores. Positive index values are associated with milder winters and strong westerly winds, while a negative NAO index is related to tougher and colder winters with weaker winds (Kröncke et al., 1998, 2013). The NAO index could successfully predict the macrobenthic community structure over time in the southern North Sea (Kröncke et al., 1998; Dippner and Kröncke, 2003). The AMO climatic index shows a cyclic pattern in the sea surface temperature (SST) of the North Atlantic with a period of 60 to 80 years (Garcia-Soto and Pingree, 2012). This pattern is thought to be driven by internally induced variations in the Atlantic Meridional Overturning circulation, caused by the coupling of the atmospheric and oceanic systems (Gulev et al., 2013; Dippner et al., 2014). Patterns in pelagic fish densities in the English Channel and the Southern North Sea (McLean et al., 2018), as well as multidecadal spatial patterns in Arcto-Norwegian cod spawning areas could be linked to changes in the AMO index (Sundby and Nakken, 2008), showing its importance as a potential predictor of fish behaviour when studying long-term trends in fish communities.

Temperature anomalies in relation to climate regime shifts (CRS) can cause major reorganizations in the biological community structure, often referred to as biological regime shifts (BRS) (Dippner et al., 2010; Drinkwater et al., 2010; Kröncke et al., 2013). Several BRSs have been identified in the southern North Sea over the last few decades. In 1988-'89, a 'smooth' BRS (characterized by a linear relationship between driver and response variable) was coupled with a negative to positive shift in the NAO index, while an 'abrupt' BRS (i.e. non-linear relationship) was identified in 2000-'01 (Scheffer et al., 2001; Meyer et al., 2016). The latter has been linked to shifts in the benthic macrofaunal community structure and species composition near Norderney, an East Frisian island in German waters (Dippner et al., 2014). Further, Kröncke et al. (2019) suggested that a new BRS took place around 2010, which coincided with a shift in several climatic indices and thus hints at a concurrent CRS.

The current study focuses on the demersal and benthopelagic fish communities of the Belgian part of the North Sea (BPNS) to investigate: (1)

whether environmental and climate-related forces (SST, AMO and NAO) drive fish density at small spatial scales, (2) if shifts in community structure within fish assemblages are related to differences in trends between Lusitanean and Boreal species, (3) if potential BRSs can be identified in fish density time series, and (4) if shifts in length took place for a number of fish species over the studied time period. We used a combination of multivariate and univariate modelling techniques to facilitate the long-term trend analyses (34-year time span), both at the level of fish assemblages and at the individual species level for the most common fish species. Due to its key position as "gateway" to the larger North Sea basin, knowledge on the BPNS study area is particularly interesting, as species displacement related to climatic drivers will be picked up at an early stage in this more southern area, providing a good indication of what can be expected in the more northern areas if temperature continues to rise in the future. The results contribute to our knowledge on the environmental variability and the influence of climatic forces on the local demersal and benthopelagic ecosystem, allowing us to better understand and further discriminate the more direct effects of different human activities.

2.2 MATERIALS AND METHODS

Previous research conducted within the BPNS revealed the existence of different species assemblages for zooplankton, macrobenthos and epibenthos (Van Hoey et al., 2004; Degraer et al., 2008; De Backer et al., 2010; Van Ginderdeuren et al., 2014; Breine et al., 2018). As we expected similar differences in the spatial structure of the demersal and benthopelagic fish assemblages, we first conducted a community structure analysis by means of a clustering approach. Subsequently, we investigated the long-term trends in relation to climate and weather-related indices (e.g. NAO, AMO and SST) within each identified fish assemblage, based on the dominant characteristic species of each cluster group. Finally, individual species trends in density and length were identified within each fish assemblage and linked to relevant climatic variables using a combination of time series analysis and Spearman rank correlation.

2.2.1 STUDY AREA

The Belgian part of the North Sea covers only 0.5% of the entire North Sea basin (3,454 km^2), but it is one of the busiest marine areas in the world: fisheries, shipping, dredging, sand extraction and offshore wind farm development all take place side by side, creating a complex combination of stressors that act on the local environment (Verhalle and Van de Velde, 2020). The presence of natural sand banks parallel to the coastline provide quite unique features in terms of habitat characteristics, creating different opportunities for many organisms, including demersal and benthopelagic fish species (Figure 2.1). Moreover, due to its location at the most southern tip of the North Sea basin, it is an interesting area to investigate the impact of climate related drivers.

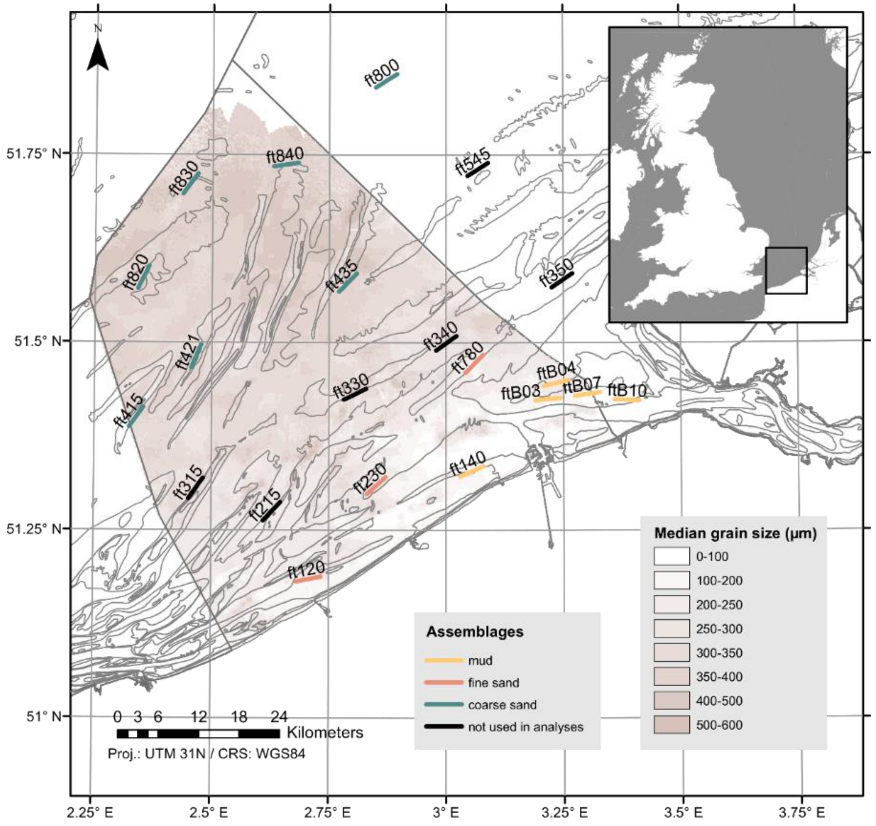

Figure 2.1: Belgian part of the North Sea with indication of the fish sampling locations on top of the median grain size map (Verfaillie et al., 2006). Fish assemblages are based on the community structure cluster analysis. The grid indicates the resolution (0.25 ° x 0.25 °) on which the SST-related variables were calculated. Stations that did not consistently cluster within the same assemblage over the study period were removed from further time series analyses.

2.2.2 FISH DATA

Demersal and benthopelagic fish data are collected as part of yearly sampling surveys in the BPNS in the framework of long-term environmental monitoring, ongoing since 1985. For the current study, data were selected from a number of fixed locations in the Belgian (and small part of the Dutch) EEZ, sampled on an annual basis in autumn (September-December) over the period 1985-2018 (Figure 2.2).

Due to logistic problems, no samples could be taken in 2015 and 2016. Sampling was conducted with an 8-m beam trawl with a cod-end mesh size of 22 mm and a bolder chain in front of the ground rope, targeting mainly smaller fish and younger year classes. Sampling time, start and stop coordinates and sampling depth were logged to enable a correct standardisation towards sampled surface units (1000 m^2). Till 2009, the net was towed for a total of 30 minutes at an average speed of 4 knots over the ground along with the current; from 2010 onwards, tow duration was reduced to 15 minutes. A comparative field study revealed no difference in catch composition for the different tow durations (Derweduwen et al., 2010). All fish were identified to species level, counted and measured. Pelagic species, such as sprat (*Sprattus sprattus*) and Atlantic mackerel (*Scomber scombrus*), were excluded from further analyses, as they were not sampled quantitatively with the used gear (Froese R. and Pauly, 2022). Some fish species that were difficult to correctly identify to species level on board due to morphological similarities, were lumped at a higher taxonomic level (e.g. sand goby and Lozano's goby were lumped into goby species *Pomatoschistus* spp.). All species were grouped according to their biogeographic affinities into Boreal (preferring cold water) species and Lusitanean (preferring warm water) species, following the classification by Wheeler (1969) and Yang (1982).

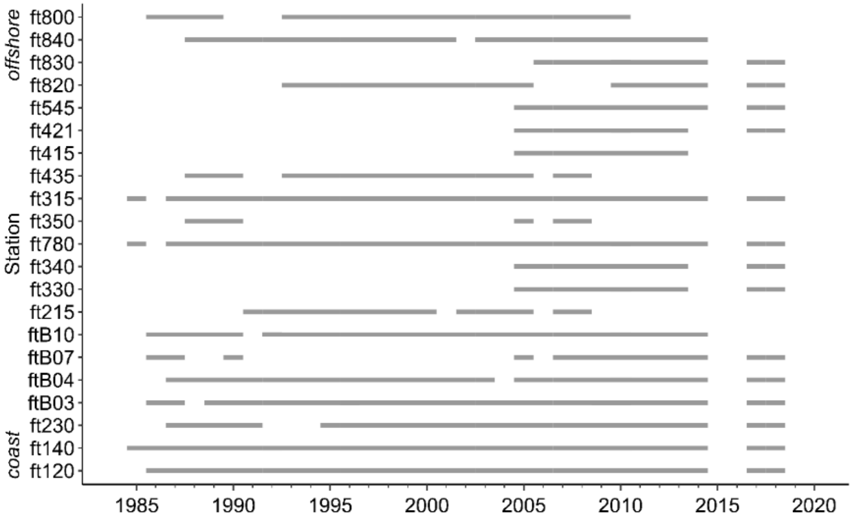

Figure 2.2: Overview of the sampled locations per year in the period 1985-2018.

2.2.3 ENVIRONMENTAL VARIABLES

SST data were obtained from monthly L4 satellite data through the EU Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu/). SST data were averaged per year over 0.25 ° x 0.25 ° grid cells and assigned to the sampling locations falling within those grid cells (Figure 2.1). SST_{winter} for each year per grid cell was calculated as the mean SST value from December till March. Additionally, lagged SST values of one to three years were used in the analyses to account for potential delayed biological responses.

The AMO index derived from the detrended Kaplan SST dataset was downloaded from the NOAA Earth System Research Laboratory's Physical Sciences Division website (https://www.esrl.noaa.gov/psd/data/timeseries/AMO/). NAO index values were downloaded from the NOAA Climate Prediction Centre website (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). Yearly averages were calculated from the monthly data. Winter index values for both indices were again calculated as the mean index value from December until March (see Annex 2.1).

We also included daily discharge values from the Scheldt estuary in the analyses as a weather-related variable. These data were obtained through the Flemish Hydrological Information Centre (www.waterinfo.be), mean values for each year were calculated.

Pairwise and multi-collinearity of the environmental variables was tested through correlation coefficients (>0.70) and variance inflation factors (VIF, >3.0), respectively. High collinearity was found for SST_{winter} and SST ($r = 0.77$) and for AMO_{winter} and AMO ($r = 0.80$). We decided to only include SST and AMO_{winter} for further analyses, the latter because initial data exploration revealed slightly higher correlations (compared to AMO) with different species densities. All data operations were carried out in R, version 3.6.1 (R Core Team, 2019).

2.2.4 COMMUNITY STRUCTURE ANALYSIS

A community structure analysis was carried out to determine spatial fish assemblages in the study area, after which the temporal variability within these assemblages was studied using more specific time series-related techniques. Density values (ind. 1000 m^{-2}) per sampling location were calculated for each fish species and averaged over three 10-year time periods (1985-1995, 1996-2006, and 2007-2018). Time bins were used to incorporate the variability in community structure over time, so that sampling locations better represented stable assemblages and not local changes in habitat. A hierarchical cluster analysis together with a SIMPROF test was carried out based on the Bray-Curtis similarity index calculated after a square root transformation of the data. The significance level was set more stringent to 1% given the multiple testing inherent to this hierarchical approach, as suggested in Clarke et al. (2008). Only locations that consistently clustered within the same cluster from the moment they were first sampled were included in further analyses. A SIMPER analysis with a cut-off level of 90% was performed to identify the species that contributed most to the within-group similarity of the identified clusters. Both analyses were performed using the PRIMER-E v6.1.13 software (Clarke and Gorley, 2006).

2.2.5 COMMON TRENDS PER FISH ASSEMBLAGE

Dynamic factor analysis (DFA) was used to study common trends in fish densities for each assemblage determined by the community analysis, using only the species identified by the SIMPER analysis (90% cut-off level). DFA is a dimension-reducing technique based on structural time series analysis to estimate common trends and effects of explanatory variables together with their possible interactions for multiple time series (Harvey, 1990; Zuur et al., 2003, 2007; Erzini et al., 2005). Mean species density values were calculated for each year for each cluster group or fish species assemblage and log-transformed to stabilise the variance in the data. Furthermore, environmental variables were linked to each fish assemblages by averaging their values over all 0.25 ° x 0.25 ° grid cells in which sampling locations were located belonging to that fish assemblage/cluster group. All environmental variables and species densities were further standardised by subtracting the mean and dividing by the standard deviation, so that a similar scale was obtained, to ease the interpretation.

Time series of fish species density were then modelled as linear combinations of an intercept, one to three common trends, one or two explanatory variables and noise. All models were fitted with a diagonal and a symmetric error covariance matrix, where the latter allows for two-way interactions between time series. Best models were selected using the Akaike information criterion (AIC), with preference given to the simpler model, together with a stepwise approach to identify the best set of explanatory variables. Factor loadings with a threshold of 0.2 were used as a measure for the relative importance of a common trend for a specific fish species and to identify groups of species that are related to a common trend (Zuur et al., 2003; Erzini et al., 2005). Effects of environmental variables were evaluated based on t-values resulting from the regression of these environmental variables and individual species densities, where an absolute threshold value of 3 indicates an important relationship (Zuur et al., 2003; Erzini et al., 2005). The analyses were conducted using the Brodgar software, version 2.7.5 (http://www.brodgar.com/, Highland Statistics).

2.2.6 INDIVIDUAL SPECIES TRENDS

While common trends give an idea about general temporal trends in fish communities, single species time series analysis enables to identify significant increases or decreases for each individual species.

Temporal trends in individual species densities were identified for each assemblage through structural time series analyses together with a Kalman filter using the TrendSpotter-software (Harvey, 1990; Visser, 2014). Smoothed density values and their associated standard deviations were estimated for each time series with N equidistant measurements over time. TrendSpotter also allows to estimate the standard deviation values for differences between two smoothed density values of consecutive time points (Soldaat et al., 2007; Tulp et al., 2008). After adding a constant value of 0.01 to the species densities (corresponding to the lowest density value), a log10-transformation was applied to reduce the data variation. To avoid nonsense fits, trends were only fitted for common species identified by the SIMPER analysis.

To explore if trends in individual species could be linked to certain environmental variables, Spearman rank-order correlation tests were conducted for each combination of fish species and environmental variable per assemblage identified by the cluster analysis. This method was chosen over a parametric alternative as non-normality was determined in some of the time series. The correlation coefficients were calculated using the log10(x+0.01) transformed density data to stabilize the variation.

Finally, trends over time in fish length were analysed for the most important commercial species for which sufficient data was available, i.e. sole *Solea solea*, dab *Limanda limanda*, plaice *Pleuronectes platessa*, whiting *Merlangius merlangus*, and pouting *Trisopterus luscus*. The yearly 0.8 quantile of fish length, based on length-frequency data, was calculated for each commercial species per fish assemblage (cluster group). Quantile values are preferred over mean length as a response variable, as they are less sensitive to outliers or skewed distributions due to the presence of overlapping age classes. If a trend over time for the 0.8 quantile values was observed by visual inspection, a linear model containing year, cluster group and their interaction factor was fitted, followed by a type-III ANOVA to test for statistical significance. If the interaction was found significant, secondary linear models were fitted for each cluster group to test the significance of the slope. In case the interaction was not significant, it was excluded from the model. A thorough model validation was carried out by visual inspection of the residuals. The analyses and validation were executed in R, version 3.6.1 (R Core Team, 2022).

2.3 RESULTS

2.3.1 COMMUNITY STRUCTURE ANALYSIS

Although hierarchical cluster analysis discriminated eight significant clusters at the 70% similarity level (Figure 2.3), only three clusters contained sampling locations that were consistently put together within the same cluster over the different time periods. The spatial distribution of the three clusters clearly showed similarities with the macrobenthic communities identified in Breine et al. (2018), which were coupled to habitat (sediment) type, and as such used to define the fish assemblages.

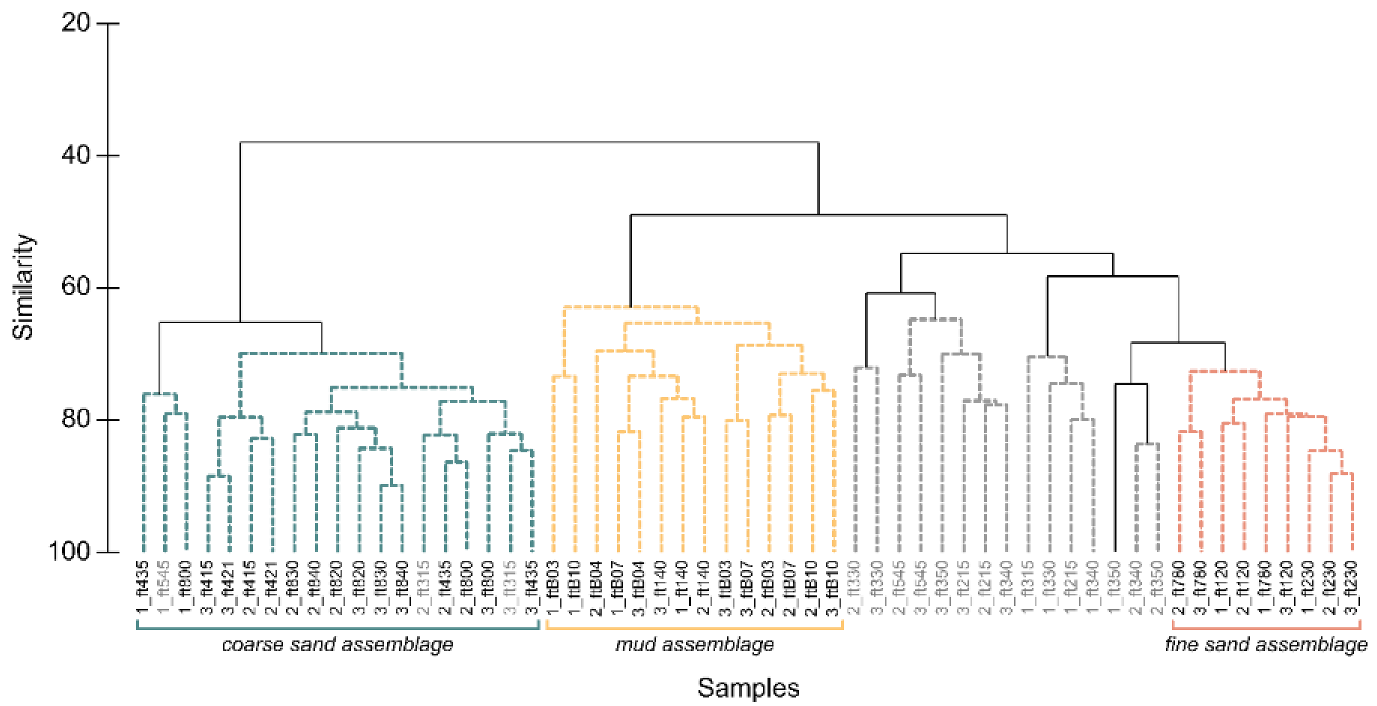

Figure 2.3: Group-average hierarchical cluster analysis dendrogram. SIMPROF significant clusters are depicted with dotted lines, and the three consistent clusters over time are indicated. The numbers (1-3) in front of the station names refer to the time bins.

The ‘mud’ assemblage (avg. similarity = 67%) consists of five locations close to the Scheldt estuary in the eastern part of the study area and is mainly characterized by goby species, sole and plaice (together 55% of within-group similarity). The ‘fine sand’ assemblage (avg. similarity = 77%) includes three coastal locations parallel to the coastline with dab, goby species and hooknose *Agonus cataphractus* as its most typical species (46% within-group similarity). Finally, the ‘coarse sand’ assemblage (avg. similarity = 73%) contains seven deeper, more offshore locations (Figure 2.1) and was mainly determined by lesser weever *Echiichthys vipera*, dragonet species *Callionymus* spp. and dab (50% of the within-group similarity). These locations and clusters were withheld for further analyses, data from five other locations were discarded.

Table 2.1: Characterization of the three demersal fish assemblages (cluster groups) identified by the hierarchical cluster analysis, showing the average within-group similarity, and the species contributing cumulatively to 90% of the within-group similarity and their average densities (ind. 1000 m^{-2}) within each assemblage.

Mud assemblage (avg. similarity = 67%)			Fine sand assemblage (avg. similarity = 77%)			Coarse sand assemblage (avg. similarity = 73%)		
Species	%	avg. density	Species	%	avg. density	Species	%	avg. density
Pomatoschistus spp.	33.46	23.14	*Limanda limanda*	18.81	23.91	*Echiichthys vipera*	31.21	16.00
Solea solea	11.47	4.04	*Pomatoschistus* spp.	16.25	26.52	*Callionymus* spp.	10.77	1.69
Pleuronectes platessa	9.92	3.88	*Agonus cataphractus*	11.37	11.36	*Limanda limanda*	8.07	0.90
Merlangius merlangus	8.40	1.56	*Callionymus* spp.	10.42	9.86	*Pomatoschistus* spp.	7.56	1.00
Agonus cataphractus	7.53	1.85	*Merlangius merlangus*	9.76	7.29	*Pleuronectes platessa*	6.41	0.67
Limanda limanda	6.50	1.64	*Solea solea*	8.12	5.95	*Mullus surmuletus*	6.32	0.62
Trisopterus luscus	6.16	1.42	*Pleuronectes platessa*	7.57	4.88	*Buglossidium luteum*	4.81	0.58
Liparis liparis	4.92	0.92	*Trisopterus luscus*	7.32	4.12	*Arnoglossus laterna*	4.31	0.26
Triglidae spp.	2.61	0.20	*Buglossidium luteum*	1.55	0.41	*Hyperoplus lanceolatus*	4.05	0.22
						Ammodytes tobianus	4.04	0.22
						Merlangius merlangus	4.02	0.30

2.3.2 COMMON TREND ANALYSIS

The best DFA model for the mud assemblage contained one common trend and was fitted with a diagonal covariance matrix (Figure 2.4). The lowest AIC-value of 786 was obtained by combining SST and AMO$_{winter}$ index values in the model (Table 2.2). The common trend showed an increasing course over time with peaks in 1992 and 2013, and a seemingly decreasing course in the last five years.

Figure 2.4: DFA trends based on the final model with ribbons showing 95% confidence intervals for the period 1985-2018 (middle), their associated factor loadings for each species identified by SIMPER analysis (right), and the explaining environmental variables fitted with a LOESS smoother (left), for the mud assemblage (A), the fine sand assemblage (B), and the coarse sand assemblage (C) (full line = trend 1, dashed line = trend 2).

Factor loadings indicated that gurnard species *Triglidae* spp. and sea snail *Liparis liparis* were positively correlated with this trend (0.23 and 0.28, respectively), while pouting showed a negative correlation (-0.29). Based on the t-values of the environmental variables, hooknose, whiting and sea snail showed a strong negative relationship with SST, while sole densities, next to plaice and pouting, were positively correlated with AMO_{winter} index values (see Annex 2.2).

The final DFA model (AIC = 779) for the fine sand assemblage was obtained by using SST and SST with a lag of 3 years in a one-trend model that was fitted using a diagonal covariance matrix (Figure 2.4, Table 2.2). This model is characterized by an erratic common trend over time, with troughs in 1985, 1993, 2006 and 2010 and peaks in 2003 and 2008, although a general decreasing trend may be noticed between 2004 and 2018. All species included in the analysis showed a positive correlation with the identified trend, with highest values for hooknose, dab and dragonet species. High negative t-values for SST were found for hooknose and sole, positive t-values for dragonet species. and whiting, while only a small, though significant, negative correlation was found with SST_{lag3} for sole.

The best model for the coarse sand assemblage contained two common trends and was fitted with a symmetric covariance matrix. The addition of NAO index and AMO_{winter} index values to the model resulted in the lowest AIC value of 873. The first trend for the coarse sand assemblage showed a relatively stable course over time with a smaller peak around 1999 and a larger peak around 2007, after which the trend steadily decreased to the lowest value in 2018. The second trend showed a linear increase between 1985 and 2018. For the first DFA trend, relatively high factor loadings were noted for dragonet species. (0.40), greater sandeel[1] *Hyperoplus lanceolatus* (0.38), solenette *Buglossidium luteum* and dab. Although no clear correlation was

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[1] Sandeels (*Ammodytes* and *Hyperoplus* species) are not representatively sampled with a beam trawl, because these species tend to bury themselves deep into the sand. This behaviour can cause a bias in the results, especially with absolute numbers and if variation exists in catchability over time. However, as sampling occurred only at daylight hours and each year during the same season and using the same setup, variation in catchability is probably limited. Therefore, the results reported for the sandeels should only be considered within the context of this study and not be compared with other studies.

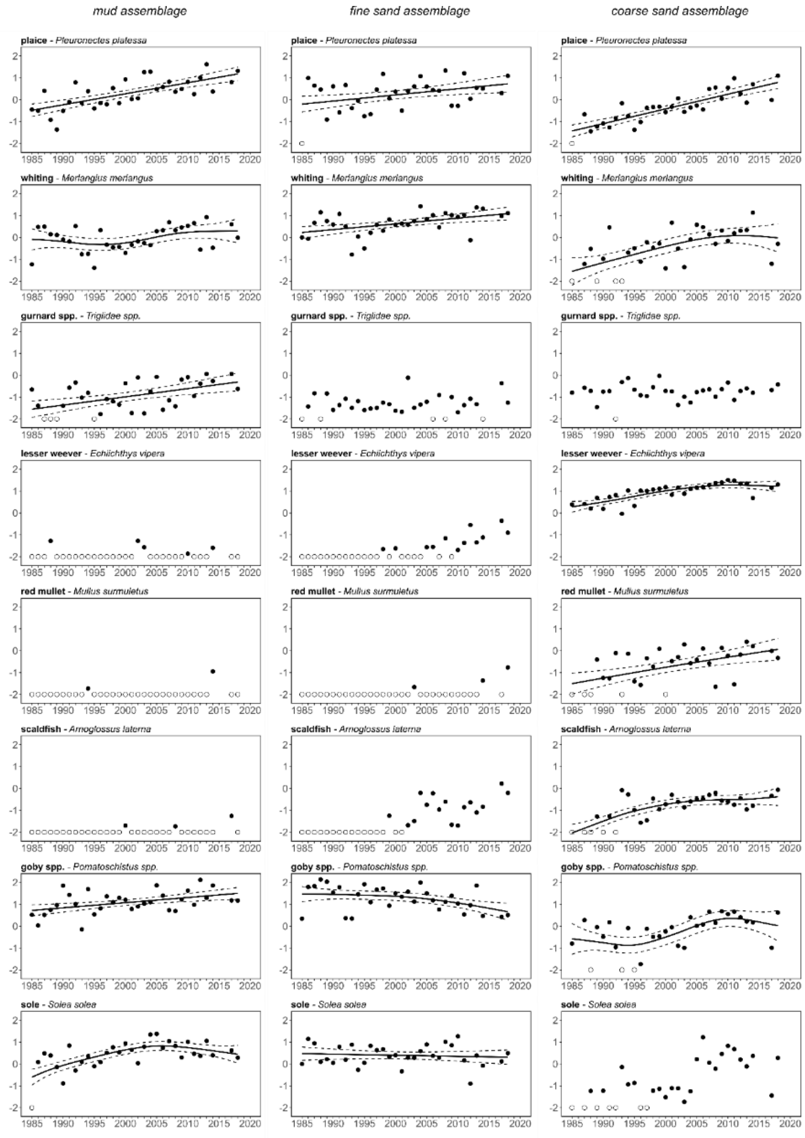
identified for any species with the second trend (all factor loadings <0.2), a positive factor loading was found for all but two species. High positive t-values for AMO_{winter} were recorded for solenette and lesser weever; while greater sandeel, lesser sandeel *Ammodytes tobianus* and solenette showed a positive relationship with NAO index values.

Table 2.2: Akaike information criterion (AIC) values for the fitted DFA models using one to three common trends (CT), and the five best models using a combination of the common trends (1-3) with one or two explanatory environmental variables. “Diagonal” and “symmetric” refer to the covariance matrix used in the model. The final model that was selected for each assemblage (lowest AIC) is shown in bold.

Model	Common trends	Explanatory variables	Diagonal	Symmetric
Mud assemblage				
CTs + noise	1	-	822	843
	2	-	808	841
	3	-	822	854
CTs + expl. variables + noise	2	SST	789	
	1	SST + $\text{AMO}_{\text{winter}}$	**786**	
	2	SST + $\text{AMO}_{\text{winter}}$	791	
	2	SST + NAO	794	
	2	SST + $\text{NAO}_{\text{winter}}$	793	
Fine sand assemblage				
CT + noise	1	-	830	830
	2	-	820	838
	3	-	831	847
CT + expl. variables + noise	1	SST + SST_{lag2}	788	
	1	SST + SST_{lag3}	**779**	
	1	SST + SST_{lag3}		786
	1	SST + $\text{NAO}_{\text{winter}}$	788	
	2	SST + SST_{lag3}	779	
Coarse sand assemblage				
CTs + noise	1	-	900	886
	2	-	883	882
	3	-	879	897
CTs + expl. variables + noise	1	$\text{AMO}_{\text{winter}}$		878
	2	SST_{lag3}	877	
	3	NAO	876	
	2	SST_{lag3} + NAO	878	
	2	$\text{AMO}_{\text{winter}}$ + SST		878
	2	$\text{AMO}_{\text{winter}}$ + NAO		**873**

2.3.3 INDIVIDUAL SPECIES TRENDS

The identified density trends showed quite a lot of variation, with some species showing a similar increasing trend in all three assemblages (e.g. plaice, whiting and to a lesser extent gurnard species), whereas others (e.g. goby species and sea snail) displayed different patterns in the different assemblages (Figure 2.5). Lusitanean species, like lesser weever, red mullet *Mullus surmuletus* and scaldfish *Arnoglossus laterna*, equally showed an increasing trend, but mainly in the more offshore coarse (and fine sand) assemblage. Some species (including the five boreal species) showed a rather stable (e.g. greater sandeel in the coarse sand assemblage) or slightly increasing trend (e.g. sole in the mud assemblage) between 1985 and 2005, often followed by a decrease during the last decade, such as hooknose and pouting in the mud and fine sand assemblages, and lesser sandeel, dab, solenette and dragonet species in the coarse sand assemblage.


mud assemblage
fine sand assemblage
coarse sand assemblage
plaice - Pleuronectes platessa
whiting - Merlangius merlangus
gurnard spp. - Triglidae spp.
lesser weever - Echiichthys vipera
red mullet - Mullus surmuletus
scaldfish - Arnoglossus laterna
goby spp. - Pomatoschistus spp.
sole - Solea solea
2
1
0
-1
-2
1985
1990
1995
2000
2005
2010
2015
2020

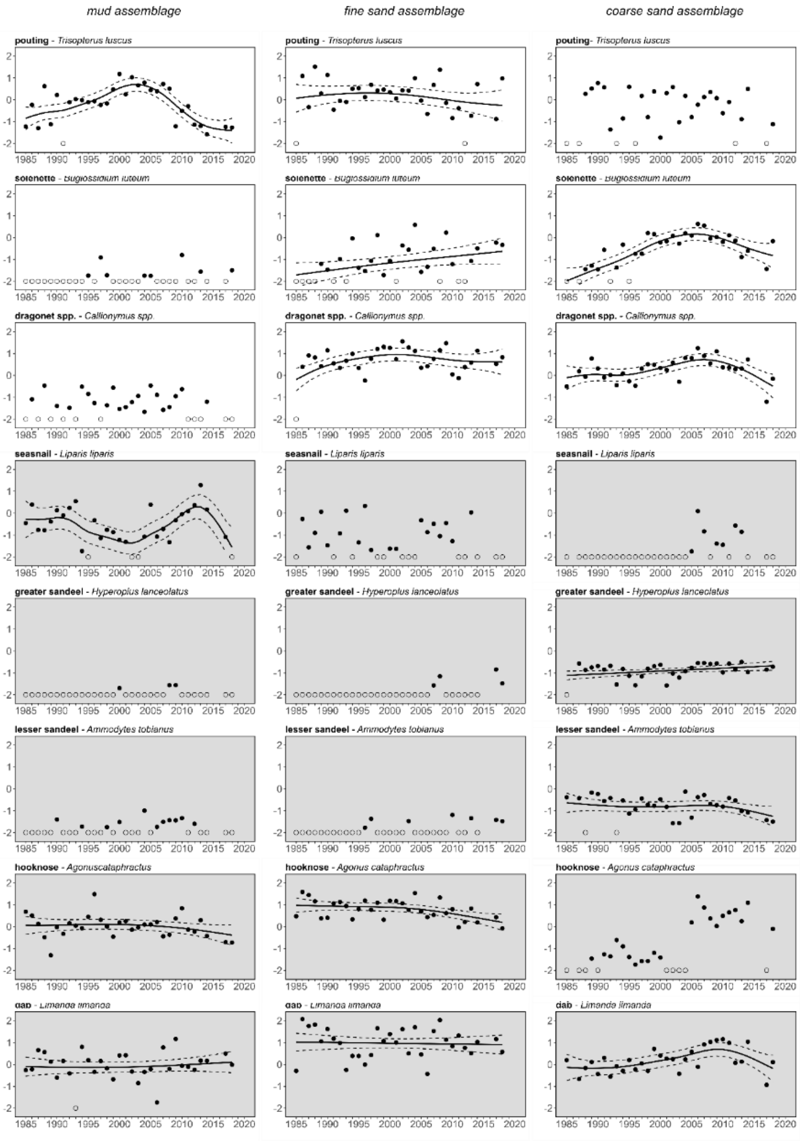


Figure 2.5: Time series of the sixteen averaged species densities over the period 1985-2018 for the three fish assemblages. A TrendSpotter-model was only fitted when a species was identified as important for a certain assemblage by the SIMPER-analysis. Vertical axes represent (log10+1)-transformed and standardized fish densities with open dots representing zero values. Dashed lines show 95% confidence intervals for the modelled density values, which are represented by a solid line. Boreal species are indicated with a light grey background, Lusitanian species with a white background.

Spearman rank correlation tests revealed various significant relationships between fish species and environmental variables (Table 2.3). On the one hand, positive correlations were noted with all or most SST-related variables and AMO_{winter}-index values for some species in all three assemblages (e.g. plaice and whiting), and for other species in only one or two assemblages (e.g. gurnard species in the mud assemblage; sole in the mud and fine sand assemblages; solenette and dragonet species in the fine and coarse sand assemblages; scaldfish, lesser weever, greater sandeel and red mullet in the coarse sand assemblage). On the other hand, a clear negative relationship with SST, AMO and both NAO-related variables was found for a number of species dependent on the assemblage (e.g. sea snail in the mud assemblage; hooknose in the mud and fine sand assemblages; lesser sandeel (not with NAO) in the coarse sand assemblage). Some species trends even showed opposite correlations with variables in different assemblages (e.g. goby species positively correlated with SST and AMO_{winter} in the mud and coarse sand assemblages, but negatively correlated in the fine sand assemblage[2]; positive correlations for pouting in the mud assemblage, negative in the fine sand assemblage; negative correlations for dab with SST time lag variables in the mud and fine sand assemblages, but positive in the coarse sand assemblage).

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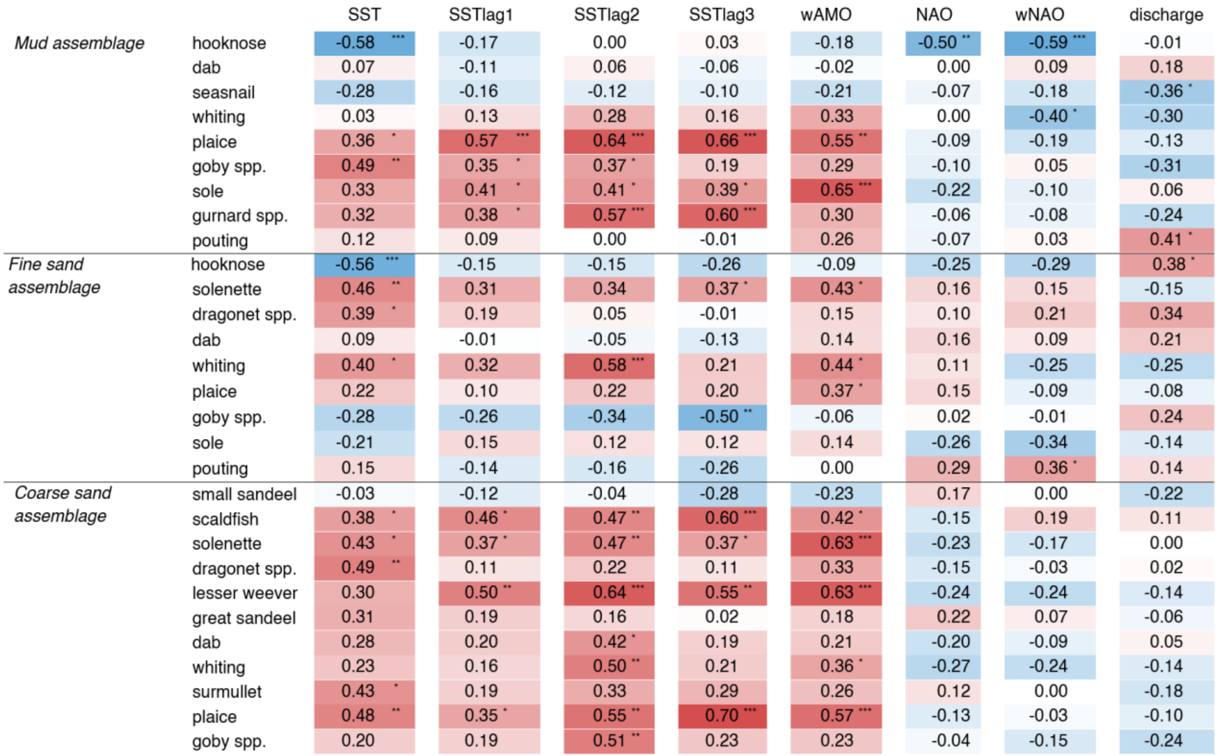
[2] Goby species (*Pomatoschistus* spp.) is likely a mix of *Pomatoschistus minutus* and *Pomatoschistus lozanoi*, which could explain the observed difference in trends.

Table 2.3: Spearman rank correlation coefficients between species, identified by SIMPER analysis for the three fish assemblages, and the used environmental variables. Significance: * = $p<0.1$, ** = $p<0.01$, *** = $p<0.001$.



		SST	SSTlag1	SSTlag2	SSTlag3	wAMO	NAO	wNAO	discharge
Mud assemblage	hooknose	-0.58 ***	-0.17	0.00	0.03	-0.18	-0.50 **	-0.59 ***	-0.01
	dab	0.07	-0.11	0.06	-0.06	-0.02	0.00	0.09	0.18
	seasnail	-0.28	-0.16	-0.12	-0.10	-0.21	-0.07	-0.18	-0.36 *
	whiting	0.03	0.13	0.28	0.16	0.33	0.00	-0.40 *	-0.30
	plaice	0.36 *	0.57 ***	0.64 ***	0.66 ***	0.55 **	-0.09	-0.19	-0.13
	goby spp.	0.49 **	0.35 *	0.37 *	0.19	0.29	-0.10	0.05	-0.31
	sole	0.33	0.41 *	0.41 *	0.39 *	0.65 ***	-0.22	-0.10	0.06
	gurnard spp.	0.32	0.38 *	0.57 ***	0.60 ***	0.30	-0.06	-0.08	-0.24
	pouting	0.12	0.09	0.00	-0.01	0.26	-0.07	0.03	0.41 *
Fine sand assemblage	hooknose	-0.56 ***	-0.15	-0.15	-0.26	-0.09	-0.25	-0.29	0.38 *
	solenette	0.46 **	0.31	0.34	0.37 *	0.43 *	0.16	0.15	-0.15
	dragonet spp.	0.39 *	0.19	0.05	-0.01	0.15	0.10	0.21	0.34
	dab	0.09	-0.01	-0.05	-0.13	0.14	0.16	0.09	0.21
	whiting	0.40 *	0.32	0.58 ***	0.21	0.44 *	0.11	-0.25	-0.25
	plaice	0.22	0.10	0.22	0.20	0.37 *	0.15	-0.09	-0.08
	goby spp.	-0.28	-0.26	-0.34	-0.50 **	-0.06	0.02	-0.01	0.24
	sole	-0.21	0.15	0.12	0.12	0.14	-0.26	-0.34	-0.14
	pouting	0.15	-0.14	-0.16	-0.26	0.00	0.29	0.36 *	0.14
Coarse sand assemblage	small sandeel	-0.03	-0.12	-0.04	-0.28	-0.23	0.17	0.00	-0.22
	scaldfish	0.38 *	0.46 *	0.47 **	0.60 ***	0.42 *	-0.15	0.19	0.11
	solenette	0.43 *	0.37 *	0.47 **	0.37 *	0.63 ***	-0.23	-0.17	0.00
	dragonet spp.	0.49 **	0.11	0.22	0.11	0.33	-0.15	-0.03	0.02
	lesser weever	0.30	0.50 **	0.64 ***	0.55 **	0.63 ***	-0.24	-0.24	-0.14
	great sandeel	0.31	0.19	0.16	0.02	0.18	0.22	0.07	-0.06
	dab	0.28	0.20	0.42 *	0.19	0.21	-0.20	-0.09	0.05
	whiting	0.23	0.16	0.50 **	0.21	0.36 *	-0.27	-0.24	-0.14
	surmullet	0.43 *	0.19	0.33	0.29	0.26	0.12	0.00	-0.18
	plaice	0.48 **	0.35 *	0.55 **	0.70 ***	0.57 ***	-0.13	-0.03	-0.10
	goby spp.	0.20	0.19	0.51 **	0.23	0.23	-0.04	-0.15	-0.24

2.3.4 TRENDS IN PLAICE LENGTH

Only for plaice, a visual inspection of the 0.8 quantile values for length revealed a decline over time in two of the three assemblages, with the largest decrease found for the coarse assemblage (Figure 2.6). The first linear model followed by an ANOVA test (type III), showed a significant interaction between *assemblage* and *year* ($p = 0.02$). Secondary linear models, with only *year* as explanatory variable, were fitted to test the significance for each assemblage. For the coarse sand assemblage, a highly significant ($p<0.001$) linear decrease of 0.36 cm per year in the 0.8 length quantile of plaice (20% largest individuals) was observed between 1985 and 2018. Also, for the fine sand assemblage the decrease in plaice length was significant ($p<0.05$) with a slope of -0.21 cm, while length remained more or less stable (slight decrease) over the years for the mud assemblage ($p = 0.64$).

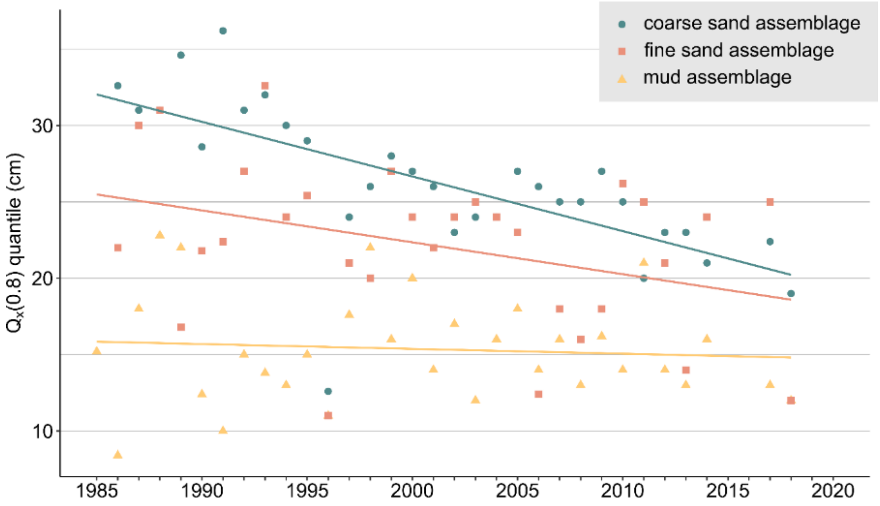


Figure 2.6: Regression lines of the fitted linear models for plaice *Pleuronectes platessa* showing the yearly 0.8 length quantile values over the period 1985-2018 for the three fish assemblages.

2.4 DISCUSSION

Trends in fish densities and length were analysed based on a long-term time series of beam trawl catch data in the BPNS. A clear spatial structure in fish communities was detected and common trends, as well as species trends, within the identified assemblages were studied using a combination of multivariate (dynamic factor analysis) and univariate methods (time series analysis and Spearman rank correlation). Observed trends in fish density, correlated with different environmental indices, showed high variability among species and assemblages and may be linked to biological regime shifts. Differences in patterns were also detected between Lusitanean and Boreal species, indicating influences of climate change in the study area. Finally, a decrease in length of plaice was obvious in two of the three assemblages, which might be linked to a combination of climate change and fishing-induced selection.

2.4.1 THREE SPATIALLY STRUCTURED DEMERSAL AND BENTHOPELAGIC FISH ASSEMBLAGES

Several studies already showed a clear spatial distribution in macrobenthos with four, and more recently, five macrobenthic communities delineated in the BPNS linked to habitat/sediment type (Degraer et al., 2003, 2008; Van Hoey et al., 2004; Breine et al., 2018). The three fish assemblages clearly overlap with these macrobenthos habitats, which might be explained by the fact that macrobenthos is an important food source for the early life stages of demersal and benthopelagic fish species in this shallow coastal area (Rijnsdorp and Vingerhoed, 2001; Heindler et al., 2019). Moreover, this overlap indicates that both biological groups seem to be structured by similar environmental variables. For the transitional locations that were not further used in the time trend analyses, most probably a combination of the trends found in the fine and coarse sand assemblages will be relevant.

2.4.2 TEMPERATURE, AMO$_{\text{WINTER}}$ AND NAO AS IMPORTANT DRIVERS FOR THE DEMERSAL AND BENTHOPELAGIC FISH ECOSYSTEM

Clear differences were noted for both common trends at fish assemblage level and trends at individual fish species level per assemblage, but in all cases temperature (SST) and AMO_{winter} or NAO climate indices were included by the models as important explanatory variables. The other weather related variable, river discharge from the Scheldt estuary, was never retained in any of the models. Most probably, this variable only influences the system on a smaller spatial and temporal scale than the scales investigated in this study, which proves the importance of real temperature-related forces.

