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The proportion of flatfish recruitment in the North Sea potentially affected by offshore windfarms

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Abstract

Understanding the influence of man-made infrastructures on fish population dynamics is an important issue for fisheries management. This is particularly the case because of the steady proliferation of offshore wind farms. Several flatfish species are likely to be affected because areas with offshore wind farms in place or planned for show a spatial overlap with their spawning grounds. This study focuses on six commercially important flatfish species in the North Sea: common sole (*Solea solea*), European plaice (*Pleuronectes platessa*), turbot (*Scophthalmus maximus*), brill (*Scophtalmus rhombus*), European flounder (*Platichthys flesus*) and common dab (*Limanda limanda*). We used a particle-tracking model (LARVAE&CO) coupled to a 3D hydrodynamic model to assess the effects of spatial overlap of offshore wind farms with the species' spawning grounds on the larval fluxes to known nursery grounds. An important overlap between planned areas of offshore wind farms and flatfish spawning grounds was detected, with a resulting proportion of settlers originating from those areas varying from 2 to 16%. Our study suggests that European plaice, common dab and brill could be the most affected flatfish species, yet with some important local disparities across the North Sea. Consequently, the study represents a first step to quantify the potential impact of offshore wind farms on flatfish settlement, and hence on their population dynamics.

Key words:

Coastal zone management, connectivity, dispersal, flatfish, individual based modelling, North Sea, spawning ground, offshore wind farms

Running title:

Impact likelihood of offshore wind farms on flatfish settlement

Introduction

The capacity and number of offshore wind farms (OWFs) is increasing in European waters due to the growing demand for renewable energy. Many are either operational, under construction or planned for (Lindeboom *et al.*, 2015; OECD, 2016). The European Union has set the target to have 20% of all energy needs covered by renewables by 2020 (Renewable Energy Directive 2009/28/EC). In this context, the recent widescale extension of OWFs in the southern and central North Sea is of particular significance (Kalaydjian and Girard, 2017). However, the installation of thousands of turbines covering wide areas of the central and southern North Sea (OSPAR Commision, 2014, see Figure 1) in the near future across the entire North Sea raises questions about the environmental impact and the effects on the marine ecosystem (Petersen and Malm, 2006; Bergström *et al.*, 2013, 2014).

Several studies have highlighted the effects of OWFs during the construction, operation and decommissioning phases (Petersen and Malm, 2006; Bergström *et al.*, 2014). While impacts relating to the construction phase are significant, they occur over a relatively short time span (Vaissière *et al.*, 2014). Given the short time span involved, Wilhelmsson (2010) suggested that the perturbation is most likely to be of an acceptable level. Other impacts however persist throughout the lifespan of the OWFs. These include underwater sound related to gearbox vibrations and shipping traffic (Nedwell and Howell, 2004; Wahlberg and Westerberg, 2005), electromagnetic fields (Gill *et al.*, 2012) and alterations in the local hydrodynamic conditions (Broström, 2008). Major effects are linked to the introduction of hard substrates in sandy or muddy habitats, increasing the local habitat heterogeneity and providing substrates for fouling organisms. This phenomenon is known as the ‘artificial reef effect’ (Petersen and Malm, 2006; Langhamer, 2012; De Mesel *et al.*, 2015). Additionally, OWFs may limit fisheries related activities. A reduction in the deployment of towed fishing gear decreases the disturbance of benthic communities and may facilitate the recovery of previously disturbed communities (Leonhard *et al.*, 2011; Lindeboom *et al.*, 2011; Wilhelmsson and Langhammer, 2014), creating new opportunities for organisms such as fish.

Both OWFs and other artificial hard substrates have been reported to attract and concentrate fish (Bohnsack, 1989; Pickering and Whitmarsh, 1997; Leitão *et al.*, 2008, 2009), which find shelter against currents, predators, human-induced and natural stressors (e.g: Langhamer, 2012; Reubens *et al.*, 2014;

