On the Food-Web Ecology of Offshore Wind Farms, the Kingdom of Suspension Feeders

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To my family,

Antonis, Milly, and Sofianna

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Ninon,

May 2020

Summary

In the North Sea, the offshore wind farm (OWF) industry is rapidly developing, with new wind farms being under construction, licenced or planned. These installations induce changes to the marine environment, by adding artificial hard substrates into soft-bottom areas. Multiple vertebrate and invertebrate species are attracted to these structures altering the biodiversity, arising concerns about the impacts of OWFs on the environment, including effects on ecosystem functioning.

In this PhD thesis, the effects of offshore wind turbines on the local food web properties were investigated at two levels: (a) detailed food web structure on one gravity-based foundation (Chapters 2 and 3), and (b) local (Belgian part of the North Sea) effects on primary productivity and on fish (Chapter 4 and 5). Colonising assemblages along the entire depth gradient of a gravity-based foundation in the Belgian part of the North Sea (BPNS) and fish species in close proximity to the same turbine were sampled to get insights in the in situ food web structure. Laboratory experiments with fully colonised PVC panels obtained from a tripod inside an OWF in the BPNS allowed for detailed ex situ observation of the carbon assimilation by colonising species.

In Chapters 2 and 3, the food web structure of the colonising assemblages along the depth gradient of the offshore wind turbine, its scour protection layer (SPL) and the surrounding soft substrate were investigated. The objective of Chapter 2 was to investigate whether structural differences in community composition would be reflected in the food web complexity and whether resource partitioning could contribute to the co-existence of such dense communities. This chapter, therefore, focused on the local food web properties between and within different communities along the depth gradient to investigate resource partitioning at both levels (i.e. community-specific study). The aim of Chapter 3 was to investigated whether trophic plasticity is one of the mechanisms contributing to the wide distribution and survival of invertebrate organisms occurring at different depths along the depth gradient of the gravity-based foundation (i.e. species-specific study). For the purposes of these two chapters, stable isotope analysis was performed on the organisms collected from

the turbine foundation. The results (Chapter 2) showed that structural community differences are reflected in the food web structure of communities occurring in different depth zones. Resource partitioning was detected both between and within the assemblages. The highest food web complexity was found at the SPL and the soft substrate, where a strong accumulation of organic matter is expected. This high food web complexity was further supported by the results of the species-specific study (Chapter 3), demonstrating that the organisms occurring in these two zones exploited a wider range of resources compared to the organisms found higher up at the turbine. Moreover, this study indicated that most of the investigated invertebrate species found at the offshore wind turbine are trophic generalists, with depth-specific resource use strategies. This suggests that trophic plasticity contributes to the co-existence of invertebrate species within and across the depth zones. In these two chapters, the importance of the SPL and the soft substrate near the turbine foundation is highlighted, since in these zones high resource quantity is accumulated, supporting the presence of organisms of multiple trophic levels.

In Chapter 4, the carbon assimilation by colonising assemblages that typically occur at offshore wind turbines in the North Sea was investigated. While the role of colonising species in reducing the primary producer standing stock has previously been modelled for the southern North Sea, real data to validate these models are still scarce. Therefore, an *ex-situ* pulse-chase experiment was conducted to track the processing of organic matter by colonising organisms on the wind turbine foundations. The results indicated that the blue mussel *Mytilus edulis* showed the highest biomass-specific carbon assimilation, while the local amphipod *Jassa herdmani* population as a whole assimilated the highest amount of carbon. This study showed that *J. herdmani* and *M. edulis* contributed the most to the local consumption of the primary producer standing stock, since their assimilation was ca. 97 % of the total faunal carbon assimilation. The results of this experiment were upscaled to the total number of all the currently installed turbines (264 monopiles, 48 jackets, and 6 gravity-based foundations) in the BPNS. The total amount of carbon assimilated by the total number of *J. herdmani* and *M. edulis* individuals on every type of foundation was calculated and compared with the total annual primary production in the BPNS. It was estimated that 1.3 % of the local annual primary producer standing stock is grazed upon by *M. edulis* and *J. herdmani*. This value was compared with the amount of carbon that is not assimilated by the soft sediment macrofauna due to the loss of habitat by the installation of the different foundation types. The data suggest that the presence of offshore wind turbines and their subsequent colonisation by colonising fauna remarkably increases the carbon assimilation compared to the permeable sediment macrofauna inhabiting the same surface area (i.e. footprint of the turbines). As compared to the soft sediments, the presence of jacket foundations causes the highest and the gravity-based foundations the lowest increase in the local carbon assimilation.

Chapter 5 aimed at understanding the feeding ecology of fish species that are attracted to artificial reefs, such as OWFs, in the BPNS. Two pelagic (*Scomber scombrus* and *Trachurus trachurus*), two benthopelagic (*Gadus morhua* and *Trisopterus luscus*) and one benthic (*Myoxocephalus scorpioides*) species abundantly present close to a gravity-based foundation were sampled. Stomach content and stable isotope analyses were performed to respectively investigate the short- and the long-term dietary composition of these fish species. Both short- and the long-term analyses showed that the benthic and benthopelagic species (species highly associated with the SPLs) feed on the colonising species *J. herdmani* and *Pisidia longicornis*. These results imply that these species utilize artificial reefs, such as OWFs, as feeding grounds for a prolonged period. The short-term dietary analysis of *Trachurus trachurus* indicated a diet based on *J. herdmani*, but the long-term analysis suggested that this species feeds on zooplankton. Thus, this species feeds only occasionally on the colonising fauna, using the artificial reefs as oases of enhanced resources. *Scomber scombrus* in contrary does not utilize the artificial habitats of OWFs as feeding grounds at all, since both analyses indicated a diet based on zooplankton. The dietary results of this chapter on the benthic and benthopelagic species corroborate the hypothesis that their local production could potentially be increased. However, this study did not support such statement for the pelagic species.

In conclusion, OWFs do influence the local food web properties, with the occurrence of colonising organisms slightly lowering the water column primary producer standing stock, but also being an important resource for organisms of higher trophic levels. Altogether, the major role of suspension feeding organisms with key roles *M. edulis* and *J. herdmani* was highlighted in this thesis. These organisms were responsible for the reduction of the local annual primary producer standing stock and they increased the local food web complexity, mainly through their biodeposition process. Furthermore, the importance of SPLs as newly introduced habitats was highlighted throughout this thesis: (a) a high food web complexity was found in this area; (b) their invertebrate species exploit a wide range of resources; and (c) fish species associated with SPLs remain in the area to feed for a prolonged period. Moreover, an over-representation of trophic generalists and an under-representation of trophic specialists were observed, suggesting that more generalist organisms will occur in the North Sea in the future due to the development of more OWFs. Finally, it was shown that the introduction of jacket foundations causes the highest increase in carbon assimilation compared to the other types of foundations, reducing significantly the carbon content of the water column. From the above, it is implied that foundations with SPLs, such as gravity-based and monopile foundations, are possibly more beneficial for the local food webs, but further investigation is necessary to completely understand the effects of OWFs on the marine food webs.

Samenvatting

Offshore windmolenparken (OWPs) vormen een succesvolle bron van hernieuwbare energie en als gevolg daarvan groeit de ontwikkeling van OWPs wereldwijd snel. Ook in de Noordzee worden OWP projecten continu vergund en gebouwd. Deze installaties zorgen voor een verandering in het natuurlijke mariene milieu o.a. door de introductie van kunstmatig hard substraat in een omgeving die van nature veelal enkel uit zacht substraat bestaat. De constructies trekken een verscheidenheid aan gewervelde en ongewervelde soorten aan waardoor de biodiversiteit in het gebied verandert. Dit roept vragen op over de impact van OWPs op hun omgeving, waaronder vragen naar de effecten op het fuctioneren van het mariene ecosysteem.

In deze doctoraatsverhandeling worden de resultaten gepresenteerd van een onderzoek naar de effecten van offshore windturbines op de karakteristieken van het voedselweb in de OWPs. Daartoe werden de aangroeigemeenschappen over de gehele dieptegradiënt van een gravitaire turbine in het Belgische deel van de Noordzee (BdNZ) bemonsterd. Daarnaast werden ook de verschillende vissoorten die zich ophouden in de nabijheid van de betreffende turbine verzameld om de in situ karakteristieken van het voedselweb in beeld te brengen. Via experimenten met gekoloniseerde PVC plaatjes, afkomstig van een tripode uit het windmolengebied, werden gedetailleerde ex situ observaties gedaan met betrekking tot het voedselweb en de koolstofassimilatie door de aangroeiende organismen.

In de Hoofdstukken 2 en 3 onderzochten we de karakteristieken van het voedselweb van de aangroeigemeenschappen langsheen de diepte gradiënt van de offshore windturbine, de erosiebeschermingslaag (EBL) en het omringende zachte substraat van de zeebodem. De focus lag hier op het onderzoeken van mogelijke 'resource partitioning' tussen en binnen de verschillende dieptezones (i.e. gemeenschapsniveau). Voor de ongewervelde soorten die in verschillende diepte zones voorkomen, werd ook het voedingsgedrag onderzocht om na te gaan of trofische plasticiteit een mechanisme is dat kan bijdragen aan hun wijde verspreiding en overleving in een competitieve omgeving (i.e. soort-specifiek onderzoek). Dit onderzoek werd uitgevoerd via stabiele isotoop analyses (SIA) van de organismen

die werden bemonsterd op en nabij de turbine. De resultaten hiervan duiden op een verschil in voeselwebstructuur tussen gemeenschappen die verzameld werden op verschillende dieptes langsheen de turbine. ‘Resource partitioning’ werd duidelijk, zowel tussen als binnen de verschillende dieptezones. De meest complexe structuur werd gevonden op de EBL en het omringende zachte substraat, waar een sterke accumulatie van organisch materiaal wordt verwacht. Deze bevindingen werden verder ondersteund door de resultaten van het soort-specifieke onderzoek dat aantoont dat de organismen die in deze zones voorkomen een grotere diversiteit aan voedingsbronnen gebruiken dan de organismen die hoger op de turbine worden aangetroffen. Daarnaast blijkt uit onze resultaten ook dat de meerderheid van de ongewervelde soorten die op de turbine gevonden worden zich gedragen als trofische generalisten, waarbij hun voedselkeuze afhankelijk is van de diepte. Dit suggereert dat trofische plasticiteit bijdraagt aan het samen voorkomen van ongewervelde soorten binnen en tussen de diepte zones. Deze twee hoofdstukken belichten dat de EBL en het omringende zachte substraat belangrijk zijn voor organismen van meerdere trofische niveaus wat kan worden verklaard door de accumulatie van veel organisch materiaal in deze zones.

In Hoofstuk 4 onderzochten we de koolstofassimilatie door de aangroeigemeenschappen op de turbine. Hoewel het effect van deze gemeenschappen op de hoeveelheid primaire producenten al eerder werd gemodelleerd, ontbreekt het nog aan gemeten data om deze modellen te valideren. Wij hebben een “pulse-chase” experiment uigevoerd om te kunnen volgen in welke mate organische materie wordt verwerkt door de aangroeigemeenschappen. De resultaten tonen aan dat de hoogste biomassa-specifieke koolstof assimilatie wordt gerealiseeerd door de blauwe mossel *Mytilus edulis*. Op gemeenschapsniveau wordt de grootste hoeveelheid koolstof geassimileerd door de vlokreeft *Jassa herdmani*. Het onderzoek toont aan dat *J. herdmani* en *M. edulis* de voornaamste bijdrage leveren aan de totale consumptie van de voedselvoorraad: 97% van de totale koolstofopname verloopt via deze twee soorten. De resultaten van dit experiment werden vervolgens geëxtrapoleerd naar het huidige totale aantal geïnstalleerde windturbines in het BdNZ (264 monopiles, 48 jackets en 6 gravitaire funderingen). We berekenden de hoeveelheid koolstofopname door het totale aantal *J. herdmani* en *M. edulis* individuen voor elk type fundering en vergeleken dit met de totale jaarlijkse primaire productie in dit gebied. Onze resultaten tonen aan dat in de huidige situatie, 1.3% van de jaarlijkse voedselvoorraad wordt aangesproken door *M. edulis* en *J. herdmani*. We vergeleken deze waarde met de hoeveelheid koolstof die niet langer wordt geassimileerd door verlies van de macrofauna in de zachte substraten als gevolg van het habitatverlies door de constructie van de funderingen. De data suggereert dat de aanwezigheid van de offshore windturbines en de bijbehorende kolonisatie door aangroeigemeenschappen zorgt voor een opmerkelijke toename in koolstofassimilatie in vergelijking met de natuurlijke macrofauna in het permeabele sediment van een zelfde oppervlakte (i.e. de voetafdruk van de turbine). Vergeleken met het natuurlijke zachte sediment veroorzaakt de aanwezigheid van jacket funderingen de grootste toename, en die van gravitaire funderingen de kleinste toename in de lokale koolstofassimilatie.

In Hoofdstuk 5 ligt de focus op de vissoorten die worden aangetrokken door OWPs. We verzamelden exemplaren van twee pelagische soorten (*Scomber scombrus* en *Trachurus trachurus*), twee benthopelagische soorten (*Gadus morhua* en *Trisopterus luscus*) en een benthische soort (*Myoxocephalus scorpioides*), die abundant aanwezig zijn in de nabijheid van de funderingen. Maaganalyse en stabiele isotoop analyse werden uitgevoerd om respectievelijk de korte en lange termijn dieetsamenstelling van deze soorten in kaart te brengen. Beide analysetechnieken laten zien dat de benthische en benthopelagische soorten (voornamelijk voorkomend in de EBLs) zich voeden met de aangroeisoorten *J. herdmani* en *Pisidia longicornis*, beide energierijke en vetzuurrijke voedingsbronnen. Deze resultaten suggereren dat deze soorten de OWPs benutten als foerageergebied voor langere periodes. De analyse van het dieet van *T. trachurus* op korte termijn liet voornamelijk *J. herdmani* als voedsel-item zien, waar de langetermijn analyse aantoont dat deze soort zich voornamelijk voedt met zooplankton. Dit wijst erop dat *T. trachurus* zich eerder sporadisch voedt met de aangroeifauna en de OWPs tijdelijk als oase van energierijke voedingsbronnen benut. *Scomber scombrus* blijkt de de OWPs niet als foerageergebied te benutten; beide analysestrategieën wijzen op een dieet gebaseerd op zooplankton. De resultaten van de dieetanalyses voor de benthische en benthopelagische soorten bevestigen dat deze soorten rijkelijk gebruik maken van de aanwezige voedselbronnen en dus de hypothese dat hun productie lokaal zou kunnen toenemen. Voor de pelagische soorten kunnen de resultaten van dit onderzoek deze stelling niet bevestigen.

Concluderend kan gesteld worden dat de aanwezigheid van OWPs wel degelijk een invloed op de karakteristieken van het lokale voedselweb heeft, waarbij de aangroeiende fauna er enerzijds voor zorgt dat de voedselvoorraad in de waterkolom enigszins wordt verlaagd, maar waar deze organismen zelf ook een belangrijke voedselbron vormen voor organismen van een hoger trofisch niveau. Samengevat, deze doctoraatsverhandeling belicht de hoofdrol van de suspensievoeders *M. edulis* en *J. herdmani*. Deze organismen zijn verantwoordelijk voor een reductie in de hoeveelheid primaire producenten en verhogen daarnaast de complexiteit van het lokale voedselweb, voornamelijk door biodepositieprocessen. Daarnaast toont deze studie het belang aan van de EBLs als nieuw geïntroduceerd habitat: (a) de complexiteit van het voedselweb is hier verhoogd; (b) de ongewervelde soorten die hier voorkomen benutten zeer gevarieerde voedingsbronnen; en (c) sommige vissoorten die in de nabijheid van de EBL leven blijven hier voor langere tijd om te voeden. Ook werd er een oververtegenwoordiging van trofische generalisten en een ondervertegenwoordiging van trofische specialisten waargenomen. Dit suggereert dat verdere ontwikkeling van OWPs ervoor zal zorgen dat er in de toekomst meer generalisten in de Noordzee zullen voorkomen. Ten slotte werd aangetoond dat de aanleg van jacket funderingen leidt tot de grootste toename van koolstofassimilatie in vergelijking met andere funderingstypes, wat eventueel kan leiden tot een betekenisvolle afname van de hoeveelheid koolstof in de waterkolom. Uit bovenstaande kan worden afgeleid dat funderingstypes die worden aangelegd met een EBL, zoals gravitaire of monopile funderingen, mogelijk voordeliger zijn voor het lokale voedselweb. Echter, verder onderzoek is nodig om de effecten van OWPs op de structuur van mariene voedselwebben volledig te begrijpen.

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Chapter 1

General Introduction

1.1 Combating climate change with renewable energy

1.1.1 Climate change causes and predictions

Climate change is among the most severe threats that the planet is facing today. It is defined as the changes in climate caused by direct or indirect human activities that change the global atmosphere and that are detected additionally to the natural climate variability that is observed over comparable time periods (UNFCCC, 1992). Another common definition introduces climate change as the changes observed in climate over time due to natural variability and human activity and can be identified by changes in the mean and/or the variability of its properties (IPCC, 2007). Climate change is driven mainly by the increased anthropogenic greenhouse gas emissions, which are accumulated in the atmosphere since the pre-industrial era (IPCC, 2007, 2014; Cook *et al.*, 2016). The main greenhouse gas emitted by human activity is carbon dioxide (CO_2) with concentrations that have been increased by more than a third since the beginning of the industrial revolution (Hartmann *et al.*, 2013; IPCC, 2014, 2018). Global emission of CO_2 is continually increasing and was measured at 34 billion tonnes in 2017 (Malhotra, 2020). Temperature records over the last 1000 years indicate that the rate of increase from 1976 onwards has doubled compared to the period between 1910 and 1945 (Walther *et al.*, 2002). Nowadays, the global average air temperature is approximately 1.0^0C higher than during the pre-industrial era (with a range of 0.8 to 1.2^0C – IPCC, 2014, 2018).

The effects of climate change on the terrestrial and marine ecosystems are already prominent (Walther *et al.*, 2002; Thomas *et al.*, 2004). The main effects of climate change to the environment include the increasing frequency of extreme weather phenomena, such as storms and heat waves, ocean warming, ocean acidification (decreasing ocean pH), and sea level rise (ICPP, 2007; Wernberg *et al.*, 2014). Moreover, climate change has an impact on the species distributions and phenology of organisms (Walther *et al.*, 2002; Parmesan and Yohe, 2003; Ohlberger, 2013). Distribution shifts have been registered for both marine (Poulard and Blanchard, 2005; Beaugrand *et al.*, 2008; Birchenough *et al.*, 2015) and terrestrial species (Walther *et al.*, 2002; Rouget *et al.*, 2003). Climate change can also affect the growth rate and development of species by impacting their metabolism and resource acquisition (Ohlberger, 2013), alter the abundance of different marine species (Beaugrand *et al.*, 2008), change the life cycle events of species that depend on temperature fluctuations (Birchenough *et al.*, 2015), but also cause thermal stress on reefs with dramatic effects that lead to total loss of corals (Walther *et al.*, 2002). Finally, it can enhance the extinction rate of all species (globally) up to 58 % (for species with poor dispersal capability and for the scenario of maximum expected climate change - Thomas *et al.*, 2004).

To moderate the consequences of climate change, there has been an international agreement for the reduction of global carbon emissions and the limitation of the temperature rise to 2^0C in December 2015 at the Paris Climate Agreement of the United Nations Framework Convention on Climate Change. In 2018, the Paris Climate Agreement decided to limit global warming to 1.5^0C. In order to maintain global warming to this level, the emission of greenhouse gases (including CO_2 and nitrous oxide N_2O) needs to be minimized (Allen *et al.*, 2018). Different approaches for the reduction of the CO_2 emission are considered and/or adopted by various countries, such as the increased usage of low carbon fuels, the improvement of energy efficiency, the application of geoengineering approaches, the capture and storage of CO_2 and not at least, the deployment of renewable energy installations (Leung *et al.*, 2014).

1.1.2 Renewable energy resources

Renewable energy is the energy source that is continuously provided by nature and does not require energy sources from fossil fuels, waste products from fossil fuels or waste from inorganic sources (Ellabban *et al.*, 2014). Renewable energy resources (RERs) seem to be one of the most promising and effective solutions to reduce CO_2 emissions and moderate the environmental problems caused by climate change (Hepbasli, 2008). These resources are inexhaustible, offer many environmental benefits and they do not release any pollutants during operation (Demirbas, 2005; Hepbasli, 2008). Since the renewable sources vary geographically, their potential tends to be geographically diverse (Gross *et al.*, 2003). The different renewable energy technologies include the photovoltaic, wind turbines, concentrating solar power, batteries, wave energy devices, etc. (Blaabjerg and Ionel, 2015). The demand for renewable energy is globally increasing, in sync with the challenge to reduce carbon dioxide (CO_2) emission and mitigate global warming (Bergström *et al.*, 2014). In 2001, the European Commission requested that part of the electricity is produced by renewable energy sources. A few years later, the European Union set the target of 20 % of energy consumption to be derived from renewable sources (European Commission, 2009). A variety of renewable energy developments has been implemented, such as wave energy converters (Veigas *et al.*, 2014), solar panels (Dincer, 2000), hydropower (Demirbas, 2005), geothermal fields (Barbier, 2002), etc. In this thesis we will focus on the wind energy and, specifically, on offshore wind energy.

Wind energy is a great success for renewable energy production (Gross *et al.*, 2003) and has seen a rapid market growth since 1991. By 2001, the total installed capacity worldwide (both on- and offshore) had increased from 2 GW to more than 20 GW (Wind Power Monthly, 2001), while in Europe, this capacity is expected to reach 70 GW by 2030 (WindEurope, 2018). In 2011, almost 4 % of Europe's electricity demands were fulfilled by wind power, while this is expected to increase to 25 % by 2030 (Bilgili *et al.*, 2011). The wind turbine technology is the most commonly used method for the transformation of the wind kinetic energy to electrical energy by rotating blades (Herbert *et al.*, 2007). Onshore wind farms have been developed at a large scale (Gross *et al.*, 2003), but they cause e.g. aesthetic concerns and rivalry with land users (Taylor, 2004). This, in combination with the better wind conditions and the availability of space in offshore areas, has led to the increasing development of offshore wind farms (Inger *et al.*, 2009).

1.2 Offshore wind farms

The offshore wind farm (OWF) industry is rapidly developing in Europe (Fig. 1.1). Denmark was the first country in 1991 to build an OWF consisting of 11 turbines (EWEA, 2011) and some other northern European countries followed later, with The Netherlands building its first OWF in 2006 (Lindeboom *et al.*, 2011), Belgium in 2008

(Brabant and Degraer, 2010) and Germany having its first operational wind farm in 2010 (Kirchgeorg *et al*., 2018). By 2012, more than 1600 turbines allocated to 55 offshore wind farms (OWFs) were established and operational (EWEA, 2013), while more OWFs are continuously being constructed, licensed and/or scheduled (Soma *et al*., 2019). In 2018, 15.8 GW of capacity corresponding to 4,149 offshore wind turbines were installed in Europe (Kirchgeorg *et al*., 2018; WindEurope, 2018). This number is expected to increase to 48 GW by 2030 with most of this capacity present in the North Sea (Fig. 1.2 - WindEurope, 2018). In the Belgian part of the North Sea, there are currently six operational offshore wind farms, consisting of 318 turbines, while by the end of 2020 there will be 399 turbines installed and operational (Rumes and Brabant, 2019). During the last revision of the marine spatial plan (MRP 2020-2026), the Belgian federal government reserved a surface area of 284 km^2 located at 35-40 km offshore for the construction of new offshore wind farms (Rumes and Brabant, 2019). Since this zone is partly located in the Habitats Directive area "Vlaamse Banken", research is needed to determine whether the establishment of the new OWFs is compatible with the natural values of this marine protected area (Rumes and Brabant, 2019).

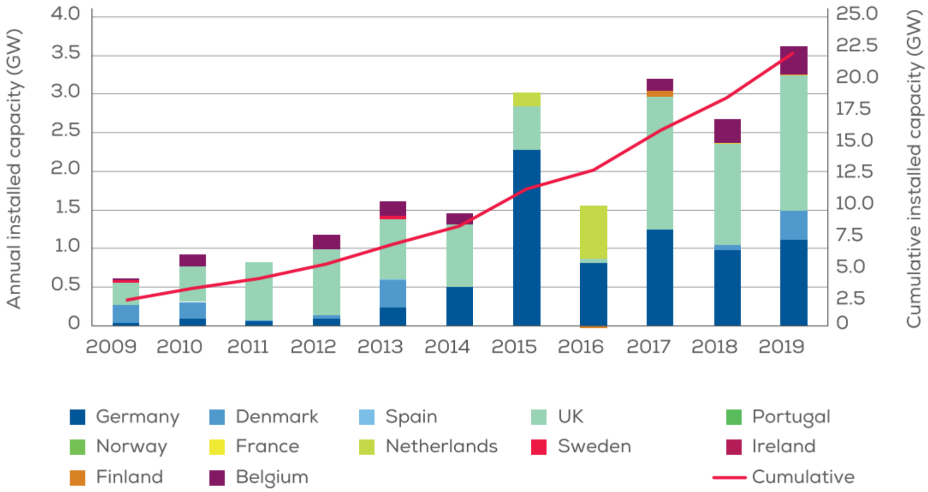


Figure 1.1: Annual installed capacity (left axis) and cumulative installed capacity (right axis) of offshore wind installations by country and year in Europe (source: WindEurope, 2020).

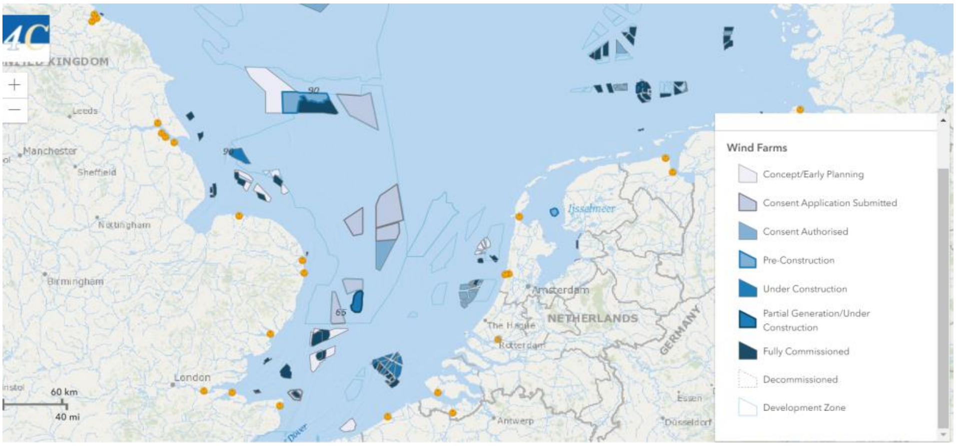


Figure 1.2: Map of the offshore wind farms (fully commissioned, under construction, in the pre-construction phase, authorised) and the zones reserved for the offshore wind farms to be constructed in the future in the southern part of the North Sea (source: https://www.4coffshore.com/offshorewind/).

Even though the establishment of OWFs contributes to the mitigation of the effects of climate change, their introduction can induce changes in the marine environment (Gill, 2005; Lindeboom *et al.*, 2011), both above and under the sea. However, the potential effects of OWFs will differ between the different phases of the progression of the foundations (under construction, operational, decommissioning), and are also location-specific (i.e. North Sea, Baltic Sea, etc.) and species-specific (depending on their likelihood of interacting with the different structures of the turbines - Bailey *et al.*, 2014). Our understanding of the potential effects of these structures on the marine ecosystem is steadily improving as we are gathering empirical evidence from operational offshore wind farms (Lindeboom *et al.*, 2011; Krone *et al.*, 2013a; De Mesel *et al.*, 2015) and also from decommissioning for both oil and gas platforms and offshore wind installations (Jøgersen, 2009, 2012). Defining the effects as positive/good/favourable or negative/bad/unfavourable is viewpoint dependent. Here, a selection of predominant direct pressures (*in casu* effects that are caused only by the presence of the foundations when they are in the operational phase) of OWFs on the marine environment of the North Sea are presented. These pressures were identified as the ones most frequently mentioned in literature and they are rated as favourable or unfavourable depending on the presumed effect on the local abundance of marine organisms (favourable: increased local abundance, unfavourable: decreased local abundance).

1.2.1 Overview of main pressures of OWFs

Offshore wind foundations produce sound (both during the operational and mainly during the constructional phase), which is considered an unfavourable effect (Fig. 1.3) influencing the marine life (Nedwell *et al.*, 2004; Gill, 2005; Madsen *et al.*, 2006; Petersen and Malm, 2006; Inger *et al.*, 2009). Sound is transmitted through water affecting a variety of species (Petersen and Malm, 2006). Underwater sound affects mainly organisms sensitive to sounds (Inger *et al.*, 2009), such as marine mammals that have very sensitive hearing (Mangi, 2013) and use sound for communication, echolocation, breeding and predation avoidance (Madsen *et al.*, 2006). Fish and crustaceans are sensitive to sound as well, and they may avoid the OWF areas during the construction period (Popper *et al.*, 2001; Petersen and Malm, 2006; Inger *et al.*, 2009). The knowledge on the impact of sound on the macrofaunal organisms is generally poor, since the sensitivity of these organisms to sound, needs to be further examined (Roberts and Elliott, 2017). However, recent studies have shown that sound might influence the behaviour of some species, such as the bioirrigation of the species *Nephrops norvegicus* (Solan *et al.*, 2016).

In order to transfer power among devices, to transformers and to the mainland, submarine cables are used (Inger *et al.*, 2009). During operation, electromagnetic fields are created due to the transportation of the electricity through those cables (Gill, 2005; Bailey *et al.*, 2014). The possibility that electromagnetic fields might cause unfavourable effects has been rated low (Gill *et al.*, 2012; Bergström *et al.*, 2014). However, they can affect the movements, navigation and predation capabilities of species that use electromagnetic signals for these purposes, such as electrosensitive fish (particularly elasmobranches and teleosts), large decapods (e.g. *Cancer pagurus* - Scott *et al.*, 2018) and marine mammals (Gill, 2005; Inger *et al.*, 2009; Gill *et al.*, 2012; Bailey *et al.*, 2014). The impacts of electromagnetic fields could be reduced by using improved cable armours and a subsequent cable burial (Petersen and Malm, 2006).

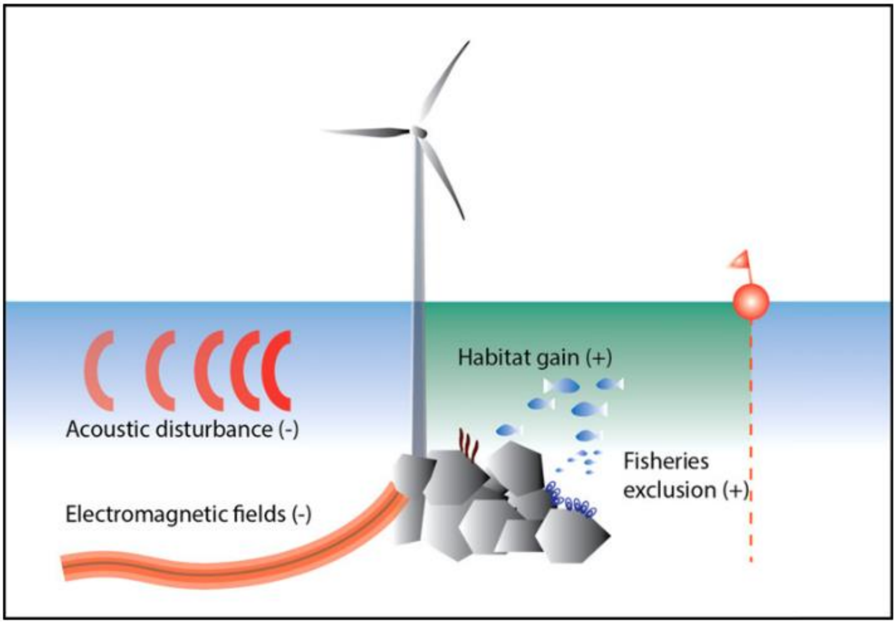


Figure 1.3: Overview of the pressures (unfavourable: left and favourable: right) of the offshore wind foundations during the operational phase on the marine organisms (source: Bergström *et al.*, 2014).

The installation of OWFs may have some favourable effects onto the local abundance of marine organisms as well (Fig. 1.3). The deployment of turbines and scour protection layers results in habitat creation (Wilson and Elliott, 2009). The added hard substrates increase the habitat availability for many species (Andersson and Öhman, 2010; Langhamer, 2012). The addition of the scour protection layers surrounding the base of monopiles and gravity-based foundations can further change the natural habitat (Wilson and Elliott, 2009; Langhamer, 2012). This habitat creation (Fig. 1.4) increases the heterogeneity of the marine environment (Petersen and Malm, 2006; Langhamer, 2012). Finally, the new habitat might lead to increased production in the area, since newly established substrates are linked with increased settling, foraging and protection against predators (Bohnsack, 1989).

Fisheries activities may be restricted in the OWF area as a consequence of excluding shipping for safety reasons (Bergström *et al.*, 2014). Fisheries exclusion could lead to an increase in the species abundances and growth by reducing mortality rates of target species (Leonhard *et al.*, 2011; Lindeboom *et al.*, 2011) that could potentially contribute to a spill-over effect (Brabant *et al.*, 2013). Hence, OWFs might have the potential to act as refugia for many species (Wilson and Elliott, 2009). The crevices of the scour protection layer can provide protection against predators and currents for several fish species (Bohnsack, 1989; Reubens *et al.*, 2011). The introduced habitats in combination with the fisheries exclusion and the enhanced protection against predation can increase the species abundances on and around the OWFs, a phenomenon known as artificial reef effect.

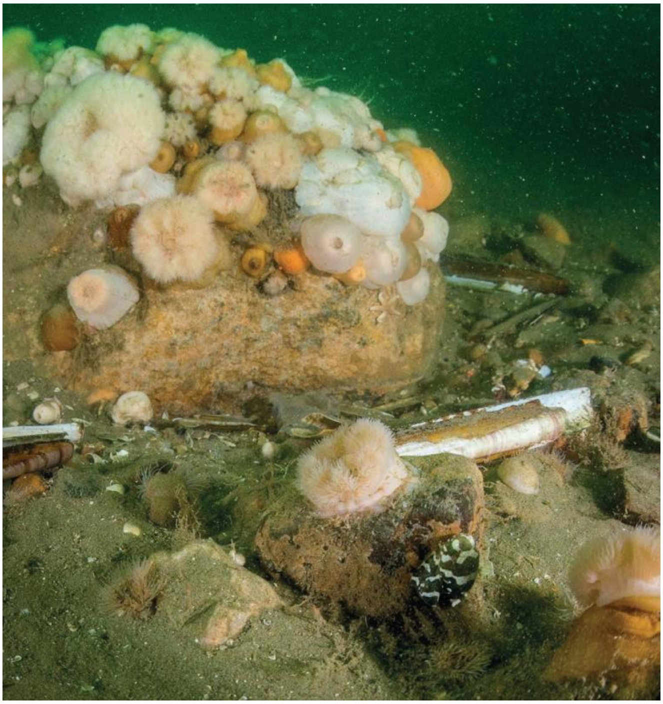


Figure 1.4: Rock from a scour protection layer in the Dutch part of the North Sea increasing the available habitat for sessile organisms (source: Coolen, 2017).

1.2.2 Artificial reef

Seven different types of OWF foundations (5 fixed – Fig. 1.5, and 2 floating – Fig. 1.6) have been introduced in the North Sea: monopile, gravity-based, jacket, tripod, tripile floating spar buoy and floating barge foundations (WindEurope, 2018). The monopiles are the most common foundations, representing 87% of the installed foundations in the North Sea and counting 3,720 turbines in 2017 (WindEurope, 2018). Jacket foundations (315 turbines and 9% of the total installed foundations) are the second most common foundations, followed by the gravity-based (283 turbines, 7.6% of the total installed foundations), the tripods (132 foundations), the tripiles (80 foundations) and finally the floating spar buoy (6 foundations) and the floating barge (only 1 foundation) (WindEurope, 2018).

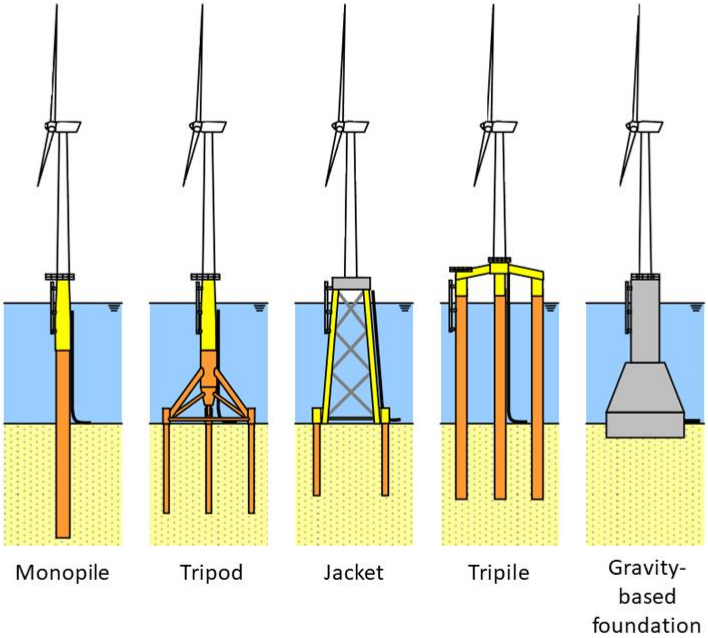


Figure 1.5: The five different types of fixed offshore wind foundations. From left to right: monopile, tripod, jacket, tripile and gravity-based foundation (modified by source: Fischer, 2011).

The main underwater modification caused by the establishment of OWFs is the creation of an artificial reef (Petersen and Malm, 2006; Langhamer, 2012). The term 'artificial reef' refers to all kinds of submerged man-made structures placed either deliberately (to influence physical, biological or socioeconomic processes and regulate climate change, i.e. oil and gas platforms, OWFs), or accidentally (i.e.

shipwrecks) on the seafloor and function as habitats for marine biota (Jensen *et al*., 2000; Svane and Petersen, 2001). The combined effect of all these man-made structures is known as artificial reef effect (Dannheim *et al*., 2020). These artificial constructions provide new habitat for colonising sessile, or 'fouling', species (Svane and Petersen, 2001; Brown, 2005) and associated mobile fauna, such as crustaceans, molluscs and fish (Chapman, 2006; Page *et al*., 2006). Artificial reefs generally hold higher densities and biomass of fish and colonising fauna compared to the surrounding soft-bottom areas (Bohnsack and Sutherland, 1985; Bohnsack, 1989; Relini *et al*., 1998). The effects of artificial reefs on the recruitment rates differ per species because of differences in limitation by refuge, food sources, territory and/or behavioural requirements (Inger *et al*., 2009). Artificial reefs that enhance growth, reproduction and survival rates can play an important role on population structure and dynamics (Gibson, 1994; Lowry *et al*., 2013).

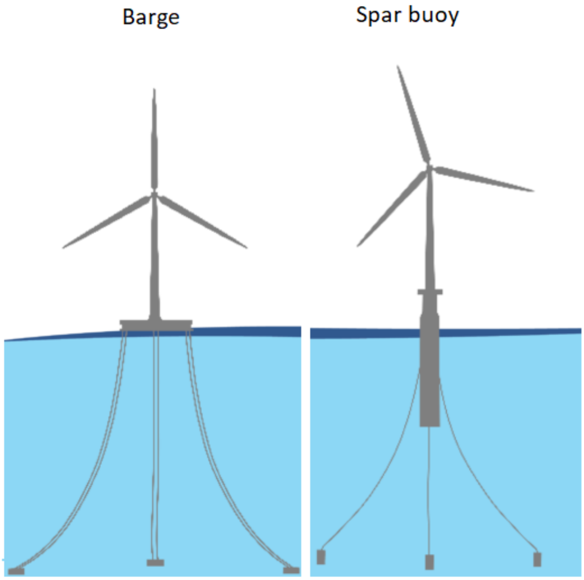


Figure 1.6: The two different types of floating offshore wind foundations: barge and spar buoy (modified by source: Quest Floating Wind Energy – questfwe.com).

The colonisation of artificial reefs by epibenthic organisms occurs via settlement of pelagic larvae, but also juvenile and adult individuals, which accounts for more than 90 % of the initial colonists attaching at the artificial reef (Osman, 1977). Water depth can have an effect on the composition of colonising assemblages (Perkol-Finkel *et al.*, 2008), since abiotic factors, such as light and temperature, could lead to a decrease of the species diversity and biomass at lower depths (Relini *et al.*, 1994; Ardizzone *et al.*, 1996). Over time, the organisation and complexity of the assemblages increase (Sammarco *et al.*, 2004), together with the biomass (Relini and Relini, 1997) and the biodiversity (Ardizzone *et al.*, 1996). It is only after approximately 5 years that stable assemblages are established (Jensen *et al.*, 2000), with only a few species dominating the artificial hard substrates (Kerckhof *et al.*, 2019).

Most of the knowledge we have obtained about vertically elongated artificial reefs in the North Sea derives from research on oil and gas platforms, while research on the artificial reef effect by offshore wind foundations is increasing the last two decades. The installation of oil and gas platforms in the North Sea initiated ca. 60 years ago (Olsgard and Gray, 1995) and since then, extensive research on their effects on the marine environment has been conducted (Olsgard and Gray, 1995; Guerin *et al.*, 2007; Guerin, 2009; van der Stap *et al.*, 2016; Almeida and Coolen, 2020). Indeed, a plethora of information about the zonation patterns along the depth gradient of colonising organisms (van Buuren, 1984; van der Stap *et al.*, 2016) and fish attraction towards the oil and gas platforms (Soldal *et al.*, 2002; Wright *et al.*, 2020) exists. Knowledge of the effects of such installations on marine life is of great significance for understanding the influence of the presence of the offshore wind foundations (van der Stap *et al.*, 2016). This is due to the structural similarities between oil and gas platforms and some offshore wind foundations, that stretch along the entire depth gradient. OWFs and oil and gas platforms are the only artificial reefs that create this link between the seabed and the sea-surface.

1.2.3 Zonation patterns along the depth gradient

As with natural habitats, distinct zonation patterns of highly abundant species (animal and algae) colonise the offshore wind turbines in the North Sea, rising from the sea-bottom up to the sea-surface (Petersen and Malm, 2006). The typical vertical zonation pattern that has been found at the offshore wind turbines in the North Sea (Fig. 1.7) consists of the intertidal zone, the *Mytilus edulis* zone (from now on mentioned as *Mytilus* zone), the *Jassa herdmani* zone (from now on mentioned as *Jassa* zone) and the *Metridium senile* zone (from now on mentioned as *Metridium* zone) (Whomersley and Picken, 2003; Lindeboom *et al.*, 2011; Krone *et al.*, 2013a; De Mesel *et al.*, 2015). The zonation pattern is not clearly defined, i.e. individuals of *M. edulis* can be found in lower depths and individuals of *J. herdmani* can occur at different zones; however, the abundance of the dominant species is higher in their zones of dominance compared to other zones.

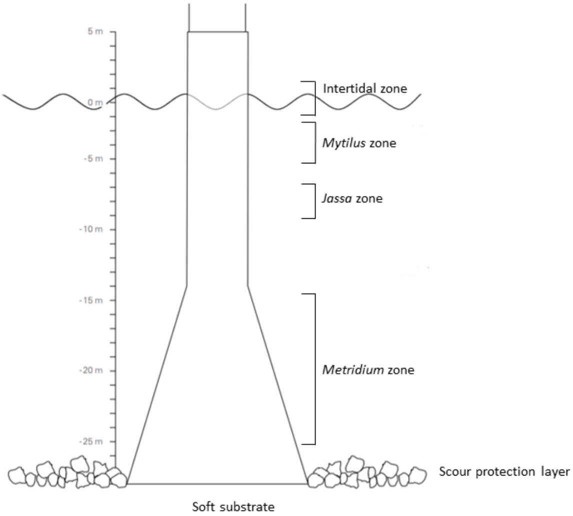


Figure 1.7: Zonation pattern as it is formed by the macrofauna species and the structure of the turbine along the depth gradient of a gravity-based foundation (modified by the source: De Mesel *et al.*, 2013).

The offshore intertidal zone does not naturally occur in the southern North Sea (De Mesel *et al.*, 2015). This zone is mainly structured by tides and wave action. It comprises typical intertidal species (De Mesel *et al.*, 2015; Liversage, 2017), such as the decapod *Carcinus maenas* (Langhamer *et al.*, 2016) and the macroalge *Ulva* spp. (Bouma and Lengkeek, 2008). In the Belgian part of the North Sea, this zone mainly comprises both indigenous species, such as the barnacle *Semibalanus balanoides*, and non-indigenous species, such as the barnacle *Balanus perforatus*, the limpet *Crepidula fornicata* and the midge *Telmatogeton japonicus* (De Mesel *et al.*, 2015).

The blue mussel *Mytilus edulis* dominates the shallow subtidal zone. Offshore wind turbines are heavily colonised by this species after only a few years (Krone *et al.*, 2013a). *Mytilus edulis* individuals form a dense belt in the *Mytilus* zone. Parts of this belt might fall off under its own weight (Leewis *et al.*, 2000). The large densities of this species at the thousands of offshore wind turbines that are already established and planned to be constructed in the future, will lead to the "*Mytilus*ation" of the offshore regions within the North Sea (Krone *et al.*, 2013a). *Mytilus*ation will most probably affect the local ecosystem (OWF scale) through the production of secondary hard substrates that are created by this species (Krone *et al.*, 2013; Kerckhof *et al.*, 2019). This can lead to slightly larger impacts of OWFs since there is more space available for organisms to settle (Janßen *et al.*, 2015). Indeed, *M. edulis* is considered an engineer species because it creates new habitats thereby changing the structure of the existing communities (Gili and Coma, 1998; Maar *et al.*, 2009; Cresson *et al.*, 2016). It also plays an important role in bentho-pelagic coupling, since it can alter the nutrient and organic matter pool (Gili and Coma, 1998; Cresson *et al.*, 2016).

Below the *Mytilus* zone, there is a zone dominated by the tube-building amphipod *Jassa herdmani*, the *Jassa* zone. This tube-building amphipod occurs along the entire depth gradient of offshore wind turbines (Leonhard and Pedersen, 2006), but they reach highest densities right below the *Mytilus* zone, at ca. 8-9 m depth. *Jassa herdmani* often represents more than 85 % of the total density of the assemblages found at the turbines, which corresponds to ca. 10,000 individuals m^{-2} (De Mesel *et al.*, 2015).

Finally, the anemone *Metridium senile* is abundantly present at the lower parts of the turbines, the *Metridium* zone. *Metridium senile* is a strong spatial competitor, having a strong structuring influence on the colonising assemblages. It rapidly colonises new substrates (Nelson and Craig, 2011). This competitive behaviour might explain the lower species richness that has been observed in the *Metridium* zone (van der Stap *et al.*, 2016), where *M. senile* is the dominant species, a phenomenon known as "slimeification" (Kerckhof *et al.*, 2019).

At the base of the monopiles and gravity-based foundations, a scour protection layer (SPL) is surrounding the turbines to prevent erosion. SPLs are made of rocks, which form a rock collar around the turbines (Baeye and Fettweis, 2015) that expands 15 m from the edge of the foundations (Peire *et al.*, 2009). The rock layer consists of 20 % - 80 % mixture of 5 - 40 kg and 40 - 200 kg of compact limestone rocks (Peire *et al.*, 2009). SPLs enhance the habitat complexity and provide further habitat (Causon and Gill, 2018), which provides shelter against currents and predators for sessile and mobile species (Petersen and Malm, 2006; Reubens *et al.*, 2011; Langhamer, 2012; Liversage and Chapman, 2018). This leads to increased densities of organisms attached to the rocks of the SPL (Bouma and Lengkeek, 2008) and of fish species, whose densities might get on average 37 times higher above the SPL than in the surrounding soft sediments (Couperus *et al.*, 2010).

Finally, OWFs are placed on the sandbanks with naturally coarse sediments. A few years after the installation, the sediment characteristics seem to change. The soft substrates close to the offshore wind turbines have a lower median grain size and higher organic carbon content compared to the local soft sediments. This is caused by the biodeposition of organic matter produced by the colonising fauna on the turbine and the locally altered hydrodynamic conditions (Coates *et al.*, 2014). This leads to increased abundances and species richness close to the turbines (Coates *et al.*, 2014; Lefaible *et al.*, 2018). The biodiversity of the soft substrate communities is further enhanced by the occurrence of some typical colonising species, which have probably been detached by the turbine and/or by the SPL rocks (Bouma and Lengkeek, 2012; Mavraki *et al.*, 2020).

1.2.4 Artificial structures and the attraction-production hypotheses

Apart from the changes induced to the biodiversity of invertebrate species, artificial structures influence fish as well. The addition of such structures can alter the habitat composition, affecting the local fish biodiversity (Wilhelmsson *et al.*, 2006a; Andersson *et al.*, 2009). Furthermore, the length of some fish species has been found to be larger when near artificial reefs in comparison to sandy areas (Reubens *et al.*, 2013a), indicating that these structures could affect the fish physiology. Artificial reefs have been extensively used to support small-scale fisheries, to restore degraded habitat and to manage coastal zones (Neves Santos and Costa Monteiro, 1998; Claudet and Pelletier, 2004). These structures are a successful management tool, resulting in enhanced local catches in both professional and recreational fisheries (Bohnsack and Sutherland, 1985). The origin of the increased fish biomass has been largely debated the last decades. This issue is known as the "attraction-production" debate. This debate was first raised during the Third International Artificial Reef Conference in 1983. During this conference, the investigation on whether artificial reefs can lead to production or only to attraction was initiated (Lindberg, 1997).

The attraction hypothesis suggests that fish are attracted from the natural environment (including the soft sediments) to artificial reefs, where they aggregate, but there is no net increase in their production (Bohnsack, 1989; Brickhill *et al.*, 2005). The reefs act as fish aggregation devices, providing behavioural cues that fish can exploit (Brickhill *et al.*, 2005). The attraction to artificial reefs can be caused by the increased structural complexity, resulting in the enhanced protection against predators, shelter from the currents (Bohnsack and Sutherland, 1985; Bohnsack, 1989) and/or the increased food availability (Leitão *et al.*, 2007; Reubens *et al.*, 2011).

Alternatively, the production hypothesis proposes a more positive outcome concerning the fish biomass. It states that the carrying capacity of the original environment increases due to the establishment of the new habitat (Bohnsack, 1989; Lindberg, 1997). Increased feeding and shelter opportunities provided by the artificial reefs encourage fish larvae to settle at these structures, survive to spawn, grow and contribute new individuals to the local population, increasing the net production (Lindberg, 1997; Powers *et al.*, 2003; Brickhill *et al.*, 2005).

Attraction and production were determined as the two extremes of a continuum of ecological situations (Svane and Petersen, 2001; Brickhill *et al.*, 2005). The attraction to the artificial reefs could potentially lead to production, since they are not mutually exclusive (Reubens *et al.*, 2013a; Cresson *et al.*, 2019). The degree of attraction or production following the establishment of the artificial reefs will depend on the surrounding habitat concerning spatial heterogeneity and nutrient availability (Brickhill *et al.*, 2005). The introduction of a single artificial reef will most likely induce the fish attraction. Numerous and more complex reefs are more likely to increase production (Brickhill *et al.*, 2005). The use of isotopic functional indices can provide an innovative sight of the mechanisms of production involved in the biomass increase in artificial reefs (Cresson *et al.*, 2019). Recently, Cresson *et al.* (2019) combined isotopic and biomass data of various fish species that were near artificial reefs to calculate isotopic indices. The isotopic data were plotted in the isospace to identify any potential dietary switch towards the organic matter of benthic (artificial reefs) origin. Results indicating a diet based on organic matter of benthic origin, together with increased fish biomass and a decrease of the values of the isotopic indices suggest increased local secondary production (Cresson *et al.*, 2019). Hence isotopic functional indices can be used to provide insights towards secondary production, but the link between them cannot be directly proven.

1.2.5 Predicted effects of artificial habitats

A variety of anthropogenic activities in the North Sea for many centuries has created a highly perturbed environment. The southern part of the North Sea has multiple ship wrecks deriving from the First and the Second World Wars (Zintzen, 2007), offshore test drilling for oil and gas started already since 1966, and by 2018 the North Sea region contained 184 offshore rigs, making it the region with the most rigs in the world (Statistica, 2018). Commercial fisheries in the area are largely performed by trawling, affecting the natural soft sediments. Overfishing has created an unproductive environment, disturbing marine food web dynamics (Clover, 2004).

The introduction of offshore wind turbines provokes further perturbations to this environment, changing the biodiversity. In addition to that, the installation of such artificial structures may modify the hydrodynamic conditions of the area (Dannheim *et al.*, 2020). This can potentially lead to an increase in the vertical water mixing and subsequently to the nutrient transport throughout the water column (Floeter *et al.*, 2017). Moreover, the increased resuspension of particulate organic matter, caused by the OWF installations, increases the turbidity (Baeye and Fettweis, 2015), which in turn leads to reduced light affecting primary productivity (Devlin *et al.*, 2008).

The increasing numbers of OWF installations in the North Sea promote the colonisation of these structures by sessile filter feeding organisms. It has been hypothesized that the filtering activity of these organisms could alter the clearance rates of the water (Newell, 2004) and significantly reduce the phytoplankton but also the micro- and meso-zooplankton biomass in the area (Maar *et al.*, 2007). Furthermore, data deriving from long-term chlorophyll a monitoring in the Belgian part of the North Sea and beyond (MSFD-Eutro: https://www.deltares.nl/en/projects/msfd-eutro/) has shown that chlorophyll *a* concentrations have decreased over the last years, especially in coastal areas (Fig. 1.8). Coastal chlorophyll *a* concentrations can be influenced by anthropogenic nutrient supply deriving from agricultural and industrial sources (Peters *et al.*, 2005). When reducing the river dissolved inorganic nitrogen and phosphorous loads by 50 %, a 15-20 % reduction of the coastal primary production is detected, whereas offshore waters remain roughly unaffected (OSPAR, 2008). However, the establishment of OWFs with its subsequent colonisation depletes the phytoplankton in and around OWF areas, reducing the chlorophyll *a* in offshore waters as well (Slavik *et al.*, 2019). This will eventually alter the entire food web and biogeochemical cycling (Slavik *et al.*, 2019).

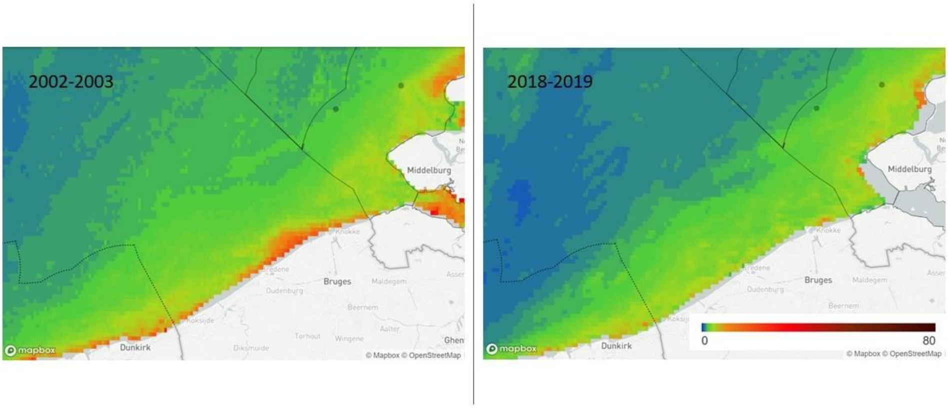


Figure 1.8: Changes in the mean chlorophyll *a* concentrations in the Belgian part of the North Sea within 16 years. On the left, the chlorophyll *a* concentrations of the year 2002-2003 and on the right the chlorophyll *a* concentrations of the year 2018-2019. On the bottom right, the range of chlorophyll *a* concentrations is illustrated by the different colours, with blue indicating the absence and dark red/purple the elevated concentrations of chlorophyll *a* (modified by source: MSFD-Eutro: https://www.deltares.nl/en/projects/msfd-eutro/).

Furthermore, it has been predicted that the SPLs at the base of some artificial structures will act as the main artificial reefs, given the provision of habitat heterogeneity (Petersen and Malm, 2006; Whitehouse *et al.*, 2011). The increased heterogeneity in the area can play an important role in species diversity and density (Langhamer, 2012). It is anticipated that SPLs will facilitate the settling of larvae, attracting more invertebrate and vertebrate organisms (Petersen and Malm, 2006). Moreover, they can alter the nature of the soft substrate near offshore wind foundations, turning exposed and/or biodiversity poor soft substrates into species-rich ecosystems (Langhamer, 2012). Finally, Langhamer (2012) estimated that the food provisioning in between the rocks of SPLs will get up to 60 times higher compared to the natural soft sediment.