The fact that SST and the other climate-related indices play an important role in explaining common trends in fish density corroborates the findings of several other studies (Dulvy et al., 2008; Kröncke et al., 2019). Variation in SST is a combination of various environmental drivers, such as temporal fluctuations (extremely warm summers and cold winters or *vice versa*), a linear warming trend and long-term climatic oscillations, all acting simultaneously on the marine environment (Cannaby and Hüsrevolu, 2009; Harris et al., 2014). The latter study showed that the linear warming trend contributes most to the variability in water temperature for the entire North Atlantic (which includes the southern North Sea), while Cannaby and Hüsrevolu (2009) found a clear correlation with AMO and patterns in the East Atlantic (EA) and NAO climatic modes. As such, SST can also be seen as a real, overall climate index, as it encompasses both natural and human-induced variability.

2.4.3 COMMON TRENDS AT FISH ASSEMBLAGE LEVEL

Observed trends in both coastal assemblages were best explained by SST-related variables (in the fine sand assemblage) or a combination of SST and AMO_{winter} (for the mud assemblage). This suggests that, in contrast to the third more offshore coarse sand assemblage, the trends at demersal fish assemblage level in the shallow coastal area are more sensitive to year-to-year fluctuations in temperature and other weather or temperature-related variables. In contrast to long-term climatic variation, these short-term fluctuations can have a bigger influence on species densities through a direct effect on recruitment (Brunel and Boucher, 2007; Sundby and Nakken, 2008). This is supported by the erratic common DFA-trend model for the coastal fine sand assemblage, where the troughs (lower values) coincide with higher SST-values three years earlier (e.g. 1993 trough ≈ 1990 high SST, 2010 trough ≈ 2007 SST, etc.). Indeed, these years were characterized by the highest yearly averaged temperatures recorded in Belgium (https://klimaat.be/in-belgie/klimaat-en-uitstoot/waarmeningen). This means that warmer years may be linked to lower overall fish densities two or three years later, at least for the fine sand fish assemblage. Additionally, the link with SST itself shows that extreme cold winters (e.g. 1985, 1996, 2010) lead to higher fish density values in the subsequent years in both mud and fine sand assemblages.

Trends for the more offshore coarse sand fish assemblage are mainly related to the climate indices NAO and AMO_{winter}. This indicates that this offshore assemblage is more influenced by the circulation of Atlantic water along the European continent. This water circulation is known to have a major influence on the water properties of the North Sea, including seawater temperature (Leterme et al., 2008). The latter study showed that a minor inflow of warm and saline water, influenced by the prevailing wind regimes in the region, enters the offshore region of the BPNS through the English Channel. Wind regimes themselves are associated with the phases of the NAO index, which could explain the correlation between the fish densities and the NAO index in the offshore coarse sand assemblage. Kröncke et al. (2019), who conducted a DFA analysis on epibenthic time series in the German Bight of the North Sea, also found the best model to include SST and North Sea Environmental index, a multivariate predictor similar to NAO.

For the coarse sand assemblage, a model with two trends was selected as best model. Although model selection based on AIC-values is a widely accepted method, caution is needed when interpreting the results. In the mud and fine sand assemblages, all top five models contained the variable SST, suggesting this variable plays an important role in explaining fish density trends in these assemblages. For the offshore assemblage, the variables were less consistent over the different models, which complicates the indication of the most important variables. Burnham and Anderson (2004) suggest that if the absolute difference between the model with the lowest AIC-value and any other model is >2, that model should be selected. Most of the peaks (1994, 1999, 2007) and troughs (1987, 1996, 2004, 2010) in the first trend of fish densities for the coarse sand assemblage correspond with similar peaks and troughs in the NAO index. However, this relation seems to be lost since the major trough in 2010 followed by a subsequent increasing trend in NAO, whereas the fish density trend keeps declining. Several studies have described climate and biological regime shifts (CRS, BRS) in 1988-'89 and 2000-'01 (Beaugrand et al., 2009; Kröncke et al., 2013; Meyer et al., 2016), which partly overlap with the decreasing periods in the first fish density trend we recorded for the coarse sand assemblage. Moreover, Kröncke et al. (2019) suggested that a new BRS took place around 2010, based on the common trends from five different marine sites in the Northern hemisphere. The minimum value for the NAO index in 2010 and the continuous decrease in fish density trend may equally indicate the existence of a CRS and a coupled BRS.

2.4.4 TRENDS IN INDIVIDUAL SPECIES DENSITIES AND LENGTH WITHIN THE FISH ASSEMBLAGES

Some species like dab, plaice, whiting and goby species. are common over the entire study area, while other species prefer more coastal (e.g. sole, hooknose, pouting) or offshore waters (e.g. lesser weever and greater sandeel). Overall, several species showed different patterns in different fish assemblages, which supports the choice for studying the different assemblages independently. Several species, such as dab, solenette, dragonet species and goby species all showed a decreasing trend in density after 2006-'07 in the coarse sand assemblage, largely driven by changes in NAO. In the shallower coastal area, the influence of NAO is smaller and the densities of these species remained stable.

Small, Lusitanean species with a southern habitat range such as lesser weever, red mullet, solenette and scaldfish, showed considerable density increases, mainly in the coarse sand assemblage, during the last decade(s). This increase showed a significant positive relationship with SST suggesting a northward expansion of their habitat, corroborating the findings of (van Hal et al., 2010). Additionally, there is a clear correlation with AMO_{winter} for these species. The trend for this index equally increased till 2003 after which it more or less stabilized, which is also noted for the trend in fish densities.

Opposite to the above-described trend for small Lusitanian species, three Boreal species (sea snail (mud assemblage), hooknose (mud and fine sand assemblage), and lesser sandeel (coarse sand assemblage)) are negatively correlated with SST and AMO_{winter}. For the latter two fish species, we see a declining trend after 2000 (the trend for sea snail is more difficult to explain). Also, other studies found changes in the fish community structure with an increasing number of Lusitanean species and a decreasing number of Boreal species over time (Rijnsdorp and Van Leeuwen, 1996; Ter Hofstede and Rijnsdorp, 2011). A decline in hooknose and sea snail densities over time was also observed by Tulp et al. (2008) in different coastal areas in the Netherlands. The decrease in densities for these boreal species may be linked to the BRS in 2000, which was described by several studies (Swanson and Tsonis, 2009; Kröncke et al., 2013; Beaugrand et al., 2014; Meyer et al., 2016). However, while hooknose densities in the mud and fine sand assemblage decreased, the opposite pattern is distinguished in the coarse assemblage. A possible explanation for this could be that, even on such a local scale, this species has relocated towards deeper waters as a reaction to rising water temperatures. Such deepening, or redistribution in general, is found to be a common coping strategy of species in relation to climate change (Dulvy et al., 2008). The fact that several Lusitanean species are able to expand their habitat range northward due to the raising seawater temperature, while the upper thermal limit seems to be reached for only few Boreal species, may lead to an overall increase in fish species richness within temperate areas, as was noted by Hiddink et al. (2008).

For plaice we showed a steady increase in density over time, while for sole the pattern differed per fish assemblage, although an overall stable or increasing trend (limited decrease in the mud assemblage in last decade) may be seen as well. Plaice and sole are commercially important flatfish species. There are no long-term fisheries data at such a high resolution spanning the entire study period, but at the North Sea level a steady decrease in fishing pressure is recorded since 1997 for both species (ICES, 2020; Vansteenbrugge et al., 2020). Since we mainly focused on the smaller length classes (1-3 years) in this study, the decreased fishing pressure in the past decades may have resulted in more juveniles in the nursery areas. Still, a clear correlation was found between SST/AMO_{winter} and fish densities for both species, proving the strength of the models and the importance of temperature-related variables as explaining factors. Moreover, although SST_{lag3} was only withheld in the overall model for the fine sand assemblage, significant correlations with the SST-lagged variables were noted for plaice, gurnard and whiting. Most probably this time lag is also relevant for the other assemblages (but due to the higher AIC, as such, not selected), meaning that at least for some (commercially important) species a cold winter will often be followed by strong cohorts in the subsequent years.

Over the 34-year time span, the overall length of plaice clearly decreased in the fine and coarse sand assemblages (and to a limited extend in the mud assemblage), a trend that had already been observed in the North Sea (Grift et al., 2003; van Walraven et al., 2010). Possible explanations for the observed length decrease are: (1) fisheries-induced selection towards fish that mature at a smaller size (Grift et al., 2003); (2) climate change-driven faster maturation at earlier ages (Bromley, 2000; Grift et al., 2003); (3) climate change-driven shift in distribution of larger individuals towards deeper waters (van Keeken et al., 2007) and (4) climate change-driven selection towards smaller fish due to physical constraints (Pauly and Cheung, 2018). Most probably, the decrease in length we observed for plaice is best explained by a combination of fisheries-induced variability and the influence of climatic change. A steadily increasing trend in plaice density was recorded in all assemblages since the beginning of the study period, clearly correlating with SST-related variables. As such, there seems to be an overall selection towards more, but smaller, individuals. Whether they reach maturity at an earlier age or smaller length, as suggested by Baudron et al. (2014), is out of scope of the current study.

2.4.5 CONCLUDING REMARKS

This study shows that long-term datasets are necessary to understand how environmental and climate-related forces drive demersal and benthopelagic fish densities and length. Trends in fish densities in the coastal mud and fine sand assemblages in the Belgian part of the North Sea seem to be mainly driven by temperature, whereas AMO_{winter} and NAO as larger climate modes explained most variation in fish densities in the offshore coarse sand assemblage. This indicates that the two coastal assemblages are more sensitive to climate change than the more offshore assemblage, as SST also encompasses a linear warming trend. As such, it can be expected that observed trends related to temperature will further continue or even strengthen (Harris et al., 2014; IPCC Panel, 2014). On the other hand, AMO is a natural oscillating climate index with a period of 60-80 years, currently approaching a warming phase peak (Garcia-Soto and Pingree, 2012; Trenberth et al., 2019). Therefore, a cooling AMO phase could slow down or even reverse the current observed trends in density.

We observed a climate change-driven increase of Lusitanean species densities (northern habitat expansion), as has been shown by other studies in the wider North Sea area. The decreasing trend in length of plaice coupled to a steadily increasing trend in density is most probably an effect of both climate change and fisheries-induced selection. For some Boreal species, a negative correlation was found between fish density and SST/AMO_{winter}. A movement towards deeper water might be suggested for at least one species. The current study shows that environmental and climate-related drivers are important to explain part of the biological variability and should be taken into account when investigating the direct impact of human activities on the marine environment.

2.5 ACKNOWLEDGEMENTS

The first author acknowledges funding for a doctoral fellowship through the WinMon.BE programme, outlining long-term trends in fish assemblages as a baseline for offshore wind farm assessments. This study is based on data gathered (and funded) within the framework of environmental monitoring for sand extraction, dredge disposal and offshore wind farms. The authors want to thank the crew of the RV Belgica (and RBINS-ODNature and Belspo for providing ship time) and RV Simon Stevin (VLIZ) for their commitment during the sampling campaigns, the many colleagues of ILVO who collected and processed the samples over this large time period, and especially Bart Ampe for his well-constructed statistical advice.

PART 2

ECOLOGICAL EFFECTS OF OFFSHORE WIND FARMS ON PLAICE

3 OFFSHORE WIND FARMS AFFECT THE SPATIAL DISTRIBUTION PATTERNS OF PLAICE *PLEURONECTES PLATESSA* AT BOTH THE TURBINE AND WIND FARM SCALE

This chapter is a modified version of the paper published as Buyse, J., Hostens, K., Degraer, S., De Backer, A. (2022) Offshore wind farms affect the spatial distribution patterns of plaice *Pleuronectes platessa* at both the turbine and wind farm scale. ICES Journal of Marine Science.

Abstract

We investigated how the distribution of plaice *Pleuronectes platessa*, a typical soft-sediment fish species, has been affected by the introduction of hard substrate (turbine foundations and scour protection layer (SPL) at both turbine and wind farm scales in two Belgian offshore wind farms (OWFs). Diving transects (40 m) at 11 monopiles revealed four times higher plaice abundances on the sandy patches in the SPL (average radius 16.5 m) compared to the surrounding sand. We suggest that the configuration of the SPL, i.e. an open rock field, offering increased food and shelter opportunities, with sandy patches in between, facilitating the natural burrowing behaviour of plaice, forms the basis for the increased plaice abundances at the turbine scale. At the wind farm scale, beam trawl catches in-between the turbines and reference zones revealed significantly increased plaice abundances for one OWF, which suggests that wind farms can act as refuge areas for plaice, at least under specific conditions. Differences in environmental conditions, turbine foundation type and surrounding fishing pressure, explain the equivocal findings between both OWFs, whereas low statistical power could have hampered the detection of general refuge effects. Next to the integration of different spatial scales (turbine/wind farm) within one study, longer-term monitoring, and extra life history parameters (e.g. length, sex ratio) may enhance the detectability of potential refuge effects.

Key words

artificial reef, North Sea, fisheries exclusion, plaice, BACI, scour protection layer

3.1 INTRODUCTION

Offshore wind farms (OWFs) are proliferating to meet the increasing demands for renewable energy. The introduction of artificial structures (turbine foundations, scour protection and cables) in soft-sediment areas can influence species distribution patterns directly through attraction to or avoidance of these structures (the so-called artificial reef effect), and indirectly through the fisheries exclusion effect (Bohnsack and Sutherland, 1985; Lindeboom et al., 2015; Stenberg et al., 2015; Gill et al., 2020; Mooney et al., 2020; van Berkel et al., 2020).

Hard structures related to OWFs are rapidly colonized by fouling communities, which in their turn attract various fish species and epibenthic organisms that profit from the increased forage and shelter opportunities (Leonhard and Pedersen, 2006; Wilhelmsson et al., 2006; Degraer et al., 2020). Higher densities of benthopelagic fish and large invertebrates have been observed around hard substrates in different European wind farms, e.g. cod *Gadus morhua* (Reubens et al., 2013a), edible crab *Cancer pagurus* and European lobster *Homarus gammarus* (Krone et al., 2017).

In most European wind farms, vessel movements are restricted due to safety considerations, except for maintenance and scientific research purposes. As a consequence, no fisheries activities are allowed within OWFs, making them essentially no-take zones, which creates opportunities for fish and crustacean species that experience high fishing pressure (Ashley et al., 2014; Coates et al., 2016). Studies regarding marine protected areas (MPAs) have shown that fisheries exclusion can affect fish distribution patterns through increased local fish densities and spill-over effects in adjacent areas (Guidetti et al., 2014). Spatial food web models calculated that up to seven percent higher catches were to be expected near a wind farm in the extended Bay of Seine (Halouani et al., 2020), while a spillover effect for plaice was demonstrated in the field for some Belgian wind farms (De Backer et al., 2019).

So far, most studies on the effects of OWFs on fish have concentrated on hard substrate-associated fish species (Reubens et al., 2013a; Krone et al., 2017). The consequences for soft-sediment associated species such as flatfish are less studied (Vandendriessche et al., 2015). Since flatfish spend the majority of their life in close contact with the seabed, their spatial distribution response to the introduction of artificial hard substrates might differ from that of (bentho)pelagic fish species (Wilber et al., 2018). A number of studies found no attraction of flatfish towards the scour protection layer (SPL) (Krone et al., 2017; van Hal et al., 2017) and no clear positive nor negative effects at the wind farm level (Lindeboom et al., 2011; Stenberg et al., 2015; Wilber et al., 2018). However, these studies might have missed the real effect, as refuge effects are often only observed after a prolonged period (>5 years) (Babcock et al., 2010; De Backer et al., 2020).

Within the Belgian part of the North Sea (BPNS), a weak attraction of plaice was found in the C-Power wind farm with higher densities at a distance of approx. 200 m from the turbines compared to the control areas (De Backer et al., 2020). Additionally, Derweduwen et al. (2016) showed that the diet of dab *Limanda limanda* in the same wind farm clearly differed from the control areas. Furthermore, numerous plaice individuals were observed between the rocks of the SPLs by divers in the Belgian Belwind wind farm (Jan Reubens, personal communication). These findings suggest that attraction of soft-sediment associated fish species might occur at both the wind farm scale, and the much smaller turbine scale.

In this study, we investigated the spatial distribution patterns of plaice *Pleuronectes platessa*, a commercially important flatfish species, in two Belgian offshore wind farms at two spatial scales i.e. the turbine and wind farm scale. We hypothesised that plaice is attracted at both spatial scales by the presence of hard substrate in the form of turbine foundations and their surrounding SPL, and due to the exclusion of fisheries.

3.2 MATERIALS AND METHODS

3.2.1 STUDY AREA

In 2004, a 238 km^2 zone was designated for the production of renewable energy in the eastern part of the BPNS along the Dutch EEZ-border, and nine OWF concessions (in total 2.26 GW) have been granted (Maes et al., 2005; Rumes and Brabant, 2020) (Figure 3.1). Our study focused on the oldest OWF concessions, namely C-Power and Belwind. Construction of C-Power on the Thorntonbank started in 2007 at a distance of 27–30 km from the shore at water depths of 14-28 m. The pilot phase finished by the end of 2008 and consisted of six turbines on gravity-based foundations (GBFs, 5 MW Senvion). These were surrounded by an SPL consisting of a filter layer of pebble with an armour layer of rocks on top (width: 44-58 m, median rock size = 0.35 m) to prevent erosion of the sand due to changed current patterns (Sumer and Fredsøe, 2001; Rumes et al., 2013). The second and third phases of C-Power were carried out between 2010 and 2013, with 46 turbines (6 MW Senvion) being installed on jacket foundations without surrounding scour protection, as currents can pass freely through the foundation structures (Rumes et al., 2013). Fishing activities were suspended around the 6 GBFs (+500 m safety zone) in February of 2008, while the rest of the concession zone was closed off in January of 2011 (Table 3.1). The construction of the Belwind OWF started in September 2009 (fisheries exclusion from June 2009) and this OWF has been operational since 2010. Belwind is located on the Bligh Bank (46-52 km off the coast, 15-37m water depth) and exists of 56 monopile turbines (55 Vestas (3 MW); 1 Haliade (6 MW, 2013)), all surrounded by a SPL with a radius of approx. 16.5 m from the monopile. The SPL in the Belwind wind farm exists of a filter layer of smaller rocks with an armoured layer of larger rocks on top (median rock size = 0.37 m, solid rock density = 2.65 ton/m^3). In most locations (especially further from the turbines), sandy patches are present in between the rocks of the armoured layer due to sedimentation and the relatively low density of rocks.

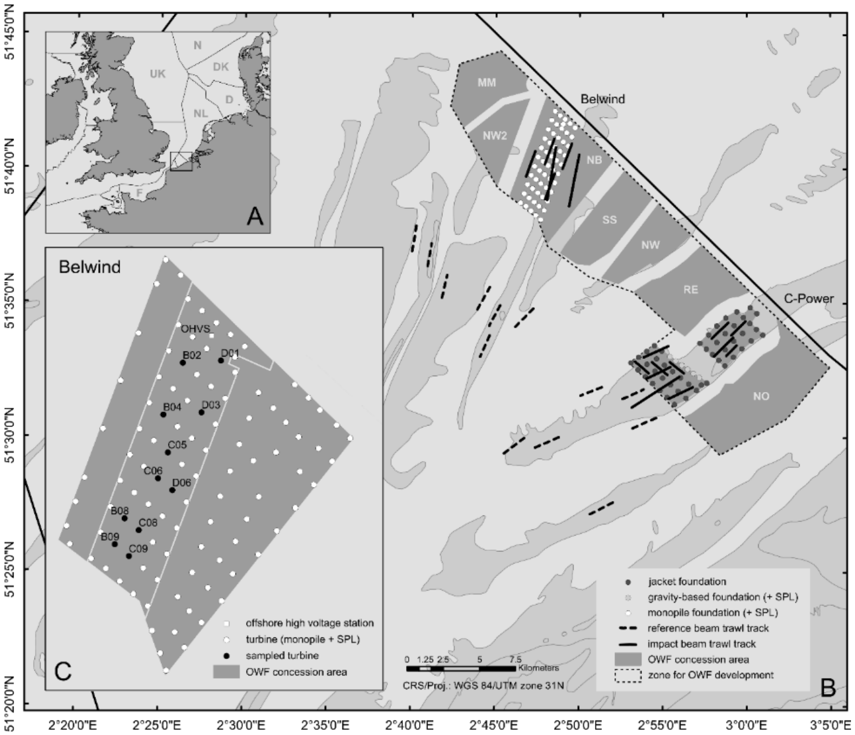


Figure 3.1: A) Map indicating the location of the Belgian part of the North Sea (BPNS). B) Sampling design used at the wind farm scale, showing the beam trawl tracks in the impact and reference sites for C-Power and Belwind; the other OWF concessions are also shown (NO: Norther (2019), RE: Rentel (2018), NW: Northwind (2014), SS: Seastar (2020), NB: Nobelwind (2017), NW2: Northwester 2 (2020), MM: Mermaid (2020)). C) Map of Belwind OWF highlighting the turbines where the diving transects were conducted to investigate the turbine scale patterns.

Table 3.1: Overview of construction start and fisheries closure at the different Belgian concession areas. The area closed for fishing corresponds with the concession area (500 m of safety buffer around the turbines) for each wind farm, except for the first phase of C-Power. Corridors between two closed areas are also closed for shipping and fisheries activities.

Wind farm	Start of sustained fisheries closure	Comments	Start construction	First power generated
C-Power phase 1	02/08	6 GBFs (+500 m safety buffer)	05/08	01/09
Belwind	06/09		09/09	01/11
C-Power phase 2 & 3	01/11	Both zone A and B	04/11	09/13
Northwind (NW)	01/13		04/13	05/14
Nobelwind (NB)	02/16	South and north of Belwind	05/16	12/17
Rentel (RE)	04/17		07/17	01/19
Norther (NO)	05/18		08/18	05/19
Northwester 2 (NW2)	04/19		07/19	05/20
Seamade (MM + SS)	06/19	Seastar + Mermaid concession areas	09/19	11/20

3.2.2 FIELD SAMPLING AND DATA AVAILABILITY

3.2.2.1 Turbine-scale distribution patterns

To study whether plaice is attracted to the scour protection surrounding the wind turbine foundations, 21 visual diving transects (each 40 m length) crossing the SPL and the surrounding open sand were conducted in the Belwind concession zone (Figure 3.2) (see Annex 3.1 and 3.2). This wind farm was chosen due to the higher visibility and water transparency, and the presence of an SPL around all turbine foundations. Moreover, in contrast to

C-Power, Belwind consists entirely of monopiles, which is the most commonly used foundation type in European OWFs (WindEurope, 2022).

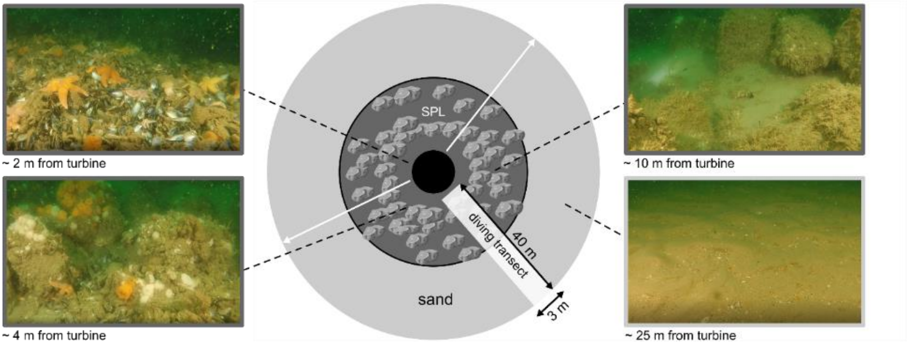


Figure 3.2: Schematic representation of the diving transects around the wind turbines in the Belwind OWF. The middle black circle represents the monopile; the dark grey circle represents the scour protection layer (SPL, approx. 16.5 m radius starting from the monopile) consisting of a visible armoured rock layer with sand in between the rocks. The number and density of rocks is higher close to the turbines and gradually decreases towards the sandy area (light grey circle without rocks) directly surrounding the SPL. In the first meter right next to the turbines almost no rocks are present as well. White arrows indicate potential transect lines conducted by the divers during one dive. The white rectangle shows a schematic representation of a diving transect of 40 by 3 m. Pictures (©Film Johan Devolder) show the typical habitat at the indicated locations.

Between June and August 2019, the presence of plaice was surveyed by divers around 11 randomly chosen turbines, each completely surrounded by other turbines to avoid fringe effects (Figure 3.1C). Depending on the prevailing conditions, such as visibility and current speed, 1-3 transects in different directions from the turbine could be covered within each dive (3 transects: turbine D1 and C6; 2 transects: turbines B2, B4, C8, C9, D3 and D6; 1 transect: turbines B8, B9 and C5). Two divers descended along the turbine foundation, secured a measuring tape at the bottom of the monopile and started swimming in a straight line away from the turbine. A fixed distance of 40 m was covered during each transect to standardise the data, covering both the SPL (a combination of the rock armour layer and sandy patches in between the rocks) and the open sand directly surrounding the SPL (Figure 3.2). One diver visually scanned the area for plaice at both sides of the measuring tape (covering approx. 3 m width), while the other diver filmed the transect with a GoPro camera. When a plaice individual was visually identified, the habitat (SPL or surrounding open sand) and its distance to the turbine were noted on a waterproof writing board. Water temperature, visibility and transect direction[3] were also logged for each transect. The end of the SPL (and thus the distinction between the two habitat types) was defined as the point where no rocks were present anymore over a distance of approximately 2 m on the transect. The searched area per habitat type was calculated for each transect as:

Searched area SPL = length of the SPL * width of the transect (±3 m)

Searched area surrounding open sand = (total length of transect – length of SPL) * width of the transect (±3 m)

Both the total searched area and the total number of plaice were then calculated per turbine by taking the sum of the searched area and the number of observed plaice per habitat type over all the transects.

3.2.2.2 Wind farm-scale distribution patterns

To investigate the wind farm-scale distribution patterns of plaice, beam trawl sampling was performed in autumn during the yearly environmental monitoring campaigns of the WinMon.BE-programme. Data from similar BACI-designs were used for the period 2004-2019 for C-Power and 2008-2019 for Belwind (Table 3.2). Beam trawl samples were taken in September-November within the concession areas and at reference locations with comparable environmental conditions both before and after the installation of the turbines (Figure 3.1). For a complete overview of the 'before'-construction sampling design, the reader is referred to Vandendriessche et al. (2015). Although the six turbines with GBFs in C-Power were already operational in 2009, for this study we considered all data up till 2010 as 'before

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[3] The results on the effects of direction, as well as on the distribution of other flatfish species, were reported in Buyse et al. (2021). Because the direction was not sampled in a standardized way and due to the low number of samples for each direction, it was decided not to report those results within the thesis.

construction' since the beam trawl tracks were located further away from these six turbines and were as such not considered to be (or at least little) affected by the first construction phase. For Belwind, the construction phase ended in February 2010, i.e. after our sampling survey of 2009. Over the entire study period, the sampling design was adapted in relation to wind farm accessibility (e.g. restricted access during construction), weather conditions and research vessel availability (e.g. no samples in 2015 due to the unavailability of RV Belgica). Sampling was conducted with an 8-m beam trawl equipped with a shrimp net (22 mm in the cod end) and a bolder-chain. Till 2009, the net was towed at an average speed of 4 knots during 30 minutes over approximately 2 NM, after which this was reduced to 15 minutes over approximately 1 NM, due to the limitations of the OWF design. Comparative studies in the BPNS and Australia did not find any significant effects of beam trawl tow duration on catch rates of individual species, which suggests that standardised results are comparable over the years (Rotherham et al., 2008; Derweduwen et al., 2010). Once on board, catches were sorted and processed and all fish individuals were identified, measured and counted at species level. For this study, we only used the data on plaice abundances for further analyses.

Table 3.2: Number of impact/reference beam trawl samples taken for each offshore wind farm over the entire study period. The horizontal dashed lines indicate the before/after construction period for each wind farm.

Year	C-Power		Belwind	
	impact	reference	impact	reference
2004	2	3	-	-
2005	4	4	-	-
2006	1	1	-	-
2007	1	1	-	-
2008	4	4	3	6
2009	3	4	2	5
2010	4	4	-	7
2011	-	1	4	6
2012	6	4	4	6
2013	4	4	4	6
2014	2	4	2	2
2015	-	-	-	-
2016	4	4	2	3
2017	4	4	3	6
2018	4	4	4	7
2019	4	4	4	7
Total	47	50	32	61

3.2.3 STATISTICAL ANALYSES

To check whether there was a turbine-scale effect due to the presence of an SPL on plaice abundance, a general linear mixed model (GLMM) with a Poisson distribution was fitted, with the number of plaice individuals as the response variable and *habitat type* (SPL/sand) as a fixed effect. Turbine was included in the model as a random effect to take into account the nested nature of the design. A log-transformed offset variable based on the searched area per habitat type was added to correct for the variation in sampling effort. The final fitted model was:

Number of plaice ~ offset(log(*area searched*)) + f(*habitat type*) + (1|f(*turbine*))

Further, mean densities of plaice over all the transects were also calculated for each 4-m segment of the standardized 40-m transect to describe distribution patterns of plaice in function of distance.

The potential wind farm-effect on plaice abundance was investigated using a GLMM with a negative binomial distribution. This distribution was chosen over a Poisson distribution to deal with the overdispersion of the data. A three-way interaction between a time factor *BA* (before/after construction), an impact level factor *RI* (reference/impacted area) and a wind farm factor *WF* (C-Power/Belwind) was added as the fixed part of the model. A significant interaction between *BA* and *RI* represents a wind farm effect (positive or negative), while a significant three-way interaction indicates that the potential wind farm effect is expressed differently for both wind farms. Two random effects *year* and *station* were included in the model to incorporate the nested nature of the sampling design at both temporal and spatial scales. A factor *top/gully* was added as random effect as well, as previous studies within this study area showed an influence of sampling location on or next to a sandbank on fish abundances (Derweduwen et al., 2010; Vandendriessche et al., 2015). To correct for the differences in sampling effort, the trawled distance was added as a log-transformed offset. The full fitted model was:

Number of plaice ~ offset(log(*distance trawled*)) + f(*BA*)*f(*RI*)*f(*WF*) + (1|f(*top/gully*)) + (1|f(*station*)) + (1|f(*year*))

An interaction analysis was conducted based on the pairwise comparisons of the estimated marginal means to test for a wind farm effect for both wind farms separately.

For both models, a thorough model validation based on visual plots of Pearson-residuals was carried out to check if all assumptions for linear regression were met. All data exploration, modelling and validation was carried out in R version 4.0.3 (R Core team, 2020).

3.3 RESULTS

3.3.1 TURBINE-SCALE DISTRIBUTION PATTERNS

A total of 31 plaice individuals were observed along the transects, of which 23 were spotted within the SPL-habitat (total searched area = 1,028 m^2), while only eight were found on the open sand surrounding the SPL (total searched area = 1,436 m^2). The GLMM showed a highly significant effect for *habitat type* (p = 0.0009, Z = -3.32), whereby four times more individuals were found on the sand between the rocks of the SPL (2.08±0.55 ind. 100 m^{-2}, 95% CI (1.24-3.49) compared to the surrounding open sand (0.53±0.20 ind. 100 m^{-2}, 95% CI (0.25-1.11) (Figure 3.3 A). Plaice abundances were high right next to the turbine foundation, much lower a few meters further away, increasing again with distance from the turbine up to the edge of the SPL, after which abundances significantly decreased. The observed numbers of plaice on the surrounding open sand, at distances between 24 and 40 m from the turbine, were much lower (Figure 3.3 B).

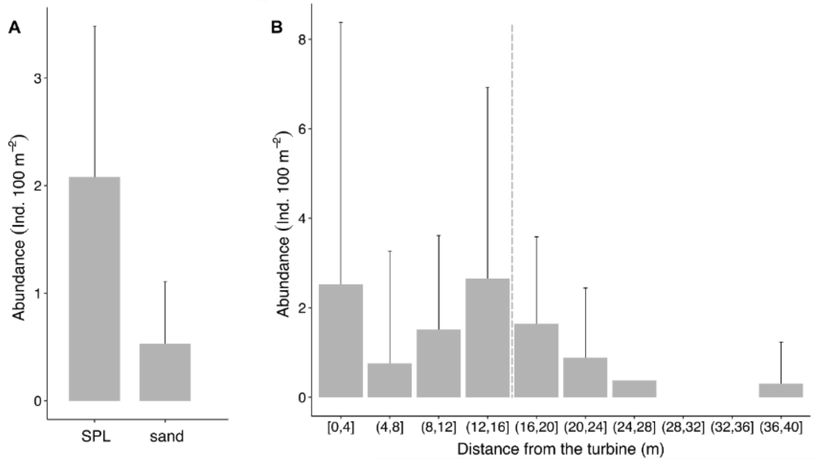

Figure 3.3: Plaice distribution in the Belwind OWF at turbine-scale A) Least-squares means for the final generalized linear mixed model showing the number of plaice per 100 m2 for both habitat types (SPL = scour protection layer). B) Plot showing the mean plaice abundances across all diving transects in relation to distance intervals starting from the turbine foundation; the vertical dashed line indicates the average width of the scour protection layer. Error bars show standard deviation values.

3.3.2 WIND FARM-SCALE DISTRIBUTION PATTERNS

A total of 5,186 plaice individuals were caught over 190 trawls ($\bar{x}$ = 0.18± 0.16 ind. 100 m^{-2}), covering a total trawled area of 3.37 km^2. The GLMM model showed a significant three-way interaction (*BA*RI*WF*, p = 0.002, Z = -3.06), mainly explained by a significant difference in wind farm effect (BA*RI) between both OWFs. For Belwind, no OWF effect was observed (BA*RI, p = 0.25, Z = 1.16), with plaice abundances showing relatively similar patterns for reference and impact areas both before and after construction (Figure 3.4). For C-Power on the other hand, a significant wind farm effect (BA*RI, p = 0.0008, Z = -3.35) was observed with 4.5 times higher plaice abundances in impacted samples (0.27±0.09 ind. 100 m^{-2}, 95% CI (0.13-0.53)) after the construction compared to before the construction (0.06±0.02 ind. 100 m^{-2}, 95% CI (0.03-0.12)), while no difference in plaice abundance before and after construction was observed for reference samples (p = 0.13, Z = -1.53). Additionally, there was a significant difference in plaice abundances between reference and impact samples after construction (p = 0.03, Z = 2.22), while this was not the case in samples before construction (p = 0.05, Z = -1.93). Actually, this effect reflects a decrease in abundances in reference samples, which was not recorded in impact samples.

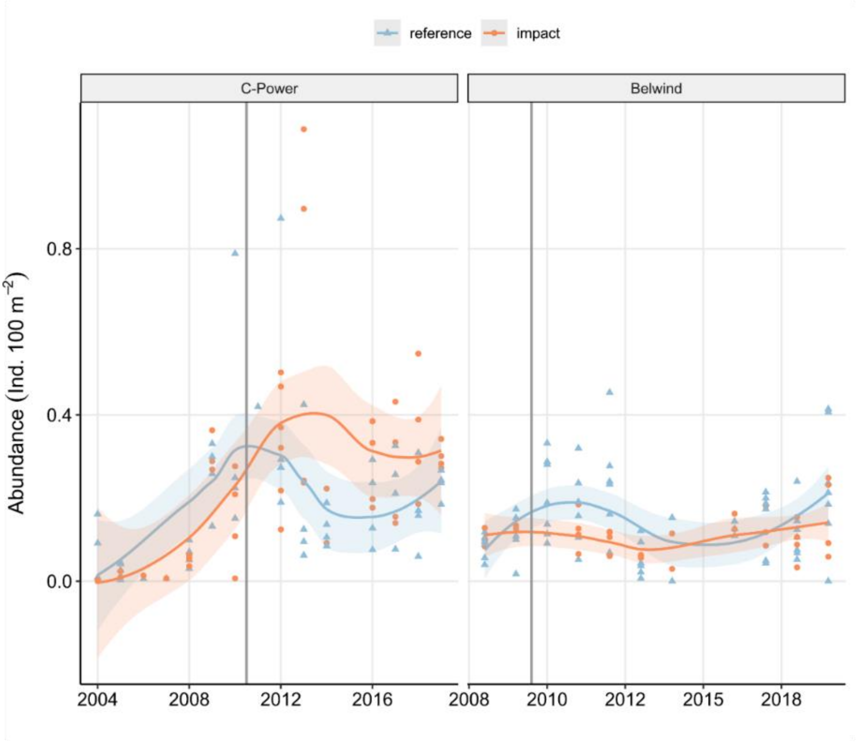

Figure 3.4: Plaice abundance in beam trawl samples (approx. 200 m from the turbines) for C-Power and Belwind in reference and impact areas over resp. the time span 2004-2019 and 2008-2019[4]. Vertical dark grey lines indicate the before and after construction period as considered in this study, which also coincides with the moment that fisheries activities were suspended for the second and third phase of C-Power and Belwind. The area around the 6 GBFs in C-Power (first construction phase) was closed in 2008. LOESS-smoothers with a span of 0.7 were fitted to the data to facilitate interpretation. Orange and blue bands indicate the standard error 95% confidence intervals for the impacted and reference areas, respectively.

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[4] There is an increase in the density of plaice in the reference and impact samples for C-Power between 2004 and 2010. This increase is probably related to factors that are driving plaice abundance or distribution on a larger scale, as it is observed in reference and impact areas. Fishing pressure on plaice in the North Sea strongly decreased after 2001, which was followed by an increase in the spawning stock biomass (Froese et al., 2015; ICES, 2022a). This change in fishing mortality might, therefore, explain the observed pattern in density during this period.

3.4 DISCUSSION

We investigated the distribution patterns of plaice in the presence of OWFs at both turbine and wind farm spatial scales. At the turbine scale, we observed that plaice was attracted towards the sandy patches between the rocks of the scour protection layer (SPL) surrounding the wind turbines, with four times higher abundances compared to the surrounding open sand system. At the wind farm scale, higher plaice abundances were recorded for one of the two OWFs, indicating that OWFs not only attract hard-substrate benthopelagic species, like pouting *Trisopterus luscus* (Reubens et al., 2013a) and edible crab *Cancer pagurus* (Krone et al., 2017), but also soft-sediment demersal species like plaice.

3.4.1 ATTRACTION OF PLAICE TO THE SCOUR PROTECTION LAYER SURROUNDING THE TURBINE

Man-made structures that are introduced deliberately into soft-sediment marine environments to increase local biodiversity for nature conservation or fishery management purposes are generally referred to as "artificial reefs" (Bohnsack and Sutherland, 1985; Petersen and Malm, 2006). Although wind turbines, their scour protection and cable toppings are not constructed to serve this particular goal, research has shown that densities of fish and epibenthic invertebrates are higher close to wind farm structures (Degraer et al., 2020). The extent of such an attraction effect is species-specific but it can generally be observed up to a maximum distance of 100 m from the artificial reef structures with a sharp decline from around 50 m (dos Santos et al., 2010; Reubens et al., 2013a).

In our study, which specifically focused on flatfish, we also recorded significantly higher abundances of plaice on the sand between the rocks of the SPL, compared to the surrounding open sand, indicating an attraction towards the SPL habitat. This is in contrast to other studies that did not find indications of an artificial reef effect of the SPL for flatfish species in OWFs or even suggested avoidance behaviour in relation to the hard substrate (Hinz et al., 2006a; Krone et al., 2017; van Hal et al., 2017). This might partly be explained by the fact that their sampling design did not specifically focus on flatfish, whose passive behaviour is different from more active benthopelagic and pelagic species, resulting in a sampling bias (Gibson, 1997).

Apart from the sampling design, the configuration of the SPL seems to be an even more important explanation why we could show an attraction effect for flatfish, while this was not found in other studies. In the Belwind OWF, the rocks of the SPL are sufficiently spread and sedimentation sufficiently high to allow for the (natural) development of sandy patches in between the hard substrate. In contrast to the 'open rock fields' observed in Belwind, Krone et al. (2017) described the rocks of the scour protection around the monopiles in the Riffgat wind farm as 'closed rock fields'. Also, in other European wind farms, such as OWEZ (NL) and Horns Rev (DK), much higher densities of rocks without visible sediment patches are shown in video footage and pictures of the SPL (Leonhard and Pedersen, 2006; Lengkeek et al., 2017). Krone *et al.* (2017) already suggested that the amount of rocks making up the scour protection may influence the distribution patterns of soft-bottom fauna.

Our results suggest that the distribution pattern of plaice may be associated with the presence of sandy patches and thus the rock density of the SPL, which supports the idea that SPL configuration is important. High abundances of plaice were found in the immediate surroundings of the turbine foundation where almost no rocks are present. A few meters away from the turbine foundation, the rocks of the armour layer are closely stacked on top of each other, leaving no patches of sand in between them, and low abundances of plaice were observed. With increasing distance from the turbines the number of rocks decreases until the edge of the SPL merges into natural sandy habitat, corresponding with a gradual increase in plaice abundance till the edge of the SPL, followed by a decrease when moving further away from the hard substrate. In conclusion, low abundances of plaice were recorded in areas without rocks and with very high densities of rocks, while higher plaice abundances were found in areas with a lower density of rocks.

The higher plaice abundance on the sandy patches of the SPL can be explained by the presence of shelter and food. The SPL increases the environmental complexity and creates crevices (Bohnsack and Sutherland, 1985), which creates a shelter against currents and predators. Food is another reason, since it has been estimated that the introduction of hard substrates may lead to a 50-fold food increase (Leonhard and Pedersen, 2006). We therefore hypothesize that plaice benefits from the presence of hard substrate in relation to the associated increase in food and shelter, but only if sandy sediments are present to facilitate their natural burrowing behaviour. Additional studies, focusing on the behaviour and diet of plaice may further elucidate the reasons behind the observed attraction for this flatfish species (Buyse et al., 2023).

Our findings, which demonstrate a flatfish species being present in higher abundances near hard substrates, are supported by Wright et al. (2020), who showed a positive association of plaice in the western North Sea with the presence of oil and gas platforms, while Krone et al. (2013) found higher flatfish abundances near a research platform compared to natural soft sediments. Attraction towards an artificial reef island was also observed for marbled flounder *Pseudopleuronectes yokohamae* in Osaka Bay using acoustic telemetry (Mitamura et al., 2021). Following the above-mentioned hypothesis, it is plausible that an attraction effect of flatfish to the hard substrate will appear in other wind farms over time where, up till now, no such effect was registered, at least if sedimentation rates and sinking rates of the rocks are high enough to allow for the formation of sandy patches in between the rocks. From our study, it is not fully clear if plaice uses the SPL only sporadically for foraging and shelter or if they spend longer time periods on the sandy patches of the hard substrate. Including the use of acoustic telemetry in future studies might help to further elucidate the habitat use of plaice in OWFs (Winter et al., 2010).

The fact that plaice is attracted to these sandy patches between the rocks might be taken into account in the design of new SPLs in other wind farms[5].

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[5] Ideas and recommendations on how the design of the scour protection could be adapted to serve the needs of plaice and other flatfish are given in the general discussion of the thesis, see 6.1.3 Design of the scour protection layer.

However, other species probably have other needs and so, eventually, choices on which species to attract or protect will have to be made. This type of discussions have implications for nature conservation, the industry and local fisheries, so they should take place already during the OWF design phase and should include as many stakeholders as possible (Gill et al., 2020).

3.4.2 INCREASED ABUNDANCES OF PLAICE IN BETWEEN THE TURBINES

Increased plaice abundances were also observed at the wind farm scale for one of the two studied OWFs. As no fisheries activities are allowed within any of the Belgian wind farm concessions due to safety restrictions, it is likely that the soft sediments in between the turbines serve as refuge areas for plaice, at least under specific conditions. Fisheries exclusion zones are widely used in nature conservation and fisheries management plans with the aim to enhance biodiversity or biomass of certain key species, preferably leading to spillover effects in the surrounding areas (Fenberg et al., 2012; Florin et al., 2013; Abecasis et al., 2014). The location of such fisheries exclusion zones is mostly based on the high intrinsic natural value or the presence of certain key species, which is not really the case for OWFs. Therefore, the potential of OWFs as refuge areas might be lower than for specifically designated areas. Notwithstanding, our study is one of the first to provide evidence that under certain conditions, *de facto* fisheries exclusion areas like OWFs can lead to increased abundances of certain commercial flatfish species.

Other studies that looked at flatfish abundances in-between the turbines of OWFs found no significant wind farm effect (Lindeboom et al., 2011; Wilber et al., 2018). The average time for the first detection of a refuge effect on a target species in a fisheries exclusion zone is over five years (Babcock et al., 2010). Most probably, the studied period in the mentioned publications was not long enough (less than five years) to detect subtle changes. This highlights the need for long-term monitoring strategies in OWFs.

Our study covered a period of more than ten years, showing significantly higher plaice abundances in C-Power after construction. However, also here results were not consistent between both studied OWFs. Other factors might play a role in explaining the observed discrepancy. First of all, fishing pressure in the areas surrounding the OWFs differed. The fisheries exclusion zone surrounding C-Power was larger and has been closed for a longer time period both northwest and southeast of the OWF, related to the construction of the neighbouring Rentel (2017) and Norther (2018) OWFs. Belwind is surrounded by the Nobelwind concession since 2016, but the construction of other neighbouring OWFs only started in 2019. A VMS (Vessel Monitoring System) analysis showed an increase in fishing effort in the vicinity of Belwind and other more offshore located wind farms in the period 2016-2017 compared to 2006-2007, probably due to fisheries displacement in combination with a potential increase in fish abundances due to spillover effects (De Backer et al., 2019). The combination of higher fishing pressure at the edges and a smaller fishing exclusion area could have counteracted a potential refuge effect in Belwind.

Further, the foundation type and presence of a SPL most probably also play an important role. The majority of turbines in C-Power (48) have jacket foundations without SPL, with an additional 6 gravity-based foundations with SPL, while all turbines in Belwind have monopile foundations surrounded by a SPL. The observed turbine-scale attraction towards the sandy patches in the SPL in Belwind may be the result of a displacement of individuals, as such creating fish hot spots near the hard substrate and a decreased detection in beam trawl samples at 200 m from the turbines. The effects at the wind farm scale in Belwind could thus be masked by the more pronounced smaller-scale attraction of plaice towards the scour protection around the turbine foundations.

Apart from the differences in foundation type and fishing pressure, environmental conditions such as depth, sediment composition, turbidity, hydrology and water temperature also differ between both concession areas in the BPNS, which also influence species distribution and food web interactions (Dannheim et al., 2014). Finally, the increase in macrobenthic biodiversity and density in the vicinity of the turbine foundations was more pronounced in C-Power than in Belwind (Lefaible et al., 2018), corroborating the results observed for plaice.

It remains a challenge to try and capture real refuge effects, as many factors are at play and sampling methods or designs might not be optimal, at least not for all species. Although we have shown that OWFs have the potential to act as refuge areas for plaice, results of this study are inconsistent, while several studies reported no effects. Not being able to demonstrate an effect, however, does not mean that there is no effect. Moving away from a BACI-design towards a before-after gradient (BAG) design might help to overcome low statistical power in monitoring studies (Methratta, 2020). In the latter design, samples are taken over a distance gradient from the impact site, which has the advantage that no specific control areas need to be identified. As shown in our study, the inclusion of different spatial scales improves our understanding of how OWFs influence species distribution patterns, as refuge effects might be masked by an attraction towards the SPL-habitat (Bergström et al., 2013). Finally, most OWF-studies focused on fish abundances, which are highly variable in space and time, while refuge effects may be more easily identified when looking at other life history parameters, such as age, length and sex ratio (Miethe et al., 2010; Florin et al., 2013). For example, Di Franco et al. (2009) showed that the observed increase in biomass for many target species within a protected area in the Mediterranean was mainly due to an increase in fish size rather than fish abundance.

