Diel variation in feeding and movement patterns of juvenile Atlantic cod at offshore wind farms

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A B S T R A C T

Atlantic cod (Gadus morhua) is a commercially important fish species suffering from overexploitation in the North-East Atlantic. In recent years, their natural environment is being intensively altered by the construction of offshore wind farms in many coastal areas. These constructions form artificial reefs influencing local biodiversity and ecosystem functioning. It has been demonstrated that Atlantic cod is present in the vicinity of these constructions. However, empirical data concerning the diel activity and feeding behaviour of Atlantic cod in the vicinity of these artificial reefs is lacking. Atlantic cod has a flexible diel activity cycle linked to spatio-temporal variations in food availability and predation risk. In this study we integrated acoustic telemetry with stomach content analysis to quantify diel activity and evaluate diel feeding patterns at a windmill artificial reef (WAR) in the Belgian part of the North Sea. Atlantic cod exhibited crepuscular movements related to feeding activity; a 12 h cycle was found and the highest catch rates and stomach fullness were recorded close to sunset and sunrise. It is suggested that the observed diel movement pattern is related to the prey species community and to predation pressure. Foraging at low ambient light levels (i.e. at dusk and dawn) probably causes a trade-off between foraging success and reducing predation pressure. Fish did not leave the area in-between feeding periods. Hence other benefits (i.e. shelter against currents and predators) besides food availability stimulate the aggregation behaviour at the WARs.

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1. Introduction

Atlantic cod (Gadus morhua Linnaeus, 1758) is a demersal fish species occurring throughout the North Atlantic Ocean (Froese and Pauly, 2012). It has a considerable commercial value and many populations have been heavily exploited for several centuries (Serchuk and Wigley, 1992). This resulted in critically low population levels for many stocks in recent years (ICES, 2010; Svedäng and Bardon, 2003). Due to its commercial importance and its dwindling stocks, the life history traits (Lund et al., 2011; Olsen et al., 2004), abundances (Rose and Kulka, 1999; Svedäng and Bardon, 2003), movements (Lindholm et al., 2007; Metcalfe, 2006; Svedäng et al., 2007) and feeding behaviour (Adlerstein and Wellemann, 2000) of Atlantic cod have been documented in many studies over a wide range of spatial and temporal scales using a variety of techniques and approaches.

However, natural behaviour, abundances and movements of Atlantic cod may be influenced by offshore human activities. Solid structures (e.g. gas platforms (Lowe et al., 2009), wind turbines (Reubens et al., 2011) and wave power foundations (Langhamer et al., 2009)) have been placed on the seabed all around the world and can be classified as artificial reefs. These artificial reefs have some environmental costs and benefits (Langhamer et al., 2009) which may influence local biodiversity and ecosystem functioning (Andersson et al., 2009). Numerous offshore wind farms are currently being constructed in the North Sea and research on the effects of these Windmill Artificial Reefs (further referred to as WARs) on the surrounding marine environment is required. Some demersal fish species for instance, are likely to be attracted to the WARs as shelter against currents or predators (Bohnsack, 1989) and increased food provisioning (Leitao et al., 2007; Reubens et al., 2011) may turn these substrates into suitable habitats for hard substrate dwelling fish.

Reubens et al. (2013) revealed the presence of large aggregations of juvenile Atlantic cod at WARs in the Belgian part of the North Sea (BPNS) during summer and autumn. However, empirical data concerning the reason why this species seems to be attracted by the reefs is unclear. Information on the diel movements and feeding behaviour of Atlantic cod in the vicinity of WARs is still lacking. The diel variation needs to be taken into account as this might shed light on the true added value of WARs. Next, Atlantic cod are also known to have a flexible diel cycle in feeding activity and habitat utilization which may differ between life stages, season and habitat (Clark and Green, 1990; Keats and Steele, 1992; Neat et al., 2006). It