Since the presence of OWFs affects a wide range of marine organisms, concerns about the potential environmental impacts induced by the OWFs on marine ecosystems and ecosystem functioning arose (Lindeboom *et al.*, 2011; Bailey *et al.*, 2014). A food web analysis would provide a rigorous and comprehensive understanding of the ecological processes (Fry, 2006) occurring on and around the offshore wind turbines.

1.3 Food web ecology

1.3.1 Marine food webs

The impact of environmental and structural changes on species in ecosystems is often induced from the base of the food webs (Paine, 1980). Food webs are complex and composed of many species and their interactions, changing spatially and seasonally, and constantly developing and adapting. Owing to this complexity, species responses to anthropogenic and/or environmental changes are complex too. The nature of these responses is usually unpredictable, which makes future states of ecosystems hard to predict (Planque, 2016). Marine food webs are mainly supported by primary production of phytoplankton in the photic zone, which is the engine of the “biological pump” that sustains the marine food web (Fig. 1.9 – Chisholm, 2000). Using sunlight and dissolved inorganic nutrients, phytoplankton converts CO_2 to organic carbon, which is the base of the food web (Chisholm, 2000). Part of this organic carbon reaches the sediment and fuels the benthic communities (benthic food web), while another part passes through consumers in surface and middle waters (pelagic food web) (Chisholm, 2000).

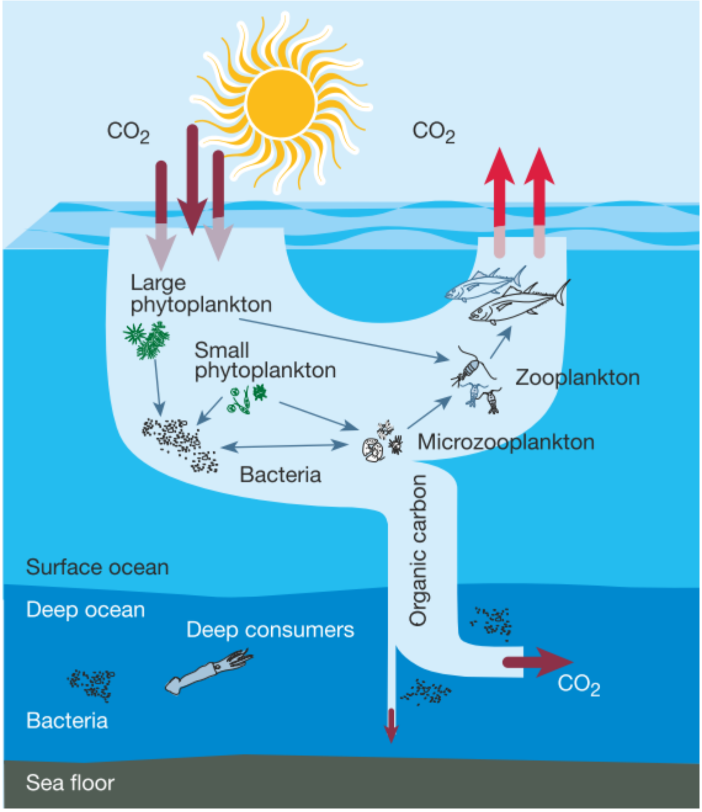


Figure 1.9: The main carbon flows in the marine ecosystem. The pelagic food web is supported by the production of organic matter by phytoplankton. The benthic food web is fuelled by the organic matter that settles on the sediment. Primary production is being supported by the remineralization of organic matter that releases nutrients, which are transported to the photic zone (modified from source: Chisholm, 2000).

Our understanding of how this carbon flows through the marine food web has led to multiple studies concerning both the pelagic and the benthic food web. Steele (1974) was the first to develop the theory on the herbivorous pathway, in which phytoplankton is being consumed by zooplankton, which in turn is being exploited by fish. There is also another theory that was introduced later, which introduces the carbon transfer through the microbial loop (Azam *et al.*, 1983). According to this theory, the dissolved organic matter, which is produced by algae and bacteria, is assimilated by bacteria and may, eventually, feed higher trophic levels through multiple transfer steps. Thus, dissolved organic carbon may still contribute to the "traditional" food chain. In coastal rocky shores, macroalgae is considered the most important primary producer, especially during winter, when the phytoplanktonic production is minimum (Duggins *et al.*, 1989). Macroalgae enter the coastal food webs through the detritic pathway (Riera *et al.*, 2009), with 10 % of the macroalgal production being immediately grazed and 90 % entering various detritus food chains as particulate organic matter (POM) and/or dissolved organic matter (DOM – Pomeroy, 1980).

Food webs have mostly been studied in closed systems that are easier to examine, such as lakes (Vander Zanden *et al.*, 1999), or in less diverse systems, such as rivers (Fisher *et al.*, 2001; Jepsen and Winemiller, 2002). However, there are also relatively detailed food web studies in open ocean areas (Davenport and Bax, 2002), deep sea (Fry, 1988), polar regions (Gillies *et al.*, 2012), estuaries (Richoux and Froneman, 2008), and in the intertidal zone (Christianen *et al.*, 2017). Food webs have been extensively studied on rocky shore assemblages (Riera, 2009; Richoux *et al.*, 2014a; Richoux and Ndhlovu, 2015), but also on artificial hard substrates, such as oil and gas platforms (Guerin, 2009). However, to our knowledge, there have been no studies on the food web structure of organisms associated with OWFs.

1.3.2 Food web structure and the role of the species

There is a complementary relationship between community and food web structure and function (Thompson *et al.*, 2012). For example, the food web structure can influence the behaviour and stability of ecological communities, by influencing the transfer of energy, and in turn, affect the community structure (MacArthur, 1955; May, 1972; Paine, 1980). Traditionally, it was stated that community stability increases with the increased number of links in a food web (MacArthur, 1955; Elton, 1958; Dunne *et al.*, 2002). However, mathematical models showed the opposite, stating that larger and more inter-connected communities were less stable (May, 1972). May's mathematical food web models relied on the representation of connections between species based on random graphs. But food web structure in nature is far from random (Allesina *et al.*, 2015). Indeed, food web stability is highly dependent on connectance and distribution of trophic links of the species comprising a food web (Borrvall *et al.*, 2000; Ebenman and Jonsson, 2005). Food webs with many and highly connected species tend to be more robust to a species loss (Borrvall *et al.*, 2000; Dunne *et al.*, 2002; Ebenman and Jonsson, 2005). Thus, increased connectance among species reduces the sensitivity of food webs to the removal of highly connected species, while the loss of random species will have minor effects on the food webs (Dunne *et al.*, 2002). On the contrary, low connectance and species-poor food webs exhibit extreme sensitivity (Dunne *et al.*, 2002), meaning that the loss of one species can result in increased risk of coextinction of multiple species (Borrvall *et al.*, 2000).

Species play different ecological, structural and functional roles in a food web, by the way they capture and exploit their resources and, hence, the trophic position they acquire in the food chain. In OWFs, organisms with different feeding traits co-exist (i.e. suspension feeders, grazers, scavengers, predators, etc.). The most common type of consumers found in OWFs are suspension feeders, e.g. the blue mussel *Mytilus edulis* and the anemone *Metridium senile*. These organisms depend on the suspended particles in the water column (Gili and Coma, 1998; Dubois and Colombo, 2014), while they exhibit different suspension feeding mechanisms to screen and collect particles (Riisgård and Larsen, 2000). Suspension feeders are capable of selecting particles based on their size and quality (Ward and Shumway, 2004).

Food webs on the intertidal part of the OWFs are based on the macroalgal production. The subtidal part of the OWFs relies on a mixture of suspended particles in the water column, such as phytoplankton, detritus and bacteria, which represent the basis of the food web (Raoux *et al.*, 2017), followed by the zooplankton, which is the primary consumer. Other types of consumers found at the offshore wind turbines include grazers, such as the limpet *Patella vulgata*, that feed by scraping material attached to benthic surfaces (Richoux and Ndhlovu, 2015). There are also deposit feeders (e.g. the polychaete *Lanice conchilega*), mainly at the soft substrates surrounding the turbines. These organisms can rework vast amounts of sediments (Iken *et al.*, 2001) and mainly feed on detritus and deposited material (Ward and

Shumway, 2004). Scavengers (e.g. the crab *Pilumnus hirtellus*) and omnivores (e.g. the common hermit crab *Pagurus bernhardus*) also occur in the area, feeding on dead material, and algae and animal tissues, respectively.

Highly mobile predators, such as fish, are recognized as the key elements of marine food webs because of their ability to link the nutrient fluxes and energy between spatially separated food chains (Quevedo *et al.*, 2009). The majority of predators can switch their diets depending on the resource availability in order to optimise their energy gain (Thums *et al.*, 2011). Therefore, predators, such as fish, exploit the enhanced food availability provided by the artificial structures and feed extensively on colonising organisms (Reubens *et al.*, 2011, 2014a).

1.3.3 Species co-existence and resource partitioning

The high macrofaunal species diversity within the colonising and natural (soft substrate) assemblages in OWFs has led to a substantial amount of studies on their species composition (for the colonising assemblages: Bouma and Lengkeek, 2008, 2012; Lindeboom *et al.*, 2011; Krone *et al.*, 2013; De Mesel *et al.*, 2015, for the natural soft-sediment communities: Coates *et al.*, 2014; Lefaible *et al.*, 2018). Species can co-exist in many ways, and in different spatial and temporal scales. The species co-existence theory often refers to species sympatric co-occurrence, meaning that multiple species co-occur in the same place and at the same time, and that this co-occurrence can continue for a long time (Turnbull *et al.*, 2013). Species co-existence and community structure are largely determined by the ability of species to exploit shared resources (Tilman, 1982). Limiting resources can affect species co-existence by introducing competition (Ross, 1986). Spatiotemporal heterogeneity in resources, in combination with limited dispersal abilities (i.e. sessile and/or hemi-sessile organisms) may affect the local population dynamics (Hernandez, 2008). This will cause a variation in the outcome of the interaction between species, which will either co-exist or lead to competitive exclusion of one species (Hernandez, 2008), although competitive exclusion occurs more frequently and rapidly between highly related (phylogenetically) species (Violle *et al.*, 2011).

In the marine environment, most considerations about competition and co-existence among different species focus on the single limiting resource of space (Ferguson *et al.*, 2013). In hard substrate benthic communities, space has long been considered as the primary limiting resource (Buss and Jackson, 1981; Ferguson *et al.*, 2013; Dubois and Colombo, 2014; Cresson *et al.*, 2016), while in soft substrate communities, competition for space plays a less significant role. Indeed, it has been shown that species compete fiercely for the available space and may overgrow and/or undercut each other to secure further space (Buss, 1979). Competition for space was also considered a major factor in an evolutionary marine life-history study (McKinney and Jackson, 1991). Stable co-existence is assumed to occur due to a trade-off between competitive ability for space and the ability to colonise new habitats (Keough, 1984; Edwards and Stachowicz, 2010).

However, food resource limitation is also considered an important factor determining species co-existence (Buss and Jackson, 1981; Dubois and Colombo, 2014; Cresson *et al.*, 2016). Trophic competition is only relevant when species with similar diet co-exist under limiting food conditions (López-Jamar *et al.*, 1984; Cresson *et al.*, 2016). It has been observed among many different taxa and feeding modes, such as adult and juvenile fish (Latli *et al.*, 2019) and suspension feeding organisms (Lefebvre *et al.*, 2009; Cresson *et al.*, 2016). The effects of trophic competition can be partly reduced when co-occurring organisms exhibit trophic plasticity and resource partitioning (Lefebvre *et al.*, 2009; Riera, 2009), and/or when the food resources are not limiting.

Trophic plasticity is a common adaptation of organisms to exploit multiple resources to minimize potential competition (MacNeil *et al.*, 1997; Lefebvre *et al.*, 2009). Some organisms exhibit trophic plasticity in their feeding strategies depending on life history stage and/or the type of the resources that are available (Pyke, 1984; Jumars and Wheatcroft, 1989). Trophic plasticity is considered an important characteristic for an organism's ability to survive in a wide range of habitats (Groenewald, 1964; Kadye and Booth, 2012), making it more adaptable to changes in resource availability (Plavan *et al.*, 2007).

Trophic plasticity can partly allow for resource partitioning between species (MacNeil *et al.*, 1997; Ashton *et al.*, 2010). Resource partitioning is the ability of organisms to divide (limited) resources as a mechanism to avoid trophic competition (Ross, 1986). The extent of the segregation can be driven by multiple factors, such as resource limitation and growth of predators (Witteveen and Wynne, 2016). Understanding the resource partitioning among species can provide insights into species interactions and the ability to predict responses to environmental and/or anthropogenic changes that are likely to affect marine food webs (Wu *et al.*, 2019). Resource partitioning has been observed for a variety of marine organisms, from co-occurring sessile suspension feeders (Dubois *et al.*, 2007) to highly mobile fish species (Latli *et al.*, 2019; Wu *et al.*, 2019). Thus, both trophic plasticity and partitioning are mechanisms that allow for avoiding trophic competition; however, this does not necessarily mean that a species exhibiting trophic plasticity will partition the available resources.

1.3.4 Studying the food web structure

1.3.4.1 Stomach content analysis

A fundamental requirement in understanding the energy flow through complex marine food webs from primary carbon fixation to upper trophic-level consumers is the knowledge of the trophic linkages among species (Hobson *et al.*, 2002). These trophic linkages can be assessed with simple methods such as stomach content analysis (SCA). SCA is the traditional and most common method for addressing this objective and acquiring information on diet composition. It is widely used to determine the diet composition of fish species but can be used for invertebrate species as well. It provides a snapshot of recently ingested (up to 10 h) food items (Hyslop, 1980). This method provides a taxonomic resolution of the ingested food that may be difficult to achieve with other methods (Lin *et al.*, 2007). However, SCA has also multiple limitations, since the diet of a species may vary substantially depending on the food availability, the size of the individuals and other factors (Stoner and Zimmerman, 1988; Pinnegar and Polunin, 2000). SCA requires high sampling frequencies to obtain a time-integrated overview of a species’ diet composition (St John, 1999; Parkyn *et al.*, 2001). Furthermore, SCA can underestimate the consumption of highly digestible material and thus, provide an indication of the food items that are still recognizable, but not actually assimilated (Parkyn *et al.*, 2001; Jensen *et al.*, 2012). This method depends on the relative digestibility of the food items (St John, 1999; Stapp, 2002), resulting in the over-representation of food items with hard parts (i.e. crustaceans) and the under-representation of highly assimilated and defaecated items, such as soft-bodied organisms (Fry, 1988; Hobson *et al.*, 1995). Finally, an inherent issue is that fish often have empty stomachs, leading to a paucity of dietary data from the sampled population (St John, 1999; Nolan and Britton, 2018).

1.3.4.2 Stable isotope analysis

Another way to study trophic linkages between resources and consumers is by using measurements of naturally occurring stable isotopes of elements, such as carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) (Michener and Schell, 1994). This approach is based on the principle that the stable isotope ratios in consumers' tissues can be related to their resources (DeNiro and Epstein, 1981). For nitrogen, ratios of ^{15}N to ^{14}N (expressed as $\delta^{15}N$) show stepwise enrichment (typically 3-4 ‰) with trophic transfers and can be used in estimating an organism's trophic position (Post, 2002). Ratios of carbon isotopes ($\delta^{13}C$) vary substantially among primary producers, but they slightly change with trophic transfers (ca. 1 ‰). Hence, $\delta^{13}C$ can be used to determine carbon sources (DeNiro and Epstein, 1981; Peterson and Fry, 1987). The combined use of carbon and nitrogen stable isotopes in marine organisms can be used to provide important information on their feeding ecology and trophic relationships (Hobson *et al.*, 1994; Michener and Schell, 1994).

The main advantages of stable isotope analysis (SIA) are that it can be applied to small sample sizes and the isotopic signatures can integrate information on resources that are truly assimilated in the tissues of field sampled organisms (Melville and Connolly, 2003; Davis *et al.*, 2012; Daly *et al.*, 2013) for a prolonged period of time (up to 6 months) (Hesslein *et al.*, 1993; Estrada *et al.*, 2003; Davis *et al.*, 2012). This method allows for the investigation of the isotopic niche of a species that provides information on the resource utilization and the trophic level of a species and is therefore, an approximation of its trophic niche (Newsome *et al.*, 2007; Jackson *et al.*, 2011). An isotopic niche can be a useful proxy for understanding the ecological niche, where $\delta^{13}C$ and $\delta^{15}N$ represent the environmental and trophic axes, respectively (Newsome *et al.*, 2007; Jackson *et al.*, 2011). It can be used for the direct comparison of individuals or populations, combining information on richness and evenness of resources (Bearhop *et al.*, 2004). It also allows for the temporal integration of dietary information over different timescales (Bearhop *et al.*, 2004). Therefore, the use of isotopic niches might lead to conclusions about the trophic roles of an organism in an ecosystem (McMeans *et al.*, 2015). Niche overlap can be considered as an illustration of trophic competition among species (Dubois and Colombo, 2014). The degree of overlap depends on the isotopic niche sizes and orientation (Swanson *et al.*, 2015). For example, the isotopic niche of species A can be completely overlapped by the isotopic niche of species B, while the probability of finding an individual of species B in species A's niche can be very small. Similarly, an overlap of 1 ‰ of an isotopic niche of size 1.2 ‰ is considered large, while for a niche size of 10 ‰ is considered relatively small.

Isotopic niches are extensively used as a proxy of trophic niches (Bearhop *et al.*, 2004; Layman *et al.*, 2007a; Jackson *et al.*, 2011). A trophic niche constitutes all the trophic interactions that connect a species to others in the ecosystem (Elton, 1927). This means that a trophic niche is a representation of a species' overall trophic role (Leibold, 1995). The investigation of trophic niches can provide information on the functional effects of nutrient loading on ecological systems (Warry *et al.*, 2016) and thus, provide assessments of ecosystem health that can be related to ecosystem threats and pressures (Palmer and Febria, 2012).

1.3.4.3 Pulse-chase experiments

Stable isotopes can also be used at the tracer level, where the isotopic composition of an (in)organic resource is deliberately being modified. By using labelling experiments, also known as pulse-chase experiments, we can quantify the rates and pathways of short-term organic matter in benthic macrofaunal communities (Middelburg *et al.*, 2000; Witte *et al.*, 2003a, 2003b). The combination of deliberately added tracers and isotopic analysis provides the possibility to directly measure the macrofaunal carbon assimilation (Boschker and Middelburg, 2002). A change in the isotopic composition of the elements modified by the tracers included in the experiments in comparison to the background composition is denoted in the Δδ notation: $\Delta\delta = \delta_{modified} - \delta_{background}$. Modifying the isotopic composition of an (in)organic resource will lead to transfer of this modification to the other components in the food web.

Labelling experiments can be conducted in two ways: a) by introducing inorganic nutrients or simple organic substrates into a food web (Middelburg *et al.*, 2000; Hamilton *et al.*, 2001; Tobias *et al.*, 2003) and b) by cultivating algae in an isotopically enriched medium, harvesting them and feeding them to the investigated assemblages (Moodley *et al.*, 2000; Nomaki *et al.*, 2005). In both cases, the organic matter processing by aquatic and benthic organisms is monitored through time and is used to quantify the assimilation of the added (in)organic substrate. These studies provide important insights in the structure of marine food webs. They have been successfully applied in a wide range of soft sediment areas, from organic carbon rich (Woulds *et al.*, 2007) to oligotrophic sediments (Bühring *et al.*, 2006a), from polar (Gontikaki *et al.*, 2011a, 2011b; Braeckman *et al.*, 2019) to the tropic regions (Aspetsberger *et al.*, 2007; Sweetman *et al.*, 2010) and from estuaries (Middelburg *et al.*, 2000; Moodley *et al.*, 2000) to abyssal areas (Witte *et al.*, 2003a; Woulds *et al.*, 2009, 2016). However, to our knowledge, labelling experiments have not been applied to hard substrate assemblages yet.

1.4 Thesis scope

This PhD thesis is part of the Belspo funded BRAIN-be project "Functional biodiversity in a changing sedimentary environment: implications for biogeochemistry and food webs in a managerial setting", also known as "FaCE-It". This project aims at understanding the effects of major human activities, such as the installation of OWFs, beam trawling, aggregate extraction, etc., on the marine environment. Specifically, FaCE-It investigates the effects of "fining" and "hardening" on coastal marine ecosystems by examining the marine food web structure, C-flows and biogeochemical cycling. The final aim is to understand how these activities affect the local (Belgian part of the North Sea) and the regional (southern North Sea) coastal ecosystems and how they might affect the implementation of the marine strategy framework directive (MSFD).

This PhD focuses on the food web structure and C-flows of the organisms associated with an offshore wind turbine in the Belgian part of the North Sea (BPNS). The aim was to understand the effects of these structures on various aspects of the trophic niche and feeding habits of these species. Food web structure, assemblages' and species' isotopic niches, and the diet composition of invertebrate and vertebrate species are examined. In parallel, the carbon assimilation by colonising organisms and thus, the amount of primary production that is being processed by them is being investigated by conducting pulse-chase experiments. The final aim is to provide knowledge on how OWFs can affect the local food web properties associated with these structures.

1.4.1 Study area

In 2008, the first six offshore wind turbines were installed in the BPNS initiating the Belgian OWF zone. In 2018, 318 offshore wind turbines, belonging to 6 OWFs were constructed and operational (Fig. 1.10), with a total capacity of 1556 MW (Degraer *et al.*, 2019). The number of the offshore wind turbines will continue to increase, and by the end of 2020, approximately 400 wind turbines will be installed in the BPNS (Rumes and Brabant, 2019). The current surface area of the existing OWFs is 238 km^2, while an additional area of 284 km2 is reserved for installation of OWFs in the near future (Rumes and Brabant, 2019).

The research in this PhD thesis has been conducted in the C-Power wind farm. This wind farm is located on the Thornton Bank, a natural sand bank in the BPNS. Thornton Bank is characterised by large dynamic dunes, which were levelled/dredged to facilitate the construction of the offshore wind turbines (Brabant and Jacques, 2010). The BPNS has a total surface of ~ 3500 km^2 and its depth ranges between 0 m and 46 m (Kerckhof and Houziaux, 2003). The offshore waters in the BPNS are influenced by the water masses from the Atlantic Ocean, being highly saline and having a low nutrient content, while the coastal waters receive nutrient-rich fresh water from the rivers (Kerckhof and Houziaux, 2003). The temperature of the seawater varies seasonally between 4 and 18 ^{0}C (Reubens, 2013).

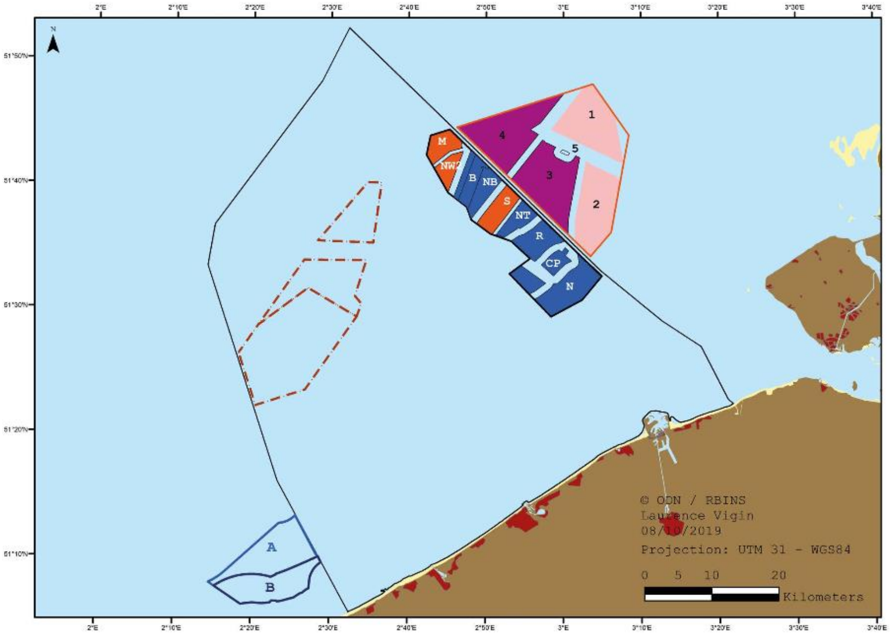


Figure 1.10: Installed and planned offshore wind farm zones in and around the Belgian part of the North Sea. The six operational (blue), three currently under construction (orange) and the locations for the new offshore wind farms that are proposed to be installed in the Habitats Directive area "Vlaamse Banken" (dashed lines). Purple and pink areas represent the Dutch offshore wind farms that have been set to start construction in 2019 and 2020, respectively, while the A and B sites are the proposed French offshore wind farms (map made by L. Vigin, 2019).

The C-Power wind farm is situated 27 km offshore, at the east side of the BPNS, close to the border with the Netherlands. This was the first OWF constructed in the BPNS in 2008 consisting of six gravity-based foundations (Brabant *et al.*, 2012). This wind farm now entails 48 more turbines, which were installed on jacket foundations (Brabant *et al.*, 2012). The water depth ranges between 18 m and 24 m and the total surface area of the wind farm is 19.84 km^{2}.

All the samples for the chapters 2, 3 and 5 of this thesis were collected from the gravity-based foundation D6 (coordinates: 51°33.04'N - 02°55.42'E – Fig. 1.11) within the C-Power wind farm. Gravity-based foundations have a diameter of 6 m at the sea surface, which increases to 14 m at the seabed (Reubens *et al.*, 2011). They are surrounded by a scour protection layer, which consists of a filter and an armour layer of quarried rock materials (Peire *et al.*, 2009). The diameter for the armour and filter layer is 58 m and 62.6 m, respectively (Peire *et al.*, 2009). The total hard substrate surface area of the turbine foundation with its scour protection layer represents ca. 2043 m^2 (Peire *et al.*, 2009). The natural soft sediments around the gravity-based foundations have a mean grain size that ranges between 312 µm (north-west gradient) and 427 µm (south-east gradient) at 15 m away from the turbines (Coates *et al.*, 2014).

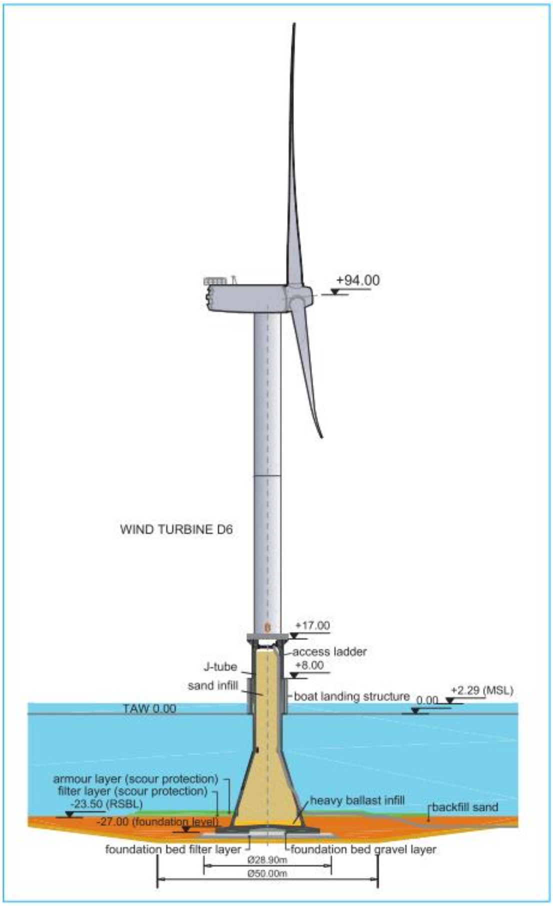


Figure 1.11: Design layout of the gravity-based foundation D6 in the C-Power offshore wind farm (source: Peire *et al.*, 2009).

The samples for chapter 4 were collected from a tripod that was placed within the C-Power wind farm area (coordinates: 51°54.08′N - 2°91.68′E), which was part of the artificial hard substrate garden (AHSG) provided by the European Marine Biological Resource Centre (EMBRC). The tripod was placed on the sea floor, approximately 500 m away from the turbines. PVC panels (15 × 15 cm) were attached to the tripod, which were roughened on one side to facilitate colonisation (Beermann and Franke, 2012). These panels remained in the sea for one year before their collection by scientific divers.

1.4.2 Assemblages and species of interest

In this thesis, we focused on colonising assemblages that are attached to the gravity-based foundation D6. We particularly paid attention to invertebrate species that occurred in multiple zones along the depth gradient of the turbine, such as *Diadumene cincta* (Stephenson, 1925), *Jassa herdmani* (Walker, 1983), *Metridium senile* (Linnaeus, 1761), *Mytilus edulis* (Linnaeus, 1758), *Necora puber* (Linnaeus, 1767), *Ophiothrix fragilis* (Abildgaard in O.F. Müller, 1789) and *Pisidia longicornis* (Linnaeus, 1767). Moreover, we studied the fish species *Gadus morhua* (Linnaeus, 1758), *Trisopterus luscus* (Linnaeus, 1758), *Myoxocephalus scorpioides* (Fabricius, 1780), *Scomber scombrus* (Linnaeus, 1758) and *Trachurus trachurus* (Linnaeus, 1758) that have been frequently observed in close proximity to these structures.

Colonising (or fouling) assemblages are defined as the biota that at any point in time develop on artificial reefs (Wahl, 1989; Svane and Petersen, 2001). Marine colonising assemblages may colonise man-made surfaces that are placed in marine and estuarine environments (Kingsbury, 1981) and may damage artificial structures, such as oil and gas platforms (Kingsbury, 1981; Picken, 1986) and offshore wind turbines by enhancing their corrosion (Kingsbury, 1981). However, they can also protect the artificial structures, by an increased frictional drag by waves (Kingsbury, 1981; Picken, 1986) and the prevention of inspections (Kingsbury, 1981; Picken, 1986). Colonising assemblages can increase the local species richness (Degraer *et al.*, 2013) and can be an important resource for larger predatory species, e.g. fish (De Troch *et al.*, 2013). They can further generate habitat for new epifaunal assemblages but also influence the benthic communities underneath them and the surrounding pelagic zone (Maar *et al.*, 2009). Colonising assemblages show seasonal (short-term) variations in species composition, which are known as seasonal fluctuations (Kerckhof *et al.*, 2010a). These fluctuations (or temporal dynamics) are the result of the competition between individuals for the available space, which is caused by the settlement of larvae on the foundations (Kerckhof *et al.*, 2010a).

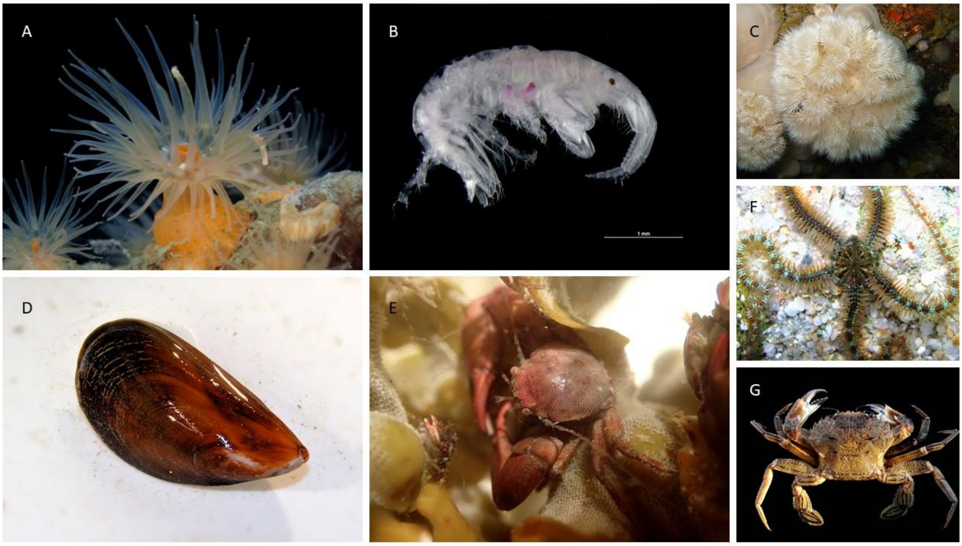


Figure 1.12: Invertebrate species studied in this thesis. A: *Diadumene cincta* (source: www.nederlandsesoorten.nl), B: *Jassa herdmani* (source: Hillewaert, H.), C: *Metridium senile* (source: Norro, A.), D: *Mytilus edulis* (source: Hillewaert, H.), E: *Pisidia longicornis* (source: Hillewaert, H.), F: *Ophiothrix fragilis* (source: WoRMS), and G: *Necora puber* (source: Wikipedia.org).

Diadumene cincta (Fig. 1.12A) is an anemone species that mainly occurs in inshore waters and especially in brackish areas (Braber and Borghouts, 1977). It is a suspension feeder, exploiting mainly zooplankton (Sebens, 1981; Östman *et al.*, 2010). It has a bright orange or light brown colour and resembles young specimens of certain colour-varieties of *Metridium senile* (Stephenson, 1925). It mainly lives on stone-covered dikes in muddy habitats, while it avoids sandy habitats (Braber and Borghouts, 1977). This organism prefers localities with a certain amount of water movement. It has a wide vertical range, from ca. 0.8 m below the mid-tide level to about 48 m depth (Braber and Borghouts, 1977). *Diadumene cincta* can be consumed by jellyfish (www. sealifebase.ca).

Jassa herdmani (Fig. 1.12B) is a hemi-sessile, suspension and scavenging feeding amphipod species (Conlan, 1994; Dixon and Moore, 1997). *Jassa* species are known to be the most abundant amphipods on artificial structures, dominating the colonising assemblages of ship wrecks, navigational buoys and offshore wind turbines, where they can reach remarkably high abundances (Nair and Anger, 1980; Conradi *et al.*, 1997; Zintzen *et al.*, 2008; De Mesel *et al.*, 2015). This amphipod creates its own microhabitat by building tubes made of "amphipod silk" and deliberately incorporating mucus and detritus (Franz and Mohamed, 1989; Clancy, 1997; Dixon and Moore, 1997). The amphipod silk mainly consists of organic material that derives from the water column (Beermann and Franke, 2012). The tubes have elastic walls and are attached to hard substrates (Dixon and Moore, 1997). *Jassa herdmani* individuals sit at the tube's opening, extending their prolonged antennae into the water column, from which they obtain their food (Beermann and Boos, 2015). The tubes are attached to any kind of hard substrate in multiple layers, forming thick fouling mats (Franz, 1989; Dixon and Moore, 1997). *Jassa herdmani* is a prey for fish species, such as cod and pouting (Reubens *et al.*, 2011, 2013).

Metridium senile (Fig. 1.12C) is a sessile suspension feeding anemone that uses its tentacles to capture zooplankton (Sebens, 1981; Östman *et al.*, 2010). It is a ubiquitous member of the colonising assemblages (Hoffmann, 1976; Fautin *et al.*, 1989), occurring in different size distributions at different environmental conditions (Anthony and Svane, 1994; Anthony, 1997). *Metridium senile* can be attached to any suitable hard substrate, such as gravel and shell debris (Riis and Dolmer, 2003). This species can slowly move across a substrate, leaving a piece of the pedal disc behind, which is part of its asexual reproduction (Riis and Dolmer, 2003). The piece of the pedal disc is usually fragment and each piece generates into a new individual (Bucklin, 1987). Organisms preying on *M. senile* include jellyfish and anemones of the family Goniasteridae (www.sealifebase.ca).

Blue mussels (*Mytilus edulis* – Fig. 1.12D) are the most abundant bivalves in the North Sea and the Western Baltic Sea (Darr *et al.*, 2014). They are an important food source for starfish, birds and fish, but also for human, and thus, they are of great economic importance (Lemmen, 2018). They are suspension feeding organisms and occur in large numbers near the water surface of hard substrates (Freire and Gonzalez-Gurriaran, 1995; Riis and Dolmer, 2003). Blue mussels can significantly reduce the concentration of phytoplankton and of micro- and meso-zooplankton (Maar *et al.*, 2009) by filtering vast volumes of water (Cloern, 1982; Kreeger and Newell, 1996). At the same time, they actively deposit large amounts of organic and inorganic materials, such as faecal pellets, pseudofaeces and empty shells, to the benthos (Freire and Gonzalez-Gurriaran, 1995; Krone *et al.*, 2013a). Mussels are predated by a variety of fish species, lobsters, echinoderms, etc. (www.sealifebase.ca).

The anomuran decapod *Pisidia longicornis* (Fig. 1.12E) is typically found on rocky substrates and other solid structures that provide suitable habitat for this short-lived, suspension feeder (Robinson and Tully, 2000). It has been shown that it largely feeds on pseudofaeces of mussels (Tenore and González, 1975), while it is the main resource of many dominant crustaceans and fish (Freire and Gonzalez-Gurriaran, 1995; Sampedro *et al.*, 1997).

The brittle star *Ophiothrix fragilis* (Fig. 1.12F) is widely distributed in the eastern Atlantic (Moyse and Tyler, 1990) and it forms dense aggregations mainly on coarse sediments and on muddy gravel bottoms (Warner, 1971). Specimens of this species are frequently found on artificial hard substrates, such as oil and gas platforms (van der Stap et al., 2016) and offshore wind turbines (Lindeboom *et al.*, 2011; Mavraki *et al.*, 2020). It is a passive deposit and suspension feeder, largely feeding on detritus (Warner and Woodley, 1975) and fine particulate suspended matter (Warner, 1971). Brittle stars are predated by fish (www.sealifebase.ca).

The velvet swimming crab *Necora puber* (Fig. 1.12G) is typically found on hard substrates of the Northeast Atlantic. It is a commercially important species and it is abundant from the extreme lower intertidal to depths of ca. 20 m, although some specimens have been found at greater depth (Ingle, 1980; Clark, 1986). In colonising assemblages, it may be a dominant predator, regulating the abundance and distribution of the prey assemblages (Aronson, 1989; Freire and Gonzalez-Gurriaran, 1995). The diet composition of this species varies both spatially and seasonally, as well as over its life cycle (Choy, 1986; Norman and Jones, 1993). In summer and spring, the diet of *N. puber* mainly contains bivalves, while in winter, it mainly feeds on gastropods (Freire and Gonzalez-Gurriaran, 1995). The same authors observed an increase in the consumption of fish (by scavenging), molluscs and Brachyura with size, while there were no significant diet differences between male and female individuals.

The benthopelagic fish pouting (*Trisopterus luscus*) and cod (*Gadus morhua*) aggregate around offshore wind turbines in the BPNS (Reubens *et al.*, 2011, 2013a). Pouting (Fig. 1.13A) occurs in the North Sea, the Mediterranean Sea, at the British Isles and along the Northwest African coast (Cohen *et al.*, 1990). It is omnivorous, mainly feeding on benthic crustacean (Hamerlynck and Hostens, 1993).

Cod (Fig. 1.13B) is one of the most important fish species on the planet (Link and Garrison, 2002) regarding its historical and cultural importance (Jensen, 1972). It is a highly valued commercial species that has been heavily exploited, leading to a significant decrease of its stocks (e.g. Murawski *et al.*, 1997; Link and Garrison, 2002; ICES, 2010). The North Sea spawning stock of cod is also continuously declining, while the recruitment remains poor since 1998 (ICES, 2019). ICES (2019) recommends that the 2020 North Sea cod catch should not exceed 10457 metric tons, which is 70 % less than the total allowable catch for 2019. Research has indicated that the fishing mortality rates are equivalent to those evoked by climate drivers (Frank *et al.*, 2016). Ocean warming causes mismatches of the time of occurrence between cod larvae and their prey items, leading to larval starvation (Klein *et al.*, 2017). Cod occurs in the entire North Atlantic Ocean and it is distributed in a variety of different habitats (Cohen *et al.*, 1990). It is an omnivorous and opportunistic feeder, with its juveniles mainly feeding on crustaceans, while older specimens feed on other fish (Link and Garrison, 2002).

The sculpin *Myoxocephalus scorpioides* (Fig. 1.13C) is a common benthic species that has a wide distribution, from temperate waters up in to the high Arctic (Robins and Ray, 1986). This species is a generalist opportunistic feeder (Link and Almeida, 2002), consuming macroinvertebrates and other fish specimens (Cui *et al.*, 2012).

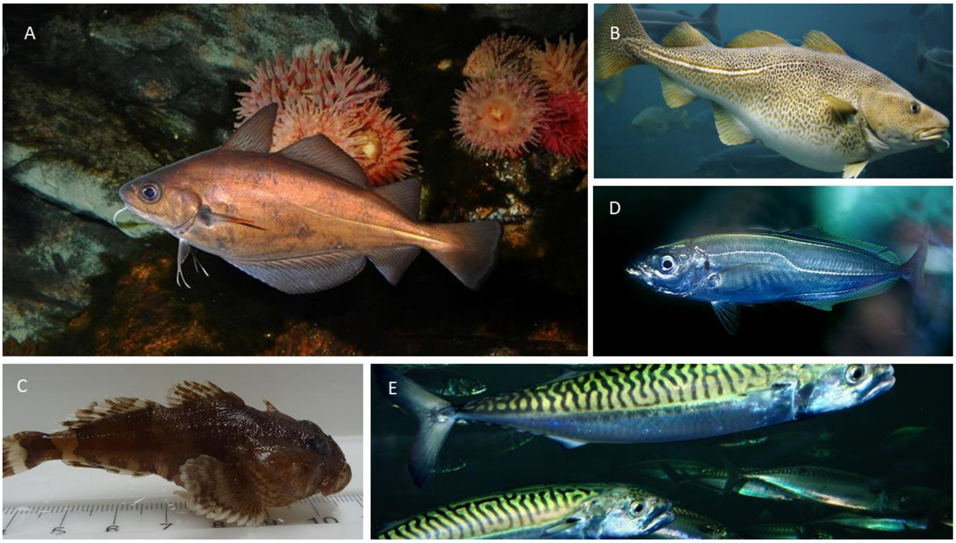


Figure 1.13: Fish species under study. A: *Trisopterus luscus* (pouting – source: Biopix: Sloth, N.), B: *Gadus morhua* (cod - source: Dieter Craasmann), C: *Myoxocephalus scorpioides* (sculpin – source: Wikipedia), D: *Trachurus trachurus* (horse mackerel – source: www.fishbase.org, photo by JJPhoto), E: *Scomber scombrus* (mackerel – source: Biopix: Schou, J. C.).

The pelagic fish horse mackerel (*Trachurus trachurus*) and mackerel (*Scomber scombrus*) have been found in close proximity to artificial hard substrates in the BPNS (Reubens *et al.*, 2011). Horse mackerels (Fig. 1.13D) are found from the tropical to the temperate east Atlantic and Mediterranean Sea (Smith-Vaniz, 1986), where it is also targeted by fisheries for human consumption (Rumolo *et al.*, 2017). They feed on zooplankton (Hecht, 1990), but also on non-plaktonic crustaceans and small fish (Bayhan and Sever, 2009). Mackerels (Fig. 1.13E), on the other hand, are widely distributed along the North Atlantic Ocean (Jansen *et al.*, 2016) and are major consumers of zooplankton and at a smaller extent of small fish (Bachiller *et al.*, 2018). They are opportunistic feeders, ingesting their prey either by biting or by filter feeding (Macy *et al.*, 1998), while their diet varies annually, seasonally, diurnally and spatially (Óskarsson *et al.*, 2015).

1.5 Thesis outline and main objectives

Currently, thousands of offshore wind turbines have been installed in the North Sea, and even more are planned, licensed and/or under construction (Soma *et al.*, 2019). These foundations are established in soft bottom areas that are already affected by human activities, such as dredging, fisheries, etc. However, the installation of offshore wind foundations induces further changes to the marine environment and influences the local biodiversity and ecosystem functioning (Andersson *et al.*, 2009).

The aim of this thesis was to investigate the impact of OWFs on the local food web properties by examining different aspects of the trophic niche of colonising assemblages, invertebrate and vertebrate species. Resource partitioning, diet composition, carbon assimilation and the attraction-production debate were also investigated. The different aspects and chapters of this thesis are presented in Figure 1.14. Apart from the general introduction (Chapter 1) and the general discussion (Chapter 6), specific research questions and the detailed scientific results of this thesis are divided in four chapters, which are stand-alone research articles that are published, under review or in preparation. This thesis is structured around one main theme: the impact of OWFs in the local food web properties. This is examined both at a detailed level and at a larger scale, with each scale subdivided into two chapters.

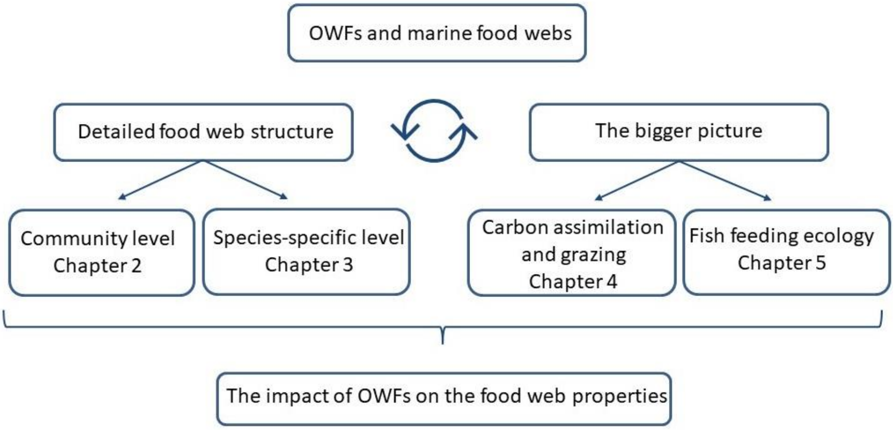


Figure 1.14: Schematic overview of the different chapters of this thesis.

Chapter 2 – Food web structure along the depth gradient of an offshore wind turbine

In this study, insights of the food web structure of colonising assemblages from different zones along the depth gradient of an offshore wind foundation are provided. Stable isotope data are used to create isotopic niches and identify whether resource partitioning is the mechanism allowing the co-existence of the dense colonising assemblages. Food web complexity is linked with areas where organic matter accumulation occurs, such as the scour protection layer and the soft substrate surrounding these foundations. This indicates that there is higher food quality and quantity in these zones, and thus, they can accommodate organisms with a wide range of trophic levels. Furthermore, resource partitioning was observed within and between the colonising assemblages of the deeper zones. This led to the next research question, which is to identify whether the colonising organisms exhibit trophic plasticity, which may allow for the resource partitioning found in this chapter.

Chapter 3 – Isotopic niches of co-existing invertebrate species

In Chapter 3, the feeding habits of invertebrate species that occur in more than one zones along the depth gradient were examined to investigate whether trophic plasticity is the key mechanism allowing for their wide vertical distribution and survival in a competitive environment. Isotopic niches and diet composition of the same species found in different zones are examined. Stable isotope analysis allowed for the investigation of the isotopic niches. The results of this study indicated that most of the species found at an offshore wind turbine are trophic generalists, exploiting different resources in different zones. Thus, even though the water column in the area is well mixed, dietary differences can arise, allowing for the co-existence of many individuals in a limited space.

Chapter 4 – Carbon assimilation by colonising assemblages

Once the resource partitioning and trophic plasticity of the species associated with the offshore wind farms are confirmed, it is crucial to investigate which of these organisms are processing the highest amount of the organic matter in the area. Thus, the carbon assimilation by different colonising organisms was estimated to calculate the amount of the primary producer standing stock that is grazed upon by these organisms. This allowed for the identification of the key species that play the most important role in the reduction of the organic carbon in the area. Labelling experiments were conducted, where colonising assemblages were incubated in experimental tanks containing labelled fragmented algae. This ex-situ study provided valuable information on the way the organic matter is processed by colonising organisms. The results of this experiment were upscaled to the total number of offshore wind turbines in the BPNS in order to estimate the percentage of the reduction of primary producer standing stock caused by the increased abundances of colonising organisms. Finally, the ratio turbine/sediment was estimated to calculate the additional amount of carbon that is assimilated by the colonising fauna due to the establishment of one foundation.

Chapter 5 – Diet composition of fish species around an offshore wind turbine

The high densities of colonising organisms on the OWFs attract mobile predators, such as fish. In this chapter, the short- and the long-term diet composition of fish species associated with offshore wind turbines are investigated. The short-term diet composition was examined by conducting stomach content analysis, while the time-integrated dietary analysis was shown with the use of stable isotopes. These two techniques were compared in order to acquire information on whether the fish species remain in the area to feed for a prolonged period of time or whether they opportunistically take advantage of the enhanced resource availability while passing by the OWF areas.

Finally, in Chapter 6 (General Discussion), the results of the different chapters are discussed, aiming to unravel the complex aspects of the food web structure of the offshore wind foundations and the trophic ecology of the species found there. The results of this thesis are examined under the prism of the construction of many more turbines in the future of the North Sea. Recommendations for future research directions on the food web structure of species at offshore wind turbines and/or other artificial reefs are also provided.

This study provides crucial knowledge on the impact of offshore wind farms on the local food web properties, focusing on the trophic ecology of the assemblages and species associated with these foundations. The diet composition of vertebrate and invertebrate species was investigated, while the carbon assimilation by invertebrate colonising fauna was estimated. Upscaling the results of this thesis to the multiple turbines that have already been and will be constructed in the North Sea might allow for the understanding of the effects of these structures on the ecosystem and the trophic ecology of the marine fauna.

Chapter 2

Functional differences in trophic structure of offshore wind farm communities: a stable isotope study

This chapter is a modified version of the paper published as: Mavraki, N., Degraer, S., Moens, T., Vanaverbeke, J. (2020). Functional differences in trophic structure of offshore wind farm communities: A stable isotope study. Marine Environmental Research, 157; 104868.

Author contributions: NM conducted the sampling, sample preparation, data analysis and wrote the manuscript. JV guided the data analysis and the writing. TM and SD provided valuable suggestions for improving the content of the manuscript.

Abstract

The proliferation of offshore wind energy installations causes a local change in biodiversity because these structures become heavily colonised by large quantities of colonising fauna, attract large mobile crustaceans and fish, and alter the macrofaunal communities in the soft sediments surrounding the wind turbines. Here, we analysed the stable isotope signals ($\delta^{13}C$ and $\delta^{15}N$) of the faunal communities associated with a wind turbine, its scour protection layer (SPL) and the surrounding soft sediments. We hypothesised that structural differences in community composition would be reflected in food web complexity and that resource partitioning could be one of the mechanisms contributing to the co-existence of such dense communities. Sampling was conducted at a gravity-based foundation in the Belgian part of the North Sea, where both sessile and mobile organisms were collected along the depth gradient of the turbine, the SPL and the surrounding soft substrate. The results indicated that the structural differences of the communities are reflected in the food web complexity as indicated by the trophic niche size, the trophic diversity and the redundancy of the communities along the depth gradient. Higher food web complexity was associated with zones where high accumulation of organic matter occurs (soft substrate and SPL). Low food web complexity was

observed in depth zones that are dominated by sessile suspension-feeding organisms (intertidal and *Mytilus* zone). The high trophic diversity and low redundancy observed within the trophic clusters of the soft substrate and the *Metridium* zone indicated that resource partitioning can be a mechanism allowing the co-existence of large densities of a wide variety of species.

2.1 Introduction

As a contribution to the mitigation of climate change, there has been an increasing installation of offshore wind farms (OWFs) to generate renewable energy. By 2018, 15.8 GW capacity, corresponding to 4149 offshore wind turbines, had been installed in European marine waters (Kirchgeorg *et al.*, 2018), and this capacity is expected to increase to 70 GW by 2030, with most of it (48 GW) being produced by the offshore wind farms in the North Sea (WindEurope, 2018). This will result in a further addition of hard substrate into otherwise soft-bottom areas (Lindeboom *et al.*, 2011).

The increase of man-made structures at sea also leads to an alteration of the composition of the biological communities at and around offshore wind farm installations with a particular increase in the biomass and density of filter feeders (Lindeboom *et al.*, 2011) and other colonising species (Slavik *et al.*, 2019). Colonising organisms form dense communities and develop a clear inter- and subtidal vertical zonation along the depth gradient of the OWF foundations (Krone *et al.*, 2013a; De Mesel *et al.*, 2015). In southern North Sea waters, both the intertidal and the subtidal parts of the turbines are densely colonised by 26 and 80 different species, respectively (De Mesel *et al.*, 2015). The intertidal zone is colonised by typical intertidal species, such as the barnacle *Semibalanus balanoides* (De Mesel *et al.*, 2015). The upper subtidal meters of the turbines become densely populated by the blue mussel *Mytilus edulis*, a phenomenon called "*Mytilus*ation" because of its predominance on constructions at sea (Krone *et al.*, 2013a). Below the mussel zone, there is a zone dominated by the amphipod *Jassa herdmani*, while the anemone *Metridium senile* is abundantly present at the lower parts of the piles (Lindeboom *et al.*, 2011; Krone *et al.*, 2013a; De Mesel *et al.*, 2015). Finally, the scour protection layer (SPL) surrounding the turbine accommodates a variety of species (Langhamer, 2012), including cod *Gadus morhua* and pouting *Trisopterus luscus* (Reubens *et al.*, 2011). The macrofaunal communities in the (usually) soft sediments surrounding the scour protection layer exhibit an increased abundance and species richness in response to the deposition of faecal pellets and detritus by the colonising fauna (Coates *et al.*, 2014). The presence of offshore wind farms can also affect ecosystem functioning, with the increased abundance of *Mytilus edulis* altering the pelagic primary productivity, by reducing the concentration of phytoplankton (Maar *et al.*, 2007;

Slavik *et al.*, 2019). This reduction affects both the benthic and the colonising communities, with the latter influencing both the basis of the marine food web and the local biogeochemical cycling (Slavik *et al.*, 2019). Moreover, the water column close to the offshore wind turbines is affected by the resuspension of sediment organic matter, which causes suspended particulate organic matter plumes (Baeye and Fettweis, 2015).

As colonising communities on wind turbines are characterised by the co-existence of large densities of a variety of species, competition for food may play an important role in structuring these communities (Richoux and Ndhlovu, 2015). However, resource partitioning may allow for the co-existence of multiple species (Pianka, 1974). Resource partitioning is the division of limited resources amongst different species to avoid trophic competition (Ross, 1986). Resource differentiation among assemblages associated with the offshore wind turbines can be assessed by studying their trophic niche through stable isotope analysis (SIA) (Peterson and Fry, 1987; Newsome *et al.*, 2007). A trophic niche represents all the trophic interactions that link a species to others in the ecosystem (Elton, 1927). In other words, it is a representation of its overall trophic role (Leibold, 1995). By studying the trophic niches of the different colonising communities, we can acquire information about the food source preferences and trophic levels of the organisms composing these communities and investigate their trophic diversity. In order to examine the trophic niche, we need to estimate the isotopic niche, which provides information on the resource utilization and trophic level of a species and is therefore an approximation of its trophic niche (Newsome *et al.*, 2007; Jackson *et al.*, 2011). Isotopic data are presented as bi-plots, where the isotopic values (δ-values) of animal tissues are represented in δ-space, delineating the isotopic niche of a species (Newsome *et al.*, 2007).

The structural differences in communities associated with offshore wind farms may well have extended effects on ecological relationships and food webs (Langhamer, 2012). In this study, we sampled the colonising assemblages of all depth zones of a wind turbine in the Belgian part of the North Sea (BPNS), as well as the scour protection layer and the soft sediments surrounding the turbine to test the following two hypotheses: (1) differences in the structural community composition along the depth gradient of a wind turbine are reflected in the trophic characteristics of these communities, and (2) food resource partitioning is an important mechanism promoting the co-existence of colonising species within depth zones. To our knowledge, this is the first investigation of the trophic structure of the assemblages associated with offshore wind farms with the use of stable isotope analysis.

2.2 Methodology

2.2.1 Sampling

Sampling was conducted at a gravity-based wind turbine (D6, coordinates: 51◦ 33.04′N - 02◦ 55.42′E) in the C-Power offshore wind farm on the Thornton Bank, in the Belgian part of the North Sea (BPNS) in August 2016 and August 2017. This was the first wind farm constructed in the BPNS, where the first 6 gravity-based foundation turbines were installed in spring 2008 (Degraer *et al.*, 2010). The tidal range at the area is 4 - 5 m during spring tide (Van den Eynde *et al.*, 2010). The location and turbine were selected based on the data availability on the communities of colonising fauna, the scour protection layer and in the surrounding sediments (Reubens *et al.*, 2011; Coates *et al.*, 2014; De Mesel *et al.*, 2015). The age of the wind farm was an additional argument, since we aimed to investigate a community in an advanced successional stage. We focused on one gravity-based wind turbine and one season because of the logistic effort associated with sampling within offshore wind farms in highly dynamical conditions. However, it has been shown that similar colonisation patterns are observed on all the gravity-based turbines in the area (De Mesel *et al.*, 2013), and hence, we believe that our samples represent the typical colonising communities attached to such turbine foundations.