3.4.3 CONCLUSION

Our study showed that the presence of OWFs, together with the associated absence of fisheries activities, does affect soft-sediment fish species, *in casu* plaice, at both turbine and wind farm spatial scales. At the turbine scale, we observed higher plaice abundances in the sandy patches of the open-rock SPL habitat. We state that the SPL configuration has an important effect on the attraction and distribution patterns of plaice, especially the presence of sandy patches between the rocks, providing both food and shelter, and facilitating the natural burrowing behaviour of this flatfish species. Future studies should also focus on the diet and behaviour of soft-sediment fish near turbine foundations and SPLs to further elucidate the potential functions of this introduced habitat for such species. Based on acquired scientific knowledge, SPL design could then be optimized to meet the ecological needs of certain target species (e.g. the presence of sand patches between rocks for plaice). However, decisions related to SPL design depend on the species of interest with each species (group) having different needs concerning habitat configuration and complexity.

At the wind farm scale, we observed increased plaice abundances for one OWF, suggesting that OWFs can act as refuge areas for flatfish. However, factors such as differences in environmental conditions, fishing pressure and foundation type potentially play an important role, as they create specific circumstances that might influence fish species and communities in different ways. Moreover, OWF-related refuge effects are difficult to pick up, due to the high year-to-year variability in fish abundances, compared to the relatively small differences between impact and control sites. Additionally to fish abundances, we recommend to monitor other life history parameters such as length, sex ratio, weight and age, to enhance the detection of potential refuge effects. We advise monitor programmes to take into account multiple spatial scales, as attraction at both turbine and wind farm scales might influence each other, thus creating a bias when focusing on only one scale. Alternative monitoring methods, such as ROVs and environmental DNA, can be used to study fish abundance and biomass in OWFs when traditional methods cannot be used due to safety regulations (Lengkeek et al., 2017; Ruppert et al., 2019; Rourke et al., 2022; Staehr et al., 2022). The first Belgian wind farm zone of 238 km^2 has been completed in 2020 with nine OWF concessions, with no fisheries activities allowed within this entire area. We expect potential refuge effects to become more pronounced in the near future, enabling a better understanding of the effects of OWFs on fish distribution on an even larger scale.

3.5 ACKNOWLEDGEMENTS

We want to thank Parkwind NV for the cooperation and logistic support during planning and sampling. We also want to thank all voluntary scientific divers, Alain Norro (RBINS), the VLIZ scientific diving team and ILVO colleagues for all data collection. We acknowledge the crew of R.V. Belgica for the excellent cooperation during numerous sampling campaigns in the OWFs, as well as the Belgian Science Policy (Belspo and RBINS-OD Nature) for providing ship time on the R.V. Belgica. Also, the commitment of the R.V. Simon Stevin crew is greatly appreciated, as is the support of VLIZ for providing ship time on the R.V. Simon Stevin. This research contributes to the Belgian wind farm monitoring programme (WinMon.BE).

4 INCREASED FOOD AVAILABILITY AT OFFSHORE WIND FARMS AFFECTS TROPHIC ECOLOGY OF PLAICE *PLEURONECTES PLATESSA*

This chapter is a modified version of the paper published as Buyse, J., Hostens, K., Degraer, S., De Troch, M., Wittoeck, J., De Backer, A., (2023) Increased food availability at offshore wind farms affects trophic ecology of plaice *Pleuronectes platessa*. Science of the Total Environment.

Abstract

Offshore wind farms (OWFs) and their associated cables, foundations and scour protection are often constructed in soft sediment environments. This introduction of hard substrate has been shown to have similar effects as artificial reefs by providing food resources and offering increased habitat complexity, thereby aggregating fish around the turbine foundations. However, as most studies have focused their efforts on fish species that are typically associated with reef structures, knowledge on how soft sediment species are affected by OWFs is still largely lacking. In this study, we analysed the trophic ecology and condition of plaice, a flatfish species of commercial interest, in relation to a Belgian OWF. The combination of a stomach and intestine content analysis with the use of biomarkers (i.e. fatty acids and stable isotopes) identified a clear shift in diet with increased occurrences of typical hard substrate prey species for fish in the vicinity of the foundations and this both on the short and the long term. Potential effects of OWFs on the condition and fecundity plaice of was studied by calculating a combination of different morphometric and organosomatic condition indices. Despite some condition indices suggesting that the hard substrate provides increased food availability, no clear increases of overall plaice condition or fecundity were found. Samples from within the wind farm, however, contained larger fish and had a higher abundance of females compared to control areas, potentially indicating a refuge effect caused by the cessation of fisheries activities within the OWF. These results suggest that soft sediment species can potentially benefit from the presence of an OWF, which could lead to fish production. However, more research is still needed to further elucidate the behavioural ecology of plaice within OWFs to make inferences on how they can impact fish populations on a larger spatial scale.

Key words

OWFs, fish condition, trophic ecology, North Sea, artificial reef effect, plaice (*Pleuronectes platessa*)

4.1 INTRODUCTION

Offshore wind farm (OWF) are rapidly expanding in European waters and especially in the North Sea region (WindEurope, 2022). This OWF growth is associated with the introduction of hard substrate in the form of e.g. foundations, cables and scour protection in environments often characterised by soft sediments (Lindeboom et al., 2011; Reubens et al., 2011a; Stenberg et al., 2015). As these artificial reefs are typically inhabited by faunal communities other than sandy bottom communities, local biodiversity and species interactions are altered (Bohnsack and Sutherland, 1985; Kerckhof et al., 2010; Zintzen and Massin, 2010; De Mesel et al., 2013; Coolen et al., 2020). While much is known about this artificial reef effect (Degraer et al., 2020), several knowledge gaps on the effects of OWFs on soft sediment organisms still exist (Wilhelmsson et al., 2006; Wilber et al., 2018, 2022b). Addressing these gaps is especially important for species that have commercial value, as OWF effects might not only have ecological consequences, but may also impact fisheries resources (Gill et al., 2020; Mooney et al., 2020).

Although many hard structures, such as offshore platforms and OWFs, are not introduced into the marine environment with the primary intention of increasing local biomass and biodiversity, they have been shown to act in a similar way as artificial reefs (Soldal et al., 2002; Coolen, 2017). Various studies have demonstrated the attraction of hard substrate-associated fish to the foundations and SPL of OWFs, e.g. cod *Gadus morhua* and pouting

Trisopterus luscus (Reubens et al., 2013a), black sea bass *Centropristis striata* (Carey et al., 2020), shorthorn sculpin *Myoxocephalus scorpius* and goldsinny wrasse *Ctenolabrus rupestris* (Bergström et al., 2013). While for sand-dwelling species, usually no such effects are found (Lindeboom et al., 2011; Van Deurs et al., 2012; Wilber et al., 2018), a recent study did show an attraction of plaice *Pleuronectes platessa,* a typical soft-sediment species, towards the sandy patches in between the rocks of the SPL in a Belgian OWF (Buyse et al., 2022a).

Increased food availability and habitat complexity, offering shelter from currents and predators are the main reasons why fish and other organisms aggregate around artificial reefs (Bohnsack and Sutherland, 1985; Bohnsack, 1989; Leonhard and Pedersen, 2006; dos Santos et al., 2010). An important question to answer is whether an observed attraction towards the hard structures also leads to an increase in local production, commonly referred to as the 'attraction-production'-hypothesis (Lindberg, 1997; Brickhill et al., 2005). Colonizing fauna on the turbine foundations and scour protection layers (SPLs) of OWFs enrich the surrounding sediments through their deposition of faecal pellets and detritus, thereby increasing the food availability in the area (Maar et al., 2009; Degraer et al., 2020). Together with the increase in structural complexity, this might simply redistribute individual fish without having an effect on the overall fish density in the area. On the other hand, higher prey biomass could support higher numbers of fish and, therefore, increase the carrying capacity of the original habitat, resulting in higher production (Powers et al., 2003; Brickhill et al., 2005). To investigate the attraction-production hypothesis in relation to OWFs, it is thus vital to integrate knowledge on fish spatial distribution with an analysis of their trophic ecology (De Troch et al., 2013; Schwartzbach et al., 2020; Mavraki et al., 2021).

Colonizing fauna inhabiting natural and artificial reefs are very specific for that habitat type and many of those species are only present under particular environmental conditions (Zintzen, 2007). For example, many species found around the foundations and SPL of wind farms do not occur in the surrounding, natural soft sediment (De Mesel et al., 2013). Fish feeding on these structures, might hence have a different diet and trophic ecology compared to their conspecifics feeding on sandy bottoms. Stomach content analysis (SCA) gives a very high taxonomic resolution of what individual fish have consumed over a period of approximately 10 hours and is widely used to answer research questions related to short-term feeding ecology (Hyslop, 1980; Mavraki et al., 2021). Although no major shifts in stomach content composition were found for seven different demersal fish species in Block Island Wind Farm (Rhode Island, U.S.), increases of typical hard substrate species such as blue mussel *Mytilus edulis* were found in stomachs of fish sampled in between the turbines (Wilber et al., 2022b). Further, diet changes were also identified for dab *Limanda limanda*, lesser weever *Echiichthys vipera* (Derweduwen et al., 2016) and pouting *Trisopterus luscus* (Reubens et al., 2011) in a Belgian wind farm. Besides the analysis of fish stomach contents, food web studies related to artificial reefs have also used biomarkers (i.e. stable isotopes and fatty acids (FAs)) to assess both differences in trophic ecology among certain habitat types and trophic interactions among different species (Mavraki et al., 2021; Plumlee et al., 2021). Compared to SCA, biomarkers offer a lower taxonomic resolution, but they give insights into feeding habits integrated over longer time scales (weeks up to months) and provide information on what is eventually assimilated in the tissues. Therefore, the combination of both SCA and biomarkers provides the best insights when studying potential changes in trophic ecology (Davis et al., 2012; Nithirojpakdee et al., 2014; Mavraki et al., 2021).

The quantification of trophic interactions related to OWFs is important to get insight in how they can affect local food webs and what kind of implications this might have on their surrounding environment (Cresson et al., 2019). For example, if the hard substrate provides easier prey accessibility and the composition is of the same or even better quality, secondary production might be enhanced. Especially within OWFs this can be true, as in most European wind farms no fishing activities are allowed, thereby additionally increasing their potential to act as refuge areas for fish of commercial interest (Halouani et al., 2020). In this study, we investigated the effects of an OWF in the Belgian part of the North Sea on the trophic ecology and condition of plaice, a commercially valuable species. We hereby defined fish condition in a broad sense, not only referring to the purely physiological status of an individual, but also to its overall health (Lloret et al., 2014). We specifically aimed at determining (1) whether the diet of plaice is influenced by the presence of hard substrate and its colonizing fauna, (2) if plaice is feeding off the hard substrate for long periods of time, and (3) if plaice condition is influenced by the presence of the wind farm. We hypothesized that plaice diet and condition is affected by the presence of the hard substrate in the OWF, at least for individuals that are caught close to the foundations.

4.2 MATERIALS AND METHODS

4.2.1 STUDY AREA

Plaice individuals were sampled in and around the Belwind OWF in the Belgian part of the North Sea in 2020 (Figure 4.1 when working in Belgian OWFs.). Belwind is located 49 km off the coast of Zeebrugge on the Bligh Bank with average depths varying between 15 and 37 m. Since 2010, the wind farm is fully operational consisting of 55 turbines on monopile foundations and 1 turbine on a jacket foundation, which was added in 2013. Each foundation is surrounded by a SPL (~16.5 m radius) to avoid sediment erosion in its vicinity due to increased current speeds. The SPL consists of a filter layer of smaller rocks, covered by sand after some time, and an armoured layer of larger boulders on top. These boulders, as well as the turbines themselves, are covered with fouling organisms dominated by *Jassa herdmani*, *Metridium senile*, *M. edulis* and *Ophiothrix fragilis* (De Mesel et al., 2013; Rumes et al., 2021). The soft sediment in between the foundations of Belwind consists mainly of medium sand (250-500 µm), with *Nephtys cirrosa*, *Nemertea* sp. and *Bathyporeia elegans* characterizing the associated macrobenthic community (Lefaible et al., 2018). Although the macrobenthic community in between the turbines differs from the one surrounding the SPL in terms of its composition, there is no indication of organic enrichment of the sediments near the SPL.

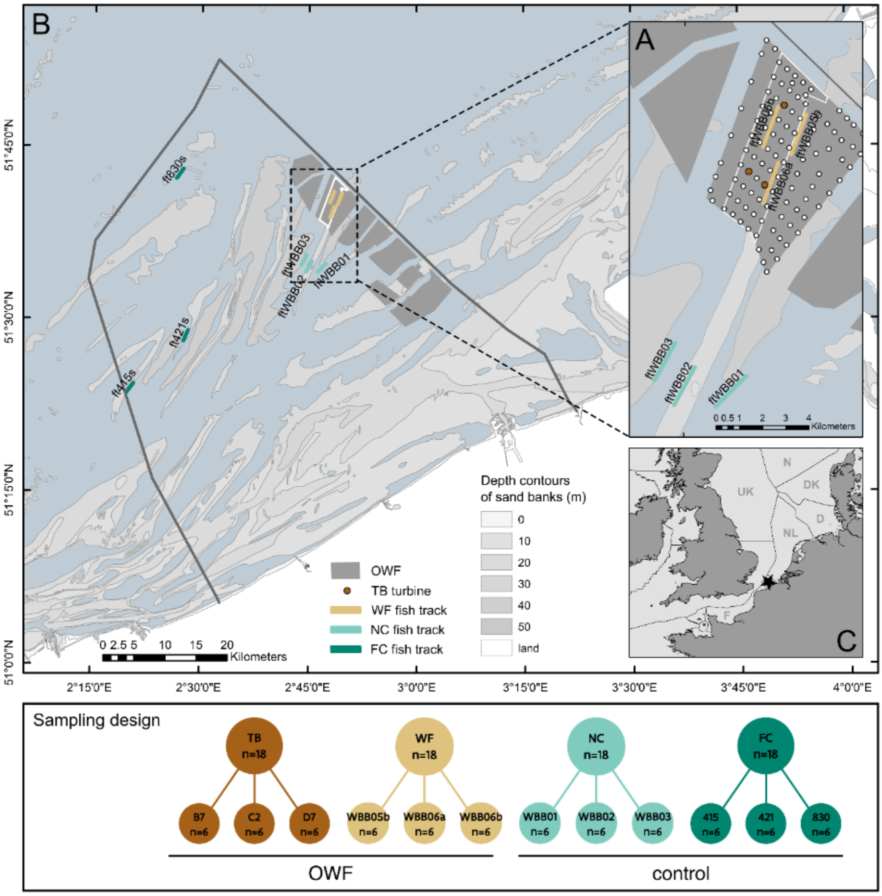

Figure 4.1: (A) The Belwind offshore wind farm with locations of the beam trawl tracks of the WF group and the randomly chosen turbines of the TB group; (B) the locations of the different beam trawl tracks for the WF, NC and FC groups and (C) the location of the Belgian part of the North Sea. The contour lines indicate the presence of sand banks in the study area.

4.2.2 STUDY DESIGN AND SAMPLING

To study the effects of the Belwind OWF on the trophic ecology and condition of plaice, samples were collected close to the turbines (TB) by hook-and-line fishing and in between the turbines (WF), in a near control area (NC) and a far control area (FC) by beam trawl. For each area, a total of 18 plaice individuals (total length >15 cm) were sampled at three replicate locations (6 fish at each location) to incorporate as much randomization within the sampling design as possible, while still respecting the safety measures to be complied with when working in Belgian OWFs.

TB fish were caught between 10 and 15 September 2020 by hook-and-line fishing (hooks: Gamakatsu size 1/0, bait: *Arenicola marina*) from a small zodiac in the immediate vicinity (2-10 m) of three randomly chosen turbines in the wind farm. The fish were kept alive in a small holding tank until they were transferred onto the research vessel. WF fish consisted of individuals caught in between the turbines at a distance of approximately 200 m using an 8-m wide beam trawl equipped with a shrimp net (mesh size 22 mm in the cod end) on board RV Belgica. NC and FC fish were collected during the same sampling campaign (same beam trawl setup, WF and NC group: 15 September 2020, FC group: 23 September 2020) and each group included fish from three different locations with comparable environmental conditions as within the Belwind OWF (De Backer et al., 2010). The NC-trawls were located 6-7 km from the edge of the wind farm, while the FC-trawls were located further away at a distance ranging from 24-40 km. Fish caught by beam trawl (WF, NC and FC) were randomly sampled from the catch, while the TB-group existed of the first six fish that were caught with a minimum length of 15 cm.

Once on board of the research vessel, the fish were euthanized with MS-222 (500 mg L^{-1}) and their length, sex and total wet weight were determined. Subsequently, the entire gastrointestinal tract was removed and preserved in 100% ethanol and stored in the freezer (-20 °C). The liver and gonads were also dissected and fixed in a 4% formaldehyde-sea water solution. Afterwards in the lab, the wet blotted weight of all three organs was determined on an analytical scale, as the swell compensated scale on board of the research vessel could not measure at 0.1 g precision. The organs were weighed after 20 days in ethanol or formaldehyde, as shrinkage effects are strongest in the first few days after preservation (Mills et al., 1982). After the removal of all the organs, the fish were weighed again on board to obtain the eviscerated weight. For the stable isotope and FA analyses, small pieces of muscle tissue (approx. 2 x 2 x 1 cm) were cut out and stored dry in the freezer (-20 °C). In the lab, the muscle tissue samples were transferred to a temperature of -80 °C until further processing. Lastly, the otholiths of each fish were also removed for age determination.

To link stable isotope signals and FA signatures of the fish muscle tissue to potential prey items, we also sampled macrobenthic, epibenthic and fouling organisms from the four sample groups. For the TB-group, divers collected scrape samples from the rocks of the SPL and took macrobenthic samples from in between the rocks. For each of the other sample groups, three sediment samples were collected using a 0.1 m^2 Van Veen grab at one of the locations where the beam trawl samples of that group were also taken. The samples were sieved on a 1 mm sieve and living prey items were collected and identified to the lowest taxonomic level possible. If possible, three replicates were collected for each prey item per sample group. To avoid the influence of food items in the stomach and intestines on the stable isotope signals, prey species were kept overnight in filtered sea water to facilitate the emptying of their gastrointestinal tract. All prey items were then stored dry in the freezer on board (-20 °C) and transferred on land to a -80 °C freezer until further processing.

4.2.3 STOMACH AND INTESTINE CONTENT ANALYSIS

The stomach and intestine of each fish were analysed separately to account for differences in the degree of digestion of prey items. Both stomach and intestine were rinsed with 100% ethanol and all prey items (full or incomplete organisms) were morphologically identified to the lowest taxonomic level possible under a stereomicroscope. For each prey species found in the stomach and/or gut, the typical habitat (soft sediment/hard substrate) was determined based on different literature sources (De Mesel et al., 2013; Kerckhof et al., 2010; Tyler-Walters et al., 2022). To determine the contribution of each prey item to the stomach/intestine content, three different methods were used: (1) the numerical method, (2) the gravimetrical method and the (3) relative fullness method (Amundsen and Sánchez-Hernández, 2019). The numerical method consists of counting each prey item, while the gravimetrical method is based on their biomass. The biomass of each prey species was obtained by determining its blotted wet weight using an analytical balance (Mettler Toledo, 0.00001 g precision). Even though the numerical and gravimetrical method are both considered reliable and are often used in fish diet studies, they also have several disadvantages. Sometimes it is not possible to obtain a reliable count of a prey item when it is highly fragmented. Moreover, a bias can exist when not all prey items are of a similar size. The gravimetrical method can overcome these biases, but still induces problems when prey items cannot be easily separated when digestion is too advanced. In the relative fullness method, on the other hand, the contribution of each prey item is scored visually in percentage of the total stomach fullness. Although this could be perceived as a subjective method, a comparison test showed no significant differences between inexperienced and experienced analyzers, which supports its consistency and reliability. Furthermore, this method is also considered as one of the most time-efficient approaches when studying relative prey composition (Amundsen and Sánchez-Hernández, 2019).

4.2.4 STABLE ISOTOPE ANALYSIS

Both muscle and potential prey samples were rinsed with milli-Q water to remove any salts and dried overnight at 60 °C. All dried samples were grounded using mortar and pestle to homogeneous powder. For muscle tissue samples and prey items that did not contain calcareous structures, the residue was homogenized and 1.0±0.2 mg was transferred into Sn-capsules (5 x 8 mm, Elemental Microanalysis). Prey items that did contain calcareous structures, such as amphipods, ophiuroids and decapods, were acidified to remove non-dietary, inorganic C in carbonates (Schlacher and Connolly, 2014). After drying, two subsamples of 1.0±0.2 mg were taken, of which one was transferred into a Sn-capsule and left untreated for δ^{15}N-assessment, while the other one was transferred into an Ag-capsule (5 x 8 mm, Elemental Microanalysis) for the acidification process. The sample was acidified with a 1%-HCl solution using the 'drop-by-drop'-method and dried again (Mavraki et al., 2020). All capsules were then folded and transferred into 96-well plates.

For most of the smaller prey, the entire individual (or multiple individuals) was used, while for some larger prey items only parts were dissected (e.g. blue mussel). The samples were shipped to the UC Davis Stable Isotope Facility, United States, California where they got analysed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The results are expressed relative to the Vienna Pee Dee Belemnite international standard for carbon and atmospheric standard for nitrogen (Wieser and Brand, 1999).

4.2.5 FATTY ACID ANALYSIS

The FA analysis, consisting of the hydrolysis of total lipid extracts and methylation to FA methyl esters (FAME) was carried out according the method described by Abdulkadir and Tsuchiya (2008) and adapted by De Troch et al. (2012). Composition analysis of the FAMEs was carried out using a gas chromatograph system (GC; HP 7890B, Agilent Technologies, Diegem, Belgium) equipped with a flame ionization detector (FID) and connected to an Agilent 5977A Mass Selective Detector (MSD; Agilent Technologies). The FID signal was used for FAME quantification, while the MSD-signal allowed for FAME identification. Chromatogram analysis was done with MassHunter Quantitative Analysis software (Agilent Technologies). Peaks were identified based on their retention times, compared with external standards as a reference (Supelco 37 Component FAME Mix, Sigma-Aldrich, Overijse, Belgium) and by the mass spectra obtained with the MSD. FAME quantification was based on the area of the internal standard and on the conversion of peak areas to the weight of the fatty acid by a theoretical response factor for each fatty acid (Ackman and Sipos, 1964; Wolff et al., 1995). The FA absolute concentration (in mg FA/g dry weight), as well as the FA relative concentration (in % of total) were determined for each individual FA.

4.2.6 DATA ANALYSES

4.2.6.1 Morphometric and organosomatic condition indices

A combination of morphometric and organosomatic condition indices were calculated for each fish to obtain a more complete view on its overall condition. The Fulton's K index (K) is a simple morphometric index, which assumes that a heavier fish is in better condition than a lighter fish for a given length and is calculated as

$K_{TW/EW} = (W/L^3)*100$

with W representing the total weight or the eviscerated weight of the individual for K_{TW} and K_{EW}, respectively, and L its total length. An important assumption for using these formulae is that fish growth should be isometric; in other words, the b-value in the species length-weight relationship ($W = aL^b$, with W = total weight of the fish, L = total length of the fish) needs to be 3 (or very close to it) to ensure the applicability (Lloret et al., 2014). For plaice this condition is met (b-value = 3.009) (Robinson et al., 2010), so K can be used as a proxy for the condition of an individual fish.

Additionally, three organosomatic indices were calculated: the hepatosomatic index (HSI), the gonadosomatic index (GSI) and the digestive-somatic index (DSI). The HSI, GSI and the DSI were calculated as:

$HSI = 100*(W_L/W_E)$

$GSI = 100*(W_O/W_E)$

$DSI = 100*(W_{GI}/W_E)$

with W_L, W_O, W_{GI} and W_E representing liver weight, ovary weight, gastro-intestinal tract weight and fish eviscerated weight, respectively.

Furthermore, a stomach fullness index (FI) of each non-empty stomach (n = 53/72) was also calculated using

$FI = (W_S/ W_T)*100$

with W_S representing the total weight of all stomach contents and W_T the total weight of the fish (Mahesh et al., 2018).

4.2.6.2 Stomach and intestine content, and fatty acid analyses

The results for the stomach and intestine content were combined for each fish to obtain a more comprehensive view of its diet and to maximize the available information, especially when stomachs were empty. This could cause a bias due to the difference in level of digestion of prey items in the intestine compared to the stomach and due to differences in sensitivity to digestion of different prey items (Hyslop, 1980). Nevertheless, we are confident that our outcomes are trustworthy, because our main objective was to check for differences in composition between sample groups, and not to describe the diet of plaice in as much detail as possible. Moreover, we found numerous polychaetes, which are soft-bodied and thus most prone to digestion, that were identifiable up to family level in both the stomach and hindgut, which supports the choice for combining the data.

The results from the numerical and gravimetrical method were combined by summing the abundance or biomass of each prey species for the stomach and intestine. For the relative abundance method, this was done by taking the mean contribution of each prey species with stomach and intestine each accounting for 100%. The abundance data from the numerical method were fourth-root transformed, while the biomass data from the gravimetrical method were square-root transformed to reduce the variance. The relative abundance data, on the other hand, were treated with an arcsine transformation (Sokal et al., 1995). Further, a SIMPER analysis was also performed on the relative abundance data to find the most important prey items for each sample group (Clarke, 1993). The relative FA concentration data were treated with an arcsine transformation. Mean relative polyunsaturated FA (PUFAs) concentrations, as well as mean relative microbial FAs (uneven carbon atoms), were calculated per sample group.

4.2.6.3 Multivariate statistical analyses

Potential differences in stomach/intestine contents and relative FA profiles between sample groups were investigated using a multivariate approach. The transformed abundance/concentration data were used as the input for the calculation of a Bray-Curtis similarity matrix. A principal coordinates analysis (PCO) was conducted together with a PERMANOVA-test on each of the resemblance matrices. *Sample group* (TB, WT, NC and FC) was added as a fixed effect, while *turbine* or *haul* was added as a nested random factor. If sample group was found to be significant, a post-hoc pairwise PERMANOVA-test using Monte-Carlo approximation was performed to test for differences among the sample groups. Additionally, a PERMDISP-test was carried out to check the homogeneity of dispersions using distances among centroids. All multivariate analyses were carried out in PRIMER-E v7 (Clarke and Gorley, 2015).

4.2.6.4 Univariate statistical analyses

To check whether potential differences among sample groups existed in condition indices, individual relative FA concentrations, mean relative PUFA concentrations, mean relative microbial FAs (uneven carbon atoms) and isotope values ($\delta^{13}C$ and $\delta^{15}N$), linear mixed models were fitted with *sample group* as a fixed effect and *haul* or *turbine* as a random factor. Additionally, *fish length* was also added as a fixed effect to test if differences between groups were not mainly explained by individual fish characteristics. The Akaike Information Criterion (AIC) values of the models with and without fish length were compared and only when the AIC-value of the simpler model was substantially lower (<5), fish length was removed from the model (Burnham and Anderson, 2004). The model was then validated using different plots of the residuals checking for heteroscedacity, non-normality and non-linear relationships. If non-normality of the residuals was determined due to a high number of zero values, a zero-inflated linear mixed model was used instead. Statistical testing of the group-variable was done using a type-III F-test. Finally, if the sample group variable was significant, a post-hoc test based on the estimated marginal means was carried out to test all possible pairwise combinations. A Tukey adjustment was applied to the p-values to correct for multiple testing. All calculations and statistical analyses related to univariate analyses were carried out in R version 4.1.2 (R Core Team, 2022).

4.3 RESULTS

A total of 72 plaice individuals were sampled with lengths ranging from 17.5 to 36.5 cm (mean = 25.8±4.3 SD) (see Annex 4.1). Length differed significantly among the sample groups, except between the two control groups, with the largest fish found in the TB and WF-group (median length TB: 30.2 cm, WF: 26.2 cm, NC: 23 cm, FC: 23 cm ; $F_{3,68}$ = 21.8, $p<0.001$). Sex ratio also varied strongly across the different groups with a strong dominance of females in the TB (0.88) and WF group (0.83), while sexes for the control groups were more evenly distributed (NC: 0.67, FC: 0.5). Age of the fish did not differ among the sample groups (mean = 3.42±1.77 SD; $F_{3,68}$ = 0.62, p = 0.60).

4.3.1 CONDITION INDICES

The fullness index (FI), as well as the Fulton's K index based on fish total weight (K_{TW}), were highest for the TB group and decreased with increasing distance from the hard substrate (Figure 4.2). For FI, however, sample group was not significant ($F_{3,7.5}$ = 2.656, p = 0.12). For $K_{TW,}$ on the other hand, sample group was highly significant ($F_{3,8}$ = 11.061, p = 0.003), but the post-hoc test revealed only lower values for the FC-group compared to all other groups ($p<0.05$). Values of the Fulton's K index calculated with the fish eviscerated weight (K_{EW}) were again lower for the FC-group ($F_{3,8}$ = 6.3096, p = 0.02), compared to the other three groups ($p < 0.05$), but no gradient with distance from the hard substrate was present. For none of the three indices, fish size significantly explained variation in the data and was therefore removed from the models.

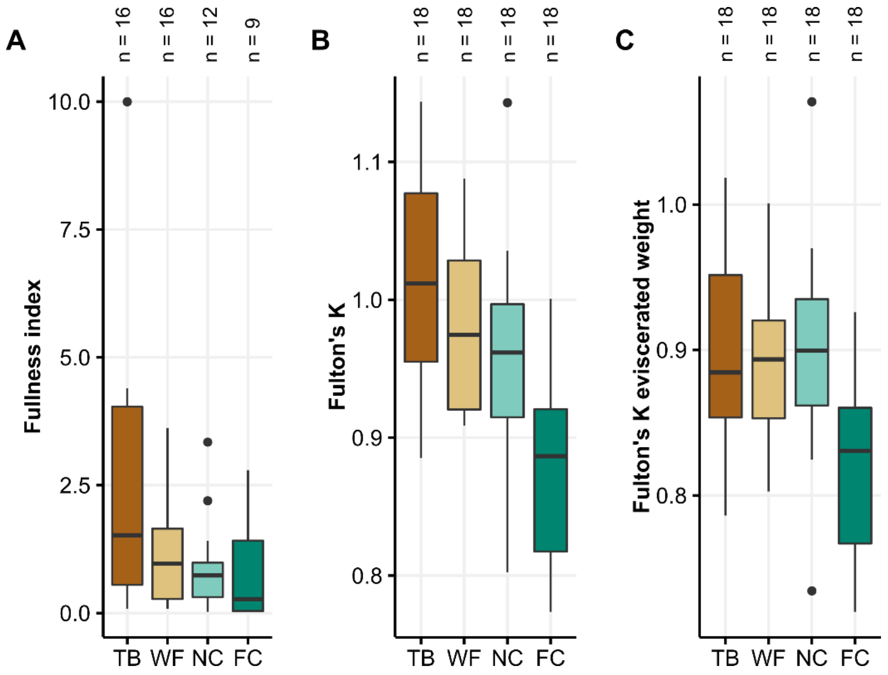

Figure 4.2: (A) Boxplots of fullness index of non-empty stomachs (n = 53), (B) Fulton's K condition index calculated with fish total weight and (C) Fulton's K condition index calculated with fish eviscerated weight for each of the sample groups with n representing the number of samples used.

The gonadosomatic index (GSI) did not show any significant differences between groups ($F_{3,9} = 1.02$, $p = 0.43$), although the FC group had lower values (1.34±0.5) compared to the others (TB: 2.3±0.5, WF: 1.98±0.5, NC: 2.4 ±0.5) (Figure 4.3). Fish length was highly significant in explaining the variation in the GSI ($F_{1,42} = 15.7$, $p = 0.0003$). Both the hepatosomatic index (HSI) and the digestive-somatic index (DSI) differed significantly between sample groups (HSI: $F_{3,8} = 4.17$, $p = 0.05$, DSI: $F_{3,8} = 10.07$, $p = 0.004$). Here fish length was not retained in the final model and thus not significant in explaining variation. For the HSI, pairwise differences were found between WF and FC ($p = 0.04$), while for the DSI there were significant differences between the TB-group and both control groups (NC: $p = 0.006$, FC = 0.008). Similar patterns for males and females were observed for all condition indices (except for GSI).

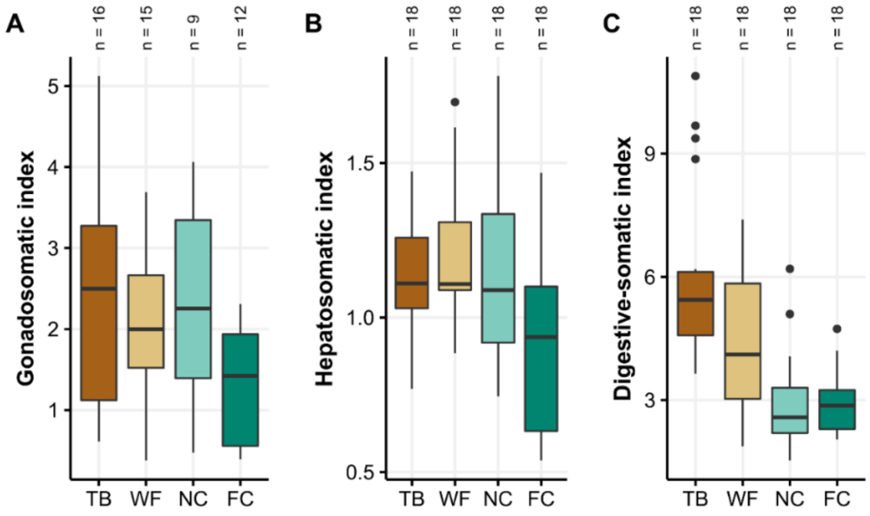

Figure 4.3: Boxplots of the (A) gonadosomatic (GSI), (B) hepatosomatic (HSI) and (C) digestive-somatic (DSI) indices for each of the sample groups with n representing the number of samples used. For the calculation of the GSI, only females were used.

4.3.2 STOMACH AND INTESTINE CONTENT ANALYSIS

Of the 72 sampled fish, 18 had empty stomachs (25%) and most were found in the control groups (TB: 2, WF: 2, NC: 6, FC: 8) (see Annex 4.2). Empty intestines, on the other hand, were found for a total of 6 individuals (8.3%) in the NC-and WF-group (TB: 0, WF: 2, NC: 4, FC: 0). When stomach and intestine contents were combined, only 4 fish (5.6%) had a completely empty digestive system (TB: 0, WF: 1, NC: 3, FC: 0).

Multivariate analyses of abundance, biomass and relative abundance data gave very similar results, so only the latter are presented here (Figure 4.4 A). Principal coordinates analysis (PCO) showed that the samples of the TB-group clustered apart from the other groups. Diet composition was significantly different among sample groups ($p_{Permanova}$, pseudo-$F_{3,67}$ = 3.15, p = 0.005) and pairwise tests revealed significant differences between the TB-group and all other groups (WF: p_{MC} = 0.001, NC: p_{MC} = 0.0008, FC: p_{MC} = 0.0002), while no significant differences were found between the WF-, NC- and FC-group. The PERMDISP test did not show any significant differences among the group variances. SIMPER results showed that the TB-group mainly fed on *O. fragilis*, *J. herdmani* and *M. edulis*, typical hard-substrate species found on the SPL and turbine foundations. In contrast, diet of the other groups consisted of soft-sediment species such as *Echinocardium cordatum*, *Gastrosaccus spinifer* and polychaetes (Figure 4.4 B).

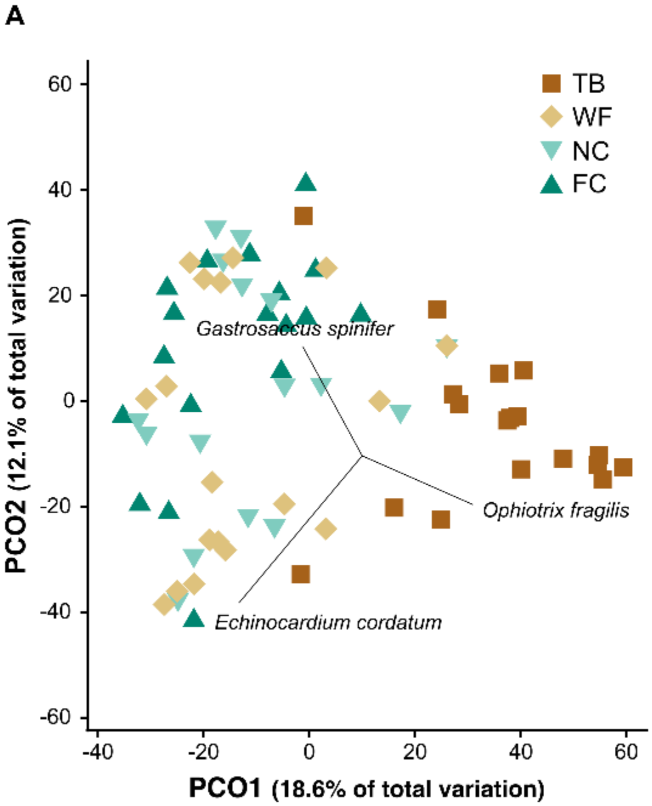

Figure 4.4: (A) Principal coordinates analysis (PCO) results of combined stomach and intestine content using relative abundances of prey items plotted by sample group. The overlay vector shows prey species with a multiple correlation >0.4. (B) Most abundant prey species (contribution) in stomach and intestine per sample group according to a SIMPER analysis. The cut-off level for importance was set at 90%.

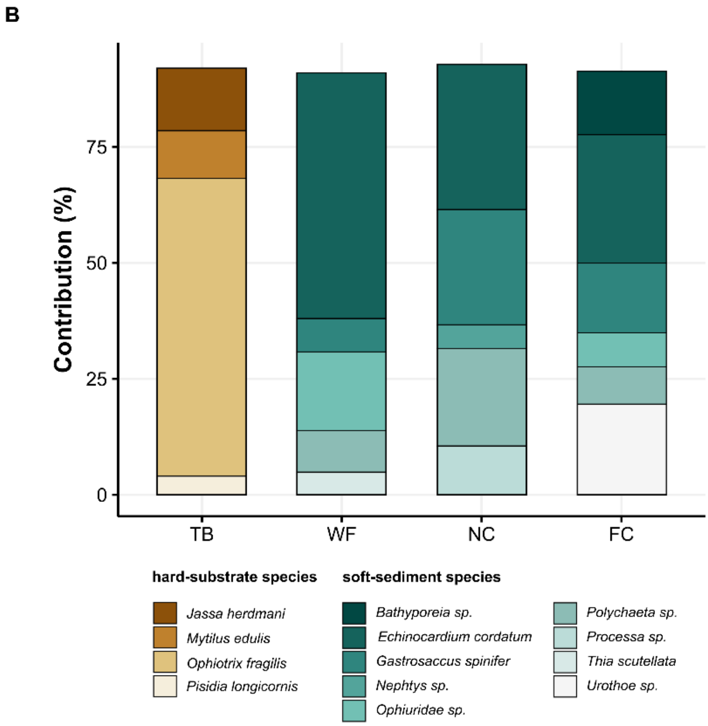

Figure 4.4: continued.

4.3.3 STABLE ISOTOPE ANALYSIS

δ^{13}C-values for plaice muscle tissue samples ranged between -17.7‰ and -14.8 ‰, while the range of the potential prey samples was much wider (between -22.4‰ and -10.4‰) (Figure 4.5). δ^{15}N-values differed more among the different plaice sample groups ranging from 12.2‰ to 15.9‰, while prey items spanned a range from 8.4‰ to 15.1‰. For some prey species, a very large variance in isotopic values was found for the different replicates (e.g. *O. fragilis, Crangon crangon*), while for other species the values were more similar (e.g. *Pisidia longicornis).* A linear model for δ^{13}C-values did not show any significant differences among sample groups ($F_{3,68}$ = 1.13, p = 0.34), while significantly lower δ^{15}N-values were found for the FC-group (13.7±0.7‰) compared to the NC- (14.7±0.7‰) and WF-group (14.6±0.8‰) ($F_{3,68}$ = 7.51, p = 0.0002).

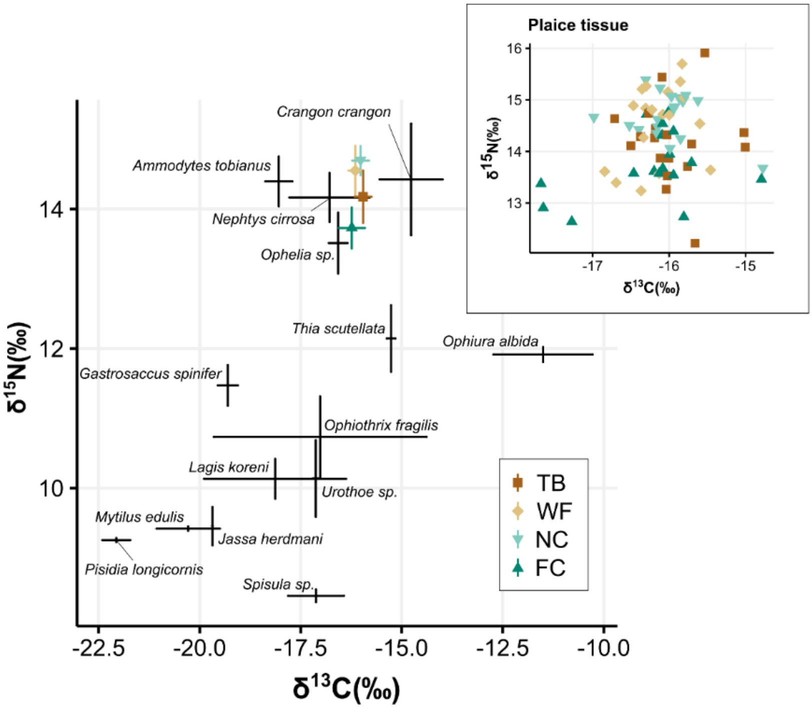

Figure 4.5: Biplot of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) values of prey items and plaice muscle samples per sample group. Error bars represent 95% confidence intervals. Inset only shows values for plaice muscle tissue samples.

4.3.4 FATTY ACID ANALYSIS

A PCO-analysis together with a main PERMANOVA-test revealed significant differences in relative FA concentrations among the different sample groups (pseudo-$F_{3,8}$ = 2.41, p = 0.04) (Figure 4.6). Despite a clear visual separation, pairwise tests showed that the TB group differed significantly from both control groups (NC: t = 2.92, p_{MC} = 0.001, FC: t = 2.95, p_{MC} = 0.001), but not from the WF group (t = 1.24, p_{MC} = 0.24). The PCO also showed a larger spreading for the TB group along the second axis, while the samples of the other groups had more variation along the first axis. The PERMDISP-results indicated that significant differences among sample groups were not explained by a heterogeneity of variances (TB/NC: p = 0.14, TB/FC: p = 0.19). A SIMPER analysis showed that DHA was the principal FA for the WF, NC and

FC group (WF: $\bar{x}$ = 22.3±5.2%, NC: $\bar{x}$ = 23.8±3.8%, FC: $\bar{x}$ = 23.8±5.1%), while it was equally important to EPA for the TB group (22:6 n-3, $\bar{x}$ = 20.4±3.6%; 20:5 n-3, $\bar{x}$ = 20.4±1.9%). Furthermore, the importance of EPA seemed to decrease with increasing distance from the hard substrate (WF: $\bar{x}$ = 19.2±2.6%, NC: $\bar{x}$ = 18.1±2.3%, FC: $\bar{x}$ = 17.7±2.0%) and stearidonic acid (18:4 n-3) contributed considerably more to the FA profile of the TB group ($\bar{x}$ = 1.25±0.8%) compared to all other groups (WF: $\bar{x}$ = 0.7±1.2%, NC: $\bar{x}$ = 0.25±0.08%, FC: $\bar{x}$ = 0.27±0.2%). Statistical univariate analyses of individual FAs showed significant differences among sample groups for different FAs, with the TB group often showing lower or higher FA concentrations compared to the other groups.

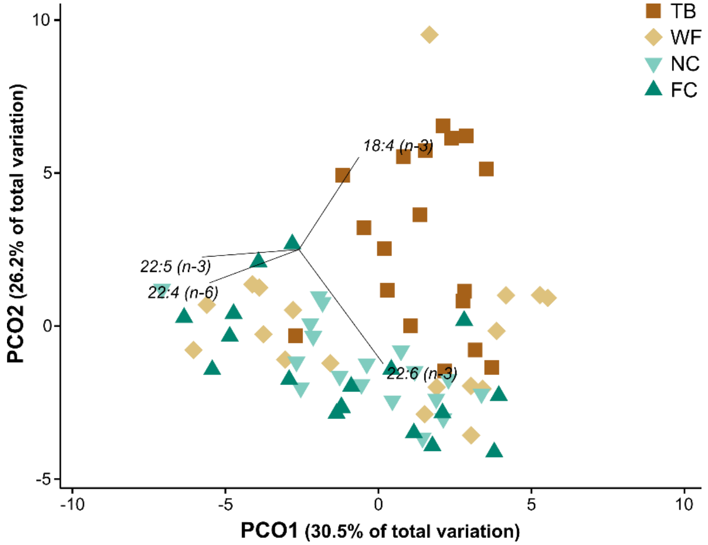

Figure 4.6: Principal coordinates analysis (PCO) of relative fatty acid (FA) concentrations for plaice muscle samples for the different sample groups. Overlay vector shows FAs with multiple correlations >0.4.

The mean relative concentration of PUFAs did not differ among sample groups ($F_{3,68}$ = 0.19, p = 0.90). Higher mean concentrations of (n-3)-PUFAs ($F_{3,8}$ = 4.30, p = 0.04) were found for the TB-group (6.96±0.13%), but none of the pairwise comparisons were significant (WF: 6.46±0.13%, NC: 6.51±0.13%, FC: 6.51±0.13%), while no differences in relative concentrations for (n-6)-PUFAs were found among sample groups ($F_{3,8}$ = 0.30, p = 0.83). When looking at the mean relative concentration of microbial FAs (FAs with uneven number of carbon atoms), a clear gradient was found with values increasing with distance from the turbines ($F_{3,8}$ = 7.63, p = 0.01) (Figure 4.7). However, only the TB-group (0.33±0.03%) was significantly different from both control groups (NC 0.44±0.04%, FC: 0.51±0.04%). Fish length was not considered as important in any of the FA linear models and was therefore removed.

Table 4.1: Results of F-tests and mean values (±SD) for the individual relative fatty acid (FA) concentrations with S = saturated FA, M = monounsaturated FA, P = polyunsaturated FA, B = uneven carbon FA (bacterial origin). Significant p-values (<0.05) are indicated in bold. The asterisk indicates the use of a zero-inflated linear model and a Chi-square test.