Wilhelmsson and Langhammer, 2014) and an increase in food provision (Pike and Lindquist, 1994; Fabi *et al.*, 2006; Leitão *et al.*, 2007). This behaviour is known to fishermen who increase their fishing effort in the vicinity of artificial hard structures such as oil and gas pipelines in the North Sea (Rouse *et al.*, 2018). Several studies have indicated an increase in abundances of fish close to OWFs, including commercially important species such as Atlantic cod (*Gadus morhua*) and pollock (*Pollachius pollachius*) (Bergström *et al.*, 2013; Stenberg *et al.*, 2015). The concentration of adult fish around windfarm could increase eggs production in OWF areas. OWFs are also known for their positive impact on flatfish biomass as predicted by a modelling study in the Eastern English Channel (Raoux *et al.*, 2017) and illustrated by an apparent size increase of European plaice (*Pleuronectes platessa)* in Belgian OWFs (Vandendriessche *et al.*, 2015). Furthermore, general increases in flatfish density have been observed around artificial structures in the North West Atlantic (Walton, 1982). The closure of fishing grounds, a general practice in OWFs, has had a positive impact on the egg production of turbot (*Scophthalmus maximus*) in the Baltic Sea (Florin *et al.*, 2013).

Fisheries management requires an understanding of the present and prediction of the future state of the environment, including the future state of fish populations after the introduction of OWFs. Many studies have addressed the question of the impact of OWFs on the ecosystem but most of them focus on local scale effects. However, local scale effects may have knock-on effects at the population level. This spillover effect can be either positive as in the case of marine protected area (Stobart *et al.*, 2009; Abecasis *et al.*, 2014) or negative in the case of nursery habitat degradation (Rochette *et al.*, 2010). From an ecosystem functioning perspective, these local studies must be extrapolated to the wider environment, e.g. the North Sea at large. One route to achieve such spatial extrapolation is via a modelling approach, which can provide valuable insights into the potential impact of OWFs onto species-specific population dynamics.

In this context, North Sea flatfishesform an interesting group of species to model. In addition to their high economic value, flatfishes have a complex bentho-pelagic life cycle spanning broad geographical scales. There is high potential for interaction with OWFs during their different life stages, each of which involving spatially distinct habitats. During the adult phase, despite differences among species, most migration occurs between feeding and spawning grounds (Gibson, 1997; Hunter *et al.*, 2003), and the effects of OWFs may differ in each of these areas. For some flatfish, such as European plaice, the feeding and spawning grounds are located at different sites. Feeding grounds with increased macrobenthic biomass, for example as a consequence of the presence of OWFs (Coates *et al.*, 2016), could positively impact the fish' condition, while spawning grounds may be strongly impacted by fisheries restrictions, as it has been shown for temporal closure during spawning season (van Overzee and Rijnsdorp, 2014). Indeed, the fishing pressure is higher for target species such as common sole (*Solea solea*) or European plaice due to spawning aggregations. Flatfish produce a large number of eggs, with variable but generally low chances of survival (Juanes, 2007; Le Pape and Bonhommeau, 2015). Large variations in recruitment are at least partially due to the sensitivity of larval survival to environmental conditions and hydrodynamics, which may explain the current lack of stock-recruitment relationships in many exploited fish species (Houde, 2008; Cury *et al.*, 2014). Finally spawning grounds, due to their role in connectivity and recruitment, can be considered a critical habitat for flatfish.

Settlement is not directly related to the number of eggs spawned because of a pelagic larval phase with recruitment constraints at the nursery grounds. In the present study, a model is used to investigate how OWFs throughout the southern and central North Sea, whatever their stage (operational, under construction or planned), may spatially interfere with the population dynamics of flatfish. The study focuses on the ontogenetic phases of the early life cycle because of its important role in the population dynamics. The general aim of this study represents a first step to quantify the potential impact of OWFs on population dynamics. The specific aims are to assess (1) the proportion of overlap between spawning grounds and OWFs, (2) the proportion of settlers originating from (realised and planned) OWFs, (3) the potential connectivity between OWFs and nursery grounds, and (4) how the expansion of OWFs across the North Sea may spatially affect flatfish nursery grounds.

Materials and Methods

Research strategy

The spatial overlap in spawning grounds and the consequent arrival of settlers from (realised and planned) OWFs at the nursery grounds can be used to study the likelihood that an OWF affects flatfish populations. The use of biophysical models is considered a valid methodology to study connectivity and settlement of early pelagic life stages in the open ocean for two reasons (Miller, 2007; Pineda *et al.*, 2007; Cowen and Sponaugle, 2009). First, a direct observation of fish eggs and larvae trajectories is difficult in the open ocean and secondly, direct or indirect tagging such as genetics or otolith microchemistry have a limited power to spatially track fish recruits in a well-mixed sea such as the North Sea. For the present purpose, the Lagrangian larval transport model LARVAE&CO (Lacroix *et al.*, 2013), resulting from the coupling between a hydrodynamical model and an Individual-Based Model (IBM), was used to simulate the dispersal of early life stages of flatfish. This model has shown to explain a significant part (31%) of recruitment variability of sole in the North Sea (Lacroix *et al.*, 2013). The simulations were carried out for a 10-year period (1997-2006), in order to span most of the year-to-year variability over the typical timescale of the North Atlantic Oscillation (NAO) cycle (Berglund *et al.*, 2012).