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is often assumed that these differences in diel activity patterns are linked to spatio-temporal variations in predation pressure and food availability (Løkkeborg and Fernö, 1999; Righton et al., 2001). The wind farm under consideration harbours a diverse epifaunal community with high species abundances (Kerckhof et al., 2010b). Many of these epifaunal species are potential prey for juvenile Atlantic cod (Froese and Pauly, 2012). Several natural predators of Atlantic cod are also present in the area. The harbour porpoise (Phocoena phocoena Linnaeus, 1758) is present year round and may reach high abundance during late winter, early spring. The harbour seal (Phoca vitulina Linnaeus, 1758), grey seal (Halichoerus grypus Fabricius, 1791) and the white-beaked dolphin (Lagenorhynchus albirostis Gray, 1846) are also observed in Belgian waters, be it in much lower numbers compared to harbour porpoises (Haelters et al., 2011). All types of fisheries are excluded in the wind farm, leading to less human disturbance of the associated fish aggregations. Therefore, this wind farm provides an ideal opportunity to investigate the diel behaviour of an Atlantic cod aggregation in relation to food availability and predator pressure. However, directly observing the behaviour of marine fish in the wild is logistically very difficult. As a result, other methods are essential to infer fish behaviour (Hall et al., 1995). In this study we integrated acoustic telemetry with stomach content analysis. The former method was used to empirically quantify diel movement behaviour, while the latter is used to evaluate diel feeding patterns. Several questions were addressed: (1) do Atlantic cod at WARs exhibit predictable diel activity and movement patterns? (2) is there a diel pattern in feeding rates and prey composition?

2. Material and methods

2.1. Study site

The wind farm under consideration is situated in the BPNS at the Thorntonbank (Fig. 1), a natural sandbank 27 km offshore (coordinates WGS 84: 51°33′N-2°56′E). Two types of foundations are present in this farm: concrete gravity based and steel jacket foundations. Both function as WARs. All Atlantic cod used in the present study were caught at gravity based foundations. These foundations have a width of 14 m at the seabed, at a depth of about 22.5 m at mean low water spring (MLWS). The gravity based foundations are surrounded by a scour protection layer of pebbles and rocks with a total width of 44 m (1520 m²). The surrounding soft sediment is composed of medium sand (mean median grain size 374 μm, SE 27 μm) (Reubens et al., 2009).

2.2. Sampling methods

2.2.1. Acoustic telemetry

To quantify the diel movement pattern of Atlantic cod at the WARs, the Vemco VR2W acoustic monitoring system was used. In this system self-contained, single channel (69 kHz) submersible VR2W receivers were used to detect the signals of pulse-coded acoustic transmitters (Vemco V9-1 L). Each transmitter has a unique ID, emitting a signal every 110 to 250 s.

The Atlantic cod tracked at the WARs, were collected between May and July 2011 (Table 1) in the study area using hook and line gear. After capture the individual fishes were kept in an aerated water tank for 2 h before surgical implantation of the transmitter (i.e. tagging). Surgical procedures were similar to those of Reubens et al. (2012), Arendt et al. (2001) and Jadot et al. (2006). Prior to tagging, the fish were anaesthetized in a 0.3 ml l⁻¹ 2-phenoxyethanol solution. Following anaesthesia (i.e., fish showing no reaction to external stimuli, slow opercular rate and loss of equilibrium (McFarland and Klontz, 1969)), the fish were placed, ventral side up, in a V-shaped support. Most of the body, except the ventral side, stayed in the water and a continuous flow of aerated water was pumped over the gills to avoid dehydration and provide continuous oxygenation. A small incision (15–22 mm) was made on the mid-ventral line and an acoustic transmitter was inserted in the visceral cavity. The incision was closed with two sutures (polyamide...
monofilament, DS19 3/0). In total, 22 cod specimens were tagged. The fish were further externally tagged with a T-bar anchor tag. After full recovery and up to 2 h observation for survival, the fish were released at their capture site.

The acoustically tagged Atlantic cod specimens were tracked with three automated acoustic receivers. The receivers were placed around one WAR (Fig. 1) and recorded the presence of any acoustic transmitter within a range of 250 to 500 m. On the 20th of October 2011 the receivers were retrieved for data analysis.

2.2.2. Stomach content analysis

To quantify the feeding rate of Atlantic cod and prey composition in their diet on a diel base, line fishing was conducted. A 24 h sampling campaign was performed on the 29th and 30th of July 2010 at a WAR. Sampling was performed for 30 min at 3 h time intervals. Times of sunrise and sunset were recorded at 04:06 h and 19:33 h (Coordinated Universal Time) respectively. Angling (hooks: Arca, size 4; bait: Aremicola marina) was performed 1 to 10 m away from a turbine (i.e. within the erosion protection layer radius) just above the bottom of the seabed, assuring catching individuals hovering at the WAR. The fish were measured (total length), weighed (wet weight) and stomachs were removed and preserved in an 8% formaldehyde–seawater solution. All food components in the stomachs were identified to the lowest possible taxonomic level. Crabs that could not be identified to the genus level were named as ‘Brachyura sp.’. Wet weight, dry weight (60 °C for 48 h) and ash free dry weight (500 °C for 2 h) were measured for all separate food contents in each stomach.