	Mean relative FA concentrations				F-test results	
Fatty acid	TB	WF	NC	FC	$F_{3,8}$	p-value
14:0 S	2.34±0.79	1.81±0.78	1.53±0.28	1.48±0.49	5.73	**0.022**
15:0 S, B	0.49±0.07	0.58±0.10	0.58±0.09	0.55±0.10	3.04	0.093
16:0 S	18.5±1.04	19.9±1.51	19.3±0.96	19.4±1.17	4.63	**0.037**
iso-17:0 S, B	0.22±0.09	0.35±0.17	0.45±0.15	0.50±0.21	7.68	**0.010**
16:1 M	0.38±0.13	0.36±0.09	0.33±0.05	0.28±0.06	3.94	0.054
16:1 n-7 M	2.77±0.71	3.29±0.88	3.55±1.17	3.74±1.87	2.01	0.191
anteiso-17:0 S, B	0.47±0.10	0.46±0.15	0.56±0.11	0.53±0.09	3.02	0.094
18:0 S	7.39±0.73	6.74±0.56	6.73±0.46	6.76±0.63	4.87	**0.033**
18:1 n-9 M	7.68±1.31	7.18±1.10	7.30±0.97	6.59±1.09	2.53	0.131
18:1 n-7 M	3.08±0.35	3.11±0.55	3.36±0.51	3.35±0.70	0.99	0.446
18:2 n-6 P	0.49±0.10	0.46±0.15	0.48±0.11	0.48±0.12	0.15	0.926
20:0 S	0.13±0.07	0.08±0.07	0.07±0.07	0.07±0.08	0.90	0.482
18:3 n-6 P	0.02±0.04	0.02±0.05	0.02±0.04	0.02±0.05	0.62*	0.890*
18:3 n-3 P	1.04±0.49	0.60±0.56	0.63±0.2	0.66±0.24	3.81	0.058
20:1 n-9 M	0.72±0.17	0.59±0.18	0.6±0.13	0.58±0.20	1.50	0.286
20:1 n-7 M	0.22±0.12	0.21±0.10	0.43±0.17	0.42±0.30	6.44	**0.016**
18:4 n-3 P	1.25±0.80	0.70±1.16	0.25±0.08	0.27±0.18	5.28	**0.027**
20:4 n-6 P	7.13±0.96	6.33±1.58	5.82±0.96	6.00±1.17	1.77	0.230
20:5 n-3 P	20.4±1.91	19.2±2.61	18.1±2.26	17.7±1.99	5.43	**0.025**
24:1 M	0.80±0.16	0.75±0.22	0.68±0.19	0.67±0.24	1.40	0.312
22:4 n-6 P	0.44±0.37	0.70±0.66	0.90±0.44	1.10±0.60	1.45	0.298
22:5 n-3 P	3.73±1.11	4.21±1.67	4.59±1.45	5.03±2.04	0.90	0.482
22:6 n-3P	20.4±3.55	22.3±5.18	23.8±3.78	23.8±5.10	1.22	0.365

When looking at the mean relative concentration of microbial FAs (FAs with uneven number of carbon atoms), a clear gradient was found with values increasing with distance from the turbines ($F_{3,68}$ = 7.63, p = 0.01) (Figure 4.7). However, only the TB-group (0.33±0.03%) was significantly different from both control groups (NC: 0.44±0.04%, FC: 0.51±0.04%). Fish length was not considered as important in any of the FA linear models and was therefore removed.

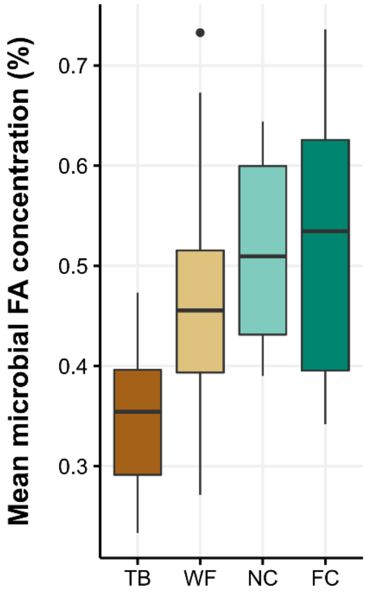

Figure 4.7: Mean relative concentration (n = 18) of microbial fatty acids (15:0, iso-17:0 and anteiso-17:0) for each sample group.

4.4 DISCUSSION

This study showed that the trophic ecology of plaice is affected by the presence of hard substrate within OWFs. The stomach and intestine content analysis demonstrated that fish caught in the vicinity of the turbines mainly fed on hard substrate organisms. The FA profiles of these fish, furthermore, indicated that these are not occasional feeding events, but that they feed off these hard substrates for a prolonged period of time (weeks up to months). In contrast, plaice individuals caught outside the wind farm or on the sand in between the wind turbines preyed on typical soft sediment species, which was reflected in a different FA profile. Stable isotope analysis, however, could not discern these differences in trophic ecology. Finally, some evidence was presented that the presence of hard substrate provides an easier accessibility to food (i.e. DSI), suggesting a positive effect on plaice condition. However, results related to other fish condition indices could not corroborate this.

4.4.1 PLAICE NEAR TURBINE FOUNDATIONS HAVE A HIGHER FOOD INTAKE AND MAINLY FEED ON HARD SUBSTRATE SPECIES

Plaice individuals that were caught on the SPL had a different diet composition, existing mainly of hard substrate-associated species such as *J. herdmani, Ophiothrix fragilis* and *M. edulis*. These prey species are typically found on the turbines and scour protection of OWFs and other AR structures, with the latter two being found in extremely high densities on monopile foundations during the climax succession stage (>6 years after construction) (De Mesel et al., 2013, 2015; Coolen et al., 2019; Kerckhof et al., 2019). Prey items observed in stomachs and intestines of plaice caught in sandy control areas and on the sand in between the turbines generally resembled the diet described for individuals sampled on typical sandy sediments in Dutch, German and Danish coastal areas (e.g. *E. cordatum, G. spinifer, Bathyporeia* sp.) (Rijnsdorp and Vingerhoed, 2001). We did find a few typical hard-substrate species (i.e. *J. herdmani, M. edulis, O. fragilis, Pisidia longicornis*) in the diet of fish caught in between the turbines, while this was not the case for the control groups. It is plausible that those fish had fed off the hard substrate during that same day and thus travel between the sand and the hard substrates when foraging. On the other hand, the effects of the presence of hard substrate can spread out towards the soft sediments over time. For example, aggregations of *M. edulis* were observed at a distance of 90 m from the turbine foundations at the Block Island Wind Farm three years post-construction (Hutchison et al., 2020a; Wilber et al., 2022b). Also in the Belgian OWFs, an expansion of the artificial reef effect with increased abundances of hard-substrate species in the soft sediments (±250 m from the turbines) was observed seven years after construction (De Backer et al., 2021). So plaice in between the turbines can have access to hard-substrate prey species in the soft sediment as well.

Other studies that analysed stomach contents of benthopelagic and demersal fish near OWF structures also recorded more hard substrate species (e.g. *J. herdmani*, *Pisidium longicornis* and *M. edulis)*, typically found on the turbine foundations and the scour protection (Reubens et al., 2011a, 2013c; Derweduwen et al., 2016a; Mavraki et al., 2021). Divers even observed pouting *T. luscus* actively ingesting pieces of epibenthic material from the rocks of the SPL in a Belgian wind farm, which was reflected in their stomach contents and FA profiles (Reubens et al., 2014b). Although significant diet shifts linked to the presence of OWFs have not been reported for flatfish before, sampling distance from the turbines may explain why we did observe a clear shift. Individuals from the TB-group in this study were caught in the immediate vicinity of the turbine foundations (<10m), while flatfish in other studies were collected on the soft sediment in between the turbines (250 m or further) using a beam or bottom trawl (Derweduwen et al., 2012; Wilber et al., 2022b). These fish probably best resemble our WF-group (±200 m from hard substrate), for which no clear shift in diet was found either, only an increased presence of hard-substrate species for some of the individuals. Our results thus suggest a spatial gradient in short-term flatfish diet composition with increased importance of hard-substrate prey when moving closer to the turbine. This gradient might reflect the typical opportunistic feeding behaviour of flatfish, which eat what is readily available in their surroundings (Gibson et al., 2015).

Fish close to the turbine foundations also had fuller stomachs (although not significant) and heavier digestive tracts (digestive-somatic index) compared to fish on the sand in between the turbines and in control areas. This indicates that the presence of hard substrate offers increased food availability and/or prey items that are more easily accessible compared to the sandy habitat. This is in line with estimations from a Danish wind farm, suggesting a 50-fold increase of food availability for fish after its construction (Leonhard and Pedersen, 2006). It is assumed that the colonizing fauna on the turbines and scour protection, together with the increased habitat complexity, attract fish and other organisms, which is generally referred to as the artificial reef effect (Bohnsack and Sutherland, 1985; Reubens et al., 2013b; Krone et al., 2017; Degraer et al., 2020). The presence of such an attraction effect within the Belwind OWF has not only been demonstrated for cod and pouting, species known to be associated with hard substrates (Reubens et al., 2013a), but also for plaice increased abundances (x4) on the sandy patches in between the rocks of the SPL were observed (Buyse et al., 2022a). Alongside with the results of this study, plaice seems to be attracted towards the SPL because of the higher food availability.

4.4.2 BIOMARKERS SUGGEST LONG-TERM FEEDING ON SPL AND NEAR TURBINE FOUNDATIONS

Distinct FA profiles were observed for plaice near the turbine, further supporting the short-term differences in diet composition. As FAs reflect what fish have eaten on a time scale of weeks up to months, this indicates that they feed off the hard substrate for prolonged time and thus reside near the turbines and/or inside the wind farm for longer time periods. Plaice is known to have a very high site fidelity to feeding and spawning grounds (Solmundsson et al., 2005; Gibson et al., 2015), so it is possible that individuals reside in the OWF during spring, summer and autumn to feed. The FA profiles of plaice caught on the sandy sediments between the turbines (WF group) appear to be a transition between or combination of those of the TB and control groups, as no significant differences were found with any of the other groups. This pattern was also observed in the gut content analysis and may be explained either by an expansion of the artificial reef effect or by a mixed foraging strategy on the soft sediments with occasional trips to the hard substrates. Acoustic telemetry focusing on the small-scale movements of plaice in an OWF might be able to determine which of these hypotheses is correct (see Chapter 5).

Although SIA did not clearly reflect the presence of hard substrate on the isotopic niche of plaice, we did find lower δ^{15}N-values for the TB-group compared to the WF and NC-group and higher values compared to the FC-group (not significant). The discrepancy with the FA analysis might be related to hard substrate prey having a similar isotopic signature as prey found within soft sediments. Indeed, a trophic niche analyses of benthic organisms on and around the turbine foundations and SPL in the C-Power wind farm (BE) and across different depth zones found the largest standard ellipse areas for the SPL and the soft sediment habitat, which also largely overlapped (Mavraki et al., 2020). Other studies have indicated as well that FA profiles of different prey sources were more distinct compared to their stable isotope signatures (Rooker et al., 2006; Plumlee et al., 2021). Therefore, FA analysis might be a more suitable method for detecting shifts in diet when the trophic discreteness in consumers is expected to be low, such as with opportunistic or omnivorous feeding strategies (Persson et al., 1996).

No clear differences in the mean total concentration of PUFAs and the concentrations of (n-3) and (n-6) PUFAs were found among the sample groups, suggesting no major shifts in FA patterns (Dalsgaard et al., 2003; De Troch et al., 2012). Essential PUFAs cannot be synthesized in sufficient quantities by an organism itself and must therefore be obtained through its diet. In marine fish, docosahexaenoic acid (DHA, 22:6 n-3), eicosapentaenoic acid (EPA, 20:5 n-3) and arachidonic acid (AA, 20:4 n-6) are three essential dietary PUFAs that are required for normal growth and development (Sargent et al., 1999). This makes them particularly interesting to use as biomarkers in trophic interaction studies, especially because they are stored in tissues in their original state (De Troch et al., 2013; Plumlee et al., 2021). Higher relative concentrations of the essential PUFAs eicosapentaenoic acid (EPA) and arachidonic acid (AA) were found in individuals from the TB group compared to the control groups, while lower concentrations of docosahexaenoic acid (DHA) were found. These differences in essential PUFA-ratios support the presence of a diet shift associated with long-term feeding off the hard substrates, but do not indicate a difference in quality of diet (Dalsgaard et al., 2003).

Lower concentrations of bacterial FAs were found in the muscle tissue of plaice that were caught near the turbines compared to the control groups. Bacteria differ from eukaryotes in their ability to synthetize odd-numbered FAs such as 15:0, 17:0, 15:1, and 17:1. Therefore, such FAs can be used as a biomarker for bacterial food intake (Dalsgaard et al., 2003). One explanation for the observed results might be that plaice feeding off the hard substrate ingest less sediment and thus less organic material and associated bacterial compounds (Coates et al., 2011; Oni et al., 2015). Additionally, this pattern could be related to the feeding mode and diet composition of the prey themselves. Organisms that colonize the rocks of the SPL and turbine foundations mainly consist of suspension feeders (e.g. *J. hermani, M. edulis*), which mainly take up suspended particles in the water column (Mavraki et al., 2020). Prey species associated with the soft sediment, on the other hand, are more typically deposit feeders that consume higher amounts of organic matter and thus bacterial compounds (Braeckman et al., 2012; De Mesel et al., 2013; Mavraki et al., 2020). This difference in prey selection could explain the lower bacterial FA concentrations observed for plaice feeding off the hard substrates in OWFs. It is, however, not clear if and how this could impact plaice on the long term.

4.4.3 OWF EFFECTS ON PLAICE CONDITION

Fish caught within the wind farm were significantly larger than in the control areas, while age did not differ among sample groups. Further, a higher proportion of females was observed within the two impact groups compared to the control groups. Due to the sexual dimorphism that exists for plaice, with females being generally larger than males (Bromley, 2000), high fishing pressure is expected to involuntarily select for male fish that are smaller at a certain age. A larger fish size and a sex ratio that is skewed towards more females could therefore indicate that the presence of the OWF offers a refuge effect for plaice against fishing mortality (Di Franco et al., 2009; Florin et al., 2013). These results, together with the apparent increased food availability offered by the hard substrates, suggest that plaice can benefit from the presence of OWFs.

Hook-and-line fishing was used to collect the fish in the TB-group, while the fish of the other sample groups were caught using a beam trawl. This combination of two sampling methods could result in a bias due to differences in gear selectivity, especially for fish length. However, we are confident that this did not influence our results. Despite the fact that we found that fish size was significantly larger for the TB-group compared to the other groups, fish size was also higher for the WF-group that was sampled with a beam trawl. Further, the hook size (1/0), which was chosen based on the knowledge of an experienced recreational fisherman, targets both larger and smaller sized fish. This is corroborated by the fact that we also caught small sized dab (< 20 cm) using the same setup. Other sources of bias could be linked to the ontogeny or sex of the fish influencing their diet or condition. However, ontogenetic changes in diet are thought to be minimal for fish of larger size classes (Piet et al., 1998) and no differences were found between males and females for the calculated condition indices (except for GSI).

The diet and biomarker analyses further indicate that OWFs offer good quality prey items for fish. For example, the tube-building amphipod *J. herdmani*, found in high numbers in the guts of plaice caught near the turbines, has a very high energy content and optimal levels of the most important essential PUFAs (De Troch et al., 2013). Furthermore, prey items living on the rocks of the SPL and on the foundations are more accessible and thus require less energy to capture than prey living in the soft sediment. Also, the composition of the SPL in Belwind (large rocks in combination with sandy patches in between them) allow for plaice to bury, and thus hide from predators, in a structurally complex environment (Buyse et al., 2022b). By doing so, they can save energy that can be used for other purposes than predator avoidance, such as somatic growth or reproduction (Schwartzbach et al., 2020). All of this points to wind farms being favourable feeding grounds for plaice, which is confirmed by our study.

The combined results of different morphometric (i.e. Fulton's K with total (K_{TW}) and eviscerated fish weight (K_{EW})) and organosomatic condition indices (i.e. GSI, DSI and HSI), however, showed no clear effect of wind farm presence on the overall condition and fecundity of plaice. However, a spatial gradient can be recognized in the Fulton's K_{TW} index with higher values found for fish caught closer to turbines and a significantly lower overall condition for fish in the FC group. This could indicate a positive effect of the hard substrates on plaice condition, but might be mainly explained by a higher overall organ weight (liver, gonads and gut) rather than muscle tissue, as no such gradient was found for K_{EW}. The increased organ weight of fish caught near the turbines is probably due to a combination of a higher fullness, as the DSI was determined with gut contents, and a higher organ tissue weight. The observed gradient could then be an indication that the positive influence of the wind farm has spread beyond its borders. Although the selection of the control area locations was based on the similarity of environmental conditions such as sediment composition and depth, it is possible that the sampling locations of the FC group might not be truly comparable to the others, thereby explaining the large differences in fish condition and fecundity. These locations may be associated with lower food quality and supply, thereby negatively influencing fish condition (Lloret et al., 2002).

It is also possible that an overall wind farm effect on plaice condition is present, but could not be picked up due the large variation in the data (fish size, gender and age) and the relatively small sample size. However, differences in Fulton's K were found between juvenile common sole from different nursery areas in the southern North Sea using comparable sample sizes as in our study (Amara et al., 2007). In contrast, only increases in fullness index and length were determined for pouting between reference and impacted sites in and around the C-Power (BE) wind farm, while no differences in Fulton's K were found (Reubens et al., 2013c). It is possible that the presence of hard substrate has therefore no direct effect on fish condition or ovary weight, but rather leads to increased food intake and larger fish sizes due to the combination of an artificial reef and refuge effect, indicating that production could be occurring.

Combining a stomach and intestine content analysis with the use of biomarkers has enabled us to show that the presence of hard substrate in an OWF causes a clear diet shift for plaice, especially in the vicinity of the turbine foundations. Our findings highlight the need for the combination of diet analyses methods that give a high resolution in potential prey items on the short term (i.e. gut content analysis) and methods that provide insight in what is getting assimilated in the fish tissues on the long term (i.e. FA analysis and SIA) (Dance et al., 2018; Mavraki et al., 2021). By doing so, a more comprehensive understanding was obtained on the trophic ecology of plaice in relation to an OWF, from which inferences on its feeding behaviour on short and longer time scales were drawn. Although no significant differences in overall condition and fecundity were found related to the presence of hard substrate, larger individuals and a higher occurrence of females within the wind farm can point to a potential refuge effect of the OWF due to the absence of fishing activities. However, very small sampling sizes were used in this study, so follow-up studies that focus specifically on studying refuge effects in OWFs are needed to corroborate these findings. In addition, we found evidence that OWFs act as artificial reefs for plaice by providing higher food abundances that are potentially easier to access than soft sediment prey, thereby saving energy that can be used for different purposes such as somatic growth. Further, we recommend an analysis of plaice movement in relation to an OWF, as it would substantially increase the understanding of the observed patterns (Chapter 5).

4.5 ACKNOWLEDGEMENTS

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5 HARD SUBSTRATES IN OFFSHORE WIND FARMS INFLUENCE SPATIAL MOVEMENTS OF PLAICE *PLEURONECTES PLATESSA*

This chapter is in preparation to be submitted as Buyse, J., Hostens, K., Degraer, S., Reubens, J., Goossens, J., De Backer, A., Hard substrates in offshore wind farms influence spatial movements of plaice *Pleuronectes platessa*.

Abstract

The development of offshore wind farms (OWFs) is expanding rapidly in the North Sea in order to make the shift towards more renewable energy sources. The construction of OWFs takes up a lot of marine space, often not available anymore to commercial fisheries causing a conflict of space. At the same time, knowledge is still lacking on how OWFs influence soft sediment fish species, such as flatfish, which are an important fisheries resource in the southern part of the North Sea. To assess how OWFs can influence flatfish, it is vital to have information on their spatial behaviour within the wind farm and how they are connected to other areas. Therefore, this study aimed at investigating the small-scale movement patterns of European plaice *Pleuronectes platessa* around the turbines and scour protection, and its large-scale movements in relation to the OWF. We found a high residency for plaice within the small study area (4 km^2) during the feeding period in spring and summer; and a high site fidelity to the area as many fish returned after their winter spawning migrations. Although small-scale movements of fish around the turbine and scour protection revealed that they mainly stayed on the soft sediments around the hard substrate, a clear diurnal pattern was found in their distance to the hard substrate with fish being closer to the turbines during the day than at night. Based on knowledge of their trophic ecology and spatial distribution around the OWF hard substrates, we hypothesize that plaice undertakes feeding excursions towards the SPL due to an increase in food availability. This suggests that an increase in fish production might be occurring within the

OWF, which can potentially lead to a spillover. However, their high residency and site fidelity might limit this effect. This study provides important insights into the movement behaviour of plaice in relation to OWFs, which can inform management on how OWFs can influence local fisheries.

Key words

Passive acoustic tagging, YAPS, fish positioning, residency, site fidelity

5.1 INTRODUCTION

Offshore wind is expanding fast in the North Sea area to meet with the renewable energy goals set by the European Union, who aims to be climate neutral by the end of 2050 (European Commission, 2019; WindEurope, 2022). At the end of 2021, a total of 5,785 turbines divided over 122 offshore wind farms (OWFs) supply 28.3 GW of power to twelve different European countries (WindEurope, 2022). These developments take up a vast amount of marine space, which is often not available anymore for commercial fisheries activities as the concession holders apply strict safety rules within the wind farm areas. As a consequence, fishers are forced to relocate to potentially less ideal fishing grounds, which can cause a decrease in revenue (Stelzenmüller et al., 2021). This causes a spatial conflict between the two sectors that will likely increase in the future, as the majority of OWF projects are still in the planning phase (Stelzenmüller et al., 2022). As it looks now, present and planned OWFs will occupy ten percent of the total surface area of the North Sea basin in the future (EMODnet, 2022).

The development of OWFs does not only affect fisheries directly through a decrease in their fishable space, but the introduction of hard substrate in an often soft sediment environment can also influence fisheries resources such as finfish (Gill et al., 2020). Up till now, no clear negative effects of OWFs on fish have been found (Langhamer et al., 2009; Leonhard et al., 2011; Lindeboom et al., 2011; Wilhelmsson and Langhamer, 2014; Stenberg et al., 2015; Wilber et al., 2022a). On the contrary, due to the cessation of bottom trawling activities within their concession areas, it is thought that OWFs can cause a refuge effect for fished species similar to what is observed for marine protected areas (Fenberg et al., 2012; Halouani et al., 2020). Moreover, the hard substrate in the form of turbines, their foundations and the surrounding scour protection is found to aggregate various hard-substrate fish species. This is referred to as the artificial reef effect and is often explained by an increase in food and/or shelter opportunities (Degraer et al., 2020). However, evidence-based information on the ecological effects of OWFs on soft-sediment species, such as flatfish, is still largely lacking. This while two of the most important target species in the southern North Sea are flatfish (i.e. plaice and sole *Solea solea*) (Polet et al., 2022).

To be able to assess how OWFs can influence local fisheries resources, it is crucial to have thorough knowledge on the spatial behaviour of target species within the wind farm area and their connection to other areas. Spatial movements of fish individuals around artificial structures in OWFs can give an indication of their importance and the role they play for the species (Winter et al., 2010; Reubens et al., 2013b; Mitamura et al., 2021). Further, to investigate whether a protected area can benefit a certain species, it is crucial to have information on its movement patterns in relation to the area (Shipp, 2003). Fish that constantly move in and outside the protected area, for example, will profit less from its protection than fish that remain within its boundaries. However, fish that do not leave the area cannot support local fisheries through spillover (Miethe et al., 2010). There is thus a trade-off between the level of protection an area can offer and its ability to support local fisheries, depending on the spatial behaviour of the target species.

This study aims at investigating the spatial movements of plaice in relation to an OWF. Plaice *Pleuronectes platessa* is an economically valuable flatfish species common in the North Sea. Plaice exhibits large-scale migrations from their feeding grounds, where they reside during spring, summer and early autumn, to various spawning locations during the winter months (December-March) (Rijnsdorp, 1989; Gibson, 1997). Their main spawning areas are located in deeper waters in the North Sea, English Channel and the Irish Sea (Ellis et al., 2012). Plaice shows high fidelity towards both their feeding and spawning areas and were often recaptured years later only hundreds of meters away from their original release location (Solmundsson et al., 2005). They are typical visual daytime feeders that exhibit a diurnal feeding pattern (Gibson et al., 2015). When the light intensity reaches a certain threshold during morning hours, they start swimming just above the sea bottom in search of prey. During the evening, when light intensities drop below their visibility threshold, they leave the bottom and go higher up in the water column. However, if light intensity is too high during the day (e.g. at noon during a sunny day), they enter an inactive phase by digging themselves into the sand (Verheijen and De Groot, 1967; De Groot, 1971). This observed feeding pattern is reflected in the catch rates of plaice, which are higher during the day than at night when bottom trawls can pass under the fish as they are swimming closer to the sea surface (De Groot, 1971).

Diving transects in the Belwind wind farm (Belgium) together with an analysis of their trophic ecology showed that plaice was attracted towards the sandy patches in between the rocks of the SPL and that they fed on typical hard-substrate species when they were present in the vicinity of the turbines (Buyse et al., 2022, Buyse et al., in revision). However, it remains unclear how strongly plaice is associated with the SPL and whether they use it for foraging and/or as shelter against predators and currents. In addition, knowledge on their spatial movements in relation to an offshore wind farm is also lacking. An interesting method for studying the spatial movements of fish within the marine environment is acoustic telemetry, especially in areas with limited accessibility where traditional sampling methods such as nets or trawls cannot be deployed (Reubens et al., 2013b; Keller et al., 2017). It has already been used in artificial reef research to study residency, site fidelity and feeding habits of fish in relation to artificial structures (Winter et al., 2010; Reubens et al., 2013b, 2014a; Mitamura et al., 2021). Further, it was also successfully applied to assess the benefits of marine protected areas for fish and investigate its possibilities for spillover to adjacent areas (Abecasis et al., 2014; Novak et al., 2020). The specific aims of this study were to investigate the (1) residency of plaice within an OWF (2) their site fidelity towards the wind farm in relation to their yearly spawning migrations and (3) their habitat association near the artificial hard substrates.

5.2 MATERIALS AND METHODS

5.2.1 STUDY SITE

This study was carried out in the Belwind (51° 39′ 36″ N, 2° 48′ 0″ E) offshore wind farm (OWF) in the Belgian part of the North Sea (Figure 5.1 A). Belwind is located on the Bligh Bank, a natural sandbank situated 40 km off the Belgian coastline at depths between 15-37 m. The construction of the wind farm started in 2009 and included the installation of 55 turbines (Vestas, 3 MW) on monopile foundations with a diameter of 5 m at a distance of 450-670 m from each other. In 2013, one additional larger turbine on a jacket foundation was added in the northern part of the wind farm (Haliade, 6 MW) for demonstration. A scour protection layer (SPL) with a radius of approximately 16.5 m, consisting of a filter layer and an armoured layer on top, was added around each turbine to prevent the surrounding sand from eroding due to the change in current patterns (Coates et al., 2016). About three months before construction started, the entire concession zone was closed off for all vessel traffic, except for scientific or maintenance purposes.

5.2.2 RECEIVER ARRAYS

In the period May 2020-August 2021, three different arrays of VR2AR receivers (69 kHz, InnovaSea Systems Inc., USA) were deployed during three different periods in the southern part of the OWF (Figure 5.1 B-D). This part of the wind farm has less variation in bathymetry compared to the northern part, which increases the detectability of the transmitters by the bottom-anchored receivers. Each array setup had its specific objectives and was constrained by the availability of receivers. The first array (May 2020–October 2020) existed of 28 receivers and was specifically designed to assess small-scale movement patterns of plaice relative to the SPL during the summer-autumn feeding period (Gibson, 1997). Therefore, three turbines (B9, C8 and D9) were each surrounded by six receivers at a distance of ±150 m from the turbine (Figure 5.1B). In addition, ten receivers were put on the sand in between the turbines to cover a larger area for studying the residency of plaice in relation to (that area of) the wind farm. During the first month of the study, a range test was carried out to assess the relationship between the distance of a transmitter to a receiver, the influence of different environmental conditions and the detection probability (Goossens et al., 2022). This study indicated that, for the array used during the first period, the predicted cumulative detection probability over an entire day was 100% up to a distance of 600 m from a receiver and this under average noise conditions. Taking this modelled range into account, it was highly unlikely that plaice, considered a slow-moving species, was present on a certain day within the study area without being detected. The second array (n = 28, October 2020-February 2021) was deployed during the spawning period of plaice and mainly aimed at assessing if plaice left the OWF and if they returned to the OWF after spawning was over. As several tagged fish were still being detected around turbine B9 in October 2020, we chose to keep the design with the six receivers surrounding it, while the rest of the receivers were redeployed either in the middle of four turbines or in the vicinity of a turbine. Therefore, this design allowed for both the studying of small-scale movement patterns and the assessment of the homing behaviour of plaice in relation to the study area. Finally, the third array (n = 15, February 2021-August 2021) was purposed to detect the return of the plaice individuals to the OWF after spawning. To increase the detectability of the fish on their return, the available receivers were evenly spread out over the study area. All receivers were deployed on the sea bottom using tripod moorings. For a detailed description of the mooring method, the reader is referred to Goossens et al. (2020).

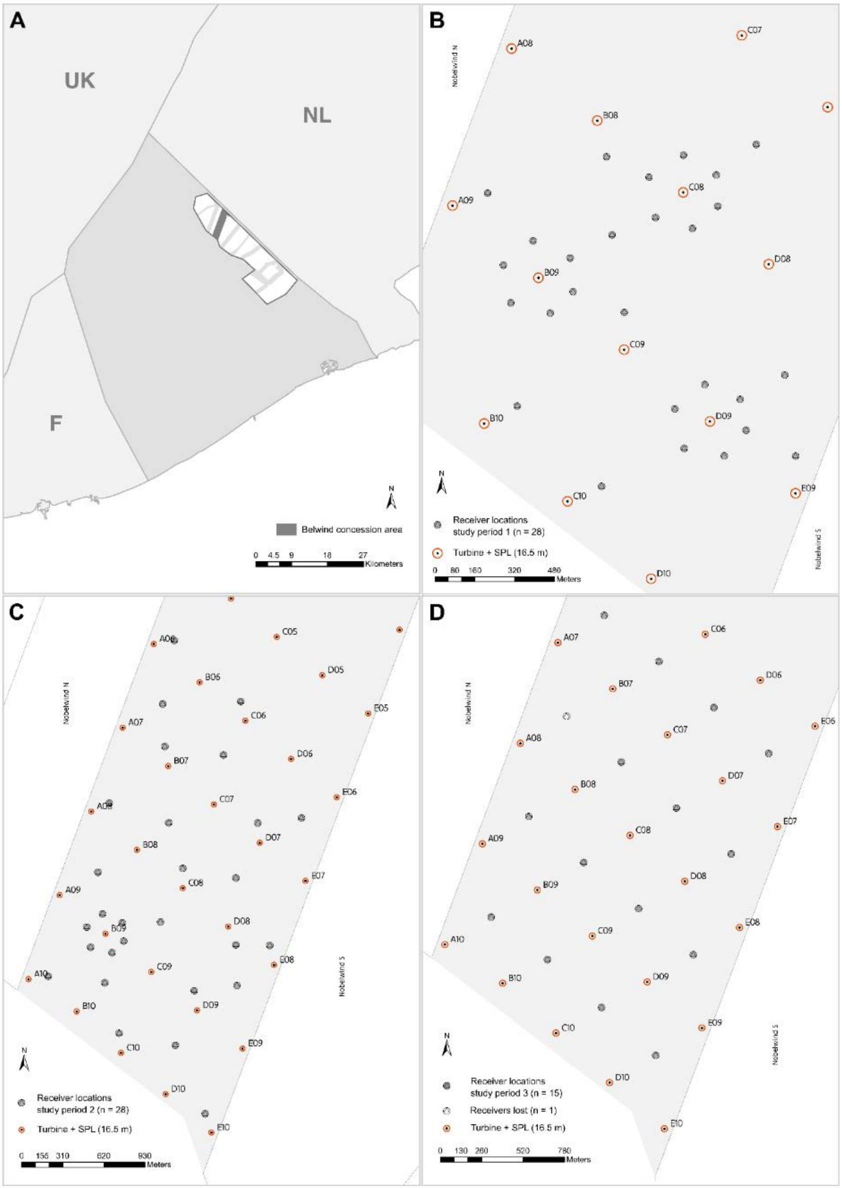

Figure 5.1: (A) Map showing the location of the Belwind wind farm in the Belgian part of the North Sea. (B) Overview of the receiver array used during the first study period (May 2020–October 2020), (C) second study period (October 2020–February 2021) and (D) third study period (February 2021–July 2021) within the Belwind wind farm to analyse movement patterns of plaice.

5.2.3 TAGGING PROCEDURE

For the tagging of plaice, Thelma Biotel MP9 transmitters (69 kHz, 146 dB, 9 x 24.4 mm, 3.6 g in air, 2.1 g in water) were used, which emit an acoustic signal that can be translated to a unique ID. The transmitters were preprogrammed to emit an acoustic signal with an interval between 70–130 seconds for the first 200 days after activation and then switched to a transmission interval of 150–210 seconds for the following 90 days. For the remaining battery life of the transmitter, the interval was switched again to 70–130 s. These settings were chosen to maximise the battery life of the transmitters (estim. 522 days) without compromising the data resolution. The 90 days with the longer transmission interval was timed to coincide with the spawning period of plaice, when they were assumed to have moved out of the study area.

A total of 31 plaice individuals were caught between May 2020–October 2020 near the turbines of the study array using one of two methods: (1) hook and line fishing from a research vessel or zodiac or (2) diving combined with the use of a small hand net (Table 5.1). Hooks (Gamakatsu, size 1/0) without barbs were used to minimise the tissue damage to the mouths of the fish. After a fish was caught, it was transferred to an aerated water tank until the tagging was carried out. Total fish length ranged from 29-39.5 cm. Based on the length-weight relationship for plaice, it was calculated that the transmitters made up between 0.6-1.5% of the fish body weight in air (Froese R. and Pauly, 2022). The tags were externally mounted to the fish, which is a commonly used tagging method for dorsoventrally compressed species as their peritoneal cavities are usually very small. In general, external tagging was found to be favourable for bottom-dwelling flatfish that live on flat surfaces (Jepsen et al., 2015) (Figure 5.2). Further, external attachment of transmitters to European flounder *Platichthys flesus* was found to cause fewer adverse effects for the fish compared to the internal tagging procedure (Neves et al., 2018). The tagging method used in this study was based on procedures described in previous studies, but was slightly adapted to decrease the handling time of the fish (Bridger and Booth, 2003; Hunter et al., 2003; Neves et al., 2018). In order to make external tagging possible, the transmitters were first secured to a stainless steel wire (0.6 mm) using a piece of heat shrink tubing. The fish were first transferred onto a piece of foam soaked in sea water with a wet cloth covering their heads and gills. Next, the transmitter was attached anterior to the dorsal fin by first passing two 19-gauge syringe needles (Terumo Agani) ventrally through the dorsal musculature at a distance equal to the length of the transmitter. Next, both wires at each side of the transmitter were passed through the needles, after which the needles were removed. On the ventral side, a small piece of rubber (25 x 10 x 1 mm) was fixed against the fish skin to protect it from abrasions. Finally, both wires were secured together using a small metal fishing crimp.

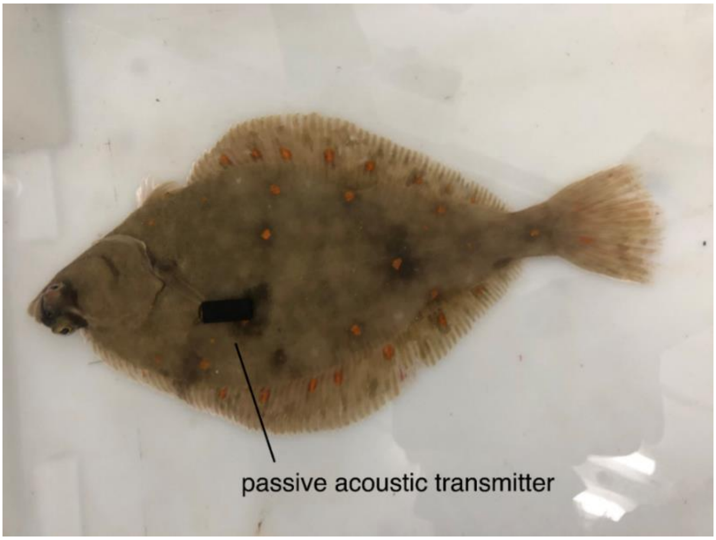

Figure 5.2: Plaice equipped with an externally attached ID-MP9 transmitter (Thelma Biotel).

Throughout the procedure, all wounds were disinfected using betadine and all equipment was sterilized with 70% ethanol beforehand. The time it took to complete the entire procedure was approximately three minutes. Afterwards, the fish were transferred into a large, aerated holding tank and, after normal swimming behaviour was observed, the fish were carefully released as close to their catch position as possible. The experimental protocol was approved by the ethical committee of the Flanders Research Institute for Agricultural, Fisheries and Food (ILVO) (Permit Number: EC 2020/366).

Table 5.1: Summary of the metadata and acoustic monitoring data for the 31 tagged plaice individuals. Days in the field is defined as the period between the release date and the end of the overall study period (11/07/2021).

Fish ID	Release date	Last detected	Capture method	Capture/release location	Total length (cm)	Days in the field	Days detected
T9246	15/05/2020	28/09/2020	hook and line	SPL D09	32	423	131
T9247	15/05/2020	11/11/2020	hook and line	SPL C08	29	423	62
T9248	19/06/2020	19/11/2020	hook and line	SPL C08	34	388	135
T9249	15/09/2020	07/10/2020	hook and line	SPL C09	32	300	15
T9250	17/06/2020	10/07/2021	diving	SPL C08	32	390	195
T9251	19/06/2020	14/11/2020	hook and line	SPL B09	38.5	388	149
T9255	14/07/2020	11/07/2021	hook and line	SPL C08	34.5	363	192
T9256	14/07/2020	25/03/2021	hook and line	SPL C08	39.5	363	98
T9257	17/10/2020	18/10/2020	hook and line	SPL C08	36	268	2
T9258	15/09/2020	19/09/2020	hook and line	SPL D09	33	300	5
T9259	14/08/2020	04/07/2021	hook and line	Sand near B09	31	332	282
T9260	19/06/2020	20/06/2021	hook and line	SPL B09	34	388	250
T9262	17/10/2020	21/10/2020	hook and line	SPL C08	31	268	5
T9263	17/06/2020	24/03/2021	hook and line	SPL D09	34.5	390	151
T9264	16/06/2020	08/12/2020	diving	SPL B09	35	391	92
T9265	17/06/2020	10/11/2020	hook and line	SPL D09	34.5	390	100

Table 5.1 continued

Fish ID	Release date	Last detected	Capture method	Capture/release location	Total length (cm)	Days in the field	Days detected
T9268	10/09/2020	22/02/2021	hook and line	Sand near E08	32.5	305	2
T9269	15/09/2020	11/07/2021	hook and line	SPL D08	39	300	98
T9272	17/06/2020	23/03/2021	hook and line	SPL D09	34.5	390	244
T9273	17/06/2020	13/12/2020	hook and line	SPL D09	35	390	82
T9274	16/06/2020	20/06/2021	diving	SPL B09	30	391	156
T9275	15/09/2020	15/06/2021	hook and line	SPL D08	33.5	300	38
T9276	16/06/2020	04/07/2021	diving	SPL B09	31.5	391	40
T9277	17/06/2020	11/07/2021	hook and line	SPL D09	37.5	390	180
T9279	13/08/2020	21/12/2020	hook and line	SPL D09	33	333	67
T9280	10/09/2020	10/07/2021	hook and line	SPL C09	31.5	305	179
T9281	17/06/2020	29/09/2020	diving	SPL C08	32	390	103
T9282	19/06/2020	31/10/2020	hook and line	SPL B09	32.5	388	135
T9283	17/06/2020	12/08/2020	hook and line	SPL B09	36	390	5
T9284	14/07/2020	20/06/2021	hook and line	SPL C08	35	363	127
T9285	17/06/2020	06/08/2020	hook and line	Sand between row B & C, 9 &10	33	390	11

5.2.4 DATA ANALYSIS

5.2.4.1 Residency and long-term presence

The residency of plaice within the study area was studied using daily binary presence/absence data of the tagged fish that were present during the first monitoring period (May 2020-October 2020). A fish was considered to be present in the study area on a certain day when it was detected at least twice on that particular day (Meyer et al., 2007; Ramsden et al., 2017). Data was scanned for erroneous detections based on visual inspections using graphs and spatial maps. The residency index (RI) was calculated for each individual fish as

RI = number of days detected/days at large

with days at large = last day of detection during first monitoring period – release date of the fish

Only the data of fish that were at least 20 days at large were used to calculate the mean residency index for plaice in the study area. Further, the presence/absence data per day from the three receiver arrays was used to describe the long-term movement patterns of plaice in relation to the wind farm.

5.2.4.2 Site fidelity of plaice towards the OWF

The site fidelity of plaice in relation to the study area was analysed using the presence/absence data of all three receiver arrays. Although it was not possible to follow the fish when they moved outside of the study area, long term absences during the spawning period followed by regular presences after spawning would strongly suggest that fish migrated to the spawning grounds and returned to the study area to feed during spring and summer.

5.2.4.3 Small-scale movements around the turbine

Estimation of positions

The data from the first sampling array (May 2020-October 2020) were used to estimate fish positions of five fish (9250, 9251, 9260, 9272 and 9282) that were present during long uninterrupted periods in the study area. The day on which a fish was tagged and the following day were removed from the dataset to avoid any effects of the tagging procedure on their behaviour. A fine-scale positioning system was used to the estimate the spatial positions using YAPS (Yet Another Position Solver), a model that combines the signal time of arrival (TOA) at fixed receiver positions with a random walk movement model (Baktoft et al., 2017, 2019). This method was chosen over other more traditional methods as it allows for complete transparency of the data analysis and was shown to offer better accuracy and error control than alternatives (Baktoft et al., 2017). Before any positions could be estimated, the receiver array first had to be synchronized to ensure the quality of the output. The VR2AR's built-in transmitters of all the receivers were used as sentinel tags (mean transmission interval of 10 s) for the development of the synchronisation model. Synchronisation of the array and the validation of the model was applied using the yaps package in R (github.com/baktoft/yaps), following the method described in Baktoft et al. (2019).

After the synchronisation model was applied to all the detections, the positions of each fish were estimated separately using the YAPS model. To make the estimation process easier, each dataset was split up in 4-hour bins with a shift of 1 hour. These overlaps were used to reduce any edge effects. The model was run on each chunk of data five times and only the output of the model with the lowest object score (comparable to the Akaike Information Criterion) was retained for further analysis (Hendrik Baktoft, personal communication). In addition, only detections that were logged by three or more receivers were retained (Espinoza et al., 2011) and estimated positions with a standard deviation for the x or y position of more than 10 m were also deleted. The filtered positions had an average standard deviation of 1.22 m for the x-coordinate and 1.23 m for the y-coordinate. This stringent filtering was done to ensure that the estimated positions were as reliable as possible before they were used in any further analyses.

Habitat selectivity, distance and angle in relation to the turbine

The filtered estimated positions were used to calculate the distance between each position and the nearest turbine of the selected five fish. Based on the distance to the turbine, each estimated position was then assigned to one of three different habitat types: (1) scour protection layer when the estimated position was located closer than 16.5 m from the turbine, (2) soft sediments close to the hard substrate between 16.5 and 50 m from the turbine and (3) soft sediments further away from the hard substrates for positions >50 m from the turbine. To test for a diurnal pattern in the distance of the fish to the hard substrate, data on sunlight times were used to create a categorical variable *light* with four different levels: dawn, day, dusk and night. Nautical dusk and dawn times (sun is 12° below the horizon) were used to differentiate between night and dusk/dawn, while sunrise and sunset times were used to distinguish between day and dusk/dawn. A linear mixed model (LMM) with a Gaussian distribution was fitted using distance of the fish to the nearest turbine as a response variable. *Light* was added as a fixed effect to the model and fish ID was included as a random variable to incorporate the variance between the different fish. The final model that was fitted was

Distance ~ light + (1 | fish ID)

Furthermore, the angle between the turbine and each estimated position was calculated to analyse whether the fish showed a preference of direction in relation to the hard substrate. The main current direction was also calculated based on modelled forecast data for the Bligh Bank area (Legrand and Baetens, 2021). Distance calculations were carried out in ArcMap version 10.4, while all other calculations were performed in R version 4.2.1 (R Core Team, 2022).

5.3 RESULTS

5.3.1 RESIDENCY AND LONG-TERM PRESENCE IN THE WIND FARM

During the first study period (May 2020-October 2020), the 29 fish tagged were detected for 1–131 days (Table 5.2). Many fish were present in the wind farm for long uninterrupted periods after their release date during the summer and autumn months and most of them were still present at the end of the first study period (11/10/2020) (Figure 5.3). Three fish (9257, 9258 and 9262) were only detected for a few days after their release date and were never detected again. Eleven of the 31 fish were (re)detected after one year and seven fish were detected in the wind farm until the last two weeks of the study. During the winter months, fewer detections in the study area were observed. Residency for fish that were at least 20 days at large during the first period (n = 24) ranged from 0.09–1 with an average residency of 0.78±0.29 and most fish had a high index value (70% of the fish had an RI of at least 0.75).

Table 5.2: Residency index (RI) for all 29 fish that were present during the first period of the study (15/05/2020–11/10/2020). Days at large and last detections are given for the first study period only.

Fish ID	Release date	Last detection	Days detected	Days at large	RI
9246	15/05/2020	28/09/2020	131	137	0.96
9247	15/05/2020	27/07/2020	61	74	0.82
9248	19/06/2020	11/10/2020	109	115	0.95
9249	15/09/2020	07/10/2020	15	23	0.65
9250	17/06/2020	11/10/2020	115	117	0.98
9251	19/06/2020	11/10/2020	115	115	1.00
9255	14/07/2020	11/10/2020	85	90	0.94
9256	14/07/2020	25/09/2020	72	74	0.97
9258	15/09/2020	19/09/2020	5	5	1.00
9259	14/08/2020	11/10/2020	59	59	1.00
9260	19/06/2020	11/10/2020	115	115	1.00
9263	17/06/2020	11/10/2020	76	117	0.65
9264	16/06/2020	10/10/2020	71	117	0.61
9265	17/06/2020	21/09/2020	97	97	1.00
9268	10/09/2020	14/09/2020	1	5	0.20
9269	15/09/2020	11/10/2020	21	27	0.78
9272	17/06/2020	10/10/2020	103	116	0.89
9273	17/06/2020	31/07/2020	45	45	1.00
9274	16/06/2020	11/10/2020	115	118	0.97
9275	15/09/2020	09/10/2020	3	25	0.12
9276	16/06/2020	16/06/2020	1	1	1.00
9277	17/06/2020	11/10/2020	80	117	0.68
9279	13/08/2020	06/10/2020	16	55	0.29
9280	10/09/2020	11/10/2020	31	32	0.97
9281	17/06/2020	29/09/2020	103	105	0.98
9282	19/06/2020	11/10/2020	115	115	1.00
9283	17/06/2020	12/08/2020	5	57	0.09
9284	14/07/2020	11/10/2020	69	90	0.77
9285	17/06/2020	06/08/2020	11	51	0.22

5.3.2 SITE FIDELITY OF PLAICE TOWARDS THE OWF

Several fish (9250, 9255, 9256, 9260, 9269, 9275, 9277, 9280 and 9284) were absent for consecutive months, which coincided with the spawning period of plaice (December-March), after which they returned to the study area during spring. One fish (9277) was tagged on 23/05/20 and remained in the wind farm, with the exception of two longer periods of absence, until 16/10/20. After being completely absent for more than 111 days, it was detected twice on 5/02/21 at receiver station bpns-Westhinder (51° 22' 52" N, 2° 27' 10" E) in the western part of the Belgian part of the North Sea (BPNS). Almost 11 days later, it was detected again within the Belwind wind farm and remained present there until the end of the study period (17/07/21).