Organisms living along the depth gradient on the wind turbine, on the scour protection layer and inhabiting the surrounding sediments (Fig. 2.1), as well as benthopelagic, benthic and pelagic fish near the turbine were collected. Along the subtidal parts of the turbine, colonising organisms were collected for community composition and stable isotope analyses at different depths corresponding to the dominant colonising taxa by scraping (25 x 25 cm quadrat/frame) by scientific divers: (a) *Mytilus* zone (5 m depth; 2 scrape replicates), (b) *Jassa* zone (~ 8.5 m depth; 3

scrape replicates), (c) *Metridium* zone (15 and 25 m depth; 2 x 3 scrape replicates). Three rocks (~ 15 cm length, 10 cm width and 5 cm height – completely scraped) were collected from the scour protection layer and two sediment samples from the surrounding soft sediments were taken using an airlift suction device to collect the upper 5 cm of sediment from within a 25 x 25 cm frame. The different numbers of replicates between the zones are a result of the practical limitations linked to the restricted diving time available. Finally, non-quantitative scrape samples (i.e. the sampling surface differed between the samples because of practical constraints linked to sampling from an inflatable boat) of the intertidal community were collected at low and at high tide from a detached rigid-hulled inflatable boat. The intertidal samples were used only for the stable isotope analysis. Benthopelagic and pelagic fish were caught by line-fishing (hooks: Arca, size: 2 and 4, bait: *Arenicola marina*), while spear-fishing was conducted at the SPL for the collection of the benthic fish species. Line-fishing was conducted at two different depths - above the SPL and at midwater (~ 10 m) - to collect the benthopelagic and pelagic species, respectively. Large crustaceans, such as lobsters and crabs, were hand-picked by scientific divers along the depth gradient. Organisms were identified to the lowest taxonomic level possible. Whenever possible, five individuals per species from each zone were subsampled from the replicate scrape samples and stored for stable isotope analysis, while the rest was preserved for the community composition analysis (see below). Macrofaunal organisms for stable isotope analysis were starved in filtered seawater overnight to allow gut evacuation (Nilsen *et al.*, 2008). Large organisms, such as fish and lobsters, were killed on site and specific muscle tissues (see section 2.2.2) were sampled for stable isotope analysis. Large crustaceans were freeze-killed (Zhang *et al.*, 2018), while fish were sacrificed by pithing with a metal rod (Kadye and Booth, 2012).

All samples for stable isotope analysis (whole organisms or muscles) were stored at -20^{0}C until further processing. The remaining organisms for the community composition analysis were stored in different buckets per zone and replicate in a formaldehyde-seawater solution (8%). In the lab, the species for the community composition analysis were sieved through a 1 mm sieve in order to separate the macrofaunal organisms from the meio- and microfauna. The macrofaunal organisms were subsequently identified under a stereomicroscope to the lowest taxonomic level possible and counted (see 2.2.3).

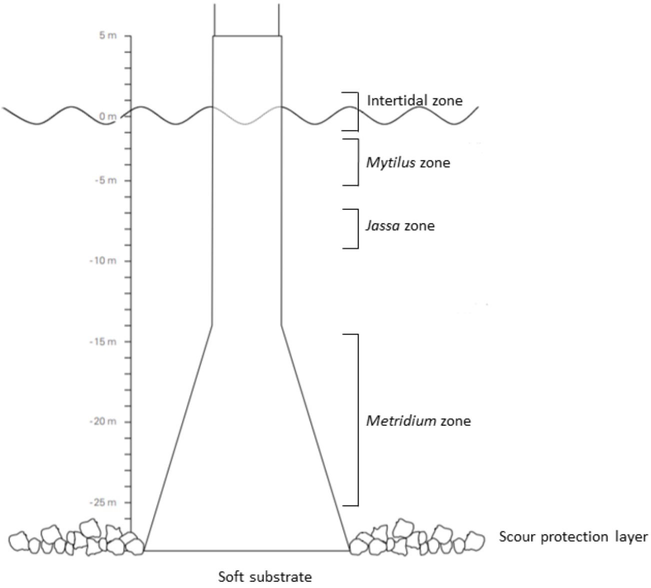


Figure 2.1: The different community depth zones formed along a gravity-based wind turbine.

2.2.2 Stable isotope analysis

Entire individuals of small invertebrates, such as amphipods, polychaetes, crabs (De Smet *et al.*, 2015) and sponges (Renaud *et al.*, 2015) were processed for stable isotope analysis (SIA) after an overnight gut evacuation in vials containing filtered sea-water. For large invertebrates and for vertebrates, parts of their muscles were extracted: cheliped muscle from large decapods (Reid *et al.*, 2016), peristomial membrane from sea stars and brittle stars (Andrade *et al.*, 2016), foot from bivalves (Richoux and Ndhlovu, 2015) and dorsal muscle from fish (Hertz *et al.*, 2017). Individuals of similar size per species were selected, hence size-specific shifts in diet were not considered here (Cresson *et al.*, 2016). We tried to analyse at least three replicates per species, but this was not always possible for all the taxa in each zone. Individuals and muscle samples were rinsed with milli-Q water to remove salts (Nilsen *et al.*, 2008) and dried overnight at 60°C. Subsequently, samples were pulverized using a pestle and mortar, homogenized, and depending on the sample type, 1 mg of dried sample was either acidified or not. Organisms lacking calcareous structures do not require acidification; hence ca 1 mg of the dried sample was immediately encapsulated into Sn capsules (8 x 5 mm, Elemental Microanalysis UK), weighed and stored dry until further analysis. The organisms with calcareous structures, such as amphipods, crabs and isopods, were pulverised and then their dried tissues were subsampled; one subsample (for $\delta^{13}C$ analysis) was transferred to Ag capsules (8 x 5 mm, Elemental Microanalysis UK) and the other (for $\delta^{15}N$ analysis) to Sn capsules. The first subsample was further processed by adding 1% HCl "drop-by-drop" until CO_2 was eliminated (Jacob *et al.*, 2005), since acidification removes the carbonates from organisms with such calcareous structures (Vafeiadou *et al.*, 2013). The second subsample was not acidified, since acidification may affect the organic matter $\delta^{15}N$ (Goering *et al.*, 1990; Bunn *et al.*, 1995). The acidified sample was subsequently rinsed with distilled water, dried again, closed and stored in multiwell Microtitre plates in a desiccator until further analysis. When the weight of the organisms was not sufficient to prepare two subsamples, more individuals of the same species and depth zone were pooled to provide enough dry tissue.

The samples were analysed at the UC Davis Stable Isotope Facility (University of California, USA) using a PDZ Europa ANCA-GSL elemental analyser, interfaced to a continuous flow isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The results are expressed in the standard delta (δ) notation in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{Sample} / R_{Standard}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

2.2.3 Data analysis

Differences in community composition between the different subtidal depth zones were visualised using non-metric multi-dimensional scaling (MDS) and analysed using one-way analysis of similarity (ANOSIM). Species abundance data were square-root transformed before calculating a Bray-Curtis similarity matrix. Colonial organisms, such as sponges, were not included in the analysis, since they could not be individually counted (Boaventura *et al.*, 1999; Carvalho *et al.*, 2013). Data collected in the intertidal zone were not incorporated in this analysis since the sampling strategy was different (see 2.2.1). Following a significant ANOSIM result, pair-wise tests were conducted to test the differences in species composition between every subtidal zone. ANOSIM and MDS were performed using the PRIMER-E package (Clarke and Gorley, 2006).

In order to investigate whether differences in community composition were reflected in differences in food web structure along the depth gradient of a wind turbine, at the scour protection layer and in the surrounding sediment, we used a combination of a classical and a more integrative approach. The classical approach involved the clustering of species into isotopic groups, while the integrative approach estimated community-wide metrics by using Bayesian statistics. Following De Smet *et al.* (2015), Cresson *et al.* (2016) and Bell *et al.* (2016), we allocated the species to clusters according to their isotopic signatures. This allows for the allocation of the organisms according to their feeding preferences, as revealed by their isotopic signatures, and not according to their feeding types based on literature (as indicated by feeding traits). We used the similarity profile (SIMPROF) permutation tests based on Euclidean distance (Whitaker and Christman, 2015) to cluster species in groups with similar isotopic signatures (De Smet *et al.*, 2015; Cresson *et al.*, 2016). This resulted in the delineation of 'trophic clusters', irrespective of species identity, zone and feeding trait. These trophic clusters were subsequently used to investigate the isotopic niches of the different communities found in different zones (see below). In addition, all species were allocated to feeding types based on De Smet *et al.* (2015) and the World Register of Marine Species (WoRMS; http://www.marinespecies.org/) in order to investigate whether species with the same feeding traits indeed belong to the same isotopic cluster. The invertebrate species were categorized as either predators, suspension feeders, deposit feeders, suspension/deposit feeders, grazers, omnivores, omnivores/predators/scavengers or suspension feeders/scavengers. Fish formed one separate category, since all fish species in our study were predators and a separation between invertebrate and vertebrate predators was necessary to reflect ecological differences between fish and invertebrate species.

For the comparison of the isotopic niches of the assemblages sampled in the six zones, we estimated the standard ellipse areas (SEAs, ‰^{2}) using the trophic clusters produced by SIMPROF as input. By doing so, we used the prevailing functional entities (trophic clusters) in order to estimate the isotopic niche of the assemblages sampled from every sampling zone, rather than starting our analysis from structural characteristics (species identity) or from a literature-derived (trophic groups) basis. In addition, this allowed us to make maximum use of the available data, since we were able to make use of data collected from species that were not sampled in sufficient numbers (at least three individuals) by allocating them to trophic clusters in order to generate the ellipses. However, some trophic clusters (i.e. cluster A from the *Jassa* zone and the soft substrate, cluster K from the intertidal, etc.) were not included in the Bayesian analysis as they consisted of less than three individuals in the respective depth zones.

The benthic and benthopelagic fish species were allocated to the scour protection layer, since the species in our study are highly associated with rocky bottoms (Nickell and Sayer, 1998; Smith, 2014; Barrett *et al.*, 2018) and they were collected from inside and just above the scour protection layer. Specifically, the benthopelagic *Gadus morhua* and *Trisopterus luscus* have higher densities (up to 37 times) above the scour protection layer in comparison to the surrounding soft sediment (Couperus *et al.*, 2010). The pelagic species *Trachurus trachurus* was allocated to the *Jassa* zone, since stomach content analysis has shown that this species mainly feeds on the amphipod *Jassa herdmani* (Mavraki *et al.*, in prep.). However, we do acknowledge that it is a highly mobile species and it could have been feeding on other subtidal zones as well.

SEA provides an estimate of the trophic niche space occupied by the members of a community (Layman *et al.*, 2007a; Jackson *et al.*, 2011). As SEAs can be sensitive to small sample sizes (Brind'Amour and Dubois, 2013), both SEA$_C$ (the corresponding metric corrected for small sample size) and the Bayesian estimation of ellipse size SEA_B were calculated. SEA_C was used to estimate the trophic niche overlap among the communities sampled from different zones. SEA_B illustrates the total amount of niche space that can be occupied by a community (Demopoulos *et al.*, 2017) and can be used for the probabilistic comparison of the isotopic niches between the different communities (Jackson *et al.*, 2011). Trophic structure – in terms of trophic diversity and trophic redundancy – of the communities from the different zones was investigated by calculating six quantitative community-wide Layman metrics using mean carbon and nitrogen isotope ratios of the consumers (Layman *et al.*, 2007a). Trophic diversity is reflected by (1) $\delta^{15}N$ range (NR), which represents the vertical food web structure and indicates the length of the trophic chain and hence the diversity of trophic levels, (2) $\delta^{13}C$ range (CR), which represents the niche diversification with respect to the food sources; higher CR reflects the utilization of a broader spectrum of food sources; (3) total area (TA), which is the convex hull area and reflects the total niche space occupied by the members of a community; and (4) mean distance to centroid (CD), which is the mean Euclidean distance of the isotopic signature of each specimen from the $\delta^{15}N$-$\delta^{13}C$ centroid and is a proxy of the trophic diversity of the investigated food web. Trophic redundancy, then, is characterised by (5) the mean nearest neighbour distance (MNND), which is the mean Euclidean distance in the bivariate isotopic space of each specimen to its nearest neighbour, and as such reflects the average trophic (dis)similarity of specimens; and (6) the standard deviation of nearest neighbour distance (SDNND), which is calculated as the standard deviation of these Euclidean distances and is a measure of the evenness of the spatial density and packing of the specimens in the isotopic space. Low MNND values (increased trophic redundancy) are an indication of food webs with a large proportion of species characterised by similar trophic ecologies, while low SDNND values suggest more even distribution of the isotopic niches (Layman *et al.*, 2007a). The probabilities that any of these metrics in one depth zone is higher than the same metric in other zones were also calculated.

In a next step, we wanted to investigate whether the organisms belonging to the same trophic cluster and zone partition resources. Here again, we generated standard ellipse areas corrected for small sample sizes (SEA_C) for every trophic cluster of each zone. Since these ellipses are made up of isotopically separated trophic clusters, we expected no or very small overlap between them within a zone. In order to investigate the resource partitioning within the trophic clusters of every zone, we calculated the Layman indices CD, MNND and SDNND (see above). Relatively high values of these indices indicate resource partitioning, while relatively low values are an indication of competition for the available food sources. All trophic clusters were included in the analysis for the standard ellipse areas in order to investigate their position in the isotopic spaces of the different zones. For the Layman indices, only the trophic clusters that had more than 5 replicates per zone were included in the model, since trophic clusters with less than 5 replicates showed very narrow distributions in isotopic space and their Layman indices were always 0, which was caused by their similar isotopic signatures (Layman *et al.*, 2007a). All isotopic metrics were calculated using the SIBER package (Jackson *et al.*, 2011) in R (R Development Core Team, 2013).

2.3. Results

2.3.1 Community composition

The ANOSIM analysis revealed significant differences in community composition between different subtidal depth zones (Fig. A1.1 - Global R = 0.641, P = 0.001), particularly between communities inhabiting the soft substrate and those found in the other zones, but also between the scour protection layer and most of the other communities (Table 2.1). The least dissimilar communities (pairwise R = 0.531) were those from the *Metridium* zone and the scour protection layer (SPL).

Table 2.1: Results of ANOSIM pair-wise tests. Global R = 0.641, P = 0.001.

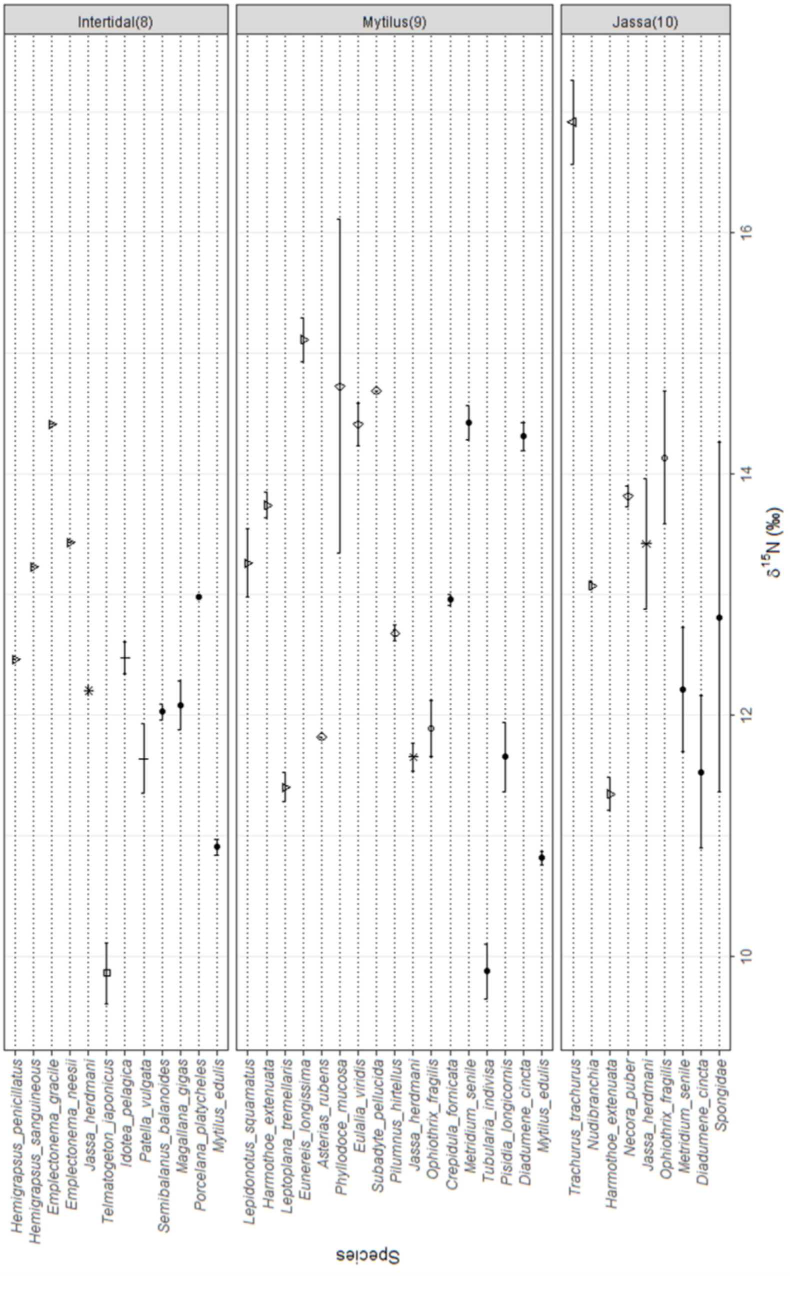
Groups	R statistic
Mytilus, *Jassa*	0.583
Mytilus, *Metridium*	0.542
Mytilus, Scour protection layer	0.917
Mytilus, Soft substrate	1.000
Jassa, *Metridium*	0.549
Jassa, Scour protection layer	1.000
Jassa, Soft substrate	1.000
Metridium, Scour protection layer	0.531
Metridium, Soft substrate	0.906
Scour protection layer, Soft substrate	1.000

2.3.2 Isotopic signatures

The $\delta^{13}C$ values of 478 individuals belonging to 46 invertebrate and 8 vertebrate taxa (Table A1.1) ranged between -23.2 ± 2.5 ‰ (individuals of the brittle star *Ophiothrix fragilis* from the *Jassa* zone) and -8.3 ‰ (one individual of the nudibranch species 2 from the *Jassa* zone). $\delta^{15}N$ values (Fig. 2.2) ranged between 9.9 ± 0.5 ‰ (individuals of the hydroid *Tubularia indivisa* from the *Mytilus* zone) and 18.4 ± 1.7 ‰ (individuals of the fish species *Myoxocephalus scorpioides* from the scour protection layer).

2.3.3 Trophic clusters

The SIMPROF analysis revealed the existence of 14 significantly different trophic clusters (Table A1.2), which did not coincide with the depth zones nor with the feeding groups nor with a combination of these two factors. Two trophic groups (clusters C and D) consisted of only fish and/or predatory invertebrate species. While cluster D consisted only of three individuals of the fish species *Myoxocephalus scorpioides* from the SPL, cluster C included vertebrate and invertebrate predators originating from 4 zones (SPL, *Jassa*, and *Metridium* zones, and soft substrate). One trophic cluster (K) consisted of suspension feeders from 2 zones (intertidal and *Mytilus*). However, some trophic clusters comprised a variety of different feeding traits. Cluster G, for instance, contained one fish species, suspension feeders,


Intertidal(8)
Mytilus(9)
Jassa(10)
Hemigrapsus_penicillatus
Hemigrapsus_sanguineous
Emplectonema_gracile
Emplectonema_neesii
Jassa_herdmani
Telmatogeton_japonicus
Idotea_pelagica
Patella_vulgata
Semibalanus_balanoides
Magallana_gigas
Porcelana_platycheles
Mytilus_edulis
Lepidonotus_squamatus
Harmothoe_extenuata
Leptoplana_tremellaris
Eunereis_longissima
Asterias_rubens
Phyllodoce_mucosa
Eulalia_viridis
Subadyte_pellucida
Pilumnus_hirtellus
Jassa_herdmani
Ophiothrix_fragilis
Crepidula_fornicata
Metridium_senile
Tubularia_indivisa
Pisidia_longicornis
Diadumene_cincta
Mytilus_edulis
Trachurus_trachurus
Nudibranchia
Harmothoe_extenuata
Necora_puber
Jassa_herdmani
Ophiothrix_fragilis
Metridium_senile
Diadumene_cincta
Spongidae
Species
10
12
14
16
δ15N (‰)

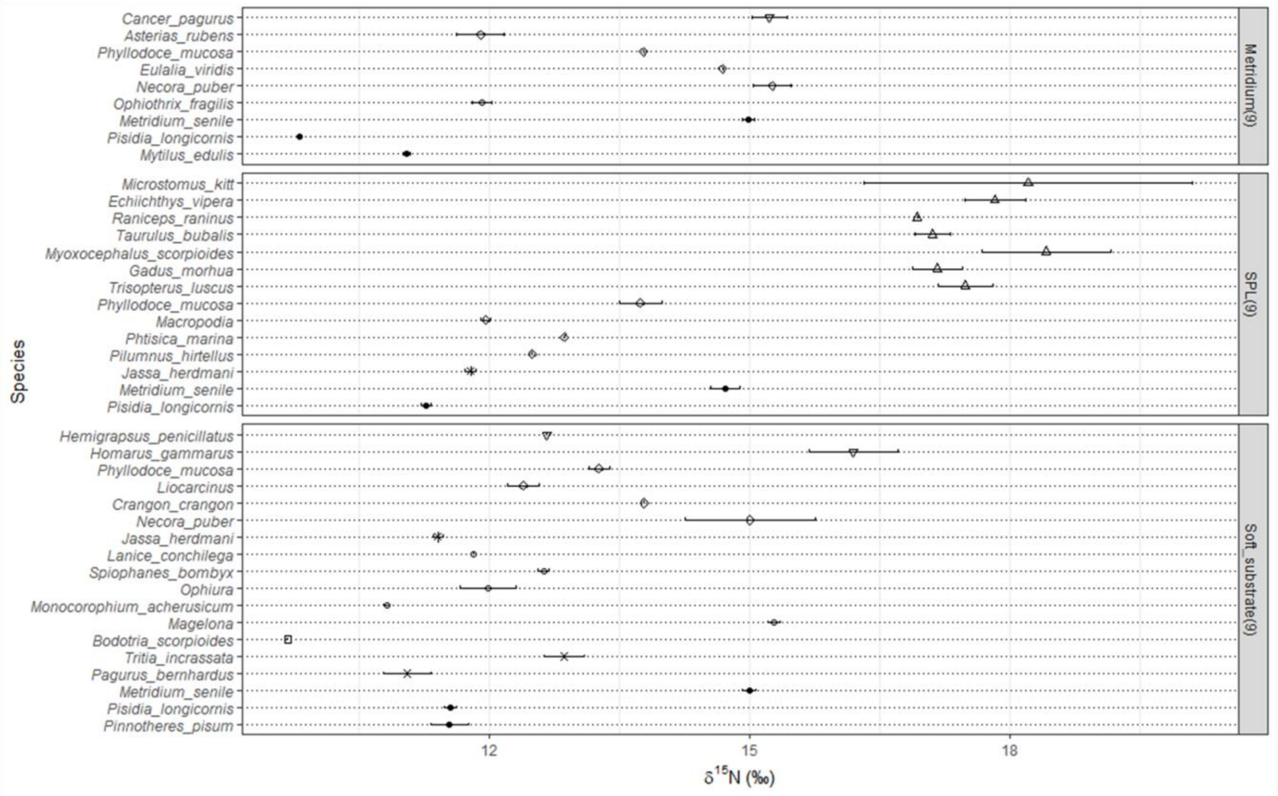


Figure 2.2: Mean and standard deviation of the $\delta^{15}N$ values (‰) of the species present at each zone. On the right, the zones with the numbers of trophic clusters in brackets. On the left, the names of the different species. Different symbols represent different feeding traits: Δ Fish, ● Suspension feeder, ◇ Omnivore/predator/scavenger, ∇ Predator, + Grazer, × Omnivore, □ Deposit feeder, ✱ Suspension/scavenger, ◦ Deposit/suspension feeder.

invertebrate predators and omnivores/predators/scavengers from 5 depth zones (*Mytilus*, *Jassa*, *Metridium*, SPL and soft substrate), while cluster N consisted of invertebrate predators, suspension feeders, grazers, deposit feeders, scavengers/suspension feeders and omnivores from 3 zones (intertidal, *Metridium* zone and soft substrate).

Lowest $\delta^{13}C$ values were found in cluster B (min. = -27.8 ‰, max. = -24.8 ‰) consisting of deposit/suspension feeders, suspension feeders and omnivores/predators/scavengers from 4 zones (*Mytilus*, *Jassa*, *Metridium* and SPL). $\delta^{15}N$ values in this cluster were also low (min. = 11.2 ‰, max. = 13.4 ‰). Highest $\delta^{13}C$ values were found in cluster A (min. = -9.6 ‰, max. = -8.3 ‰), which consisted of a predator from the *Jassa* zone and a deposit/suspension feeder from the soft substrate. The values of $\delta^{15}N$ of cluster A were low (min. = 12.8 ‰, max. = 13.3 ‰). However, the lowest $\delta^{15}N$ values were found in cluster K (min. = 9.1 ‰, max. = 10.7 ‰). The $\delta^{13}C$ values of this cluster were intermediate (min. = -19.0 ‰, max. = -18.3 ‰). Highest $\delta^{15}N$ values were found in the monospecific cluster D (*Myoxocephalus scorpioides*) from the SPL. Individuals of some species, such as the anemone *Diadumene cincta*, grouped in one specific cluster (F) independent of the zone of collection. However, most of the species were distributed over multiple clusters; some species, such as the polychaete *Eulalia viridis*, were found in different clusters according to their sampling zone. Others, such as the blue mussel *Mytilus edulis*, were spread over the clusters independent of the depth zone they were sampled in.

2.3.4 Food web structure within sampling zones

The number of the trophic clusters per zone did not differ much: the intertidal zone consisted of 8 trophic clusters; 9 trophic clusters were found in the *Mytilus*, *Metridium*, scour protection layer and soft substrate, while 10 were present in the *Jassa* zone (Table 2.2, Fig. 2.3). Most of the clusters were present at all zones, while cluster D (comprising three individuals of the fish *Myoxocephalus scorpioides*) was present only at the SPL. Cluster K (suspension feeding species, such as *Tubularia indivisa* and *Mytilus edulis*) was restricted to the upper zones of the turbine (intertidal and *Mytilus* zone). Cluster N had a relatively large SEA_C (9.00 ‰2) at the soft substrate and was elongated along the x-axis (from $\delta^{13}C$~ -11.6 to ~ -16.8 ‰). In the intertidal, this cluster had fewer members, smaller SEA$_C$ (1.90 ‰2) and occupied a smaller δ^{13}C range (~ -14 to ~ -16.6 ‰). At the same time, cluster G (comprising a variety of species such as *Metridium senile*, *Homarus gammarus*, *Harmothoe extenuata* and *Trachurus trachurus*) was vertically elongated when found in the *Jassa* zone and the SPL and horizontally elongated when found in the *Mytilus*, the *Metridium* and the soft substrate zones.

Table 2.2: Total convex hull area (TA), standard ellipse area (SEA) and small sample size corrected standard ellipse area (SEA$_C$) of the trophic clusters in the different communities formed at the different zones.

Zone	Trophic Clusters	TA	SEA	SEA$_C$
Intertidal	F	NA	NA	NA
	H	0.73	0.36	0.39
	I	NA	NA	NA
	J	0.42	0.21	0.23
	K	NA	NA	NA
	L	0.12	0.22	0.44
	M	2.10	1.30	1.48
	N	1.53	1.43	1.90
Mytilus	B	NA	NA	NA
	F	3.22	0.92	0.96
	G	0.78	1.41	2.81
	H	0.82	0.37	0.38
	I	NA	NA	NA
	J	0.58	0.26	0.27
	K	0.41	0.50	0.75
	L	0.87	0.45	0.52
	M	0.32	0.50	0.60
Jassa	A	NA	NA	NA
	B	NA	NA	NA
	C	0.10	0.18	0.35
	E	NA	NA	NA
	F	2.71	0.91	0.96
	G	0.18	0.32	0.64
	H	0.16	0.09	0.11
	J	NA	NA	NA
	L	NA	NA	NA
	M	4.05	2.18	2.50
Metridium	B	NA	NA	NA
	C	NA	NA	NA
	F	0.40	0.39	0.51
	G	2.42	0.98	1.06
	H	1.30	0.91	1.10
	J	0.01	0.02	0.05
	L	NA	NA	NA
	M	3.57	2.88	3.61
	N	NA	NA	NA

Scour protection layer	B	NA	NA	NA
	C	2.52	0.98	1.04
	D	0.09	0.16	0.31
	E	NA	NA	NA
	F	0.68	0.39	0.45
	G	0.55	0.78	1.17
	H	0.03	0.03	0.03
	L	NA	NA	NA
	M	2.06	1.12	1.21
Soft substrate	A	NA	NA	NA
	C	0.81	0.57	0.68
	F	2.81	1.04	1.12
	G	0.91	0.51	0.58
	H	0.85	0.42	0.46
	J	0.06	0.08	0.12
	L	0.52	0.41	0.55
	M	2.77	1.31	1.46
	N	9.94	7.20	9.00

Overall, the trophic diversity (CD) and the trophic redundancy (MNND and SDNND values) differed within the trophic clusters of the different zones (Table 2.3). The largest trophic diversity was found for the trophic clusters in the *Metridium* zone and the soft substrate, while the largest absolute trophic redundancy values were observed for the trophic clusters at the soft substrate. In contrast, the trophic clusters of the *Mytilus* zone had the lowest absolute trophic diversity and redundancy values. The lowest absolute trophic diversity (CD - 0.46) and trophic redundancy values (MNND - 0.59 and SDNND - 0.22) were observed for the trophic cluster F in the *Mytilus* zone that consisted of different species, including *Metridium senile*, *Harmothoe extenuata* and *Diadumene cincta* (Table 2.3). The largest absolute trophic diversity (CD - 2.00) and trophic redundancy values (MNND - 2.60 and SDNND - 1.02) were observed for the trophic cluster N from the soft substrate comprising different species, such as *Necora puber*, *Jassa herdmani* and *Pinnotheres pisum*. The trophic cluster M, consisting of a variety of species in every zone, showed the highest trophic diversity and redundancy values in every zone, except for the soft substrate and the *Mytilus* zone. In the *Mytilus* zone, the largest trophic diversity and redundancy were observed for the trophic cluster L, which consisted of different species, such as *Crepidula fornicata*, *Pilumnus hirtellus* and *Ophiothrix fragilis*.

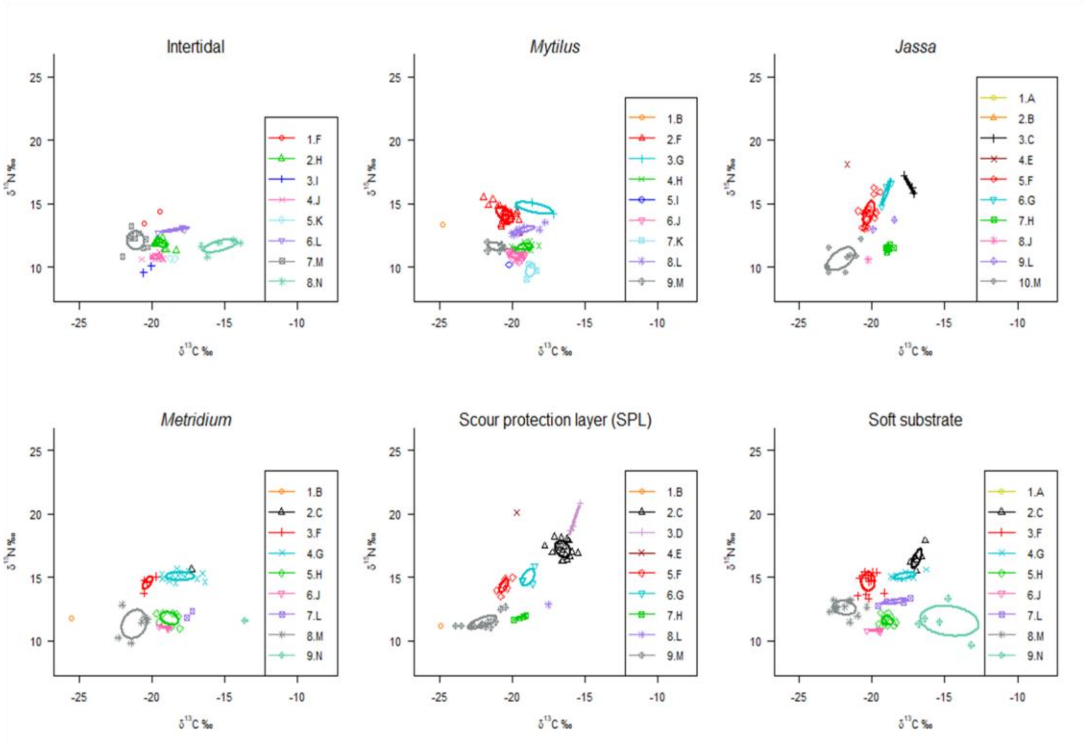


Figure 2.3: Standard ellipse areas corrected for small-size samples (SEA_C - solid lines) of the different trophic clusters found at the six communities. Different colours and shapes represent the different trophic clusters found at each location, whereas the number of the different trophic clusters in every zone is specified in the legend of each plot. The different letters in the legends represent the trophic clusters that are found in every zone.

Table 2.3: Mean values of the Layman community-wide metrics mean distance to centroid (CD), mean nearest neighbour distance (MNND) and standard deviation of the nearest neighbour distance (SDNND) for every trophic cluster that had more than five replicates per zone.

Zone	Cluster	CD	MNND	SDNND
Intertidal	H	0.78	1.00	0.37
	J	0.85	1.08	0.40
	M	0.94	1.18	0.50
Mytilus	F	0.46	0.59	0.22
	H	0.67	0.86	0.32
	J	0.72	0.95	0.30
	L	1.06	1.32	0.57
	M	0.88	1.07	0.51
Jassa	F	0.55	0.71	0.27
	H	0.88	1.08	0.49
	M	1.09	1.33	0.61
Metridium	G	0.90	1.13	0.46
	H	1.10	1.34	0.53
	M	1.32	1.63	0.71
Scour protection layer	C	0.67	0.84	0.33
	F	0.84	1.05	0.45
	M	1.08	1.38	0.49
Soft substrate	C	1.12	1.38	0.61
	F	0.79	1.01	0.38
	G	1.05	1.31	0.57
	H	0.84	1.06	0.43
	M	0.87	1.10	0.44
	N	2.00	2.60	1.02

2.3.5 Comparison of trophic structure between zones

Standard ellipse areas corrected for small sample sizes (SEA_C) indicated differences in the sizes of the isotopic niches between the different depth zones (Fig. 2.4). The smallest SEA_C was observed in the *Mytilus* zone (4.14 ‰^{2}), followed by the intertidal (4.31 ‰^{2}) (Table 2.4). The largest SEA_C was observed for the soft substrate (12.63 ‰^{2}) and mainly reflected a broader range along the x-axis ($\delta^{13}C$). The most elongated SEA_C along the y-axis was observed for the SPL, which exhibited the second largest isotopic niche space (9.54 ‰^{2}).

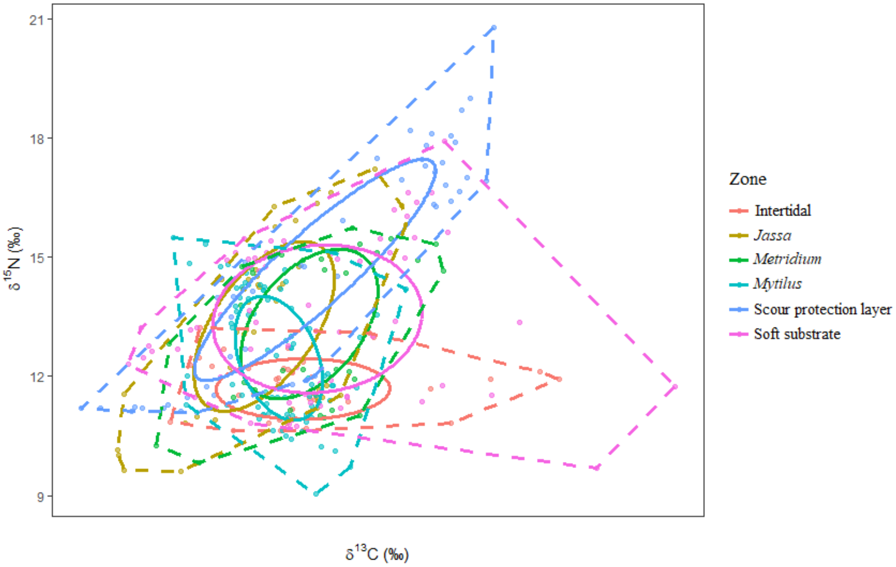


Figure 2.4: Standard ellipse areas corrected for small sample sizes (SEA_C - full lines) and convex hull areas (dotted lines) for the communities in the six zones. The different colours represent different zones.

Table 2.4: Standard ellipse areas corrected for small sample size (SEA_C), overlaps (‰^{2}) of the SEA_C ellipse areas and probability that the SEA_B of g 1 is smaller than the SEA_B of g 2 for all the communities in the different zones.

g1	**g2**	**SEA_C1**	**SEA_C2**	**Overlap (‰²)**	**SEA_B Probability**
Intertidal	*Mytilus*	4.31	4.14	1.93	0.43
Intertidal	*Jassa*	4.31	8.09	1.24	1.00
Intertidal	*Metridium*	4.31	7.53	1.49	0.99
Intertidal	Scour protection layer	4.31	9.54	0.01	1.00
Intertidal	Soft substrate	4.31	12.63	1.77	1.00
Mytilus	*Jassa*	4.14	8.09	2.81	1.00
Mytilus	*Metridium*	4.14	7.53	3.20	1.00
Mytilus	Scour protection layer	4.14	9.54	1.63	1.00
Mytilus	Soft substrate	4.14	12.63	3.32	1.00
Jassa	*Metridium*	8.09	7.53	4.19	0.37
Jassa	Scour protection layer	8.09	9.54	5.22	0.87
Jassa	Soft substrate	8.09	12.63	6.23	0.99
Metridium	Scour protection layer	7.53	9.45	3.52	0.92
Metridium	Soft substrate	7.53	12.63	7.29	0.99
Scour protection layer	Soft substrate	9.54	12.63	5.37	0.88

The extent of the overlap of the SEA_C of the different depth zones ranged from 0.01

‰^{2} (between SPL and the intertidal) to 7.29 ‰^{2} (between the *Metridium* zone and the soft substrate – large overlap) (Table 2.4). On the upper part of the turbine, there was only a small overlap of SEA_C between neighbouring zones, such as between the intertidal and the *Mytilus* zone (overlap = 1.93 ‰^{2}). The overlaps (both in absolute values and in proportions) between zones increased slightly when closer to the sea floor. Trophic niche sizes were compared based on their Bayesian estimates (SEA_B). The largest isotopic niche was that of the soft substrate; the probability that the SEA_B of the soft substrate was larger than those of the other zones was almost 100%, except for the comparison with the SPL, where the probability of a difference was 0.88 (Fig. 2.5, Table 2.4). In turn, the SEA_B of the SPL generally exceeded (probability > 0.87) those of the other zones, excluding the soft substrate.

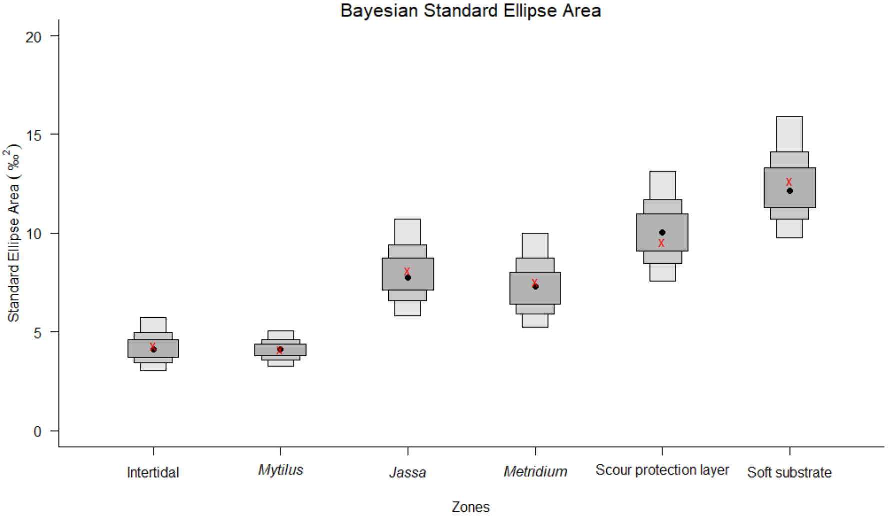


Figure 2.5: Standard ellipse area Bayesian estimations (SEA_B) for each zone. Black dots show the SEA_B mode, the red crosses represent the SEA_C and the grey boxes the probability of data distribution (50% dark grey boxes, 75% lighter grey boxes and 95% lightest grey boxes).

The Layman metrics for the trophic diversity and redundancy further confirmed the observed differences in the trophic structure of the zones (Figures 2.6-2.7 and Table 2.5). Overall, the lowest trophic diversity and highest trophic redundancy were found in the intertidal and in the *Mytilus* zone. Specifically, the *Mytilus* zone had the smallest mean δ^{13}C range (CR - 3.03), distance to centroid (CD – 1.78) (trophic diversity), mean nearest neighbour distance (MNND – 1.39) (trophic redundancy) and standard deviation of the mean nearest neighbour distance (SDNND – 0.57), while the lowest mean δ^{15}N range (NR - 2.31) and the smallest convex hull area (TA – 6.75) values were observed in the intertidal zone. The probabilities that the metrics of these two zones were smaller than at any of the other zones were large (mainly > 0.7), except for SDNND (mainly < 0.7) and CR for the intertidal in comparison to *Jassa* and *Metridium* zones. On the other hand, almost all indices (except CR and SDNND) reached their largest mean values at the SPL, showing that this zone is characterised by a high trophic diversity and low trophic redundancy. The probability that the values of this zone were larger than those of the other zones generally exceeded 0.7, except for SDNND.

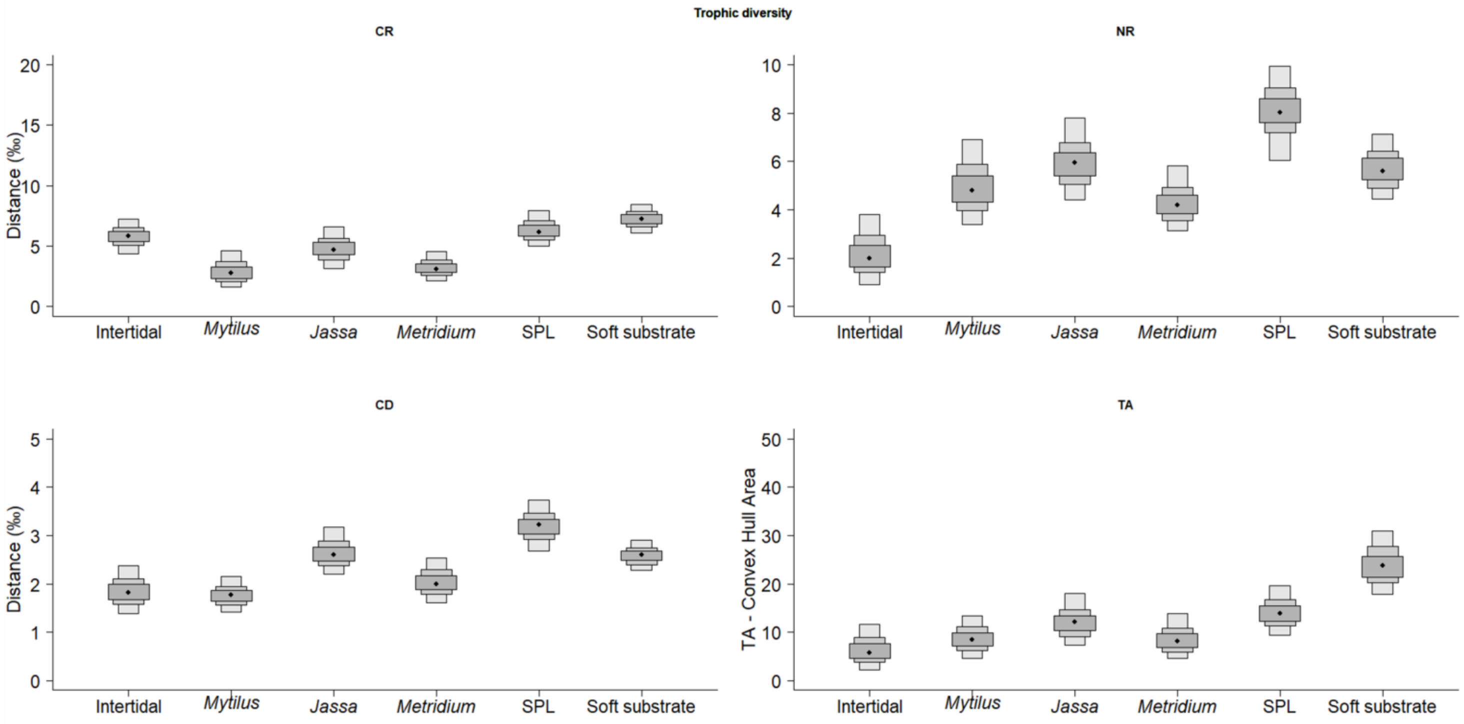


Figure 2.6: Bayesian results for the three trophic diversity community-wide metrics: CR is the δ^{13}C range, NR is the δ^{15}N range, CD is the mean distance to centroid and TA is the convex hull area. The boxes represent the 50% (dark grey), 75% (lighter grey) and 95% (lightest grey) credibility intervals and the black dots represent the mode (‰).

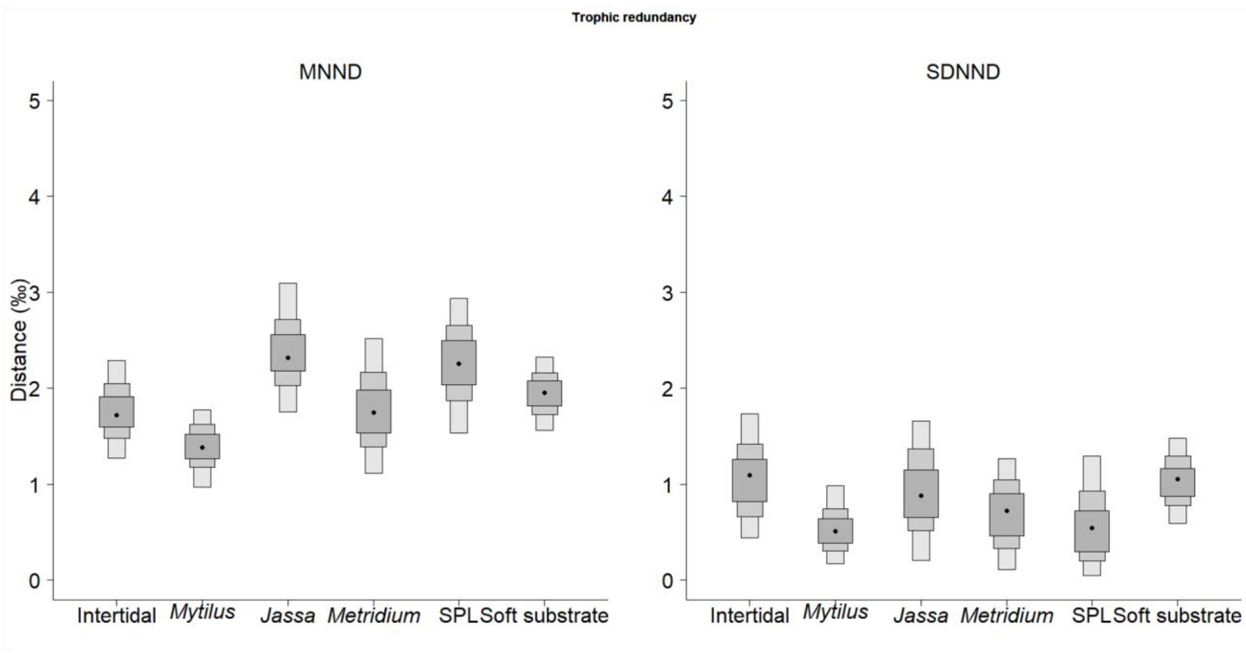


Figure 2.7: Bayesian results for the two trophic redundancy community-wide metrics: MNND is the mean nearest neighbour distance and SDNND is the standard deviation of nearest neighbour distance. The boxes represent the 50% (dark grey), 75% (lighter grey) and 95% (lightest grey) credibility intervals and the black dots represent the mode (‰).

Table 2.5: Probability that the Layman metric of the column is smaller than that of the row.

$\delta^{13}C$ range (CR)

	Intertidal	***Mytilus***	***Jassa***	***Metridium***	**Scour protection layer**
Mytilus	0.014	-	-	-	-
Jassa	0.175	0.94025	-	-	-
Metridium	0.01275	0.6415	0.06425	-	-
Scour protection layer	0.73	0.9925	0.91875	0.99575	-
Soft substrate	0.94275	0.99675	0.977	0.99725	0.81375

$\delta^{15}N$ range (NR)

	Intertidal	*Mytilus*	*Jassa*	*Metridium*	Scour protection layer
Mytilus	0.98725	-	-	-	-
Jassa	0.9945	0.8075	-	-	-
Metridium	0.9735	0.26625	0.605	-	-
Scour protection layer	0.998	0.98525	0.94725	0.99625	-
Soft substrate	0.99425	0.7485	0.39675	0.923	0.02075

Mean distance to centroid (CD)

	Intertidal	*Mytilus*	*Jassa*	*Metridium*	Scour protection layer
Mytilus	0.37875	-	-	-	-
Jassa	0.9795	0.9965	-	-	-
Metridium	0.72375	0.83675	0.03925	-	-
Scour protection layer	0.99575	0.99975	0.9355	0.99575	-
Soft substrate	0.9805	0.99575	0.40755	0.95875	0.023

Total Area (TA)

	Intertidal	*Mytilus*	*Jassa*	*Metridium*	Scour protection layer
Mytilus	0.7605	-	-	-	-
Jassa	0.937	0.7605	-	-	-
Metridium	0.756	0.937	0.15475	-	-
Scour protection layer	0.978	0.756	0.73425	0.93975	-
Soft substrate	0.99825	0.9995	0.98975	0.9975	0.98625

Mean nearest neighbour distance (MNND)

	Intertidal	*Mytilus*	*Jassa*	*Metridium*	Scour protection layer
Mytilus	0.10975	-	-	-	-
Jassa	0.93925	0.9965	-	-	-
Metridium	0.52125	0.8545	0.107	-	-
Scour protection layer	0.8565	0.97825	0.3775	0.8115	-
Soft substrate	0.71725	0.97525	0.095	0.6555	0.20525

Standard deviation of the nearest neighbour distance (SDNND)					
	Intertidal	*Mytilus*	*Jassa*	*Metridium*	Scour protection layer
Mytilus	0.09725	-	-	-	-
Jassa	0.399	0.814	-	-	-
Metridium	0.2115	0.65275	0.316	-	-
Scour protection layer	0.177	0.54925	0.2655	0.43175	-
Soft substrate	0.4685	0.929	0.5855	0.80325	0.836

2.4. Discussion

In the offshore wind farm (OWF) areas of the Belgian part of the North Sea and beyond, the water column is well-mixed, suggesting that the pelagic food sources are available over the entire depth gradient (Jago and Jones, 1998; van Oevelen *et al.*, 2009; Franco *et al.*, 2010; Floeter *et al.*, 2017). Despite this homogeneity, our results indicated differences in the trophic structure between the depth zones. The structural differences in community composition on and in the vicinity of an offshore wind turbine are thus reflected in the trophic niches occupied by those communities, suggesting that different food sources are exploited in different zones. Our analysis shows that the size of the isotopic niche spaces is larger where we expect the highest organic matter accumulation, i.e. the soft substrate, the scour protection layer and the *Jassa* zone (see 2.4.4), where food diversity and availability are increased. This was also supported by the high trophic diversity and low trophic redundancy observed for these zones. The food web study indicated that the trophic clusters in the *Metridium* zone and the soft substrate had the highest trophic diversity and lowest trophic redundancy (Table 2.3), suggesting resource partitioning. The number of trophic clusters was constant throughout the entire depth gradient.

2.4.1 Community composition

The observed differences in the community composition of the colonising fauna along a depth gradient on a wind turbine are in accordance with earlier observations in the Belgian (De Mesel *et al.*, 2015), Dutch (Lindeboom *et al.*, 2011) and German (Krone *et al.*, 2013a) parts of the North Sea. The general patterns, with the blue mussel *Mytilus edulis* dominating the zones closest to the sea surface, and the amphipod *Jassa herdmani* and the anemone *Metridium senile* dominating the middle and lower sections of the turbine, confirmed earlier observations on various types of wind turbines (Krone *et al.*, 2013a; De Mesel *et al.*, 2015). As such, we are confident that our results reflect the food web properties of a 'standard' gravity-based foundation community. Similar zonation patterns have also been observed at oil and gas platforms in the North Sea (van der Stap *et al.*, 2016). In addition, we are certain that we included the most abundant species in terms of densities and biomass, hence we are confident that our dataset includes the main building blocks of the food web associated with an offshore wind turbine, thus reflecting the major trophic patterns.

Even though we sampled only in one season (summer), the community composition of the colonising species was in line with the previous findings. However, we do acknowledge that the fish community composition would be largely affected by the season of sampling. For example, the catches of the fish species *Gadus morhua* and *Trisopterus luscus* are significantly higher during summer and autumn compared to winter and spring (Reubens *et al.*, 2014b). Since the occurrence of fish largely affects the isotopic niche size of the community in the scour protection layer (see 2.4.4), it is possible that seasonality would affect the food web complexity in this zone. Further research is needed to evaluate whether seasonality has an effect on the food web complexity in the area.

2.4.2 Clusters according to isotopic signatures

The SIMPROF analysis did not classify individual organisms according to feeding traits or depth zone but according to isotopic signatures. The fact that organisms with the same feeding traits were not allocated to the same trophic clusters suggests that organisms sharing the same feeding traits may still utilize different food sources (Brind'Amour and Dubois, 2013), reinforcing the idea that a categorisation of benthic and colonising organisms into feeding guilds does not reliably reflect their actual resource consumption (Gerino *et al.*, 2003; De Smet *et al.*, 2015; Richoux and Ndhlovu, 2015).

2.4.3 Resource partitioning within trophic clusters of each zone

The trophic diversity and redundancy values differed among the zones and the trophic clusters (Table 2.3). This suggested that there is resource partitioning at two levels: between different co-occurring clusters within the same zone, and within trophic clusters as demonstrated by the Bayesian indices mean distance to centroid (CD), mean nearest neighbour distance (MNND) and standard deviation of the nearest neighbour distance (SDNND).

Within clusters, resource partitioning ranged from low to high. Specifically, a low trophic diversity (low CD absolute values) and high trophic redundancy (low MNND and SDNND absolute values) were observed in the *Mytilus* zone (Table 2.3), reflecting low levels of resource partitioning. The *Mytilus* zone mainly consists of sessile suspension feeders, such as *Mytilus edulis* and *Crepidula fornicata*. Our results contradict previous findings about suspension feeding organisms, which exhibited resource partitioning and different selection mechanisms (Dubois and Colombo, 2014).

High levels of resource partitioning within trophic clusters were observed in the *Metridium* zone, the soft substrate and to some extent the scour protection layer that showed the highest trophic diversity (high mean distance to centroid – CD – absolute values) and lowest trophic redundancy (high mean nearest neighbour distance – MNND – and standard deviation of the nearest neighbour distance – SDNND absolute values, Table 2.3). This implies that resource partitioning is an important mechanism allowing the co-existence of a variety of species in these zones.

The highest trophic diversity and lowest trophic redundancy were observed for the trophic cluster N at the soft substrate, for the cluster M in the intertidal, the *Jassa*, the *Metridium* zones and the scour protection layer, and for the cluster L in the *Mytilus* zone. This is caused by the species exploitation of multiple food sources with distinct isotopic signatures. On the other hand, the low trophic diversity and high trophic redundancy that was observed for cluster F in the *Mytilus* zone, the *Jassa* zone and the soft substrate indicates that the species comprising this cluster exploit largely the same food sources.