No analysis was performed if stomachs were not preserved appropriately. In total 305 stomachs were used for analysis. Atlantic cod length varied between 25.2 and 53.7 cm (mean ± SD was 35.7 ± 4.2 cm).

The set up for acoustic telemetry and line fishing were not organised at the same turbine. Telemetry was performed at wind turbine D5, while fishing was organised at D1. In 2010 a test study was running at D5 to analyse the possibility to perform acoustic telemetry. It was decided not to perform the 24 h fishing sampling campaign at the same wind turbine, to minimize the chance of catching tagged fish. However, D1 is in close proximity to D5 (approximately 2 km), it is also a gravity based foundation and environmental parameters are very much comparable.

2.3. Data analysis

2.3.1. Acoustic telemetry

First, the data were filtered for spurious detections. A fish was defined as being present in the study area on a given day if it was detected at least two times on that day. Single transmitter detections were defined as false detections and removed from the analyses (Meyer et al., 2007).

The Fast Fourier Transformation (FFT) time series analysis was used to investigate periodicity in the behaviour. FFT breaks down a time series into the sum of its sinusoidal components. It describes fluctuations in a time series by comparing them to sinusoids. Frequencies of dominant patterns are identifiable as peaks (Bloomfield, 2004; Meyer et al., 2007). In FFT algorithms, the number of cases must be equal to a power of 2. If this is not the case, additional computations have to be performed (Statistica, Statsoft). The input dataset was not padded, exact length was used. Prior to FFT the detections of each fish were pooled into hourly bins. FFT was applied on data of 18 Atlantic cod as the remaining fish had insufficient detections for analysis (fish that were detected less than five days were left out). We further investigated possible diel patterns in detections linked to the photoperiod. Therefore, detections of each specimen were binned by period (i.e. sunrise, day, sunset and night) and daily average detections (weighted for the length of each period throughout the study) were compared between periods using the non-parametric Kruskal–Wallis test.

Sunrise and sunset information was obtained by the Royal Observatory of Belgium. The FFT was performed in Statistica (version 7.0, Statsoft, Tulsa, Oklahoma), while Kruskal–Wallis tests were performed in R 2.15.1 software (www.r-project.org).

2.3.2. Stomach content analysis

To investigate the diel pattern in feeding rates, a stomach content fullness index (IF) was calculated for each stomach of Atlantic cod. IF = \(10,000 \times c L^{-2}\), where c is the stomach content mass (wet weight, g) and L is the fish length (total length, cm). The IF adjusts for variation in fish size (Darbyson et al., 2003). Only non-empty stomachs were used in the analysis as regurgitation could have occurred while fish were being hauled. The non-parametric Kruskal–Wallis test was used to compare stomach content fullness between the 3 h sampling intervals (i.e. fishing batches). Statistical analysis was performed in R 2.15.1 software (www.r-project.org).

Further, prey composition of the diet was also examined by time of the day. Dietary composition was assessed by gravimetric abundance (ash-free dry weight) of each prey species for each batch. Prey composition was compared within and between time frames using non-metric multi-dimensional scaling and was statistically tested using a randomization test (analysis of similarity) based on permutations of the similarity matrix (Clarke and Gorley, 2006). Prior to analysis the community abundance data were standardized (De Crespin de Billy et al., 2000) and a similarity matrix was constructed using the Bray–Curtis index of similarity. Statistical analyses were performed using the Plymouth Routines in Multivariate Ecological Research (PRIMER) package, version 6.1.6 (Clarke and Gorley, 2006). A significance level of p < 0.05 was used in all tests. Results are expressed as mean ± standard error (SE).

3. Results

3.1. Diel movement patterns

The acoustic monitoring ran between May and October 2011. The receivers were recovered on 20/10/2011. The receivers detected 20 of

<table>
<thead>
<tr>
<th>Fish ID</th>
<th>Length (cm)</th>
<th>Release date</th>
<th>Date first detected</th>
<th>Date last detected</th>
<th>Time at liberty</th>
<th>Days detected</th>
</tr>
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<td>24/05/2011</td>
<td>16/07/2011</td>
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<td>54</td>
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<td>34</td>
<td>24/05/2011</td>
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<td>5</td>
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<td>33</td>
<td>24/05/2011</td>
<td>24/05/2011</td>
<td>21/06/2011</td>
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<td>02/10/2011</td>
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<td>71</td>
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<tr>
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<td>32</td>
<td>27/07/2011</td>
<td>27/07/2011</td>
<td>24/06/2011</td>
<td>29</td>
<td>29</td>
</tr>
</tbody>
</table>
the 22 acoustically tagged Atlantic cod. The total number of days on which a fish was detected ranged between 1 and 150 days (median 53.5 days) (Table 1).