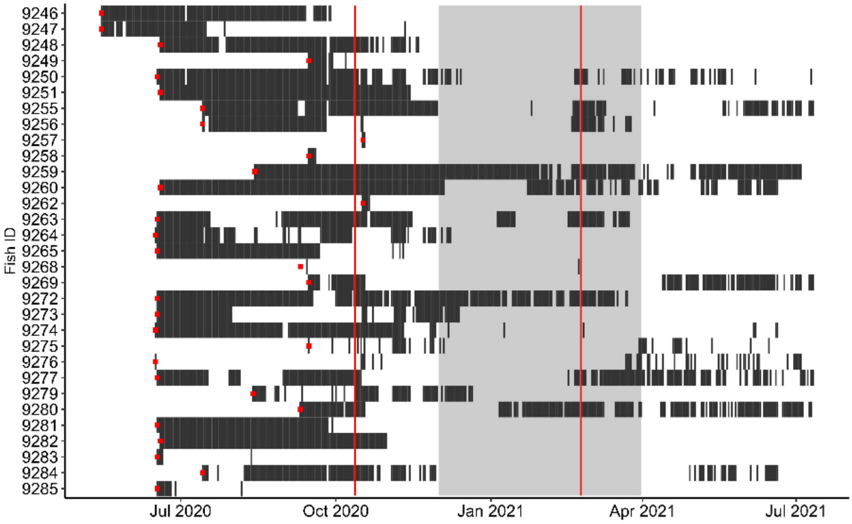

Figure 5.3: Presence per day of the 31 tagged plaice over all study periods (15/05/2020-11/07/2021) in Belwind. Red squares indicate the tagging and release date of the fish, while the red vertical lines show the change in receiver array design and thus represent the divisions between the 3 different study periods (period 1: 15/05/2020-11/10/2020; period 2: 14/10/2020-22/02/2021; period 3: 25/02/2021-11/07/2021). The grey box represents the yearly spawning period for plaice in the southern North Sea (December-March with a peak in January). A fish was considered to be present in the study area if it was at least detected two times on that particular day.

5.3.3 HABITAT SELECTIVITY, DISTANCE AND ANGLE

The habitat selectivity and angle in relation to the turbines was determined for 79137 estimated positions of five fish with a high residency index (RI>0.89) and almost continuous presence in the study area during the first period (Table 5.3). Overall, the fish stayed relatively close to the hard substrate with a mean distance of 69.1±46.3 m from the turbine and 52.6±46.3 m from the SPL. For two fish (9251, 9282), more than 50% of their estimated positions were located on the SPL or on the soft sediment close to the hard substrate (<50 m). The other fish were mainly detected further away from the hard substrate (9250, 9260, 9272) (>50 m). Only a minority of the detections were located within the range of the SPL (4.55±4.76%), but large variation existed between the different fish (0.1%-9.6%).

Table 5.3: Habitat selectivity based on the distance of the estimated positions of the five plaice individuals to the nearest turbine.

Fish ID	9250	9251	9260	9272	9282
Total estimated positions	1280	19822	19653	11905	26477
SPL (0-16.5 m)	10 0.8%	1901 9.6%	24 0.1%	304 2.6%	2098 7.9%
Soft sediment close (16.5-50 m)	99 7.7%	8170 41.2%	4638 23.6%	1200 11.2%	13444 50.8%
Soft sediment far (>50 m)	1171 91.5%	9751 49.2%	14991 76.3%	10401 86.2%	10935 41.3%

The linear mixed model identified the presence of a diurnal pattern in the distance of the fish to the hard substrate ($\chi^2 = 4176.8$, $p<0.001$) with fish being closer to the turbine during dawn (75.7 m, $CI_{0.95}$[51.1-100]) and daylight hours (78.3 m, $CI_{0.95}$[53.8-103]), while they were positioned further away during dusk (104.2 m, $CI_{0.95}$[79.5-129]) and at night (97.4 m, $CI_{0.95}$[72.8-122]) (Figure 5.4).

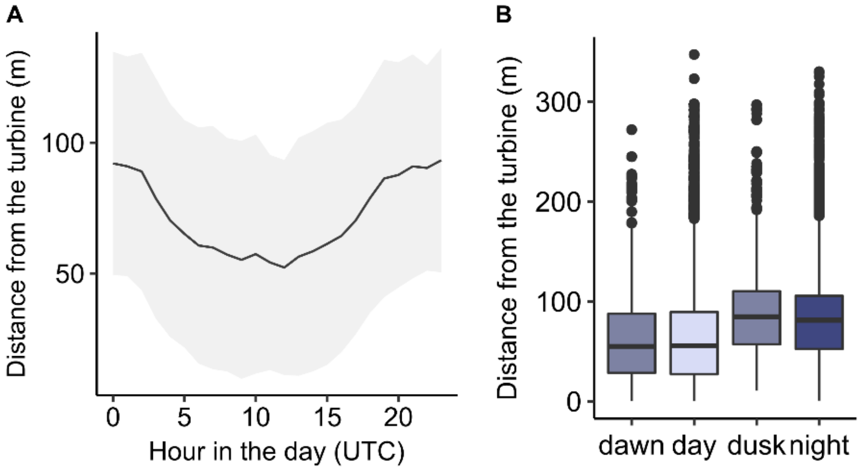

Figure 5.4: (A) Relationship between the distance of the fish from the turbine and the hour in the day. The black line represents mean values for all five fish and for all days of the first monitoring period, while the grey band represents SD-values. (B) Boxplot showing the distance of the fish from the turbine in relation to the four levels of the categorical variable *light*.

There is an increase in the number of detections during morning and evening hours, while a lower number of detections are observed during night and midday (Figure 5.5 A). Fish were positioned on the SPL almost exclusively during daylight hours.

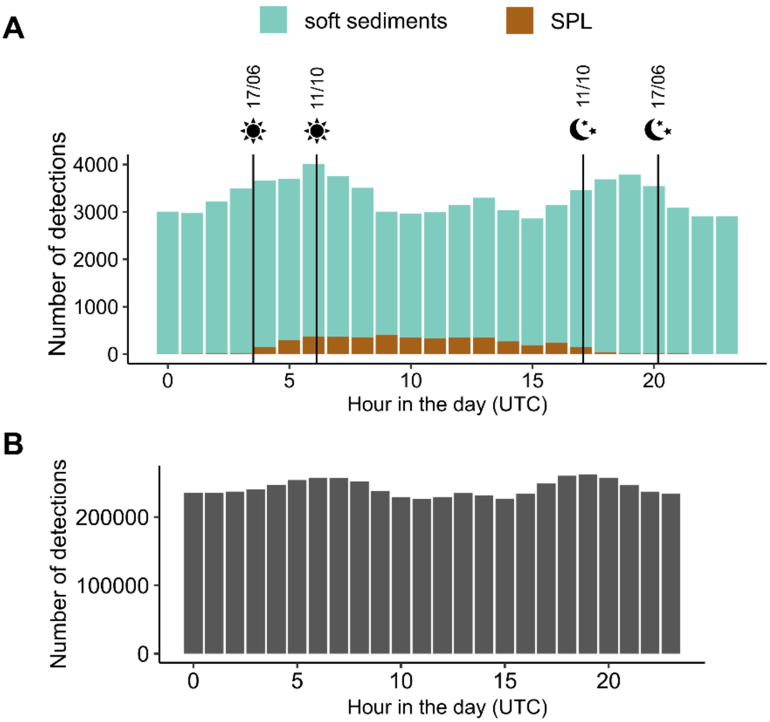

Figure 5.5: (A) Number of estimated positions over hour in the day for the first monitoring period (May 2020-October 2020). Vertical lines indicate the sunrise and sunset times for the first and last day of the monitoring period. Detections are considered to be on the SPL if the distance to the turbine <16.5 m. (B) Total number of detections over the hour of day for the first monitoring period (May 2020-October 2020).

The mean angle between the estimated positions and the turbine showed large differences between the different fish (Figure 5.6). While one fish (9260) clearly preferred to position itself along the direction of the main current (218°-38°), other fish did not show this pattern (9250, 9251). Most fish did show a preference for a certain direction in relation to the hard substrate with most positions located between 0 and 90°. It is also clear from the estimated fish positions that individuals preferred to stay around a certain turbine, with only occasional straying towards other turbines (Figure 5.7).

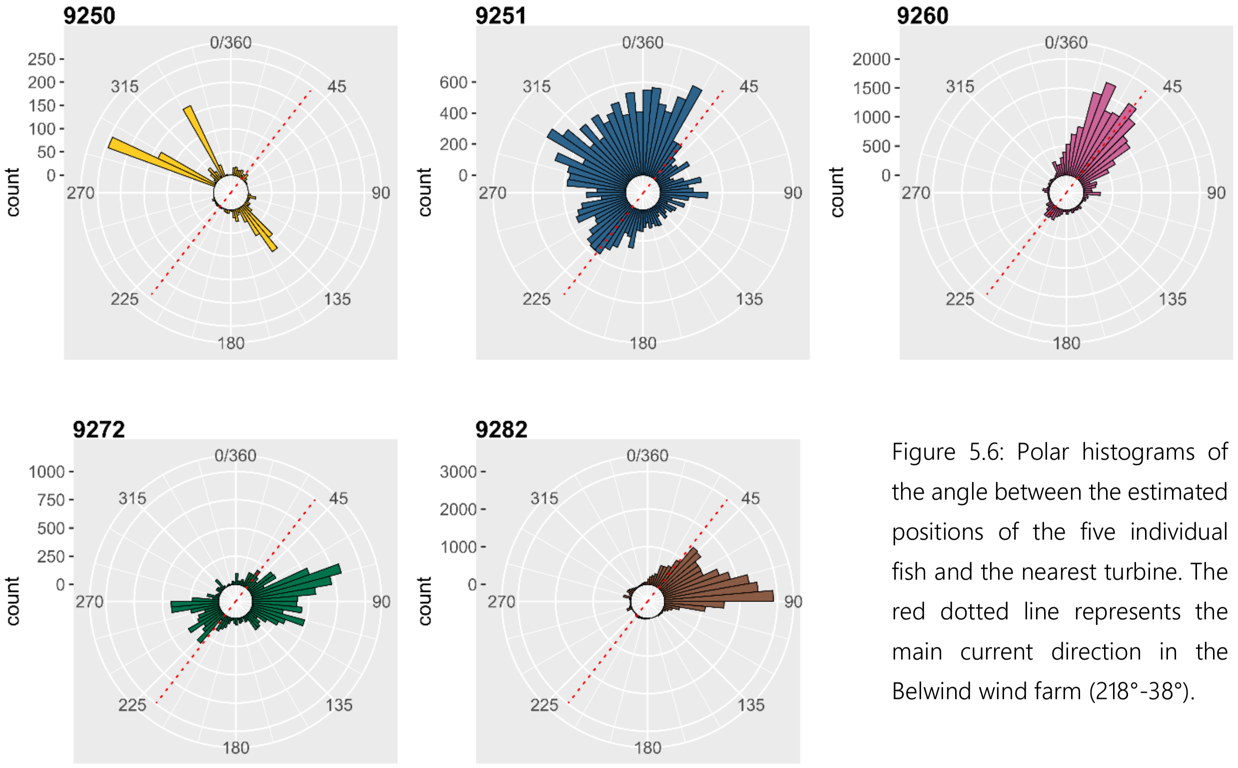

Figure 5.6: Polar histograms of the angle between the estimated positions of the five individual fish and the nearest turbine. The red dotted line represents the main current direction in the Belwind wind farm (218°-38°).

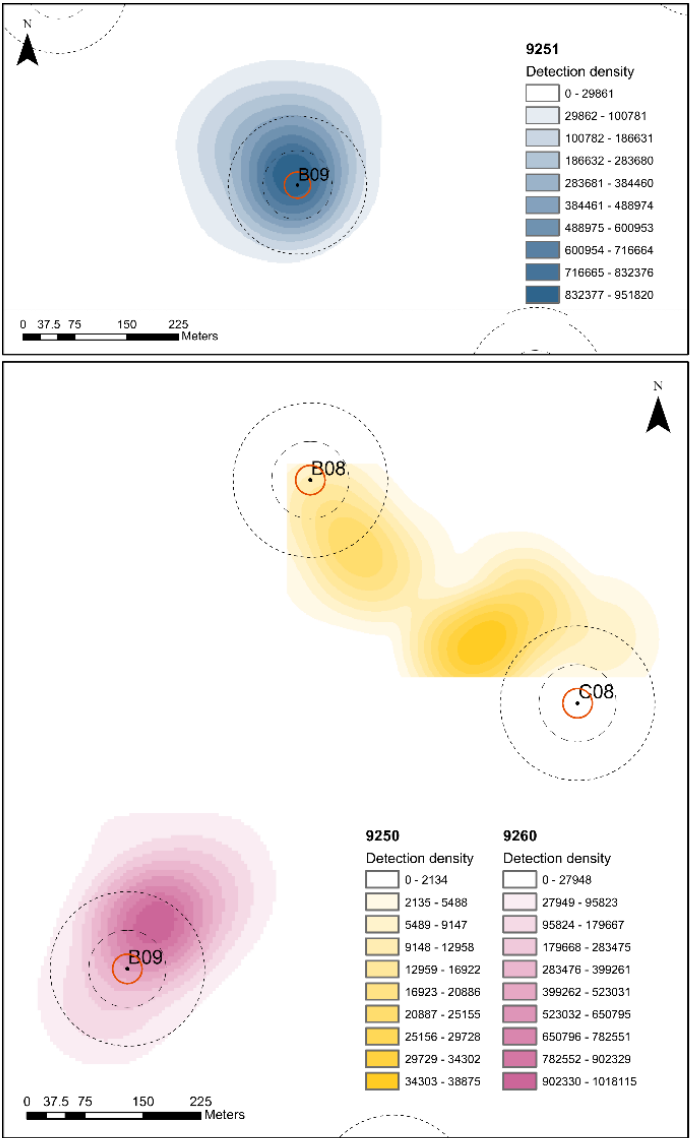

Figure 5.7: Spatial distribution (Kernel densities) of individual fish (9250, 9251, 9260, 9272 and 9282) based on the number of their estimated positions during the first study period (May 2020–October 2020). Turbines (diameter 5 m) are represented by black dots. The extent of the scour protection (16.5 m from the turbine) is shown as a red line, the dashed line shows a buffer of 50 m and the dotted line represents a buffer of 100 m.

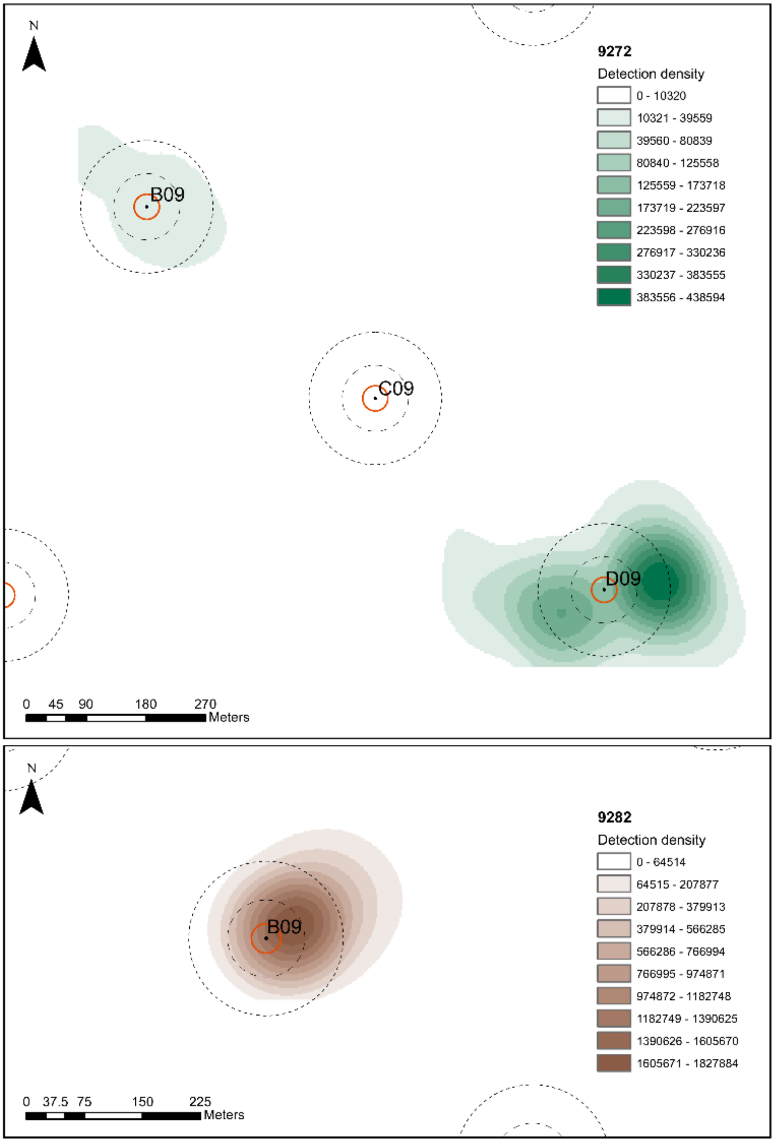

Figure 5.7 continued.

5.4 DISCUSSION

5.4.1 RESIDENCY AND SITE FIDELITY

Even though the study area was very limited in surface area (4 km^2), a relatively high residency was found for the 29 fish that were followed during summer and early autumn (first receiver array). This residency indicates that, during the feeding season, individuals do not travel over very large distances in search of their food and mainly remain within the borders of the wind farm. Despite some fish showing absences of days up to weeks during the first study period, it is still possible that they remained within the wind farm, but were not detected as they travelled outside of the study area. Plaice, like most other flatfish, is an opportunistic feeder that forages on what it can find in its immediate surroundings and their spatial distribution is, therefore, largely driven by the availability of prey (Gibson, 1997; Shucksmith et al., 2006). A high residency within a small area thus suggests that there is a sufficient amount of food available. This is supported by the findings of the trophic analysis, which showed that plaice had fuller digestive tracts when present in the vicinity of the turbines (Buyse et al., 2023). The clear preference of the studied fish for a particular turbine further corroborates this.

The presence-absence data for the three receiver arrays indicated that 11 out of 31 (35%) fish were still present within the study area one year after tagging. Tagging studies of plaice in the North Sea generally indicate a very strong site fidelity towards the spawning and feeding grounds, however, only limited quantitative information is available (De Veen, 1978; Rijnsdorp and Pastoors, 1995; Hunter et al., 2003). A mark-recapture study on European plaice conducted off the coast of Iceland estimated that their fidelity to the feeding grounds was 90% after one year and at 100% after two and three years from tagging. However, this is on a scale of tens of kilometres, while our study area is much smaller (4 km^2). This same study reported that 38.1% of males and 50% of females were recaptured within 5 km of their tagging site, with 19% of males and 26.5% of females being recaptured within 1 km of their tagging site (Solmundsson et al., 2005). These results align with our result of 35%, thereby indicating a strong site fidelity to the study area within the OWF. Based on these findings, it is suggested that plaice exhibits high site fidelity towards the feeding grounds located in the OWF area and that fish present within OWF are likely to return there after their spawning period.

Nine out of the 31 fish (29%) disappeared from the study area during several consecutive months in autumn and winter, only to return in spring to the study area. During the winter months (December-March), mature plaice exhibit large spawning migrations from their feeding grounds to their spawning grounds that are mainly located in deeper waters in the English Channel, Irish Sea and North Sea (Gibson, 1997; Ellis et al., 2012). Although the use of ID-tags did not allow to follow the fish individuals when they moved outside of the receiver array, the timing and duration of their absence strongly suggest that they left the study area to spawn. Moreover, one fish (9277) tagged in May 2020 was detected by a receiver in the western part of the BPNS in February 2021, after being absent from the study area within the Belwind OWF for almost 4 months during autumn and winter. Eleven days later, the fish was detected again within the study area, where it was observed regularly during the spring and summer months.

Some fish (e.g. 9259, 9272, 9263) remained in the study area during the spawning period. We hypothesize that these individuals might not have been mature yet and, therefore, did not leave the area to spawn. Although we did not collect information on the sex or maturity stage of the fish, maturity ogives and length-age keys for plaice in the southern North Sea indicate that 30-80% of females can still be immature around the age of 4-5 years, which corresponds to fish that measure 30-35 cm (Rijnsdorp, 1989). As the length of the tagged fish ranged between 29-39.5 cm, it is highly likely that some of the fish were not yet mature.

A high residency within and site fidelity towards a small area within an OWF implies that wind farms could play a role as refuge areas for plaice against fishing mortality. If adult fish would constantly move in and outside the wind farm, its protective capacity against fishing mortality would be much lower (Miethe et al., 2010). Moreover, for many fished species, plaice included, a fisheries-induced effect has been identified that caused a shift towards individuals that reach maturity at a smaller size (Heino et al., 2002; Grift et al., 2003). Low connectivity and a low migration rate of large adults from within a protected area to adjacent fished areas have been shown to counteract this evolutionary change in size at maturity (Miethe et al., 2010). On the other hand, our results also suggest that plaice leaves the wind farm area during the spawning season from December-March. Therefore, the high residency and site fidelity when present in an OWF protects them well against fishing mortality during the feeding season, but not during the spawning season when they migrate.

5.4.2 SMALL-SCALE MOVEMENT PATTERNS AROUND THE HARD SUBSTRATE

The analysis of the small-scale movements of plaice, based on the tagging data of five individual fish, identified a clear diurnal pattern with fish being closer to the hard substrate during day than during night hours. We hypothesize that this pattern is linked to their typical feeding behaviour. Plaice mainly forages during daylight hours as it relies on its sight to detect benthic invertebrates such as polychaetes, bivalves and echinoderms (Verheijen and De Groot, 1967; De Groot, 1971; Gibson et al., 2015). When searching for prey during the day, plaice swims just above the sea bottom, while at night, they position themselves higher up in the water column (De Veen, 1978). Fish were positioned closer to the hard substrate during the day, suggesting that they move closer to the turbines to feed. The increased distance of the fish to the hard substrate during the night could then be explained by their pelagic swimming behaviour in order to avoid predation (Burrows, 1994). This movement pattern can also be recognized in the number of detections over a 24-h period (Figure 5.5 B), whereby peaks are apparent during morning and evening hours when plaice supposedly feeds most intensively. Also, fish were located on the scour protection almost exclusively during day time. Furthermore, trophic and spatial distribution analyses of plaice within the Belwind wind farm showed that plaice was not only attracted to the soft sediment patches in between the rocks of the SPL (Buyse et al., 2022a), but that they also had fuller digestive tracts and a typical hard-substrate diet when present near the turbines (Buyse et al., 2023). This difference in diet was not only observed on a short time scale through a stomach content analysis, but also on a longer time scale as a distinctive fatty acid profile. These findings strongly suggest that plaice actively uses the SPL as a feeding ground during the day. However, the majority of the estimated positions were located on the soft sediments around the SPL at a distance of 69 m from the turbine. We, therefore, hypothesise that plaice undertakes feeding excursions to the SPL, but do not remain there for long consecutive periods. By doing so, they can profit from the increased food availability on the scour protection (Degraer et al., 2020), while still being able to bury themselves into the sand surrounding the hard substrates.

While the main observed angle between the turbines and the estimated positions of the five fish showed large variation between individuals, each fish seemed to have a preferred direction or even side in relation to the hard substrate. These preferences might be explained by individual differences between fish in combination with a very limited home range, which is supported by the clear preference of fish for a certain turbine and the high observed residency. Furthermore, the SPLs of the different turbines are not uniform and, for a given turbine, the rocks are not evenly distributed around the foundation. This can also partly explain the observed differences in plaice behaviour. As most of the estimated fish positions do not fall within the range of the SPL, it is unlikely that they use the rocks of the SPL as shelter against currents or predators. Also, by burying themselves into the sand, plaice can easily avoid strong currents or hide from predators (Gibson et al., 2015). An in-depth analysis linking current speed and tidal direction with fish behavioural states could give a more detailed view of the role of the scour protection as shelter for plaice.

The interpretation of tagging data can only be meaningful if there are no strong biases in the detectability of the fish transmitters by the receiver network (Payne et al., 2010; Cagua et al., 2013). However, the transmission of signals from fish that are present on the SPL can be hampered by the presence of the rocks, which could also partly explain the low presence of fish on the SPL. The mean number of detections per hour for a fish on the soft sediment is twice as high (12.3±8.2) as for a fish present on the SPL (6.2±5.4). Because of this, the number of fish positions on the SPL might underestimate the level of association of plaice with the SPL. Further, fish behaviour (e.g. burial, laying in between the rocks of the SPL) might influence whether or not the YAPS-model convergences and produces reliable position estimates for that fish. However, the same diurnal pattern was found in the total number of detections and the number of reliable position estimates, suggesting that the ability of YAPS to produce reliable estimates does not depend on the behaviour of the fish (Figure 5.5 B).

5.4.3 FURTHER RESEARCH AND CONCLUSION

This study provides insights into the small-scale and larger-scale spatial movements of plaice in relation to a Belgian OWF. However, additional research could help in further assessing the value of OWFs for plaice and elucidating their use of the hard substrate. Although ID-transmitters were suitable to answer our research questions, transmitters equipped with pressure and temperature sensors, so-called archival tags, could provide additional information in support of the hypotheses put forward in this study (Wright et al., 2020). They allow the calculation of 3D-positions (cfr. 2D-positions for ID-transmitters) of fish in the water, which allows for the integration of depth information to improve the identification of feeding or swimming behaviour. The use of Hidden Markov Models, through which different behavioural states can be determined from position data, could then further validate the ‘feeding excursions-hypothesis’ put forward here (Griffiths et al., 2018; Bacheler et al., 2019). Moreover, as archival tags continuously log sensor data, a modelling analysis can estimate fish tracks outside of the receiver array and thus follow plaice from their feeding areas to their spawning grounds and back. Also, it is of vital importance in telemetry studies to take into account the circumstances that influence the detection probability of transmitter signals to ensure a correct interpretation of the data (Huveneers et al., 2016; Goossens et al., 2022). Incorporating such information in the form of an error structure into future data analyses or use it to help with the interpretation of the animal transmitter data could, therefore, further improve the reliability of the study (Goossens et al., 2022). Finally, including more fish (only five were used in this study) for position estimations, could also help in underpinning observed patterns in habitat association and distance from the hard substrate.

5.5 ACKNOWLEDGEMENTS

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PART 3

GENERAL DISCUSSION AND CONCLUSION


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6 FLATFISH IN OFFSHORE WIND FARMS: ARE THERE OPPORTUNITIES FOR FISHERIES?

The main aim of this thesis was to investigate the ecological effects of offshore wind farms (OWFs) on plaice as a fisheries resource against a background of climatic influences. Although plaice is considered a typical soft-sediment species, the hard substrates associated with OWFs were found to affect its spatial distribution, trophic ecology and movement patterns. Plaice showed an attraction towards the scour protection layer (SPL), probably due to an increase in food availability. This was reflected in fuller digestive tracts of fish present on the SPL and a distinctive diet existing of typical hard substrate species, both on the short and long term. Although tagged plaice were mainly positioned on the soft sediment around the hard substrate, a diurnal pattern in their distance to the hard substrate was revealed with fish being closer to the turbine during the day than at night. It was, therefore, hypothesized that they undertake feeding excursions to the SPL during daytime hours to feed, while they are still able to exhibit their natural burrowing behaviour in the surrounding sediments. These findings indicate that hard substrates associated with OWFs can act as artificial reefs for plaice.

A positive wind farm effect, resulting in higher abundances of plaice within the concession area, was found for one of the two studied OWFs. Moreover, larger-sized fish and a higher female-to-male ratio were observed for sample groups caught within another OWF, compared to control areas. Also, a tagging analysis revealed a high residency of plaice in an OWF and absence-presence data further indicated that plaice can return to the OWF after their winter spawning migrations. Plaice was also found to have increased in abundances over the last decades in the (Belgian part of the) North Sea, while their size at first maturity potentially decreased. This was explained by a combination of climate change effects and fisheries-induced selection. These results indicate that plaice might benefit from a refuge effect offered by OWFs, as bottom trawling activities are not allowed within most European wind farms.

In this general discussion, the results of the different chapters are combined and discussed in a broader context. First, the role of OWFs as artificial reefs is evaluated for plaice, mainly focusing on the scour protection in relation to the species' feeding behaviour (see 6.1). Here, the issue of attraction and production is also addressed. Then, the potential of OWFs as refuge areas for plaice is discussed in relation to the cessation of bottom trawling activities (see 6.2). Subsequently, the potential interaction effects between OWFs and climate change and the consequences for fisheries resources are discussed with a focus on flatfish (see 6.3). Then, recommendations on upscaling of OWF effects on plaice from individuals to populations are presented (see 6.4). Lastly, based on the findings of this thesis, recommendations, ideas for future research and lessons learned are discussed that can help in addressing existing knowledge gaps, followed by a conclusion (see 6.6).

6.1 OFFSHORE WIND FARMS AS ARTIFICIAL REEFS FOR FLATFISH

Offshore wind farms (OWFs), and in particular their foundations and associated scour protection layers, act as artificial reef structures (Stenberg et al., 2015; Degraer et al., 2020). Their introduction often creates a new hard substrate habitat in a natural soft-sediment environment. This habitat is rapidly colonized by different filter and suspension feeding species, which attract animals at higher trophic levels such as fish through an increase in food and shelter opportunities. It was thought that mainly typical hard substrate-associated fish species, such as cod (*Gadus morhua)* and pouting (*Trisopterus luscus)*, were attracted towards the foundations and scour protection. However, this thesis has shown that plaice, a typical soft-sediment species, was attracted to the sandy patches in between the rocks of the scour protection (Chapter 3). An in-depth trophic analysis showed that fish present in the vicinity of the turbine had fuller digestive tracts and a distinctive diet existing primarily of hard substrate prey, and this both on a short and longer time frame (Chapter 4). Further, the small-scale movements of plaice around the turbines suggested that fish spend most of the time on the soft sediment surrounding the hard substrates, but make feeding excursions to the SPL during daylight hours (Chapter 5). These findings suggest that the hard structures associated with OWFs can create feeding opportunities for plaice and thus act as artificial reefs for soft-sediment species as well as for typical hard substrate species.

6.1.1 THE ROLE OF THE HARD SUBSTRATE IN OWFS FOR PLAICE

Although plaice is considered a typical soft-sediment species that lives in close contact with the seabed, an attraction effect was found towards the SPL habitat. Four times higher fish abundances were found on the sandy patches in between the rocks of the scour protection, compared to the surrounding open sand. Fish are thought to aggregate around artificial reef structures, mainly because of increased food availability and/or shelter opportunities (Bohnsack and Sutherland, 1985; Brickhill et al., 2005). A combination of stomach and gut content together with a biomarker approach clearly showed that plaice fed on typical hard-substrate organisms in the vicinity of the turbine foundations. In contrast, plaice caught at a distance of >200 m from the turbines and at sandy control sites typically had a diet consisting of soft sediment prey. Differences between the control groups and fish caught on the scour protection were not only observed in stomach/gut content, but also in biomarker profiles, suggesting that these near-turbine fish had a different diet over a prolonged period of time. Plaice on the scour protection also had fuller guts than fish caught elsewhere, indicating a higher food availability. Furthermore, acoustic telemetry demonstrated that plaice was highly resident in the wind farm area and displayed a diurnal pattern in their distance to the hard substrate (closer during the day than at night) potentially coinciding with their feeding cycle (De Veen, 1978) (Chapter 5). All this empirical evidence strongly suggests that plaice actively uses the SPL to feed over long time periods. However, estimated positions of five plaice individuals indicated that they mainly reside at a distance of approximately 70 m from the turbine on the soft sediment with only a minor share of their positions located on the scour protection (4.6%). We, therefore, hypothesized that plaice mainly rests on the soft sediments surrounding the turbines and, from there, undertake feeding excursions closer to and on the SPL during daylight hours. By doing so, they can profit from the increased food availability offered by the hard substrates and still be able to bury themselves in the surrounding soft sand during peak light intensities (Verheijen and De Groot, 1967; De Veen, 1978; Gibson et al., 2015). Importantly, the presence of plaice on the SPL based on the number of fish positions might be an underestimation of their association to the hard substrate, as we found a lower detectability for fish present on the scour protection compared to the soft sediments. Furthermore, typical hard substrate species, such as *Jassa herdmani* and *Monocorophium acherusicum,* were found in the sand surrounding the SPL and even in between the turbines at distances of >350 m in two different Belgian wind farms, so plaice could even profit from the presence of the OWF structures without having to swim over the rocks (Coates et al., 2011; Lefaible et al., 2021).

Whether or not plaice uses the SPL as shelter from predators or strong currents is not clear based on our findings. However, it seems unlikely that plaice consistently uses the hard substrate as shelter, since, based on an acoustic telemetry analysis, it appears that they spend the majority of their time on the sand in near vicinity (around 70 m) of the SPL, and only (very) short periods on the SPL (Chapter 5). While predation on larvae and juvenile individuals of flatfish may be very substantial (e.g. *Crangon crangon, Carcinus maenas)*, adults are at much lower risk due to their relatively large body size. Although plaice was found to be a significant component of the diet of grey seals (Hammond et al., 1994), humans are by far its most important predators (van der Veer and Bergman, 1987). Strong currents, on the other hand, could be as easily avoided by burying themselves into the sand. For example, during their extensive spawning migrations, plaice buries itself into the sand when the tide is unfavourable to save energy (De Veen, 1978; Arnold and Metcalfe, 1996). Based on the findings of this thesis, combined with the available knowledge on their behaviour, increased food availability, rather than shelter, appears to be the major driver of the observed attraction effect of plaice towards the hard substrate.

Plaice distribution at the turbine scale together with their diet, condition and spatial movements were all studied within the Belwind wind farm where all but one turbines have monopile foundations surrounded by scour protection. Such an approach did not allow for the comparison between different foundation types or the assessment of the presence or absence of scour protection. However, we did find higher abundances of plaice within the C-Power wind farm, which consists mainly of jacket foundations without scour protection. Although this effect was observed on the wind farm scale, the increased fish abundances suggest that an artificial reef effect for plaice does not depend on the presence of scour protection. This is supported by observations of higher plaice abundances in a German wind farm in the vicinity of jacket and tripod foundations without SPL compared to monopile foundations surrounded by an SPL (Krone et al., 2017). Further, plaice was found to be more abundant in areas with a high number of oil and gas platforms in the North Sea (Wright et al., 2020). Although it is suggested that SPLs are more effective as artificial reefs than the turbines and their foundations due to a higher food web complexity associated with the rocks, it is plausible that turbines without scour protection also attract plaice, but potentially to a lesser extent (Petersen and Malm, 2006; Mavraki et al., 2020, 2021). Nevertheless, on the basis of our results we can conclude that wind turbine foundations (with or without surrounding SPL) are beneficial for plaice because they offer a higher availability of food.

6.1.2 DO OWFS LEAD TO INCREASED FISH PRODUCTION FOR PLAICE?

Although this thesis demonstrated a positive wind farm effect on plaice abundance together with an attraction effect towards the SPL habitat, this does not automatically imply that fish production is occurring within the OWF. Fish may simply aggregate in the vicinity of the hard substrates as a behavioural consequence without there being an actual increase in the total biomass within the wind farm area as compared to before. This is commonly referred to as the attraction hypothesis (Bohnsack and Sutherland, 1985). In contrast, the production hypothesis states that artificial reefs can increase the carrying capacity of an area by adding additional habitat, thereby enabling them to accommodate more individuals by increasing feeding, shelter or spawning opportunities (Brickhill et al., 2005). Both hypotheses are not mutually exclusive, but can be viewed as two extremes along a wide gradient (Svane and Petersen, 2001). Another possibility is that artificial reefs appear more interesting to animals than their natural habitat, while they actually offer worse conditions and are therefore ecological traps (Robertson and Hutto, 2006). If the mismatch between the environmental cues and the habitat condition is substantial, it can affect the animal's fitness and might even cause a decline at the population level (Hale and Swearer, 2016). Furthermore, a lot of different factors can influence observed responses such as the size and age of the reef and its configuration, the life characteristics of the fish species, the fishing effort in adjacent areas and environmental conditions in general (Bohnsack and Sutherland, 1985; Peterson et al., 2003; Mavraki et al., 2021). It is, therefore, important to study fish responses on a case-by-case basis, especially because OWFs are not intended to enhance fisheries resources (Cresson et al., 2019; Gill et al., 2020).

Bohnsack (1989) defined several mechanisms that could be driving fish production at artificial reefs: (1) offering of increased food availability, (2) increasing the feeding efficiency, (3) offering protection against predation, (4) providing settlement habitat for larvae and (5) increasing the availability of naturally occurring habitat by aggregating fish around the introduced structures.

Increased food availability. Earlier studies showed that the presence of turbine foundations and scour protection increases the density and biomass of epibenthic and macrobenthic organisms (Coates et al., 2011; De Mesel et al., 2013), so more food is available. We indeed observed fuller digestive tracts for plaice near the turbines and these near-turbine plaice specifically fed on hard-substrate organisms for longer time periods (Chapter 4), suggesting that the OWF increases food availability for this species.

Increased feeding efficiency. Since plaice normally feeds on benthic invertebrates and macrobenthic organisms that are often (partially) buried in the sediment, feeding off the hard substrates, where prey items are more readily available, might increase their feeding efficiency as well (Wyche and Shackley, 1986; Gibson et al., 2015).

Protection against predation. Although we were not able to show that plaice uses the SPL for shelter, the cessation of trawling activities within the OWF can be viewed as a protection measure against human predation, which is the primary cause of mortality in adult plaice (Gibson et al., 2015). Our tagging data also indicated that most plaice individuals remained in the wind farm area, and even close to a specific turbine, during the summer period (Chapter 5). This implies a close association with the OWF and thus an increased protection against fisheries mortality (except during the spawning period). On the other hand, seals have been observed to concentrate their hunting effort around wind farm structures, which may lead to increased predation rates on plaice (Hammond et al., 1994; Russell et al., 2014).

Settlement habitat for larvae. Although it is unlikely that OWFs can provide substantial settlement habitat for plaice larvae, they can influence recruitment through different processes (Barbut et al., 2020). After plaice has spawned, their developing eggs and larvae are transported with the currents towards shallow coastal zones where they settle in nursery areas (Bergman et al., 1988). A modelling study in the North Sea estimated that 9.4% of plaice adults spawn within current and planned OWF areas and, based on field data, 8.9% of larvae settling in nursery areas originate from within those areas (Barbut et al., 2020). Importantly, potential impacts can be negative, as well as positive, depending on various factors. On the one hand, construction of OWFs in spawning areas can cause a deterioration of the spawning habitat, leading to decreased recruitment. On the other hand, it is also possible that recruitment in OWF-areas is enhanced due to the absence of bottom trawling activities (van Overzee and Rijnsdorp, 2015). Moreover, fish originating from OWFs could be in better condition and/or have a higher fecundity because of an increase in food availability (Hiddink et al., 2011). Although our study was not conclusive on increased plaice condition or fecundity in the presence of OWFs, we did find increased fish sizes and a higher female-to-male ratio for the sample groups that were caught within an OWF. If the OWF offers protection to these large, mature females against fishing mortality, they might indirectly benefit plaice recruitment through a refuge effect (but see 6.2 for more information on fisheries exclusion effects).

Increased natural habitat availability by aggregating fish. Due to the aggregation of plaice individuals around the hard substrates, which offer increased food availability, it is possible that more fish can be accommodated within an OWF compared to open sand habitat. This would imply that the introduction of hard substrates increases the carrying capacity of the area, and that fish production is thus enhanced. This is corroborated by our observations of higher plaice abundances between the turbines within the C-Power wind farm compared to control areas. Also, an ecosystem model predicted that plaice biomass would increase by a factor of 2.5 within a planned wind farm area in the Bay of Seine due to an increase of benthic invertebrate prey (Raoux et al., 2017), further supporting this hypothesis.

The argumentation above suggests that OWFs can enhance biological fish production due to an increase in the carrying capacity of the area, which is driven by a higher food availability. However, even when cumulative effects of multiple wind farms are considered, this does not necessarily imply an increase at the population level. An increase in prey biomass and protection from fishing mortality could mainly benefit individuals that are already present within the wind farm, thereby boosting their growth and increasing their chances of survival, rather than adding more individuals to the area (Powers et al., 2003). In addition, processes such as larval dispersal and survival in the nursery areas might be more important bottlenecks for plaice population dynamics than the survival of mature adults (Levin and Stunz, 2005; Nash and Geffen, 2012; Le Pape and Bonhommeau, 2015). As such, environmental factors that drive these processes may be more dominant in steering populations than enhancement of fish production at the adult fish stage. A meta-analysis that considers how OWFs influence the different life stages of plaice and in what way they influence the population level can help in clarifying this issue.

6.1.3 DESIGN OF THE SCOUR PROTECTION LAYER

Scour protection is usually added around the foundations of wind turbines to ensure that the surrounding sand is not eroded due to changed current patterns and velocities (Coates et al., 2014). The most common design in European wind farms exists of a filter layer of smaller rocks topped with an armoured layer of larger rocks (Whitehouse et al., 2011). While initially only technical and economic arguments were considered during its design and deployment, recently, the focus has shifted towards the use of more eco-friendly scour protection designs that can enhance the ecological functioning (Lengkeek et al., 2017; Glarou et al., 2020). This concept of modifying artificial structures that originally have another purpose to additionally serve nature conservation goals is commonly referred to as 'nature inclusive designs' and is now actively implemented in the Netherlands during the planning and construction phases of OWFs (van Duren et al., 2017; Ministerie van Economische Zaken, 2019).

An important ecological consideration when designing scour protection is that not all species have the same habitat requirements (Lengkeek et al., 2017). A certain adaptation can be beneficial for one species, while it can have no effects on others. Large crevices between rocks, for example, are required by larger fish species when used for shelter, while smaller crevices are preferred by smaller fish (Hixon and Beets, 1993). Nature-inclusive designs or add-on structures might even be deleterious for species in case competition exists for the same resource (Hermans et al., 2020). In that case, one species might outcompete the other, which is even worse when the better competitor is a non-indigenous species. It is therefore crucial to have a good ecological understanding of how a certain modification will affect the native biological communities that are present in the area, so that undesired effects can be limited as much as possible (Dannheim et al., 2020). However, knowledge on individual habitat requirements of single species is often not available. Experts therefore advise to group species with similar life-traits or to select and focus on a few umbrella species for which such knowledge is readily available (Lengkeek et al., 2017). Provided that these species are well-chosen, optimization of the scour protection to serve their needs should then result in a higher habitat suitability for a wide range of other species.

In this thesis, we found that plaice showed a positive attraction towards the scour protection (in particular the sandy patches in between the rocks) in the Belwind wind farm (Chapter 3), while such an effect was not found in other wind farms (Krone et al., 2017; van Hal et al., 2017; Wilber et al., 2018). We hypothesized that this difference was partly due to the design of the SPL in the different wind farms, whereby plaice actively avoids closed rock fields due to the absence of soft sediments (Gibson et al., 2015). Plaice might either prefer to forage on prey located on the sandy patches in between the rocks of the SPL or use these patches as stepping stones to target prey present on the rocks. Based on these findings, plaice can be used as a model for other flatfish, or even soft sediment species with similar life-traits, when considering the enhancement of the scour protection in terms of its ecological functioning. It is possible to reconcile the needs of hard-substrate and soft-sediment species related to the design of scour protection by changing the density of rocks of the armoured layer with distance from the turbine foundation. In the close vicinity of the foundation, rocks can be stacked on top of each other, thereby creating different sizes of crevices and adding environmental complexity, which benefits species such as cod and lobster. The density of rocks could then decrease towards the edges of the SPL, creating a more 'open rock field' with large sand patches thereby allowing soft-sediment species, such as plaice, to forage more easily near the hard substrate. However, the design of the SPL must first and foremost meet the technical requirements to ensure the structural stability of the turbine. Therefore, it might not be feasible to lower the rock density of the existing SPL, but it may be possible to add additional rocks or other structures as add-ons that enhance the biodiversity and prey biomass within the OWF instead (Whitehouse et al., 2011; Hermans et al., 2020).

6.2 FISHERIES EXCLUSION EFFECT IN OWFS

In many European wind farm areas, most fisheries activities are forbidden due to strict safety regulations. In UK waters, where trawlers are allowed within the wind farms, issues concerning liability and insurance prevent fishers from entering (Gill et al., 2020). Due to such direct or indirect restrictions, OWFs can be considered as refuge areas for fish where no extraction can take place, except when the use of passive fishing gear is allowed (Stelzenmüller et al., 2016). Research has shown that successful marine protected areas (MPAs) can support fisheries resources by reducing direct fishing mortality and enhancing fish production of target species through an increase in food, which can in time lead to an spillover of adults into adjacent areas (Friedlander et al., 2007; Florin et al., 2013; Guidetti et al., 2014). It is even suggested that marine reserves (i.e. MPA's where no extraction can take place) can prevent a fisheries-induced evolution towards maturation at a smaller size (Miethe et al., 2010). On the other hand, due to the strong growth of offshore wind in the North Sea area, traditional fishing grounds are lost, which has caused some debate between the two parties (Gill et al., 2020). Although some studies suggest that OWFs can have an overall positive effect on local fish populations in a similar way as MPAs (Ashley et al., 2014; Halouani et al., 2020), empirical evidence is still largely lacking.

6.2.1 CAN MPAS BE EFFICIENT REFUGE AREAS FOR PLAICE?

The effectiveness of an MPA to increase fish production (biomass) for a given species within its borders is mainly determined by two conditions: (1) the species needs to be overfished and (2) the species has to be more or less sedentary within the protected area (Shipp, 2003).

The species needs to be overfished. Plaice is a very important commercial flatfish species that has been fished for centuries in the North Sea (Walsh et al., 2015). Although fishing pressure has been high on the species in the past (ICES, 2022a), the spawning stock biomass has increased significantly during the last two decades and the species is now exploited under maximum sustainable yield levels (ICES, 2022a). However, we demonstrated a decrease in fish size for plaice over the last 30 years (Chapter 2). Other studies have observed a similar effect for the species and attribute it, at least partly, to a fisheries-induced evolution towards maturation at an earlier age and size (Rijnsdorp, 1989; Bromley, 2000; Grift et al., 2003; van Walraven et al., 2010). Because there exists a minimum landing size for plaice (27 cm), mainly large individuals are extracted. As a result, there is an unintentional selection for genotypes that are mature at a smaller size and age, which can eventually lead to a lower yield (Grift et al., 2003). Although the spawning stock biomass (SSB) may increase due to a higher abundance of mature fish, recruitment will not necessarily follow this trend as fecundity for plaice is positively linked with fish size of female plaice (Rijnsdorp, 1991; Murawski et al., 2001). Recruitment in the North Sea region does, indeed, not seem to follow the recent exponential increase in plaice SSB (ICES, 2022a). So, despite the fact that the North Sea plaice stock is currently not overexploited, there is evidence of a potential historic fisheries-induced effect on its size at maturation. Interestingly, a modelling study demonstrated that such an evolutionary effect could be counteracted by the establishment of a marine reserve, provided that it is sufficiently large and properly managed (Miethe et al., 2010). However, genetic changes in populations are difficult to reverse, especially on a short time frame, because they happen over the course of several generations (Reznick, 1993).

The species is resident within the protected area. Our tagging study indicated that during their feeding period in spring, summer and autumn, plaice mostly resides within a relatively small area (±4 km^2) (Chapter5). Moreover, previous research has shown that the species has a very high site fidelity towards its spawning and feeding grounds (Burrows et al., 2004; Solmundsson et al., 2005). However, mature individuals undertake seasonal large scale migrations from the feeding to the spawning grounds during the winter months (December–March). Despite their low mobility during most of the year, such migrations significantly lower the protection potential of an MPA, making them less effective fisheries management tools for flatfish in general. However, if MPAs are combined with regulations that involve a seasonal closure of critical spawning areas, this could significantly increase their effectiveness for the protection of plaice (Shipp, 2003).