Study area

The Eastern English Channel and the southern and central North Sea are shallow coastal seas, and the currents are mainly generated by tides and wind. The general circulation pattern is oriented from South to North (Turrell, 1992), with some interannual variability in the flow field related to the NAO in addition to strong seasonal variability. For the sake of this study the extent and distribution of existing and planned OWFs were extracted from the OSPAR data base on offshore windfarms (OSPAR Commision, 2014). This study addresses all OWF stages (operational, under construction or planned), distributed over nine geographic sectors of interest (Figure 1).

Species of interest

This study focuses on the six most exploited flatfish species in the North Sea: turbot (*Scophthalmus maximus L.*), brill (*Scophtalmus rhombus L.*), common sole (*Solea solea L.*), common dab (*Limanda limanda L.*), European plaice (*Pleuronectes platessa L.*) and European flounder (*Platichthys flesus L.*).

Hereafter, common sole, common dab, European flounder and European plaice will be referred to as sole, dab, flounder and plaice, respectively.

The six flatfish species display a wide range of life history traits related to growth (e.g. pelagic larval duration), behaviour and reproduction strategy (e.g. spawning period and spawning distribution, Figure 2), which impact larval drift (Cowen *et al.*, 2007; Pineda *et al.*, 2007). Nursery grounds are mostly located in shallow coastal waters associated with soft sediments. Nursery grounds are species-specific, based on bathymetry and sediment type (see in supplementary material) and further divided in six areas according to national boundaries (France, Belgium, the Netherlands and German Bight) and two geographically separated nurseries in the United Kingdom (Norfolk and Thames estuary). In addition, the Dogger Bank, which is an important offshore nursery for dab and plaice, was included in the Norfolk nursery ground (Figure 3). More details on spawning grounds and nursery grounds for the six species can be found in the supplementary material.

Modelling of the early life stage

The hydrodynamic model

The3D hydrodynamic NOS (North Sea) model, based on the COHERENS model (Luyten *et al.*, 1999), has been implemented in the Eastern English Channel and the southern and central part of the North Sea, between 48.5°N and 57°N and 4°W and 9°E in latitude and longitude respectively (Figure 1). The model domain contains a 157 x 205 horizontal grid with a resolution of 5' in longitude and 2.5' in latitude and 20 σ-coordinate vertical layers. The boundaries are formed by the northern and western open boundaries (at 4°W and 57°N) and included daily river discharges of 14 rivers (Figure S1). The model is forced by weekly sea surface temperature (SST) data on a 20×20 km grid interpolated in space and time according to the model resolution (*Bundesamt für Seeschifffahrt und Hydrographie, BSH, Germany*) (Loewe, 2003) and by six-hourly surface wind and atmospheric pressure fields provided by the Royal Meteorological Institute of Belgium based on the analyzed/forecast data of the UK Met Office Global Atmospheric Model (Hi_Res; Walters et al., 2017). Details about the model implementation can be found in Savina *et al*. (2010) and Lacroix *et al*. (2013).

Individual-based model

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The Lagrangian larval transport model LARVAE&CO (Lacroix et al., 2013) was structured in four different stages representing flatfish life stages from eggs to metamorphosis (eggs, yolk-sac larvae, first-feeding larvae and metamorphosis larvae). Each stage has a species-specific parameterisation in terms of larval duration and behaviour (*in casu* vertical migration). Spawning grounds (Figure 2) and periods are also species-specific. The parametrisation details for the six flatfish species can be found in the supplementary material. Larval trajectories were calculated online using the particle tracking model. The vertical diffusion was modelled by the random walk technique following Visser (1997). Because in the North Sea vertical turbulent diffusion is considered to be the dominant horizontal dispersal mechanism (Christensen *et al.*, 2007), explicit representation of horizontal diffusion was neglected. Specific details on the implementation can be found in Lacroix et al. (2013).