The FFT analysis, done on 2048 h of continuous observations, revealed a clear diel cycle in movements of Atlantic cod (Fig. 2). The dominant peak in detections disclosed a 12 h periodicity. A secondary 6 h peak was observed as well.

We found evidence that Atlantic cod occurs in the vicinity of the WAR during the whole diurnal cycle. Each acoustically tagged Atlantic cod. Peaks indicate the periodicity of dominant cycles.

Further, daily detection rates vary highly between individual specimens.

3.2. Diel pattern in feeding rates and prey composition

In total, 308 Atlantic cod were caught over the eight fishing batches. Average length was 35.7 ± 4.2 cm, indicating they are 2 to 3 years old (ICES Fishmap, http://www.ices.dk/marineworld/fishmap/ices/). Catch per unit effort (CPUE) was highest immediately before sunset and after sunrise (Table 3). CPUE decreased significantly during night time (mean = 11 ± 3) compared to day time (mean = 26 ± 2) (Mann-Whitney U-test, p = 0.04).

40 of the 305 stomachs analysed were empty (13.1%).

The mean fullness index was highest immediately after sunset (batch 5: 0.94 ± 0.33) and sunrise (batch 8 and 1: 0.86 ± 0.11 and 0.90 ± 0.13 respectively). Fig. 3 reveals that stomach fullness followed a clear trend. Mean stomach fullness peaked immediately after sunset and sunrise, followed by a gradual decrease. After reaching a minimum during midday/midnight stomach fullness gradually increased towards twilight periods. A significant difference in fullness index was present between the different batches (Kruskal-Wallis, p = 0.007). Post-hoc analysis revealed that B3 and B8 differed strongest in stomach fullness.

The diet of Atlantic cod showed a wide variety in prey species, many of which are epifaunal species or associated with hard substrates. The predominant prey species in the diet were *Pisidia longicornis*, *Brachyura sp.*, *Liocarcinus spp.* and *Actinaria sp.* Some amphipod species (i.e. *Jassa herdmanni*, *Phtisica marina* and

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Monocorophium acherusicum) had a high frequency of occurrence as well and reached high abundances, but contributed less to the total prey biomass. Within each batch, a broad range of prey species was present. Stomach content did not differ significantly between batches (Anosim, p = 0.27, R = 0.007).

P. longicornis had a high frequency of occurrence in all batches. Liocarcinus spp. and Brachyura sp. occurred more in stomachs of Atlantic cod caught during the night, while J. herdmani was more often present in day time samples. A comparable trend was present in the relative contribution of the predominant preys to the stomach content weight in each batch (Fig. 4).

4. Discussion

4.1. Diurnal movement patterns

The Vemco VR2W acoustic monitoring system was used to record the presence of fish equipped with an acoustic transmitter within a certain distance of a receiver. If a tagged fish was detected, this indicates that the fish was present within the detection range of that specific receiver. If a fish was absent, this indicates that the fish was outside the detection range of the receiver or the signal emitted by the transmitter was blocked before it reached the receiver (e.g. by a boulder or a wind turbine foundation). In the former situation the fish had moved outside the study area, in the latter the fish had moved to a position within the study area where it could not be detected. In this way, the presence/absence data obtained by the system can be used to measure fish movements.

FFT analysis of the data revealed a dominant 12 h peak in detections at the WAR, indicating crepuscular movements. If this 12 h periodicity is linked to the fullness index, it clearly shows that Atlantic cod is most active at the WARs during twilight periods (Fig. 5). During these periods they actively forage, resulting in enhanced food intake and stomach fullness. As a consequence, they have the highest chance to be caught by line fishing during twilight, which is consistent with the CPUE data (Table 3).