Research related to the potential refuge effects of protected areas on flatfish also showed some ambiguity of results. A European marine reserve in the Baltic Sea held higher densities of flounder *Platichthys flesus* and turbot *Scophthalmus maximus* compared to fished reference areas, suggesting a successful refuge effect for these species (Florin et al., 2013). The increase in fish age and a more even sex ratio within the reserve further supported this. In contrast, a partially closed zone located in the main nursery areas of plaice in the North Sea (the 'plaice box'), observed decreases of plaice' SSB and fishing yields after its closure (Pastoors et al., 2000). Given reasons for these unexpected effects were related to long term changes in the overall North Sea environment, climate change effects on fish distributions and a potential deterioration of the feeding grounds due to a decrease in bottom trawling effort (Pastoors et al., 2000; Hiddink et al., 2008; van Hal et al., 2010). This last effect can be explained by the intermediate disturbance hypothesis, whereby the biomass of small invertebrates, on which plaice feeds, is higher in areas that are trawled once or twice per year (Hiddink et al., 2008). This shows that there is no universal response to a reduction in fishing effort on flatfish populations and that clear management goals, comprehensive knowledge on the species and its interactions with the marine environment, and a thorough monitoring plan are crucial to mitigate any undesired effects.

Overall, plaice does not present itself as an ideal candidate species for fisheries enhancement through the establishment of an MPA, due to its extensive spawning migrations and its relatively good stock condition in the North Sea. Nevertheless, it could still profit from a reduction in fishing pressure, as research has suggested that its size and age at maturation decreased over the last decades through an evolutionary fisheries-induced effect. Such an effect is not easy to reverse over a short time frame and because plaice exhibits transnational seasonal movements, a North-Sea scale management approach will be needed. Another important consideration is that a spillover of adults into adjacent fished areas could increase the yield of local fisheries considerably, but it lowers the protection of those adults against the effects of fishing at the same time. So even if an MPA is successful in increasing the target fish biomass within its boundaries, there is a trade-off between offered protection against fishing mortality by the MPA and increases in local fisheries yield (Miethe et al., 2010). This is especially important for plaice, because benefits offered by the presence of an MPA can be completely nullified if fisheries target spawning mature adults outside the protected area. Another consequence related to a fisheries exclusion in MPAs is that fisheries will have to move to other areas. Such displacement can locally increase fishing effort and mortality, which can negatively affect species that are already overexploited.

6.2.2 CAN OWFS OFFER THE SAME BENEFITS AS MPAS?

This thesis found higher abundances of plaice within the Belgian OWF C-Power compared to control areas (Chapter 3). Moreover, plaice individuals caught within the Belwind wind farm were larger compared to fish caught in control areas (Chapter 4) and samples taken within the OWF had a higher female-to-male ratio. Plaice is a sexual dimorphic species with the females growing faster and for a longer time than males. In undisturbed populations, this results in a dominance of male individuals among smaller individuals and a dominance of females among larger individuals, with an even sex ratio for the total population. A higher catchability of larger (and thus more likely female) individuals in fished areas can lead to a decrease in fish size and a higher proportion of males (van Walraven et al., 2010; Florin et al., 2013). Although our sample size was very small, the higher female-to-male ratio together with increased fish size for the two groups caught within the OWF, may be a sign of a fisheries exclusion effect (Di Franco et al., 2009; Florin et al., 2013). This potential refuge effect might even increase in the future, as the entire Belgian wind farm zone (238 km^2) is now completely occupied by wind turbines and no fishing vessels are allowed within the entire area. However, further investigation of this potential refuge effect based on larger sample sizes is needed to support these findings.

Although there seems to be potential for OWFs to offer plaice protection against fishing mortality, there are important aspects to consider. The designation of OWF areas is mainly based on technical aspects such as water depth, sediment composition and available wind speed (Gil-García et al., 2019), while MPAs are often chosen based on their natural value or conservation potential. In addition, OWFs do not aim to enhance biodiversity or increase fisheries resource densities and completely lack the design aspects and clearly defined management goals that are key elements in successful MPAs (Gaines et al., 2010). Therefore, OWFs should not be considered as a replacement for thoroughly protected areas, as their establishment is based on completely different principles. Even though fisheries can be excluded within OWFs, energy emissions (e.g. noise, EMFs), changes in food webs or their construction in sensitive areas (e.g. nursery grounds) might still negatively impact fish. This makes the comparison with MPAs somewhat problematic and, therefore, care should be taken when results of MPA studies are used to underpin research hypotheses related to possible effects of OWFs. Using the results of MPA studies to formulate hypotheses on the potential effects of OWFs can be helpful, but these always need to be validated in the field. Constructing and adapting OWFs in such a way that they have the maximum potential to enhance the ecological function of the area may, however, partly compensate for the lack of well-protected MPAs in the North Sea caused by the limited amount of marine space (Florin et al., 2013).

6.3 INTERACTION EFFECTS BETWEEN CLIMATE AND OWFS ON FISH

6.3.1 EFFECTS OF CLIMATE CHANGE AND VARIABILITY ON FISHERIES RESOURCES

Many different factors are simultaneously affecting the marine environment and its associated biological communities (Beaugrand et al., 2009). Understanding which factors are important and how they affect species is crucial to correctly interpret effects of direct anthropogenic activities (e.g.

OWFs), especially when they can influence each other. Climate is one of the major factors affecting fish populations on the long term. Natural variability in the system together with human-induced climate change influences water temperature, which is the major driver for changes in fish abundances, their spatial distribution, body size and other life-history traits (Perry et al., 2005; Dulvy et al., 2008; Edwards et al., 2013; Crozier and Hutchings, 2014). Even on a very small spatial scale such as the Belgian part of the North Sea (BPNS), we found potential links between climate-related variables, such as sea temperature and climatic modes (i.e. Atlantic Multidecadal Oscillation and North-Atlantic Oscillation) and fish abundances over a period of 30 years (Chapter 2). These results underline the importance of taking climate effects, from both natural as well as human-induced sources, into account when studying fish abundances.

Fish can react in various ways to changing environmental conditions due to long-term climate influences (Engelhard et al., 2011). One of the most commonly observed responses is a shift in their distribution towards locations that offer more suitable habitat conditions (Perry et al., 2005). In the case of increasing sea water temperature that exceeds species limits, this can result in a deepening or northward movement of entire fish stocks (Dulvy et al., 2008). For southerly species, on the other hand, warming temperatures can shift their northern habitat boundary and allow them to expand their distribution towards higher latitudes. Typically, this is observed through an increase in the abundance of warm-water species (Lusitanean) and/or a decline of cold-water species (Boreal) within a small study area (Rijnsdorp et al., 2009), which we also found in the BPNS (Chapter 2). Such shifts in distribution can lead to increases of the overall fish biodiversity in temperate areas (Hiddink and ter Hofstede, 2008), but might, at the same time, affect entire ecosystem dynamics through a change in species food web interactions.

Typically, fish species at lower latitudes that are adapted to higher temperatures have smaller body sizes due to physiological restraints in oxygen uptake (Atkinson, 1994; Baudron et al., 2014; Pauly and Cheung, 2018). A northward range expansion of such species would therefore result in a decline in the community-average fish length in areas at higher latitudes. Moreover, a decline in length possibly linked to temperature was also identified for different commercial fish species in the North Sea over a period of 40 year (Baudron et al., 2014). As growth rates are usually higher in warmer regions, and growth rate is negatively correlated with adult body size, it is suggested that increasing temperatures in temperate regions can cause a decline in individual fish size (Thresher et al., 2007). The combination of these two mechanisms (i.e. northward expansion of smaller species and lower individual fish body sizes) led to the prediction that under future climate change scenarios average body weight of fish communities will shrink by 14-24% globally (Cheung et al., 2013). Our trend analyses support this as we observed the highest increases in abundance for typical small-sized southerly species such as lesser weever *Echiichthys vipera*, solenette *Buglosssidium luteum*, red mullet *Mullus surmuletus* and scaldfish *Arnoglossus laterna* (Chapter 2*)*, whose distribution ranges increased significantly during the last decades (Hiddink and ter Hofstede, 2008). Further, we found evidence that the length of the 20% largest plaice individuals had shrunk over 10 cm over the last 30 years. Although some studies suggest that fisheries-induced selection effects may partially explain the decrease in plaice length, other studies attribute it to an increase in temperature (Grift et al., 2003; Baudron et al., 2014). As these two impacts are acting simultaneously on commercial fish stocks, they might amplify observed biological responses (Hiddink and ter Hofstede, 2008; Hermant et al., 2010).

Climatic influences on fish can potentially lead to lower catch rates for commercial fisheries, especially for flatfish as they are more vulnerable because of their lower mobility compared to more active pelagic and demersal species (Cheung and Oyinlola, 2018). Following the predictions, the adult body size of commercial flatfish in the North Sea will decline, stocks will move northward or to deeper waters and large valuable species are gradually replaced by smaller non-target species. Furthermore, if dispersal rates differ between species, competition over food sources with native fish can arise. A study conducted in the North Sea suggests that this is already the case for solenette *Buglosssidium luteum*, because of its dietary overlap with plaice and sole (Jennings et al., 2008; van Hal et al., 2010). Fishers will have to adapt to these changes by increasing their effort, finding new fishing grounds (probably located further away) or by switching target species. Despite the numerous negative impacts of a temperature increase on fisheries resources, the influx of warm-water species can also offer new opportunities for the fishing industry. Common squid *Loligo vulgaris*, for example, showed a large expansion of its habitat range during the last decades, resulting in much higher catch rates in the North Sea (van der Kooij et al., 2016). This trend was positively linked to sea surface temperature, suggesting that this increase will further continue in the future.

6.3.2 INTERACTION EFFECTS BETWEEN CLIMATE AND OWFS ON FISH

Natural climate variability and human-induced climate change influence fish populations on a global scale (Brunel and Boucher, 2007; Cheung et al., 2013). Trying to mitigate the undesired impacts of climate change has led to a proliferation of offshore wind as an alternative energy source (WindEurope, 2022). Although our understanding of the ecological effects of OWFs on fish has substantially increased over the years, a lot of uncertainty remains about their interaction with other impacts such as climate change. Although this thesis did not investigate any interaction effects directly, we can hypothesize about some potential outcomes by combining our findings with available studies related to MPAs.

Some potential effects of OWFs might help in tackling undesired impacts of climate change on fish populations. Areas where no fishing is allowed, such as OWFs, can be used as stepping stones by dispersing species that are already under environmental stress. By taking away fishing mortality as a major stressor, such species can adapt more gradually to a changing environment, giving them higher chances of survival (Roberts et al., 2017). OWFs can offer refuge to species that are less mobile, and thus have less adaptive capabilities, or protect species that have reached the outer limits of their distribution. Although fisheries do not profit from these refuge effects directly, it may benefit them in the longer term by protecting species that are already under threat from fishing mortality (Roberts et al., 2017). Furthermore, OWFs may also help in reducing fisheries-induced effects amplified by climate change. For example, the fisheries-induced evolution for plaice towards fish that are mature at a smaller size might be accelerated by a rise in water temperature. This is based on the hypothesis that higher temperatures will lead to a decrease in fish size as a consequence of the temperature size rule (Atkinson, 1994; Baudron et al., 2014). By taking away fisheries as a stressor within the OWF, this effect might be slowed down. Our findings of larger plaice within the wind farm area, thereby, support this hypothesis; as well as other studies that reported increased fish sizes within the boundaries of MPAs (Halpern, 2003; Claudet and Pelletier, 2004; Di Franco et al., 2009; Fenberg et al., 2012). Climate change not only causes a rise in sea temperature, but also reduces the pH of the water in a process called 'ocean acidification' (Nagelkerken et al., 2021). A lower pH can be detrimental for species that have calcareous structures, such as bivalves, and it is therefore predicted that climate change will decrease invertebrate biomass (Roberts et al., 2017). This can affect fish species that feed on these invertebrates, especially since a rise in temperature causes higher metabolic rates and thus requires a higher energy uptake to compensate for this (Denman et al., 2011). The higher prey availability in OWFs might help to partially overcome this increased energy need for fish.

It is also possible that OWFs can strengthen climate-induced effects on fish. For example, the introduction of hard substrate in sandy environments can help the establishment of reef-associated southerly species that might compete for the same resources as native species (van Hal et al., 2010; Hermans et al., 2020). This can negatively affect native fish through a decrease in prey availability. Also, the development of OWFs can cause fishers to relocate to other areas as a reaction to the loss of fishing grounds. This might concentrate their efforts in some areas, putting even more pressure on fish populations that are already overexploited (Stelzenmüller et al., 2016, 2020, 2022). Such a displacement of fishing effort due to the presence of offshore wind has already been observed within the Belgian part of the North Sea (De

Backer et al., 2019) and will likely increase in the future as more wind farms are being constructed (Stelzenmüller et al., 2022). Moreover, increased fishing pressure due to displacement could lower the capability of target species to deal with climatic stress, which can decrease fisheries yield even further (Roberts et al., 2017; Cheung and Oyinlola, 2018). Therefore, close monitoring of fishing effort on a regional scale in relation to the construction of wind farms is crucial to avoid the overexploitation of fisheries resources (Stelzenmüller et al., 2022).

6.4 HOW TO UPSCALE OWF EFFECTS FROM INDIVIDUALS TO POPULATIONS?

This PhD study focused mainly on the ecological impacts of OWFs on adult plaice at the level of individuals. While this work filled some important knowledge gaps, it is crucial to understand the impacts not only on individuals, but also on populations, as this is the level that is most relevant for fisheries management (May et al., 2019). Translating individual OWF effects to the population level is somewhat problematic due to the discrepancy in temporal and spatial scales on which effects might be occurring. For example, adult fish that profit from increased prey availability around the turbine foundations in an OWF might not induce any changes in the population, even though the effect size on the individual level is very high. Fish populations are determined by mortality processes, which can be natural (e.g. predation) or human-induced (e.g. fisheries, pollution), and by the recruitment and growth of individuals. To understand how OWFs can affect fish populations, it is crucial to gather knowledge on how their presence affects these processes of mortality, recruitment and growth (Gill et al., 2020).

Growth and mortality processes occur at each life stage of a species, while recruitment occurs at a specific point in a species' lifetime (van Der Veer et al., 2000). Therefore, upscaling an impact (e.g. OWFs) from individuals to populations requires the integration of knowledge on how the impact affects all different life stages of a given species. Moreover, growth, mortality and recruitment occur at different temporal and spatial scales, which also need to be taken into account when assessing an impact on a population.

This part will discuss how we can upscale OWF effects on plaice from individuals to populations by identifying knowledge gaps that need to be addressed based on knowledge obtained in this thesis. Potential OWF effects on the different life stages of plaice (egg, larva, juvenile and adult) are discussed for the different processes (recruitment, growth and mortality), along with the relevant spatial and temporal scales at which the effect may occur.

6.4.1 RECRUITMENT

Fish recruitment is defined as the number of individuals that make the transition between two life stages (e.g. from juvenile to the mature population) (van Der Veer et al., 2000). The recruitment process includes anything that can influence the survival of the early life stages (egg, larva and juvenile) from the fecundity of the adults to the mortality of juveniles on the nursery grounds. For female plaice, the number of eggs produced (= fecundity) increases with age and size of the individual. Therefore, on the population level, egg production can be influenced by sex ratio, length-frequency distribution and total abundances (van der Veer et al., 1990; van Der Veer et al., 2000). This thesis suggested that OWFs can positively influence the abundances, size composition and sex ratio (higher number of females) of plaice (Chapter 4), which might indirectly affect egg production on the population scale, especially when cumulative impacts of OWFs are considered. The sample sizes in this thesis were very small to provide sufficient evidence, but larger field studies may be able to support our findings.

On the individual level, the fecundity of female plaice is determined by body condition and nutritional status (Bromley, 2000). A study spanning seven years showed that the inter-annual variability in plaice fecundity ranged from 7%-15% for different size classes and correlated with condition. Therefore, this variability in fecundity may be explained by the rate of energy acquisition during the feeding season (Rijnsdorp, 1990; Rijnsdorp, 1991). Based on these findings, OWFs could positively affect the individual fecundity of female plaice if they offer increased prey abundances and/or improve accessibility to prey. However, while we found indications that plaice had access to higher prey availability in the vicinity of turbine foundations, our results could not show that this translated into a positive effect on fish condition or ovary weight (≈ fecundity) (Chapter 4). It is possible that this effect was not picked up due too low sample sizes or because we did not measure fecundity directly by determining the number of oocytes. On the other hand, fish are able to regulate the way they allocate energy towards somatic growth or reproduction, with smaller individuals making more energy available for growth, while large fish prioritize reproduction (Rijnsdorp and Ibelings, 1989; Rijnsdorp, 1991; van Walraven et al., 2010). This regulating mechanism might bias the interpretation of condition metrics or ovary weight and, therefore, data on how much of the acquired energy is allocated towards growth or reproduction might be needed to increase our understanding of the effects on OWFs on fish condition and fecundity.

Electromagnetic fields (EMFs) emitted by cables within OWFs might also affect recruitment of plaice indirectly through the disturbance of individuals during their spawning migrations. For many migratory fish species, lab and tagging studies have indicated that they use the Earth's magnetic field for orientation (Formicki et al., 2019). If EMFs from cables interfere with this natural field, it is possible that fish become disorientated and do not reach the spawning areas or take more time to get there, which can affect recruitment. However, research related to the effects of offshore wind-associated EMFs on fish is still in its infancy and a lot of knowledge gaps still need to be addressed (Hutchison et al., 2020b).

Another recruitment process that could be affected by OWFs is the transport of the pelagic eggs and larvae towards the nursery areas, which occurs at the scale of hundreds of kilometres (Barbut et al., 2020). Turbine foundations can modify the hydrodynamics at local and regional scales by modifying the wind fields and oceanographic parameters (Rivier et al., 2016; van Berkel et al., 2020). Modelling studies on plaice in the southern North Sea have suggested that meteorological-driven variability in circulation patterns during the early pelagic stages might be a key factor in determining year-class strength (van der Veer et al., 1998; Bolle et al., 2009). Therefore, it is possible that the development of offshore wind might alter the hydrographic relationship between spawning and nursery areas, which can impact the number of eggs or larvae that reach the nursery areas. It is not clear whether disturbances in hydrological patterns due to OWFs surpass the natural variability in the system (van Berkel et al., 2020) and what the effects are for fish recruitment, which is an important knowledge gap that needs addressing. Filling this knowledge gap is especially important given the planned increase in the number of wind farms within the coming decades.

OWFs might also impact plaice recruitment when they are constructed inside coastal nursery areas. Currently, there are already some OWFs present within plaice nursery areas and this number will further increase in the future (Figure 6.1). Following the 'nursery size hypothesis', a positive relationship was found between year-class strength of 0-group plaice and the surface area of available nursery areas (van Der Veer et al., 2000). Anthropogenic disturbances have been found to substantially decrease nursery capacity (Rochette et al., 2010), and so the construction of OWFs in nursery areas might lead to a decrease in their surface area and quality, thereby affecting recruitment. Quality of the nursery areas is mainly determined by food availability and predation risk (Gibson, 1994) and both could be affected by OWFs. Their presence has been shown to provoke large-scale changes in primary production, dissolved oxygen and sediment resuspension (Rivier et al., 2016; Daewel et al., 2022), which can result in changes to the food web. Predators of juvenile plaice, mainly crustaceans and fish (van der Veer and Bergman, 1987), might be attracted to the OWF hard substrates through the artificial reef effect, leading to increased mortality of juveniles on the nursery grounds. On the other hand, a higher prey availability through enrichment of the surrounding sediments (Lefaible et al., 2018) and an increase in shelter opportunities due to increased habitat complexity might also have positive effects on the survival of juveniles in the nursery areas. Presently, it is still largely unknown what the effects are of OWF construction in flatfish nursery areas. However, addressing this knowledge gap is key to assess OWF effects on the population level.

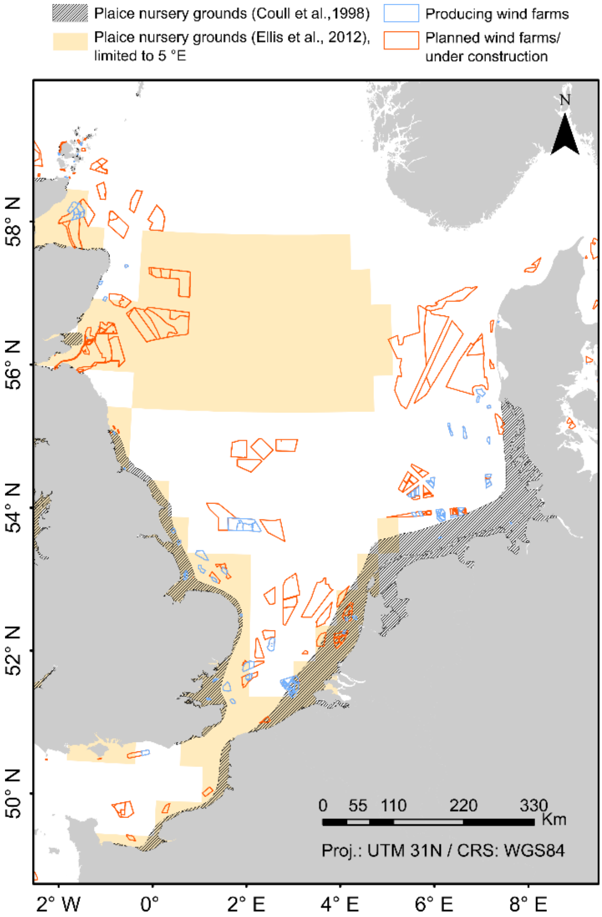

Figure 6.1: Locations of plaice nursery grounds from Coull et al., (1998) and Ellis et al., (2012), together with present (blue) and planned (red) offshore wind farms.

OWFs might also affect plaice recruitment when they are constructed within spawning areas (Figure 6.2). The locations of the spawning areas seem to be mainly determined by their hydrographic relationship with the nursery areas (Bolle et al., 2009). The effects of OWFs on the local hydrology are substantial and include changes in upwelling and increases in turbulence and water retention times (van Berkel et al., 2020). These local effects can hamper or delay the dispersion of eggs to the nursery areas and may lead to changes in recruitment. During spawning, plaice ceases to eat almost completely, so effects of OWFs on prey availability are probably less important than for the nursery areas. However, the artificial reef effect can increase predator presence and thus change food web dynamics, which might lead to changes in survival on the spawning grounds. On the other hand, a positive effect on adult survival can be expected due to the cessation of trawling activities. A recent study calculated that, currently, 9.4% of plaice spawning grounds overlap with present and planned OWFs, but this number will likely increase in the future (Barbut et al., 2020). As for nursery grounds, the effects of constructing OWFs in spawning areas of plaice are still largely unknown.

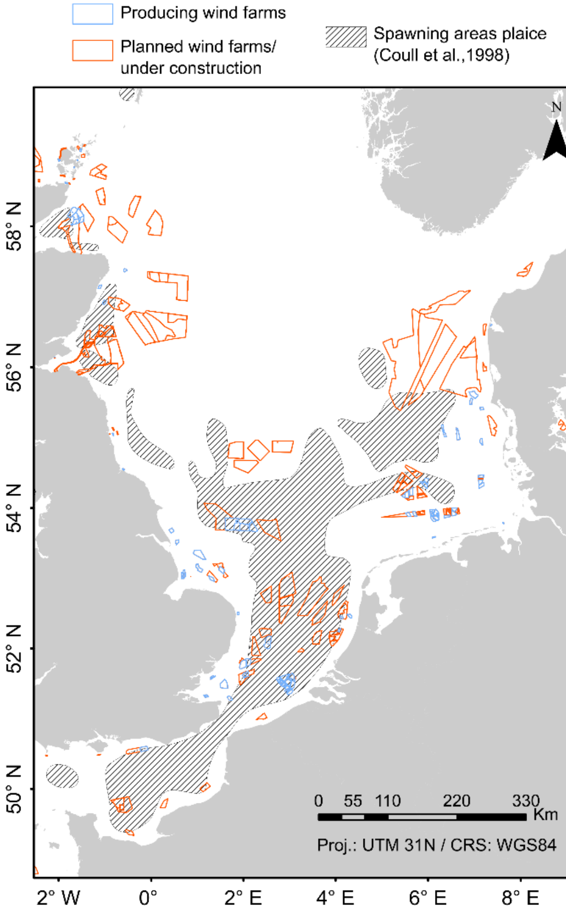

Figure 6.2: Locations of the plaice spawning areas from Coull et al., (1998), together with present (blue) and planned offshore wind farms (red).

6.4.2 GROWTH

The growth rate of adult plaice is mainly determined by food intake and temperature (Rijnsdorp and van Beek, 1991). Increased growth rates of plaice in the southern North Sea around the 1960s have been linked to increases in food intake (Rijnsdorp and van Beek, 1991). Therefore, as OWFs increase the prey availability for plaice, they might also positively affect growth rates. However, growth in plaice is very complex and is suggested to be density-dependent, whereby higher abundances of fish lead to decreased growth rates (Modin and Pihl, 1994). We showed that plaice present within a wind farm were larger, which could be an indication of increased growth (or a refuge effect), but no apparent effects were found on body condition. However, in order to answer the questions if and how much OWFs affect plaice growth, long-term length at age data is needed (Rijnsdorp and van Beek, 1991).

6.4.3 MORTALITY

OWFs can affect the natural mortality of adult plaice by the attraction of apex predators, such as grey seals *Halichoerus grypus*. Research has revealed that plaice can attribute substantially to the diet of grey seals, which have been shown to aggregate around wind turbine foundations (Hammond et al., 1994; Russell et al., 2014). An ecological modelling study also estimated a threefold increase of this species after the construction of an OWF (Raoux et al., 2017). It is not clear whether this increase in grey seals could have a significant effect on fish abundances in OWFs. Human-induced mortality of plaice can be altered due to offshore wind development through fisheries displacement. As trawling activities are forbidden in most European wind farms, fishers might need to find new fishing grounds. Such displacement can aggregate efforts and lead to local overexploitation of fisheries resources (Stelzenmüller et al., 2016).

6.4.4 METHODS FOR UPSCALING OWF EFFECTS

Assessing whether and to what extent populations can be affected by OWFs is preferably achieved by in-situ studies (e.g. BACI) investigating processes that determine populations. However, this is sometimes difficult to achieve as such population-determining processes occur on large temporal and spatial scales that are hard to capture within field studies. Moreover, the natural variability of the marine ecosystem and the influence of regional or global trends (e.g. climate change) make the extraction of specific impacts difficult (van Berkel et al., 2020). Therefore, modelling approaches might be considered as an interesting alternative for or addition to field studies. Predictive models often require knowledge of the effect sizes of individual effects and how they change over time (May et al., 2019). As such, output from studies performed on the turbine and OWF scale is needed as input for models that aim to estimate impacts over larger scales. In conclusion, upscaling OWF effects from individuals to populations can be achieved by the combination of modelling and in-situ approaches that focus on processes determining populations.

6.5 RECOMMENDATIONS, FUTURE RESEARCH IDEAS AND LESSONS LEARNED

The main aim of this thesis was to study the ecological effects of offshore wind farms on plaice. Based on the findings of our study, together with experience gained during field sampling and data analyses, some recommendations are formulated on how flatfish monitoring in OWFs could be improved. Further, ideas for future research are presented that builds further on the knowledge gained in this work. Finally, some points of attention are raised in the form of learned lessons that can be taken into account when addressing similar research questions.

6.5.1 RECOMMENDATIONS FOR MONITORING FLATFISH IN OWFS

6.5.1.1 Alternative sampling techniques

Due to the many safety restrictions in OWFs, it is often difficult to collect high resolution scientific fish data on ecologically relevant time and spatial scales. The use of traditional sampling gear, such as trawls or dredges, is often not allowed within wind farm areas while diver-based methods are time-consuming and limited by sampling depth and currents.

A promising non-invasive method for sampling within OWFs is the use of remotely operated vehicles (ROVs). Footage of the foundations and scour protection can inform researchers about biomass, biodiversity, zonation patterns and the succession of organisms that are associated with the hard substrate (Karlsson et al., 2021) and could, as such, be used instead of diving transects for studying (flat)fish distribution patterns on the hard substrates in an OWF. This method is particularly interesting when combined with automatic video analysis techniques, which can significantly reduce the time it takes to analyse the footage (Boavida et al., 2016). Also, these systems are not limited by water depth and are less dependent on tidal cycles than traditional diving methods. Especially for sampling hard substrates at greater depths, they might be the only feasible method to use. Moreover, it could also be interesting to work together with the industry, as most wind farm operators use ROVs equipped with cameras to inspect turbine foundations on a regular basis. Cooperation could increase the data frequency and reduce the sampling costs substantially (Coolen et al., 2019). The suitability of ROV footage as a sampling method will off course depend on the research question that needs to be answered. While this method has already been successfully used to study the dominant communities on submerged hard structures, it is less ideal for the identification of very small and cryptic species due to low visibility or video resolution (Schutter et al., 2019). Furthermore, ROVs might not be ideal in areas where high turbidity can complicate the identification of organisms. Combining ROV footage and ground-truthing techniques, such as scrape samples or in-situ diver observations, can overcome the limitations of both methods (Coolen et al., 2020).

Another technique that could be used for monitoring flatfish in OWFs is environmental DNA (eDNA). Although this technique is mainly used in the marine environment for studying biodiversity (Staehr et al., 2022) or detecting the presence of non-indigenous species (Ardura and Planes, 2017), there is growing interest for its application as a cost-effective indicator of fish abundance and/or biomass for stock assessments (Rourke et al., 2022). A recent literature review reported that 90% of the sourced studies found a positive correlation between detectable DNA in the marine environment and the abundance or biomass of fish (Rourke et al., 2022). Applying this technique in OWFs could seriously reduce costs and increase efficiency, especially when an automated sampler of eDNA is combined with traditional monitoring methods for ground-truthing (Staehr et al., 2022). Moreover, such an approach would allow for the integration of seasonality in the sampling design, as samples could be taken year round. Another advantage of this method compared to visual techniques is its independency of good water visibility, making it interesting to use in the more turbid coastal waters of the North Sea. However, the technique still needs further development and validation, especially for biomass estimations, before it can be used in actual monitoring campaigns and stock assessments (Ruppert et al., 2019; Rourke et al., 2022).

Overall, it is recommended to use a combination of different methods to obtain a detailed overview of the ecological effects of OWFs on flatfish. The best approach, thereby, combines alternative non-invasive techniques that increase the sampling frequency, with more traditional ones that are thoroughly validated, but often more labour-intensive. Off course, the choice of an appropriate sampling or monitoring method is highly dependent on the research questions that need to be answered and the temporal or spatial scale at which information is required.

6.5.1.2 The importance of spatio-temporal scales

Offshore wind farms affect the marine environment in various ways and on many different spatial and temporal scales. The artificial reef effect, for example, is mainly occurring at the scale of a turbine, its foundation and the surrounding SPL (dos Santos et al., 2010), while the fisheries exclusion effect might influence fish population on a much wider scale (Dannheim et al., 2020). The extent of these spatial scales is thereby not only dependent on the species' characteristics, but also changes over time and differs between life stages and even seasons (Gill et al., 2020). Therefore, to capture these changes over space and time, studies should not only focus on the adult life stage or sample in a particular season. Moreover, the Belgian monitoring campaign could only find an extension of the artificial reef effect towards the soft sediment after seven years (De Backer et al., 2021). Monitoring should be a continued process that is not only conducted during the first few years after the construction of the wind farm, but spans a longer time frame (Langhamer, 2012). Our results also suggested that effects occurring at different spatial scales can influence each other. The observed attraction of plaice towards the SPL on the small scale might have caused a relocation of the fish in between the turbines and, as such, create a sampling bias when only one of the scales is studied (Chapter 3). Thorough knowledge on the temporal and spatial scales at which effects take place in OWFs is thus crucial to avoid biases during sampling or monitoring.

Another issue concerning the monitoring in OWFs is that their potential effects are often studied on spatial scales that are too small to properly inform management. The effects of a single turbine or wind farm might be extensive from an ecological point of view, but may not be able to influence populations at the regional level. For the fisheries sector, for example, an OWF-effect is only considered important if it causes changes in the fish stocks, as these have a direct influence on their catch sizes (Gill et al., 2020). The upscaling of effects, however, is not easy, as it requires extensive ecological knowledge about a particular species and a mechanistic understanding of all the possible cause-effect relationships (Dannheim et al., 2020; Gill et al., 2020). Modelling studies can help in tackling this problem of upscaling, but require large amounts of detailed species and food web information that can only be acquired through targeted research on much smaller scales (Raoux et al., 2017). Moreover, the importance of upscaling will further increase in the near future, as the number of wind farms is growing exponentially, especially in the North Sea (EMODnet, 2022; Stelzenmüller et al., 2022).

In conclusion, it is recommended to use a combination of different methods that allow for the integration of information on different temporal (e.g. stomach content analysis and fatty acid analysis) and spatial scales (e.g. diving transects for turbine scale, beam trawling for wind farm scale). Off course, the choice of an appropriate sampling or monitoring method is highly dependent on the research questions that need to be answered and the temporal or spatial scale at which information is required. In a long-term monitoring programme, alternative, non-invasive methods that increase the sampling frequency should be combined with more traditional methods that are thoroughly validated, but often more labour intensive. As such can the limitations of both types of methods (time consuming vs. high uncertainty) be compensated. For studying refuge effects on flatfish in OWFs, we recommend to not only focus on fish abundances, but to include other variables such as fish size, sex ratio, age and condition to increase the chances of picking up a potential effect.

6.5.2 IDEAS FOR FUTURE RESEARCH

This thesis focused on the ecological effects of OWFs on plaice, a soft sediment species with a high commercial value. Field studies demonstrated that the presence of turbines and scour protection, together with the absence of fisheries, influenced plaice ecology in terms of their spatial distribution, diet and movements. Although this thesis already filled some important knowledge gaps related to the effects of OWFs on soft sediment species, there are still many unanswered questions that remain. Here, some ideas for future research are presented based on the results obtained throughout this PhD study.

This thesis included a baseline study that analysed long term trends in fish length and abundances in relation to climatological variables with the aim of better understanding how climate change and variability is influencing different fish species (Chapter 2). In the overall discussion, some hypotheses were formulated on potential cumulative impacts of climate change and OWFs on plaice based on our findings. However, modelling studies that take into account both impacts simultaneously are needed to fully understand how their cumulative effects could influence fish communities (Voet et al., 2021). Moreover, as the impact of both OWFs and climate change will likely further increase in the future, especially in the North Sea (Garcia-Soto and Pingree, 2012; Stelzenmüller et al., 2022), knowledge on potential interaction effects is key to draw up more effective mitigation measures.

All of the field work included in this thesis was carried out within two separate OWFs (Belwind, and to a lesser extent C-Power) in the BPNS. However, as more and more wind projects are being constructed, it is important to consider their cumulative impact on the larger marine ecosystem (Gill et al., 2020). Only by upscaling the observed local ecological effects and linking them to changes in catch size or individual fish quality for regional fish stocks, the interaction between the OWF and fisheries sector can be fully understood. An important question is, therefore, whether OWFs can cause a spillover of fish into adjacent fishable areas that is large enough to support local or even regional fisheries (Halouani et al., 2020). It is clear from our thesis that plaice has access to increased prey availability, which suggests that fish production might be occurring within the Belwind wind farm. Moreover, we also found larger individuals within the wind farm, supposedly a result of the cessation of bottom trawling within the area (Vandendriessche et al., 2015). These results indicate that spillover from the OWF is possible, however, large scale in-situ studies are needed to confirm this and further investigate if the potential effect is sufficient enough to cause changes on the population level.

As a result of the OWF expansion, larger, contiguous wind farm zones are being formed. It would be interesting to assess whether there is a size effect on their refuge potential, similar to what is observed for MPAs (Vandeperre et al., 2011). Although species densities, biomass and individual fish size do not proportionally increase with the size of a marine reserve, large reserves are essential to obtain sufficient increases in absolute numbers (Halpern, 2003). As changes in catches are often the main concern for fisheries, larger OWF zones might be more efficient than multiple smaller ones in supporting fisheries resources. In 2020, the first OWF zone (238 km^2) in the BPNS was completed. Together with the finished adjacent wind energy area Borssele (344 km^2), it forms a contiguous area of 582 km^2 where no bottom-trawl fisheries are allowed (Noordzeeloket, 2022). Its large size, together with the existing ban on the usage of bottom-disturbing fishing gear in the entire zone, makes it an interesting area for studying OWF-effects on a larger scale as well as spillover effects into adjacent waters.

Our tagging study (Chapter 5) used acoustic ID transmitters to follow plaice movements within the Belwind wind farm. Although this type of transmitters was suitable to answer the research questions related to the residency and small-scale movements of plaice within and in relation to an OWF, they also have some limitations. ID-transmitters do not store depth information, so triangulation can only estimate the position of a fish in a 2D-plane and, therefore, says nothing about the location of the fish in the water column. For plaice, whose vertical movements in the water column are linked to their feeding behaviour (De Groot, 1971), depth information could be useful for linking movement of fish to certain behaviour (Heffernan et al., 2004; Bacheler et al., 2019). Further, ID-transmitters can only give information on fish movement when the fish is present in the vicinity of a receiver or inside a receiver network. This dependence on the presence of receivers limits the data continuity, especially when fish are known to migrate outside the area (e.g. spawning migrations of plaice). Data storage tags (DSTs) equipped with temperature, pressure or activity sensors could offer complementary information on depth preferences and spatial behaviour of plaice on their movements outside of the OWF area. The combination of acoustic and data storage tags can further increase the amount of data that can be collected (Goossens et al., 2023).

This thesis focused on plaice due to its commercial importance and the knowledge gaps that existed concerning its ecology in OWFs. Future research on OWF effects should include other marine resource species that can be affected by the presence of hard substrates or energy emissions. Although many of the observed effects might be similar for all flatfish species due to their high association with the seabed, individual differences between species might still be substantial. Sole, for example, is a night-time feeder and relies on chemical cues for catching its prey (Gibson, 1997). Moreover, its distribution and temperature-preferences are very different from those of plaice, which might lead to different impacts or effect sizes. Electroreceptive species such as sharks and rays may be very sensitive to the EMFs emitted by the cables, which can comprise their ability to locate their prey or orientate themselves in the water column (Wilhelmsson and Langhamer, 2014). Further, although not a fish species, it might also be interesting to study common squid *Loligo vulgaris* in relation to OWFs. Increased densities of the species were found in C-Power, which can be an indication that these cephalopods use the steel structured of jacket foundations for the deposition of their eggs (De Backer et al., 2020).

6.5.3 LESSONS LEARNED

During the analyses of the data and the interpretation of the results, some limitations of the used sampling design were encountered. Here we discuss some of these limitations and give recommendations on how they can be dealt with in future studies.

During the analysis of the diving transect data that was collected in Belwind, it became clear that the scour protection is not homogenously distributed around the turbine foundations and that this might have affected the observed patterns in distribution. Especially the amount of open space in between the rocks was suggested to be an important factor determining plaice distribution. However, we did not collect any information on the configuration of the scour protection and only median values of rock size were available over all turbines. Therefore, it is recommended that in future research on soft-sediment fish distribution around wind turbines, this kind of information is collected during sampling.

In the tagging study, the built-in transmitters of the receivers were used to perform the range detection analysis (Goossens et al., 2022) and to synchronise the receiver network. However, it would have been interesting to combine the data of these build-in transmitters with data from fixed animal transmitters used as sentinel tags. Such sentinel tags could have been put between the rocks of the SPL and on the open sand. Such a setup would have allowed for the calculation of the difference in detection efficiency between the SPL and the surrounding sand, which would have helped in assessing the performance of the yaps model.

During the analysis of the tagging data, we formulated the hypothesis that the observed small scale pattern in plaice movement were linked to their feeding behaviour, which is largely driven by light intensity. Now, the relation between light and plaice distance to the turbine was assessed using time of the day as a proxy for light conditions. The concurrent collection of data on this variable in the field could have improved the data analysis considerably.

6.6 CONCLUSION

The presence of offshore wind farms affects plaice ecology in terms of spatial distribution, diet and movement patterns. Although plaice is considered a typical soft-sediment fish species, it is attracted to the habitat formed by the scour protection (i.e. rocks interspersed with sandy patches). Plaice present on the scour protection have, compared to fish caught on the soft sediment, a distinctive diet composition dominated by hard substrate prey, on which they feed over longer periods of time. Moreover, their digestive tracts are fuller, indicating that the hard substrate offers an increased availability and/or accessibility of prey items. Their small scale movements suggest that plaice are mainly resting on the soft sediments relatively close (±70 m) to a particular turbine during the day and, from there, undertake ‘feeding excursions’ to or near the scour protection during daylight hours. At night when they generally do not feed, their distance to the scour protection increases, probably because they swim higher up in the water column. Altogether, this indicates that the hard substrate in OWFs, and mainly the scour protection, exerts an artificial reef effect on plaice by creating 'feeding hot spots'. Although this could lead to fish production, a post-construction increase in plaice abundance was only clear for one of the two studied wind farms. Furthermore, no statistical differences in condition and fecundity were found between fish caught within the OWF and in control areas. These ambiguous results highlight the need for further investigation related to the attraction-production hypothesis for flatfish. Such research is preferably carried out on a broader regional scale, at which fisheries are usually managed.

Apart from their role as artificial reefs, OWFs may also offer refuge to fished species as most fisheries activities are not allowed within many European wind farms. Although plaice is not the ideal species for protection against fishing mortality through closed areas because of their large-scale spawning migrations, this thesis provided evidence that it can benefit from OWFs as refuge areas. We observed larger plaice in higher abundances with a higher female-to-male ratio within an OWF compared to control areas, which might be explained by the cessation of trawling activities within the wind farm and thus the occurrence of a refuge effect. Such a refuge effect could especially be interesting for plaice, as a combination of climate change and fisheries-induced selection probably leads to a decrease in its size-at-first maturity. Therefore, it is possible that by excluding the negative effects of fishing, OWFs could facilitate plaice adaptation to climate change by providing stepping stones for dispersal and may even counteract evolutionary fisheries-induced effects on the species.

This thesis demonstrated that OWFs benefit plaice through the combination of an artificial reef and refuge effect. It remains, however, unclear whether the abovementioned positive effects can affect the plaice population beyond the borders of an OWF. If a spillover exists, this could create opportunities for commercial flatfish fisheries through increased catch rates or fish sizes on fishing grounds outside OWFs. Thus far, knowledge on the effects of OWFs on fish population level is still largely missing. In the meantime, fishers are worried about the loss of fishing grounds due to the large-scale expansion of offshore wind in the North Sea, which can lead to conflicts. Therefore, future research needs to focus on upscaling the observed ecological effects and assess cumulative impacts to answer the question if fishers might profit from wind farm development. This is vital information needed to inform discussions between both sectors, especially because offshore wind will further grow during the coming decade.

ANNEXES

Annex 2.1: Atlantic Multidecadal and North Atlantic Oscillation index values for 1985-2019.

Year	NAO index	AMO index	Year	NAO index	AMO index
1985	-0.183	-0.284	2003	0.098	0.214
1986	0.503	-0.292	2004	0.243	0.189
1987	-0.123	0.050	2005	-0.268	0.275
1988	-0.013	-0.022	2006	-0.209	0.249
1989	0.702	-0.100	2007	0.174	0.130
1990	0.594	-0.055	2008	-0.378	0.121
1991	0.268	-0.149	2009	-0.244	0.022
1992	0.581	-0.236	2010	-1.153	0.333
1993	0.179	-0.228	2011	0.294	0.085
1994	0.576	-0.194	2012	-0.456	0.197
1995	-0.081	0.118	2013	0.209	0.150
1996	-0.214	-0.075	2014	0.184	0.085
1997	-0.157	0.035	2015	0.434	0.097
1998	-0.481	0.355	2016	-0.039	0.326
1999	0.391	0.101	2017	0.225	0.299
2000	0.207	0.011	2018	1.084	0.052
2001	-0.183	0.102	2019	-0.318	0.157
2002	0.039	0.047			

Annex 2.2: T-values for the correlations between the selected environmental variables of the three final DFA-models and the used species for each fish assemblage. Values > 2 in absolute sense are considered as meaningful and are indicated in bold.

Mud assemblage

species	SST	AMOwinter
Agonus cataphractus	-4.69	1.52
Limanda limanda	1.00	-1.37
Liparis liparis	-2.74	-0.63
Merlangius merlangus	-2.86	1.93
Pleuronectes platessa	-0.66	2.33
Pomatoschistus spp.	1.91	-0.60
Solea solea	-1.22	4.61
Triglidae spp.	-0.74	0.94
Trisopterus luscus	1.99	2.37

Fine sand assemblage

species	SST	SSTlag3
Agonus cataphractus	-3.69	1.62
Buglossidium luteum	0.75	1.19
Callionymus spp.	2.33	-0.51
Limanda limanda	0.20	-0.22
Merlangius merlangus	2.24	0.11
Pleuronectes platessa	0.32	1.21
Pomatoschistus spp.	-0.40	-1.82
Solea solea	-3.30	2.51
Trisopterus luscus	1.49	-1.70

Coarse sand assemblage

species	AMOwinter	NAO
Ammodytes tobianus	-0.71	2.51
Arnoglossus laterna	0.32	0.97
Buglossidium luteum	4.83	2.23
Callionymus spp.	1.28	1.79
Echiichthys vipera	3.13	0.54
Hyperoplus lanceolatus	0.88	4.41
Limanda limanda	-0.80	0.38
Merlangius merlangus	-1.03	-0.52
Mullus surmuletus	-0.51	0.62
Pleuronectes platessa	-0.03	1.63
Pomatoschistus spp.	-1.12	1.53

Annex 3.1: Metadata of all visual diving transects performed in the Belwind offshore wind farm to study small–scale distribution patterns of plaice *Pleuronectes platessa* around the wind turbine foundations. SPL = scour protection layer.

Date	Month	Turbine	Transect number	Effort surrounding sand (m^2)	Effort SPL (m^2)	Total area (m^2)	Total distance (m)	Direction (°)
09/07/2019	7	B9	1	57	48	105	35	360
09/07/2019	7	C9	1	84	36	120	40	315
09/07/2019	7	C9	2	33	57	90	30	45
10/07/2019	7	B8	1	60	45	105	35	45
10/07/2019	7	C8	1	66	54	120	40	292.5
10/07/2019	7	C8	2	60	60	120	40	157.5
24/07/2019	7	D1	1	69	51	120	40	270
24/07/2019	7	D1	2	72	48	120	40	135
24/07/2019	7	D1	3	78	42	120	40	180
24/07/2019	7	D3	1	63	45	108	36	45
24/07/2019	7	D3	2	75	45	120	40	225
26/07/2019	7	C6	1	60	60	120	40	90
26/07/2019	7	C6	2	60	60	120	40	180
26/07/2019	7	C6	3	60	60	120	40	270
26/07/2019	7	D6	1	78	42	120	40	225
26/07/2019	7	D6	2	73.5	46.5	120	40	45
08/08/2019	8	B4	1	66	54	120	40	180
08/08/2019	8	B4	2	63	57	120	40	360
08/08/2019	8	C5	1	75	45	120	40	135
27/08/2019	8	B2	1	81	39	120	40	315
27/08/2019	8	B2	2	87	33	120	40	135

Annex 3.2: Video recording of a visual diving transect conducted on 8/08/2019 around the foundation of turbine B4 in the Belwind wind farm. ©Film Johan Devolder.

Visual diving transect Belwind (8 August 2019) - Turbine B4, Transect 1

Link to video: https://youtu.be/o5ip_PXEw8I

Annex 4.1: Metadata, length, age and wet weight (W_{TOT} = total wet weight, W_E = eviscerated wet weight, W_{GUT} = gut wet weight, W_{GON} = gonad wet weight, W_{LIV} = liver wet weight) of all fish that were included in the study described in chapter 4.