2.4.4 Functional differences reflected in isotopic niches

The structural differences in communities sampled along the depth gradient (ANOSIM results – Table 2.1) were reflected in their trophic characteristics, as indicated by the small overlaps between the zone-specific trophic niches (Table 2.4). This suggests substantial shifts in resource use with depth. This is partly unexpected in view of the fact that the water column at the study location is well-mixed (Franco *et al.*, 2010; Floeter *et al.*, 2017).

The largest resource range and highest trophic diversity (in terms of food chain length and food sources range) were observed in the soft substrate and the scour protection layer (SPL) (Fig. 2.4, Table 2.4), probably as a result of the accumulation of organic matter at these sites (but see further for SPL). The soft substrates in the study area are permeable sediments that efficiently recycle organic matter, resulting in low organic matter concentrations (Braeckman *et al.*, 2014). However, in the close vicinity of the wind turbines, these sediments have a lower median grain size and a higher organic carbon content, which is largely a consequence of the biodeposition of organic matter by the colonising fauna on the turbine (Coates *et al.*, 2014). This in turn alters macrofaunal community structure, with increased abundances and species richness close to the turbines (Coates *et al.*, 2014; Lefaible *et al.*, 2018). One example is the high abundance of the tube-dwelling polychaete *Lanice conchilega*, the aggregations of which can further increase local retention of organic matter and enhance local biodiversity (Rabaut *et al.*, 2007; De Smet *et al.*, 2016). These alterations in biodiversity result in a more diverse local food web with a higher number of trophic groups in the soft sediments close to the wind turbines. Similar impacts of colonising fauna on the community and food web of nearby soft sediments were observed in Lake Constance, where zebra mussels, growing on hard substrates, increased the organic matter accumulation in the benthic zone due to biodeposition, resulting in higher abundances of benthic macroinvertebrates and longer food chains as well as a broader resource range (Gergs *et al.*, 2011).

An additional explanation for the enhancement of the soft sediment biodiversity is that the soft substrate community sampled close to the pile is comprised of a mixture of true soft sediment and colonising species (*Monocorophium acherusicum*, *Pisidia* *longicornis* and *Jassa herdmani*) (Table A1.1). We believe that some colonising species are capable of temporarily surviving in the soft substrate, after having been dislocated from the turbines and/or the scour protection layer (Bouma and Lengkeek, 2012; Fernandez-Gonzalez *et al.*, 2016), thus increasing the natural species richness of the soft sediments. The presence of colonising species did not affect the isotopic niche space (SEA_C surface) of the soft substrate community, since most of these species were located in the centre of the sediment community's isotopic niche space.

The community at the scour protection layer had the second largest SEA_C (Fig. 2.4, Table 2.4), the largest trophic diversity (CD) and the largest $\delta^{15}N$ range (NR) (Fig. 2.6). Scour protection layers are made of rocks, forming a collar around the piles (Baeye and Fettweis, 2015), adding complexity and providing habitat (Causon and Gill, 2018). The density of epibenthic species on the SPL rocks is high (Bouma and Lengkeek, 2008), attracting fish species, which can reach densities up to 37 times higher than those found in other zones of the wind farm (Couperus *et al.*, 2010). The occurrence of fish at the SPL increases its isotopic niche space and food-chain length. We therefore also analysed the data after exclusion of the fish (not shown here), which resulted in a considerably smaller isotopic niche size (from 9.54 ‰^{2} to 5.60 ‰^{2}), trophic diversity and $\delta^{15}N$ range for the SPL. Removal of fish from the SPL community also decreased the mean distance to the centroid of the isotopic niche space and the size of the convex hull volume but left the trophic redundancy metrics unaltered.

We observed the lowest trophic redundancy (high MNND absolute values) in the *Jassa* zone (Fig. 2.7), which is an indication that a wide variety of resources is used in that zone (Abrantes *et al.*, 2014; Rigolet *et al.*, 2015; Kaymak *et al.*, 2018). Our results can partly be explained by the behaviour of the dominant amphipod *Jassa herdmani* in that zone. *Jassa herdmani* is a tube-building amphipod that produces large mats, known as "amphipod silks" that largely consist of organic matter derived from the water column (Beermann and Franke, 2012). Tube-building amphipods perform grooming motions, which dissociate aggregates and loosen the organic matter that is accumulated between these mats (Dixon and Moore, 1997). Hence, part of the organic matter that is trapped in the mats becomes available to nearby suspension-feeders, increasing the range of the available food sources in this zone. Moreover, the community of the *Jassa* zone included a pelagic fish species (*Trachurus*

trachurus), which is highly mobile and can exploit different habitats and food sources. Upon removal of fish from the data analysis, the isotopic niche size of the *Jassa* community decreased (from 8.09 ‰^{2} to 6.81 ‰^{2}), but not so drastically as the isotopic niche space of the SPL. However, excluding the fish from the analysis resulted in a higher trophic diversity (high δ^{15}N range and mean distance to centroid), while the MNND remained unaltered. This indicates that *T. trachurus* contributes much less to the food web structure in the *Jassa* zone than do fish species in the SPL.

The assemblage in the intertidal zone occupied a completely different trophic niche than those of the other zones, resulting in the smallest isotopic niche overlap with all other communities (Fig. 2.4, Table 2.4). The intertidal community mainly consisted of sessile suspension feeders that are constrained in their access to food (Richoux *et al.*, 2013). The *Mytilus* community located below the intertidal area is also mainly composed of sessile suspension-feeders and had the second smallest trophic niche overlap with other communities, as well as the smallest isotopic niche size. Sessile suspension feeders generally have narrow trophic niches (Dubois and Colombo, 2014), which explains the small SEA_C sizes of zones dominated by sessile suspension feeders. Narrow trophic niches may also result in small niche overlap. In addition, the community in the *Mytilus* zone was also characterised by a high trophic redundancy, indicating that the species of this community had very similar diet compositions (Catry *et al.*, 2016; Kaymak *et al.*, 2018).

The high food web complexity, in terms of food chain length, found in our study has not been observed in another study, which compared the food web complexity between artificial (oil and gas platforms) and adjacent natural hard substrates in the Celtic Sea, showed similar complexity at these two substrates (Guerin, 2009). In this study, the δ^{15}N range was small, suggesting that the fauna at those structures occupied the same trophic level (Guerin, 2009). This contrasts with the higher food web complexity we observed in communities associated with the offshore wind turbines, a difference which might be related to the age of the respective colonising communities, since most of the oil and gas platforms were 25 years old (Guerin, 2009), while the turbine examined here had been constructed 8 years before the present study.

2.5. Conclusions

Our study provides fundamental knowledge on the food web structure associated with offshore wind turbines. The structural differences in communities sampled in different depth zones on and in the vicinity of the turbine are reflected in their trophic characteristics. Higher food web complexity, in terms of isotopic niche width, trophic diversity and trophic redundancy, was associated with the zones where organic matter accumulation occurs (soft substrate, *Jassa* zone, scour protection layer). Lower food web complexity was associated with zones where sessile filter-feeding species dominate (intertidal and *Mytilus* zone). The increasing overlap of the isotopic niches of the communities in deeper areas indicates a higher complexity of the food web in the deeper zones. On the other hand, the clear separation of the isotopic niches of the zones found at higher depths from those at lower depths indicates the exploitation of a variety of food sources and the occupation of different trophic levels in the different depth zones. Furthermore, trophic differentiation within clusters of every zone pointed at food resource partitioning as an important mechanism allowing species co-existence.

Chapter 3

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Resource niches of co-occurring invertebrate species at an offshore wind turbine indicate a substantial degree of trophic plasticity

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Author contributions: IDM, TM, SD, JV conceived this study. NM collected the data, analysed the data with support of JV and TM and wrote the manuscript with valuable inputs and edits by all the other co-authors.

Abstract

Offshore wind farms in the North Sea are proliferating, causing alterations in local ecosystems by adding artificial hard substrates into naturally soft-bottom areas. These substrates are densely colonised by epibenthic organisms, which may compete for the available resources. While the distribution of some species is restricted to specific parts of the turbine, others occur across depth zones and may therefore face different competitive environments. Here we investigate the trophic niches of seven invertebrate species: three sessile, one hemi-sessile and three mobile species that occur in multiple depth zones. We hypothesised that these species would be trophic generalists at the turbine level, but would exhibit trophic plasticity, selecting different food resources in different depth zones, to cope with the different competitive environments in which they occur. We analysed $\delta^{13}C$ and $\delta^{15}N$ of these species and their potential food resources across depth zones. Our results show that most of these invertebrates are indeed trophic generalists which display substantial trophic plasticity, selecting different resources in different zones. Degree of trophic plasticity was not related to mobility of the species. There are two possible explanations for these dietary changes with depth: either consumers switch diet to avoid competition

with other (dominant) species, or they benefit from the consumption of a non-limiting resource. Only *Diadumene cincta* was a trophic specialist that consumed suspended particulate organic matter independent of its zone of occurrence. Altogether, trophic plasticity appears an important mechanism for the co-existence of invertebrate species along the depth gradient of an offshore wind turbine.

3.1 Introduction

In many countries across the world, and in Europe in particular, offshore wind farms (OWFs) are increasingly being considered a potentially significant contributor in the quest to reduce CO_2 emissions. By 2018, 4149 offshore wind turbines had been installed in European marine waters, producing a total of 15.8 GW, while this capacity is expected to increase up to 70 GW in 2030 (WindEurope, 2018). In the North Sea, new wind farms are continuously being constructed, licensed or scheduled (Soma *et al.*, 2019).

The construction of offshore wind turbines creates a new benthic habitat, adding hard substrate to naturally soft-bottom areas. These hard substrates are colonised by dense hard-bottom assemblages (Wilhelmsson and Malm, 2008; Krone *et al.*, 2013a; De Mesel *et al.*, 2015), consisting mainly of filter-feeders (Lindeboom *et al.*, 2011) and other colonising (or fouling) organisms (Slavik *et al.*, 2019) that may compete for food and space (Buss and Jackson, 1981; Dubois and Colombo, 2014; Cresson *et al.*, 2016). Filter-feeders capture suspended food particles that are highly diluted in the water column (Gili and Coma, 1998). These organisms have developed mechanisms to select specific food particles from the available spectrum (Dubois *et al.*, 2007; Dubois and Colombo, 2014) and exploit a variety of food sources that may change through space and time (Bode *et al.*, 2006; Richoux *et al.*, 2014b). Hence, species within the same feeding guild can have different resource use strategies, limiting competition for food through trophic niche partitioning (Lefebvre *et al.*, 2009; Richoux *et al.*, 2014b).

In the North Sea, colonising communities living on wind turbines form a clear vertical zonation pattern along the depth gradient (De Mesel *et al.*, 2015). Despite this general zonation pattern, some species occur in multiple depth zones or along the entire depth gradient of the turbine. These include both sessile organisms, such as the blue mussel *Mytilus edulis* and the anemone *Metridium senile*, and mobile species, such as the porcelain crab *Pisidia longicornis*, the brittle-star *Ophiothrix fragilis* and the crab *Necora puber* (Mavraki *et al.*, 2020). The latter are not considered fouling organisms, but their presence is highly linked to the presence of artificial hard substrates (Lindeboom *et al.*, 2011; De Mesel *et al.*, 2015; van der Stap *et al.*, 2016).

Pisidia longicornis and *O. fragilis* can feed on suspended material, such as phytoplankton and pseudofaeces (Warner, 1971; Smaldon, 1972; Sampedro *et al.*, 1997; Allen, 1998), while *N. puber* also preys on a variety of colonising species, such as amphipods and mussels (Freire and Gonzalez-Gurriaran, 1995). The occurrence of these species in multiple zones does not necessarily imply that they are successfully established in these zones. Temporal dynamics influence the species distribution along the depth gradient. For example, the dominance of *J. herdmani* decreases with increasing depth in summer and in winter, while *M. edulis* can only be found at lower depths during winter (Kerckhof *et al.*, 2010a).

The occurrence of certain species in more than one zone suggests that they may be competing both for the available food resources and/or for space with the dominant species in those zones. In benthic communities, space has long been considered as the main limiting resource (Buss and Jackson, 1981; Côté *et al.*, 1994; Dubois and Colombo, 2014; Svensson and Marshall, 2015). However, food limitation (henceforth referred to as food or resource limitation in this paper) by co-occurring species is also recognised as an important factor influencing community functioning (Buss and Jackson, 1981; Dubois and Colombo, 2014; Cresson *et al.*, 2016). Resource partitioning and trophic plasticity have been proposed as strategies of co-occurring organisms to limit the effects of trophic competition (Lefebvre *et al.*, 2009; Riera, 2009). Resource partitioning is the division of limiting resources among species as a mechanism to avoid trophic competition (Ross, 1986), while trophic plasticity is the adaptation of organisms to minimize potential competition for food by (partly) shifting their diets (MacNeil *et al.*, 1997; Lefebvre *et al.*, 2009). Resource partitioning often entails some form of trophic specialisation, leading – in the case of the invertebrate fauna associated with wind turbines – to the utilization of a narrow range of food sources by specific taxa (Van Valen, 1965; Bearhop *et al.*, 2004). Trophic plasticity, on the other hand, is a form of trophic generalism, implying that a species is capable of feeding on a broad food spectrum, but will exploit only a (partly different) part of that spectrum depending on the competitive environment in which it occurs (here, e.g., in the different depth zones) (Hazlett, 1988; Bearhop *et al.*, 2004; Gutt, 2006; Riera, 2009). The scenario of the existence of mainly trophic generalists on offshore wind turbines is plausible, because the species would be able to co-occur in a limited amount of space by exhibiting considerable trophic plasticity (Araújo *et al.*, 2011; Páez-Rosas *et al.*, 2017). In any case, the co-occurrence of multiple invertebrate species on offshore wind turbines could be partly explained by their feeding behaviour.

In this study, we sampled invertebrate species that occur across different zones along the depth gradient of a gravity-based offshore wind turbine, its scour protection layer (SPL) and the surrounding soft sediments in the Belgian part of the North Sea (BPNS). We hypothesised that these species would be trophic generalists that are capable of modifying their resource exploitation in different depth zones, implying that trophic plasticity is the key mechanism allowing their wide distribution and survival in a competitive environment. We used stable isotope analysis (SIA) to investigate trophic niches and pathways (Riera, 2009). The isotopic niche of a species can be estimated using SIA and is a proxy for its trophic niche (Newsome *et al.*, 2007; Jackson *et al.*, 2011). We would therefore expect partly different isotopic niches across depth zones within the same consumer species. In addition, we anticipated that such a niche differentiation across depth zones would translate into overall large depth-integrated isotopic niches of these species, as they are expected to be overall trophic generalists (Layman *et al.*, 2007b).

3.2 Methodology

3.2.1 Study site

Samples were collected from a gravity-based wind turbine (D6, coordinates: 51° 33.04′N - 02° 55.42′E) within the C-Power wind farm on the Thornton Bank (BPNS). We chose this particular location because a wealth of data on colonising assemblages and soft-substrate fauna were available (Coates *et al.*, 2014; De Mesel *et al.*, 2015). Sampling of all the consumers and of most of their potential resources was conducted from the RV Simon Stevin in August 2016. Macroalgae from the intertidal were collected from an inflatable boat in August 2017.

3.2.2 Sampling scheme

Invertebrate organisms living along the depth gradient on the wind turbine, the scour protection layer (SPL) and the surrounding soft sediment, as well as possible resources from the water column and the intertidal area of the turbine, were collected. Six sampling zones (Fig. 3.1) based on macrofaunal zonation patterns (Lindeboom *et al.*, 2011; Krone *et al.*, 2013a; De Mesel *et al.*, 2015) and on structural/habitat differences (Baeye and Fettweis, 2015) were chosen for the collection of the consumer organisms: (a) the intertidal, (b) the *Mytilus* zone (5 m depth), (c) the *Jassa* zone (~ 8.5 m depth), (d) the *Metridium* zone (15-25 m depth), (e) the scour protection layer (SPL) and (f) the soft sediment surrounding the turbine (soft substrate). Scientific divers collected consumer species from the *Mytilus* (2 samples), the *Jassa* (3 samples) and the *Metridium* (6 samples) zones by scraping (25 x 25 cm frame), from the SPL by collecting 3 rocks (~ 15 cm length, 10 cm width and 5 cm height) and from the sediment by using an airlift suction device (surface sampled: 25 x 25 cm, sediment depth: 5 cm, 2 samples). Consumers from the intertidal zone (2 samples) were collected by scraping from an inflatable boat at low tide. Different numbers of samples collected in the different zones are a result of the practical limitations linked to the restricted available diving time (Fig. 3.1). Samples were collected during the turn of the tide at neap tide. Finally, large consumers, such as large crustaceans and ophiuroids, were handpicked by scientific divers in the different subtidal zones. All consumers were identified to the lowest taxonomic level possible. Whenever possible, five individuals per species were collected from each zone for the stable isotope analysis to include intraspecific variation. The individuals were randomly selected to more accurately quantify the width of the trophic niche of the species and ultimately understand the mechanism(s) responsible for species co-existence (Bolnick *et al.*, 2011; Violle *et al.*, 2012). Macrofaunal organisms were starved overnight in filtered sea-water in order to allow them to clear their gut contents. Larger crustaceans were immediately freeze-killed (Zhang *et al.*, 2018) and cheliped tissues were subsequently isolated and retained for stable isotope analysis (SIA).

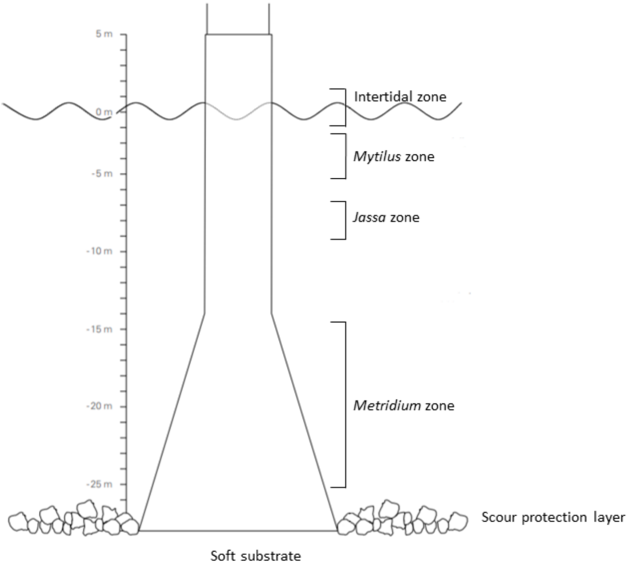

Figure 3.1: The six sampling zones along the depth gradient of the gravity-based foundation D6 in the Belgian part of the North Sea (modified by the source: De Mesel *et al.*, 2013).

For the collection of candidate resources, three replicate samples (one 1-l sampling vial for each replicate) of suspended particulate organic matter (SPOM) were collected by scientific divers from the lower (~ 1 m above the sea floor – referred to as SPOM-bottom) and the upper (~ 3 m below the sea surface – referred to as SPOM-surface) water column. Water samples were initially sieved through a 200-µm sieve to remove large detritus and zooplankton (Lorrain *et al.*, 2003; Bănaru *et al.*, 2014), and then filtered through pre-combusted and pre-weighed Whatman GF/F 47-mm filters (mesh size: 0.7 µm) using a vacuum pump. Zooplankton was collected one meter away from the turbine, using a vertical haul of the plankton net (diameter: 0.57 m, mesh size: 200 µm). Subsequently, it was concentrated by sieving over different mesh sizes (800 and 250 µm) and separated into different size groups. The subsamples were kept in filtered sea water for 2-4 h to allow gut clearance (Smyntek *et al.*, 2007). Macroalgae were scraped off from the intertidal both at low (algae-lower) and at high (algae-upper) tide from an inflatable boat. Since the macroalgae on the wind turbine are perennial, they are constantly available to consumers; year-round studies revealed no or only very small inter-annual variation in their isotopic signatures (Bordeyne *et al.*, 2017). Hence, sampling macroalgae in a different year would not have an effect on their isotopic signatures. Epiphytes were scraped off the algae using a sterilized dull scalpel under a stereomicroscope prior to drying to acquire the isotopic signature of the algae (Moncreiff and Sullivan, 2001; Renaud *et al.*, 2015). We additionally included data for sediment organic matter (SOM) that were collected during the same sampling period from the same wind farm area (Toussaint *et al.*, pers. comm.), since re-suspended SOM is a potential resource, e.g. for species inhabiting the SPL and the soft substrate.

All samples for SIA (sources and consumers) were stored in a -20⁰C freezer until further analysis. In total, seven species were sampled in sufficient replicates from more than one depth zones: the sessile filter-feeding species *Mytilus edulis*, *Diadumene cincta* and *Metridium senile*, the hemi-sessile filter-feeder *Jassa herdmani*, the mobile filter-feeding species *Pisidia longicornis* and *Ophiothrix fragilis*, and the mobile omnivore/predator *Necora puber* (Table 3.1).

3.2.3 Sample preparation

Filters for the analysis of SPOM were thawed, dried overnight at 60⁰C and prepared for $\delta^{13}C$ and $\delta^{15}N$ isotope analysis. The preparation included the bisection of the filter; one half was immediately enclosed in a tin (Sn) capsule and the other half was acidified through exposure to hydrochloric acid fumes (HCl 37%) in a desiccator for the removal of the inorganic carbon (Lorrain *et al.*, 2003). The acidified halves of the filters were dried again overnight (60⁰C) and then enclosed in silver (Ag) capsules. Acidification was necessary to eliminate traces of carbonates, which can significantly affect the $\delta^{13}C$ values of the SPOM samples (Lorrain *et al.*, 2003). The non-acidified samples were then analysed for $\delta^{15}N$, which do not require pre-treatment, since acidification may contribute to some shifts in $\delta^{15}N$ (Goering *et al.*, 1990; Vafeiadou *et al.*, 2013).

Entire individuals of the small-sized species *Jassa herdmani*, *Pisidia longicornis*, *Metridium senile* and *Diadumene cincta* were processed for SIA after gut content clearance. For the other organisms, specific muscle tissues were sampled: cheliped muscle from *Necora puber* (Reid *et al.*, 2016), foot from *Mytilus edulis* (Richoux and Ndhlovu, 2015) and peristomial membrane from *Ophiothrix fragilis* (Andrade *et al.*, 2016). For each species, individuals of similar size were selected to exclude effects of any size-specific shifts in diet (Cresson *et al.*, 2016). Zooplankton subsamples were first thawed and then analysed under a stereomicroscope for the separation of the organisms into broad taxonomic groups (Bănaru *et al.*, 2014). The largest size class (800-1000 µm) contained mainly crab larvae (referred to as "Crab larvae") and other unidentified larvae (referred to as "Other larvae"). The smaller size-class (250-800 µm) contained mainly copepods. The different taxonomic groups were further analysed for SIA. Finally, macroalgae samples were also thawed and analysed under a stereomicroscope to ensure that epiphytes had been effectively removed.

Individuals, muscle tissues, zooplankton samples and macroalgae were rinsed with milli-Q water to avoid contamination and dried overnight at 60^0C, after which they were pulverised using a mortar and pestle and homogenized. Depending on the tissue type, approximately 1 mg of dried tissue was immediately encapsulated in a Sn capsule, weighed and stored in a desiccator until further analysis, or it was first split into two subsamples of equal dry weight (ca 1 mg); one subsample was used for the analysis of δ^{15}N and immediately encapsulated in a Sn capsule without prior treatment, whilst the other was transferred in a Ag capsule, acidified by adding 1% HCl "drop by drop" until elimination of all CO_2 from the carbonates in the sample (Jacob *et al.*, 2005), and used for analysis of δ^{13}C. The latter sample was subsequently rinsed with distilled water, dried again and stored dry in multi-well Microtitre plates in a desiccator until further analysis (Pinnegar and Polunin, 1999). When the weight of the organisms was not sufficient to prepare two subsamples, more individuals of the same species and location were pooled in the same sample. Only the organisms containing calcareous structures, i.e. *Jassa herdmani*, *Ophiothrix fragilis*, *Pisidia longicornis* and zooplankton, were acidified.

In total, 206 samples (both resources and consumers – Table A2.1 in Appendix) were analysed on a PDZ Europa ANCA-GSL elemental analyser, interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the UC Davis

Stable Isotope Facility (University of California, USA). The results for carbon and nitrogen isotope ratios were expressed in the standard delta (δ) notation:

$$\delta X = [(R_{Sample} / R_{Standard}) - 1] \times 10^{3} \text{ (in ‰)}$$

where X is ^{13}C or ^{15}N and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. For both sources and consumers, we strived to analyse at least three replicates per species, but for some zooplankton groups this was not possible.

3.2.4 Data analysis

We used two different approaches to investigate the diet composition of each consumer in the different zones. For each species, we first characterised the isotopic niche by calculating the following metrics: the sample-size corrected standard ellipse area (SEA_C) for every consumer species and in every zone combination, the SEA_C overlap of a given species between different depths, the Bayesian standard ellipse area (SEA_B), as well as the ellipse metrics eccentricity (E) and angle (theta – θ) for every species in the different zones. Then we assessed the potential contribution of each possible resource to the diet of the examined species. SEA_C reflects the two-dimensional ($\delta^{13}C$ and $\delta^{15}N$) isotopic niche of a group of individuals. It is insensitive to sample size and is a proxy of the trophic niche of that group of individuals (Jackson *et al.*, 2011). The Bayesian estimation of the standard ellipse area (SEA_B) provides a range of ellipse surfaces that can be valid given the input data (Jackson *et al.*, 2011). SEA_B was calculated from 10^4 posterior iterations of SEA_B. Bayesian inference allows a direct probabilistic interpretation of the differences in SEA_B depending on the grouping level, (i.e. between the individuals of the same species sampled at different depth zones). Pair-wise comparisons of SEA_B estimate the probability that the isotopic niche of a species in one zone is larger than in another zone (Jackson *et al.*, 2011). Eccentricity E is a measure of the circularity of the SEA_C and therefore of the variance along the x ($\delta^{13}C$) and y ($\delta^{15}N$) axes. Eccentricity (E) values of the standard ellipse range between 0 and 1, where $E = 0$ is a perfect circle, while $E \sim 1$ indicates higher elongation of the standard ellipse (Reid *et al.*, 2016). Hence, low E (values ~ 0) reflects similar variance on both axes and high E (values ~ 1) indicates that the ellipse is more elongated along one of the two axes (Reid *et al.*, 2016). Theta (θ) is a measure of the inclination of the ellipse and is returned as a value between 0 and π (Jackson *et al.*, 2011). It is reported here in an angular range between -90 and +90°, with positive and negative values indicating that $\delta^{13}C$ and $\delta^{15}N$ are, respectively, directly or inversely proportional (Demopoulos *et al.*, 2017). θ values close to 0 (ellipse dispersed along the x-axis) indicate utilization of multiple resources while θ values close to (-) 90 (ellipse dispersed along the y-axis) indicate that the individuals within a site feed across different trophic positions within (a) basal carbon source(s) (Reid *et al.*, 2016; Demopoulos *et al.*, 2017). The combination of E and θ can distinguish isotopic niche areas, which have similar sizes, but the relationship between $\delta^{13}C$ and $\delta^{15}N$ among locations (in this case depth zones) and/or species is different (Reid *et al.*, 2016). SEA_C, SEA_C overlap, SEA_B and the ellipse metrics E and θ were calculated using the SIBER (Stable Isotope Bayesian Ellipses in R) package (Jackson *et al.*, 2011).

The contribution of each potential resource to the diet of each species was calculated using the R-package SIMMR (Stable Isotope Mixing Models in R) (Parnell *et al.*, 2013; Parnell and Inger, 2019). Bayesian isotope mixing models are based on the assumption that all dietary resources are included in the analysis (Phillips *et al.*, 2014). Therefore, we attempted to sample as many of the known resources in the area as possible. However, we acknowledge that we probably did not collect all of them. The main advantage of this model is that it takes into account both the mean (μ_{prey}) and the standard deviation (σ_{prey}) of the prey stable isotope ratios in order to evaluate the likelihood of the proportion of a given prey item in the diet (Moore and Semmens, 2008). We investigated the species-specific variation in resource preferences between zones by running the mixing models separately for each species and zone. This yielded information on the contribution of each food resource to the diet of every species in every zone of occurrence. Resources that are not mixed along the depth gradient, such as macroalgae and SOM, were only included as possible resources in those zones where they were available for the consumers, i.e. the intertidal for macroalgae and the soft substrate and SPL for SOM. A trophic enrichment factor (TEF) was added to the model. Applying the relevant TEF is crucial to the design of mixing models (Phillips *et al.*, 2014). Therefore, we ran the model multiple times, using different TEFs applied to similar consumers (Dubois and

Colombo, 2014; Richoux *et al.*, 2014b; Cresson *et al.*, 2016); based on the results of the different model runs, we chose the same TEFs as reported in Cresson *et al*. (2016), i.e. 1.28 ± 0.72 for carbon and 3.25 ± 0.67 for nitrogen. The choice was based on the position of the consumers within the convex polygons in the isotope space defined by the resources (Phillips *et al.*, 2014). According to the same authors, if the consumer is positioned within the range of its resources in the $\delta^{13}C$ – $\delta^{15}N$ isospace, there is at least one solution explaining the consumer's isotopic values as a combination of the available resources. Since different species feed on different food items, the mixing models only included species-specific and zone-specific relevant food items, as deduced from literature (Table 3.1). *Necora puber* is a predator/omnivore and feeds on a combination of primary resources and invertebrate fauna. Isotope values ($\delta^{13}C$ and $\delta^{15}N$) for its possible invertebrate prey resources (Table 3.1) were obtained from Mavraki *et al.* (2020), who sampled these candidate prey species during the same sampling period and at the same site as reported here.

In order to avoid increasing the uncertainty of the mixing model by unnecessarily inflating the number of potential resources for a consumer (Phillips and Gregg, 2003), an *a posteriori* approach for combining resources was used (Table 3.1) (Phillips *et al.*, 2005). We used matrix plots to test the correlation between the isotopic signatures of potential resources (Parnell *et al.*, 2010, 2013) and we combined the resources that were strongly and positively correlated for each species. Highly correlated food sources generally included SPOM-surface and SPOM-bottom and were then combined and renamed to "SPOM"; the zooplanktonic organisms (copepods, crab larvae and other larvae) were often combined and referred to as "Zooplankton". Finally, algae-upper and algae-lower were combined in a "Macroalgae" food source. All data analyses were conducted in R (R Development Core Team 2018).

Table 3.1: The seven dominant species (consumers) sampled in the different depth zones with the relative resources that were used in the mixing model per depth zone after the *a posteriori* combination of sources. The potential resources for every species according to the literature and the respective references are found at the last two columns.

Consumers	Zones of occurrence (number of replicates per consumer)	Resources used in the model (number of replicates)	Potential resources according to the literature	References
Diadumene cincta	*Mytilus* (6), *Jassa* (10)	SPOM (6) Copepods (3) Crab larvae (1) Other larvae (1)	Zooplankton, Invertebrate larvae	Sebens, 1981; Östman *et al*.. 2010; Nelson and Craig, 2011
Jassa herdmani	*Mytilus* (9), *Jassa* (8)	SPOM-bottom (3) SPOM-surface (3) Zooplankton (5)	*Ulva* thalli, *Artemia* nauplii	Beermann and Boos, 2015
	Scour protection layer (3), Soft substrate (5)	SPOM-bottom (3) SPOM-surface (3) Zooplankton (5) SOM (6)		
Metridium senile	*Mytilus* (6), *Jassa* (7), *Metridium* (10)	SPOM (6) Zooplankton (5)	Zooplankton, Invertebrate larvae	Sebens, 1981; Östman *et al*., 2010; Nelson and Craig, 2011
	Scour protection layer (10), Soft substrate (9)	SPOM (6) Zooplankton (5) SOM (6)		
Mytilus edulis	Intertidal (18)	SPOM (6) Copepods (3) Crab larvae (1) Other larvae (1) Macroalgae (20)	Diadoms, Phytoplankton, Particulate Organic Matter, Micro- and meso-zooplankton	Bayne *et al*., 1989; Maar *et al*., 2007
	Mytilus (14), *Metridium* (5)	SPOM (6) Copepods (3) Crab larvae (1) Other larvae (1)		

Necora puber	*Metridium* (5)	SPOM-bottom (3) SPOM-surface (3) Copepods (3) Crab larvae (1) Other larvae (1) *Pisidia longicornis* (24) *Pilumnus hirtellus* (5) Amphipods (31) Mussels (20) Sponges (2)	*Pisidia longicornis*, Amphipods, Mussels, Sponges, Fish	Freire and Gonzalez-Gurriaran, 1995
	Soft substrate (6)	SPOM-bottom (3) SPOM-surface (3) Copepods (3) Crab larvae (1) Other larvae (1) SOM (6) *Pisidia longicornis (24)* *Pilumnus hirtellus (5)* Amphipods (31) Mussels (20) Sponges (2)	*Pisidia longicornis*, Amphipods, Mussels, Sponges, Fish	Freire and Gonzalez-Gurriaran, 1995
Ophiothrix fragilis	*Mytilus* (7), *Jassa* (10), *Metridium* (6)	SPOM (6) Copepods (3) Crab larvae (1) Other larvae (1)	Fine particulate organic matter, Phytoplankton	Warner, 1971; Allen, 1998
Pisidia longicornis	*Mytilus* (8)	SPOM (6) Copepods (3) Crab larvae (1) Other larvae (1)	Pseudofaeces, suspended material	Sampedro *et al.*, 1997; Smaldon, 1972
	Scour protection layer (13)	SPOM (6) Copepods (3) Crab larvae (1) Other larvae (1) SOM (6)		

3.3 Results

3.3.1 Isotopic niche characteristics

Average δ^{13}C values of the resources ranged between -22.3 ± 0.3 ‰ (SPOM-surface) and -16.6 ± 0.0 ‰ (Other larvae), while the average δ^{15}N values ranged between 6.0 ± 0.8 ‰ (Algae-upper) and 11.4 ± 0.1 ‰ (copepods) (Table 3.2). The δ^{13}C signatures of the consumers (Table 3.3) ranged between -23.2 ± 2.5 ‰ (*Ophiothrix fragilis* in the *Jassa* zone) and -17.6 ± 2.2 ‰ (*O. fragilis* in the *Metridium* zone), while the δ^{15}N signatures ranged between 10.8 ± 1.0 ‰ (*O. fragilis* in the *Jassa* zone) and 16.1 ± 0.3 ‰ (*Necora puber* in the *Jassa* zone).

Table 3.2: Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values (‰, mean and standard deviation when possible) and number of samples (n) of the resources sampled, where SPOM: suspended particulate organic matter and SOM: sediment organic matter.

Resources	**δ^{13}C**	**δ^{15}N**	**n**
SPOM-surface	-22.3±0.3	11.3±0.2	3
SPOM-bottom	-21.4±1.3	10.7±0.2	3
Algae-upper	-19.5±0.3	6.0±0.8	10
Algae-lower	-18.9±0.4	6.7±0.3	10
SOM	-22.3±1.93	6.9±1	6
Copepods	-19.7±0.4	11.4±0.1	3
Crab larvae	-19.7	10.7	1
Other larvae	-16.6	11.2	1

The isotopic niche sizes (SEA$_C$) differed between species and within a species between different depth zones (Table 3.4). The largest SEA$_C$ (8.1 ‰^{2}) was observed for the brittle star *O. fragilis* in the *Jassa* zone, while the smallest SEA$_C$ (0.01 ‰^{2}) was found for the hemi-sessile species *J. herdmani* in the SPL (Fig. 3.2, Table 3.4). The extent of overlap of the isotopic niches differed between the species and zones (Table 3.5). For *P. longicornis*, *M. senile* and *O. fragilis*, there was little or no overlap between their isotopic niches in the different zones, while for *D. cincta* and *N. puber* considerable overlap was observed between the isotopic niches of the occupied zones (Fig. 3.2, Table 3.5). *Jassa herdmani* and *M. edulis* exhibited intermediate patterns. For the former species, the isotopic niche in the SPL did not show any

Table 3.3: Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values (‰, mean and standard deviation when possible) and number (n) of the consumers sampled at the six depth zones.

	Zones																	
	Intertidal zone			***Mytilus* zone**			***Jassa* zone**			***Metridium* zone**			**Scour protection layer**			**Soft substrate**		
Species	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n
Diadumene cincta	-	-	-	-20.0 ±0.5	14.3 ±0.3	6	-20.3 ±0.4	14.3 ±0.2	10	-	-	-	-	-	-	-	-	-
Metridium senile	-	-	-	-20.1 ±0.7	14.4 ±0.3	6	-20.2 ±0.4	13.6 ±0.8	7	-19.3 ±0.9	15.0 ±0.2	10	-19.8 ±0.9	14.7 ±0.5	10	-20.0 ±0.9	15.0 ±0.2	9
Mytilus edulis	-19.56± 0.8	10.9± 0.3	18	-19.7 ±0.3	10.8 ±0.2	14	-	-	-	-18.8 ±0.5	11.1 ±0.1	5	-	-	-	-	-	-
Jassa herdmani	-19.7	12.2	1	-18.9 ±0.2	11.7 ±0.4	9	-18.9 ±0.2	11.5 ±0.2	8	-	-	-	-19.5 ±0.3	11.8 ±0.1	3	-18.3 ±0.9	11.4 ±0.1	5
Necora puber	-	-	-	-	-	-	-17.2 ±0.1	16.1 ±0.3	2	-17.7 ±0.6	15.3 ±0.5	5	-	-	-	-17.1 ±1.0	15.0 ±1.9	6
Pisidia longicornis	-	-	-	-20.1 ±0.8	11.7 ±0.8	8	-	-	-	-21.4	9.8	1	-22.5 ±1.1	11.3 ±0.2	13	-20.3 ±1.7	11.6 ±0.1	2
Ophiothrix fragilis	-	-	-	-19.7 ±1.2	11.9 ±0.6	7	-23.2 ±2.5	10.8 ±1.0	10	-17.6 ±2.2	11.9 ±0.3	6	-	-	-	-	-	-

overlap with any of the isotopic niches from the other zones, but these other zones had ellipses that showed considerable overlap. For *M. edulis*, the isotopic niches in its two most important depth zones, i.e. the *Mytilus* and the *Metridium* zone, were completely separate, but the isotopic niche in the intertidal zone overlapped with that of the two other zones.

The abovementioned differences in the isotopic niches were further corroborated by the SEA_B, which was used to compare the isotopic niche sizes. Differences were observed at the species-specific level, as the SEA_B of the mobile species had high probabilities (generally > 0.8) of being larger than those of sessile and hemi-sessile species, with the exception of *P. longicornis* in the SPL (Fig. 3.3, Table 3.6, Table A2.2). The strongest differences were observed between the hemi-sessile species *J. herdmani* and the mobile species *N. puber* and *O. fragilis* (Fig. 3.3). Furthermore, differences were also detected within a species sampled in different zones, i.e. the probability that the SEA_B of *J. herdmani* in the SPL is smaller than in any of the other zones exceeded 0.69 (Table A2.2).

Generally, isotopic niches were elongated (E values close to 1) and stretched along the x-axis (absolute θ values < 45^0 - Table 3.4). This indicates the exploitation of multiple resources by each species within every zone. However, lower E values were also observed for *J. herdmani* in the *Jassa* zone (E = 0.68), for *N. puber* in the *Metridium* zone (E = 0.66), for *M. edulis* in the *Mytilus* zone (E = 0.79) and for *P. longicornis* in the *Mytilus* zone (E = 0.62). For most of the species, there was a general tendency for E values to increase with increasing water depth (Fig. 3.4, Table 3.4). The θ values were generally < 45^0, corroborating the major trends in E values, which also indicated utilization of a range of resources (larger spread along the x-axis). There were nevertheless some exceptions (absolute θ values > 45^0) that reflected an isotopic niche stretched along the y-axis. Such exceptions included *J. herdmani* in the *Mytilus* zone (θ = 76^0), *M. senile* in the *Jassa* zone (θ = 68^0), *N. puber* in the soft substrate (θ = -68^0) and *P. longicornis* in the *Mytilus* zone (θ = -53^0).

Table 3.4: Sample size-corrected standard ellipse area (SEA$_C$ - ‰^{2}), eccentricity (E), angle of the ellipse (θ), mode of the Bayesian standard ellipse area (SEA$_B$) and the lower and upper 95% credible intervals showing the uncertainty of SEA$_B$ (95% CI) of the consumer species collected at the different zones.

Species	**SEAc**	**E**	**θ**	**SEA$_B$**	**95 % CI**
Diadumene cincta					
Mytilus zone	0.55	0.86	-15.31	0.50	0.21 to 1.34
Jassa zone	0.24	0.87	-2.74	0.15	0.08 to 0.30
Jassa herdmani					
Mytilus zone	0.24	0.85	76.00	0.12	0.06 to 0.26
Jassa zone	0.11	0.68	41.95	0.10	0.04 to 0.22
Scour protection layer	0.01	1	17.84	0.06	0.02 to 0.25
Soft substrate	0.45	0.99	-3.31	0.30	0.10 to 0.88
Metridium senile					
Mytilus zone	0.29	0.99	24.61	0.42	0.20 to 1.14
Jassa zone	1.04	0.92	68.01	0.93	0.47 to 2.45
Metridium zone	0.41	0.99	13.28	0.38	0.20 to 0.79
Scour protection layer	1.28	0.91	25.38	0.67	0.34 to 1.36
Soft substrate	0.73	0.97	2.91	0.56	0.30 to 1.23
Mytilus edulis					
Intertidal zone	0.73	0.95	5.54	0.64	0.42 to 1.09
Mytilus zone	0.23	0.79	-15.7	0.18	0.10 to 0.31
Metridium zone	0.17	0.99	-4.69	0.09	0.03 to 0.27
Necora puber					
Metridium zone	1.32	0.66	11.25	0.87	0.30 to 2.49
Soft substrate	6.04	0.92	-68.03	4.57	1.80 to 12.30
Ophiothrix fragilis					
Mytilus zone	2.82	0.86	3.65	2.17	0.99 to 5.43
Jassa zone	8.10	0.93	-9.08	5.50	2.81 to 11.34
Metridium zone	2.31	0.99	-1.35	1.74	0.77 to 4.74
Pisidia longicornis					
Mytilus zone	2.24	0.62	-53.01	2.32	1.11 to 5.12
Scour protection layer	0.63	0.99	4.78	0.43	0.24 to 0.78

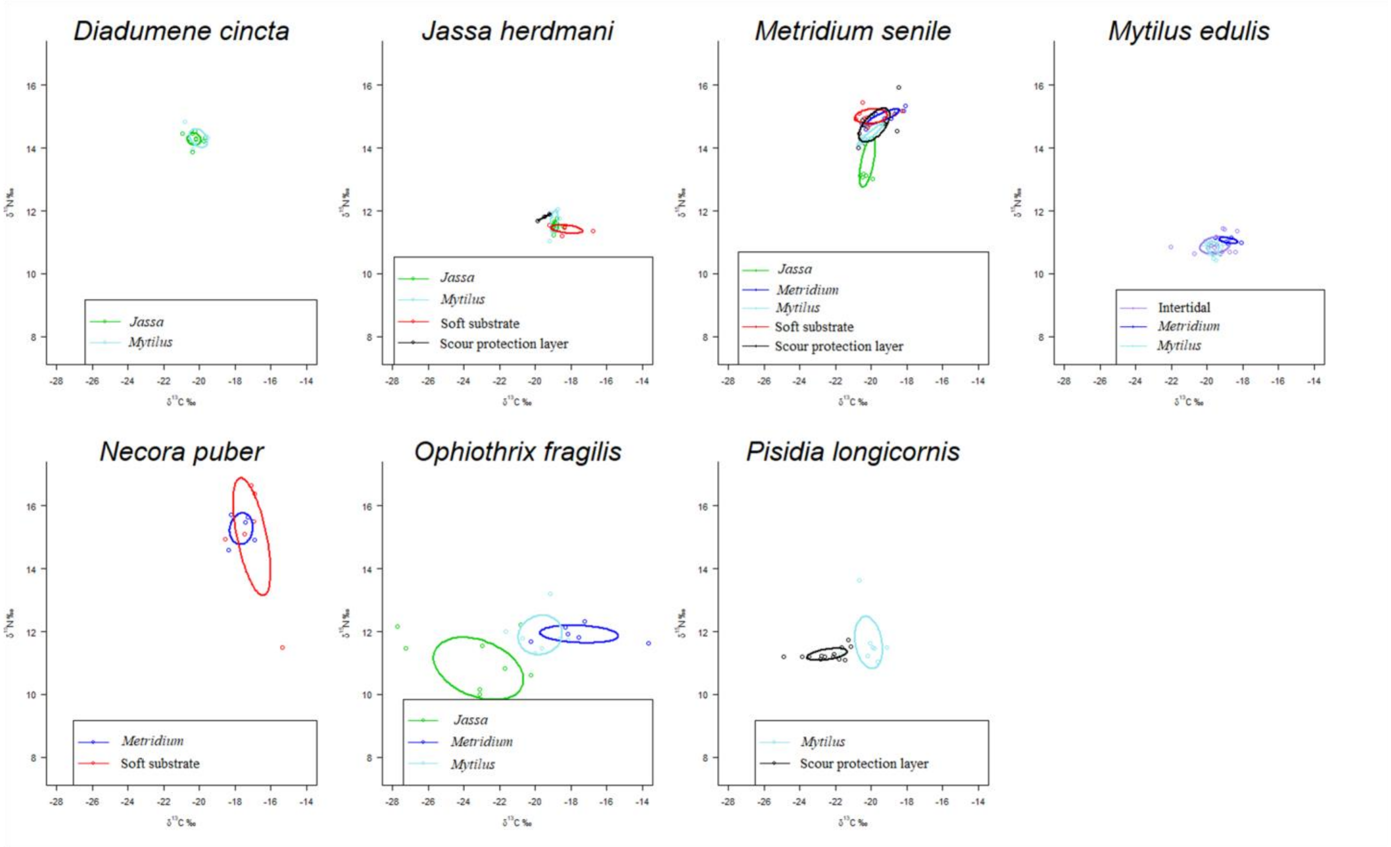

Figure 3.2: Sample-size corrected standard ellipse areas (SEA$_C$) calculated from $\delta^{13}C$ and $\delta^{15}N$ values for the seven species under study collected from different zones. The SEA$_C$ includes the 40 % of the data. The different colours represent different zones.

Table 3.5: Overlaps (‰^{2}) of the sample-size corrected standard ellipse areas (SEA$_{C}$) between the groups of the same species collected in different zones.

Diadumene cincta		
Mytilus zone	*Jassa* zone	0.20
Jassa herdmani		
Scour protection layer	*Jassa zone*	0.00
Scour protection layer	*Mytilus* zone	0.00
Scour protection layer	Soft substrate	0.00
Jassa zone	*Mytilus* zone	0.09
Jassa zone	Soft substrate	0.07
Mytilus zone	Soft substrate	0.07
Metridium senile		
Scour protection layer	*Jassa* zone	0.07
Scour protection layer	*Metridium* zone	0.31
Scour protection layer	*Mytilus* zone	0.25
Scour protection layer	Soft substrate	0.43
Jassa zone	*Metridium* zone	0.00
Jassa zone	*Mytilus* zone	0.02
Jassa zone	Soft substrate	0.00
Metridium zone	*Mytilus* zone	0.00
Metridium zone	Soft substrate	0.26
Mytilus zone	Soft substrate	0.00
Mytilus edulis		
Intertidal zone	*Metridium* zone	0.10
Intertidal zone	*Mytilus* zone	0.22
Metridium zone	*Mytilus* zone	0.00
Necora puber		
Metridium zone	Soft substrate	1.08
Ophiothrix fragilis		
Jassa zone	*Metridium* zone	0.00
Jassa zone	*Mytilus* zone	0.00
Metridium zone	*Mytilus* zone	0.63
Pisidia longicornis		
Scour protection layer	*Mytilus* zone	0.00

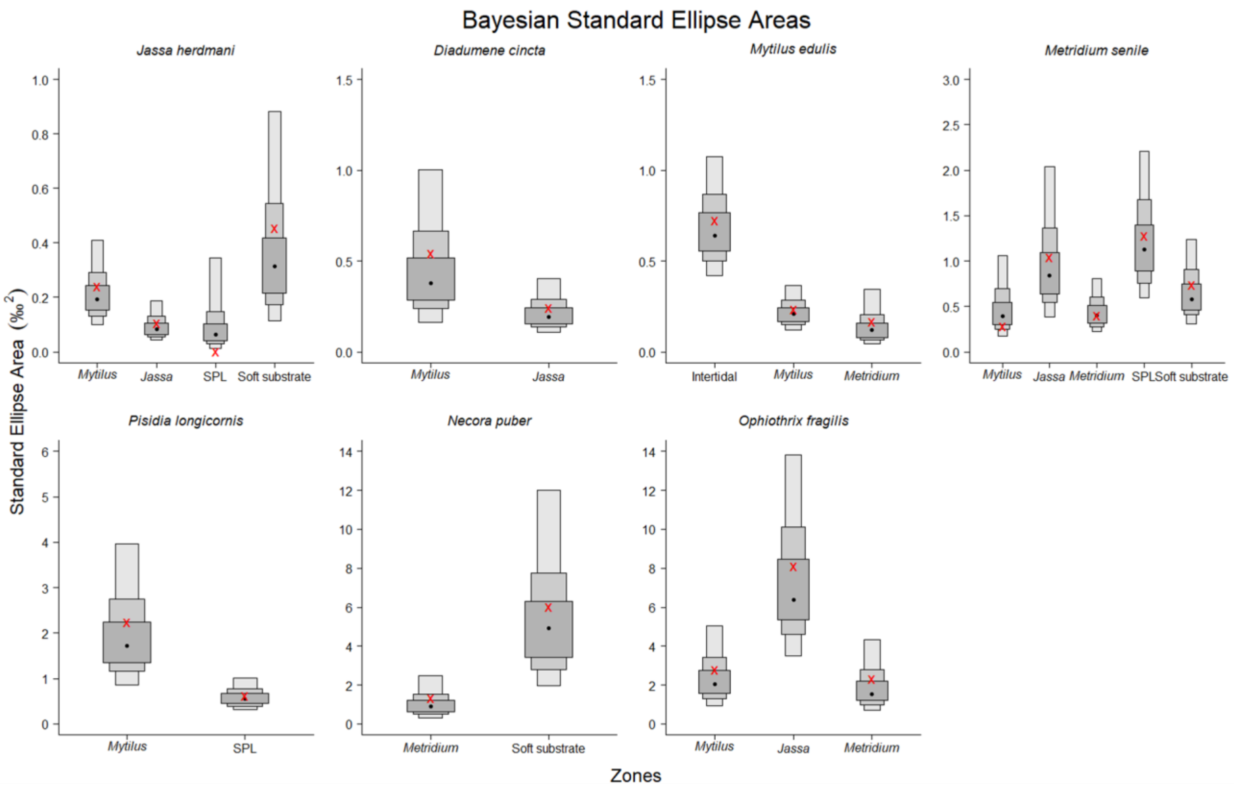

Figure 3.3: The posterior Bayesian estimates of the standard ellipse area (SEA_B) for the seven studied species in the different zones. Shaded density plots represent 50, 75 and 97 % credible intervals. SEA_B mode is represented by a black circle and SEA_C by a red x mark. The scale of the y-axis differs per species; smallest scale on the top left and largest scale to the bottom right.

Table 3.6: Bayesian standard ellipse area (SEA$_B$) probabilities (prob) that the ellipse area of one group is smaller than the other (g2).

Diadumene cincta		
g1	**g2**	**Probability**
Mytilus	*Jassa*	0.0055
Jassa herdmani		
g1	**g2**	Probability
Mytilus	*Jassa*	0.32475
Mytilus	Scour protection layer	0.22075
Mytilus	Soft substrate	0.9555
Jassa	Scour protection layer	0.3175
Jassa	Soft substrate	0.98125
Scour protection layer	Soft substrate	0.96875
Metridium senile		
g1	**g2**	**Probability**
Mytilus	*Jassa*	0.91075
Mytilus	*Metridium*	0.36175
Mytilus	Scour protection layer	0.7485
Mytilus	Soft substrate	0.65925
Jassa	*Metridium*	0.024
Jassa	Scour protection layer	0.19825
Jassa	Soft substrate	0.1305
Metridium	Scour protection layer	0.88425
Metridium	Soft substrate	0.81675
Scour protection layer	Soft substrate	0.3785
Mytilus edulis		
g1	**g2**	**Probability**
Intertidal	*Mytilus*	0.0005
Intertidal	*Metridium*	0.00075
Mytilus	*Metridium*	0.1725
Necora puber		
g1	**g2**	**Probability**
Metridium	Soft substrate	0.99225
Ophiothrix fragilis		
g1	**g2**	**Probability**
Mytilus	*Jassa*	0.94775
Mytilus	*Metridium*	0.3625
Jassa	*Metridium*	0.02675
Pisidia longicornis		
g1	**g2**	**Probability**
Mytilus	Scour protection layer	0.00025

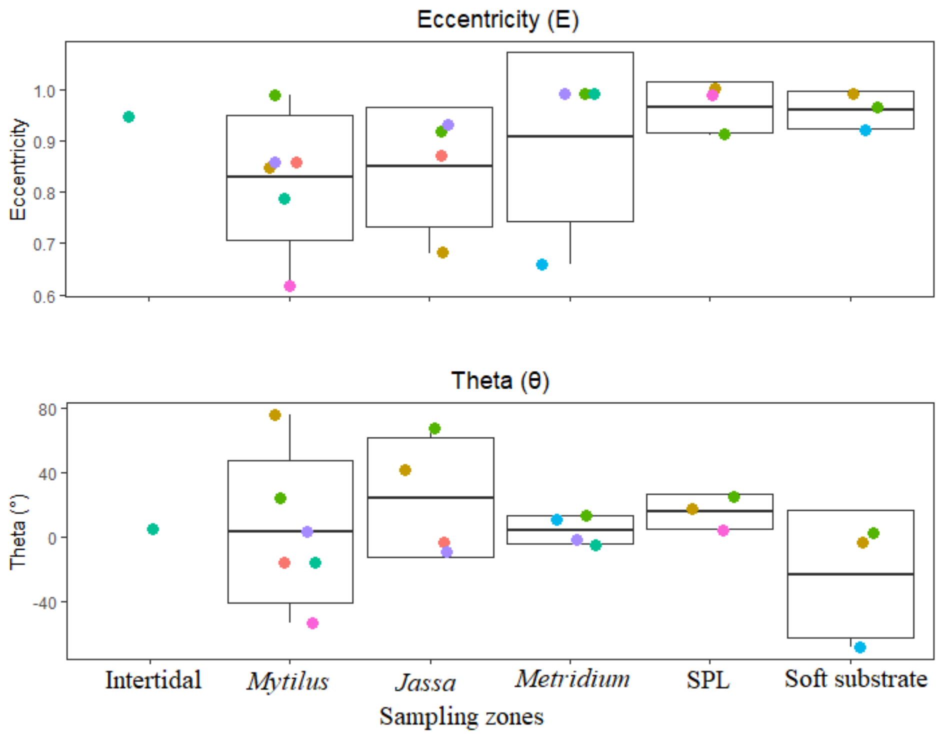

Figure 3.4: Eccentricity (E – upper graph) and theta (◦) (θ – lower graph) values of every species in the different zones (Intertidal, *Mytilus*, *Jassa*, *Metridium*, Scour Protection Layer – SPL and soft substrate). Each boxplot represents the median (middle horizontal line) and the lower and upper quartile (the lower and upper end of the boxplots respectively) of eccentricity and theta in the different zones, while the whiskers represent the extreme highest and lowest observations. Intertidal was the only zone without enough replicates to generate a boxplot.

3.3.2 Food resource contribution per consumer

The Bayesian stable isotope mixing models (SIMMR) revealed depth-dependent differences in resource utilization of species (Fig. 3.5, Table A2.3). *Diadumene cincta* was the only species that did not show any dietary differences between the different zones it occupied, exploiting mainly SPOM in both the *Mytilus* and the *Jassa* zone (mean and standard deviation: 63 ± 11.2 % and 72 ± 6.8 % contribution to its diet, respectively). *Necora puber* was the only species that exploited more or less equal shares (usually < 20 %) of multiple resources at every depth zone.