Our results are in agreement with the results from similar studies on North Sea cod in which also morning and evening peaks in stomach fullness were found, reflecting intensive feeding at sunrise and sunset (Adlerstein and Wellemann, 2000; Rae, 1967). However, this is not always the case. Atlantic cod is known to have a flexible diel feeding activity cycle (Helfman, 1993) that may differ between regions. Clark and Green (1990) found that 3-year-old Atlantic cod in Newfoundland were nocturnally active during summer, switching to daytime activity in autumn. Lekkeborg et al. (1989) found that Atlantic cod exhibited a morning and afternoon peak in activity. Rae (1967) concluded that Atlantic cod in the North Sea displays crepuscular feeding patterns, while Daan (1973) found no consistent pattern.

4.2. Prey availability and feeding behaviour

Patterns in diel feeding activity have been demonstrated to be influenced by the activity pattern of prey species and the predation pressure (Clark and Green, 1990; Lekkeborg and Fernö, 1999; Neat et al., 2006). If important prey species have a specific diel activity cycle, Atlantic cod is expected to follow this cycle. Meanwhile, they need to minimize the predation risk. Therefore active foraging will coincide with light conditions that maximize the feeding success in relation to predation pressure (Helfman, 1993). Adlerstein and Wellemann (2000) for instance, found that the most intensive feeding period of Atlantic cod coincided with the diel migration of sandeels, a dominant prey in their diet. In the present study however, sandeel was seldomly encountered. Atlantic cod is an opportunistic feeder and their diet is known to be largely determined by availability (Daan, 1973), which is in agreement with the present findings. The predominant preys in this study (i.e. P. longicornis, Liocarcinus spp., Actiniaia sp. and J. herdmani) are known to occur in high densities (up to 13,000 and 4000 ind./m² for J. herdmani and P. longicornis respectively) at the WAR studied (Kerckhof et al., 2010a).

The observed diel feeding activity pattern of Atlantic cod in the present study is supposed not to be linked to the activity pattern of one or several dominant prey species. Although some trends are present in relative contribution of dominant prey species in the diet among batches (Fig. 4) none of these can be clearly linked to the activity cycle of Atlantic cod. There were no significant differences in stomach contents between the batches and a large variety of potential prey species were present in high densities, both day and night (Kerckhof et al., 2009). Some preys may contribute more to the diet during daytime (e.g. J. herdmani), other more during night time (e.g. Liocarcinus spp. and Brachyura sp.), while some (e.g. P. longicornis) are important throughout the day. Hence, the prey composition may change somewhat during the course of a day, but the prey availability remains constantly high. Therefore Atlantic cod behaviour is suggested not to be linked to specific prey species, but to the prey community as a whole.

Feeding behaviour is expected to reflect the optimal energy gain (Kerr 1982). Atlantic cod can use both visual and chemical senses to
localize prey (Brawn, 1969). However, during the daytime they have a bigger chance to encounter and locate prey (Løkkeborg and Fernø, 1999), making it energetically more profitable to forage during this period of the day.

4.3. Predation pressure

Based on the previous arguments Atlantic cod is expected to actively forage during daytime. However, crepuscular feeding behaviour was observed. Therefore, the risk of predation is probably influencing their feeding behaviour as well. Lakkeborg and Fernø (1999) investigated diel food search behaviour in Atlantic cod in a Norwegian fjord where the predation pressure was assumed to be negligible. The results indicated that Atlantic cod was more active during daytime, supporting our idea. Gregory and Anderson (1997) observed that 2–4 year old Atlantic cod were often associated with specific substrate features (such as rocks, crevices and holes) which represent potential cover against predators. At the WARs, the scour protection forms a habitat with a high complexity. The stone mattress of boulders and rocks creates an ideal hiding place, with many holes and crevices. During scuba diving operated visual surveys at these WARs Reubens et al. (2011) occasionally observed Atlantic cod of 2 to 3 years old in these crevices.

The harbour porpoise, harbour seal, grey seal and white-beaked dolphin are four natural predators of Atlantic cod that occur in the BPNS (Haelters et al., 2011). The harbour porpoise is present year round and may reach seasonally high abundances (more than 1 ind./km²) (Haelters et al., 2012). Based on stranding and sighting information it has been shown that the numbers of this species have increased in recent years in the southern North Sea (Haelters and Camphuysen, 2009). Harbour porpoises feed on a wide variety of fish species, with Atlantic cod (and gadoid species in general) often as one of the main species in their diet (Santos and Pierce, 2003). Harbour porpoises are regularly present at offshore installations in the North Sea and an acoustic monitoring study in a Dutch offshore wind farm revealed that the activity of harbour porpoises was significantly higher inside the wind farm than in the reference areas. It is suggested that these structures may play an important role as porpoise feeding stations (Scheidat et al., 2011; Todd et al., 2009).