Analysis

We assume that the production of eggs has a one to one relationship with the spawning ground surface area and spawning distribution (Figure 2). The overlap between the geographic distribution of the spawning grounds and (planned and existing) OWFs is consequently expected to show a one to one relationship with the proportion of eggs spawned in areas with OWFs. The dispersal model was used to assess how much the dispersal and settlement success of flatfish are likely to be affected by OWFs over a 10 years period. The proportion of settlers at a given spawning location originating from OWFs is the relative contribution of settlers originating from OWFs to the total number of settlers in a given spawning ground. Finally, to assess the eventual repercussion of a change in egg production inside OWF areas on settlement, four scenarios were tested. These scenarios consider an hypothetical change of egg production of-20%, +10%, +25% and +50% inside the OWFs and an absence of change outside. No change in the spatial distribution of eggs was considered in these scenarios.

Results

Contribution of spawning events in offshore wind farms to total egg production and recruitment

The proportion of eggs spawned in the areas with OWFs varies among species (Table 1). Dab, which has the largest spawning ground (see Figure 2) of the six selected species, present the highest level of overlap: 16.7% of the eggs produced in the model domain by this species will be derived from an area where OWFs are or will be present in the near future. Plaice has a large spawning ground but showed a lower level of overlap with OWFs (about 9%). The spawning distribution of brill showed likewise a 15% of overlap with OWF areas whereas turbot presented a lower level. Flounder and sole, which spawn in more coastal waters, present the lowest level of spatial overlap with OWFs (around 3%).

The six species displayed interannual variation in the mean arrival of settlers from OWFs at the nursery grounds for the period 1997-2006 (Table 1 and Figure 4). Dab showed the highest proportion of settlers originating from OWFs compared to the other species (16.1%). For brill and plaice this proportion was lower while turbot, flounder and sole showed the lowest level of larval arrivals from OWFs (about 2% of the settlers).

Table 1: Proportion of eggs spawned in realised and planned offshore wind farms (OWFs) for the different species and mean, minimum, maximum and standard deviation of the proportion of settlers originating from OWFs during the period 1997-2006.

Species	**Proportion of spawning in OWFs (%)**	**Proportion of settlement from OWFs (%)**			
		Mean	**Min**	**Max**	**Sd**
Plaice	9.4	8.9	7.4	10.3	0.97
Turbot	9.5	2.2	1.3	3	0.6
Dab	16.7	16.1	13.3	20.1	2.2
Sole	2.9	1.8	1.1	2.4	0.4

Brill	15.3	6.9	5.5	10.2	1.7
Flounder	3.3	2.3	1.5	3.7	0.7

The inflow of settlers originating from OWFs varied between the years (Table 1). The difference between the maximum and minimum proportion of settlers coming from OWFs drew attention (about 30%-60%). In addition to year-to-year variability, the model also predicted spatial heterogeneity (Figure 4). For turbot, the Thames nursery was the most affected, with an average of 7.8% of settlers coming from OWFs. The Nl, Ge and No nurseries were also affected (2.6%, 1.4% and 3.9% from OWFs, respectively), while Fr and Be received less than 1% of settlers from OWFs. For brill, Nl, Ge and No were the most impacted nursery grounds. For sole, the most impacted nursery ground was Nl, with about 5% of the settlers coming from OWFs and less than 1.5% for other spawning grounds. For dab, OWF arrivals were important in No, Tha and Ge (30%, 14% and 13%, respectively), while for the French nursery 8% of the settlers on average came from OWFs, with high interannual variability (from 42% in 1999 to low input in 2001 or 2002). For plaice, No and Ge nursery grounds presented the highest number of arrivals from OWFs (12% and 10%, respectively). For Nl and Tha the number of settlers from OWFs was important (5% and 4%, respectively), but limited for Be and Fr (2% and <1%, respectively). Flounder displayed the same interannual variability than dab. While overall, Fr, Tha and Be were the least impacted, a high year-to-year variability was observed, with particularly high values for the Belgian nursery in 1997 and 2001 (13% and 29% from OWFs, respectively). Nl was the most affected nursery ground for this species (on average 6%).