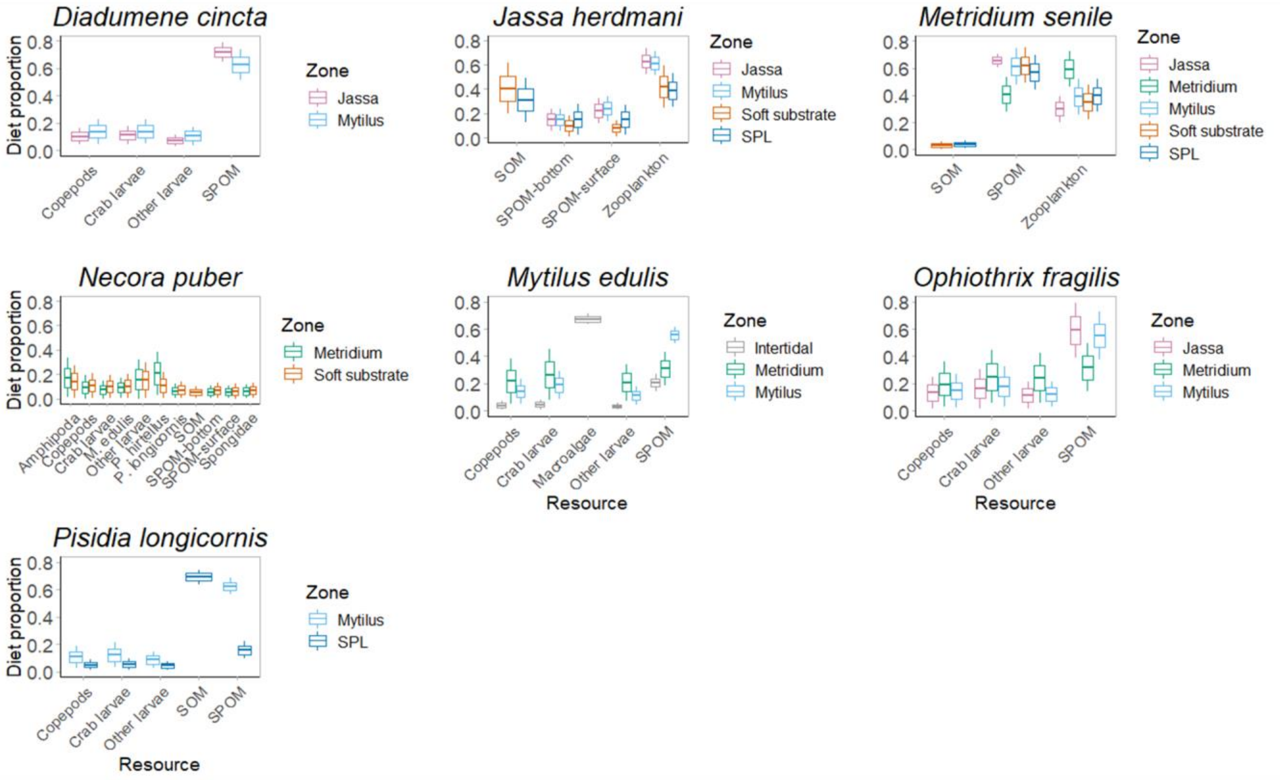

Figure 3.5: Potential contribution of each food resource to the diet of each species in the different zones. The different colours represent the different zones. The coloured boxplots represent the 25th percentile, the median and the 75th percentile of the dietary proportions, while the whiskers represent the 1.5*Interquartile ranges (IQR) of the upper and lower quartile.

The other consumers showed higher variability in their diets when sampled at different depth zones. *Jassa herdmani* mainly exploited zooplankton in the *Jassa* and *Mytilus* zones, while SOM was an important resource for *J. herdmani* from the SPL and soft substrate. The brittle star *O. fragilis* consumed SPOM in the *Mytilus* and *Jassa* zones (55.2 ± 17.4 % and 59 ± 20.1 %, respectively), but in the *Metridium* zone, the contribution of SPOM to its diet was considerably lower (31.6 ± 17.6 %). The contributions of crab and other zooplankton larvae to its diet (25.0 ± 19.4 % and 23.9 ± 18.3 %, respectively) were higher in the *Metridium* zone. The suspension-feeding crab *P. longicornis* mainly consumed SPOM (69 ± 11.7 %) in the *Mytilus* zone but SOM (69 ± 5.4 %) in the SPL. Finally, *M. edulis* mainly fed on macroalgal material in the intertidal (67.2 ± 3.9 %), while SPOM was an important food source in the subtidal zones (55.5 ± 5.9 % and 30.9 ± 12.3 % in the *Mytilus* and *Metridium* zones, respectively). However, in the *Metridium* zone, different resources contributed more or less equally to the diet of *M. edulis*.

3.4 Discussion

Competition may drive species to alter their niche, thus facilitating co-existence (Svanbäck and Bolnick, 2007). The most common mechanism to avoid resource competition is niche variation, where generalist species narrow down their resource use (Van Valen, 1965; Huss *et al.*, 2008). From this point of view – and in contrast to the alternative niche pre-emption theory (May and Arthur, 1972) – a strong competitor is not one that outcompetes other species at using the most favourable food, but one that exhibits high (‘dominant’) resource plasticity as a function of its competitive environment (Ashton *et al.*, 2010).

Our results partly confirmed our hypothesis that most species that are found across multiple depth zones at an offshore wind turbine would exhibit depth-specific resource use strategies. This was demonstrated both by the limited overlaps of the isotopic niches of a given species between different depths, and by depth-specific differences in their diet composition. These data support the idea of a considerable trophic plasticity, which was not related to the mobility of the species, since it was observed for both sessile and mobile species. Only the anemone *Diadumene cincta* proved to be a resource specialist, consuming suspended particulate organic matter (SPOM) irrespective of the zone where it was sampled.

3.4.1 Food resources and isotopic niches

The organisms occurring on offshore wind turbines have access to a wide range of food resources. These resources are generally well-mixed along the depth gradient (Jago and Jones, 1998; van Oevelen *et al.*, 2009; Franco *et al.*, 2010). Suspended particulate matter has been reported to be homogenously mixed in the water column in the southern part of the North Sea (Jago and Jones, 1998) and in close proximity to the OWFs (Floeter *et al.*, 2017; Forster, 2018). Similarly, chlorophyll *a* concentrations at the Belgian part of the North Sea (BPNS) have been observed to be comparable in surface and bottom waters (van Oevelen *et al.*, 2009; Franco *et al.*, 2010). From the potential resources that we sampled, zooplankton, suspended particulate organic matter (SPOM), sediment organic matter (SOM) and macroalgae were highly exploited by most of the invertebrate species (excluding *Necora puber* – Fig. 3.5). The carbon and energy content of these resources differs, with zooplankton being the most energy-rich, followed by macroalgae, SPOM, and finally SOM (Wilson and Parkes, 1998).

The results of our study indicate that the organisms occurring in deeper zones have generally broader trophic niches than those in the upper zones (Table 3.4). This implies that these organisms have access to a wide range of sedimentary sources, which are enriched around the base of the turbine foundations. Indeed, the biodeposition of faeces and pseudofaeces by filter-feeders (mainly *Mytilus edulis*) growing on offshore wind turbines enriches the nearby surroundings (Coates *et al.*, 2014), increasing both the availability, diversity and quality range of resources in the SPL and the soft substrate close to the turbines (Mavraki *et al.*, 2020). This may well explain why organisms from deeper zones generally exhibited isotopic niches that were more stretched along the x-axis (high E values and $\theta < 45°$ - Fig. 3.4), compared to their conspecifics from shallower zones (Reid *et al.*, 2016; Tabak *et al.*, 2016). *Diadumene cincta*, *M. edulis* and *O. fragilis* mainly had negative θ values (Table 3.4) indicating that an increase in their $\delta^{13}C$ values was associated with a decrease in $\delta^{15}N$, while the other species mainly had positive θ values, implying that $\delta^{13}C$ and $\delta^{15}N$ covaried positively (Reid *et al.*, 2016).

3.4.2 Trophic plasticity of colonising fauna

The resource utilization patterns shown by the mixing models at least partly confirmed the depth-dependence of feeding strategies indicated by the isotopic niche descriptors (section 3.4.1). As a direct consequence of these depth-specific feeding strategies, species like *M. edulis*, *M. senile*, *J. herdmani*, *O. fragilis*, *N. puber* and *P. longicornis* act as resource generalists at the turbine scale, while having narrower diets at the scale of single depth zones. This leads to zone-specific isotopic niches (Fig. 3.2), often with limited or no overlap (Table 3.5). Such switching between resource-use strategies can be an important mechanism to avoid resource competition (Bolnick *et al.*, 2003; Lefebvre *et al.*, 2009), and demonstrates a large degree of trophic plasticity of these species.

The diet of *M. edulis* in the *Mytilus* zone consisted mainly of SPOM (55.5 ± 5.9 %), which is considered an energy-poor resource (Wilson and Parkes, 1998; David *et al.*, 2006), while it largely obtained carbon from macroalgae (67.2 ± 3.9 %) when in the intertidal (Table A2.3). Macroalgae are abundantly present on offshore wind turbines in the North Sea, where they mostly consist of *Porphyra* spp. and *Ulva* spp. (Bouma and Lengkeek, 2008). While *M. edulis* cannot directly graze on macroalgae, it can filter fine particulate macroalgal detritus which becomes suspended due to waves and tidal action (Dubois *et al.*, 2007). In the *Metridium* zone, by contrast, 70 % of the diet of *M. edulis* consisted of various zooplankton groups (mainly crab larvae and copepods), SPOM still accounting for the remaining 30 %. A large dependence of *M. edulis* on zooplankton is in line with previous studies (Lehane and Davenport, 2002; Wong and Levinton, 2006; Maar *et al.*, 2007), but could result in resource competition with *M. senile*, which is the dominant species in this zone and feeds mainly on zooplankton. However, we suggest that zooplankton is abundant enough to fulfil the energy demands of both species.

Still, it should be noted that *M. edulis* feeds on a lower-quality food resource in its own zone of dominance. There are two possible explanations for this; either SPOM is much more abundant closer to the sea surface compared to the deeper areas, or there is higher intraspecific competition within the *Mytilus* zone than there is interspecific competition. Support for the higher availability of SPOM near the surface can be found in the diet of most species (*D. cincta*, *M. edulis*, *M. senile*, *P. longicornis*, *O. fragilis*), which exploited SPOM in the *Mytilus* and *Jassa* zones, while zooplankton was mainly exploited in deeper zones. Indeed, high surface concentrations of suspended particulate matter have been documented as sediment plumes by aerial photography (Vanhellemont and Ruddick, 2014) and acoustic data (Baeye and Fettweis, 2015) in the OWF areas in the BPNS. These are normally obvious shortly after strong storm events (Pleskachevsky *et al.*, 2005), but the construction of turbines induces their production due to the changes in the hydrodynamics and sediment transport, affecting the turbidity (Baeye and Fettweis, 2015). Plumes are associated with the wakes of single turbines, and their tidal stream and direction change with the tide cycle (Vanhellemont and Ruddick, 2014). The duration of the plumes differs with the tidal cycle and seasonality (Baeye and Fettweis, 2015), but they are persistent, since they are continuously repeating with each current reversal (Vanhellemont and Ruddick, 2014). Plumes are mainly caused by the resuspension of relatively small, fast-settling, predominantly inorganic particles (Eleveld *et al.*, 2008), while particles of organic origin are also part of them (Fettweis *et al.*, 2011; Baeye and Fettweis, 2015). This indicates that the concentration of SPOM can often be very high near the water surface, and therefore zooplankton densities will be relatively decreased there. Thus, it is possible that the organisms exploit the food resource that is *ad libitum*, shifting their diets synchronously towards this non-limiting food resource (Lefebvre *et al.*, 2009). Alternatively, it is possible that *M. edulis* shows higher intraspecific than interspecific competition in its own zone of dominance, leading to high competition between the *M. edulis* individuals for the limiting energy-rich resources and finally, to the exploitation of the non-limiting SPOM by the majority of them (Troost *et al.*, 2010).

Metridium senile fed on both zooplankton (59.3 ± 12.9 %) and SPOM (40.7 ±12.9 %) in its own depth zone, while in other depth zones, it mainly utilized SPOM (> 56 %, Table A2.3). The latter strategy may allow it to coexist with *J. herdmani* in the *Jassa* zone, where the highly abundant *J. herdmani* predominantly feeds on zooplankton

(Table A2.3). In the *Mytilus* zone, the feeding strategy of *M. senile* with a focus on SPOM may bring it in direct competition with *M. edulis*. There are two possible explanations for this dietary shift; either *M. senile* avoids competition with *J. herdmani* in the *Mytilus* zone, or it is energetically more favourable to feed on SPOM which is probably available in non-limiting quantities (see above), given that most of the species in the *Mytilus* and *Jassa* zones (except *J. herdmani*) primarily relied on SPOM (Table 3.7).

Jassa herdmani mainly fed on zooplankton in every depth zone. In the SPL and in soft substrate, the contribution of SOM increased substantially to 30 % and more (Table A2.3), but zooplankton remained the predominant resource. However, *J. herdmani* is not a sediment dwelling organism and its presence there can be explained by individuals that have become dislodged from the turbine (Bouma and Legkeek, 2012; Mavraki *et al.*, 2020). Their isotopic signatures likely reflect in part their original position along the turbine depth gradient and in another part an opportunistic and little selective use of the most available resource(s) at or near the sediment. In general, our results suggest that *J. herdmani* is a strong competitor for zooplankton, as evidenced by the higher contribution of zooplankton to its diet than to that of any other consumer in every zone where *J. herdmani* occurred (Table A2.3). Indeed, other species largely exploited zooplankton in the *Metridium* zone, where *J. herdmani* was rare.

Similarly, dietary shifts were also observed for mobile consumer species (Fig. 3.2), suggesting that these do not dwell the turbine and its environment in search of a preferred food source. *Pisidia longicornis* individuals sampled from the *Mytilus* zone mainly fed on SPOM (68.5 ± 11.7 %), while the diet of individuals from the SPL was dominated by SOM (69.3 ± 5.4 %). The size of the trophic niche (SEA_C) of *P. longicornis* was also considerably larger in the *Mytilus* zone than in the soft sediments (Fig. 3.2, Table 3.4), which may be a strategy of minimizing competition with *M. edulis* by broadening its trophic niche while sharing a substantial part of its resources with that species.

Table 3.7: The food resources that the species exploit in every zone of occurrence. Larger font size indicates higher exploitation of the food resources (> 50 %), while the food resources that are consumed by the dominant species in their zones of dominance are bold.

	Intertidal	*Mytilus* zone	*Jassa* zone	*Metridium* zone	Scour protection layer	Soft substrate
Diadumene cincta	-	SPOM Zooplankton	SPOM Zooplankton	-	-	-
Jassa herdmani	-	Zooplankton SPOM	**Zooplankton** SPOM	-	Zooplankton SOM SPOM	Zooplankton SOM SPOM
Metridium senile	-	SPOM Zooplankton	SPOM Zooplankton	**Zooplankton** SPOM	SPOM Zooplankton SOM	SPOM Zooplankton SOM
Mytilus edulis	Macroalgae SPOM Zooplankton	**SPOM** Zooplankton	-	Zooplankton SPOM	-	-
Necora puber	-	-	-	*Pilumnus hirtellus* Amphipods Mussels *Pisidia longicornis* Sponges SPOM-surface SPOM-bottom	-	Amphipods *Pilumnus hirtellus* Mussels *Pisidia longicornis* Sponges SPOM-surface SPOM-bottom
Ophiothrix fragilis	-	SPOM Zooplankton	SPOM Zooplankton	Zooplankton SPOM	-	-
Pisidia longicornis	-	SPOM Zooplankton	-	-	SOM SPOM Zooplankton	-

Ophiothrix fragilis is a deposit/suspension feeder that mainly consumed SPOM in the *Mytilus* (55.2 ± 17.4 %) and *Jassa* (59 ± 20.1 %) zones, but the contribution of SPOM to its diet dropped by almost half in the *Metridium* zone, where *O. fragilis* mainly fed on crab and other larvae (up to 70 %). These feeding strategies may bring *O. fragilis* in direct competition with *M. edulis* in the *Mytilus* zone and with *M. senile* in the *Metridium* zone. At the same time, it would limit competition between *O. fragilis* and *J. herdmani*, a strategy that is further enforced by a pronounced increase in the size of its trophic niche ($\mathrm{SEA_B}$, Fig. 3.3) in the *Jassa* zone. It is nevertheless important to note that niche expansion at the population level may not only follow from a decrease in interspecific competition, but also from an increase in intraspecific competition, because the latter may drive individuals to minimize niche overlap with conspecifics by narrowing their resource use (Svanbäck and Bolnick, 2007; Violle *et al.*, 2012). As such, the considerably larger isotopic niche of *M. edulis* in the intertidal zone, for instance, may also reflect strong intraspecific competition. Because isotopic niches are calculated at a 'population level' (i.e. for a group of individuals) rather than at an individual level, our data can only demonstrate the degree of variation within a population, but not the niche width of individual consumers, and hence cannot prove the ecological mechanism causing the observed variation.

In contrast to *O. fragilis*, *Necora puber*, exhibited no or only small differences in trophic niche between the *Metridium* zone and the soft substrate (Fig. 3.2). In the *Metridium* zone, *N. puber* was partly feeding on the small crab *Pilumnus hirtellus* (20.6 ± 17.9 %), while in the soft substrate, no specific dietary preferences were observed. This indicates that *N. puber* does not narrow its resource range and/or shifts to different food sources depending on the depth zone where it occurs, and exhibits very little trophic plasticity.

Finally, *D. cincta* was the only trophic specialist observed in our study, and hence, the only species that did not show any trophic plasticity. *Diadumene cincta* mainly consumed SPOM in both the *Mytilus* (62.5 ± 11.2 %) and the *Jassa* (71.9 ± 6.8 %) zones (Fig. 3.2, Table A2.3). The specialist diet of this species suggests that it cannot avoid competition with other, more dominant species. Because of their shared reliance on SPOM, trophic competition with *M. edulis* in the *Mytilus* zone is likely to occur, but in turn, limited competition is to be expected with *J. herdmani*, since the latter species predominantly preys on zooplankton.

3.4.3 Methodological considerations

The $\delta^{13}C$ values of SPOM and SOM were highly similar, which is in line with a previous study conducted in the area (Franco *et al.*, 2008). This could be explained by the composition of SOM, which partly consists of deposited SPOM particles and partly of the faecal pellets derived from the biodeposition of the colonising organisms (Coates *et al.*, 2014). The $\delta^{15}N$ values of SPOM were almost identical to the $\delta^{15}N$ values of zooplankton. Such similarities in the $\delta^{15}N$ values between SPOM and zooplankton have been previously reported in summer and autumn in the Mediterranean Sea (Bănaru *et al.*, 2014). Therefore, SPOM in our samples could contain a range of different particles, each with somewhat different isotopic signatures, that influenced the overall SPOM isotopic values but also the estimates of the contributions of SPOM and SOM to the diet of consumers.

In addition, we probably did not collect all the available potential resources (i.e. diatoms, bacteria, detritus, etc.). A significant contribution of bacteria to the diet of suspension feeding organisms, such as the blue mussel *Mytilus edulis* (Kreeger and Newell, 1996) and the brittle star *Ophiothrix fragilis*, might explain the unexpectedly low $\delta^{15}N$ values measured for suspension feeding organisms (Cresson *et al.*, 2016). Bacteria represent an important proportion of the organic carbon content in marine food webs (Richoux and Froneman, 2008) and are considered a potential food resource both for bivalves (Maar *et al.*, 2007; Mueller *et al.*, 2013; Cresson *et al.*, 2016; Demopoulos *et al.*, 2017) and for *O. fragilis* (Migne *et al.*, 2012).

3.5 Conclusions

Our study provides insight into the feeding strategies and dietary composition of invertebrate species associated with offshore wind turbine foundations. A considerable degree of trophic plasticity was observed for both sessile and mobile species, indicating that they exploit at least partly different resources in different depth zones. The isotopic niches of most species were highly horizontally elongated in deeper zones, which suggests that organisms consumed resources with distinct $\delta^{13}C$ values that are accumulated in the scour protection layer (SPL) and the surrounding soft sediments, but also that there was considerable intraspecific variation in diet. Our results suggested that *Diadumene cincta* was the only trophic specialist, since it predominantly fed on suspended particulate organic matter (SPOM) in both zones where it occurred. All the other species showed zone-specific dietary shifts, which may well represent a way to avoid trophic competition with the dominant species of each zone and/or a strategy to feed on energetically more favourable food sources. *Jassa herdmani* appeared to be a dominant competitor for zooplankton, since its occurrence in any depth zone coincided with a very limited or no contribution of zooplankton to the diets of the other species in that zone. Finally, this study suggests that trophic plasticity is likely a key mechanism allowing the co-existence of invertebrate organisms within and across depth zones at an offshore wind turbine.

Chapter 4

Organic matter assimilation by hard substrate fauna in an offshore wind farm area: a pulse-chase study

This chapter is a modified version of the manuscript submitted as: Mavraki, N., Degraer, S., Vanaverbeke, J., Braeckman, U. Organic matter assimilation by hard substrate fauna in an offshore wind farm area: a pulse-chase study. ICES Journal of Marine Science

Author contributions: NM setup and performed the pulse-chase experiment, sample preparation, data analysis and wrote the manuscript. UB guided the data analysis and the writing. JV and SD provided valuable suggestions for the experimental setup and for improving the context of the manuscript.

Abstract

The installation of offshore wind farms (OWF) adds artificial hard substrates into soft-bottom areas, changing the local biodiversity. The turbine foundations are rapidly colonised by colonising organisms, mainly consisting of suspension feeders that can potentially reduce the local primary producer standing stock. In this study we estimated the amount of organic matter processed by colonising assemblages of OWFs. We conducted a laboratory pulse-chase experiment, by offering ^{13}C-labelled fragmented algae to PVC panels colonised by OWF epibenthic fauna. The blue mussel *Mytilus edulis* showed the highest biomass-specific carbon assimilation, while the high densities of the amphipod *Jassa herdmani* resulted in the highest total carbon assimilation. By upscaling our results to the total number of the installed offshore wind turbines in the Belgian part of the North Sea, we estimate that these species can reduce the local primary producer standing stock in the area by ca. 1.3 %. *Mytilus edulis* and *J. herdmani* communities colonising offshore wind turbine foundations remarkably increase carbon assimilation compared to natural soft sediment macrofauna inhabiting the same surface area (i.e. footprint of the turbines).

As compared to natural soft sediments, jacket foundations cause the highest and gravity-based foundations the lowest increase in the local carbon assimilation.

4.1 Introduction

In recent years, the offshore wind farm (OWF) industry is rapidly increasing in order to meet green energy requirements. As a result, OWFs are continuously under construction and/or scheduled in the North Sea (Soma *et al.*, 2019), since they allow a high total level of energy production (EC, 2008; EWEA, 2012). In the beginning of 2018, 4149 offshore wind turbines were installed in European marine waters, corresponding to a capacity of 15.8 GW, while in 2020 this capacity is expected to reach 25 GW and up to 48 GW in 2030 (WindEurope, 2018).

The establishment of OWFs induces changes to the marine environment (Lindeboom *et al.*, 2011; Gill *et al.*, 2018). Wind turbines are being rapidly colonised by epibenthic communities (Krone *et al.*, 2013a; De Mesel *et al.*, 2015; Nall *et al.*, 2017), which mainly consist of suspension feeders (Lindeboom *et al.*, 2011). Suspension feeders capture food particles that are in suspension and are highly diluted in the water column (Gili and Coma, 1998). These organisms (i.e. the blue mussel *Mytilus edulis*) may reduce both the phytoplankton and the micro- and meso-zooplankton biomass (Maar *et al.*, 2007; Slavik *et al.*, 2019). This could eventually lead to an alteration of food webs and biogeochemical cycling in and around the OWFs (Slavik *et al.*, 2019).

Understanding the nature and fate of organic matter in marine communities is important in order to estimate the extent of and variability in carbon consumption in marine ecosystems and their contribution to the marine carbon budget (Cebrian, 2002). Especially in OWFs, the increased abundances of colonising organisms (Lindeboom *et al.*, 2011; De Mesel *et al.*, 2015) might lead to increased reduction of phytoplankton around these installations (Slavik *et al.*, 2019). In the southern North Sea, such high abundances of colonising species were not present before the construction of the thousands of offshore wind turbines. Thus, estimating the organic matter consumption by colonising species is important in understanding the effects of these organisms on the pelagic ecosystem (Slavik *et al.*, 2019). Currently, such estimations are available from modelling exercises, which only considered the role of the blue mussel *M. edulis* for the reduction of the annual primary producer standing stock (Slavik *et al.*, 2019). However, obtaining experimental data to validate model estimates and also considering species other than *M. edulis* are lacking so far. A way to acquire such data is to perform labelling experiments.

Labelling organic matter with stable carbon and/or nitrogen isotopes has been shown to be a useful method for quantifying the consumption and assimilation of food resources by benthic organisms (Middelburg *et al.*, 2000; Boschker and Middelburg, 2002; Aberle and Witte, 2003). By conducting pulse-chase experiments, the rates and pathways of short-term organic matter cycling in benthic communities can be quantified (Middelburg *et al.*, 2000; Witte *et al.*, 2003a, 2003b; Woulds *et al.*, 2007). This approach has been extensively applied in a wide range of soft sediment habitats, from estuaries (Middelburg *et al.*, 2000; Moodley *et al.*, 2000) to abyssal areas (Witte *et al.*, 2003a; Woulds *et al.*, 2009, 2016), from polar (Gontikaki *et al.*, 2011a, 2011b; Braeckman *et al.*, 2019) to the tropic regions (Aspetsberger *et al.*, 2007; Sweetman *et al.*, 2010) and from organic carbon-rich (Woulds *et al.*, 2007) to oligotrophic sediments (Bühring *et al.*, 2006a). However, to our knowledge, this type of experiment has not been applied to hard substrate communities yet.

In the present study, we aimed at investigating the hard substrate macrofaunal carbon (C) assimilation by the colonising fauna that occurs at offshore wind turbines. We conducted a mesocosm experiment in which we applied a carbon stable isotope labelling approach to track the organic matter into the macrofaunal biomass. We hypothesized that the different colonising taxa would demonstrate significant differences in carbon assimilation, with the blue mussel *M. edulis* showing the highest assimilation rate, since this species is known to be a key player in the reduction of the primary producer standing stock (Slavik *et al.*, 2019). Furthermore, we upscaled the results of this study to the total number of wind turbines in the Belgian part of the North Sea to estimate the grazing effect of colonising fauna on the local primary producer standing stock. Finally, we compared the amount of carbon assimilated by the colonising fauna to that of a natural soft sediment macrofauna inhabiting the same surface area as the footprint of a monopile, a jacket and a gravity-based foundation.

4.2 Materials and methods

4.2.1 Organism collection

Colonising organisms are typically attached on the offshore wind turbine foundations and they can disperse to newly established hard substrates either via their planktonic larvae or as adults (Lange *et al.*, 2010; Lindeboom *et al.*, 2011; Krone *et al.*, 2013a). To bring naturally grown hard substrate assemblages from OWFs to the laboratory, nine PVC panels (15 x 15 cm) were attached on a tripod (1.5 - 2 m above the sea floor – Fig. 4.1) and deployed in April 2017 in the C-Power OWF on the Thornton Bank (water depth: ca. 25 m, coordinates: 51°54.08′N – 2°91.68′E) in the Belgian part of the North Sea (BPNS). The distance between the tripod and the turbines was approximately 500 m. The panels were roughened on one side to facilitate colonisation (Beermann and Franke, 2012), while their distance apart was approximately 5 cm. The panels remained in the water for one year in order to be fully colonised by epibenthic organisms and were recovered in April 2018. The PVC panels were randomly and carefully collected in sealed plastic bags by scientific divers (1 PVC panel per bag) before being taken to the surface. Upon recovery, the PVC panels were fully colonised (Fig. 4.2) and were immediately placed in buckets with filtered seawater, since we aimed at conducting the mesocosm experiment with starved organisms. Thus, using filtered seawater would ensure that gut evacuation would start immediately after recovery. Air supply was also provided until the plates were transferred to the laboratory, within four hours.

4.2.2 Experimental set-up

In the laboratory, four PVC panels were immediately scraped in order to provide background ^{13}C data. At least five individuals per species per PVC panel were isolated whenever possible, kept overnight in filtered seawater for gut evacuation and stored in -20 °C until further analysis (see 4.2.3). Only females and non-thumbed males were collected for the species *Jassa herdmani*, since the thumbed males do not feed extensively (Beermann and Franke, 2012). The remaining organisms were kept in a formaldehyde-seawater solution (8 %) for species identification, counting and biomass measurements. The other five PVC panels were incubated in five separate experimental tanks (one PVC panel per experimental tank) that contained in total 17 l of 0.2 µm filtered sea water, at an in situ temperature of 10 °C and air supply, in a dark climate room. An experimental tank consisted of two chambers (lower and upper) connected by two water pipes to enable water circulation (Fig. 4.3). The lower chamber contained an air pump and a water pump circulating the water (speed of water circulation 9 l min-1), since most of the colonising species found at OWFs are suspension-feeders (Lindeboom *et al.*, 2011) and need water current that can keep the food particles in suspension (Gili and Coma, 1998). The upper chamber contained a colonised PVC panel hanging in the chamber and a mesh (mesh size: 1 mm) that was preventing the mobile and hemi-sessile macro-organisms to flow to the lower chamber.

Figure 4.1: Image of the set-up of the PVC panels on the tripod before they were deployed at sea in April 2017.

Figure 4.2: Image of a fully colonised PVC panel after recovery.

After 24 h of acclimation, approximately 0.1 g of lyophilized fragmented algae corresponding to 43 mg C (99 atom % ^{13}C, Sigma-Aldrich ® 478,945) was suspended in 1 l of filtered (0.2 µm) sea water to assure a homogenous mixing of the algal cells. The suspended fragmented algae were subsequently added to the upper chamber of every experimental tank. Hence, the total volume of each experimental tank was 18 l after the addition of the algae. We aimed at providing the food resources *ad libitum* to assure sufficient food particles in every experimental tank. Therefore, we initially calculated the amount of carbon that naturally occurs in the BPNS. Previous chlorophyll *a* measurements in the same sampling season in the BPNS indicated that the chl *a* concentration is ca. 40 mg m^{-3} (Provoost *et al.*, 2013). We recalculated this amount to organic carbon content following Legendre and Michaud (1999):

$$\log_{10} [\mathrm{POC}] = 2.27 + 0.35 \log_{10} [\mathrm{chl}\ a]$$

From this equation, the amount of carbon that naturally occurs in the BPNS in spring was estimated at 0.68 mg C l^{-1} corresponding to ca. 12 mg C per tank. Soft sediment macrofaunal organisms can rapidly assimilate ^{13}C-labelled material (Witte *et al.*, 2003a) and thus, three days of experimental duration was assumed to be sufficient for the enrichment of all the individuals. Since we wanted to have unlimited food conditions during three days of incubation, we added ca. 43 mg C per tank.

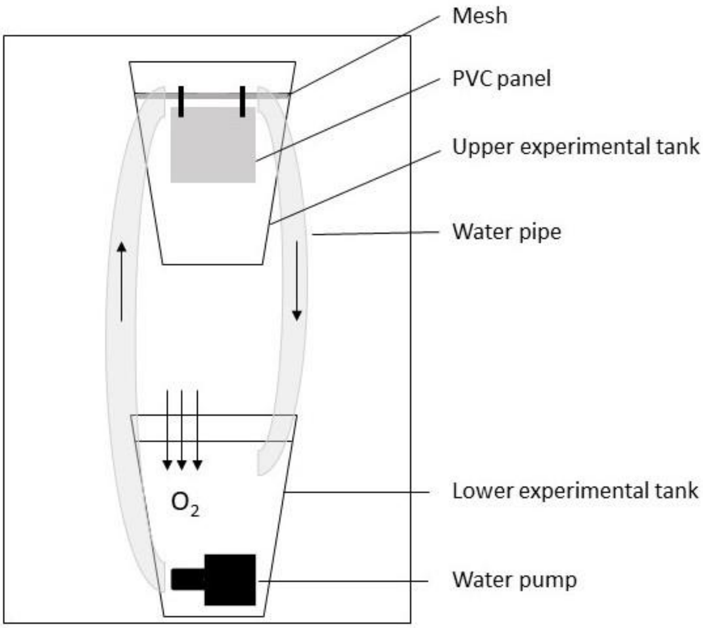

Figure 4.3: Experimental set-up. The colonised PVC panel hanged from the mesh in the upper experimental tank. The lower experimental tank contained a water and an oxygen pump. The two tanks were connected with two water pipes that allowed for the circulation of the water as it is shown by the two single arrows.

At the end of the incubation period, the PVC plates of every experimental tank were isolated and completely scraped. The organisms were consequently processed as described above for the background data. Furthermore, the water from the tanks was sieved and the remaining algal material was stored in -20 °C. The few organisms that were in the water were isolated and included in the identification, counting and biomass measurements of the respective replicate.

4.2.3 Laboratory analysis

The total species abundance of each PVC panel (including the ones for the background data – see 4.2.2) was counted. The organisms were identified under a stereomicroscope to the lowest taxonomic level possible, counted and weighed (dry weight and ass-free dry weight). Densities of the amphipod *J. herdmani* were derived from subsamples since this was a very abundant species on the PVC panels. The abundances per taxon and per experimental tank were then used to estimate the total carbon assimilation per unit of biomass in the entire colonising assemblage (see 4.2.4).

The frozen macrofaunal samples from both the background and the incubated PVC panels were thawed, rinsed with milli-Q water and further processed for stable isotope analysis (SIA). Entire individuals of amphipods, polychaetes, nudibranchs, anemones, crabs and small mussels, and foot tissues from gastropods were dried overnight at 60 ℃ (Pinnegar and Polunin, 1999). The dried tissues were grounded to a homogenous powder using a pestle and a mortar. Approximately 1 mg of dried tissue of calcareous-shelled organisms and crustaceans was placed in silver (Ag) cups (8 x 5 mm, Elemental Microanalysis UK) and was decarbonated by adding 1 % HCl "drop by drop" until the elimination of CO_2 (Jacob *et al.*, 2005). After the decarbonation, the acidified samples were rinsed with distilled water, dried and encapsulated. Dried tissue from organisms without calcareous parts was immediately encapsulated in tin (Sn) cups and stored dry in multi-well Microtitre plates in a desiccator until further analysis. The majority of the specimens were encapsulated individually. However, the dry weight of some small in size organisms was not sufficient, and hence, more individuals of the same species and from the same plate were pooled together for the isotopic analysis.

All the samples for carbon stable isotope analysis were analysed at the UC Davis Stable Isotope Facility (University of California, USA). The carbon isotopic composition was determined with a PDZ Europa ANCA-GSL elemental analyser 230 interfaced to a PDZ Europa 20-20 isotope ration mass spectrometer. The results were expressed in the standard delta (δ) notation in parts per thousand (‰) as stated by the following equation:

$$\delta^{13}C = [(R_{Sample} / R_{Standard}) - 1] \times 10^3$$

where R is the corresponding ratio of $^{13}C/^{12}C$.

4.2.4 Carbon assimilation

Carbon assimilation was calculated according to Middelburg *et al.* (2000). The total specific uptake was calculated as the product of excess ^{13}C (E) and organic carbon in the biomass. Excess ^{13}C was calculated as the difference between the fraction ^{13}C of the background ($F_{background}$) and the sample (F_{sample}):

$$E = F_{sample} - F_{background}$$

where

$$F = {}^{13}C/({}^{13}C + {}^{12}C) = R/(R + 1)$$

and

$$R = (\delta^{13}C/1000 + 1) \times R_{VPDB}$$

where $R_{VPDB} = 0.0111802$ is the carbon isotopic ratio of the Vienna Pee Dee Belemnite standard.

Macrofaunal ^{13}C assimilation was calculated as the product of the ^{13}C excess (E) and the carbon content of the sample, divided by the fraction of ^{13}C in the total carbon content of the labelled algae (99 %). The mean carbon assimilation was calculated for every species and multiplied by their abundance in every experimental tank. Assimilation into total biomass is expressed as total assimilation per species and replicate (summed individual assimilation × abundance; in µg C assimilation µg C biomass^{-1}).

4.2.5 Data analysis

One-way analysis of variance (ANOVA) was used to test for differences in: (a) carbon biomass, (b) total carbon assimilation, and (c) total carbon assimilation per unit of biomass between the different macrofaunal species. Species present on less than three replicates (N < 3, *Pilumnus hirtellus*, *Leptoplana tremellaris* and *Lanice conchilega*) were excluded from these analyses since their contribution to the carbon assimilation and/or biomass was assumed to be only marginal. Prior to the ANOVA analyses, the assumption of homogeneity of variances (Levene's test) and the assumption of normality of the data (Shapiro test) were tested and proved valid. Post hoc multiple comparisons were performed using the Tukey's Honest Significant Difference (HSD) test. All statistical analyses were carried out in R 3.5.3 (R Development Core Team 2018). Results are expressed as mean ± standard deviation (sd).

4.2.6 Upscaling rationale and calculations

To upscale our results to the total OWF area in the BPNS, calculations were performed by combining the results of this and previous studies (Table 4.1). Only *J. herdmani* and *M. edulis* were included in the upscaling calculations, since these two species assimilated the largest amount of carbon compared to the other colonising fauna (see 4.3) and they are two of the most abundant species on the offshore wind turbine foundations. The surface area that each species occupies on the gravity-based foundations was estimated by Ivanov *et al.* (pers.com.). Similar zonation patterns to gravity-based foundations have been observed for monopiles. On jacket foundations, mussels occupy the upper one third of the foundations while *J. herdmani* expands its distribution at the lower two thirds (Kerckhof pers. com.). Each type of foundation has a different footprint area on the seafloor (Rumes *et al.* 2013). As a footprint here we considered the surface area of the soft sediment that is lost due to the construction of each type of foundation, while changes caused to the soft sediment after the construction of the foundations were not taken into account. Data concerning the respiration, defaecation and - for *J. herdmani* - moulting rates (Hawkins and Bayne, 1985; Yamada and Ikeda, 2006) of these two species were also considered to calculate the actual carbon assimilation rate per species and from that, the actual carbon consumption rates (see below). Finally, the total primary production (213 g C m^{-2} y^{-1}) in the BPNS (Lancelot *et al.*, 2005) and the amount of carbon that is assimilated by macrofaunal communities in permeable North Sea sediments (mg C m^{-2} d^{-1} - Bühring *et al.*, 2006b) were also included in the data used for the upscaling calculations.

Using these data, we calculated the total carbon biomass per foundation type (µg C m^{-2}) by multiplying the mean individual biomass (µg C ind^{-1}) with the total density (individuals m^{-2}) per type of foundation. Then, the carbon assimilation per type of foundation (µg C m^{-2} d^{-1}) was estimated and was upscaled to the total carbon assimilation (g C y^{-1}) for all the different types of foundations in the BPNS (monopiles, jackets and gravity-based foundations). We estimated the total carbon assimilation for one year assuming equal carbon assimilation by these two species throughout the year. Using the results of this study combined with the annual primary production in the BPNS (Lancelot *et al.*, 2005), we determined the percentage of the primary producer standing stock in the BPNS OWFs that is assimilated by *J. herdmani* and *M. edulis*. By dividing the carbon assimilation of *J. herdmani* and *M. edulis* occurring in all the OWF foundations in the BPNS with their assimilation rates (as provided by the literature) we estimated the percentage of the primary producer standing stock that is processed/grazed upon by these two species. Finally, we determined the amount of carbon that is not assimilated by the natural permeable sediment macrofauna due to the construction of each type of foundation and defined the ratios turbine (mg C)/sediment (mg C) to evaluate the additional amount of carbon that is assimilated due to the presence of colonising fauna.

Table 4.1: Data used for the upscaling calculations for the two different colonising species, the turbine foundations in the Belgian part of the North Sea (BPNS), the annual primary production in the area and the carbon assimilation of macrofaunal organisms typically occurring at permeable sediments.

DATA					**References**
	Jassa herdmani	***Mytilus edulis* (<1cm)**	***Mytilus edulis* (1-3cm)**	***Mytilus edulis* (>3cm)**	*J. herdmani* and *M. edulis* (1-3cm): this study; *M. edulis* weight (>3cm): Bouma and Lengkeek, 2012; *M. edulis* weight (<1cm): Mallet *et al.*, 1987
Mean individual biomass (µg C)	285	51	238	394	
Mean individual biomass-specific C assimilation (µg C/µg C ind^{-1})	0.30	1.11	1.11	1.11	this study

Total surface area (m^2) on MONOPILES per species	384	192	192	192	Rumes *et al.*, 2013
Total surface area (m^2) on JACKETS per species	887	444	444	444	Rumes *et al.*, 2013
Total surface area (m^2) on GRAVITY-BASED per species	173	123	123	123	Ivanov *et al.*, pers. comm.
Total density (individuals m^{-2}) per MONOPILE	24339	251	1368	224	Kerckhof, pers. comm.
Total density (individuals m^{-2}) per JACKET	68848	22208	7800	0	Kerckhof, pers. comm.
Total density (individuals m^{-2}) per GRAVITY-BASED	47765	3268	5196	304	Mavraki *et al.*, unpublished data
Number of MONOPILES in BPNS	264				
Number of JACKETS in BPNS	48				
Number of GRAVITY-BASED foundations in BPNS	6				
Footprint per MONOPILE (m^2)	573				Rumes *et al.*, 2013
Footprint per JACKET (m^2)	10.5				Rumes *et al.*, 2013
Footprint per GRAVITY-BASED (m^2)	2227				Rumes *et al.*, 2013
Respiration fraction	0.28	0.36	0.36	0.36	*Mytilus edulis*: Hawkins and Bayne, 1985 *Jassa herdmani*: Yamad and Ikeda, 2006
Moulting fraction	0.04				
Defaecation fraction		0.48	0.48	0.48	
Assimilation fraction	0.32	0.16	0.16	0.16	
Surface area OWF in BPNS (km^2)	238				
Total production in BPNS (g C m^{-2} y^{-1})	213				Lancelot *et al.*, 2005
Carbon assimilation (mg C m^{-2} d^{-1}) by macrofauna in sediment	Min: 3.3	Max: 42			Bühring *et al.*, 2006b

4.3 Results

4.3.1 Macrofaunal abundance and biomass

The amphipod *Jassa herdmani* was the most abundant species with 12963 ± 10015 individuals per incubated PVC panel (Table 4.2). The second most abundant species was the amphipod *Monocorophium acherusicum* (250 ± 188 ind.), followed by the blue mussel *Mytilus edulis* (86 ± 10 ind.). The other species/taxa showed lower abundances (ranging from 1 to 10 individuals per PVC panel).

Significant differences between the species carbon biomass were observed (ANOVA $F_{6,23} = 50.78$, $p < 0.001$). The total *J. herdmani* carbon biomass per PVC panel at the end of the experiment averaged 1052 ± 823 mg C d^{-1}, followed by the amphipod *M. acherusicum* with a carbon biomass that averaged 20 ± 15 mg C d^{-1}. In contrast, *M. edulis* carbon biomass per PVC panel was significantly lower than that of *J. herdmani* and *M. acherusicum*, averaging 6.8 ± 1.2 mg C d^{-1}. The carbon biomass of *J. herdmani* and *M. acherusicum* was significantly higher than that of the other species (Tukey HSD, $p_{adj} < 0.05$), implying that they contributed the most to the total carbon biomass on the panels. All the other species showed similarly small carbon biomass (< 8.5 mg C d^{-1}) (Tukey HSD, $p_{adj} > 0.05$), including the species that were not tested in the ANOVA (*Lanice conchilega*, *Leptoplana temellaris* and *Pilumnus hirtellus*).

4.3.2 Biomass specific C assimilation

The $\delta^{13}C$ signatures (Table 4.3) of 228 individual specimens at the end of the experiment ranged between -18.8 ± 0.1 ‰ (the polychaete *L. conchilega*) and 1894 ± 1094 ‰ (the blue mussel *M. edulis*).

The biomass specific carbon assimilation differed significantly between the species (ANOVA $F_{6,23} = 18.49$, $p < 0.001$ – Fig. 4.4). *Mytilus edulis* was the species with the highest biomass-specific carbon assimilation (9.8 ± 6.5 µg C assimilation per mg C biomass d^{-1}, Tukey HSD, $p_{adj} < 0.05$), while *J. herdmani* showed very low biomass specific carbon assimilation (0.2 ± 0.15 µg C assimilation per mg C biomass d^{-1}). *Crepidula fornicata* showed the second highest biomass-specific carbon assimilation (0.62 ± 0.18 µg C assimilation per mg C biomass d^{-1}), which was not significantly

Table 4.2: Taxa, A: abundance (ind panel^{-1}) and B: biomass (mg C panel^{-1})s of the organisms found in the five experimental panels.

Taxa	**PVC Panel 1**		**PVC Panel 2**		**PVC Panel 3**		**PVC Panel 4**		**PVC Panel 5**	
	A	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Crepidula fornicata	2	0.94	3	0.94	2	0.64	2	0.51	3	1.16
Jassa herdmani	3023	738	5933	1537	15551	3838	11702	2611	28608	7050
Lanice conchilega	-	-	-	-	69	30.92	-	-	194	91.49
Leptoplana tremellaris	-	-	-	-	-	-	-	-	1	0.33
Metridium senile	21	8.81	-	-	2	0.67	8	2.79	7	2.74
Monocorophium acherusicum	48	9.79	61	18.15	477	120	333	65.6	333	87.39
Mytilus edulis	-	-	93	25.07	96	19.63	74	16.52	80	20.50
Nudibranchia	-	-	-	-	7	2.89	1	0.44	3	1.22
Oerstedia dorsalis	2	0.68	5	1.66	2	0.55	-	-	8	3.82
Pilumnus hirtellus	-	-	-	-	-	-	-	-	5	1.12

lower than that of *M. edulis* (Tukey HSD p_{adj} < 0.05). The biomass-specific carbon assimilation of the other species was significantly lower than that of *Mytilus edulis* (values ranging from 0.002 to 1.36 µg C assimilation per mg C biomass d^{-1}, Tukey HSD p_{adj} > 0.05).

Table 4.3: Natural and enriched stable carbon isotope values (‰, mean and standard deviation when possible) of all the background panels together and of the five panels included in the experimental tanks.

Taxa	**Natural δ^{13}C**	**Reference**	**PVC panel 1**	**PVC panel 2**	**PVC panel 3**	**PVC panel 4**	**PVC panel 5**
Crepidula fornicata	-19.6 ± 0.1	this study	114	132±124	141±67	198±181	217±330
Jassa herdmani	-19.44 ± 0.35	this study	71±59	14±24	6±25	97±181	-1±11
Lanice conchilega	-18.90	Mavraki et al. (2020)	-	-	-	-	-19±0
Leptroplana tremellaris	-20.7 ± 0.2	Mavraki et al. (2020)	-	-	-	-	-17
Metridium senile	-18.80 ± 0.42	this study	-13±7	-	-8±1	-7±8	-13±6
Monocorophium acherusicum	-20.85 ± 0.32	this study	186±110	136±32	119±91	191±166	108±45
Mytilus edulis	-20.75 ± 1.62	this study	-	1159±272	1235±631	3187±576	1644±843
Nudibranchia	-18.86	this study	-	-	-17±1	-17	-17±0
Oerstedia dorsalis	-19.72 ± 0.02	this study	-6±3	-17±2	-12	-	-17±5
Pilumnus hirtellus	-19.98 ± 0.6	Mavraki et al. (2020)	-	-	-	-	18

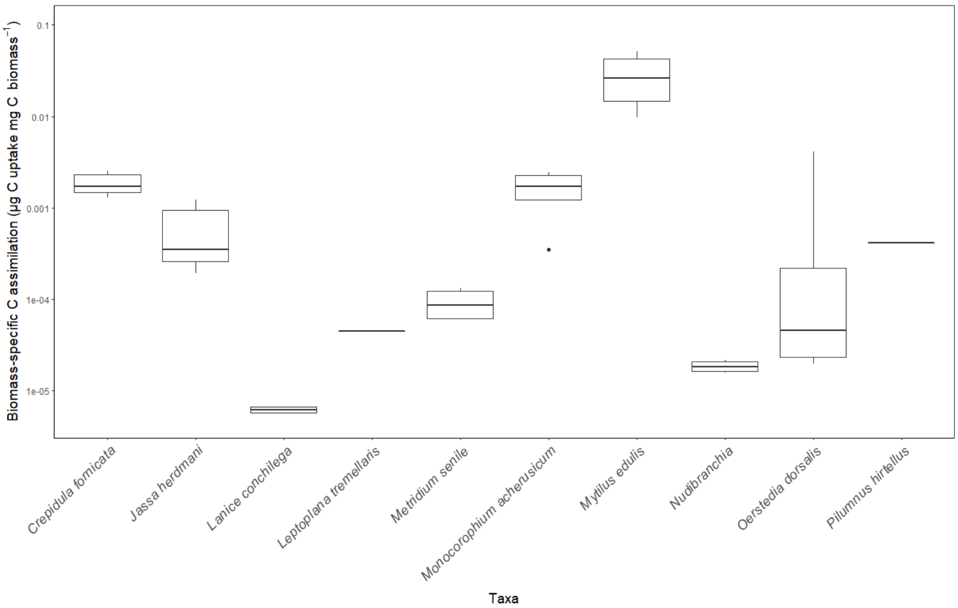

Figure 4.4: Biomass-specific carbon assimilation (µg C uptake mg C biomass^{-1}) per species and per day on a logarithmic scale. The boxplots represent the 25th, median and 75th percentile of the biomass-specific assimilation, while the whiskers represent the 1.5*Interquartile ranges (IQR) of the upper and lower quartile.

4.3.3 Total C assimilation

The total carbon assimilation by the colonising organisms in the experimental tanks ranged between 0.003 (nudibranch individuals) and 1070 (*J. herdmani* individuals) µg C d^{-1} per panel. This high variability was driven by the significantly different biomass and biomass-specific carbon assimilation observed for the different species (Fig. 4.5 ANOVA $F_{6,23} = 72.13$, $p < 0.001$). *Jassa herdmani* showed the highest total carbon assimilation (431 ± 367 µg C d^{-1}), followed by *M. edulis* (84.7 ± 35.7 µg C d^{-1}) and *M. acherusicum* (14.7 ± 11.0 µg C d^{-1}, Tukey HSD, $p_{adj} < 0.05$). The assimilation by the other species (including the species that were not tested in the ANOVA) was smaller than 3.3 µg C and significantly lower than *J. herdmani*, *M. edulis* and *M. acherusicum* (Tukey HSD, $p_{adj} > 0.05$).

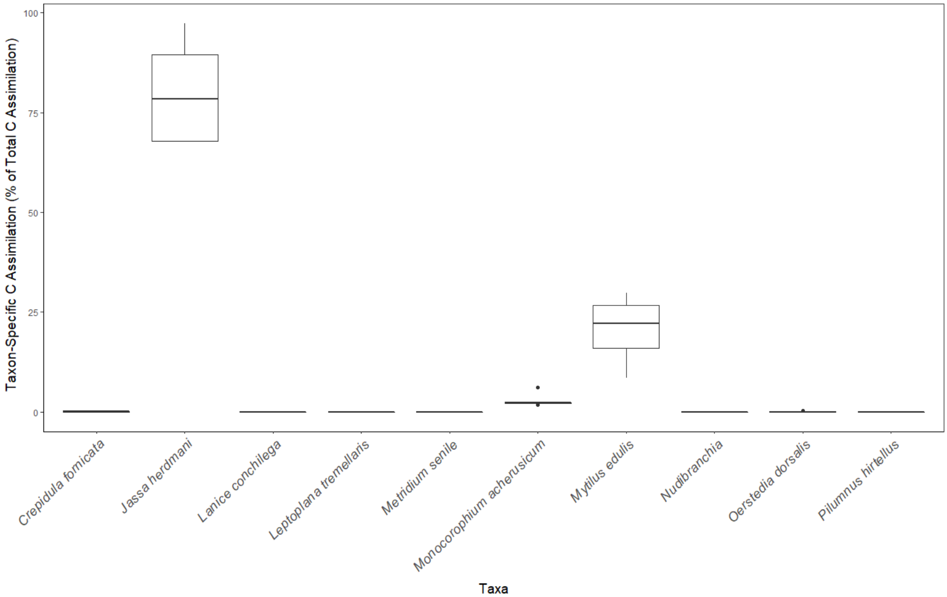

Figure 4.5: Taxon-specific carbon assimilation (expressed as % of the total carbon assimilation by all the consumers) of the different taxa found in the experimental tanks. The boxplots represent the 25th, median and 75th percentile and the whiskers show the 1.5*Interquartile ranges (IQR) of the upper and lower quantile.

4.3.4 Upscaling

The results from the upscaling calculations indicated that *J. herdmani* and *M. edulis* on all the offshore wind foundations in the BPNS assimilate in total 200 ton C y^{-1}, which is ca. 0.40 % of the primary producer standing stock in the OWF area of the BPNS in their tissues (Table 4.4). Furthermore, the carbon processing (ingestion) by these two species occurring on all the offshore wind foundations in the BPNS was estimated at 657 ton C y^{-1} (Table 4.5). This suggests that 1.3 % of the annual local primary producer standing stock is grazed upon by *J. herdmani* and *M. edulis*.

The calculations for the comparison of carbon assimilation between the different types of foundations and the natural permeable sediments indicated that the introduction of jacket foundations results in the highest increase in the carbon assimilation (ratio turbine/sediment: min: 14242 – max: 181259 – Table 4.6). The presence of monopile foundations results in the second highest increase in carbon assimilation (ratio turbine/sediment: min: 38 – max: 485), while the introduction of gravity-based foundations causes the smallest increase (ratio turbine/sediment: min: 9 – max: 116).

Table 4.4: Assimilation of the primary producer standing stock by the species *Jassa herdmani* and *Mytilus edulis*.

Assimilation of primary productivity	***Jassa herdmani***	***Mytilus edulis* (<1cm)**	***Mytilus edulis* (1-3cm)**	***Mytilus edulis* (>3cm)**
Total Biomass C per MONOPILE (µg C m^{-2} d^{-1})	2309790	4243	108708	29420
Total Biomass C per JACKET (µg C m^{-2} d^{-1})	6533675	375416	619825	0
Total Biomass C per GRAVITY-BASED (µg C m^{-2} d^{-1})	4532899	55244	412899	39927
Total C assimilation per MONOPILE (µg C m^{-2} d^{-1})	701736	4699	120399	32584
Total C assimilation per JACKET (µg C m^{-2} d^{-1})	1984993	415791	686485	0
Total C assimilation per GRAVITY-BASED (µg C m^{-2} d^{-1})	1377138	61185	457305	44222
Total C assimilation per MONOPILE (mg C $turbine^{-1}$ d^{-1})	886959	902	23117	6256
Total C assimilation per JACKET (mg C $turbine^{-1}$ d^{-1})	5797548	184486	304571	0
Total C assimilation per GRAVITY-BASED (mg C $turbine^{-1}$ d^{-1})	782498	7495	56002	5417
Total assimilation for all MONOPILES in BPNS (g C d^{-1})	234157	238	6103	1652
Total assimilation for all JACKETS in BPNS (g C d^{-1})	278282	8855	14619	0
Total assimilation for all GRAVITY-BASED foundations in BPNS (g C d^{-1})	4695	45	336	33
Total assimilation (kg C d^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	549			
Total assimilation (kg C y^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	200391	in 365 days		

Total assimilation (ton C y^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	200		
Total production in OWF BPNS (ton C y^{-1})	50694	assuming equal primary productivity throughout OWFs since enhanced primary productivity hasn't been quantified yet	
		0.40	% of primary productivity in BPNS OWFs is assimilated by *Jassa herdmani* and *Mytilus edulis*

Table 4.5: Processing of local primary producer standing stock by the species *Jassa herdmani* and *Mytilus edulis* occurring in all the currently installed offshore wind farms in the Belgian part of the North Sea.

Processing of primary productivity	***Jassa herdmani***	***Mytilus edulis* (<1cm)**	***Mytilus edulis* (1-3cm)**	***Mytilus edulis* (>3cm)**
SUMMED assimilation (kg C d^{-1}) for all OWF foundations	517	9.14	21	1.68
SUMMED PP processing (kg C d^{-1}) for all OWF foundations	1600	57	132	11
Total processing (kg C d^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	1799			
Total processing (kg C y^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	656654	in 365 days		
Total production in OWF BPNS (ton C y^{-1})	50694	assuming equal primary productivity throughout OWFs since enhanced primary productivity hasn't been quantified yet		
		1.30	% of primary productivity in BPNS OWFs is grazed upon by *Jassa herdmani* and *Mytilus edulis*	

Table 4.6: Comparison of the carbon assimilation between the hard substrate and the permeable sediment macrofauna related to the surface of each type of foundation.