Group	Catch method	Length (mm)	Sex	Age	W_{TOT}	W_E	W_{GUT}	W_{GON}	W_{LIV}
TB	BB_B7	Line	32F2	11/09/2020	340	F	6	351	309
TB	BB_B7	Line	32F2	11/09/2020	310	F	5	274	246
TB	BB_B7	Line	32F2	11/09/2020	260	F	3	201	179
TB	BB_B7	Line	32F2	11/09/2020	300	F	6	239	216
TB	BB_B7	Line	32F2	11/09/2020	320	F	6	353	317
TB	BB_B7	Line	32F2	11/09/2020	320	F	5	355	310
TB	BB_C2	Line	32F2	10/09/2020	270	F	4	189	171
TB	BB_C2	Line	32F2	10/09/2020	310	F	4	323	284
TB	BB_C2	Line	32F2	10/09/2020	280	F	3	247	213
TB	BB_C2	Line	32F2	10/09/2020	290	F	4	257	214
TB	BB_C2	Line	32F2	10/09/2020	310	F	4	288	255
TB	BB_C2	Line	32F2	10/09/2020	360	F	9	468	416
TB	BB_D7	Line	32F2	11/09/2020	305	M	8	276	255
TB	BB_D7	Line	32F2	11/09/2020	270	F	4	201	172
TB	BB_D7	Line	32F2	15/09/2020	295	M	7	262	238
TB	BB_D7	Line	32F2	15/09/2020	310	F	3	284	254
TB	BB_D7	Line	32F2	15/09/2020	275	F	3	224	202
TB	BB_D7	Line	32F2	15/09/2020	290	F	4	232	208
WF	ftWBB05bs	Trawl	32F2	15/09/2020	285	F	5	226	206
WF	ftWBB05bs	Trawl	32F2	15/09/2020	365	F	9	444	400
WF	ftWBB05bs	Trawl	32F2	15/09/2020	270	F	3	180	158
WF	ftWBB05bs	Trawl	32F2	15/09/2020	270	F	4	204	180
WF	ftWBB05bs	Trawl	32F2	15/09/2020	255	F	3	170	154
WF	ftWBB05bs	Trawl	32F2	15/09/2020	250	M	5	142	132
WF	ftWBB06as	Trawl	32F2	15/09/2020	325	F	4	334	308
WF	ftWBB06as	Trawl	32F2	15/09/2020	300	F	4	266	244
WF	ftWBB06as	Trawl	32F2	15/09/2020	210	F	2	100	90
WF	ftWBB06as	Trawl	32F2	15/09/2020	220	F	1	102	94
WF	ftWBB06as	Trawl	32F2	15/09/2020	220	M	2	98	92
WF	ftWBB06as	Trawl	32F2	15/09/2020	230	F	2	112	106
WF	ftWBB06bs	Trawl	32F2	15/09/2020	310	F	7	272	250
WF	ftWBB06bs	Trawl	32F2	15/09/2020	355	F	6	420	380
WF	ftWBB06bs	Trawl	32F2	15/09/2020	280	F	4	226	202
WF	ftWBB06bs	Trawl	32F2	15/09/2020	250	F	3	170	154
WF	ftWBB06bs	Trawl	32F2	15/09/2020	225	M	3	120	114
WF	ftWBB06bs	Trawl	32F2	15/09/2020	220	F	2	106	98

Annex 4.1: continued.

Group	Catch method	Length (mm)	Sex	Age	W_{TOT}	W_{E}	W_{GUT}	W_{GON}	W_{LIV}
NC	ftWBB01s	Trawl	32F2	15/09/2020	250	M	4	148	138
NC	ftWBB01s	Trawl	32F2	15/09/2020	255	F	3	164	154
NC	ftWBB01s	Trawl	32F2	15/09/2020	245	F	2	118	108
NC	ftWBB01s	Trawl	32F2	15/09/2020	240	M	3	120	114
NC	ftWBB01s	Trawl	32F2	15/09/2020	220	F	2	102	94
NC	ftWBB01s	Trawl	32F2	15/09/2020	210	M	3	88	86
NC	ftWBB02s	Trawl	32F2	15/09/2020	230	F	2	126	114
NC	ftWBB02s	Trawl	32F2	15/09/2020	220	M	2	94	90
NC	ftWBB02s	Trawl	32F2	15/09/2020	210	F	2	92	84
NC	ftWBB02s	Trawl	32F2	15/09/2020	195	F	1	74	70
NC	ftWBB02s	Trawl	32F2	15/09/2020	210	M	2	82	78
NC	ftWBB02s	Trawl	32F2	15/09/2020	175	M	1	52	48
NC	ftWBB03s	Trawl	32F2	15/09/2020	310	F	4	302	282
NC	ftWBB03s	Trawl	32F2	15/09/2020	240	F	3	158	148
NC	ftWBB03s	Trawl	32F2	15/09/2020	230	M	2	124	118
NC	ftWBB03s	Trawl	32F2	15/09/2020	220	F	2	102	96
NC	ftWBB03s	Trawl	32F2	15/09/2020	245	M	4	142	132
NC	ftWBB03s	Trawl	32F2	15/09/2020	230	M	2	110	104
FC	ft830s	Trawl	32F2	23/09/2020	240	F	2	138	128
FC	ft830s	Trawl	32F2	23/09/2020	260	F	2	138	128
FC	ft830s	Trawl	32F2	23/09/2020	240	F	2	129	121
FC	ft830s	Trawl	32F2	23/09/2020	240	F	4	112	104
FC	ft830s	Trawl	32F2	23/09/2020	240	M	4	116	111
FC	ft830s	Trawl	32F2	23/09/2020	230	F	2	106	98
FC	ft421s	Trawl	32F2	23/09/2020	225	F	2	114	104
FC	ft421s	Trawl	32F2	23/09/2020	215	M	3	90	84
FC	ft421s	Trawl	32F2	23/09/2020	225	F	2	92	86
FC	ft421s	Trawl	32F2	23/09/2020	215	M	3	92	86
FC	ft421s	Trawl	32F2	23/09/2020	220	M	3	94	90
FC	ft421s	Trawl	32F2	23/09/2020	210	M	1	82	78
FC	ft415s	Trawl	32F2	23/09/2020	230	F	2	108	100
FC	ft415s	Trawl	32F2	23/09/2020	215	F	2	94	90
FC	ft415s	Trawl	32F2	23/09/2020	265	M	4	144	134
FC	ft415s	Trawl	32F2	23/09/2020	235	F	2	102	96
FC	ft415s	Trawl	32F2	23/09/2020	240	F	2	124	116
FC	ft415s	Trawl	32F2	23/09/2020	205	F	3	78	70

Annex 4.2: Frequency of occurrence (% FO) of all prey items found in the non-empty stomachs and intestines of sampled plaice individuals.

	Stomach (% FO)				Intestine (% FO)			
Sample group	TB	WF	NC	FC	TB	WF	NC	FC
N	16	16	12	10	18	16	14	18
Ammodytidae spp.					6			
Anomia ephippium	6							
Aora gracilis	6							
Bathyporeia spp.		19	8	30	6	38	29	67
Bivalvia spp.	6			10	11			
Brachyura larvae		6			17			
Bryzoa spp.	6							
Callianassidae spp.								6
Centraloecetes spp.				10				
Cephalopoda spp.						6		
Cirripedia spp.					6			
Crangonidae spp.						6		6
Crepidula fornicata	6							
Crustacea spp.		6				6	7	11
Cumacea spp.				10		13	21	22
Diogenes pugilator				10				
Ebalia spp.				10				
Echinocardium cordatum	19	50	33	30	17	88	64	44
Echinocyamus pusillus		13		10	11	13	7	
Ensis spp.					6			
Epitonium clathratulum					6			
Eurydice spp.						6	7	
Gastrosaccus spinifer	6	25		20	28	38	57	44
Glycera spp.				10			7	
Hinia reticulata	6				11			
Jassa herdmani	31	6			44	6		
Lagis koreni		6						
Lanice conchilega	13	6		20	17	25		
Liocarcinus pusillus						6		
Macropodia spp.	6				28	6		
Monocorophium acherusicum	25				28			
Mysida spp.		6			6			11
Mytilus edulis	31				50	6		
Nematoda spp.					6			
Nemertea spp..	6	19	8	10				
Nephtys spp.	13	19	25					
Notomastus spp.				10				6
Nototropis spp.						6		
Ophiotrix fragilis	75	6			61	6		

Annex 4.2: continued.

	Stomach (% FO)				Intestine (% FO)			
Sample group	TB	WF	NC	FC	TB	WF	NC	FC
N	16	16	12	10	18	16	14	18
Ophiuridae spp.	6	38	25	20	17	63	36	33
Owenia fusiformis			8					
Paguridae spp.			8		6			6
Phyllodoce lineata	6							
Pilumnus hirtellus	13				22			
Pisidia longicornis	25				39	6		
Pisces spp.	6				6			
Platyhelminthes spp.				20				
Poecilochaetus serpens				10				
Polychaeta spp.	6		17	20		56	57	44
Pontocrates spp.					6	13	29	11
Processa spp.			25		17	19	29	6
Scolelepis spp.		13	8				7	
Spionidae spp.			25	10				
Spisula spp.		6			17	25	14	17
Stenothoe spp.	13				11	6		
Synchelidium maculatum				10				
Tellinidae spp.			8		17	25	7	
Terebellidae spp.			8	10	11	6		17
Thia scutellata		19		20	33	31	21	17
Unidentified		6	8		6			
Urothoe spp.	6			20	11	6		56

REFERENCES

ABDULKADIR, S., and TSUCHIYA, M., 2008. One-step method for quantitative and qualitative analysis of fatty acids in marine animal samples. J. Exp. Mar. Bio. Ecol. 354, 1–8. https://doi.org/https://doi.org/10.1016/j.jembe.2007.08.024

ABECASIS, D., AFONSO, P., and ERZINI, K., 2014. Can small MPAs protect local populations of a coastal flatfish, Solea senegalensis? Fish. Manag. Ecol. 21, 175–185. https://doi.org/10.1111/fme.12061

ACKMAN, R.G., and SIPOS, J.C., 1964. Application of specific response factors in the gas chromatographic analysis of methyl esters of fatty acids with flame ionization detectors. J. Am. Oil Chem. Soc. 41, 377–378. https://doi.org/10.1007/BF02654818

AMARA, R., MEZIANE, T., ET AL., 2007. Growth and condition indices in juvenile sole Solea solea measured to assess the quality of essential fish habitat. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps07154

AMUNDSEN, P.A., and SÁNCHEZ-HERNÁNDEZ, J., 2019. Feeding studies take guts – critical review and recommendations of methods for stomach contents analysis in fish. J. Fish Biol. 95, 1364–1373. https://doi.org/10.1111/jfb.14151

ANSELL, A.D., and GIBSON, R.N., 1990. Patterns of feeding and movement of juvenile flatfishes on an open sandy beach, in: Barnes, M., Gibson, R.N. (Eds.), Trophic Relationships in the Marine Environment. Proceedings of the 24th European Marine Biology Symposium. Aberdeen University Press, Aberdeen, Scotland, pp. 191–207.

ARDURA, A., and PLANES, S., 2017. Rapid assessment of non-indigenous species in the era of the eDNA barcoding: A Mediterranean case study. Estuar. Coast. Shelf Sci. 188, 81–87. https://doi.org/https://doi.org/10.1016/j.ecss.2017.02.004

ARNOLD, G.P., and HOLFORD, B.H., 1995. A computer simulation model for predicting rates and scales of movement of demersal fish on the European continental shelf. ICES J. Mar. Sci. 52, 981–990. https://doi.org/10.1006/jmsc.1995.0093

ARNOLD, G.P., and METCALFE, J.D., 1996. Seasonal migrations of plaice (Pleuronectes platessa) through the Dover Strait. Mar. Biol. 127, 151–160. https://doi.org/10.1007/BF00993655

ASHLEY, M.C., MANGI, S.C., and RODWELL, L.D., 2014. The potential of offshore windfarms to act as marine protected areas - A systematic review of current evidence. Mar. Policy 45, 301–309. https://doi.org/10.1016/j.marpol.2013.09.002

ATKINSON, D., 1994. Temperature and organism size-A biological law for ectotherms? Advances in Ecological Research 25: 1. Res. 25.

BABCOCK, R.C., SHEARS, N.T., ET AL., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proc. Natl. Acad. Sci. U. S. A. 107, 18256–18261. https://doi.org/10.1073/pnas.0908012107

BACHELER, N.M., MICHELOT, T., ET AL., 2019. Fine-scale movement patterns and behavioral states of gray triggerfish Balistes capriscus determined from acoustic telemetry and hidden Markov models. Fish. Res. 215, 76–89. https://doi.org/10.1016/j.fishres.2019.02.014

BAILEY, H., BROOKES, K.L., and THOMPSON, P.M., 2014. Assessing environmental impacts of offshore wind farms: Lessons learned and recommendations for the future. Aquat. Biosyst. https://doi.org/10.1186/2046-9063-10-8

BAKTOFT, H., GJELLAND, K., ET AL., 2019. Opening the black box of high resolution fish tracking using yaps. bioRxiv. https://doi.org/10.1101/2019.12.16.877688

BAKTOFT, H., GJELLAND, K.Ø., ET AL., 2017. Positioning of aquatic animals based on time-of-arrival and random walk models using YAPS (Yet Another Positioning Solver). Sci. Rep. 7, 1–10. https://doi.org/10.1038/s41598-017-14278-z

BARBUT, L., VASTENHOUD, B., ET AL., 2020. The proportion of flatfish recruitment in the North Sea potentially affected by offshore windfarms. ICES J. Mar. Sci. 77, 1227–1237. https://doi.org/10.1093/icesjms/fsz050

BAUDRON, A.R., NEEDLE, C.L., ET AL., 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Glob. Chang. Biol. 20, 1023–1031. https://doi.org/10.1111/gcb.12514

BEAUGRAND, G., GOBERVILLE, E., ET AL., 2014. Marine biological shifts and climate. Proc. R. Soc. B Biol. Sci. 281. https://doi.org/10.1098/rspb.2013.3350

BEAUGRAND, G., LUCZAK, C., and EDWARDS, M., 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. Glob. Chang. Biol. 15, 1790–1803. https://doi.org/10.1111/j.1365-2486.2009.01848.x

BERGMAN, M.J.N., VAN DER VEER, H.W., and ZULSTRA, J.J., 1988. Plaice nurseries: effects on recruitment. J. Fish Biol. 33, 201–218. https://doi.org/10.1111/j.1095-8649.1988.tb05574.x

BERGMAN, M.J.N., and VAN SANTBRINK, J.W., 1994. Direct effects of beam trawling on macrofauna in sandy areas off the Dutch coast. BEON Rapport. Den Haag.

BERGMAN, M.J.N., and VAN SANTBRINK, J.W., 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES J. Mar. Sci. 57, 1321–1331. https://doi.org/10.1006/jmsc.2000.0917

BERGSTRÖM, L., SUNDQVIST, F., and BERGSTRÖM, U., 2013. Effects of an offshore wind farm on temporal and spatial patterns in the demersal fish community. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps10344

BOAVIDA, J., ASSIS, J., ET AL., 2016. Comparison of small remotely operated vehicles and diver-operated video of circalittoral benthos. Hydrobiologia 766, 247–260. https://doi.org/10.1007/s10750-015-2459-y

BOHNSACK, J.A., 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bull. Mar. Sci. 44, 631–645.

BOHNSACK, J.A., and SUTHERLAND, D.L., 1985. Artificial reef research: a review with recommendations for future priorities. Bull. Mar. Sci. 37, 11–39.

Bolle, L.J., Dickey-Collas, M., et al., 2009. Variability in transport of fish eggs and larvae. III. Effects of hydrodynamics and larval behaviour on recruitment in plaice. Mar. Ecol. Prog. Ser. 390, 195–211. https://doi.org/10.3354/meps08177

Braeckman, U., Provoost, P., et al., 2012. Temporal dynamics in the diet of two marine polychaetes as inferred from fatty acid biomarkers. J. Sea Res. 68, 6–19. https://doi.org/10.1016/j.seares.2011.11.003

Breine, N.T., De Backer, A., et al., 2018. Structural and functional diversity of soft-bottom macrobenthic communities in the Southern North Sea. Estuar. Coast. Shelf Sci. 214, 173–184. https://doi.org/10.1016/J.ECSS.2018.09.012

Brickhill, M.J., Lee, S.Y., and Connolly, R.M., 2005. Fishes associated with artificial reefs: Attributing changes to attraction or production using novel approaches. J. Fish Biol. 67, 53–71. https://doi.org/10.1111/j.0022-1112.2005.00915.x

Bridger, C.J., and Booth, R.K., 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Rev. Fish. Sci. 11, 13–34. https://doi.org/10.1080/16226510390856510

Bromley, P.J., 2000. Growth, sexual maturation and spawning in central North Sea plaice (Pleuronectes platessa L.), and the generation of maturity ogives from commercial catch data. J. Sea Res. 44, 27–43. https://doi.org/10.1016/S1385-1101(00)00043-5

Brunel, T., and Boucher, J., 2007. Long-term trends in fish recruitment in the north-east Atlantic related to climate change. Fish. Oceanogr. 16, 336–349. https://doi.org/10.1111/j.1365-2419.2007.00435.x

Bulgin, C.E., Merchant, C.J., and Ferreira, D., 2020. Tendencies, variability and persistence of sea surface temperature anomalies. Sci. Rep. 10, 1–13. https://doi.org/10.1038/s41598-020-64785-9

Burnham, K.P., and Anderson, D.R., 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304. https://doi.org/10.1177/0049124104268644

Burrows, M.T., 1994. Foraging time strategy of small juvenile plaice: a laboratory study of diel and tidal behaviour patterns with Artemia prey and shrimp predators. Mar. Ecol. Prog. Ser. 115, 31–39.

Burrows, M.T., Gibson, R.N., et al., 2004. Alongshore dispersal and site fidelity of juvenile plaice from tagging and transplants. J. Fish Biol. 65, 620–634. https://doi.org/10.1111/j.0022-1112.2004.00467.x

Buyse, J., De Backer, A., and Hostens, K., 2021. Small-scale distribution patterns of flatfish on artificial hard substrates in a Belgian offshore wind farm, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea. Attraction, Avoidance and Habitat Use at Various Spatial Scales. pp. 69–76.

Buyse, J., Hostens, K., et al., 2022a. Offshore wind farms affect the spatial distribution pattern of plaice Pleuronectes platessa at both the turbine and wind farm scale. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsac107

Buyse, J., Hostens, K., et al., 2022b. Long-term series demonstrate small-scale differences in trends within fish assemblages explained by climate variability. Estuar. Coast. Shelf Sci. 264, 107663. https://doi.org/10.1016/j.ecss.2021.107663

Buyse, J., Hostens, K., et al., 2023. Increased food availability at offshore wind farms affects trophic ecology of plaice Pleuronectes platessa. Sci. Total Environ. 862, 160730. https://doi.org/https://doi.org/10.1016/j.scitotenv.2022.160730

Cagua, E.F., Berumen, M.L., and Tyler, E.H.M., 2013. Topography and biological noise determine acoustic detectability on coral reefs. Coral Reefs 32, 1123–1134. https://doi.org/10.1007/s00338-013-1069-2

Cannaby, H., and Hüsrevolu, Y.S., 2009. The influence of low-frequency variability and long-term trends in north Atlantic sea surface temperature on irish waters. ICES J. Mar. Sci. 66, 1480–1489. https://doi.org/10.1093/icesjms/fsp062

Carey, D., Wilber, D., et al., 2020. Effects of the Block Island Wind Farm on Coastal Resources: Lessons Learned. Oceanography 33, 70–81. https://doi.org/10.5670/oceanog.2020.407

Catchpole, T., Keeken, O., et al., 2008. The discard problem – A comparative analysis of two fisheries: The English Nephrops fishery and the Dutch beam trawl fishery. Ocean Coast. Manag. 51, 772–778. https://doi.org/10.1016/j.ocecoaman.2008.06.015

Cheung, W.W.L., Lam, V.W.Y., et al., 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish. 10, 235–251. https://doi.org/10.1111/j.1467-2979.2008.00315.x

Cheung, W.W.L., and Oyinlola, M.A., 2018. Vulnerability of flatfish and their fisheries to climate change. J. Sea Res. 140, 1–10. https://doi.org/10.1016/j.seares.2018.06.006

Cheung, W.W.L., Reygondeau, G., and Frölicher, T.L., 2016. Large benefits to marine fisheries of meeting the 1.5°C global warming target. Science (80-.). 354, 1591–1594. https://doi.org/10.1126/science.aag2331

Cheung, W.W.L., Sarmiento, J.L., et al., 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nat. Clim. Chang. 3, 254–258. https://doi.org/10.1038/nclimate1691

Christie, N., Smyth, K., et al., 2014. Co-location of activities and designations: A means of solving or creating problems in marine spatial planning? Mar. Policy 43, 254–261. https://doi.org/10.1016/j.marpol.2013.06.002

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. https://doi.org/https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke, K.R., and Gorley, R., 2006. PRIMER v6: User Manual/Tutorial.

Clarke, K.R., and Gorley, R.N., 2015. Primer v7: User Manual/Tutorial. Prim. Ltd., Plymouth, UK 93.

Clarke, K.R., Somerfield, P.J., and Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. https://doi.org/10.1016/j.jembe.2008.07.009

CLAUDET, J., and PELLETIER, D., 2004. Marine protected areas and artificial reefs: A review of the interactions between management and scientific studies. Aquat. Living Resour. 17, 129–138. https://doi.org/10.1051/alr:2004017

COATES, D., VANAVERBEKE, J., ET AL., 2011. Soft-sediment macrobenthos around offshore wind turbines in the Belgian Part of the North Sea reveals a clear shift in species composition., in: Degraer, S., Brabant, R., Rumes, B. (Eds.), Offshore Wind Farms in the Belgian Part of the North Sea: Selected Findings from the Baseline and Targeted Monitoring. Royal Belgian Institute of Natural Sciences, Management Unit of the North Sea Mathematical Models. Marine ecosystem management unit., p. 157.

COATES, D.A., DESCHUTTER, Y., ET AL., 2014. Enrichment and shifts in macrobenthic assemblages in an offshore wind farm area in the Belgian part of the North Sea. Mar. Environ. Res. 95, 1–12. https://doi.org/10.1016/j.marenvres.2013.12.008

COATES, D.A., KAPASAKALI, D.-A., ET AL., 2016. Short-term effects of fishery exclusion in offshore wind farms on macrofaunal communities in the Belgian part of the North Sea. Fish. Res. 179, 131–138. https://doi.org/10.1016/J.FISHRES.2016.02.019

COLLIE, J., HIDDINK, J.G., ET AL., 2017. Indirect effects of bottom fishing on the productivity of marine fish. Fish Fish. 18, 619–637. https://doi.org/10.1111/faf.12193

COOLEN, J.W.P., 2017. North Sea reefs : benthic biodiversity of artificial and rocky reefs in the southern North Sea. PhD-thesis North Sea Reefs. Benthic Biodivers. Artif. rocky reefs South. North Sea 203.

COOLEN, J.W.P., LENGKEEK, W., ET AL., 2019. Upscaling positive effects of scour protection in offshore wind farms.

COOLEN, J.W.P., VAN DER WEIDE, B., ET AL., 2020. Benthic biodiversity on old platforms, young wind farms, and rocky reefs. ICES J. Mar. Sci. 77, 1250–1265. https://doi.org/10.1093/icesjms/fsy092

COOMBS, S.H., NICHOLS, J.H., and FOSH, C.A., 1990. Plaice eggs (Pleuronectes platessa L.) in the southern North Sea: abundance, spawning area, vertical distribution, and buoyancy . ICES J. Mar. Sci. 47, 133–139. https://doi.org/10.1093/icesjms/47.2.133

COULL, K.A., JOHNSTONE, R., and ROGERS, S.I., 1998. Fisheries Sensitivity Maps in British Waters.

CRESSON, P., LE DIREACH, L., ET AL., 2019. Functional traits unravel temporal changes in fish biomass production on artificial reefs. Mar. Environ. Res. 145, 137–146. https://doi.org/10.1016/j.marenvres.2019.02.018

CRESSON, P., RUITTON, S., and HARMELIN, M., 2014. Artificial reefs do increase secondary biomass production: Mechanisms evidenced by stable isotopes. Mar. Ecol. Prog. Ser. 509, 15–26. https://doi.org/10.3354/meps10866

CROZIER, L.G., and HUTCHINGS, J.A., 2014. Plastic and evolutionary responses to climate change in fish. Evol. Appl. 7, 68–87. https://doi.org/10.1111/eva.12135

CUSHING, D.H., 1969. The Regularity of the Spawning Season of Some Fishes. ICES J. Mar. Sci. 33, 81–92. https://doi.org/10.1093/icesjms/33.1.81

DA SILVEIRA, E.L., SEMMAR, N., ET AL., 2020. Methods for Trophic Ecology Assessment in Fishes: A Critical Review of Stomach Analyses. Rev. Fish. Sci. Aquac. 28, 71–106. https://doi.org/10.1080/23308249.2019.1678013

DAEWEL, U., AKHTAR, N., ET AL., 2022. Offshore wind farms are projected to impact primary production and bottom water deoxygenation in the North Sea. Commun. Earth Environ. 3, 292. https://doi.org/10.1038/s43247-022-00625-0

DALSGAARD, J., ST. JOHN, M., ET AL., 2003. Fatty acid trophic markers in pelagic marine environment. Adv. Mar. Biol. 46.

DANCE, K.M., ROOKER, J.R., ET AL., 2018. Feeding ecology of fishes associated with artificial reefs in the northwest Gulf of Mexico. PLoS One 13. https://doi.org/10.1371/journal.pone.0203873

DANNHEIM, J., BERGSTRÖM, L., ET AL., 2020. Benthic effects of offshore renewables: Identification of knowledge gaps and urgently needed research. ICES J. Mar. Sci. 77, 1092–1108. https://doi.org/10.1093/icesjms/fsz018

DANNHEIM, J., BREY, T., ET AL., 2014. Trophic look at soft-bottom communities - Short-term effects of trawling cessation on benthos. J. Sea Res. 85, 18–28. https://doi.org/10.1016/j.seares.2013.09.005

DAVIS, A.M., BLANCHETTE, M.L., ET AL., 2012. Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. Freshw. Biol. 57, 2156–2172. https://doi.org/10.1111/j.1365-2427.2012.02858.x

DE BACKER, A., BUYSE, J., and HOSTENS, K., 2020. A decade of soft sediment epibenthos and fish monitoring at the Belgian offshore wind farm area, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Empirical Evidence Inspiring Priority Monitoring, Research and Management. Brussels: Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brussels, pp. 79–113.

DE BACKER, A., and HOSTENS, K., 2017. Effects of Belgian Offshore Windfarms on soft sediment epibenthos and Fish: an updated time series, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: A Continued Move towards Integration and Quantification. Brussels: Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management Section.

DE BACKER, A., POLET, H., ET AL., 2019. Fishing activities in and around Belgian offshore wind farms: trends in effort and landings over the period 2006-2017, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Marking a Decade of Monitoring, Research and Innovation. Brussels: Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, p. 134.

DE BACKER, A., VAN HOEY, G., ET AL., 2022. Describing the epibenthos and demersal fish communities in the Belgian part of the North Sea in view of future OWF monitoring, in: WinMon Report (in Preparation).

DE BACKER, A., VANDENDRIESSCHE, S., ET AL., 2010. Weighing natural variability and anthropogenic impacts: a case study of demersal fish and epibenthic communities in the Belgian Part of the North Sea.

DE BACKER, A., WYNS, L., and HOSTENS, K., 2021. Continued expansion of the artificial reef effect in soft-sediment epibenthos and demersal fish assemblages in two established (10 years) Belgian offshore wind farms, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea. Attraction, Avoidance and Habitat Use at Various Spatial Scales. pp. 61–68.

DE GROOT, S.J., 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (pisces: pleuronectiformes). Netherlands J. Sea Res. 5, 121–196. https://doi.org/10.1016/0077-7579(71)90008-1

DE MESEL, I., KERCKHOF, F., ET AL., 2013. Fouling community on the foundations of wind turbines and the surrounding scour protection, in: Degraer, S., Brabant, R., Rumes, B. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Learning from the Past to Optimise Future Monitoring. Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management Section, p. 239.

DE MESEL, I., KERCKHOF, F., ET AL., 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. Hydrobiologia 756, 37–50. https://doi.org/10.1007/s10750-014-2157-1

DE TROCH, M., BOECKX, P., ET AL., 2012. Bioconversion of fatty acids at the basis of marine food webs: Insights from a compound-specific stable isotope analysis. Mar. Ecol. Prog. Ser. 465, 53–67. https://doi.org/10.3354/meps09920

DE TROCH, M., REUBENS, J.T., ET AL., 2013. Energy profiling of demersal fish: A case-study in wind farm artificial reefs. Mar. Environ. Res. 92, 224–233. https://doi.org/10.1016/j.marenvres.2013.10.001

DE VEEN, J.F., 1978. On selective tidal transport in the migration of North Sea plaice (Pleuronectes platessa) and other flatfish species. Netherlands J. Sea Res. 12.

DEGRAER, S., CAREY, D.A., ET AL., 2020. Offshore wind farm artificial reefs affect ecosystem structure and functioning: a synthesis. Oceanography Special Is.

DEGRAER, S., VERFAILLIE, E., ET AL., 2008. Habitat suitability modelling as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea. Cont. Shelf Res. 28, 369–379. https://doi.org/10.1016/j.csr.2007.09.001

DEGRAER, S., VOLCKAERT, A., and VINCX, M., 2003. Macrobenthic zonation patterns along a morphodynamical continuum of macrotidal, low tide bar/rip and ultra-dissipative sandy beaches. Estuar. Coast. Shelf Sci. 56, 459–468. https://doi.org/10.1016/S0272-7714(02)00195-6

DENIRO, M.J., and EPSTEIN, S., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta 45, 341–351. https://doi.org/https://doi.org/10.1016/0016-7037(81)90244-1

DENMAN, K., CHRISTIAN, J.R., ET AL., 2011. Potential impacts of future ocean acidification on marine ecosystems and fisheries: current knowledge and recommendations for future research. ICES J. Mar. Sci. 68, 1019–1029. https://doi.org/10.1093/icesjms/fsr074

DERWEDUWEN, J., RANSON, J., ET AL., 2016a. Feeding behaviour of lesser weever (Echiichthys vipera) and dab (Limanda limanda) in the C-power wind farm, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Environmental Impact Monitoring Reloaded. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management Section, p. 287.

DERWEDUWEN, J., VANDENDRIESSCHE, S., ET AL., 2012. The diet of demersal and semi-pelagic fish in the Thorntonbank wind farm: tracing changes using stomach analyses data., in: Degraer, S., Brabant, R. & Rumes, B. (Ed.), Offshore Wind Farms in the Belgian Part of the North Sea: Heading for an Understanding of Environmental Impacts. Management Unit of the North Sea Mathematical Models, Marine ecosystem management unit, p. 155 pp. + annexes.

DERWEDUWEN, J., VANDENDRIESSCHE, S., and HOSTENS, K., 2010. Monitoring the effects of the Thorntonbank and Bligh Bank wind farms on the epifauna and demersal fish fauna of soft bottom sediments. Thorntonbank: status during construction (T2). Bligh Bank: status during construction (T1). Offshore Wind farms Belgian part North Sea early Environ. impact Assess. Spat. Var. 218.

DERWEDUWEN, J., VANDENDRIESSCHE, S., and HOSTENS, K., 2016b. Effects of Belgian wind farms on the epibenthos and fish of the soft sediment, in: Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Environmental Impact Monitoring Reloaded. Operationele Directie Natuurlijk Milieu.

DI FRANCO, A., BUSSOTTI, S., ET AL., 2009. Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. Mar. Ecol. Prog. Ser. 387, 275–285. https://doi.org/10.3354/meps08051

DICKENS, L.C., GOATLEY, C.H.R., ET AL., 2011. Quantifying Relative Diver Effects in Underwater Visual Censuses. PLoS One 6, e18965.

DIPPNER, J.W., and KRÖNCKE, I., 2003. Forecast of climate-induced change in macrozoobenthos in the southern North Sea in spring. Clim. Res. 25, 179–182. https://doi.org/10.3354/cr025179

DIPPNER, J.W., MÖLLER, C., and KRÖNCKE, I., 2014. Loss of persistence of the North Atlantic Oscillation and its biological implication. Front. Ecol. Evol. 2. https://doi.org/10.3389/fevo.2014.00057

DOS SANTOS, L.N., BROTTO, D.S., and ZALMON, I.R., 2010. Fish responses to increasing distance from artificial reefs on the Southeastern Brazilian Coast. J. Exp. Mar. Bio. Ecol. 386, 54–60. https://doi.org/10.1016/j.jembe.2010.01.018

DULVY, N.K., ROGERS, S.I., ET AL., 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. J. Appl. Ecol. 45, 1029–1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x

DUPONT, C., HERPERS, F., and LE VISAGE, C., 2020. Recommendations for positive interactions between offshore wind farms and fisheries: Short Background Study.

EDGAR, G.J., BARRETT, N.S., and MORTON, A.J., 2004. Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. J. Exp. Mar. Bio. Ecol. 308, 269–290. https://doi.org/10.1016/j.jembe.2004.03.004

EDWARDS, M., BEAUGRAND, G., ET AL., 2013. Marine Ecosystem Response to the Atlantic Multidecadal Oscillation. PLoS One 8, e57212. https://doi.org/10.1371/journal.pone.0057212

EGGLETON, J.D., DEPESTELE, J., ET AL., 2018. How benthic habitats and bottom trawling affect trait composition in the diet of seven demersal and benthivorous fish species in the North Sea. J. Sea Res. 142, 132–146. https://doi.org/10.1016/j.seares.2018.09.013

EIGAARD, O.R., BASTARDIE, F., ET AL., 2016. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES J. Mar. Sci. 74, 847–865. https://doi.org/10.1093/icesjms/fsw194

ELLIS, J.R., MILLIGAN, S.P., ET AL., 2012. Spawning and nursery grounds of selected fish species in UK waters. Sci. Ser. Tech. Rep. 147, 56.

EMODNET, 2022. Wind Farms (Polygons) [WWW Document]. URL https://www.emodnet-humanactivities.eu/search-results.php?dataname=Wind+Farms+%28Polygons%29 (accessed 6.12.22).

ENGELHARD, G.H., ELLIS, J.R., ET AL., 2011. Ecotypes as a concept for exploring responses to climate change in fish assemblages. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsq183

ERZINI, K., INEJIH, C.A.O., and STOBBERUP, K.A., 2005. An application of two techniques for the analysis of short, multivariate non-stationary time-series of Mauritanian trawl survey data. ICES J. Mar. Sci. 62, 353–359. https://doi.org/10.1016/j.icesjms.2004.12.009

ESPINOZA, M., FARRUGIA, T.J., ET AL., 2011. Testing a new acoustic telemetry technique to quantify long-term , fine-scale movements of aquatic animals. Fish. Res. 108, 364–371. https://doi.org/10.1016/j.fishres.2011.01.011

EUROPEAN COMMISSION, 2018. Review of fisheries management measures in Natura 2000 sites.

EUROPEAN COMMISSION, 2019. What is the European Green Deal? [WWW Document]. URL https://ec.europa.eu/commission/presscorner/detail/en/fs_19_6714 (accessed 10.19.22).

EUROPEAN COMMISSION, 2020. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions: An EU Strategy to harness the potential of offshore renewable energy for a climate neutral future. COM(2020) 741.

FAO, 2014. MSY.

FENBERG, P.B., CASELLE, J.E., ET AL., 2012. The science of European marine reserves: Status, efficacy, and future needs. Mar. Policy 36, 1012–1021. https://doi.org/10.1016/j.marpol.2012.02.021

FLORIN, A.-B., BERGSTRÖM, U., ET AL., 2013. Effects of a large northern European no-take zone on flatfish populations a. J. Fish Biol. 83, 939–962. https://doi.org/10.1111/jfb.12097

FORMICKI, K., KORZELECKA-ORKISZ, A., and TAŃSKI, A., 2019. Magnetoreception in fish. J. Fish Biol. 95, 73–91. https://doi.org/10.1111/jfb.13998

FRIEDLANDER, A.M., BROWN, E.K., and MONACO, M.E., 2007. Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. Ecol. Appl. 17, 715–730. https://doi.org/10.1890/06-0536

FROESE, R., DEMIREL, N., and SAMPANG, A., 2015. An overall indicator for the good environmental status of marine waters based on commercially exploited species. Mar. Policy 51, 230–237. https://doi.org/10.1016/j.marpol.2014.07.012

FROESE R., and PAULY, D. (EDS)., 2022. FishBase [WWW Document]. URL www.fishbase.org, version (08/2019)

GAINES, S.D., WHITE, C., ET AL., 2010. Designing marine reserve networks for both conservation and fi sheries management 107, 18286–18293. https://doi.org/10.1073/pnas.0906473107

GARCIA-SOTO, C., and PINGREE, R.D., 2012. Atlantic Multidecadal Oscillation (AMO) and sea surface temperature in the Bay of Biscay and adjacent regions. J. Mar. Biol. Assoc. United Kingdom 92, 213–214. https://doi.org/10.1017/S0025315410002134

GIBSON, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Netherlands J. Sea Res. 32, 191–206. https://doi.org/10.1016/0077-7579(94)90040-X

GIBSON, R.N., 1997. Behaviour and the distribution of flatfishes. J. Sea Res. 37, 241–256. https://doi.org/10.1016/S1385-1101(97)00019-1

GIBSON, R.N., NASH, R., ET AL., 2015. Flatfishes: Biology and Exploitation, 2nd ed. Wiley Blackwell, Oxford.

GIL-GARCÍA, I.C., GARCÍA-CASCALES, M.S., ET AL., 2019. Categorization and analysis of relevant factors for optimal locations in onshore and offshorewind power plants: A taxonomic review. J. Mar. Sci. Eng. 7, 0–21. https://doi.org/10.3390/jmse7110391

GILL, A.B., DEGRAER, S., ET AL., 2020. Setting the context for offshore wind development effects on fish and fisheries. Oceanography 33, 118–127.

GLAROU, M., ZRUST, M., and SVENDSEN, J.C., 2020. Using artificial-reef knowledge to enhance the ecological function of offshore wind turbine foundations: Implications for fish abundance and diversity. J. Mar. Sci. Eng. 8. https://doi.org/10.3390/JMSE8050332

GOOSSENS, J., BUYSE, J., ET AL., 2022. Taking the time for range testing : an approach to account for temporal resolution in acoustic telemetry detection range assessments. Anim. Biotelemetry 1–13. https://doi.org/10.1186/s40317-022-00290-2

GOOSSENS, J., DENEUDT, K., and REUBENS, J., 2020. Mooring scientific instruments on the seabed — Design , deployment protocol and performance of a recoverable frame for acoustic receivers 2020, 974–979. https://doi.org/10.1111/2041-210X.13404

GOOSSENS, J., WOILLEZ, M., ET AL., 2023. Acoustic and archival technologies join forces: A combination tag. Methods Ecol. Evol. 1–7. https://doi.org/10.1111/2041-210X.14045

GRIFFITHS, C.A., PATTERSON, T.A., ET AL., 2018. Scaling marine fish movement behavior from individuals to populations. Ecol. Evol. 8, 7031–7043. https://doi.org/10.1002/ece3.4223

GRIFT, R.E., RIJNSDORP, A.D., ET AL., 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Mar. Ecol. Prog. Ser. 257, 247–257. https://doi.org/10.3354/meps257247

GROSSMAN, G.D., JONES, G.P., and SEAMAN, W.J., 1997. Do Artificial Reefs Increase Regional Fish Production? A Review of Existing Data. Fisheries 22, 17–23. https://doi.org/10.1577/1548-8446(1997)022<0017:darirf>2.0.co;2

GUIDETTI, P., BAIATA, P., ET AL., 2014. Large-scale assessment of mediterranean marine protected areas effects on fish assemblages. PLoS One 9, 91841. https://doi.org/10.1371/journal.pone.0091841

GULEV, S.K., LATIF, M., ET AL., 2013. North Atlantic Ocean control on surface heat flux on multidecadal timescales. Nature 499, 464–467. https://doi.org/10.1038/nature12268

GUSATU, L.F., YAMU, C., ET AL., 2020. A spatial analysis of the potentials for offshore wind farm locations in the North Sea region: Challenges and opportunities. ISPRS Int. J. Geo-Information 9. https://doi.org/10.3390/ijgi9020096

HAGGETT, C., BRINK, T. TEN, ET AL., 2020. OFFSHORE WIND PROJECTS AND FISHERIES. Oceanography 33, 38–47.

HALE, R., and SWEARER, S.E., 2016. Ecological traps: Current evidence and future directions. Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2015.2647

HALOUANI, G., VILLANUEVA, C.M., ET AL., 2020. A spatial food web model to investigate potential spillover effects of a fishery closure in an offshore wind farm. J. Mar. Syst. 212, 103434. https://doi.org/10.1016/j.jmarsys.2020.103434

HALPERN, B.S., 2003. The impact of marine reserves: Do reserves work and does reserve size matter? Ecol. Appl. 13. https://doi.org/10.1890/1051-0761(2003)013[0117:tiomrd]2.0.co;2

HALPERN, B.S., LESTER, S.E., and KELLNER, J.B., 2009. Spillover from marine reserves and the replenishment of fished stocks. Environ. Conserv. 36, 268–276. https://doi.org/10.1017/S0376892910000032

HAMMOND, P.S., HALL, A.J., and PRIME, J.H., 1994. The Diet of Grey Seals Around Orkney and Other Island and Mainland Sites in North-Eastern Scotland. J. Appl. Ecol. 31, 340–350. https://doi.org/10.2307/2404548

HARRIS, V., EDWARDS, M., and OLHEDE, S.C., 2014. Multidecadal Atlantic climate variability and its impact on marine pelagic communities. J. Mar. Syst. 133, 55–69. https://doi.org/10.1016/j.jmarsys.2013.07.001

HARVEY, A.C., 1990. Forecasting, Structural Time Series Models and the Kalman Filter. Cambridge University Press. https://doi.org/10.1017/CBO9781107049994

HEFFERNAN, O., RIGHTON, D., and MICHALSEN, K., 2004. Use of data storage tags to quantify vertical movements of cod: Effects on acoustic measures. ICES J. Mar. Sci. 61, 1062–1070. https://doi.org/10.1016/j.icesjms.2004.07.003

HEINDLER, F.M., MAES, G.E., ET AL., 2019. Diet composition and gut microbiome of 0-group European plaice Pleuronectes platessa L. - Strong homogeneity and subtle spatial and temporal differences. J. Sea Res. https://doi.org/10.1016/j.seares.2018.11.004

HEINO, M., DIECKMANN, U., and GODØ, O.R., 2002. Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod Mikko Heino , Ulf Dieckmann and Olav Rune Godø.

HERMANS, A., PRUSINA, I., ET AL., 2020. Nature-Inclusive Design: a catalogue for offshore wind infrastructure 37. https://doi.org/10.13140/RG.2.2.10942.02882

HERMANT, M., LOBRY, J., ET AL., 2010. Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France). J. Sea Res. 64, 45–53. https://doi.org/10.1016/j.seares.2009.07.001

HIDDINK, J.G., JOHNSON, A.F., ET AL., 2011. Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. J. Appl. Ecol. 48, 1441–1449. https://doi.org/10.1111/j.1365-2664.2011.02036.x

HIDDINK, J.G., MORANTA, J., ET AL., 2016. Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors. J. Appl. Ecol. 53, 1500–1510. https://doi.org/10.1111/1365-2664.12697

HIDDINK, J.G., RIJNSDORP, A.D., and PIET, G., 2008. Can bottom trawling disturbance increase food production for a commercial fish species? Can. J. Fish. Aquat. Sci. 65, 1393–1401. https://doi.org/10.1139/F08-064

HIDDINK, J.G., and TER HOFSTEDE, R., 2008. Climate induced increases in species richness of marine fishes. Glob. Chang. Biol. 14, 453–460. https://doi.org/10.1111/j.1365-2486.2007.01518.x

HINZ, H., BERGMANN, M., ET AL., 2006a. Habitat association of plaice, sole, and lemon sole in the English Channel. ICES J. Mar. Sci. 63, 912–927. https://doi.org/10.1016/j.icesjms.2006.03.011

HINZ, H., BERGMANN, M., ET AL., 2006b. Habitat association of plaice, sole, and lemon sole in the English Channel. ICES J. Mar. Sci. 63, 912–927. https://doi.org/10.1016/j.icesjms.2006.03.011

HIXON, M.A., and BEETS, J.P., 1993. Predation, Prey Refuges, and the Structure of Coral-Reef Fish Assemblages. Ecol. Monogr. 63, 77–101. https://doi.org/https://doi.org/10.2307/2937124

HOARAU, G., RIJNSDORP, A., ET AL., 2002. Population structure of plaice (Pleuronectes platessa L.) in northern Europe: Microsatellites revealed large-scale spatial and temporal homogeneity. Mol. Ecol. 11, 1165–1176.

https://doi.org/10.1046/j.1365-294X.2002.01515.x

HUNTER, E., METCALFE, J.D., ET AL., 2004. Vertical activity patterns of free-swimming adult plaice in the southern North Sea. Mar. Ecol. Prog. Ser. 279, 261–273. https://doi.org/10.3354/meps279261

HUNTER, E., METCALFE, J.D., and REYNOLDS, J.D., 2003. Migration route and spawning area fidelity by North Sea plaice. Proc. R. Soc. B Biol. Sci. 270, 2097–2103. https://doi.org/10.1098/rspb.2003.2473

HUTCHISON, Z.L., BARTLEY, M.L., ET AL., 2020a. Offshore wind energy and benthic habitat changes lessons from block island wind farm. Oceanography 33, 58–69. https://doi.org/10.5670/oceanog.2020.406

HUTCHISON, Z.L., SECOR, D.H., and GILL, A.B., 2020b. The interaction between resource species and electromagnetic fields associated with electricity production by offshore wind farms. Oceanography 33, 96–107. https://doi.org/10.5670/oceanog.2020.409

HUVENEERS, C., SIMPFENDORFER, C.A., ET AL., 2016. The influence of environmental parameters on the performance and detection range of acoustic receivers. Methods Ecol. Evol. 7, 825–835. https://doi.org/10.1111/2041-210X.12520

HYSLOP, E.J., 1980. Stomach contents analysis-a review of methods and their application. J. Fish Biol. 17, 411–429. https://doi.org/10.4067/s0718-19572009000200016

ICES, 2020. Sole (Solea solea) in Subarea 4 (North Sea).

ICES, 2022a. Plaice (Pleuronectes platessa) in Subarea 4 (North Sea) and Subdivision 20 (Skagerrak). ICES Advice Recurr. Advice. https://doi.org/https://doi.org/10.17895/ices.advice.7819

ICES, 2022b. Sole (Solea solea) in Subarea 4 (North Sea). https://doi.org/10.17895/ices.advice.19453814.v1

INGER, R., ATTRILL, M.J., ET AL., 2009. Marine renewable energy: Potential benefits to biodiversity? An urgent call for research. J. Appl. Ecol. 46, 1145–1153. https://doi.org/10.1111/j.1365-2664.2009.01697.x

IPCC PANEL, 2014. Climate Change 2014: Synthesis Report.

IUCN, 1988. The World Conservation Union, 1988. Resolution 17.38 of the 17th General Assembly of the IUCN. Gland, Switzerland and Cambridge.