The harbour seal, grey seal and the white-beaked dolphin are also occasionally observed in Belgian waters (Haelters et al., 2011). The diet of both seals is linked to availability of prey species and Atlantic cod is often consumed (Hall et al., 1998; Hammond et al., 1994). Both harbour and grey seals have been observed within the offshore wind farms in the North Sea (pers. obs., Tougaard et al., 2003). The white-beaked dolphin has become the most numerous cetacean after the harbour porpoise in the Southern North Sea (Jansen et al., 2010; www.waarnemingen.be). The dolphins are highly selective and mainly feed upon whiting and Atlantic cod. In addition, Atlantic cod present in stomachs of stranded white-beaked dolphins in the Netherlands, had an average length of 38 and 36 cm in adult and juvenile dolphins respectively (Jansen et al., 2010). The average length of Atlantic cod that occurred at the WARs in the BPNS is 36 cm, rendering them the ideal prey size for the dolphins.

Although no direct observations of predation events on Atlantic cod at the WARs are available it is assumed, based on the previously mentioned literature information, that the risk of predation influences the observed diel feeding behaviour of Atlantic cod. Foraging at low ambient light levels (i.e. at dusk and dawn) probably causes a trade-off between foraging success and reducing predation pressure.

4.4. Other benefits stimulating aggregation

Next, the present results indicated that Atlantic cod occurs in the vicinity of the WAR throughout the 24 h of a day. High detection rates were observed for acoustically tagged fish during both day and night (Table 2). This indicates that they do not leave the area in-between feeding periods. There might be other benefits stimulating the aggregation behaviour at the WARs besides food. Shelter against currents and reduced predator pressure are suggested to influence this behaviour (Bohnsack and Sutherland, 1985; Wilhelmsen et al., 2006).

The FFT (Fig. 2) revealed a secondary 6 h periodicity peak in the detection data. This peak is probably related to the tidal regime of the studied area (Fig. 5). Tides are semi-diurnal in this region and the tidal currents can reach high velocities (varying between 0.2 and 0.6 m/s at neap tide and 0.3 and 0.9 m/s at spring tide). The swimming activity of Atlantic cod is known to decrease in periods of strong currents (Lakkeborg et al., 1989), which is probably related to energy optimization. Around the concrete turbines there is always
one side that provides shelter against the currents and many hiding places are present between the rocks of the scour protection (pers. obs.). Atlantic cod may also maintain position by heading upstream at slow swimming performance (Løkkeborg et al., 1989, pers. obs.). The energetic cost associated with this sustainable swimming speed is very low for Atlantic cod (Soofi and Priede, 1985).

4.5. Offshore wind power development — a broader context

In recent years offshore wind farms arose all across the North Sea (Arapogianni et al., 2013; Brabant et al., 2012) and member states are planning a further monumental development (Willemsson and Malm, 2008). As a result thousands of wind turbines will be present in the North Sea in the near future. In the BPNS two wind farms are already (partially) operational: C-Power and Belwind. In the near future five more wind farms will be constructed. As a result more the 400 wind turbines will be present in the BPNS (Brabant et al., 2012; Rumes et al., 2011a, 2011b). This creates a large potential for Atlantic cod populations in the Belgian part of the North Sea and beyond. As long as fisheries activities are banned inside the wind parks, the fish residing in this habitat are less vulnerable to fishing mortality; resulting in higher survival rates. From a management perspective, it is therefore essential to carefully monitor the fish populations present in offshore wind farms to broaden the knowledge on fish ecology at WARs. Thorough management restrictions should be implemented to allow fish populations to fully exploit the benefits from this protective habitat.

This study provided the first empirical data on the diel movements patterns of Atlantic cod at WARs in the BPNS (Fig. 5). They exhibited crepuscular movements related to feeding activity. We suggest that this crepuscular behaviour is related to the prey species community and to predation pressure. Preys are available throughout the day, but also predators may occur at the WARs. Therefore, foraging at low ambient light levels (i.e. at dusk and dawn) probably causes a trade-off between foraging success and reducing predation pressure.

Next, the results showed that Atlantic cod resided at the WAR in-between feeding periods. The integrated approach, combining acoustic telemetry with stomach content analysis and catch rate information, greatly contributed to the interpretation of the data. We therefore strongly encourage multidisciplinary approaches in future research to investigate fish ecology.

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