CALCULATIONS FOR COMPARISON WITH PERMEABLE SEDIMENTS	**min. assimilation**	**max. assimilation**	**References**
Carbon assimilation (mg C m^{-2} d^{-1}) by macrofauna in sediment	3.3	42	Bühring *et al.*, 2006b
Total C assimilation per MONOPILE (mg C $turbine^{-1}$ d^{-1})	917234		
Total C assimilation per JACKET (mg C $turbine^{-1}$ d^{-1})	6286605		
Total C assimilation per GRAVITY-BASED (mg C $turbine^{-1}$ d^{-1})	851412		
Amount of C that is NOT assimilated by soft sediment macrofauna due to the construction of 1 MONOPILE (mg C)	1889	24048	
Amount of C that is NOT assimilated by soft sediment macrofauna due to the construction of 1 JACKET (mg C)	35	441	
Amount of C that is NOT assimilated by soft sediment macrofauna due to the construction of 1 GRAVITY-BASED (mg C)	7349	93536	
Ratio C assimilation per MONOPILE (mg C m^{-2}) / C not assimilated in permeable sediments (mg C m^{-2})	485	38	
Ratio C assimilation per JACKET (mg C m^{-2}) / C not assimilated in permeable sediments (mg C m^{-2})	181259	14242	
Ratio C assimilation per GRAVITY-BASED (mg C m^{-2}) / C not assimilated in permeable sediments (mg C m^{-2})	116	9	

4.4 Discussion

In this study, we experimentally quantified the carbon assimilation by colonising organisms of offshore wind farms (OWFs). Our results partly confirmed our initial hypothesis: the biomass-specific carbon assimilation was highest in the blue mussel *Mytilus edulis* followed by the limpet *Crepidula fornicata*. Nevertheless, the amphipod *Jassa herdmani* assimilated the highest total amount of carbon, which is related to its high abundance and total biomass values. The other species showed very low carbon assimilation, both in terms of total and biomass-specific assimilation. Altogether, the distribution of total carbon assimilation amongst the faunal taxa in our study is in line with previous studies performed in soft sediments, where total carbon assimilation can be largely determined by the relative biomass of each taxon group (Middelburg *et al.*, 2000; Kamp and Witte, 2005; Woulds *et al.*, 2007, 2016; Hunter *et al.*, 2012).

The species composition on the PVC panels resembled the typical colonising assemblages found at the rocks of scour protection layers of an offshore wind turbine, with high *J. herdmani* and low *M. edulis* abundances (Bouma and Lengkeek, 2008). However, lower abundances of the anemone *Metridium senile* were observed on the PVC panels in comparison to what is normally found on the rocks of the scour protection layer, where this species is usually dominant (Bouma and Lengkeek, 2008). It has been shown that communities at the scour protection layer develop slowly (De Mesel *et al.*, 2013). As our PVC plates remained at sea for one year, the establishment of dense *M. senile* assemblages was probably not yet completed. The coverage of the PVC panels incubated in the experimental tanks was comparable among the panels. However, different species abundances were observed (Table 4.2). The main coverage was caused by the *Jassa herdmani* mats, in which multiple species (mainly *J. herdmani*) can occur. Since we aimed at avoiding any further disturbance of the colonising communities, we did not examine the species abundance before the incubation in the experimental tanks, resulting in dissimilar species abundances among the replicates.

4.4.1 Carbon assimilation by colonising fauna

The high total carbon assimilation by *J. herdmani* (83.8 % of all carbon assimilated by colonising fauna) reflects its high abundance in the experimental tanks and its opportunistic feeding behaviour, since this species has been reported to feed on any resource that is in suspension, such as *Ulva* thalli, *Artemia* nauplii (Beermann and Franke, 2012), smaller sympatric amphipods (Armsby and Tisch, 2006) and zooplankton (Mavraki *et al.*, subm.).

The blue mussel *M. edulis* accounted for a higher carbon assimilation than it accounted for macrofaunal biomass and it showed the highest biomass-specific carbon assimilation (9.8 ± 6.5 µg C assimilation per mg C biomass d^{-1}). These results suggest that the individuals of *M. edulis* consume a relatively high share of the primary producer standing stock compared to the individuals of other species. Our findings are supported by the feeding habits of this species. *Mytilus edulis* often filters fine particulate macroalgal detritus (Dubois *et al.*, 2007), decreasing significantly the net primary producer standing stock (Lemmen, 2018; Slavik *et al.*, 2019). This significant decrease could be explained by the energy demands of *M. edulis* that requires an assimilation of ca. seven times its own carbon biomass to fulfil its demands (Joschko *et al.*, 2008). Moreover, this species has typical clearance rates on the order of 1 L h^{-1} per individual (Prins *et al.*, 1991; Asmus *et al.*, 1992), which is remarkably higher than the clearance rates of *J. herdmani* (0.008 L ind^{-1} h^{-1} – Mavraki unpublished data). These clearance rates are increasing when small particles are provided as resources compared to larger particles (Lehane and Davenport, 2006). This also explains the results of this study, since we provided fragmented algae, which are considered small particles. Furthermore, the size range of the mussel individuals attached to the PVC panels (1-3 cm) suggests that they were juveniles. It has been shown that juveniles can assimilate new carbon more rapidly than adults (Hentschel, 1998), and specifically mussel juveniles can filter small food items (i.e. fragmented algae) in higher rates than adults (Jacobs *et al.*, 2015).

The biomass-specific carbon assimilation was not similarly high for all the species. This can be related to the feeding preferences of these species. For example, *C. fornicata* preferably feeds on benthic diatoms (Decottignies *et al.*, 2007), while *M. senile* mainly consumes zooplankton (Östman *et al.*, 2010) but also particulate organic matter (Mavraki *et al.*, subm.). Nudibranchs and the platyhelminth species *Leptoplana tremellaris* are predators, mainly exploiting anemones (Harris, 1976) and polychaetes, isopods and amphipods (Jennings, 1957), respectively. Thus, the algal cells that were used in our experiment do not necessarily fulfil the feeding preferences of all the species attached to the PVC panels.

The total faunal carbon assimilation in our experiments amounted to 4.1 ± 3.3 % of the added algae. This amount seems quite low given that the organisms were starved for 24 h. However, limited faunal carbon assimilation is not unusual in similar studies on soft sediment macrofauna. Experiments on soft sediment macrofauna have shown a total carbon assimilation ranging between 1 % and 5 % (Witte *et al.*, 2003b; Woulds *et al.*, 2016; Braeckman *et al.*, 2019; and reviewed in Woulds *et al.*, 2009). We are not aware of any published studies conducting labelling experiments with hard substrate assemblages to compare them with our findings. However, multiple studies have been conducted on the carbon assimilation by mussels. In our study, mussels assimilated ca. 1.04 ± 0.55 µg C ind^{-1} d^{-1}. This amount is relatively low, as it is similar to values expressed hourly and per individual from an experiment conducted with *M. edulis* individuals from the Whitsand Bay, in the U.K. (Hawkins and Bayne, 1985). In another study, *M. edulis* assimilated ca. 45 µg C ind^{-1} h^{-1} in its tissue (Allison *et al.*, 1998). The higher carbon assimilation by mussels in these studies in comparison to the results of our study could be explained by the longer duration of these experiments, the lower amount of carbon added to the experimental tanks and by the fact that they included only mussels in their experiments. In contrast, we had a short experimental duration (3 days), in which a multispecies assemblage was incubated in the experimental tanks.

4.4.2 Upscaling to the OWFs in the Belgian North Sea

Jassa herdmani and *M. edulis* showed the highest total carbon assimilation and the highest biomass-specific carbon assimilation, respectively. Both species are very abundant on all the wind turbine foundations (jacket-foundations, gravity-based foundations and monopiles) in the Belgian part of the North Sea (BPNS – De Mesel *et al.*, 2015). By upscaling our results for all the offshore wind turbines, we estimated that they could assimilate ca. 0.40 % of the primary producer standing stock in the OWF area of the BPNS (Table 4.4). However, these species assimilate only a small proportion of the ingested carbon (*M. edulis* 16 % - Hawkins and Bayne, 1985) and *J. herdmani* ca. 32 % - Yamada and Ikeda, 2006). This leads us to an estimate of an annual removal of 1.3% of the primary producer standing stock by *M. edulis* and *J. herdmani* living on wind turbines (Table 4.5). This percentage is on the same order of magnitude as an earlier model estimation of 3.7 ± 1.5 % for the entire southern North Sea (Slavik *et al.*, 2019) and a study in the German Exclusive Economic Zone, suggesting a reduction of 0.06 % of the annual primary producer standing stock related to the increased mussel abundances (Joschko *et al.*, 2008). This reduction to the annual primary producer standing stock by *J. herdmani* and *M. edulis* is not significant given that ~ 25 % of the annual primary production in the BPNS is deposited in the sediment (Provoost *et al.*, 2013).

In the natural permeable sediments in the southern North Sea, carbon assimilation by macrofaunal communities ranges between 3.3 mg C m^{-2} d^{-1} and 42 mg C m^{-2} d^{-1} (Bühring *et al.*, 2006b). With the introduction of offshore wind turbines, thousands of m^2 are being replaced by the hard structures. Considering the footprint of each turbine foundation (Rumes *et al.*, 2013) and the amount of carbon that would have been assimilated by the natural soft sediment macrofauna, we indicated that the presence of these constructions colonised by epifauna significantly increases the carbon assimilation in the area. The occurrence of *J. herdmani* and *M. edulis* on a single jacket foundation can result in the most significant increase in the carbon assimilation (ratio turbine/sediment: min: 14242 - max: 181259) compared to the macrofauna in the permeable sediments underneath the turbine (Table 4.6). This is probably caused by the very small footprint that this installation has (10.5 m^2 – Rumes *et al.*, 2013), thus only slightly decreasing the carbon assimilation by the soft sediment macrofauna. The carbon assimilation by the two dominant colonising organisms found on monopiles also increases carbon assimilation remarkably, although the increase is much smaller compared to the jacket foundations (ratio turbine/sediment: min: 38 - max: 485). The presence of a single gravity-based foundation has the lowest effect on this increase (ratio range turbine/sediment: min: 9 - max: 116) compared to the macrofauna in the permeable sediments underneath the turbine and scour protection layer (Table 4.6). Therefore, the presence of offshore wind turbines significantly increases the local carbon assimilation compared to natural sediment communities, with gravity-based foundations causing the lowest increase and jacket foundations causing the highest increase in local carbon assimilation.

4.4.3 Methodological considerations

The findings of this study derive from an experiment that, to our knowledge, has never been conducted before on hard substrate communities. Although the carbon assimilation by macrofaunal organisms was found to be similar to that by soft sediment species, several methodological constraints need to be considered. This experiment was conducted under optimal conditions for carbon assimilation, i.e. food was provided *ad libitum*, there were no strong currents and the competition for the available food resources was lower than in actual conditions. Furthermore, the duration of the experiment was relatively short, although it has been proved to be sufficient for the carbon assimilation by macrofaunal organisms (Witte *et al.*, 2003a). Long-term experiments would be required to establish how the different colonising species assimilate the organic carbon (Moodley *et al.*, 2005), which would lead to solid results on the way the colonising fauna can graze the local annual primary producer standing stock. Given these experimental considerations, we consider our estimates as conservative.

4.5 Conclusions

Our study identified *Jassa herdmani* and *Mytilus edulis* as key colonising species on offshore wind turbines in terms of total carbon assimilation and biomass-specific carbon assimilation, respectively. These results suggest that *J. herdmani* is an opportunistic feeder, while the *M. edulis* is a stronger suspension feeder of the added fragmented algae than the other species. Considering the density of these species found in the offshore wind farms in the Belgian part of the North Sea (BPNS), we suggest that colonising assemblages can reduce net primary producer standing stock in the BPNS by about 1.3 %. Furthermore, we indicated that the presence of offshore wind turbines colonised by colonising fauna remarkably increases the carbon assimilation compared to the natural soft sediment macrofauna inhabiting the same surface area as the turbine footprint. However, in order to completely understand the fate of the organic matter in the colonising assemblages, long-term experiments are required.

Chapter 5

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Offshore wind farms and the attraction-production hypotheses: insights from a combination of stomach content and stable isotope analyses

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Author contribution: NM conducted the sampling, the stable isotope analysis, supervised the stomach content analysis, performed the data analysis and wrote the manuscript. JV supervised the data analysis and the manuscript writing. SD helped with sampling and provided valuable suggestions for the improvement of the manuscript.

Abstract

Offshore wind farms (OWFs) act as artificial reefs, attracting high abundances of fish, which could potentially increase their local production. This study aims at understanding the feeding ecology of fish species that abundantly occur at artificial habitats, such as OWFs, by investigating the short- and the long-term dietary composition of five species: the benthopelagic *Gadus morhua* and *Trisopterus luscus*, the pelagic *Scomber scombrus* and *Trachurus trachurus*, and the benthic *Myoxocephalus scorpioides*. We conducted combined stomach content (SCA) and stable isotope analyses (SIA) to examine the short- and the time-integrated dietary composition, respectively. Our results indicated that the benthopelagic and benthic species utilize artificial reefs, such as those available at OWFs, as feeding grounds for a prolonged period, since both SCA and SIA indicated that they exploit the colonising organisms occurring exclusively on artificial hard substrates in the study area. The pelagic *T. trachurus* only occasionally uses artificial reefs as oases of highly abundant food resources, since only SCA revealed predation on colonising organisms. On the other hand, the pelagic *S. scombrus* does not feed on colonising fauna and therefore

its augmented presence in OWFs is probably related to reasons other than the enhanced food availability at the artificial reefs. The long-termed feeding preferences of benthic and benthopelagic species contribute to the hypothesis that artificial reefs, in this case OWFs, could potentially increase the fish production in the area. However, this was not supported for the pelagic species.

5.1 Introduction

Worldwide, the number of offshore renewable energy installations is increasing fast as a measure to mitigate the effects of climate change. In the North Sea, offshore wind farms (OWFs) are being continuously constructed (Soma *et al.*, 2019), adding artificial hard substrates (the foundations and the associated scour protection layers) to usually naturally soft bottom areas. These wind turbines act as artificial reefs, drastically altering the local habitat (Petersen and Malm, 2006) and adding hard bottom communities to the original environment (Mangi, 2013).

Artificial habitats accommodate high densities of fish (Bohnsack and Sutherland, 1985). Two different hypotheses have been proposed to explain these increased abundances (Brickhill *et al.*, 2005). The attraction hypothesis proposes that fish move from the surrounding environment towards the artificial reefs, where their local production does not increase (Brickhill *et al.*, 2005). The attraction to artificial reefs can be explained by the increased structural complexity resulting in an enhanced protection against predators, shelter from currents (Bohnsack and Sutherland, 1985) and/or an increased food availability (Reubens *et al.*, 2011). The production hypothesis suggests that the carrying capacity of the original environment increases due to the creation of the new habitats, favouring attraction and enhanced growth (Lindberg, 1997; Powers *et al.*, 2003; Brickhill *et al.*, 2005). These two hypotheses were put forward as the two extremes of a wide range of ecological processes (Svane and Petersen, 2001; Brickhill *et al.*, 2005). Attraction could for example, potentially facilitate production, since these two actions are not necessarily mutually exclusive (Svane and Petersen, 2001; Brickhill *et al.*, 2005; Reubens *et al.*, 2013a; Cresson *et al.*, 2019).

Understanding the attraction-production hypotheses with respect to the artificial reefs at OWFs is crucial both for their efficient management and for the associated fisheries in the area (Cresson *et al.*, 2014). So far, the attraction-production hypotheses have mainly been investigated by using stomach content analysis (Leitão *et al.*, 2007; Reubens *et al.*, 2011) and fish movement in close proximity to artificial reefs (Reubens *et al.*, 2014b). However, approaching the attraction-production hypotheses by investigating the trophic relationships on artificial reefs and the transfer of organic matter from producers to consumers with the use of tracers remains understudied (Brickhill *et al.*, 2005).

This study aims at determining whether fish species that are found in high densities in OWFs feed on prey items exclusively associated with man-made hard substrates for a prolonged period of time (up to 6 months). The investigated fish species are pouting (*Trisopterus luscus*), cod (*Gadus morhua*), horse mackerel (*Trachurus trachurus*), mackerel (*Scomber scombrus*) and sculpin (*Myoxocephalus scorpioides*), which are abundantly present in close proximity to OWFs in the North Sea and the Baltic Sea (Reubens *et al.*, 2011; Bergström *et al.*, 2013; Kerckhof *et al.*, 2018). These species can be categorised according to their ecology into: 1) benthic fish, living exclusively on and near the bottom of the sea, i.e. sculpin (Gordon and Duncan, 1985); 2) benthopelagic fish, living in close association with the sea-floor, i.e. pouting and cod (Gordon and Duncan, 1985) and 3) pelagic fish, occupying mid-water or surface water levels and performing diel vertical migrations, i.e. mackerel and horse mackerel (Dale and Kaartvedt, 2000).

Research on the short-term feeding ecology is often reliant on stomach content analysis (SCA), providing a snapshot of the recently ingested (up to 10 h) food items (Hyslop, 1980). SCA can provide a high taxonomic resolution (e.g. at the species level) of the ingested food items that may be difficult to attain with other methods (Lin *et al.*, 2007). However, it also has multiple limitations, such as the requirement of high sampling frequencies in order to obtain a time-integrated overview of the feeding habits of a species (St John, 1999; Parkyn *et al.*, 2001; Daly *et al.*, 2013) and a minimal indication of the assimilated dietary items (Parkyn *et al.*, 2001; Jensen *et al.*, 2012). SCA further depends on the relative digestibility of each prey item (St John, 1999), leading to the under-representation of highly assimilated and defaecated items and the over-representation of food sources with hard parts (Fry, 1988). Hence, stomach contents mainly consisting of hard substrate colonising organisms can be an indication of attraction towards the artificial structures for foraging activities.

The majority of the limitations of the SCA can be overcome by combining this method with stable isotope analysis (SIA). SIA has considerable advantages, showing a time- (up to 6 months) and space-integrated dietary estimation (Bearhop *et al.*, 2004; Fry, 2006; Newsome *et al.*, 2007), providing long-term information of a species feeding ecology. The time-integrated information can be acquired with a few samples (absolute minimum three replicates - Jackson *et al.*, 2011) per species. A diet based on colonising fauna for a prolonged period could indicate a long-term residency close to artificial reefs, which is a clear indication of attraction, but could potentially also lead to increased local production. SIA provides information on the truly assimilated food items (Boecklen *et al.*, 2011), and thus on the nutritionally important food sources (Melville and Connolly, 2003; Daly *et al.*, 2013). Moreover, it allows for investigating the isotopic niche of a species, which is a proxy for its trophic niche (Jackson *et al.*, 2011). However, this method does not provide the high taxonomic resolution as provided by SCA (Daly *et al.*, 2013). Thus, a combination of SIA and SCA is a powerful approach that can provide a complete picture of the feeding ecology of fish species and can improve the interpretation of aquatic food webs (Parkyn *et al.*, 2001).

In this paper, we assessed the feeding ecology of the five fish species by using a combination of SCA and SIA. We aimed at investigating whether fish use artificial reefs as feeding grounds for prolonged periods, according to three assumptions: (a) fish species use artificial reefs as feeding grounds for a prolonged period when both the SCA and the SIA show similar results and the fish' diet relies on colonising fauna that only occurs on artificial hard substrates in the southern North Sea; (b) fish occasionally use artificial reefs as feeding grounds if SCA reflects diet composition on food items derived from artificial structures (i.e. colonising organisms) which is not confirmed by SIA; and (c) fish probably do not use the artificial reefs as feeding grounds if both methods reveal a diet based on food items that are not associated with artificial hard substrates.

5.2 Methodology

5.2.1 Sampling area and data collection

Sampling was conducted next to a gravity-based wind turbine (D6, coordinates: 51° 33.04'N - 02° 55.42'E) within the C-Power wind farm at the Thornton Bank at the Belgian part of the North Sea (BPNS). The gravity-based foundation has a diameter of 6 m at the sea surface increasing to 14 m at the sea floor (Reubens *et al.*, 2011), where it is surrounded by a rock collar forming the scour protection layer with a width of 62.5 m (SPL – Peire *et al.*, 2009). We chose this particular location because a wealth of data on the investigated fish species were available (Reubens *et al.*, 2011; Kerckhof *et al.*, 2018).

Individuals of five species were collected in August 2016 during day time: cod (*Gadus morhua*), pouting (*Trisopterus luscus*), mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*) were sampled from an inflatable boat at about 5 m from the turbine using fishing lines (hooks: Arca size 4, bait: *Arenicola marina*). Sculpin (*Myoxocephalus scorpioides*) was collected by spear-fishing by scientific divers since this benthic species lives in between the rocks of the scour protection layer. The benthopelagic species (cod and pouting) were collected above the scour protection layer, while the pelagic species (mackerel and horse mackerel) were sampled from ca. 10 m depth of the water column. Only cod juveniles, belonging to the I-group (i.e. < 50 cm Reubens *et al.*, 2013a), were sampled (from now on referred as cod). This size category is known to be abundantly frequent in the OWFs (Reubens *et al.*, 2013a), while the older age groups (i.e II-group and beyond) move towards other locations (Reubens *et al.*, 2014b). Fish were immediately killed by pithing with a metal rod (Kadye and Booth, 2012) and measured (total length in mm). Subsequently, fish stomachs were extracted and preserved in an 8% formaldehyde-seawater solution for the stomach content analysis (Reubens *et al.*, 2011). A part of the dorsal (white) muscle without skin of at least five individuals (from which we also collected the stomachs) per fish species was isolated for stable isotope analysis using a scalpel. The scalpel was cleaned with ethanol before every use (both between different species and between different individuals) to avoid cross-contamination. This tissue yields the lowest $\delta^{15}N$ and $\delta^{13}C$ variability compared to other fish tissues, such as red muscle, liver and heart, and it is considered the best tissue for use in stable isotope analysis (Pinnegar and Polunin, 1999). The muscle tissue was stored in a clean vial with filtered sea water in a -20 ^{0}C freezer until further analysis. Stomachs and muscles were extracted from similar sized individuals per species (Table 5.1) to exclude any size-related dietary shifts (Mittelbach and Persson, 1998).

Table 5.1: Length (mm), weight (g) and maturity level of the five fish species under study.

Species	Length (mm)	Weight (g)	Maturity
Gadus morhua	320 ± 35	324 ± 100	Juvenile
Myoxocephalus scorpioides	213 ± 64	168 ± 133	Adult
Scomber scombrus	289 ± 34	221 ± 66	Adult
Trachurus trachurus	254 ± 24	172 ± 51	Adult
Trisopterus luscus	237 ± 30	188 ± 80	Adult

5.2.2 Stomach content analysis

For the short-term diet analysis, we obtained stomach content samples from 62 individuals in total (pouting: 17 ind.; cod: 16 ind.; horse mackerel: 12 ind.; mackerel: 12 ind.; sculpin: 7 ind.). The number of stomachs analysed was relatively small and deriving from individuals collected only in summer due to the logistic effort of collecting all consumers and food resources in all the seasons. When the small number of stomachs is unavoidable, pairing SCA with stable isotope analysis (SIA - Davis *et al.*, 2012) can help validating trophic relationships elucidated through SCA (Clarke *et al.*, 2005) and offer additional information on trophic flows and food sources (Dalsgaard *et al.*, 2003; Melville and Connolly, 2003; Abrantes *et al.*, 2014).

In the laboratory, stomachs were dissected, cleaned three times with water to assure that they were empty, and the content was collected and rinsed thoroughly with milli-Q water. Stomach content samples were drained in a 90 µm mesh sieve to thoroughly collect the small zooplanktonic organisms and the half-digested parts of bigger organisms. Consequently, they were immediately examined under a stereomicroscope to identify prey items to the lowest taxonomic level possible, and counted. Since many prey individuals were incomplete (i.e. stomachs containing only the scales of fish or a cheliped from a decapod), we did not estimate the biomass contribution of prey species. Prey items were allocated into ten broader taxonomic groups (see 5.2.3) to facilitate the analysis.

Differences in stomach content composition between the different fish species were visualized using non-metric multi-dimensional scaling (MDS) and tested using the one-way analysis of similarity (ANOSIM) routine. As the quantity of the prey items in the stomach contents varied across the fish individuals, the underlying Bray-Curtis similarity matrix (Clarke and Gorley, 2006) was constructed based on relative prey abundance data per stomach (De Crespin De Billy *et al.*, 2000). Following a significant ANOSIM result, pair-wise tests were conducted to investigate possible diet overlap. We considered pair-wise comparisons with $R < 0.25$ as substantial dietary overlap and with $R > 0.5$ indicating relatively minimal dietary overlap, while $0.25 < R < 0.5$ was considered moderate dietary overlap (Creque and Czesny, 2012).

5.2.3 Stable isotope analysis

For the analysis of the long-term trophic ecology of the five fish species, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis was performed (5 individuals of cod, pouting, horse mackerel and sculpin, and 11 individuals of mackerel). The frozen dorsal muscle tissue was thawed, rinsed with milli-Q water to remove salts (Nilsen *et al.*, 2008) and dried overnight at 60°C. The dried samples were grounded to a homogenous powder using a pestle and a mortar and approximately 1 mg of dried tissue per individual per species was encapsulated in a Sn capsule (8 x 5 mm, Elemental Microanalysis UK). The capsules were stored in Multi-well Microtitre plates until the isotopic analysis for $\delta^{13}C$ and $\delta^{15}N$ was conducted at the UC Davis Stable Isotope Facility (University of California, USA) by a PDZ Europa ANCA-GSL elemental analyser, interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). $\delta^{13}C$ and $\delta^{15}N$ data are expressed in the standard delta (δ) notation relative to standard reference material: Vienna Pee Dee Belemnite for carbon and atmospheric N for nitrogen. The results are expressed in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{Sample}} / R_{\text{Standard}}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

The trophic niches of the five fish species were estimated using the stable isotope Bayesian ellipses package in R (SIBER package, Jackson *et al.*, 2011). SIBER generates sample size-corrected standard ellipse areas (SEA_C) that were used to estimate the isotopic niche size and the trophic overlap between the five fish species. SEA_C nullifies the bias created from small sample sizes and reflects the isotopic niche of a population, which is considered a proxy of its trophic niche (Jackson *et al.*, 2011). By estimating the SEA_C overlap, we obtained information about the isotopic niche overlap between the different fish species. Results are expressed as mean ± standard deviation (sd).

The relative contribution of each prey item to the diet of the different fish species was estimated using stable isotope mixing models in R (SIMMR package, *Parnell et al.*, 2013). SIMMR can incorporate the variability that is associated with consumers, sources and trophic enrichment factors (TEFs, Parnell *et al.*, 2013). By using Markov Chain Monte Carlo simulations, this model can determine the potential contribution of different sources to the diet of a consumer (Parnell *et al.*, 2010). As the isotopic composition of the fish species was measured by using muscle tissues, the diet estimates represent the proportion of the sources that have been assimilated by this tissue (Lamontagne *et al.*, 2016). This tissue has slower turnover rates than other body parts and thus, its isotopic signature reflects a longer-term diet history than tissues with faster turnover rates (Bruestle *et al.*, 2018). SIMMR considers the mean (μ_{prey}) and the standard deviation (σ_{prey}) of the stable isotope ratios of the prey species for the estimation of the proportion of a given prey in the diet (Parnell *et al.*, 2013; Lamontagne *et al.*, 2016). However, this model is based on the assumption that all the food resources are included in the analysis (Phillips *et al.*, 2014). In order to meet this assumption, we used the food items that were identified by the SCA as prior information for the SIMMR (Jensen *et al.*, 2012). Food resources representing < 1 % of the stomach contents per species were not included in the mixing models. The prey items were grouped into 10 broad taxonomic categories Amphipoda, Bivalvia, Cumacea, Decapoda, Echinodermata, Gastropoda, Hydrozoa, Nematoda (i.e. soft sediment and hard substrate benthos), and the pelagic prey items Fish and Zooplankton. Partially digested prey individuals that could not be allocated to one of these groups were not further considered. This grouping was performed because the discriminatory power of the mixing models decreases with the number of food sources (Phillips *et al.*, 2014). Stable isotope signatures of these broad taxonomic categories and zooplankton, sampled during the same sampling event were obtained from Mavraki *et al.*, (2020, subm.), while nematode, Cumacea and fish stable isotope data were acquired from Franco *et al.* (2008), Kürten *et al.* (2013) and

Jennings and Cogan (2015) respectively (Table 5.2). We further constrained the mixing model with the known dietary proportions acquired by the stomach content analysis using the function simmr_elicit (Parnell and Inger, 2019).

Table 5.2: Stable isotope carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) mean and standard deviation (sd) values of the food items that were found in the stomach contents (> 1%) of all fish species and were included in the mixing model.

Food item	**mean $\delta^{13}C$**	**sd $\delta^{13}C$**	**mean $\delta^{15}N$**	**sd $\delta^{15}N$**	**Reference**
Amphipoda	-18.90	0.65	11.50	0.42	Mavraki et al. 2020
Bivalvia	-19.45	0.54	10.88	0.22	Mavraki et al. 2020
Cumacea	-15.50	0.20	9.20	0.30	Kürten et al. 2013
Decapoda	-20.80	1.53	11.66	0.73	Mavraki et al. 2020
Fish	-21.28	1.52	10.18	1.35	Jennings and Cogan 2015
Hydrozoa	-19.00	0.72	9.87	0.50	Mavraki et al. 2020
Nematoda	-18.00	1.00	10.00	1.00	Franco et al. (2008)
Zooplankton	-19.50	0.56	11.20	0.30	Mavraki et al. subm.

Trophic enrichment factors (TEFs) were added to the mixing models. Mixing models are sensitive to assumptions regarding TEFs (Phillips *et al.*, 2014) because of the multiplicity of factors that can affect them (Phillips *et al.*, 2014). Hence, the use of the most appropriate TEF is crucial to produce the most accurate results. In order to accomplish this, we used the function simmr_mcm_tdf that can estimate the most appropriate TEF values for a known set of dietary proportions (Parnell and Inger, 2019). Hence, every species had different mean and standard deviation values of TEFs (Table 5.3). The TEFs defined by the model were within the reported range of -1 to 6 ‰ for nitrogen and -0.8 to 4 ‰ for carbon (Caut *et al.*, 2009). The use of these TEFs assured that the fish' isotopic ratios fitted within the polygon of the prey items (Fig. A3.1), which is one of the prerequisite of isotopic mixing models (Phillips *et al.*, 2014). The isotopic niche and the dietary proportion estimations were performed in R (R Development Core Team, 2018). The diet proportions are reported as the mean and standard deviation, but also as the median (50th percentile) and the 95 % credible intervals (2.5th and 97.5th percentiles) to avoid misinterpretations of unique (mean) values (Phillips and Gregg, 2003; Phillips *et al.*, 2014).

Table 5.3: Mean and standard deviation values of the $\delta^{13}C$ and $\delta^{15}N$ trophic enrichment factors (TEFs) for every consumer species.

Consumer species	**Mean $\delta^{13}C$ TEF**	**SD $\delta^{13}C$ TEF**	**Mean $\delta^{15}N$ TEF**	**SD $\delta^{15}N$ TEF**
Gadus morhua	2.99	0.51	5.77	0.86
Myoxocephalus scorpioides	4.36	0.73	5.50	2.04
Scomber scombrus	0.60	0.41	3.89	1.27
Trachurus trachurus	0.79	0.57	5.82	0.98
Trisopterus luscus	3.35	0.50	6.21	1.00

5.3 Results

5.3.1 Diet analysis of the fish species

The SCA showed that the stomachs of the individuals of sculpin contained the lowest, and pouting the highest number of food items. Pouting, juvenile cod and horse mackerel stomachs mainly had the amphipod *Jassa herdmani* (87.6 ± 10.2 %, 76.2 ± 19.3 % and 61.2 ± 26.5 %, respectively), mackerel stomach content was dominated by zooplankton (83.9 ± 8.3 %), while sculpin stomachs mainly contained both *Pisidia longicornis* (40.0 ± 11.3 %) and fish (30.0 ± 10.0 % - Table 5.4). After allocating the prey items to broader taxonomic groups (see 5.2.3), the stomach contents of sculpin showed the lowest variety (3 prey groups); highest prey group variety (9 groups) was observed for juvenile cod (Fig. 5.1). Occasionally, empty stomachs were found. One empty stomach was found for cod and mackerel, while the stomachs of three sculpins were empty as well.

ANOSIM revealed significant differences in the stomach contents of the different fish species (Fig. 5.2 – Global $R = 0.244$, $p = 0.001$). The pairwise tests indicated dietary overlaps between cod, horse mackerel and pouting. Moreover, dietary overlap was also observed between cod, horse mackerel and sculpin (pairwise R values < 0.25) (Table 5.5). Moderate dietary overlap was found between mackerel, horse mackerel and cod ($0.25 < R < 0.5$), while low overlap was observed between mackerel and sculpin and pouting (pairwise $R > 0.5$).

Table 5.4: List of prey items. Percentage (%) of abundance of consumed items in the diets of the five different fish species.

	Pelagic		**Benthopelagic**		**Benthic**
	Scomber scombrus	***Trachurus trachurus***	***Gadus morhua***	***Trisopterus luscus***	***Myoxocephalus scorpioides***
Amphipoda					
Jassa herdmani	2.7	61.2 ± 26.5	76.2 ± 19.3	87.6 ± 10.2	-
Monocorophium acherusicum	-	1.2	0.6	0.5	-
Phtisica marina	-	-	0.3	1.2 ± 0.2	-
Stenothoe valida	-	-	2.5 ± 1	0.2	-
Unidentified sp.	-	2.2 ± 1.5	-	0.1	-
Bivalvia					
Aequipecten opercularis	-	-	-	0.3	-
Crepidula fornicata	-	-	-	0.1	-
Mytilus edulis	-	-	0.4 ± 0.1	0.3	10.0
Unidentified sp.	-	-	0.4 ± 0.3	-	-
Cumacea					
Unidentified sp.	-	1.2	-	-	-
Decapoda					
Astacidea	-	-	-	0.1	-
Liocarcinus sp.	-	1.2 ± 0.6	-	0.2	-
Macropodia sp.	-	-	-	0.4	-
Megalopa sp.	-	1.2 ± 1	-	-	-
Pilumnus hirtellus	-	-	0.1	-	-
Pisidia longicornis	-	5.9 ± 2.8	15.3 ± 9.7	4.7 ± 1.6	40.0 ± 11.3
Processa modica	-	-	-	0.1	10.0 ± 3.6
Unidentified sp.	1.3	1.2 ± 1	0.4	-	10.0 ± 2.4
Echinodermata					
Ophiothrix fragilis	-	-	0.7	-	-
Gastropoda					
Unidentified sp.	-	-	0.1	-	-
Hydrozoa					
Sertularia cupressina	-	-	-	0.1	-
Tubularia sp.	-	-	1.2 ± 0.2	2.1 ± 1	-
Nematoda					
Unidentified sp.	2.6 ± 1.7	5.9 ± 1.6	0.4	0.1	-
Pisces					
Engraulidae	4.0 ± 1.2	-	-	-	-
Unidentified sp.	6.7 ± 2.4	9.4 ± 4.5	0.8	1.2 ± 0.2	30.0 ± 10.0
Zooplankton					
Unidentified sp.	83.9 ± 8.3	9.4 ± 6.3	0.4	0.1	-

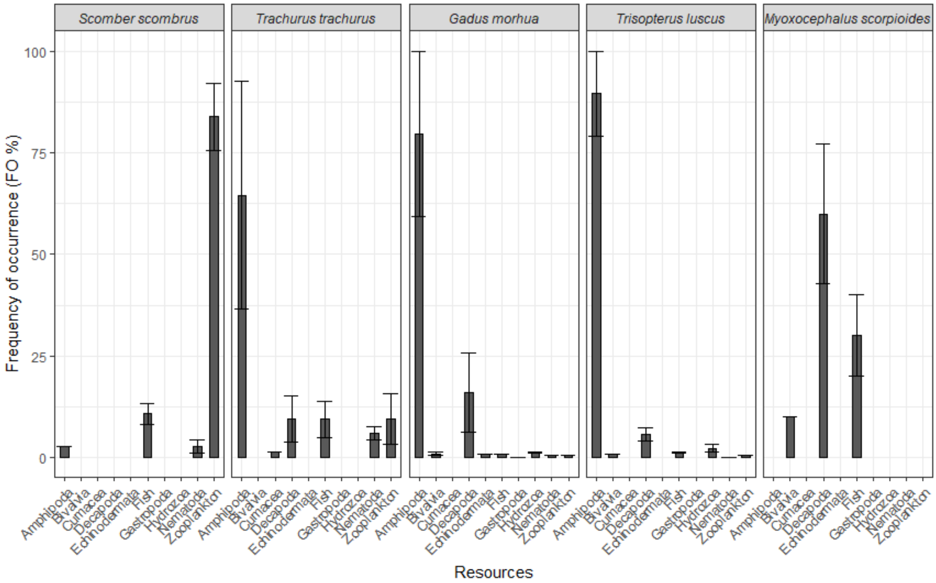

Figure 5.1: Percentage of abundance (%) of the broad taxonomic categories of the prey items found in the stomach contents of each of the five fish species, the pelagic *Scomber scombrus* and *Trachurus trachurus*, the benthopelagic *Gadus morhua* and *Trisopterus luscus*, and the benthic *Myoxocephalus scorpioides*. The error bars represent the standard deviation.

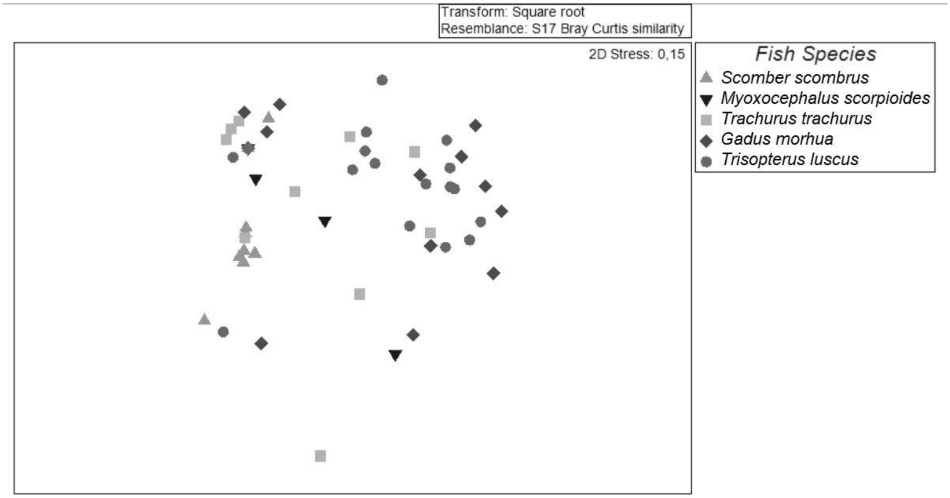

Figure 5.2: Diet composition similarity of the five fish species as visualized by the non-metric multi-dimensional scaling (MDS). The different symbols represent different species.

5.3.2 Isotopic niches

Five individuals of cod, horse mackerel, sculpin and pouting and eleven mackerels were analysed for C and N stable isotopes (Table 5.6, Fig. 5.3A). The lowest mean $\delta^{13}C$ values and $\delta^{15}N$ values were observed for mackerel (-20.5 ± 2.2 ‰ and 16.0 ± 3.7 ‰), while the highest mean $\delta^{13}C$ and $\delta^{15}N$ values (observed for all the fish individuals) were found for sculpin (-15.8 ± 0.3 ‰ and 18.4 ± 1.7 ‰). The pelagic fish species generally had depleted $\delta^{13}C$ values in comparison to the benthic and benthopelagic species. Mackerel was the species with the highest variability in the $\delta^{15}N$ values, while the $\delta^{15}N$ signatures of the other species did not differ remarkably.

Table 5.6: Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) signatures (‰, mean and standard deviation) and number of samples (n) of the five fish species collected at the offshore wind turbine.

Species	**$\delta^{13}C$**	**$\delta^{15}N$**	**Number of individuals**
Gadus morhua	-16.4 ± 0.2	17.2 ± 0.6	5
Myoxocephalus scorpioides	-15.8 ± 0.3	18.4 ± 1.7	5
Scomber scombrus	-20.5 ± 2.2	16.0 ± 3.7	11
Trachurus trachurus	-19.4 ± 1.5	16.9 ± 0.8	5
Trisopterus luscus	-16.8 ± 0.3	17.5 ± 0.7	5

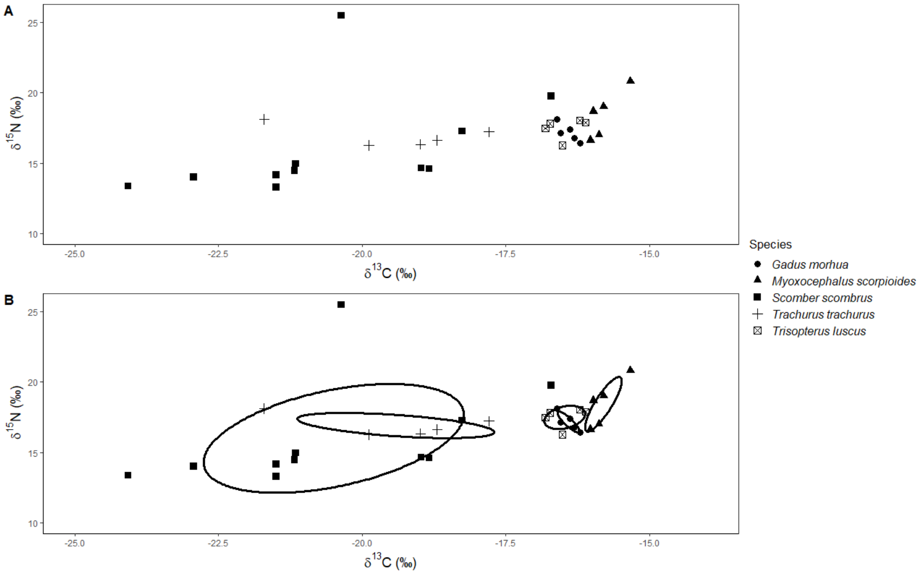

Figure 5.3: A: Individual $\delta^{13}C$ versus $\delta^{15}N$ values and B: standard ellipse areas corrected for small size samples (SEA_C) of the five targeted fish species.

Standard ellipse areas corrected for small sample sizes (SEA_C) (a proxy of the trophic niches) indicated differences between the five fish species (Fig. 5.3B, Table 5.7). The smallest SEA_C (0.22 ‰^{2}) was observed for cod, followed by pouting (0.88 ‰^{2}). The largest SEA_C (24.64 ‰^{2}) was observed for mackerel. Generally, high overlaps were observed between the isotopic niches of the species with the same ecology (Table 5.7, Fig. 5.3B). The isotopic niche of the benthic species sculpin was the only one that did not overlap with any of the isotopic niches of the other species.

Table 5.7: Standard ellipse areas corrected for small size samples (SEA_C - ‰^{2}) and overlaps (‰^{2}) between the isotopic niches of the different fish species collected at the offshore wind turbine.

Species 1	**Species 2**	**SEA_C1 (‰^{2})**	**SEA_C2 (‰^{2})**	**Overlap (‰^{2})**
Gadus morhua	*Myoxocephalus scorpioides*	0.22	1.03	0
Gadus morhua	*Scomber scombrus*	0.22	24.64	0
Gadus morhua	*Trachurus trachurus*	0.22	4.07	0
Gadus morhua	*Trisopterus luscus*	0.22	0.88	0.16
Myoxocephalus scorpioides	*Scomber scombrus*	1.03	24.64	0
Myoxocephalus scorpioides	*Trachurus trachurus*	1.03	4.07	0
Myoxocephalus scorpioides	*Trisopterus luscus*	1.03	0.88	0
Scomber scombrus	*Trachurus trachurus*	24.64	4.07	3.54
Scomber scombrus	*Trisopterus luscus*	24.64	0.88	0
Trachurus trachurus	*Trisopterus luscus*	4.07	0.88	0

5.3.3 Dietary proportions from SCA and SIA combination

The Bayesian stable isotope mixing models (SIMMR) results suggested that colonising “Amphipoda” contributed the most to the diet of cod (84.4 ± 4.7 %), horse mackerel (70.3 ± 5.1 %) and pouting (90.0 ± 8.2 %) (Fig. 5.4, Table 5.8). “Decapoda” was the second most important food item in the diet of cod (12.8 ± 3.8 %) and pouting (5.1 ± 4.2 %), however with remarkably lower contribution to their diets. The diet of horse mackerel partly relied on “Fish” (8.6 ± 2.7 %), “Decapoda” (8.5 ± 3.0 %) and “Zooplankton” (7.6 ± 1.1 %), but in notably lower contributions than “Amphipoda”. In contrast, the diet of mackerel was likely based on “zooplankton”

(89.4 ± 5.7 %), followed by “Fish” (5.9 ± 3.3 %).The diet of sculpin was mainly based on benthic “Decapoda” (66.3 ± 4.7 %), but “Fish” was also an important food item (27.3 ± 3.7 %). All the other food sources were assessed to be of minor importance (< 6.5 %) in the diet of the different fish species.

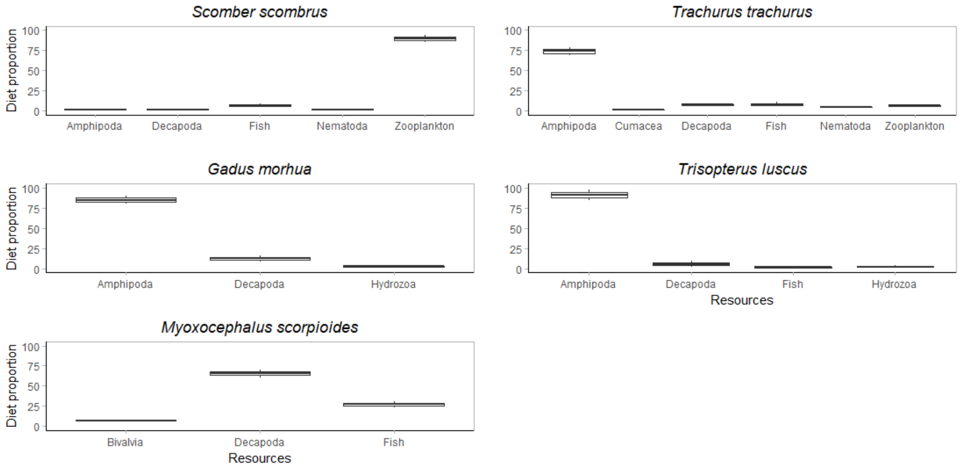

Figure 5.4: Figure 4: Potential contribution of the prey items found in the stomach contents of the pelagic species mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*), the benthopelagic cod (*Gadus morhua*) and pouting (*Trisopterus luscus*) and the benthic sculpin (*Myoxocephalus scorpioides*) in their diets as were estimated by the stable isotope mixing models. The boxplots represent the credible intervals 25 - 75 % of the dietary proportions, while the whiskers represent the 1.5* Interquartile ranges (IQR) of the upper and lower quartile.

Table 5.8: Proportion of prey categories in the diet of the five fish species sampled at close proximity from the offshore wind turbine as estimated by the combination of stomach content analysis and stable isotope mixing models.

Consumer species	Prey Category	Mean ± SD	2.5th percentile	50th percentile	97.5th percentile
Gadus morhua	Amphipoda	**84.4 ± 4.7**	74.0	85.0	92.0
	Decapoda	12.8 ± 3.8	6.6	12.4	21.4
	Hydrozoa	2.8 ± 1.1	1.3	2.6	5.3
Myoxocephalus scorpioides	Bivalvia	6.5 ± 1.1	4.6	6.4	8.7
	Decapoda	**66.3 ± 4.7**	56.9	66.3	75.1
	Fish	27.3 ± 3.7	20.2	27.2	34.8

Scomber scombrus	Amphipoda	1.2 ± 0.9	0.2	0.9	3.8
	Decapoda	1.3 ± 1.1	0.2	1.0	4.4
	Fish	5.9 ± 3.3	1.7	5.2	14.1
	Nematoda	2.1 ± 1.2	0.6	1.8	5.1
	Zooplankton	**89.4 ± 5.7**	75.1	90.7	96.8
Trachurus trachurus	Amphipoda	**70.3 ± 5.1**	59.8	70.4	79.5
	Decapoda	8.5 ± 3.0	4.0	8.1	15.3
	Fish	8.6 ± 2.7	4.4	8.3	15.0
	Nematoda	4.4 ± 1.1	2.5	4.2	6.8
	Zooplankton	7.6 ± 1.1	5.5	7.5	10.0
	Cumacea	0.5 ± 0.1	0.5	0.7	1.0
Trisopterus luscus	Amphipoda	**90.0 ± 8.2**	66.5	92.6	98.4
	Decapoda	5.1 ± 4.2	0.8	3.8	16.5
	Fish	2 ± 1.9	0.2	1.4	7.3
	Hydrozoa	2.9 ± 2.3	0.5	2.1	9.3

5.4. Discussion

Our study showed that two benthopelagic (cod and pouting) and one benthic (sculpin) fish species use artificial hard substrates, such as those in the OWFs, as feeding grounds for a prolonged period, since both the short- (stomach content analysis) and the long-term (stable isotope analysis) dietary analyses suggested that their diets are based on colonising organisms. The pelagic horse mackerel seems to feed in the OWF area only opportunistically since the short-term (stomach content analysis) and the time-integrated (stable isotope analysis) studies showed contradictory results. Finally, the pelagic mackerel was mainly feeding on zooplankton, and hence, it did not exploit the artificial hard structures as feeding habitats.

The stomach content analysis derived from a limited number of individuals that have been collected during day time in a single season (summer), hence not necessarily fully reflecting the natural dietary variability. Increasing the number of stomach samples would result in a more reliable representation of the actual diet (Ferry and Cauilliet, 1996). However, this was not possible in this study due to the logistic efforts mentioned above. While the number of replicates was small, the stomach content results pointed in the same direction as previous dietary studies for these five species. Furthermore, the stomach contents did not differ remarkably between individuals of the same species (Fig. 5.1), hence illustrating the reliability of our results.

5.4.1 Exploitation of the artificial habitats

The results of our study indicated that the benthopelagic species (pouting and juvenile cod) were mainly feeding on amphipods, and specifically on *Jassa herdmani*, while the benthic species (sculpin) was predominantly feeding on decapods, and especially on the porcelain crab *Pisidia longicornis* (Fig. 5.1, Fig. 5.4, Table 5.8). Both prey items are exclusively associated with subtidal artificial hard substrates, such as wind turbine foundations and shipwrecks, where they occur in high densities (Leonhard and Pedersen, 2006; Zintzen, 2007; De Mesel *et al.*, 2015). They are, however, rather rare in natural hard substrate communities (Zintzen, 2007). *Jassa herdmani* and *P. longicornis* have sufficient lipid levels (2.83 and 3.19 %WW respectively – Heirman, 2011) reflecting their essential energy content, which substantiates their importance as food items for highly mobile species, such as cod and pouting. Both SCA and SIA indicated remarkable dietary overlaps between cod and pouting, while SCA suggested a possible trophic competition between cod, sculpin and horse mackerel. However, the level of trophic competition depends on the degree of the food-resource availability (López-Jamar *et al.*, 1984). Since *J. herdmani* and *P. longicornis* occur in the OWF area in high densities (Zintzen, 2007; De Mesel *et al.*, 2015), consumers could exploit the same resources with no or limited competition (López-Jamar *et al.*, 1984). This in combination with the sufficient energy levels that have been reported for both *J. herdmani* and *P. longicornis* (De Troch *et al.*, 2013) supports the idea that there is no trophic competition between the fish species.

In addition to their abundance, *J. herdmani* and *P. longicornis* are energy- and fatty-acid-rich food resources (De Troch *et al.*, 2013). *Jassa herdmani* contains substantial concentrations of the fatty acid docosahexaenoic acid (DHA - De Troch *et al.*, 2013), which is an essential fatty-acid for the eye development of many fish species, such as cod (O'Brien-MacDonald *et al.*, 2006). *Pisidia longicornis*, on the other hand, has higher lipid levels than *J. herdmani* (3.19 and 2.83 %WW, respectively – Heirman, 2011) and contains considerable amounts of the essential fatty-acid eicosapentaenoic acid (EPA), which is an important fatty-acid for growth and fish development (Sargent *et al.*, 1999). These two species contain higher lipid levels than the colonising species *Monocorophium acherusicum* and the *J. herdmani* mats (Heirman, 2011; De Troch *et al.*, 2013). The energy content of *J. herdmani* and *P. longicornis* is also higher than that of food sources of pelagic origin, such as copepods (Michaud and Taggart, 2007) and of soft substrate origin, such as brown shrimp (*Crangon crangon*) larvae (Urzúa and Anger, 2013).

The pelagic horse mackerel seems to feed only occasionally on colonising organisms. This follows from the contradicting dietary results between the SCA (diet mainly based on colonising amphipods – Fig. 5.1) and the SIA, as revealed by its isotopic niche (diet mainly composed of zooplankton – since the overlap of the isotopic niches of horse mackerel and mackerel was large – Fig. 5.3B). This was the only species for which SCA and SIA did not reveal similar results, confirming that both methods can yield complementary information on dietary compositions (Kadye and Booth, 2012; Hertz *et al.*, 2017). Discrepancy between SIA and SCA can be a result of the differences in assimilation efficiencies among the food items (Hertz *et al.*, 2017). This discrepancy could also derive from the similarities in the stable isotope ratios of zooplankton and *Jassa herdmani* (Mavraki *et al.*, subm.) resulting in a less reliable resolution of the SIA for these two main food resources. A final explanation could also be found in the feeding behaviour of horse mackerels. Horse mackerels are opportunistic feeders that modify their diets according to the availability of the food items (Rumolo *et al.*, 2017), and they can feed on both benthic and pelagic prey items (Van Ginderdeuren *et al.*, 2014). Some pelagic species, such as horse mackerels, may take advantage of areas with high food availability to acquire and store energy (Jardas *et al.*, 2004). Fat and energy content of horse mackerels has been reported to be lowest during and after the spawning period in late spring and summer, when considerable energy is spent on reproduction, while it is highest in autumn (Abaunza *et al.*, 2003). In the North Sea, the energy content of horse mackerels increases rapidly in August and September (Abaunza *et al.*, 2003), which coincides with our sampling period (see 5.2.1). Hence, we suggest that horse mackerels occasionally use the artificial habitats of OWFs as feeding grounds, where they can benefit from the locally increased availability of energy-rich food sources (*J. herdmani*) to support their highly mobile life style. It is possible, though, that this is a seasonally recurring pattern that needs further research.

Mackerel was the only species that was not feeding on colonising organisms, as both the short- and the long-term analyses indicated a diet based on zooplankton (SIMMR: 89.4 ± 5.7 %, Table 5.8), which is indeed known to be its main food source (Van Ginderdeuren *et al.*, 2014; Bachiller *et al.*, 2018). Hence, the occurrence of the mackerel in the vicinity of the OWF installations may either be associated with the presence of other pelagic species in the area (Reubens pers. comm.), supporting the meeting point hypothesis that has been suggested for pelagic fish species (Dagorn and Fréon, 1999), or be linked to the enhanced protection against predation and the favourable current patterns that are provided by these habitats (Petersen and Malm, 2006). It could also be that the planktonic biomass in the area was sufficient to cover the energy demands of mackerel and/or that their highly mobile life did not allow them to exploit the sessile food items. Thus, we suggest that mackerels are not tempted, or they do not have the ability to exploit the abundant food items that are attached at the man-made structures, such as offshore wind turbines. However, further investigation is needed in order to define the way that mackerels utilize the OWFs and artificial reefs in general.

All the fish individuals in this study were caught near an offshore wind foundation. However, in the Belgian part of the North Sea, different types of artificial hard substrates exist, providing high abundance of colonising organisms (Zintzen, 2007). More than 300 shipwrecks, mainly from the World Wars I and II (Zintzen, 2007), have been mapped in the area (Fig. 5.5), while it is possible that many more unmapped wrecks are present (Reubens, 2013). Some of the wrecks are situated within the OWF area (Fig. 5.5). Even though the catch rates of pouting and juvenile cod are significantly higher at OWFs compared to shipwrecks in the Belgian part of the North Sea (Reubens *et al.*, 2013b), we cannot exclude that the fish were also foraging for food resources at shipwrecks instead of offshore wind foundations. The only exception could be cod, since research on the juvenile individuals' movement has shown strong residency towards the OWFs (Reubens *et al.*, 2013c). Cod juveniles exhibit crepuscular movements towards the OWFs, increasing their foraging success and reducing the predation pressure (Reubens *et al.*, 2014a) and, at the same time, they settle in the OWF area (Reubens *et al.*, 2014b). The combination of these studies with our results could suggest that cods remain in the OWF area to forage for a prolonged period.