IVERSON, S.J., FIELD, C., ET AL., 2004. Quantitative fatty acid signature analysis: A new method of estimating predator diets. Ecol. Monogr. 74, 211–235. https://doi.org/10.1890/02-4105

JACKSON, A.L., INGER, R., ET AL., 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

JENNINGS, S., VAN HAL, R., ET AL., 2008. Fishing effects on energy use by North Sea fishes. J. Sea Res. 60, 74–88. https://doi.org/https://doi.org/10.1016/j.seares.2008.02.007

JEPSEN, N., THORSTAD, E.B., ET AL., 2015. The use of external electronic tags on fish: An evaluation of tag retention and tagging effects. Anim. Biotelemetry. https://doi.org/10.1186/s40317-015-0086-z

JOBLING, M., 1980. Gastric evacuation in plaice, Pleuronectes platessa L.: effects of temperature and fish size. J. Fish Biol. 17, 547–551. https://doi.org/10.1111/j.1095-8649.1980.tb02786.x

JOHNSON, A.F., GORELLI, G., ET AL., 2015. Effects of bottom trawling on fish foraging and feeding. Proc. R. Soc. B Biol. Sci. 282. https://doi.org/10.1098/rspb.2014.2336

KAISER, M.J., CLARKE, K.R., ET AL., 2006. Global analysis of response and recovery of benthic biota to fishing. Mar. Ecol. Prog. Ser. 311, 1–14. https://doi.org/10.3354/meps311001

KAISER, M.J., and SPENCER, B.E., 1996. The Effects of Beam-Trawl Disturbance on Infaunal Communities in Different Habitats. J. Anim. Ecol. 65, 348–358. https://doi.org/10.2307/5881

KARLSSON, R., TIVEFÄLTH, M., ET AL., 2021. Artificial hard substrate colonisation in the offshore Hywind Scotland pilot park. Wind Energy Sci. 1–18.

KELLER, K., SMITH, J.A., ET AL., 2017. Multispecies presence and connectivity around a designed artificial reef. Mar. Freshw. Res. 68, 1489–1500. https://doi.org/10.1071/MF16127

KERCKHOF, F., RUMES, B., ET AL., 2010. Early development of the subtidal marine biofouling on a concrete offshore windmill foundation on the Thornton Bank (southern North Sea): First monitoring results. Underw. Technol. 29, 137–149. https://doi.org/10.3723/ut.29.137

KERCKHOF, F., RUMES, B., and DEGRAER, S., 2019. About "mytilisation" and "slimeification": A decade of succession of the fouling assemblages on wind turbines off the Belgian coast, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Marking a Decade of Monitoring, Research and Innovation. Brussels: Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, p. 134.

KRÖNCKE, I., DIPPNER, J.W., ET AL., 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. Mar. Ecol. Prog. Ser. 167, 25–36. https://doi.org/10.3354/meps167025

KRÖNCKE, I., NEUMANN, H., ET AL., 2019. Comparison of biological and ecological long-term trends related to northern hemisphere climate in different marine ecosystems. Nat. Conserv. 34, 311–341. https://doi.org/10.3897/natureconservation.34.30209

KRÖNCKE, I., REISS, H., and DIPPNER, J.W., 2013. Effects of cold winters and regime shifts on macrofauna communities in shallow coastal regions. Estuar. Coast. Shelf Sci. 119, 79–90. https://doi.org/10.1016/j.ecss.2012.12.024

KRONE, R., DEDERER, G., ET AL., 2017. Mobile demersal megafauna at common offshore wind turbine foundations in the German Bight (North Sea) two years after deployment - increased production rate of Cancer pagurus. Mar. Environ. Res. 123, 53–61. https://doi.org/10.1016/j.marenvres.2016.11.011

KRONE, R., GUTOW, L., ET AL., 2013. Mobile demersal megafauna at artificial structures in the German Bight – Likely effects of offshore wind farm development. Estuar. Coast. Shelf Sci. 125, 1–9. https://doi.org/10.1016/J.ECSS.2013.03.012

LANGHAMER, O., 2012. Artificial reef effect in relation to offshore renewable energy conversion: State of the art. Sci. World J. 2012. https://doi.org/10.1100/2012/386713

LANGHAMER, O., DAHLGREN, T.G., and ROSENQVIST, G., 2018. Effect of an offshore wind farm on the viviparous eelpout: Biometrics, brood development and population studies in Lillgrund, Sweden. Ecol. Indic. 84, 1–6. https://doi.org/10.1016/j.ecolind.2017.08.035

LANGHAMER, O., WILHELMSSON, D., and ENGSTRÖ, J., 2009. Artificial reef effect and fouling impacts on offshore wave power foundations and buoys - a pilot study. Estuar. Coast. Shelf Sci. 82, 426–432. https://doi.org/10.1016/j.ecss.2009.02.009

LE PAPE, O., and BONHOMMEAU, S., 2015. The food limitation hypothesis for juvenile marine fish. Fish Fish. 16, 373–398. https://doi.org/https://doi.org/10.1111/faf.12063

LEFAIBLE, N., BRAECKMAN, U., and MOENS, T., 2018. Effects of wind turbine foundations on surrounding macrobenthic communities, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Assessing and Managing Effect Spheres of Influence. pp. 57–77.

LEFAIBLE, N., VAN VOOREN, K., ET AL., 2021. Macrobenthos communities of a nearshore windfarm: distribution and first post-construction results, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea. Attraction, Avoidance and Habitat Use at Various Spatial Scales. pp. 77–92.

LEGRAND, S., and BAETENS, K., 2021. Hydrodynamic forecast for the Belgian Coastal Zone. Physical State of the Sea - Belgian Coastal Zone [WWW Document]. COHERENS UKMO R. Belgian Inst. Nat. Sci.

LENGKEEK, W., DIDDEREN, K., ET AL., 2017. Eco-friendly design of scour protection: potential enhancement of ecological functioning in offshore wind farms. Towards an implementation guide and experimental set-up. Rep. nr 17-001 98.

LEONHARD, S., STENBERG, C., and STØTTRUP, J., 2011. Effect of the Horns Rev 1 Offshore Wind Farm on Fish Communities Follow-up Seven Years after Construction. DTU Aqua Rep. 99 p.

LEONHARD, S.B., and PEDERSEN, J., 2006. Benthic Communities at Horns Rev Before, During and After Construction of Horns Rev Offshore Wind Farm - Final Report, Annual Report 2005.

LETERME, S.C., PINGREE, R.D., ET AL., 2008. Decadal fluctuations in North Atlantic water inflow in the North Sea between 1958-2003: Impacts on temperature and phytoplankton populations. Oceanologia 50, 59–72.

LEVIN, P.S., and STUNZ, G.W., 2005. Habitat triage for exploited fishes: Can we identify essential "Essential Fish Habitat?" Estuar. Coast. Shelf Sci. 64, 70–78. https://doi.org/https://doi.org/10.1016/j.ecss.2005.02.007

LINDBERG, W.J., 1997. Can science resolve the attraction-production issue? Fisheries 22, 10–13.

LINDEBOOM, H., DEGRAER, S., ET AL., 2015. Offshore wind park monitoring programmes, lessons learned and recommendations for the future. Hydrobiologia 756, 169–180. https://doi.org/10.1007/s10750-015-2267-4

LINDEBOOM, H.J., KOUWENHOVEN, H.J., ET AL., 2011. Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; Acompilation. Environ. Res. Lett. 6. https://doi.org/10.1088/1748-9326/6/3/035101

LLORET, J., GIL DE SOLA, L., ET AL., 2002. Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean. ICES J. Mar. Sci. 59, 1215–1227. https://doi.org/10.1006/jmsc.2002.1294

LLORET, J., SHULMAN, G.E., and LOVE, R.M., 2014. Condition and Health Indicators of Exploited Marine Fishes. Wiley Blackwell.

LLORET, J., TURIEL, A., ET AL., 2022. Unravelling the ecological impacts of large-scale offshore wind farms in the Mediterranean Sea. Sci. Total Environ. 824. https://doi.org/10.1016/j.scitotenv.2022.153803

MAAR, M., BOLDING, K., ET AL., 2009. Local effects of blue mussels around turbine foundations in an ecosystem model of Nysted off-shore wind farm, Denmark. J. Sea Res. 62, 159–174. https://doi.org/10.1016/j.seares.2009.01.008

MAARLEVELD, T.J., 2020. Beam trawls and bones: A reflection on dutch fisheries. Coast. Res. Libr. 35, 521–535. https://doi.org/10.1007/978-3-030-37367-2_27

MADIN, E.M.P., DILL, L.M., ET AL., 2016. Human activities change marine ecosystems by altering predation risk. Glob. Chang. Biol. 22, 44–60. https://doi.org/https://doi.org/10.1111/gcb.13083

MAES, F., VANHULLE, A., ET AL., 2005. A flood of space. Towards a spatial structure plan for sustainable management of the North Sea (GAUFRE). Belgian Science Policy.

MAHESH, V., AMBARISH, P.G., and REKHA, J.N., 2018. Stomach Content Analysis Techniques in Fishes. Recent Adv. Fish. Biol. Tech. Biodivers. Eval. Conserv. 104–115.

MAITLAND, P.S., and HERDSON, D., 1972. Key to the Marine and Freshwater Fishes of Britain and Ireland. Environment Agency, Bristol.

MATLEY, J.K., KLINARD, N. V, ET AL., 2022. Global trends in aquatic animal tracking with acoustic telemetry. Trends Ecol. Evol. 37, 79–94. https://doi.org/https://doi.org/10.1016/j.tree.2021.09.001

MAVRAKI, N., DEGRAER, S., ET AL., 2020. Functional differences in trophic structure of offshore wind farm communities: A stable isotope study. Mar. Environ. Res. 157, 104868. https://doi.org/10.1016/j.marenvres.2019.104868

MAVRAKI, N., DEGRAER, S., and VANAVERBEKE, J., 2021. Offshore wind farms and the attraction – production hypothesis: insights from a combination of stomach content and stable isotope analyses. Hydrobiologia 6. https://doi.org/10.1007/s10750-021-04553-6

MAY, R., MASDEN, E.A., ET AL., 2019. Considerations for upscaling individual effects of wind energy development towards population-level impacts on wildlife. J. Environ. Manage. 230, 84–93. https://doi.org/10.1016/j.jenvman.2018.09.062

McClanahan, T., and Mangi, S., 2000. Spillover of Exploitable Fishes From a Marine Park and Its Effect on the Adjacent Fishery. Ecol. Appl. 10, 1792–1805. https://doi.org/10.1890/1051-0761(2000)010[1792:SOEFFA]2.0.CO;2

McLean, M., Mouillot, D., et al., 2018. A Climate-Driven Functional Inversion of Connected Marine Ecosystems. Curr. Biol. 28, 3654-3660.e3. https://doi.org/10.1016/j.cub.2018.09.050

Menéndez, R., Megías, A.G., et al., 2006. Species richness changes lag behind climate change. Proc. R. Soc. B Biol. Sci. 273, 1465–1470. https://doi.org/10.1098/rspb.2006.3484

Methratta, E.T., 2020. Monitoring fisheries resources at offshore wind farms: BACI vs. BAG designs. ICES J. Mar. Sci. 77, 890–900. https://doi.org/10.1093/icesjms/fsaa026

Meyer, C.G., Holland, K.N., and Papastamatiou, Y.P., 2007. Seasonal and diel movements of giant trevally Caranx ignobilis at remote Hawaiian atolls : implications for the design of Marine Protected Areas 333, 13–25.

Meyer, J., Kröncke, I., et al., 2016. Long-term changes in species composition of demersal fish and epibenthic species in the Jade area (German Wadden Sea/Southern North Sea) since 1972. Estuar. Coast. Shelf Sci. 181, 284–293. https://doi.org/10.1016/j.ecss.2016.08.047

Meyer, L., Pethybridge, H., et al., 2019. Abiotic and biotic drivers of fatty acid tracers in ecology: A global analysis of chondrichthyan profiles. Funct. Ecol. 33, 1243–1255. https://doi.org/10.1111/1365-2435.13328

Miethe, T., Dytham, C., et al., 2010. Marine reserves and the evolutionary effects of fishing on size at maturation. ICES J. Mar. Sci. 67, 412–425. https://doi.org/10.1093/icesjms/fsp248

Mills, E.L., Pittman, K., and Munroe, B., 1982. Effect of Preservation on the Weight of Marine Benthic Invertebrates. Can. J. Fish. Aquat. Sci. 39, 221–224. https://doi.org/10.1139/f82-029

Ministerie van Economische Zaken, 2019. Kavelbesluit V windenergiegebied Hollandse Kust (noord). Staatscourant 2019.

Mitamura, H., Nishizawa, H., et al., 2021. Attraction of an artificial reef: a migratory demersal flounder remains in shallow water under high temperature conditions in summer. Environfile//clo.be/Home/Home_d1/jbuyse/Downloads/S0272771405000405.rismental Biol. Fishes. https://doi.org/10.1007/s10641-021-01153-0

Modin, J., and Pihl, L., 1994. Differences in growth and mortality of juvenile plaice, Pleuronectes platessa L., following normal and extremely high settlement. Netherlands J. Sea Res. 32, 331–341. https://doi.org/https://doi.org/10.1016/0077-7579(94)90010-8

Mooney, T.A., Andersson, M.H., and Stanley, J., 2020. Acoustic impacts of offshore wind energy on fishery resources an evolving source and varied effects across a wind farm's lifetime. Oceanography 33, 82–95. https://doi.org/10.5670/oceanog.2020.408

Moser, M.L., Myers, M.S., et al., 2005. Effects of surgically-implanted transmitters on survival and feeding behavior of adult English sole. Aquat. Telem. Adv. Appl. Proc. Fifth Conf. Fish Telem. held Eur. Ustica, Italy, 9-13 June 2003 295.

Murawski, S.A., Rago, P.J., and Trippel, E.A., 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management 1002–1014. https://doi.org/10.1006/jmsc.2001.1097

Nagelkerken, I., Alemany, T., et al., 2021. Ocean acidification boosts reproduction in fish via indirect effects. PLOS Biol. 19, e3001033.

Nash, R.D.M., and Geffen, A.J., 2012. Mortality through the early life-history of fish: What can we learn from European plaice (Pleuronectes platessa L.)? J. Mar. Syst. 93, 58–68. https://doi.org/https://doi.org/10.1016/j.jmarsys.2011.09.009

Neves, V., Silva, D., et al., 2018. Assessing the effects of internal and external acoustic tagging methods on European flounder Platichthys flesus. Fish. Res. 206, 202–208. https://doi.org/10.1016/j.fishres.2018.05.015

Nithirojpakdee, P., Beamish, F.W.H., and Boonphakdee, T., 2014. Diet diversity among five co-existing fish species in a tropical river: Integration of dietary and stable isotope data. Limnology 15, 99–107. https://doi.org/10.1007/s10201-013-0418-8

Nolan, E., and Britton, R., 2018. Diet of invasive pikeperch Sander lucioperca: Developing non-destructive tissue sampling for stable isotope analysis with comparisons to stomach contents analysis. Knowl. Manag. Aquat. Ecosyst. 49. https://doi.org/10.1051/kmae/2018037

Noordzeeloket, 2022. Borssele wind farm zone [WWW Document].

Novak, A.J., Becker, S.L., et al., 2020. Inferring residency and movement patterns of horse-eye jack Caranx latus in relation to a Caribbean marine protected area acoustic telemetry array. Anim. Biotelemetry 8, 12. https://doi.org/10.1186/s40317-020-00199-8

Oni, O.E., Schmidt, F., et al., 2015. Microbial Communities and Organic Matter Composition in Surface and Subsurface Sediments of the. Front. Microbiol. 6, 1–16. https://doi.org/10.3389/fmicb.2015.01290

Parkyn, S.M., Collier, K.J., and Hicks, B.J., 2001. New Zealand stream crayfish: Functional omnivores but trophic predators? Freshw. Biol. 46, 641–652. https://doi.org/10.1046/j.1365-2427.2001.00702.x

Pastoors, M.A., Rijnsdorp, A.D., and Van Beek, F.A., 2000. Effects of a partially closed area in the North Sea ('plaice box') on stock development of plaice. ICES J. Mar. Sci. 57, 1014–1022. https://doi.org/10.1006/jmsc.2000.0586

Pauly, D., and Cheung, W.W.L., 2018. Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. Glob. Chang. Biol. 24, e15–e26. https://doi.org/10.1111/gcb.13831

Payne, N.L., Gillanders, B.M., et al., 2010. Interpreting diel activity patterns from acoustic telemetry: The need for controls. Mar. Ecol. Prog. Ser. 419, 295–301. https://doi.org/10.3354/meps08864

Perry, A.L., Low, P.J., et al., 2005. Ecology: Climate change and distribution shifts in marine fishes. Science (80-.). 308, 1912–1915. https://doi.org/10.1126/science.1111322

PERSSON, L., BENGTSSON, J., ET AL., 1996. Productivity and Consumer Regulation---Concepts, Patterns, and Mechanisms, in: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns {\&} Dynamics. Springer US, Boston, MA, pp. 396–434. https://doi.org/10.1007/978-1-4615-7007-3_37

PETERSEN, J.K., and MALM, T., 2006. Offshore windmill farms: Threats to or possibilities for the marine environment. Ambio 35, 75–80. https://doi.org/10.1579/0044-7447(2006)35[75:OWFTTO]2.0.CO;2

PETERSON, B.J., and FRY, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18, 293–320. https://doi.org/10.1146/annurev.es.18.110187.001453

PETERSON, C.H., GRABOWSKI, J.H., and POWERS, S.P., 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: Quantitative valuation. Mar. Ecol. Prog. Ser. 264, 249–264. https://doi.org/10.3354/meps264249

PICKERING, H., and WHITMARSH, D., 1997. Artificial reefs and fisheries exploitation: A review of the "attraction versus production" debate, the influence of design and its significance for policy. Fish. Res. 31, 39–59. https://doi.org/10.1016/S0165-7836(97)00019-2

PIET, G.J., PFISTERER, A.B., and RIJNSDORP, A.D., 1998. On factors structuring the flatfish assemblage in the southern North Sea. J. Sea Res. 40, 143–152. https://doi.org/10.1016/S1385-1101(98)00008-2

PLUMLEE, J.D., HALA, D.N., ET AL., 2021. Trophic ecology of fishes associated with artificial reefs assessed using multiple biomarkers. Hydrobiologia 848, 4347–4362. https://doi.org/10.1007/s10750-021-04647-1

POLET, H., TORREELE, E., ET AL., 2022. Fisheries, in: Dauwe, S. et al. (Eds) (Ed.), Knowledge Guide Coast and Sea 2022 - Compendium for Coast and Sea. pp. 103–121.

PÖRTNER, H.O., and FARRELL, A.P., 2008. Physiology and Climate Change. Science (80-.). 322, 690–692. https://doi.org/10.1126/science.1163156

POST, D.M., 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

POWERS, S.P., GRABOWSKI, J.H., ET AL., 2003. Estimating enhancement of fish production by offshore artificial reefs: Uncertainty exhibited by divergent scenarios. Mar. Ecol. Prog. Ser. 264, 265–277. https://doi.org/10.3354/meps264265

POXTON, M.G., and NASIR, N.A., 1985. The distribution and population dynamics of O-group plaice (Pleuronectes platessa L.) on nursery grounds in the Firth of Forth. Estuar. Coast. Shelf Sci. 21, 845–857. https://doi.org/https://doi.org/10.1016/0272-7714(85)90078-2

R CORE TEAM, 2022. R: A language and environment for statistical computing.

RABAUT, M., VAN DE MOORTEL, L., ET AL., 2010. Biogenic reefs as structuring factor in Pleuronectes platessa (Plaice) nursery. J. Sea Res. 64, 102–106. https://doi.org/10.1016/j.seares.2009.10.009

RAEDEMAECKER, F., KEATING, J., ET AL., 2011. Spatial variability in diet, condition and growth of juvenile plaice (Pleuronectes platessa) at sandy beach nursery grounds on the south-west coast of Ireland. J. Mar. Biol. Assoc. United Kingdom 91, 1215–1223. https://doi.org/10.1017/S0025315410001505

RAMSDEN, S., COTTON, C.F., and CURRAN, M.C., 2017. Using acoustic telemetry to assess patterns in the seasonal residency of the Atlantic stingray Dasyatis sabina. Environ. Biol. Fishes 100, 89–98. https://doi.org/10.1007/s10641-016-0498-5

RAOUX, A., TECCHIO, S., ET AL., 2017. Benthic and fish aggregation inside an offshore wind farm: Which effects on the trophic web functioning? Ecol. Indic. 72, 33–46. https://doi.org/10.1016/j.ecolind.2016.07.037

REUBENS, J., BRAECKMAN, U., ET AL., 2013a. Aggregation at windmill artificial reefs: CPUE of Atlantic cod (Gadus morhua) and pouting (Trisopterus luscus) at different habitats in the Belgian part of the North Sea. Fish. Res. 139, 28–34. https://doi.org/10.1016/j.fishres.2012.10.011

REUBENS, J., DE RIJCKE, M., ET AL., 2014a. Diel variation in feeding and movement patterns of juvenile Atlantic cod at offshore wind farms. J. Sea Res. 85, 214–221. https://doi.org/10.1016/j.seares.2013.05.005

REUBENS, J., DEGRAER, S., and VINCX, M., 2011a. Aggregation and feeding behaviour of pouting (Trisopterus luscus) at wind turbines in the Belgian part of the North Sea. Fish. Res. 108, 223–227. https://doi.org/10.1016/j.fishres.2010.11.025

REUBENS, J., DEGRAER, S., and VINCX, M., 2011b. Spatial and temporal movements of cod (Gadus morhua) in a wind farm in the Belgian part of the North Sea using acoustic telemetry, a VPS study, in: Degraer, Steven, Brabant, R., Rumes, B. (Eds.), Offshore Wind Farms in the Belgian Part of the North Sea: Selected Findings from the Baseline and Targeted Monitoring. Royal Belgian Institute of Natural Sciences, Management Unit of the North Sea Mathematical Models. Marine ecosystem management unit., p. 157.

REUBENS, J., DEGRAER, S., and VINCX, M., 2014b. The ecology of benthopelagic fishes at offshore wind farms: A synthesis of 4 years of research. Hydrobiologia 727, 121–136. https://doi.org/10.1007/s10750-013-1793-1

REUBENS, J., PASOTTI, F., ET AL., 2013b. Residency, site fidelity and habitat use of atlantic cod (Gadus morhua) at an offshore wind farm using acoustic telemetry. Mar. Environ. Res. 90, 128–135. https://doi.org/10.1016/j.marenvres.2013.07.001

REUBENS, J., VANDENDRIESSCHE, S., ET AL., 2013c. Offshore wind farms as productive sites or ecological traps for gadoid fishes? - Impact on growth, condition index and diet composition. Mar. Environ. Res. 90, 66–74. https://doi.org/10.1016/j.marenvres.2013.05.013

REZNICK, D.N., 1993. Norms of Reaction in Fishes, in: Stokes, K., McGlade, J.M., Law, R. (Eds.), The Exploitation of Evolving Resources. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 72–90.

RIJNSDORP, A.. D., and VAN BEEK, F.. A., 1991. Changes in growth of plaice Pleuronectes platessa L. and sole Solea solea (L.) in the North Sea. Netherlands J. Sea Res. 27, 441–457. https://doi.org/https://doi.org/10.1016/0077-7579(91)90045-3

RIJNSDORP, A.D., 1989. Maturation of male and female North Sea plaice Pleuronectes platessa L. ICES J. Mar. Sci. 46, 35–51. https://doi.org/10.1093/icesjms/46.1.35

RIJNSDORP, A.D., 1990. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, Pleuronectes platessa L. Netherlands J. Sea Res. 25, 279–289. https://doi.org/10.1016/0077-7579(90)90027-E

RIJNSDORP, A.D., 1991a. Changes in fecundity of female North Sea plaice (Pleuronectes platessa L .) between 3 periods since 1900. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/48.3.253

RIJNSDORP, A.D., 1991b. Changes in fecundity of female north sea plaice (Pleuronectes platessa l.) between three periods since 1900. ICES J. Mar. Sci. 48, 253–280. https://doi.org/10.1093/icesjms/48.3.253

RIJNSDORP, A.D., BUYS, A.M., ET AL., 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES J. Mar. Sci. 55, 403–419.

RIJNSDORP, A.D., and IBELINGS, B., 1989. Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, Pleuronectes platessa L. J. Fish Biol. 35, 401–415. https://doi.org/10.1111/j.1095-8649.1989.tb02992.x

RIJNSDORP, A.D., and MILLNER, R.S., 1996. Trends in population dynamics and exploitation of North Sea plaice (Pleuronectes platessa L.) since the late 1800s. ICES J. Mar. Sci. 53, 1170–1184. https://doi.org/10.1006/jmsc.1996.0142

RIJNSDORP, A.D., and PASTOORS, M.A., 1995. Modelling the spatial dynamics and fisheries of North Sea plaice (Pleuronectes platessaL.) based on tagging data. ICES J. Mar. Sci. 52, 963–980. https://doi.org/10.1006/jmsc.1995.0092

RIJNSDORP, A.D., PECK, M.A., ET AL., 2009. Resolving the effect of climate change on fish populations. ICES J. Mar. Sci. 66, 1570–1583. https://doi.org/10.1093/icesjms/fsp056

RIJNSDORP, A.D., POOS, J.J., ET AL., 2008. The arms race between fishers. J. Sea Res. 60, 126–138. https://doi.org/https://doi.org/10.1016/j.seares.2008.03.003

RIJNSDORP, A.D., and VAN LEEUWEN, P.I., 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. ICES J. Mar. Sci. 53, 1199–1213. https://doi.org/10.1006/jmsc.1996.0145

RIJNSDORP, A.D., and VINGERHOED, B., 2001. Feeding of plaice Pleuronectes platessa L. and Sole Solea solea (L.) in relation to the effects of bottom trawling, in: Journal of Sea Research. Elsevier, pp. 219–229. https://doi.org/10.1016/S1385-1101(01)00047-8

RIVIER, A., BENNIS, A.C., ET AL., 2016. Parameterization of wind turbine impacts on hydrodynamics and sediment transport. Ocean Dyn. 66, 1285–1299. https://doi.org/10.1007/s10236-016-0983-6

ROACH, M., COHEN, M., ET AL., 2018. The effects of temporary exclusion of activity due to wind farm construction on a lobster (Homarus gammarus) fishery suggests a potential management approach. ICES J. Mar. Sci. 75, 1416–1426. https://doi.org/10.1093/icesjms/fsy006

ROBERTS, C.M., LEARY, B.C.O., ET AL., 2017. Marine reserves can mitigate and promote adaptation to climate change 114, 6167–6175. https://doi.org/10.1073/pnas.1701262114

ROBERTSON, B., and HUTTO, R., 2006. A framework for understanding ecological traps and evaluating existing evidence. Ecology 87, 1075–1085. https://doi.org/10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2

ROBINSON, L.A., GREENSTREET, S.P.R., ET AL., 2010. Length-weight relationships of 216 North Sea benthic invertebrates and fish. J. Mar. Biol. Assoc. United Kingdom 90, 95–104. https://doi.org/10.1017/S0025315409991408

ROCHETTE, S., RIVOT, E., ET AL., 2010. Effect of nursery habitat degradation on flatfish population: Application to Solea solea in the Eastern Channel (Western Europe). J. Sea Res. 64, 34–44. https://doi.org/10.1016/j.seares.2009.08.003

ROESSIG, J.M., WOODLEY, C.M., ET AL., 2004. Effects of global climate change on marine and estuarine fishes and fisheries. Rev. Fish Biol. Fish. https://doi.org/10.1007/s11160-004-6749-0

ROOKER, J.R., TURNER, J.P., and HOLT, S.A., 2006. Trophic ecology of Sargassum-associated fishes in the Gulf of Mexico determined from stable isotopes and fatty acids. Mar. Ecol. Prog. Ser. 313, 249–259. https://doi.org/10.3354/meps313249

ROTHERHAM, D., GRAY, C.A., ET AL., 2008. Effects of diel period and tow duration on estuarine fauna sampled with a beam trawl over bare sediment: Consequences for designing more reliable and efficient surveys. Estuar. Coast. Shelf Sci. 78, 179–189. https://doi.org/10.1016/j.ecss.2007.11.019

ROURKE, M.L., FOWLER, A.M., ET AL., 2022. Environmental DNA (eDNA) as a tool for assessing fish biomass: A review of approaches and future considerations for resource surveys. Environ. DNA 4, 9–33. https://doi.org/https://doi.org/10.1002/edn3.185

RUMES, B., and BRABANT, R., 2020. Offshore renewable energy development in the Belgian part of the North Sea, in: Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Empirical Evidence Inspiring Priority Monitoring, Research and Management. pp. 13–18.

RUMES, B., COATES, D., ET AL., 2013. Does it really matter? Changes in species richness and biomass at different spatial scales, in: Degraer, S., Brabant, R., Rumes, B. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Learning from the Past to Optimise Future Monitoring. Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management Section, p. 239.

RUMES, B., KERCKHOF, F., and DEGRAER, S., 2021. Blue mussel Mytilus edulis as habitat provider on offshore wind turbine foundations, in: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea. Attraction, Avoidance and Habitat Use at Various Spatial Scales. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management Section, Brussels, pp. 93–103.

RUMES, BOB, and BRABANT, ROBIN, 2021. Offshore renewable energy development in the BPNS, in: Degraer, S., Brabant, R, Rumes, B, Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea. Attraction, Avoidance and Habitat Use at Various Spatial Scales. p. 108.

Ruppert, K.M., Kline, R.J., and Rahman, M.S., 2019. Past, present, and future perspectives of environmental DNA (eDNA) metabarcoding: A systematic review in methods, monitoring, and applications of global eDNA. Glob. Ecol. Conserv. 17, e00547. https://doi.org/10.1016/j.gecco.2019.e00547

Russell, D.J.F., Brasseur, S.M.J.M., et al., 2014. Marine mammals trace anthropogenic structures at sea. Curr. Biol. 24, R638–R639. https://doi.org/https://doi.org/10.1016/j.cub.2014.06.033

Sale, P.F., Cowen, R.K., et al., 2005. Critical science gaps impede use of no-take fishery reserves. Trends Ecol. Evol. 20, 74–80. https://doi.org/10.1016/j.tree.2004.11.007

Sanders, N., Haynes, T., and Goriup, P.D., 2017. Marine Protected Areas and Offshore Wind Farms, in: Management of Marine Protected Areas: A Network Perspective. pp. 263–280. https://doi.org/10.1002/9781119075806.ch14

Sargent, J., Bell, G., et al., 1999. Recent developments in the essential fatty acid nutrition of fish. Aquaculture 177, 191–199. https://doi.org/10.1016/S0044-8486(99)00083-6

Scheffer, M., Straile, D., et al., 2001. Climatic warming causes regime shifts in lake food webs. Limnol. Oceanogr. 46, 1780–1783. https://doi.org/10.4319/lo.2001.46.7.1780

Schlacher, T.A., and Connolly, R.M., 2014. Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: A review and synthesis. Methods Ecol. Evol. 5, 541–550. https://doi.org/10.1111/2041-210X.12183

Schutter, M., Dorenbosch, M., et al., 2019. Oil and gas platforms as artificial substrates for epibenthic North Sea fauna: Effects of location and depth. J. Sea Res. 153, 101782. https://doi.org/10.1016/j.seares.2019.101782

Schwartzbach, A., Behrens, J., and Svendsen, J., 2020. Atlantic cod Gadus morhua save energy on stone reefs: implications for the attraction versus production debate in relation to reefs. Mar. Ecol. Prog. Ser. 635, 81–87. https://doi.org/10.3354/meps13192

Shipp, R.L., 2003. A Perspective on Marine Reserves as a Management Tool. Fisheries 28, 10–21.

Shucksmith, R., Hinz, H., et al., 2006. Evaluation of habitat use by adult plaice (Pleuronectes platessa L.) using underwater video survey techniques. J. Sea Res. 56, 317–328. https://doi.org/10.1016/j.seares.2006.06.001

Simpson, A.C., 1959. The spawning of the plaice (Pleuronectes platessa) in the North Sea. Fish. Invest. Ser. II 22, 1–111.

Smith, J.A., Lowry, M.B., et al., 2016. A designed artificial reef is among the most productive marine fish habitats: new metrics to address ‘production versus attraction.’ Mar. Biol. 163, 1–8. https://doi.org/10.1007/s00227-016-2967-y

Sokal, R., Sokal, R.R., et al., 1995. Biometry, Series of books in biology. W. H. Freeman.

Soldaat, L., Visser, H., et al., 2007. Smoothing and trend detection in waterbird monitoring data using structural time-series analysis and the Kalman filter. J. Ornithol. 148. https://doi.org/10.1007/s10336-007-0176-7

Soldal, A.V., Svellingen, I., et al., 2002. Rigs-to-reefs in the North Sea: Hydroacoustic quantification of fish in the vicinity of a “semi-cold” platform. ICES J. Mar. Sci. 59. https://doi.org/10.1006/jmsc.2002.1279

Solmundsson, J., Palsson, J., and Karlsson, H., 2005. Fidelity of mature Icelandic plaice (Pleuronectes platessa) to spawning and feeding grounds 200. https://doi.org/10.1016/j.icesjms.2004.11.012

Sørensen, T.K., and Thomsen, L.N., 2009. A comparison of frameworks and objectives for implementation of marine protected areas in Northern Europe and in Southeast Asia. Aquat. Ecosyst. Health Manag. 12, 258–263. https://doi.org/10.1080/14634980903140323

Staehr, P.A.U., Dahl, K., et al., 2022. Environmental DNA Monitoring of Biodiversity Hotspots in Danish Marine Waters. Front. Mar. Sci. 8, 1–15. https://doi.org/10.3389/fmars.2021.800474

Stelzenmüller, V., Diekmann, R., et al., 2016. Co-location of passive gear fisheries in offshore wind farms in the German EEZ of the North Sea: A first socio-economic scoping. J. Environ. Manage. 183, 794–805. https://doi.org/10.1016/j.jenvman.2016.08.027

Stelzenmüller, V., Gimpel, A., et al., 2020. Impact of the use of offshore wind and other marine renewables on European fisheries.

Stelzenmüller, V., Gimpel, A., et al., 2021. Sustainable co-location solutions for offshore wind farms and fisheries need to account for socio-ecological trade-offs. Sci. Total Environ. 776, 145918. https://doi.org/10.1016/j.scitotenv.2021.145918

Stelzenmüller, V., Letschert, J., et al., 2022. From plate to plug: The impact of offshore renewables on European fisheries and the role of marine spatial planning. Renew. Sustain. Energy Rev. 158. https://doi.org/10.1016/j.rser.2022.112108

Stenberg, C., Støttrup, J.G., et al., 2015. Long-term effects of an offshore wind farm in the North Sea on fish communities. Mar. Ecol. Prog. Ser. 528, 257–265. https://doi.org/10.3354/meps11261

Sumer, B.M., and Fredsøe, J., 2001. Scour around Pile in Combined Waver and Current. J. Hydraul. Eng. 127, 403–411.

Sundby, S., and Nakken, O., 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. ICES J. Mar. Sci. 65, 953–962. https://doi.org/10.1093/icesjms/fsn085

Svane, I., and Petersen, J.K., 2001. On the problems of epibioses, fouling and artificial reefs, a review. Mar. Ecol. 22, 169–188. https://doi.org/10.1046/j.1439-0485.2001.01729.x

Swanson, K.L., and Tsonis, A.A., 2009. Has the climate recently shifted? Geophys. Res. Lett. 36, 2–5. https://doi.org/10.1029/2008GL037022

Ter Hofstede, R., and Rijnsdorp, A.D., 2011. Comparing demersal fish assemblages between periods of contrasting climate and fishing pressure. ICES J. Mar. Sci. 68, 1189–1198. https://doi.org/10.1093/icesjms/fsr053

THORSTAD, E.B., RIKARDSEN, A.H., ET AL., 2013. The Use of Electronic Tags in Fish Research – An Overview of Fish Telemetry Methods. Turkish J. Fish. Aquat. Sci. 13, 881–896. https://doi.org/10.4194/1303-2712-v13

THRESHER, R.E., KOSLOW, J.A., ET AL., 2007. Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. Proc. Natl. Acad. Sci. U. S. A. 104, 7461–7465. https://doi.org/10.1073/pnas.0610546104

TRENBERTH, K.E., ZHANG, R., and NATIONAL CENTER FOR ATMOSPHERIC RESEARCH STAFF (EDS), 2019. The Climate Data Guide: Atlantic Multi-decadal Oscillation (AMO) [WWW Document]. URL https://climatedataguide.ucar.edu/climate-data/atlantic-multi-decadal-oscillation-amo (accessed 2.24.20).

TULP, I., BOLLE, L.J., and RIJNSDORP, A.D., 2008. Signals from the shallows: In search of common patterns in long-term trends in Dutch estuarine and coastal fish. J. Sea Res. 60, 54–73. https://doi.org/10.1016/j.seares.2008.04.004

TYLER-WALTERS H. HISCOCK K. (EDS), TILLIN, H.M., ET AL., 2022. Marine Life Information Network: Biology and Sensitivity Key Information Review Database [online]. Plymouth: Marine Biological Association of the United Kingdom. [WWW Document].

UHLMANN, S.S., THEUNYNCK, R., ET AL., 2016. Marine Science 73, 1244–1254.

UKMMAS, 2019. Sea surface and water column temperature in 2011-2015 [WWW Document]. UK Mar. Online Assess. Tool. URL https://moat.cefas.co.uk/

VAN BERKEL, J., BURCHARD, H., ET AL., 2020. The effects of offshore wind farms on hydrodynamics and implications for fishes. Oceanography 33, 108–117. https://doi.org/10.5670/oceanog.2020.410

VAN BOGAERT, T., ROELS, K., and PLATTEAU, J., 2020. Visserijrapport 2020. Brussels.

VAN DER KOOIJ, J., ENGELHARD, G.H., and RIGHTON, D.A., 2016. Climate change and squid range expansion in the North Sea. J. Biogeogr. 43, 2285–2298. https://doi.org/10.1111/jbi.12847

VAN DER REIJDEN, K.J., HINTZEN, N.T., ET AL., 2018. North Sea demersal fisheries prefer specific benthic habitats. PLoS One 13, 1–21. https://doi.org/10.1371/journal.pone.0208338

VAN DER VEER, H., PIHL, L., and BERGMAN, M., 1990. Recruitment mechanisms in North Sea plaice Pleuronectes platessa. Mar. Ecol. Prog. Ser. 64, 1–12. https://doi.org/10.3354/meps064001

VAN DER VEER, H.W., BERGHAHN, R., ET AL., 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia. ICES J. Mar. Sci. 57, 202–215. https://doi.org/10.1006/jmsc.1999.0523

VAN DER VEER, H.W., and BERGMAN, M.J.N., 1987. Predation by crustaceans on a newly settled 0-group plaice Pleuronectes platessa population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 35, 203–215. https://doi.org/10.3354/meps035203

VAN DER VEER, H.W., RUARDIJ, P., ET AL., 1998. Impact of interannual variability in hydrodynamic circulation on egg and larval transport of plaice Pleuronectes platessa L. in the southern North Sea. J. Sea Res. 39, 29–40. https://doi.org/https://doi.org/10.1016/S1385-1101(97)00008-7

VAN DEURS, M., GROME, T.M., ET AL., 2012. Short- and long-term effects of an offshore wind farm on three species of sandeel and their sand habitat. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps09736

VAN DUREN, L., GITTENBERGER, A., ET AL., 2017. Rich Reefs in the North Sea.

VAN GINDERDEUREN, K., VAN HOEY, G., ET AL., 2014. The mesozooplankton community of the Belgian shelf (North Sea). J. Sea Res. 85, 48–58. https://doi.org/10.1016/j.seares.2013.10.003

VAN HAL, R., GRIFFIOEN, A.B., and VAN KEEKEN, O.A., 2017. Changes in fish communities on a small spatial scale, an effect of increased habitat complexity by an offshore wind farm. Mar. Environ. Res. 126, 26–36. https://doi.org/10.1016/j.marenvres.2017.01.009

VAN HAL, R., SMITS, K., and RIJNSDORP, A.D., 2010. How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea. J. Sea Res. 64, 76–84. https://doi.org/10.1016/j.seares.2009.10.008

VAN HOEY, G., DEGRAER, S., and VINCX, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. Estuar. Coast. Shelf Sci. 59, 599–613. https://doi.org/10.1016/j.ecss.2003.11.005

VAN KEEKEN, O.A., VAN HOPPE, M., ET AL., 2007. Changes in the spatial distribution of North Sea plaice (Pleuronectes platessa) and implications for fisheries management. J. Sea Res. 57, 187–197. https://doi.org/10.1016/j.seares.2006.09.002

VAN LANCKER, V., DU FOUR, I., ET AL., 2007. Management, research and budgetting of aggregates in shelf seas related to end-users (Marebasse). Final Scientific Report.

VAN OVERZEE, H.M.J., and RIJNSDORP, A.D., 2015. Effects of fishing during the spawning period: implications for sustainable management. Rev. Fish Biol. Fish. 25, 65–83. https://doi.org/10.1007/s11160-014-9370-x

VAN WALRAVEN, L., MOLLET, F.M., ET AL., 2010. Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (Pleuronectes platessa L.). J. Sea Res. 64, 85–93. https://doi.org/10.1016/j.seares.2009.07.003

VANDENDRIESSCHE, S., DERWEDUWEN, J., and HOSTENS, K., 2015. Equivocal effects of offshore wind farms in Belgium on soft substrate epibenthos and fish assemblages. Hydrobiologia 756, 19–35. https://doi.org/10.1007/s10750-014-1997-z

VANDEPERRE, F., HIGGINS, R.M., ET AL., 2011. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. Fish Fish. 12, 412–426. https://doi.org/https://doi.org/10.1111/j.1467-2979.2010.00401.x

VANSTEENBRUGGE, L., SYS, K., ET AL., 2020. Pulsvisserij Vlaamse Kust - Deel 1.

VERFAILLIE, E., VAN LANCKER, V., and VAN MEIRVENNE, M., 2006. Multivariate geostatistics for the predictive modelling of the surficial sand distribution in shelf seas. Cont. Shelf Res. 26, 2454–2468. https://doi.org/10.1016/j.csr.2006.07.028

VERHALLE, J., and VAN DE VELDE, M., 2020. Something is moving at sea: The marine spatial plan for 2020-2026.

VERHEIJEN, F.J., and DE GROOT, S.J., 1967. Diurnal activity pattern of plaice and flounder (Pleuronectidae) in aquaria. Netherlands J. Sea Res. 3, 383–390.

VISSER, H., 2014. Detection of environmental changes. Description of the TrendSpotter software.

VOET, H.E.E., VAN COLEN, C., and VANAVERBEKE, J., 2021. Climate change effects on the ecophysiology and ecological functioning of an offshore wind farm artificial hard substrate community. Sci. Total Environ. 810, 152194. https://doi.org/10.1016/j.scitotenv.2021.152194

WALSH, S.J., DÍAZ DE ASTARLOA, J.M., and POOS, J.-J., 2015. Atlantic flatfish fisheries, in: Flatfishes: Biology and Exploitation. Wiley Blackwell, Oxford, pp. 346–394.

WHEELER, A., 1969. The Fishes of Britain and North-West Europe. Macmillan, London.

WHITEHOUSE, R.J.S., HARRIS, J.M., ET AL., 2011. The nature of scour development and scour protection at offshore windfarm foundations. Mar. Pollut. Bull. 62, 73–88. https://doi.org/10.1016/j.marpolbul.2010.09.007

WIESER, M.E., and BRAND, W.A., 1999. Isotope Ratio Studies Using Mass Spectrometry, in: Lindon, J.C. (Ed.), Encyclopedia of Spectroscopy and Spectrometry. Elsevier, Oxford, pp. 1072–1086. https://doi.org/https://doi.org/10.1006/rwsp.2000.0146

WILBER, D.H., BROWN, L., ET AL., 2022a. Demersal fish and invertebrate catches relative to construction and operation of North America's first offshore wind farm. ICES J. Mar. Sci. 79, 1274–1288. https://doi.org/https://doi.org/10.1093/icesjms/fsac051

WILBER, D.H., BROWN, L., ET AL., 2022b. Offshore wind farm effects on flounder and gadid dietary habits and condition on the northeastern US coast. Mar. Ecol. Prog. Ser. 683, 123–138. https://doi.org/10.3354/meps13957

WILBER, D.H., CAREY, D.A., and GRIFFIN, M., 2018. Flatfish habitat use near North America's first offshore wind farm. J. Sea Res. 139, 24–32. https://doi.org/10.1016/j.seares.2018.06.004

WILHELMSSON, D., and LANGHAMER, O., 2014. The Influence of Fisheries Exclusion and Addition of Hard Substrata on Fish and Crustaceans, in: Shields, M.A., Payne, A.I.L. (Eds.), Marine Renewable Energy Technology and Environmental Interactions. Springer, p. 176.

WILHELMSSON, D., MALM, T., and ÖHMAN, M.C., 2006. The influence of offshore windpower on demersal fish. ICES J. Mar. Sci. 63, 775–784. https://doi.org/10.1016/j.icesjms.2006.02.001

WINDEUROPE, 2022. Offshore wind energy 2021 statistics.

WINTER, H., AARTS, G., and KEEKEN, O. VAN, 2010. Residence time and behaviour of sole and cod in the Offshore Wind farm Egmond aan Zee (OWEZ), IMARES, Wageningen YR.

WOLFF, R.L., BAYARD, C.C., and FABIEN, R.J., 1995. Evaluation of sequential methods for the determination of butterfat fatty acid composition with emphasis on trans-18:1 acids. Application to the study of seasonal variations in french butters. J. Am. Oil Chem. Soc. 72, 1471–1483. https://doi.org/10.1007/BF02577840

WRIGHT, S.R., LYNAM, C.P., ET AL., 2020. Structure in a sea of sand: Fish abundance in relation to man-made structures in the North Sea. ICES J. Mar. Sci. 77, 1206–1218. https://doi.org/10.1093/icesjms/fsy142

WYCHE, C.J., and SHACKLEY, S.E., 1986. The feeding ecology of Pleuronectes platessa L., Limanda limanda (L.) and Scophthalmus rhombus (L.) in Carmarthen Bay, South Wales, U.K. J. Fish Biol. 29, 303–311.

YANG, J., 1982. The dominant fish fauna in the North Sea and its determination. J. Fish Biol. 20, 635–643. https://doi.org/10.1111/j.1095-8649.1982.tb03973.x

ZHANG, YING, ZHANG, C., ET AL., 2017. Offshore wind farm in marine spatial planning and the stakeholders engagement: Opportunities and challenges for Taiwan. Ocean Coast. Manag. 149, 69–80. https://doi.org/https://doi.org/10.1016/j.ocecoaman.2017.09.014

ZINTZEN, V., 2007. Biodiversity of shipwrecks from the Southern Bight of the North Sea. Dial.Uclouvain.Be 351.

ZINTZEN, V., and MASSIN, C., 2010. Artificial hard substrata from the Belgian part of the North Sea and their influence on the distributional range of species. Belgian J. Zool. 140, 20–29.

ZUUR, A.F., IENO, E.N., and SMITH, G.M., 2007. Analyzing Ecological Data, Methods. https://doi.org/10.1016/B978-0-12-387667-6.00013-0

ZUUR, A.F., TUCK, I.D., and BAILEY, N., 2003. Dynamic factor analysis to estimate common trends in fisheries time series. Can. J. Fish. Aquat. Sci. 60, 542–552. https://doi.org/10.1139/F03-030

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