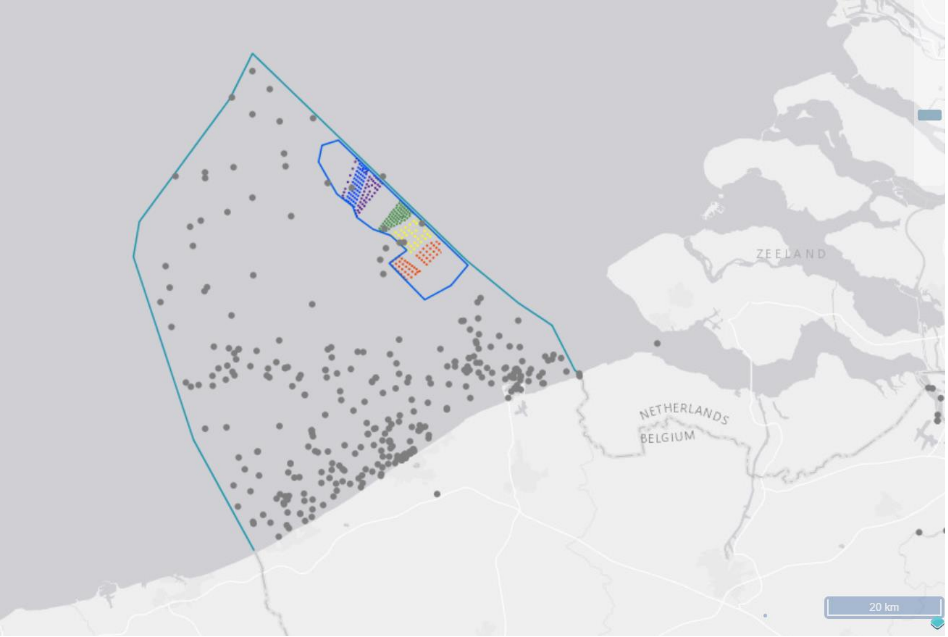

Figure 5.5: Overview of the offshore subtidal artificial reefs in the Belgian part of the North Sea. The grey dots represent the wrecks, the smaller coloured dots show the currently installed and operational offshore wind foundations and the blue line surrounding the offshore wind turbines represents the current renewable energy zone (source: www.kustportaal.be).

Overall, the results of this study indicate that there are two main pathways supporting the feeding ecology of the fish species associated with OWFs: the 'pelagic pathway' that was based on the consumption of prey items of pelagic origin, such as zooplankton, and the 'benthic pathway' that was based on the consumption of the colonising organisms, such as *J. herdmani* and *P. longicornis*. These findings are in line with earlier observations on the feeding ecology of fish species related to artificial habitats in the Mediterranean Sea (Cresson *et al.*, 2014) and could provide an indication of the co-existence of attraction and production on the same artificial reef system (Cresson *et al.*, 2019).

5.4.2. Attraction-production hypotheses

Offshore wind farms and other artificial reefs could potentially act as production sites for fish species (Leonhard and Pedersen, 2006) that feed on the abundant colonising fauna. The production hypothesis can be supported when the artificial habitat contributes to an increasing biomass and/or abundance of fish (Svane and Petersen, 2001). This is due to the increased feeding efficiency, survival rates of larvae and protection against predation at the artificial habitats, which encourage fish to settle and concentrate here (Brickhill *et al.*, 2005; Petersen and Malm, 2006). The feeding ecology of the benthic (sculpin) and benthopelagic (pouting and juvenile cod) species as revealed in this study could be an indication that these species could potentially increase their local production. This is due to their long-term feeding ecology, which suggests that they remain close to artificial habitats for a long period of time to feed.

Support for the production hypothesis has already been indicated for pouting and cod in the Belgian OWF area (De Troch *et al.*, 2013; Reubens *et al.*, 2013a). Specifically, research has shown that juvenile cod individuals indicate high residency and site fidelity in offshore wind foundations (Reubens *et al.*, 2013c) and that they settle in the area, suggesting increased production in terms of additional recruitment of individuals (Reubens *et al.*, 2014b). Furthermore, larger lengths and better fitness proxies (i.e. growth, condition index and diet) have been observed for pouting individuals in close proximity to OWFs compared to individuals occurring in sandy areas (Reubens *et al.*, 2013a). Cod and pouting exploit lipid- and fatty-acid-rich food sources (*J. herdmani* and *P. longicornis*) that can provide them with sufficient energy to sustain their metabolism and growth, and could also contribute to pouting's reproduction (De Troch *et al.*, 2013). The combination of our findings with these previous studies could corroborate the production hypothesis.

The findings of our study imply that sculpins could also increase their local production within the artificial reef area of OWFs. Indeed, artificial habitats have been reported to have a positive effect on the production of benthic carnivores, due to the increased food availability and the low fishing mortality (Cresson *et al.*, 2019). It is, thus, possible that artificial reefs, such as OWFs, could enhance the production of benthic species.

The results of our study corroborate the hypothesis that both attraction and production can co-exist on the same artificial reef, depending on the habits of every species (Cresson *et al.*, 2019). It is suggested that benthic and benthopelagic species could have an increased production within OWFs, but this cannot be demonstrated for the pelagic species. The opposite patterns observed between pelagic and benthic/benthopelagic species are typical in natural reefs but were seldomly noticed for artificial reefs (Morris *et al.*, 2018). Recently, similar patterns at the functional group-level have been observed for fish species at artificial reefs in the bay of Marseilles (Cresson *et al.*, 2019), where pelagic species do not feed on fauna associated with artificial reefs. In our study, mackerel seems not to be feeding on artificial reef fauna, while horse mackerel exploits them opportunistically. Visual observations have shown that horse mackerels approach the offshore wind foundations to predate, taking advantage of the shade that the foundations offer (Reubens pers. comm.). Hence, the pelagic species seem to be attracted towards the offshore wind turbines, but further research is needed concerning their production in the area. Previous studies have indicated that the effect of artificial reefs on the production of pelagic zooplanktivores (i.e. mackerel and horse mackerel) is negligible (Powers *et al.*, 2003), since most of these reefs are too small to significantly affect the pelagic communities (Cresson *et al.*, 2019). To conclude, further investigation is needed about whether and how the pelagic species exploit the artificial reefs.

5.5 Conclusions

Our results indicated that both benthopelagic (pouting and juvenile cod) and benthic species (sculpin), that occur abundantly at offshore wind farms (OWFs), use the artificial reefs as feeding grounds for a prolonged period, since stomach content analysis (SCA) and stable isotope analysis (SIA) reveal a diet that is based on fauna typically found on artificial hard substrates. These species mainly consume colonising amphipods (pouting and juvenile cod) and decapods (sculpin), which are abundant on these substrates. High trophic niche overlap was observed between the benthopelagic species, while the trophic niche of sculpin was not overlapping with any of the trophic niches of the other species. The pelagic species in our study either consume colonising organisms occasionally, i.e. horse mackerel, or they do not exploit them at all, i.e. mackerel. In the case of horse mackerel, artificial reefs act as feeding oases, providing high availability of food items. Mackerel continues feeding on zooplankton even when it is found in close proximity to OWFs and hence, the reason of its attraction to the artificial hard substrates requires further investigation. These findings corroborate to the hypothesis that OWFs could potentially increase the local production of fish species and especially of benthopelagic and benthic species, while further research is necessary for the pelagic species.

Chapter 6

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General Discussion

This dissertation has shown that OWFs do influence the local food webs from the basis, with the colonising fauna affecting the primary producer standing stocks, to higher trophic levels with several fish species intensively feeding on these organisms. The detailed food web analysis indicated that the food web structure of colonising assemblages differs along the depth gradient of an offshore wind turbine. Compared to epibenthic assemblages colonising the upper parts of the turbine, assemblages show larger trophic niches and thus higher food web complexity in deeper zones and in zones where organic matter accumulation occurs (scour protection layer and soft substrate near the turbine). The ecological relevance of the latter zones was highlighted by their capacity to support the presence of multiple trophic levels due to their high resource quantity (Chapter 2). Moreover, six of seven invertebrate species occurring in multiple depth zones along the depth gradient were found to be trophic generalists (*Mytilus edulis*, *Jassa herdmani*, *Metridium senile*, *Ophiothrix fragilis*, *Necora puber* and *Pisidia longicornis*). These species showed depth-specific food resource-use strategies (Fig. 6.1), indicating that trophic plasticity contributes to the co-existence and extended distribution of invertebrate species within and across different depth zones (Chapter 3).

The wider perspective (Fig. 6.2) indicates that the installation of OWFs and their subsequent colonisation by epibenthic organisms affect the primary producer standing stock (Slavik *et al.*, 2019). Here, two of the most common species on offshore wind turbines (the amphipod *Jassa herdmani* and the blue mussel *Mytilus edulis*) exhibited the highest carbon assimilation and biomass-specific carbon assimilation compared to the other colonising organisms. Moreover, by upscaling the obtained results to the total number of the installed offshore wind turbines in the Belgian part of the North Sea, it was estimated that the local annual primary producer standing stock (the baseline amount of phytoplankton that is typically present in the BPNS for one year) is reduced by 1.3 % due to the grazing activities of these two species (Chapter 4).

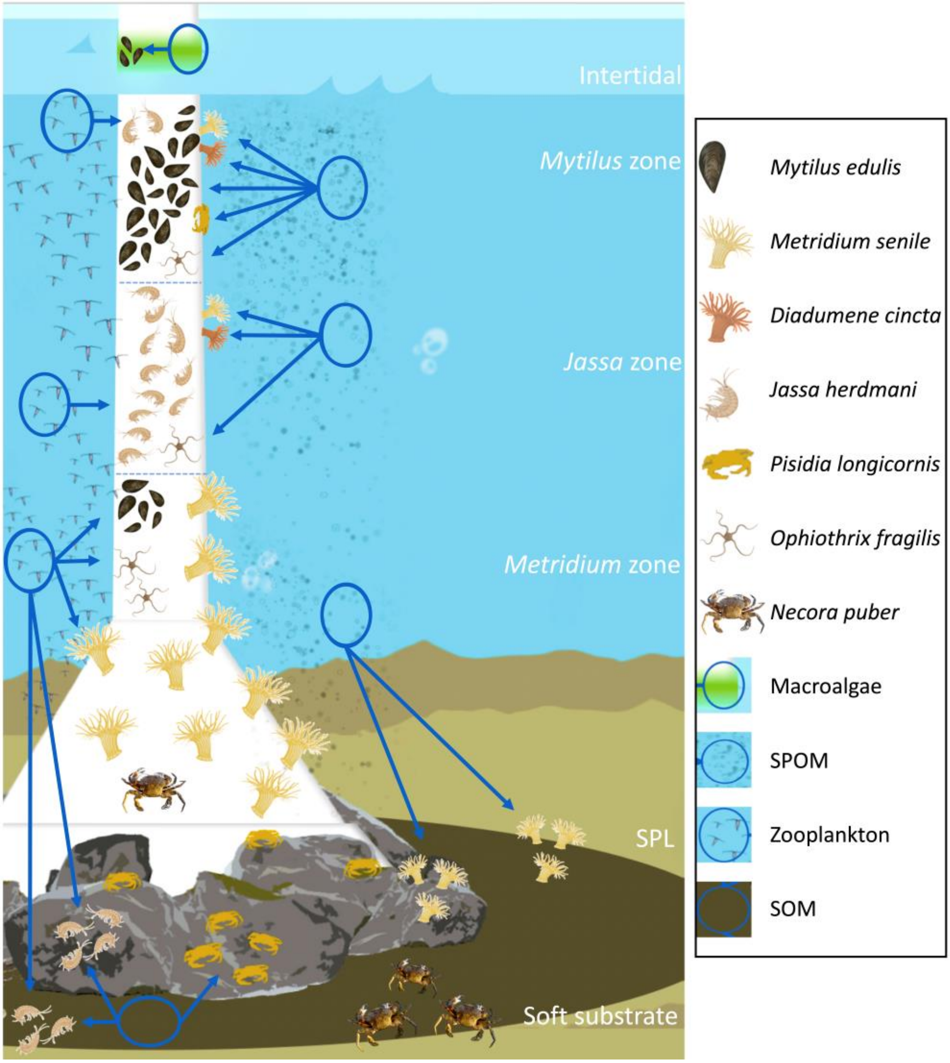


Figure 6.1: Detailed overview of the feeding ecology of the invertebrate species investigated in Chapter 3. The arrows point from the source to the consumer. *Necora puber* was the only species that did not show clear resource preference and thus, no arrows are pointing towards it. Apart from *Diadumene cincta*, all the other consumer species exhibit trophic plasticity, switching their diets according to the depth zone they occur.

Finally, OWFs attract several fish species, with several hypotheses being proposed to explain this attraction, such as provision of shelter against currents and/or predators (Bohnsack, 1989) and enhanced food availability (Leitão *et al.*, 2007; Reubens *et al.*, 2011). Three benthic and benthopelagic fish species (*Myoxocephalus scorpioides* (sculpin), *Gadus morhua* (cod) and *Trisopterus luscus* (pouting)) were found to utilize artificial reefs, such as OWFs, as feeding grounds for a prolonged period of time by consuming colonising species (*Jassa herdmani* and *Pisidia longicornis*). This could potentially increase the local benthic and benthopelagic fish production. Conversely, pelagic fish species either use the artificial habitats as feeding grounds occasionally (*Trachurus trachurus* (horse mackerel)) or not at all (*Scomber scombrus* (mackerel)) (Chapter 5).

In this chapter, the main findings of this thesis will be discussed in a wider perspective. This discussion will first focus on the functioning of OWFs as artificial reefs, with regard to the importance of scour protection layers and the surrounding soft substrate for the local food web complexity (see 6.1). Subsequently, the significance of these structures on the abundant occurrence of suspension feeding organisms, with the majority of them being trophic generalists will be addressed (sections 6.2 and 6.3). Next, the key role of *Jassa herdmani* on the reduction of the local primary producer standing stock and as a strong competitor for the available resources will be evaluated (see 6.4). Furthermore, this chapter will discuss the attraction and the potential increase in the production of particular fish species in the OWF area (see 6.5). Finally, the findings of this study will be related to the future OWF construction plans in the Belgian part of the North Sea and beyond (see 6.6) before presenting future challenges for research on OWFs, which arise from the outcome of this work (section 6.7).

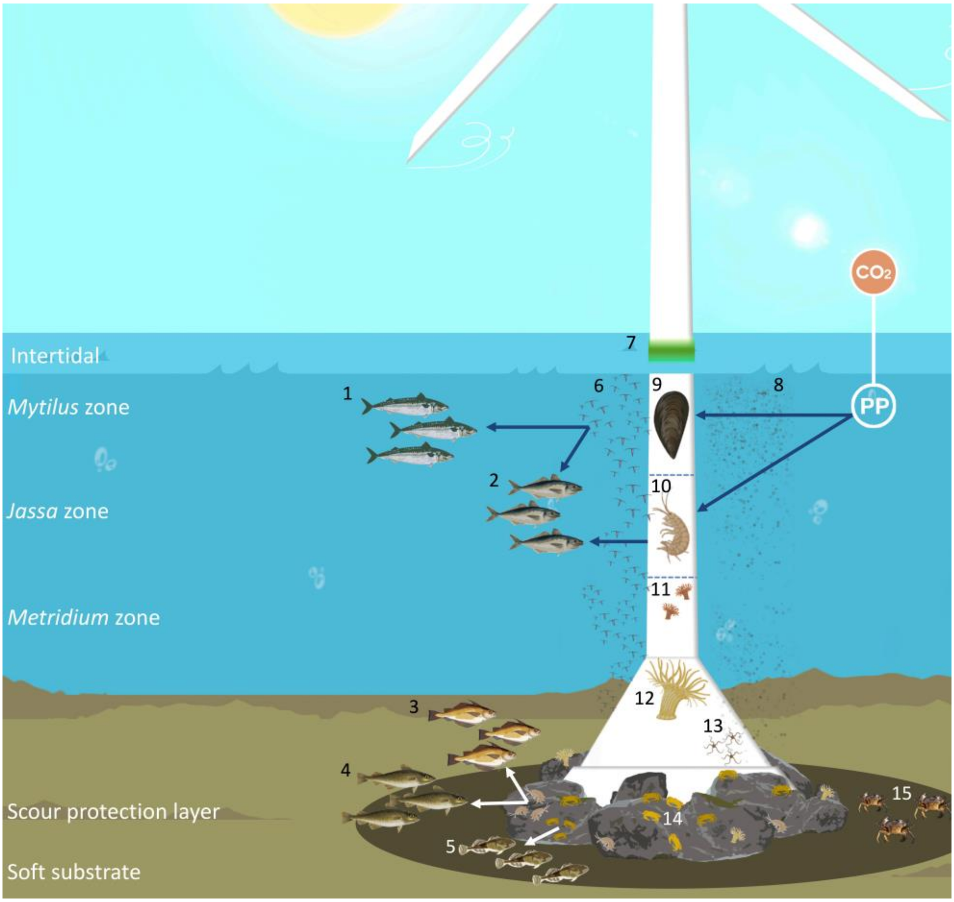


Figure 6.2: The marine environment on and around a gravity-based foundation in the Belgian part of the North Sea and illustration of the wider perspective of this thesis. The depth zones on the turbine foundation consist of different dominant species. The illustrated organisms and resources are the ones investigated in this thesis, while the arrows (pointing from the resource to the consumer) indicate trophic interactions. On the left, the feeding ecology of fish species as examined in Chapter 5. On the right, the consumption of the primary producer standing stock by *Mytilus edulis* and *Jassa herdmani*, as observed in Chapter 4. 1. *Scomber scombrus* (mackerel), 2. *Trachurus trachurus* (mackerel), 3. *Trisopterus luscus* (pouting), 4. *Gadus morhua* (cod), 5. *Myoxocephalus scorpioides* (sculpin), 6. Zooplankton, 7. Macroalgae, 8. Suspended particulate organic matter (SPOM), 9. *Mytilus edulis*, 10. *Jassa herdmani*, 11. *Diadumene cincta*, 12. *Metridium senile*, 13. *Ophiothrix fragilis*, 14. *Pisidia longicornis* and 15. *Necora puber*.

6.1 Offshore wind farms as artificial reefs

Offshore wind turbines act as *de facto* artificial reefs, representing unique features in the North Sea environment. They provide vertical surfaces stretching from the sea floor to the surface, increasing the habitat heterogeneity. Algae, sessile and mobile marine invertebrate and vertebrate species utilise the entire surface area of these turbines, with a variety of different species occupying different depths, leading to a pattern of vertical zonation. The zonation pattern found in this thesis is similar to that found in previous studies in the North Sea, both on offshore wind turbines (Lindeboom *et al.*, 2011; Krone *et al.*, 2013a; De Mesel *et al.*, 2015) and on oil and gas platforms (van der Stap *et al.*, 2016; Coolen, 2017). Furthermore, it was observed that the species occurring in the soft substrate were a mixture of typical soft-bottom and colonising species (Chapter 2), which comes in line with previous observations on the species diversity in sediments close to offshore wind turbines (Bouma and Lengkeek, 2012). This indicates that the zonation pattern identified in this thesis corresponds to a typical southern North Sea situation.

6.1.1 The importance of scour protection layers

The general pattern observed in this thesis is that the scour protection layer (SPL) plays a highly important role not only for increasing habitat heterogeneity, but also for promoting food web complexity at the base of the turbine foundations. Here, the SPL was found to accommodate species of multiple trophic levels (ranging from small suspension feeding organisms to large predatory fish species), indicating the second highest (after the soft substrate) food web complexity compared to the assemblages in the other zones (Chapter 2). This trophic complexity was further confirmed by the majority of species occurring in the SPL that exploited a wide range of resources occurring at and in between the rocks of the SPL (Chapter 3). The pivotal role of SPLs for the food web around the offshore wind turbines was further highlighted by the feeding ecology of fish species associated with it (benthopelagic and benthic), which feed for a prolonged period on colonising organisms (Chapter 5). The combination of these results indicates that SPLs function more efficiently as artificial reefs than the piles themselves, corroborating earlier predictions on the matter (Petersen and Malm, 2006; Langhamer, 2012). Moreover, this dissertation provides evidence that SPLs increase the available food quantity for both sessile and mobile fauna, as it had earlier been projected (see section 1.2.5 - Langhamer, 2012).

Initially, SPLs are colonised by a variety of sessile and hemi-sessile macrofaunal organisms, such as amphipods, in high densities (Bouma and Lengkeek, 2008; De Mesel *et al.*, 2013) and biomasses (Rumes *et al.*, 2013), which, in turn, attract predatory mobile species (Petersen and Malm, 2006). Thus, SPLs enhance the suitability of the offshore wind turbines as habitats for mobile demersal megafauna, such as fish, lobsters and crabs (Langhamer and Wilhelmsson, 2009; Reubens *et al.*, 2011; Krone *et al.*, 2013b; Scott *et al.*, 2018). Furthermore, SPLs offer habitat to rocky benthic fish species, such as *Myoxocephalus scorpioides*. Prior to the construction of offshore wind turbines, benthic fish species that normally occur in rocky areas, were rarely found in the Belgian part of the North Sea (Kerckhof *et al.*, 2018). This was mainly due to the scarcity of suitable habitats for them. With the continuous construction of offshore wind turbines and their SPLs, multiple rocky benthic fish species, such as the Ballan Wrasse *Labrus bergylta*, the tompot blenny *Parablennius gattorugine*, etc., have appeared in the area (Kerckhof *et al.*, 2018). The suitable habitat, together with the enhanced availability of prey species (Reubens *et al.*, 2011) and the provision of shelter from predation and currents (Langhamer, 2012) enhances the importance of SPLs as feeding grounds.

Turbines without SPLs, such as jacket foundations, can also serve as feeding grounds for mobile megafauna (Krone *et al.*, 2013b). Jacket foundations have higher structural complexity than monopiles and gravity-based foundations, since they consist of tubulars with multiple orientations (Krone *et al.*, 2013b; Causon and Gill, 2018). The structural complexity remains the same along the depth gradient, while the tubulars allow the main current flow to pass through the construction (Krone *et al.*, 2013b). An increased amount of empty mussel shells has been observed on the soft substrate on the bottom and around jackets foundations, providing secondary hard substrate and enhance the local spatial heterogeneity (Maar *et al.*, 2009; Krone *et al.*, 2013a). Nevertheless, the lack of SPLs leads to different biodiversity at the basis of the jacket foundations compared to foundations with SPLs (Krone *et al.*, 2017), implying that only SPLs could potentially sustain high abundances of mobile megafauna species, such as (benthic) fish. Indeed, jacket foundations seem to be less attractive to cod compared to the gravity-based foundations (Reubens *et al.*, 2013c). Furthermore, SPLs provide better hiding places for cod and pouting compared to the turbine foundations, creating suitable habitats for the feeding activities of these species (Reubens, 2013).

This thesis clearly indicates the importance of SPLs for the feeding habits of both sessile and mobile species. However, foundations without SPLs, such as jackets, were not investigated to practically compare the food web complexity between SPLs and the base of the jacket foundations. Furthermore, the location of the SPL in respect of oxygen, water salinity (Thorman, 1986), temperature (Verween *et al.*, 2007) and depth (Relini *et al.*, 1994) could also lead to different results. For example, the local accumulation of biomass in SPLs of OWFs in oxygen-poor bottom waters, such as the Baltic Sea, could foster the occurrence of anoxia (Wilding, 2014; Janßen *et al.*, 2015). The installation of SPLs in larger depths that those in the southern North Sea might result in the occurrence of fewer colonising organisms (Langhamer, 2012), which would possibly lead to lower food web complexity than the one observed in this study. Thus, the pattern observed for the SPL in this study cannot reliably be generalized for areas with different environmental characteristics.

6.1.2 The role of the soft substrate

The influence of the offshore wind turbines on the surrounding soft sediments has been studied with regard to macrofauna (Coates *et al.*, 2014) and fish (Vandendriessche *et al.*, 2015) composition and the sedimentological characteristics (Coates *et al.*, 2014). In this PhD thesis, the importance of these sediments on the food web complexity was highlighted.

The permeable soft sediments around the offshore wind turbines become finer than before the construction of these man-made structures (Coates *et al.*, 2014). Two different scenarios have been proposed for this fining: the sediment gets finer due to the pre-construction activities in the area (Van den Eynde *et al.*, 2010) and/or the changing hydrodynamics around the foundations lower the current speed in the wake of the foundation facilitating the deposition of fines (Van den Eynde, 2005).

Furthermore, high accumulation of organic matter in the soft sediments near the offshore wind turbines due to the biodeposition of the colonising organisms also leads to fining of sediments (Coates *et al.*, 2014) and increases the food quantity in the area (Mavraki *et al.*, 2020). This results in a more complex local food web (Chapter 2), with a wide range of resources that are available to both colonising and other organisms, such as the crab *Necora puber* (Chapter 3). It has been suggested that the food quantity and quality deposited on the soft substrates due to the biodeposition processes of colonising organisms is a 'shortcut within the food web' connecting different parts of the marine food web (Köller *et al.*, 2006). This is supported by the idea that in contrast to a food web based on small particulate matter, larger particles (e.g. faecal pellets) and/or even entire organisms fall from the artificial structures and become immediately available to the organisms living on the sediment (Köller *et al.*, 2006). Moreover, consumers in the soft substrates have access to particles and organisms that were not present in the area before the construction of the turbines (De Mesel *et al.*, 2015), enabling them to exploit resources that would naturally be unavailable to them.

The role of the soft sediments for the local food web complexity was only studied very close to the SPL. However, studies on the effects of OWFs on the surrounding soft sediments have shown that the organic matter accumulation expands up to 25 m away from the turbines, while increased macrofaunal density has been observed up to at least 15 m away from gravity-based foundations (Coates *et al.*, 2014). The effect of monopile foundations on the soft substrate community composition is not as apparent as with jacket foundations (Lefaible *et al.*, 2019). This indicates that the results of this study with regard to the soft substrate food web complexity could differ with distances from the turbines and with different types of foundations due to both the distinct macrofaunal composition and the extent of organic matter accumulation. Thus, further investigation of the soft substrate food web complexity at different distances and types of foundations is necessary to completely understand the effects of OWFs on the food web properties of the surrounding soft sediments.

6.2 Offshore wind turbines: the kingdom of suspension feeders

Suspension feeders dominate benthic communities that occur on hard substrates (Gili and Coma, 1998). The introduction of offshore wind turbines alters the functioning of the surrounding ecosystem by restructuring the communities at and around the foundations (Joschko *et al.*, 2008; Krone *et al.*, 2013a), enhancing the establishment of suspension feeding organisms (Wilhelmsson and Malm, 2008; Lindeboom *et al.*, 2011). Offshore wind turbines can double the biomass of suspension feeders within a wind farm area compared to the situation before its construction (Raoux *et al.*, 2017), indicating that these structures act as the "kingdom" of suspension feeders. The establishment of this kingdom results in a shift in local functional evenness towards suspension feeding (decreased functional evenness). Functional evenness is the measure of the regularity of the distribution and relative abundance of species in the functional niche space (Mason *et al.*, 2005; Villéger *et al.*, 2008; Ricotta *et al.*, 2014). The presence of high or low functional evenness is of fundamental importance to community dynamics, since it can suggest whether species are distributed over many functional traits (high evenness – Hewitt *et al.*, 2008) or they share a specific functional trait (low evenness – Mason *et al.*, 2005), such as suspension feeding. Functional evenness decreases with increased disturbance, with co-occurring species becoming highly clustered in the functional space (Mouillot *et al.*, 2013). Research has shown that low functional evenness could be an early warning signal of disturbance impacts (Mouillot *et al.*, 2013), such as the perturbed environment due to the installation of OWFs. Indeed, lower functional evenness has been observed within artificial reefs compared to natural rocky areas (Carvalho *et al.*, 2013). The co-existence of multiple functional traits could potentially increase the functional diversity (Hewitt *et al.*, 2008). In OWFs, however, where one main functional trait is observed, the evolution of the communities will probably deteriorate the functional diversity. This has already been suggested for the communities at lower depths of the turbines. The anemone *Metridium senile* dominates these depths and causes the so-called slimeification, establishing species-poor communities (Kerckhof *et al.*, 2019) and possibly decreasing the functional diversity.

The present work highlighted the important role of these organisms on the (local) food web properties. Specifically, we observed resource partitioning among and within assemblages consisting of suspension feeders (Chapter 2). Moreover, it was indicated that suspension feeding organisms occurring in multiple zones along the depth gradient of an offshore wind turbine exhibit a substantial degree of trophic plasticity (Chapter 3). This allows for the co-existence of multiple individuals by limiting the effects of trophic competition (Lefebvre *et al.*, 2009; Riera, 2009). Trophic plasticity may allow for resource partitioning (MacNeil *et al.*, 1997; Ashton *et al.*, 2010), although not all species that show trophic plasticity can partition the available resources. There are two mechanisms in which resource plasticity may occur among species (Ashton *et al.*, 2010). The first way is via niche pre-emption (Fig. 6.3A), in which individuals respond to the presence of a superior competitor by switching their diets to an alternative (either less-favourable or *ad libitum*) resource (May and Arthur, 1972; Ashton *et al.*, 2010). This is supported by the idea that generalists that change their foraging behaviour to capitalise on the most rewarding resource can co-exist with competitively superior species (Abrams, 2006). The second mechanism (Fig. 6.3B) suggests that trophic plasticity may enhance the competitive ability, with the superior competitors exhibiting trophic plasticity and the inferior competitors being unable to shift their diets (Casper and Jackson, 1997). The results of Chapter 3 imply that *J. herdmani* is possibly a superior competitor, since, once present, it forces the other species to switch their diets to an alternative resource, while it remains feeding on zooplankton.

Apart from exhibiting trophic plasticity and resource partitioning, suspension feeders were found to affect the annual primary producer standing stock (Chapter 4) and serve as important resources for fish (Chapter 5). These results corroborate predictions on the role of suspension feeders occurring at OWFs. Trophic plasticity has been previously proposed as a common mechanism for suspension feeders, which act opportunistically and exploit the variable resources they encounter (Okamura, 1990). Krone *et al.* (2013a) hypothesized that the high numbers of suspension feeders in OWFs lead to a reduction of suspended particles from the water column, and they also provide food for intermediate and top predators.

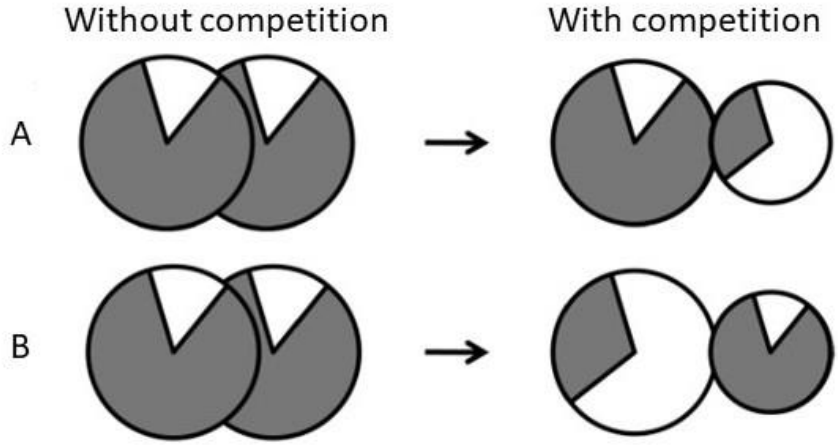


Figure 6.3: Mechanisms of resource use differentiation. Resource use of two different resources (grey and white) for two species, according to their non-competitive (on the left) and competitive (on the right) trophic niches (circles) are illustrated. The superior competitors have the leftmost niches. Two alternative scenarios are depicted: (A) niche pre-emption in which individuals respond to the superior resource competitor by switching their diets to another resource and (B) dominant plasticity, where only the superior competitor can exhibit trophic plasticity (modified from the source: Ashton *et al*., 2010).

The structure (expressed as complexity and diversity) and biomass of suspension feeding assemblages can increase with food availability, while their succession depends upon the input of the total energy deriving from the suspended particles in the water column (Gili and Coma, 1998). The high abundances and densities of suspension feeders at offshore areas in the North Sea indicate that there is sufficient food availability for these species along the entire depth gradient. The increased food availability at the deeper areas of the turbines was discussed in section 6.1. High concentrations of surface suspended particulate matter (SPM), together with the biodeposition products of the colonising organisms provide an adequate amount of resources for the suspension feeding organisms in the shallower parts of the turbines. These concentrations of surface SPM, also known as plumes, have been linked with the colonising organisms occurring on the turbines and the existence of SPLs (Baeye and Fettweis, 2015). Plumes in the North Sea were commonly observed shortly after strong storm events when high concentrations of SPM were apparent near the sea surface (Doerffer and Fischer, 1994). However, the construction of OWFs together with other anthropogenic activities in the North Sea, such as dredging, sand extraction, land reclamation and large-scale aquaculture facilities (Fredette and French, 2004; Orpin *et al.*, 2004; Bolam *et al.*, 2006; Ware *et al.*, 2010; Fettweis *et al.*, 2011) impose changes in the local hydrodynamics and fine-grained sediment dynamics (De Vos *et al.*, 2011; Whitehouse *et al.*, 2011), increasing the vertical mixing of suspended material in the water column (Floeter *et al.*, 2017). Plumes associated with OWFs can be induced by the combination of three processes: (a) localised scouring of the seabed at the base of the foundations (Vanhellemont and Ruddick, 2014), (b) the release of mud and organic matter associated with the colonising organisms (Baeye and Fettweis, 2015), and (c) the re-distribution of suspended sediment in the water column caused by the increased vertical mixing in the wake of the foundations (Forster, 2018). Recent measurements indicated that the suspended sediment concentration was higher at the sea surface compared to the concentration near the sea-bottom (Forster, 2018). The extent of the plume depends on the grain size of the substratum, with large particles settling fast, while the fine particles can be deposited over a wider area depending on the local currents (Hiscock *et al.*, 2002).

6.3 Co-existence and the increase of trophic generalists

On offshore wind turbines, a great species diversity and density is being concentrated in limited space (Petersen and Malm, 2006; Kerckhof *et al.*, 2010b). In such environments, invertebrate species compete for the available resources (space and food - Whomersley and Picken, 2003). Here, we suggested that species co-occurring on an offshore wind turbine can expand their distribution and survival through trophic plasticity, which allows them to exploit different resources and lower the interspecific competition for food (Chapter 3). This indicates that trophic generalists – individuals taking advantage of a wide range of resources (Bearhop *et al.*, 2004) - have better possibilities for thriving in this perturbed environment created by the offshore wind turbines than trophic specialists – individuals specialising in a specific food resource (Bearhop *et al.*, 2004).

Specialist dietary strategies incur greater risk to distribution due to the limited resource flexibility, while species with broad depth distribution are expected to be trophic generalists (MacDonald *et al.*, 2019). Three of the generalist species in this thesis (*Jassa herdmani*, *Mytilus edulis* and *Metridium senile*) are also dominant in specific depth zones (*Jassa*, *Mytilus* and *Metridium* zone, respectively), where they occur in high densities (De Mesel *et al.*, 2015). This indicates an over-representation of generalists over specialists, at least in terms of abundances. The over-representation of generalist over specialist feeders has been observed in multiple ecosystems, such as temperate and subtropical estuaries (Richoux and Froneman, 2008; Freeman *et al.*, 2018), bays in the North Sea (Dubois *et al.*, 2007) and the Antarctic shelf (Gutt, 2006), and also for different species, such as barnacles (Dubois *et al.*, 2007), amphipods (MacAvoy *et al.*, 2016) and fish (Quevedo *et al.*, 2009). Trophic specialists are expected to be less resilient and more vulnerable to habitat perturbation compared to trophic generalists (Gownaris *et al.*, 2015), because of their dependence on a specific (limiting) resource. Trophic generalists, on the contrary, are capable of retaining a broader range of resources and adapt to both natural and anthropogenic changes in food availability (Freeman *et al.*, 2018). Furthermore, the ability to shift between alternative resources makes trophic generalists less susceptible to extinction (Purvis *et al.*, 2000).

Concepts of specialists vs. generalists have a long history in ecological studies, but nowadays, concern is given to specialist species. A global decrease of specialists has been observed, which results in the increase of functional homogenisation (Clavel *et al.*, 2011). A decrease in specialist species coincides with a partial substitution by a small number of generalist species, with this reduction lowering the biodiversity via homogenisation (McKinney and Lockwood, 1999; Fisher and Owens, 2004; Olden and Rooney, 2006; Clavel *et al.*, 2011), altering the equilibrium of the ecosystem (Richmond *et al.*, 2005). Specialisation increases the variability, while generalisation results in homogenisation, which replaces the “unique” species by “widespread” ones (McKinney and Lockwood, 1999).

It is debatable whether the increased variability due to specialisation has consistent effects on multiple stability components or whether some stability components increase with diversity and some other decrease (Pennekamp *et al.*, 2018). As mentioned in Chapter 1, food web stability is dependent on the connectance and distribution of trophic links among species (Borrvall *et al.*, 2000; Ebenman and

Jonsson, 2005). It is also highly dependent on the strength of its interactions with other species (Ebenman and Jonsson, 2005). From that, it is implied that food web stability depends on the most connected species, which usually are resource generalists. This is because trophic generalists can create more novel linkages between different trophic levels (Fox *et al.*, 2019) and because the more connections a species has, the more potential it has to affect the food web (Dunne *et al.*, 2002). It has been suggested that the loss of generalist species with several weak links can lead to destabilisation of the entire food web (Borrvall *et al.*, 2000). However, specialist species also play an important role in the stability of the food webs. Even though they tend to have fewer links, these links are stronger compared to those of generalist species. Thus, in communities with many specialists that have strong trophic interactions, the densities of species vary remarkably in time, making species more vulnerable to stochastic extinction compared to communities dominated by weak trophic links between species (Ebenman and Jonsson, 2005). From the above, it is clear that the robustness of food webs to loss of specialists with few trophic links does not vary predictably; it will either induce large and unpredictable effects on the structure and functioning of food webs or it will cause few and/or no changes (Dunne *et al.*, 2002).

Apart from the dietary flexibility, generalist species can colonise new habitats easier than specialists (Clavel *et al.*, 2011), which makes them also known as habitat generalists. Habitat generalists are species capable of successfully establishing themselves outside of their native habitat range, for example invasive species are often indicators of habitat generalization (Marvier *et al.*, 2004). Habitat specialists cannot expand beyond their habitat range, but they are considered competitive superiors over the habitat generalists in cases of competition for the available habitat (Caley and Munday, 2003; Marvier *et al.*, 2004). However, they are unable to outcompete the generalist species on a broader range (Caley and Munday, 2003).

The concept of habitat generalist vs. specialist species has been linked with the r-K selection theory that was firstly introduced by MacArthur and Wilson (1967). This theory suggests that species can be positioned along a continuum between two endpoints; the r-endpoint represents the quantitative extreme, where the organisms allocate their energy for reproduction and the utmost offspring, while the K-endpoint is the qualitative extreme, where organisms allocate their energy for enhanced survival (Pianka, 1970, 1972). Habitat specialist species are often associated with the K-endpoint and generalists with the r-extreme (Quadros *et al.*, 2009). This relationship between habitat use and reproductive strategies allows predicting the tolerance of a species to habitat perturbations (McKinney, 1997; Purvis *et al.*, 2000; Sakai *et al.*, 2001). Hence, anthropogenic disturbances leading to habitat alteration will influence habitat specialists much more than generalists, resulting in an over-representation of the latter (Kitahara and Fujii, 1994; McKinney, 1997; Marvier *et al.*, 2004). Therefore, in introduced artificial hard substrates, such as offshore wind turbines, being a generalist species can be crucial for the survival and extended distribution along the depth gradient. With the increasing number of offshore wind turbines, more trophic generalists are expected in the BPNS and generally the North Sea, altering the balance of the North Sea ecosystem.

6.4 Primary producer standing stock: the role of *Jassa herdmani*

The results of this thesis suggest that 1.3 % of the local annual primary producer standing stock is grazed upon by the blue mussel *Mytilus edulis* and the amphipod *Jassa herdmani* (Chapter 4), which occur on the currently installed offshore wind turbines (318 turbines in total) in the BPNS. This amount is relatively small given that ~25 % of the annual primary production in the BPNS is deposited in the sediment (Provoost *et al.*, 2013). Even though this decrease is small, it extends over a large area and intensifies closer to the offshore wind turbines (Slavik *et al.*, 2019). The installation of more OWFs in the future will lead to a significant reduction of the primary productivity, which is the major energy source for ecosystems globally (Imhoff *et al.*, 2004).

OWFs are installed into permeable sediments. The carbon assimilation by the natural macrofauna in such sediments ranges between 3.3 mg C m^{-2} d^{-1} and 42 mg C m^{-2} d^{-1} (Bühring *et al.*, 2006b). However, with the construction of OWFs thousands of m^2 of permeable sediments are being replaced by hard substrates (the footprint of the turbines and - in the case of monopiles and gravity-based foundations - the scour protection layers). Thus, the natural carbon cycle changes due to the presence of these structures (Mangi, 2013). In this study, we suggest that the presence of jacket foundations leads to the most significant increase in the carbon assimilation compared to the natural soft sediment macrofauna (ratio turbine/sediment: min: 14242 max: 181259). This is mainly caused by the high densities of *J. herdmani* and *M. edulis* occurring on this type of foundation (Krone *et al.*, 2013a; Kerckhof pers. comm.), and partly by the small loss of permeable sediments since the footprint of jacket foundations averages 10.5 m^2 (Rumes *et al.*, 2013). The amount of non-assimilated carbon due to the loss of sediments is much smaller with the presence of a monopile and/or a gravity-based foundation, because these two types of foundations have larger footprints (573 m^2 and 2227 m^2, respectively – Rumes *et al.*, 2013). Owing to their large footprint and the lower densities of *J. herdmani* and *M. edulis*, monopiles have a smaller effect on the increase of the carbon assimilation compared to the soft sediment macrofauna (ratio turbine/sediment: min: 38 max: 485). The occurrence of these two species (*J. herdmani* and *M. edulis*) on gravity-based foundations causes the smallest increase in the carbon assimilation (ratio turbine/sediment: min: 9 max: 116). This indicates that the presence of monopiles and gravity-based foundations has a smaller effect on the increase of the local carbon assimilation compared to the presence of jacket foundations.

Furthermore, our results suggest that, compared to the other colonising organisms, *J. herdmani* plays the most important role in the reduction of primary producer standing stock and it is a strong resource competitor. The exclusion of mussels from the upscaling calculations results in a reduction of 1.15 % of the annual primary producer standing stock in the BPNS by *J. herdmani* alone. *Jassa* species are by far the most abundant species on artificial hard substrates, such as buoys, boulders, ship wrecks and offshore wind turbines (Nair and Anger, 1980; Franz, 1989; Conradi *et al.*, 1997; Scinto *et al.*, 2007; Zintzen *et al.*, 2008; Beermann and Franke, 2012; De Mesel *et al.*, 2015). In our study area, *J. herdmani* is extremely abundant (densities exceeding 10^4 individuals m^{-2}) (De Mesel *et al.*, 2015). Moreover, *Jassa* species have been observed to have a degree of flexibility in their feeding habits, which explains their successful establishment on multiple artificial hard substrate habitats (Dixon and Moore, 1997). This trophic flexibility was also indicated by the results of this thesis, where *J. herdmani* was feeding on zooplankton and on sediment organic matter *in-*

situ (Chapter 3), while it was largely exploiting fragmented algae in the *ex-situ* pulse-chase experiment (Chapter 4). This implies that this species is a strong competitor, since it is capable of exhibiting high resource plasticity as a function of its competitive environment (Ashton *et al.*, 2010) and it may force other organisms to feed on less favourable resources (Chapter 3).

This thesis proposes that the impact of the OWFs on the local annual primary producer standing stock is neutral, since its reduction was not remarkable. However, our results do not allow for drawing firm conclusions on the entire carbon flow within the colonising communities, since we did not perform the pulse-chase experiment in closed systems. Most pulse-chase experiments on sediment assemblages have been conducted in closed chambers (e.g. Woulds *et al.*, 2007; van Nugteren *et al.*, 2009; Braeckman *et al.*, 2010, 2018, 2019; Evrard *et al.*, 2010, 2012). The chambers remain sealed for at least some hours during the experimental duration to measure the production of ^{13}C-labelled dissolved inorganic carbon (DIC), which is necessary to determine the macrofaunal and/or bacterial respiration rates (Moodley *et al.*, 2000; Woulds *et al.*, 2009; Gontikaki *et al.*, 2011c). Therefore, the main carbon processing and, thus, the major reduction of the primary producer standing stock in the OWF areas might be caused by different processes, such as respiration. Nevertheless, we estimated the amount of carbon that is grazed upon by colonising organisms, which is, to our knowledge, the first time ever this has been experimentally determined.

Moreover, bacteria occurring within the colonising assemblages will certainly have some prominent roles in assimilating a part of the ^{13}C that was added in the experimental tanks. However, in a similar experiment on soft sediment macrofauna with the same duration (3 days) and similar feeding treatment (introducing the organic matter suspended in seawater into the water of the experimental tanks), macrofauna assimilated the highest amount of carbon compared to bacteria (van Nugteren *et al.*, 2009). This can be explained by the fact that bacteria do not intensively exploit particulate organic matter (Azam *et al.*, 1994). On the other hand, it is possible that this would change in case of a longer experimental duration, since bacteria can be responsible for the highest carbon assimilation within sediment communities (Woulds *et al.*, 2016). This occurs due to the degradation of the particulate organic matter into dissolved organic matter, which is highly exploited by bacteria (Azam *et al.*, 1994). Thus, although we did not expect a high carbon assimilation by bacteria in our experimental conditions, it is possible that they assimilate more carbon than macrofauna *in situ*. This could lead to indirect carbon reduction resulting from the mineralization by bacteria.

From the above, it is apparent that a different experimental set-up could provide further information on the carbon flow within colonising assemblages. The conditions of this experiment were not ideal, since the experimental tanks were not closed, and thus, we were not able to estimate the part of carbon that was respired by the colonising organisms. The carbon assimilation by bacteria and the labelled carbon that is excreted as faeces were also not estimated. Furthermore, the experiment was conducted for a period of three days, since our attempt to conduct the experiment for a longer period failed. Initially, we performed the same experiment for a period of 6 days. However, at the end of the experimental period, the majority of the *Jassa herdmani* individuals had depleted, which was probably the result of anoxia. Therefore, we decided to reduce the duration of the experiment and also provide more oxygen in the lower experimental tank to assure that anoxia would not occur again. It is important, hence, to conduct such experiments in a way that all the previously mentioned aspects are measured, without creating anoxic conditions. This would provide a complete insight on the fate of organic matter within the colonising assemblages and then we would be able to accurately estimate the amount of the primary producer standing stock that is processed by the colonising assemblages.

6.5 Attraction-production hypotheses

In this thesis, four fish species (cod, pouting, horse mackerel and sculpin) were found to utilize artificial reefs, such as OWFs, as feeding grounds (on a short- or a long-term basis). This result comes in line with previous studies on the feeding ecology of benthopelagic fish species in the BPNS, stating that the enhanced food availability attracts fish individuals towards the artificial reefs (Reubens *et al.*, 2011). On the contrary, mackerels are attracted to the turbines for other reason(s), since they do not seem to utilize them as feeding grounds at all.

Attraction towards the offshore wind turbines has already been investigated for the examined species from a number of studies in the OWFs in the BPNS (Reubens *et al.*, 2011, 2013a, 2013b; Kerckhof *et al.*, 2018) and other OWFs in the North and Baltic Sea (Wilhelmsson *et al.*, 2006a; Lindeboom *et al.*, 2011; Bergström *et al.*, 2013; Krone *et al.*, 2013b). The findings of this thesis further corroborate the attraction hypothesis for all the examined fish species. Even though the attraction towards the OWFs has been confirmed multiple times, there is still no clear evidence about increased production. This is because production cannot be easily measured.

This thesis cannot provide a concrete answer on whether there is increased production or not, but it supports the hypothesis that the local production of benthic and benthopelagic species could potentially increase. Mechanisms that can contribute to increased production include additional food availability, increased feeding efficiency, provision of shelter from currents and predators and provision of recruitment habitat for settling organisms (Stone *et al.*, 1979; Bohnsack, 1989; Reubens *et al.*, 2014a). The results demonstrate that OWFs provide increased feeding activity and efficiency. The integration of our dietary results with previous studies in the area can provide an insight on the possible production of the benthopelagic species (cod and pouting) that have been extensively studied in the OWFs in the BPNS. These species exploit energy- and fatty-acid-rich food sources, such as the amphipod *Jassa herdmani* and the crab *Pisidia longicornis* (De Troch *et al.*, 2013). These resources supply them with the required energy to maintain their metabolism and contribute to their growth and/or reproduction (De Troch *et al.*, 2013). Cod has shown strong residency and site fidelity towards offshore wind turbine foundations (Reubens *et al.*, 2013c), while the length and fitness proxies of pouting individuals inside the OWFs are larger than those of individuals occurring in sandy areas (Reubens *et al.*, 2013a). Thus, cod and pouting get sufficient energy supplies from foraging on colonising organisms to grow (De Troch *et al.*, 2013) and they could potentially recruit new individuals, which would possibly lead to increased local production (Reubens, 2013). However, further research on the production of fish species locally and regionally (on the scale of the southern North Sea) is needed.

The attraction-production hypotheses should also be investigated under the prism of global warming. The increased sea temperature is thought to be responsible for faunal changes throughout the world, from the Mediterranean Sea (Consoli *et al.*, 2013), to the North Atlantic (Goberville *et al.*, 2014) and the Arctic (Yurkowski *et al.*, 2018). Fish species either rapidly adapt to the temperature changes or migrate to areas with colder waters. Cod, for example, exhibits long range movements as a response to the environmental changes (Klein *et al.*, 2017). Ocean warming has catastrophic consequences for natural reefs, such as coral reefs (Pandolfi *et al.*, 2011; Frieler *et al.*, 2012), while the colonisation of artificial hard substrates by epibenthic fauna is more pronounced in warmer seas compared to colder temperatures, although this mainly refers to micro-organisms instead of macro-organisms (Rao, 2010; Smale *et al.*, 2011). This could potentially lead to an increased attraction towards the artificial habitats. However, the effects of ocean warming on the fish production are expected to be severe, since production is controlled by enrichment, concentration and retention processes, which are governed by climatic factors (Walther *et al.*, 2002). Temperature increases intensify the upwelling leading to a decline of the global fish production (Walther *et al.*, 2002).

6.6 The larger picture

This thesis particularly indicated that: (a) SPLs play a pivotal role as feeding grounds both for vertebrate and invertebrate species, (b) soft substrates near the turbine foundations show a high food web complexity, in terms of trophic diversity compared to the other zones along the depth gradient, (c) *Jassa herdmani* plays the most significant role in the consumption of primary producers, in contrast to predictions stating that *M. edulis* would cause the highest consumption, and it is possibly a strong competitor for food, and (d) benthopelagic and benthic fish species use the artificial habitats, such as OWFs, as feeding grounds for a prolonged period of time. These findings suggest that the (local – turbine and BPNS scale) food web properties are changing due to the presence of offshore wind turbine foundations. The proliferation of OWF installations and their SPLs leads to an enhanced carrying capacity, since the capacity of the environment increases with the establishment of new habitats (Bohnsack, 1989; Lidberg, 1997). This enhancement together with the organic enrichment of soft substrates close to the foundations that can host more organisms than before, confirm predictions on the way how OWFs would affect the surrounding marine environment. These findings indicate a localised (turbine scale) increase in biodiversity and complexity at the base of foundations with SPLs. The reduction of the annual primary producer standing stock and the exploitation of artificial reefs, such as OWFs, as feeding grounds by different fish species may have an effect at an even wider spatial scale (e.g. BPNS).

The findings of this thesis cannot be seen isolated from the bigger picture of the proliferation of OWFs both in the BPNS and the southern North Sea. In the future, more turbines will be installed, covering a larger surface area in the southern North Sea. The insights in the food web properties from this thesis suggest that offshore wind turbine foundations with SPLs may have a potentially enhancing effect on the local food webs. However, predicting the cumulative effects of OWFs on the larger scale remains challenging.

As mentioned above, the construction of multiple OWFs in the southern North Sea will lead to an increased environmental carrying capacity at the SPLs, which could act as ‘trophic-diversity hot spots’ at the base of gravity-based and possibly also monopile foundations. The effects of offshore wind turbines will also expand horizontally on the seafloor since, as mentioned above, the increased organic matter accumulation on the soft sediments attracts multiple organisms that show higher densities up to 15 m away from the turbines (Coates *et al.*, 2014). Moreover, the fact that all the dominant (most abundant) species along the depth gradient of an offshore wind turbine showed trophic plasticity indicates that the southern North Sea will become a sea of trophic generalists. Trophic generalists have more trophic links compared to trophic specialists. This, in turn, will possibly result in more stable food webs, since food web stability is highly dependent on the most connected species (Dunne *et al.*, 2002), which almost by definition are trophic generalists. Therefore, the increased number of trophic generalists on turbine foundations will possibly develop ‘islands’ of stable food webs. However, research on the horizontal expansion of this effect is necessary to examine the geographical scale of this effect. Also, the investigation of the feeding ecology of more invertebrate species is needed, since in this thesis, only seven species were examined, while 80 different species have been documented in subtidal zones on a gravity-based foundation in the BPNS (De

Mesel *et al.*, 2015). Naturally, not all of them occur in different depth zones in sufficient numbers to easily run such analysis.

The installation of more OWFs and their subsequent colonisation will naturally lead to a further reduction of the primary producer standing stock in the southern North Sea, influencing the very basis of the marine food webs and biogeochemical cycling (Slavik *et al.*, 2019). Slavik *et al.* (2019) estimated the reduction of the primary producer standing stock caused only by *M. edulis* attached on the installed and future planned (up to 2030) offshore wind turbines in the entire southern North Sea to be 3.7 ± 1.5 %. According to this thesis, the population of *J. herdmani* on wind turbines reduces the primary producer standing stock almost seven times more compared to *M. edulis*. Using the estimations by Slavik *et al.* (2019) for all the currently installed and future planned OWFs in the southern North Sea and assuming that *J. herdmani* shows densities and carbon assimilation rates similar to our study area, we can presume that these two organisms will cause a reduction of ~ 30 % in the southern North Sea. This amount is higher than the amount of the primary producer standing stock that is deposited in the sediments in the BPNS (~25 % - Provoost *et al.*, 2013). This indicates that OWFs could have crucial cumulative effects for the marine environment, since, by reducing the primary producers' standing stock, they affect the primary energy source for marine ecosystems (Imhoff *et al.*, 2004). Subsequently, a resource-poor environment may be created, since the organic matter will concentrate inside and close to such artificial habitats due to biodeposition processes, while it may be reduced beyond that area, as a result of the 'shadow' of the artificial habitats (Reichart *et al.*, 2017). The latter will much depend on how the increased consumption of the primary producers may be compensated for by an increased primary productivity. The enhanced vertical mixing of the water column might increase the primary production below the thermocline (Floeter *et al.*, 2017). Additionally, the increased nutrient influx into the surface waters could also result in enhanced surface primary production (Floeter *et al.*, 2017). Nevertheless, increased primary production due to the presence of OWF installations has not been proven yet and the implication of such large-scale effect of OWFs on the primary producer standing stock should be further examined, considering the conservative nature of our experiment.

This thesis supported previous findings on increased fish attraction towards the offshore wind turbines, and also corroborated the hypothesis of an enhanced production for some fish species due to the prolonged feeding on colonising organisms. Production can be facilitated by the enhanced feeding efficiency, provision of shelter against predators and currents and provision of habitat for settlement of fish larvae (Stone *et al.*, 1979; Bohnsack, 1989; Reubens *et al.*, 2014b). Fisheries exclusion can also promote the density, biomass, diversity and individual fish sizes, which could lead to increased (local) production (Reubens, 2013). Currently, extensive zones of the BPNS and the southern North Sea are dedicated to the offshore renewable energy, being partially closed for any other kind of human activity. Even in regions where fisheries are partially permitted (i.e. United Kingdom), nearly 90 % of the fishermen prefer avoiding fishing within the OWF areas due to concerns about safety, insurance and/or liability issues (Hooper *et al.*, 2015). Then, and provided that turbines are close to one another, OWFs may act as de facto marine protected areas (MPAs) with potential spill-over benefits to commercial fish stocks in the wider region (Ashley *et al.*, 2014). In BPNS, the future turbines will be more powerful and with higher efficiency than the currently installed ones, requiring more space between each turbine, which could possibly permit fisheries within the OWF area. However, in Belgium and in Germany, the implementation of IMO regulations prohibit shipping within 500 m safety zone around the wind turbines (Mehdi *et al.*, 2017). MPAs can increase the ecological resilience of marine communities in comparison to other (non-spatial) types of management measures (Barnett and Baskett, 2015). They can be used both for the conservation of endangered species and/or habitats and for the enhancement of fish stocks (Arceo *et al.*, 2013), since it has been demonstrated that they can act protectively for fish populations (Colléter *et al.*, 2014). The increased number of OWFs in the southern North Sea together with the fish attraction, prolonged residency and (partial) fisheries restrictions around these structures could lead in increased production with spill-over benefits in the region. Further research on the possible increased production is necessary via collaboration between countries to indicate the cumulative effects of the establishment of OWFs on the fish stocks.

6.7 Future perspectives

This PhD thesis addresses different aspects of the food web ecology of sessile and mobile organisms associated with an offshore wind turbine. Combined results of experimental work and field data provided evidence that offshore wind turbines do influence the local food web properties. During this thesis, several questions about the food web ecology of OWFs have been answered, providing several ideas for further research work.

Throughout this thesis, bulk stable isotope analysis (SIA) was used as the main method to investigate the trophic linkages between species and their potential food resources. SIA has been proven to be a valuable tool for the examination of trophic niches and diet proportion investigations (Fry, 2006). However, SIA does not provide detailed information of the exploited resources, especially if the isotopic signatures of the resources are not known. We examined the diet composition of invertebrate species occurring in different depth zones, with SIA allowing for the separation of the isotopic signature of the resources but we noticed similarities between the signatures of some of the resources, which need further clarification. Follow-up compound-specific SIA would help resolve whether these resources are distinct from each other (Vokhshoori and McCarthy, 2014; Demopoulos *et al.*, 2017) and would allow for the isotopic characterisation of microbial resources that are difficult to obtain with SIA (Phillips *et al.*, 2014). This analysis would accurately incorporate every possible resource of suspended material to the diet of the different consumers (Richoux *et al.*, 2014b). Phospholipid-derived fatty acid (PLFA) analysis is a powerful and promising method that is increasingly used to supplement bulk natural abundance isotopic data (Van Den Meersche *et al.*, 2009; Evrard *et al.*, 2010, 2012; Middelburg, 2014). PLFA analysis offers additional resolution, since it can differentiate the isotopic signatures of small particles, such as bacteria and eukaryotes, and allows for the estimation of the different constituents of the microbial compartments (Evrard *et al.*, 2010, 2012; Middelburg, 2014) and the phytoplankton composition (Braeckman *et al.*, 2015). Furthermore, PLFA analysis would indicate the food quality of different invertebrate species (e.g. more unsaturated fatty acids show higher quality of food resources – Wakeham *et al.*, 1984; Reemtsma *et al.*, 1990). Hence, conducting compound-specific SIA in combination with PLFA analysis would allow for more firm conclusions on the dietary composition of the invertebrate species on the OWFs.

A detailed study on the influence of mussels on the nitrogen cycle would be important, since models have shown that increased primary production is associated with a larger dissolved inorganic nitrogen (DIN) concentration observed due to the excretion of the mussels on the OWFs (Maar *et al.*, 2009). The increased mussel abundances on the offshore wind turbines could increase excretion of ammonium as well as decrease the water turbidity (Maar *et al.*, 2009; Raoux *et al.*, 2017). This could potentially lead to an increase in the growth rates of phytoplankton and filamentous algae and thus have an effect on the basis of marine food webs (Kautsky and Evans, 1987; Prins and Smaal, 1994; Norling and Kautsky, 2008). A model exercise has already estimated an increase in ammonium concentrations around offshore wind foundations of up to 25 % (Maar *et al.*, 2009). It is, hence, important to acquire the real data in order to validate this model and by that estimate the complete effect of mussels on the local phytoplankton production.

This thesis focused only on the effects of OWFs on the feeding ecology of the consumer species associated to these structures and how these species affect the local primary production standing stock. However, OWFs could have a direct effect on the primary production themselves due to the local hydrodynamic changes induced by their construction (Floeter *et al.*, 2017). Floeter *et al.* (2017) suggest an increase in phytoplankton primary production due to the increased vertical mixing caused by the construction of OWFs, with subsequent upward nutrient transport throughout the water column. In contrast, Dannheim *et al.* (2020) support the hypothesis that phytoplankton primary production will be reduced due to increased turbidity, which reduces the light in the water column. However, there is generally little information on the effects of offshore wind turbines on the primary production and further investigation is needed.

The importance of scour protection layers (SPLs) on the trophic ecology of both vertebrate and invertebrate species was highlighted. Future research may focus on the food web ecology of different turbine foundations, such as jacket foundations that lack SPLs. In these distinct types of foundations, different food web structures are expected. Investigating the food web ecology of jacket foundations that have complex structures along the entire depth gradient (Krone *et al.*, 2013b; Causon and Gill, 2018) would be a step forward to understanding the effects of different vertical structures on the food web complexity. The higher structural complexity could be reflected in the food web complexity, which could be higher in shallower parts of these foundations. Hence, the next step would be to study and compare the detailed food web between the gravity-based foundations (studied here) and the other types of foundations in the Belgian part of the North Sea and beyond. Only such a comparison would identify possible (dis)similarities in the food web complexity between the different types of foundations and understand which type of foundation would benefit the most the (local) food web properties.

In this thesis, a community of an advanced successional stage was examined. The age of the structures defines the communities that are formed on and around them. Within 5 years, stable colonising assemblages are established on artificial hard substrates (Jensen *et al.*, 2000), while on the offshore wind turbines in the BPNS a decline in species diversity is observed after ~ 6 years at 15 m depth (Kerckhof *et al.*, 2019). The gravity-based foundations are the oldest type of turbines in the BPNS. The samples in this thesis were collected 8 years after the installation of these foundations. Thus, our study can project the future situation of the local food web properties of the newly installed turbines, especially the monopiles that have similar structures. However, we can also acquire knowledge from the food web properties of even older vertical artificial constructions, such as oil and gas platforms, that have been constructed more than 20 years ago, and could project the future situation of the offshore wind farms in the North Sea. On such structures, the old communities show low species richness both in the shallow and in the deeper areas (van der Stap *et al.*, 2016). Since the community composition changes over time, studying the food web properties of older communities associated with oil and gas platforms could indicate the future situation of the currently installed offshore wind turbines.

The food web ecology was investigated only in one season (summer). However, seasonality plays an important role in marine food webs. Examining the food web complexity of the organisms associated with offshore wind turbines in different seasons would show us whether the complexity observed in the deeper zones remains stable throughout the year or whether it changes seasonally. The alteration of seasons largely influences the food supply (Lefebvre *et al.*, 2009), which can induce changes in the food web of both the intertidal and the subtidal parts of the foundations. Primary production (Bordeyne *et al.*, 2017), the availability and composition of microalgae (Schoo *et al.*, 2018), as well as the zonation patterns of the colonising organisms along the depth gradient of the turbines vary according to seasons (Kerckhof *et al.*, 2010a). The temporal variability of primary producers (in winter, primary productivity tends to be lower due to lower temperatures and light levels compared to spring and summer (Parsons and Kessler, 1987) can cascade through the marine food webs and, finally, affect the diet and/or survival of higher trophic levels (Pope *et al.*, 1994; McMeans *et al.*, 2015). Thus, seasonality can affect the diet composition of many organisms (Hertz *et al.*, 2017). Therefore, it is important to examine whether the observed effects of OWFs on food web properties are stable throughout the year.

Last but not least, more extensive studies on the impacts of OWFs on the production of (certain) fish species at a population level should be conducted. As mentioned in this thesis, there have been multiple studies supporting the idea that the production of fish increases in OWF areas (Leonhard and Pedersen, 2006; Andersson and Öhman, 2010; De Troch *et al.*, 2013; Reubens *et al.*, 2013a, 2014b), but there is no clear evidence of increased production locally or regionally at a population level yet. Thus, targeted research studies should aim at investigating the production of fish species due to the presence of OWFs. Furthermore, it would be interesting to investigate whether offshore wind turbines and their associated SPLs could be used as habitat restoration tools. This is of great importance, since natural reefs are declining and deteriorating due to human activities and climate change, which leads to a decline of certain fish species and shifts in species dominance (Abelson, 2006). The idea that offshore wind turbines can act as a tool for habitat restoration has been previously suggested (Mangi, 2013), but has, to our knowledge, not yet been studied. Targeted investigation of this idea could provide crucial information on whether these structures can potentially restore disturbed fish habitats and mitigate the impacts on the ecosystem.

6.8 Conclusion

Altogether, the introduction of offshore wind farms (OWFs) affects the local food web properties, due to the cascading trophic effects caused by epifauna organisms colonising these structures. Colonising organisms enhance the food provision for benthic organisms through the deposition of faeces and pseudofaeces, increasing the food web complexity in deeper zones of the turbines (Chapter 2). The resulting enrichment of these zones with organic matter increases the food variety in the scour protection layer (SPL) and the surrounding soft sediments, providing organisms with a wider range of food resources compared to the upper parts of the foundation. Trophic plasticity allows for an expanded distribution and survival of species in multiple depth zones along the depth gradient (Chapter 3). The high abundances of colonising organisms on the foundations do not seem to have a major effect on the reduction of the annual local primary producer standing stock. However, the dense communities of *Jassa herdmani* and *Mytilus edulis* on the jacket foundations significantly increase the carbon assimilation compared to the natural soft substrate macrofaunal communities. The less dense *J. herdmani* and *M. edulis* communities on the monopiles have minor effects on this increase, while on the gravity-based foundations there is even a decrease in the carbon assimilation compared to the permeable sediment macrofauna (Chapter 4). The increased abundance of invertebrates (due to high food availability and shelter from predators and currents, Bouma and Lengkeek, 2008) around OWF foundations attracts multiple fish species (Wilhelmsson *et al.*, 2006a, 2006b; Reubens *et al.*, 2011), indicating an effect of OWFs on higher trophic levels. Some of these fish species (cod, pouting and sculpin) benefit from the enhanced food availability and use the foundations as feeding grounds, while other fish species (horse mackerel and mackerel, respectively) use OWFs as feeding grounds only occasionally or not at all (Chapter 5).

In conclusion, this PhD thesis shows that OWFs increase the food web complexity by attracting species of different trophic levels (an effect that is more pronounced at foundations with SPLs), have minor effects on primary producer standing stocks and are utilized as feeding grounds by fish, which could potentially increase fish production. As the construction of more OWFs might, however, lead to cumulative effects that are hard to predict, further research is needed to completely understand the effects of these artificial structures on marine food webs.

Appendix

A.1 Supplementary material for Chapter 2

This section includes the results from the multi-dimensional scaling (MDS) and the stable isotope signatures and feeding traits of all the organisms sampled along the depth gradient of an offshore wind turbine, the scour protection layer and the surrounding soft substrate. Finally, the results from the similarity profile analysis (SIMPROF), which separated these organisms into trophic clusters, are also presented here.

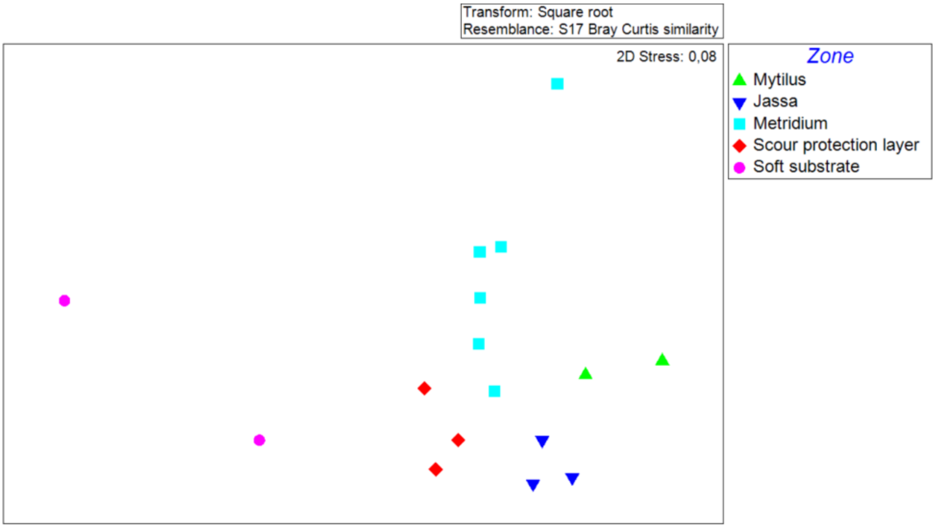


Figure A1.1: Structural similarity of species assemblages in the different zones under study as visualised by the ANOSIM analysis. The different colours and symbols represent the different zones.

Table A1.1: Stable carbon and nitrogen isotope values (‰, mean and standard deviation when possible), number of samples (n), mean trophic level and feeding traits of the organisms sampled from the six depth zones. Feeding trait abbreviations: F: Fish, SF: Suspension feeder, OPS: Omnivore/predator/scavenger, P: Predator, G: Grazer, O: Omnivore, DF: Deposit feeder, SSc: Suspension/scavenger, DS: Deposit/suspension feeder.

	Zone																		
	Intertidal			*Mytilus*			*Jassa*			*Metridium*			Scour protection layer			Soft substrate			FT
	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	
Echiicthys vipera	-	-	-	-	-	-	-	-	-	-	-	-	-17.4 ±0.5	17.8 ±0.5	2	-	-	-	F
Gadus morhua	-	-	-	-	-	-	-	-	-	-	-	-	-16.4 ±0.2	17.2 ±0.6	5	-	-	-	F
Microstomus kitt	-	-	-	-	-	-	-	-	-	-	-	-	-18.1 ±2.2	18.2 ±2.7	2	-	-	-	F
Myoxocephalus scorpioides	-	-	-	-	-	-	-	-	-	-	-	-	-15.8 ±0.3	18.4 ±1.7	5	-	-	-	F
Raniceps raninus	-	-	-	-	-	-	-	-	-	-	-	-	-17.2	16.9	1	-	-	-	F
Taurulus bubalis	-	-	-	-	-	-	-	-	-	-	-	-	-16.1 ±0.9	17.1 ±0.3	2	-	-	-	F
Trachurus trachurus	-	-	-	-	-	-	-19.4 ±1.5	16.9 ±0.8	5	-	-	-	-	-	-	-	-	-	F
Trisopterus luscus	-	-	-	-	-	-	-	-	-	-	-	-	-16.8 ±0.3	17.5 ±0.7	5	-	-	-	F

Diadumene cincta	-	-	-	-20.0 ±0.5	14.3 ±0.3	6	-20.3 ±0.4	14.3 ±0.2	10	-	-	-	-	-	-	-	-	-	**SF**
Metridium senile	-	-	-	-20.1 ±0.7	14.4 ±0.3	6	-20.2 ±0.4	13.6 ±0.8	7	-19.3 ±0.9	15.0 ±0.2	10	-19.8 ±0.9	14.7 ±0.5	10	-20.0 ±0.9	15.0 ±0.2	9	SF
Asterias rubens	-	-	-	-25.51	11.8	1	-	-	-	-20.7 ±1.9	11.9 ±0.9	10	-	-	-	-	-	-	O PS
Magallana gigas	-18.8 ±2.3	12.1 ±0.5	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	SF
Mytilus edulis	-19.6 ±0.9	10.9 ±0.3	18	-19.7 ±0.3	10.8 ±0.2	14	-	-	-	-18.8 ±0.5	11.1 ±0.1	5	-	-	-	-	-	-	SF
Spongidae	-	-	-	-	-	-	-21.3 ±0.3	10.9 ±0.1	2	-	-	-	-	-	-	-	-	-	SF
Emplectonema gracile	-19.4	14.4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P
Emplectonema neesii	-20.6	13.4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P
Crepidula fornicata	-	-	-	-19.6 ±0.1	13.0 ±0.1	2	-	-	-	-	-	-	-	-	-	-	-	-	SF
Nudibranchia sp. 1	-	-	-	-	-	-	-8.3	13.3	1	-	-	-	-	-	-	-	-	-	P
Nudibranchia sp. 2	-	-	-	-	-	-	-19.7 ±0.3	15.9 ±0.1	2	-	-	-	-	-	-	-	-	-	P
Patella vulgata	-15.7 ±1.0	11.6 ±0.6	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G

Tritia incrassata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-17.4 ±3.5	12.9 ±0.6	7	**O**
Tubularia indivisa	-	-	-	-19.0 ±0.7	9.9± 0.5	5	-	-	-	-	-	-	-	-	-	-	-	-	SF
Telmatogeton japonicus	-20.3 ±0.4	9.9± 0.4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	DF
Bodotria scorpioides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-13.2	9.7	1	DF
Cancer pagurus	-	-	-	-	-	-	-	-	-	-17.2 ±0.8	15.2 ±0.5	7	-	-	-	-	-	-	P
Crangon crangon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-19.2	13.8	1	O PS
Hemigrapsus penicillatus	-21.4	12.5	1	-	-	-	-	-	-	-	-	-	-	-	-	-20.4	12.7	1	P
Hemigrapsus sanguineus	-21.4	13.2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P
Homarus gammarus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-17.0 ±0.5	16.2 ±1.1	5	P
Idotea pelagica	-20.6 ±0,9	12.5 ±0.3	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G
Emplectonema gracile	-19.4	14.4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P
Jassa herdmani	-19.7	12.2	1	-18.9 ±0.2	11.7 ±0.4	9	-18.9 ±0.2	11.5 ±0.2	8	-	-	-	-19.5 ±0.3	11.8 ±0.1	3	-18.3 ±0.9	11.4 ±0.1	5	SS c
Liocarcinus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-19.3 ±0.4	12.4 ±0.3	3	O PS
Macropodia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-19.1 ±0.1	12.0 ±0.1	2	-	-	-	O PS

Monocorophium acherusicum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 19.8 ±0.5	10.8 ±0.1	3	DS
Necora puber	-	-	-	-	-	-	- 17.2 ±0.1	16.1 ±0.3	2	- 17.7 ±0.6	15.3 ±0.5	5	-	-	-	- 17.1 ±1.0	15.0 ±1.9	6	O PS
Pagurus bernhardus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 17.8 ±2.5	11.1 ±0.4	2	O
Phtisica marina	-	-	-	-	-	-	-	-	-	-	-	-	- 17.5	12.9	1	-	-	-	O PS
Pilumnus hirtellus	-	-	-	- 19.7 ±0.3	12.7 ±0.1	4	-	-	-	-	-	-	- 20.8	12.5	1	-	-	-	O PS
Pinnotheres pisum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 17.8 ±1.9	11.6 ±0.3	2	SF
Pisidia longicornis	-	-	-	- 20.1 ±0.8	11.7 ±0.8	8	-	-	-	- 21.4	9.8	1	- 22.5 ±1.1	11.3 ±0.2	13	- 20.3 ±1.7	11.6 ±0.1	2	SF
Porcellana platycheles	- 17.8	13.0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	SF
Semibalanus balanoides	- 19.8 ±0.7	12.0 ±0.2	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	SF
Ophiothrix fragilis	-	-	-	- 19.7 ±1.2	11.9 ±0.6	7	- 23.2 ±2.5	10.8 ±1.0	10	- 17.6 ±2.2	11.9 ±0.3	6	-	-	-	-	-		DS
Ophiura sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 17.1 ±5.1	12.0 ±0.6	4	DS
Eulalia viridis	-	-	-	- 20.6 ±0.1	14.4 ±0.3	2	-	-	-	- 18.8	14.7	1	-	-	-	-	-	-	O PS

Eunereis longissima	-	-	-	-21.5 ±0.4	15.1 ±0.4	4	-	-	-	-	-	-	-	-	-	-	-	-	P
Harmothoe extenuata	-	-	-	-19.9 ±1.2	13.7 ±0.3	8	-19.2 ±1.0	13.8 ±0.1	2	-	-	-	-	-	-	-	-	-	P
Lanice conchilega	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-18.9	11.8	1	DS
Lepidonotus squamatus	-	-	-	-17.9 ±0.3	13.3 ±0.4	2	-	-	-	-	-	-	-	-	-	-	-	-	P
Magelona sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-20.0 ±0.3	15.3 ±0.1	4	DS
Phyllodoce mucosa	-	-	-	-20.5 ±0.4	14.7 ±2.0	2	-	-	-	-20.6	13.8	1	-20.9 ±0.2	13.8 ±0.4	2	-21.3 ±0.8	13.3 ±0.3	7	O PS
Spiophanes bombyx	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-22.0 ±1.0	12.6 ±0.1	4	D
Subadyte pellucida	-	-	-	-19.7	14.7	1	-	-	-	-	-	-	-	-	-	-	-	-	O PS
Leptoplana tremellaris	-	-	-	-20.7 ±0.2	11.4 ±0.2	2	-	-	-	-	-	-	-	-	-	-	-	-	P

Table A1.2: Allocation of individuals to significantly different cluster (SIMPROF, $p<0.05$). The names of the clusters are given by the letters A-M.

Cluster	Species	Sample No	Zone	Cluster	Species	Sample No	Zone
A	Nudibranchia	1	*Jassa*	C	*Gadus morhua*	4	SPL
A	*Ophiura* spp.	1	Soft substrate	C	*Gadus morhua*	5	SPL
B	*Ophiothrix fragilis*	1	*Jassa*	C	*Microstomus kitt*	1	SPL
B	*Ophiothrix fragilis*	2	*Jassa*	C	*Myoxocephalus scorpioides*	1	SPL
B	*Asterias rubens*	1	*Metridium*	C	*Myoxocephalus scorpioides*	2	SPL
B	*Asterias rubens*	1	*Mytilus*	C	*Raniceps raninus*	1	SPL
B	*Pisidia longicornis*	1	SPL	C	*Taurulus bubalis*	1	SPL
C	*Necora puber*	1	*Jassa*	C	*Taurulus bubalis*	2	SPL
C	*Necora puber*	2	*Jassa*	C	*Trisopterus luscus*	1	SPL
C	*Trachurus trachurus*	1	*Jassa*	C	*Trisopterus luscus*	2	SPL
C	*Necora puber*	1	*Metridium*	C	*Trisopterus luscus*	3	SPL
C	*Cancer pagurus*	1	Soft substrate	C	*Trisopterus luscus*	4	SPL
C	*Homarus gammarus*	1	Soft substrate	C	*Trisopterus luscus*	5	SPL
C	*Homarus gammarus*	2	Soft substrate	D	*Myoxocephalus scorpioides*	3	SPL
C	*Homarus gammarus*	3	Soft substrate	D	*Myoxocephalus scorpioides*	4	SPL
C	*Necora puber*	1	Soft substrate	D	*Myoxocephalus scorpioides*	5	SPL
C	*Necora puber*	2	Soft substrate	E	*Trachurus trachurus*	2	*Jassa*
C	*Necora puber*	3	Soft substrate	E	*Microstomus kitt*	2	SPL
C	*Echiichthys vipera*	1	SPL	F	*Emplectonema gracile*	1	Intertidal
C	*Echiichthys vipera*	2	SPL	F	*Emplectonema neesii*	1	Intertidal
C	*Gadus morhua*	1	SPL	F	*Diadumene cincta*	1	*Jassa*
C	*Gadus morhua*	2	SPL	F	*Diadumene cincta*	2	*Jassa*
C	*Gadus morhua*	3	SPL	F	*Diadumene cincta*	3	*Jassa*

Cluster	Species	Sample No	Zone
F	*Diadumene cincta*	4	*Jassa*
F	*Diadumene cincta*	5	*Jassa*
F	*Diadumene cincta*	6	*Jassa*
F	*Diadumene cincta*	7	*Jassa*
F	*Diadumene cincta*	8	*Jassa*
F	*Diadumene cincta*	9	*Jassa*
F	*Harmothoe extenuata*	1	*Jassa*
F	*Metridium senile*	1	*Jassa*
F	*Metridium senile*	2	*Jassa*
F	*Metridium senile*	3	*Jassa*
F	*Metridium senile*	4	*Jassa*
F	*Metridium senile*	5	*Jassa*
F	*Nudibranchia*	2	*Jassa*
F	*Nudibranchia*	3	*Jassa*
F	*Trachurus trachurus*	3	*Jassa*
F	*Metridium senile*	1	*Metridium*
F	*Metridium senile*	2	*Metridium*
F	*Metridium senile*	3	*Metridium*
F	*Metridium senile*	4	*Metridium*
F	*Phyllodoce mucosa*	1	*Metridium*
F	*Diadumene cincta*	1	*Mytilus*
F	*Diadumene cincta*	2	*Mytilus*
F	*Diadumene cincta*	3	*Mytilus*
F	*Diadumene cincta*	4	*Mytilus*
F	*Diadumene cincta*	5	*Mytilus*
F	*Diadumene cincta*	6	*Mytilus*
F	*Diadumene cincta*	7	*Mytilus*
F	*Eulalia viridis*	1	*Mytilus*
F	*Eulalia viridis*	2	*Mytilus*
F	*Eunereis longissima*	1	*Mytilus*
F	*Eunereis longissima*	2	*Mytilus*
F	*Eunereis longissima*	3	*Mytilus*
F	*Eunereis longissima*	4	*Mytilus*
F	*Harmothoe extenuata*	1	*Mytilus*
F	*Harmothoe extenuata*	2	*Mytilus*
F	*Harmothoe extenuata*	3	*Mytilus*
F	*Harmothoe extenuata*	4	*Mytilus*
F	*Harmothoe extenuata*	5	*Mytilus*
F	*Harmothoe extenuata*	6	*Mytilus*
F	*Harmothoe extenuata*	7	*Mytilus*
F	*Metridium senile*	1	*Mytilus*
F	*Metridium senile*	2	*Mytilus*
F	*Metridium senile*	3	*Mytilus*
F	*Metridium senile*	4	*Mytilus*
F	*Metridium senile*	5	*Mytilus*
F	*Phyllodoce mucosa*	1	*Mytilus*
F	*Phyllodoce mucosa*	2	*Mytilus*
F	*Pisidia longicornis*	1	*Mytilus*
F	*Crangon crangon*	1	Soft substrate
F	*Magellona* spp.	1	Soft substrate

Cluster	**Species**	**Sample No**	**Zone**	**Cluster**	**Species**	**Sample No**	**Zone**
F	*Magellona* spp.	2	Soft substrate	G	*Trachurus trachurus*	5	*Jassa*
F	*Magellona* spp.	3	Soft substrate	G	*Cancer pagurus*	1	*Metridium*
F	*Magellona* spp.	4	Soft substrate	G	*Cancer pagurus*	2	*Metridium*
F	*Metridium senile*	1	Soft substrate	G	*Cancer pagurus*	3	*Metridium*
F	*Metridium senile*	2	Soft substrate	G	*Eulalia viridis*	1	*Metridium*
F	*Metridium senile*	3	Soft substrate	G	*Metridium senile*	5	*Metridium*
F	*Metridium senile*	4	Soft substrate	G	*Metridium senile*	6	*Metridium*
F	*Metridium senile*	5	Soft substrate	G	*Metridium senile*	7	*Metridium*
F	*Metridium senile*	6	Soft substrate	G	*Metridium senile*	8	*Metridium*
F	*Metridium senile*	7	Soft substrate	G	*Metridium senile*	9	*Metridium*
F	*Phyllodoce mucosa*	1	Soft substrate	G	*Metridium senile*	10	*Metridium*
F	*Phyllodoce mucosa*	2	Soft substrate	G	*Necora puber*	2	*Metridium*
F	*Phyllodoce mucosa*	3	Soft substrate	G	*Necora puber*	3	*Metridium*
F	*Metridium senile*	1	SPL	G	*Necora puber*	4	*Metridium*
F	*Metridium senile*	2	SPL	G	*Necora puber*	5	*Metridium*
F	*Metridium senile*	3	SPL	G	*Harmothoe extenuata*	8	*Mytilus*
F	*Metridium senile*	4	SPL	G	*Metridium senile*	6	*Mytilus*
F	*Metridium senile*	5	SPL	G	*Subadyte pellucida*	1	*Mytilus*
F	*Phyllodoce mucosa*	1	SPL	G	*Cancer pagurus*	2	Soft substrate
F	*Phyllodoce mucosa*	2	SPL	G	*Cancer pagurus*	3	Soft substrate
G	*Metridium senile*	6	*Jassa*	G	*Cancer pagurus*	4	Soft substrate
G	*Trachurus trachurus*	4	*Jassa*	G	*Homarus gammarus*	4	Soft substrate

Cluster	Species	Sample No	Zone	Cluster	Species	Sample No	Zone
G	*Homarus gammarus*	5	Soft substrate	H	*Jassa herdmani*	2	*Jassa*
G	*Metridium senile*	8	Soft substrate	H	*Jassa herdmani*	3	*Jassa*
G	*Metridium senile*	9	Soft substrate	H	*Jassa herdmani*	4	*Jassa*
G	*Necora puber*	4	Soft substrate	H	*Jassa herdmani*	5	*Jassa*
G	*Necora puber*	5	Soft substrate	H	*Jassa herdmani*	6	*Jassa*
G	*Metridium senile*	6	SPL	H	*Jassa herdmani*	7	*Jassa*
G	*Metridium senile*	7	SPL	H	*Jassa herdmani*	8	*Jassa*
G	*Metridium senile*	8	SPL	H	*Asterias rubens*	2	*Metridium*
G	*Metridium senile*	9	SPL	H	*Asterias rubens*	3	*Metridium*
H	*Jassa herdmani*	1	Intertidal	H	*Asterias rubens*	4	*Metridium*
H	*Magallana gigas*	1	Intertidal	H	*Asterias rubens*	5	*Metridium*
H	*Magallana gigas*	2	Intertidal	H	*Asterias rubens*	6	*Metridium*
H	*Magallana gigas*	3	Intertidal	H	*Mytilus edulis*	1	*Metridium*
H	*Mytilus edulis*	1	Intertidal	H	*Mytilus edulis*	2	*Metridium*
H	*Mytilus edulis*	2	Intertidal	H	*Ophiothrix fragilis*	1	*Metridium*
H	*Mytilus edulis*	3	Intertidal	H	*Ophiothrix fragilis*	2	*Metridium*
H	*Semibalanus balanoides*	1	Intertidal	H	*Jassa herdmani*	1	*Mytilus*
H	*Semibalanus balanoides*	2	Intertidal	H	*Jassa herdmani*	2	*Mytilus*
H	*Semibalanus balanoides*	3	Intertidal	H	*Jassa herdmani*	3	*Mytilus*
H	*Semibalanus balanoides*	4	Intertidal	H	*Jassa herdmani*	4	*Mytilus*
H	*Semibalanus balanoides*	5	Intertidal	H	*Jassa herdmani*	5	*Mytilus*
H	*Jassa herdmani*	1	*Jassa*	H	*Jassa herdmani*	6	*Mytilus*

Cluster	Species	Sample No	Zone
H	*Jassa herdmani*	7	*Mytilus*
H	*Jassa herdmani*	8	*Mytilus*
H	*Ophiothrix fragilis*	1	*Mytilus*
H	*Ophiothrix fragilis*	2	*Mytilus*
H	*Ophiothrix fragilis*	3	*Mytilus*
H	*Pisidia longicornis*	2	*Mytilus*
H	*Pisidia longicornis*	3	*Mytilus*
H	*Pisidia longicornis*	4	*Mytilus*
H	*Pisidia longicornis*	5	*Mytilus*
H	*Jassa herdmani*	1	Soft substrate
H	*Jassa herdmani*	2	Soft substrate
H	*Jassa herdmani*	3	Soft substrate
H	*Jassa herdmani*	4	Soft substrate
H	*Lanice conchilega*	1	Soft substrate
H	*Liocarcinus* spp.	1	Soft substrate
H	*Liocarcinus* spp.	2	Soft substrate
H	*Ophiura* spp.	2	Soft substrate
H	*Ophiura* spp.	3	Soft substrate
H	*Pagurus bernhardus*	1	Soft substrate
H	*Pinnotheres pisum*	1	Soft substrate
H	*Pisidia longicornis*	1	Soft substrate
H	*Jassa herdmani*	1	SPL
H	*Jassa herdmani*	2	SPL
H	*Jassa herdmani*	3	SPL
H	*Macropodia* spp.	1	SPL
H	*Macropodia* spp.	2	SPL
I	*Telmatogeton japonicus*	1	Intertidal
I	*Telmatogeton japonicus*	2	Intertidal
I	*Tubularia indivisa*	1	*Mytilus*
J	*Mytilus edulis*	4	Intertidal
J	*Mytilus edulis*	5	Intertidal
J	*Mytilus edulis*	6	Intertidal
J	*Mytilus edulis*	7	Intertidal
J	*Mytilus edulis*	8	Intertidal
J	*Mytilus edulis*	9	Intertidal
J	*Mytilus edulis*	10	Intertidal
J	*Mytilus edulis*	11	Intertidal
J	*Mytilus edulis*	12	Intertidal
J	*Mytilus edulis*	13	Intertidal
J	*Mytilus edulis*	14	Intertidal
J	*Mytilus edulis*	15	Intertidal
J	*Ophiothrix fragilis*	3	*Jassa*
J	*Mytilus edulis*	3	*Metridium*
J	*Mytilus edulis*	4	*Metridium*
J	*Mytilus edulis*	5	*Metridium*
J	*Mytilus edulis*	6	*Metridium*

Cluster	**Species**	**Sample No**	**Zone**	**Cluster**	**Species**	**Sample No**	**Zone**
J	*Jassa herdmani*	9	*Mytilus*	K	*Tubularia indivisa*	2	*Mytilus*
J	*Mytilus edulis*	1	*Mytilus*	K	*Tubularia indivisa*	3	*Mytilus*
J	*Mytilus edulis*	2	*Mytilus*	K	*Tubularia indivisa*	4	*Mytilus*
J	*Mytilus edulis*	3	*Mytilus*	K	*Tubularia indivisa*	5	*Mytilus*
J	*Mytilus edulis*	4	*Mytilus*	L	*Idotea pelagica*	1	Intertidal
J	*Mytilus edulis*	5	*Mytilus*	L	*Magallana gigas*	4	Intertidal
J	*Mytilus edulis*	6	*Mytilus*	L	*Porcellana platycheles*	1	Intertidal
J	*Mytilus edulis*	7	*Mytilus*	L	*Harmothoe extenuata*	2	*Jassa*
J	*Mytilus edulis*	8	*Mytilus*	L	*Metridium senile*	7	*Jassa*
J	*Mytilus edulis*	8	*Mytilus*	L	*Ophiothrix fragilis*	3	*Metridium*
J	*Mytilus edulis*	9	*Mytilus*	L	*Ophiothrix fragilis*	4	*Metridium*
J	*Mytilus edulis*	10	*Mytilus*	L	*Crepidula fornicata*	1	*Mytilus*
J	*Mytilus edulis*	11	*Mytilus*	L	*Crepidula fornicata*	2	*Mytilus*
J	*Mytilus edulis*	12	*Mytilus*	L	*Lepidonotus squamatus*	1	*Mytilus*
J	*Mytilus edulis*	13	*Mytilus*	L	*Lepidonotus squamatus*	2	*Mytilus*
J	*Mytilus edulis*	14	*Mytilus*	L	*Ophiothrix fragilis*	5	*Mytilus*
J	*Ophiothrix fragilis*	4	*Mytilus*	L	*Pilumnus hirtellus*	1	*Mytilus*
J	*Pisidia longicornis*	6	*Mytilus*	L	*Pilumnus hirtellus*	2	*Mytilus*
J	*Pisidia longicornis*	7	*Mytilus*	L	*Pilumnus hirtellus*	3	*Mytilus*
J	*Monocorophium acherusicum*	1	Soft substrate	L	*Pilumnus hirtellus*	4	*Mytilus*
J	*Monocorophium acherusicum*	2	Soft substrate	L	*Liocarcinus* spp.	3	Soft substrate
J	*Monocorophium acherusicum*	3	Soft substrate	L	*Tritia incrassata*	1	Soft substrate
J	*Monocorophium acherusicum*	4	Soft substrate	L	*Tritia incrassata*	2	Soft substrate
J	*Pagurus bernhardus*	2	Soft substrate	L	*Tritia incrassata*	3	Soft substrate
K	*Mytilus edulis*	16	Intertidal	L	*Tritia incrassata*	4	Soft substrate
K	*Mytilus edulis*	17	Intertidal	L	*Phtisica marina*	1	Scour protection layer

Cluster	Species	Sample No	Zone	Cluster	Species	Sample No	Zone
M	*Hemigrapsus penicillatus*	1	Intertidal	M	*Ophiothrix fragilis*	6	*Mytilus*
M	*Hemigrapsus sanguineus*	1	Intertidal	M	*Ophiothrix fragilis*	7	*Mytilus*
M	*Idotea pelagica*	2	Intertidal	M	*Pisidia longicornis*	8	*Mytilus*
M	*Idotea pelagica*	3	Intertidal	M	*Hemigrapsus penicillatus*	1	Soft substrate
M	*Idotea pelagica*	4	Intertidal	M	*Ophiura* spp.	4	Soft substrate
M	*Magallana gigas*	5	Intertidal	M	*Phyllodoce mucosa*	4	Soft substrate
M	*Magallana gigas*	6	Intertidal	M	*Phyllodoce mucosa*	5	Soft substrate
M	*Mytilus edulis*	18	Intertidal	M	*Phyllodoce mucosa*	6	Soft substrate
M	*Semibalanus balanoides*	6	Intertidal	M	*Phyllodoce mucosa*	7	Soft substrate
M	*Ophiothrix fragilis*	4	*Jassa*	M	*Pisidia longicornis*	2	Soft substrate
M	*Ophiothrix fragilis*	5	*Jassa*	M	*Spiophanes bombyx*	1	Soft substrate
M	*Ophiothrix fragilis*	6	*Jassa*	M	*Spiophanes bombyx*	2	Soft substrate
M	*Ophiothrix fragilis*	7	*Jassa*	M	*Spiophanes bombyx*	3	Soft substrate
M	*Ophiothrix fragilis*	8	*Jassa*	M	*Spiophanes bombyx*	4	Soft substrate
M	*Ophiothrix fragilis*	9	*Jassa*	M	*Tritia incrassata*	5	Soft substrate
M	*Ophiothrix fragilis*	10	*Jassa*	M	*Pilumnus hirtellus*	1	SPL
M	Spongidae	1	*Jassa*	M	*Pisidia longicornis*	2	SPL
M	Spongidae	2	*Jassa*	M	*Pisidia longicornis*	3	SPL
M	*Asterias rubens*	7	*Metridium*	M	*Pisidia longicornis*	4	SPL
M	*Asterias rubens*	8	*Metridium*	M	*Pisidia longicornis*	5	SPL
M	*Asterias rubens*	9	*Metridium*	M	*Pisidia longicornis*	6	SPL
M	*Asterias rubens*	10	*Metridium*	M	*Pisidia longicornis*	7	SPL
M	*Ophiothrix fragilis*	5	*Metridium*	M	*Pisidia longicornis*	8	SPL
M	*Pisidia longicornis*	1	*Metridium*	M	*Pisidia longicornis*	9	SPL
M	*Leptoplana tremellaris*	1	*Mytilus*	M	*Pisidia longicornis*	10	SPL
M	*Leptoplana tremellaris*	2	*Mytilus*	M	*Pisidia longicornis*	11	SPL

Cluster	Species	Sample No	Zone	Cluster	Species	Sample No	Zone
M	*Pisidia longicornis*	12	SPL	N	*Ophiothrix fragilis*	6	*Metridium*
M	*Pisidia longicornis*	13	SPL	N	*Bodotria scorpioides*	1	Soft substrate
N	*Magallana gigas*	7	Intertidal	N	*Jassa herdmani*	5	Soft substrate
N	*Patella vulgata*	1	Intertidal	N	*Necora puber*	6	Soft substrate
N	*Patella vulgata*	2	Intertidal	N	*Pinnotheres pisum*	2	Soft substrate
N	*Patella vulgata*	3	Intertidal	N	*Tritia incrassata*	6	Soft substrate
N	*Patella vulgata*	4	Intertidal	N	*Tritia incrassata*	7	Soft substrate

A.2 Supplementary material for Chapter 3

This section includes information about the number of replicates that were analysed for both the consumer species and their potential food resources, the results from the Bayesian stable isotope ellipse (SEA_B) probabilities and from the stable isotope mixing models indicating the diet proportion of every consumer species in every combination of depth zones.

Table A2.1: The taxon, sampling zone and number of replicates for each resource and consumers' species included in the study.

	Taxon	Zone	Number of replicates
Consumers	*Diadumene cincta*	*Mytilus*	6
		Jassa	10
	Jassa herdmani	Intertidal	1
		Mytilus	9
		Jassa	8
		Scour protection layer	3
		Soft substrate	5
	Metridium senile	*Mytilus*	6
		Jassa	7
		Metridium	10
		Scour protection layer	10
		Soft substrate	9
	Mytilus edulis	Intertidal	18
		Mytilus	14
		Metridium	5
	Necora puber	*Jassa*	2
		Metridium	5
		Soft substrate	6
	Ophiothrix fragilis	*Mytilus*	7
		Jassa	10
		Metridium	6
	Pisidia longicornis	*Mytilus*	8
		Metridium	1
		Scour protection layer	13
		Soft substrate	2

Resources	Algae	Upper intertidal	10
		Lower intertidal	10
	Suspended particulate organic matter (SPOM)	~1 m above the sea floor	3
		~3 m below the sea surface	3
	Sediment organic matter	Soft substrate	6
	Copepods	Water column	3
	Crab larvae	Water column	1
	Other larvae	Water column	1

Table A2.2: Bayesian stable isotope ellipse (SEA$_B$) probabilities that the ellipse area of the species in the column is smaller than the ellipse area of the species in the row. Numbers refer to the different species in the different zones: 1: *Diadumene cincta* in *Mytilus* zone, 2: *D. cincta* in *Jassa* zone, 3: *Jassa herdmani* in *Mytilus* zone, 4: *J. herdmani* in *Jassa* zone, 5: *J. herdmani* in SPL, 6: *J. herdmani* in soft substrate, 7: *Metridium senile* in *Mytilus* zone, 8: *M. senile* in *Jassa* zone, 9: *M. senile* in *Metridium* zone, 10: *M. senile* in SPL, 11: *M. senile* in soft substrate, 12: *Mytilus edulis* in intertidal, 13: *M. edulis* in *Mytilus* zone, 14: *M. edulis* in *Metridium* zone, 15: *Necora puber* in *Metridium* zone, 16: *N. puber* in soft substrate, 17: *Ophiothrix fragilis* in *Mytilus* zone, 18: *O. fragilis* in *Jassa* zone, 19: *O. fragilis* in *Metridium* zone, 20: *Pisidia longicornis* in *Mytilus* zone and 21: *P. longicornis* in SPL.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1																				
2	0,08																			
3	0,08	0,51																		
4	0,00	0,05	0,05																	
5	0,02	0,11	0,12	0,47																
6	0,37	0,83	0,83	0,99	0,96															
7	0,53	0,94	0,93	1,00	0,98	0,66														
8	0,90	1,00	1,00	1,00	1,00	0,94	0,89													
9	0,48	0,94	0,94	1,00	0,98	0,63	0,45	0,06												
10	0,96	1,00	1,00	1,00	1,00	0,97	0,95	0,68	0,99											
11	0,76	0,99	0,99	1,00	0,99	0,83	0,74	0,23	0,80	0,10										
12	0,79	1,00	0,99	1,00	0,99	0,87	0,77	0,21	0,86	0,07	0,53									
13	0,06	0,50	0,49	0,97	0,89	0,15	0,05	0,00	0,04	0,00	0,00	0,00								
14	0,04	0,22	0,22	0,74	0,72	0,07	0,03	0,00	0,03	0,00	0,01	0,00	0,20							
15	0,91	1,00	1,00	1,00	1,00	0,94	0,90	0,56	0,94	0,40	0,76	0,80	1,00	1,00						
16	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00					
17	1,00	1,00	1,00	1,00	1,00	1,00	1,00	0,96	1,00	0,91	1,00	1,00	1,00	1,00	0,92	0,07				
18	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	0,73	0,99			
19	0,99	1,00	1,00	1,00	1,00	0,99	0,99	0,89	1,00	0,81	0,98	0,99	1,00	1,00	0,84	0,04	0,34	0,01		
20	0,99	1,00	1,00	1,00	1,00	0,99	0,99	0,91	1,00	0,84	0,98	1,00	1,00	1,00	0,86	0,04	0,35	0,00	0,52	
21	0,70	0,99	0,99	1,00	0,99	0,81	0,67	0,14	0,76	0,05	0,40	0,36	1,00	0,99	0,13	0,00	0,00	0,00	0,01	0,00

Table A2.3: Mean and standard deviation (sd) of the potential contribution (%) of each resource to the diet of every species in the different zones as calculated by the Bayesian stable isotope mixing models, where SPL: scour protection layer.

***Diadumene cincta/Mytilus* zone**			***Diadumene cincta/Jassa* zone**		
Resources	**Mean (%)**	**SD (%)**	**Resources**	**Mean (%)**	**SD (%)**
Copepods	13.5	9.3	Copepods	10.1	6.2
Crab larvae	13.6	9.0	Crab larvae	11.0	6.5
SPOM	**62.5**	11.2	SPOM	**71.9**	6.8
Other larvae	10.4	6.8	Other larvae	7.0	4.3
***Necora puber/Metridium* zone**			***Necora puber*/Soft substrate**		
Resources	**Mean (%)**	**SD (%)**	**Resources**	**Mean (%)**	**SD (%)**
Copepods	10	9.2	Copepods	10.6	10.1
Crab larvae	7.3	7.3	Crab larvae	9.7	9.3
Other larvae	16.6	15.4	Other larvae	15.2	14.7
SPOM-bottom	5.4	5.1	SPOM-bottom	6.8	6.6
SPOM-surface	5.5	5.3	SPOM-surface	6.3	6.3
SOM	-	-	SOM	5.1	4.4
Pisidia longicornis	6.3	6.1	*Pisidia longicornis*	7.0	6.9
Pilumnus hirtellus	**20.6**	17.9	*Pilumnus hirtellus*	10.6	10.8
Sponges	6.0	5.7	Sponges	6.8	6.5
Mussels	8.8	8.1	Mussels	10.2	9.8
Amphipods	17.1	16.1	Amphipods	14.0	13.4
***Pisidia longicornis/Mytilus* zone**			***Pisidia longicornis*/Scour protection layer**		
Resources	**Mean (%)**	**SD (%)**	**Resources**	**Mean (%)**	**SD (%)**
Copepods	10.7	8.2	Copepods	5.0	3.6
Crab larvae	12.2	9.2	Crab larvae	5.6	4.1
SPOM	**68.5**	11.7	SPOM	15.7	6.4
Other larvae	8.6	6.1	Other larvae	4.4	3.2
SOM	-	-	SOM	**69.3**	5.4

***Mytilus edulis*/Intertidal**			***Mytilus edulis*/*Mytilus* zone**			***Mytilus edulis*/*Metridium* zone**		
Resources	**Mean (%)**	**SD (%)**	**Resources**	**Mean (%)**	**SD (%)**	**Resources**	**Mean (%)**	**SD (%)**
Copepods	4.1	3.0	Copepods	14.3	8.9	Copepods	21.8	16.6
Crab larvae	4.7	3.4	Crab larvae	18.9	10.5	Crab larvae	26.6	18.7
SPOM	20.7	6.2	SPOM	**55.5**	5.9	SPOM	**30.9**	12.3
Other larvae	3.3	2.3	Other larvae	11.2	6.5	Other larvae	20.7	13.4
Macroalgae	**67.2**	3.9	Macroalgae	-	-	Macroalgae	-	-

Ophiothrix fragilis/Mytilus zone			**Ophiothrix fragilis/Jassa zone**			**Ophiothrix fragilis/Metridium zone**		
Resources	**Mean (%)**	**SD (%)**	**Resources**	**Mean (%)**	**SD (%)**	**Resources**	**Mean (%)**	**SD (%)**
Copepods	14.7	12.0	Copepods	13.3	11.6	Copepods	19.5	16.5
Crab larvae	17.9	14.5	Crab larvae	16.3	14.5	Crab larvae	25.0	19.4
SPOM	**55.2**	17.4	SPOM	**59.0**	20.1	SPOM	**31.6**	17.6
Other larvae	12.2	9.3	Other larvae	11.5	10.0	Other larvae	23.9	18.3

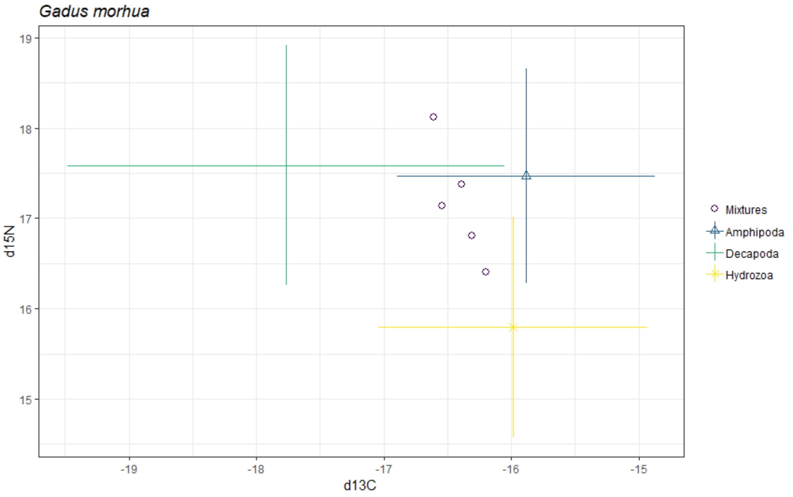
***Jassa herdmani*/*Mytilus* zone**			***Jassa herdmani*/*Jassa* zone**			***Jassa herdmani*/Scour protection layer**			***Jassa herdmani*/Soft substrate**		
Resource	**Mean (%)**	**SD (%)**	**Resource**	**Mean (%)**	**SD (%)**	**Resource**	**Mean (%)**	**SD (%)**	**Resource**	**Mean (%)**	**SD (%)**
SPOM-bottom	14.8	9.1	SPOM-bottom	15.0	9.1	SPOM-bottom	15.2	12.3	SPOM-bottom	9.9	8.6
SPOM-surface	24.0	10.3	SPOM-surface	22.2	10.3	SPOM-surface	14.9	12.3	SPOM-surface	7.8	6.5
Zooplankton	**61.2**	9.8	Zooplankton	**62.8**	10.4	Zooplankton	**38.9**	13.0	Zooplankton	**41.8**	17.4
SOM	-	-	SOM	-	-	SOM	31.0	18.0	SOM	40.5	20.8

***Metridium senile*/*Mytilus* zone**			***Metridium senile*/*Jassa* zone**			***Metridium senile*/*Metridium* zone**			***Metridium senile*/Scour protection layer**		
Resource	**Mean (%)**	**SD (%)**	**Resource**	**Mean (%)**	**SD (%)**	**Resource**	**Mean (%)**	**SD (%)**	**Resource**	**Mean (%)**	**SD (%)**
SPOM	**61.1**	13.1	SPOM	**70.3**	9.8	SPOM	40.7	12.9	SPOM	**56.7**	12.7
Zooplankton	38.9	13.1	Zooplankton	29.7	9.8	Zooplankton	**59.3**	12.9	Zooplankton	39.7	12.2
SOM	-	-	SOM	-	-	SOM	-	-	SOM	3.6	2.7

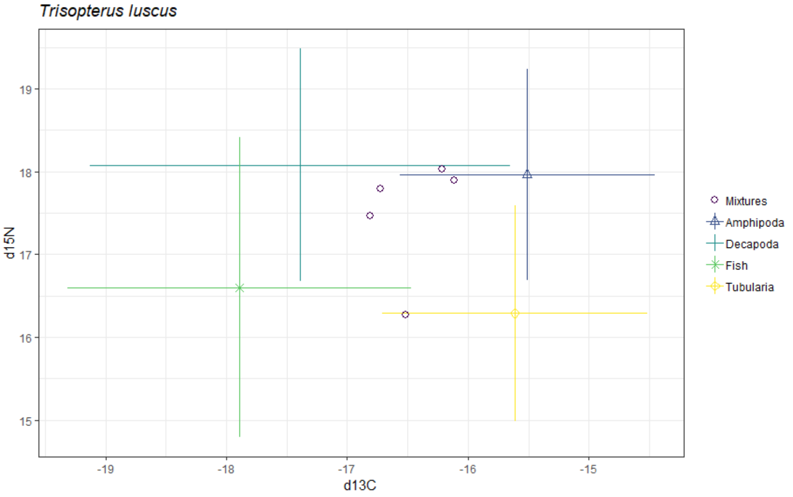
***Metridium senile*/Soft substrate**		
Resource	**Mean (%)**	**SD (%)**
SPOM	**61.9**	13.1
Zooplankton	34.8	12.6
SOM	3.3	2.8

A.3 Supplementary material for Chapter 5

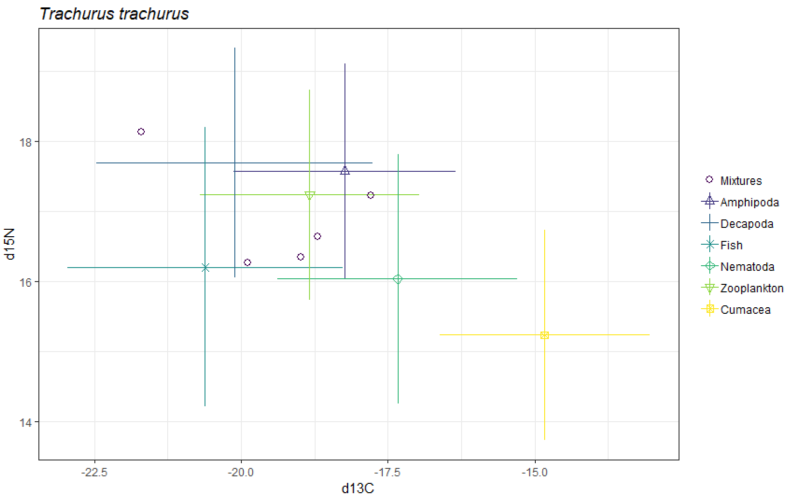
This section includes the isotopic mixing diagrams of the fish species examined in this thesis. These indicate the positions of the consumers within the convex polygon defined by the isotopic signatures of the prey items.

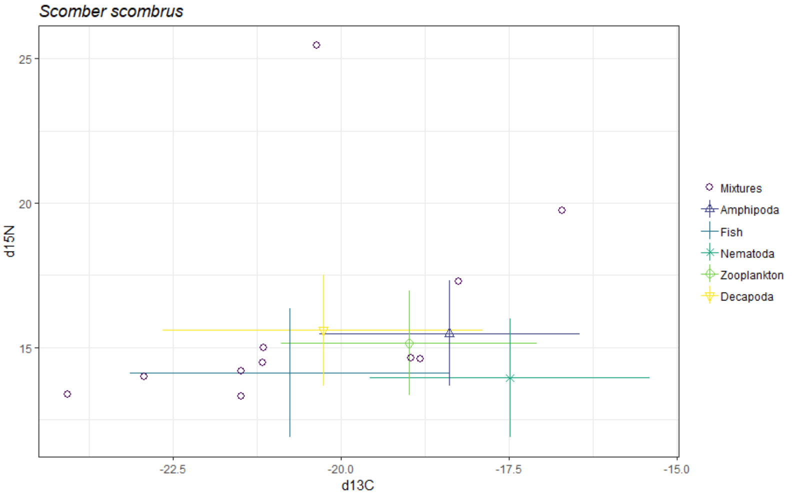


Gadus morhua



Trisopterus luscus


Trachurus trachurus


Scomber scombrus

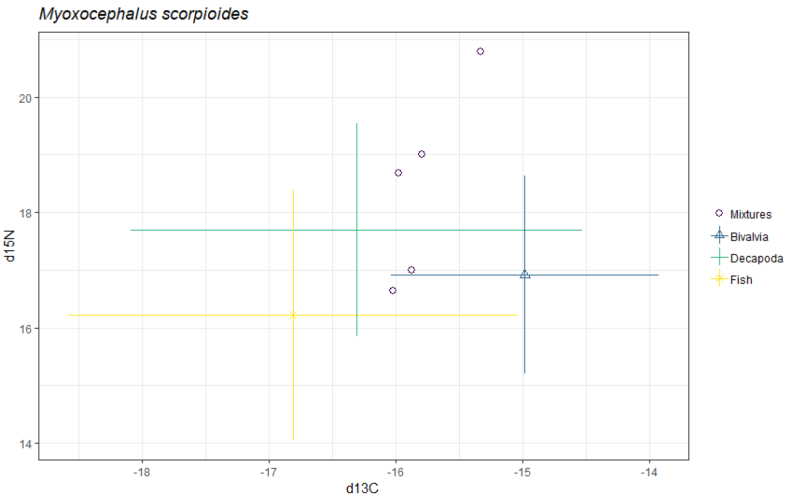


Figure A3.1: Isotopic mixing diagrams for the five fish species under study. Open circles represent the consumer fish species, while the solid coloured lines represent the potential prey items corrected with trophic enrichment factors (TEFs).

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