Specific impact of spawning event in OWF areas on the different nurseries

The inflow of settlers originating from OWFs varied between years (Table 1). In addition to the year-to-year variability, the model also predicted spatial heterogeneity (Figure 5). All nursery grounds were predicted to be prone to OWFs influences, but the impact is likely to differ among the nursery grounds, the species, and the origin of settlers. For the French nursery ground, two species presented more than 0.5% of arrivals from OWFs: dab from South UK OWFs (8.5%) and turbot from French OWFs (0.5%). The proportion of arrivals from OWFs at the Belgian nursery ground was limited compared to the other nurseries (less than 0.5% for all species, except for flounder and plaice, for which the proportion reached 4.5% and less than 2% respectively) and mainly from local OWFs (BE_NL). In the Dutch nursery ground, brill and flounder are likely to be most prone to OWFs influence, with 8% and 6%, respectively. The settlement of dab was limited. For most species, the main treat of impact comes from the Belgian and Dutch OWFs, except for flounder for which Dutch OWFs imported the majority of larvae originating from an OWF. The German nursery ground displayed a relatively high proportion of settlers from OWFs (more than 5% for brill, dab and plaice). The origin of the settlers also revealed a strong disparity between species in terms of OWFs contribution. Germany 1 OWFs was the major contributor for sole, turbot, brill and dab, and to a lesser extent a contributor for plaice. In the case of dab, there was also more than 1% of input from East UK, NL and Belgium-Netherlands OWFs. For plaice, most of the arrivals was due to East UK, Germany 1 and NL OWFs, with Belgium-Netherlands OWFs playing an important role. In the Thames nursery the origin of settlers predicted by the model indicated that 14% for dab and 8% for turbot were coming from OWFs. South UK OWFs were the major contributors for dab and to a lesser extent for plaice. Brill, sole, turbot and plaice were strongly influenced by East UK OWFs. Finally, the predicted arrivals from OWFs at the Norfolk nursery ground were considerable for dab (more than 30%), and relatively important for plaice (about 10%). East UK OWFs was the main contributor for brill, sole and turbot. North-East UK 1 OWFs played an important role in the case of dab and plaice. OWFs located further offshore or close to the North boundary of the domain (North-East UK 1, North-East UK 2 and Germany 2) had a limited impact in the Southern North Sea at the notable exception of Norfolk for East UK 1.

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Applying the model to different scenarios of OWF impact onto egg production showed changes in settlement ranging from -3% (-20% egg production scenario) to 8% (+50% egg production scenario) (Table 2). Dab was identified as the potentially most impacted species, while the lowest predicted impact goes for sole.

Table 2: Expected change of settlement (in percent) under different scenarios of altered egg production inside the offshore wind farms.

	- 20%	**+ 10%**	**+ 25%**	**+ 50%**
Plaice	-1.78	-0.89	2.25	4.45
Turbot	-0.4	0.2	0.5	1
Dab	-3.22	1.61	4.03	8.05
Sole	-0.36	0.18	0.45	0.9
Brill	-1.38	0.69	1.73	3.45
Flounder	-0.46	0.23	0.58	1.15

Discussion

This study analysed the level of overlap between spawning grounds and OWFs as well as the proportion of settlers in coastal and estuarine nursery grounds originating from OWFs for the flatfishes plaice, dab, sole, turbot, brill and flounder over a 10-year period (1997-2006). The installation of OWFs in the southern and central North Sea leads to a potential overlap with the spawning grounds of flatfishes, which might impact flatfish settlement and population dynamics. Our results showed that the proportion of settlers arriving at the nursery grounds that might originate from OWFs is not solely related to this overlap. Moreover, the model predicted high variation among species, areas and years.

Spatial overlap between spawning grounds and offshore wind farms

From an ecological and evolutionary perspective the location of spawning areas of marine fish results from a large number of constraints including fertilisation, survival from eggs to juveniles, reduced predation and transport toward suitable nursery (Ciannelli *et al.*, 2015). Also, the spawning grounds show a large variability among the six species due to the wide range of life history traits of the selected species and, hence, different levels of overlap with OWFs. These differences are explained by the species-specific reproductive strategy, spawning ground location, either coastal (e.g. sole) or more offshore (e.g. dab), and the position of spawning hotspots (higher egg densities, Figure 2). Three groups emerged: dab and brill which present the highest level of overlap with OWFs of the species studied, sole and flounder which present a lower level of overlap and turbot and plaice that exhibit an intermediate level of overlap.

Settlement of larvae originating from offshore wind farms

The overlap between spawning grounds and OWFs is an important aspect to understand the potential effect of OWFs on the species' population dynamics. Due to the specific life history of flatfish, this overlap is not directly related to recruitment as there is no linear relation between spawning and settlement (Cury *et al.*, 2014). In this context, using hydrodynamic models coupled to individual-based model was useful to understand how spawning grounds and nursery grounds are connected (Pineda *et al.*, 2007). The model predicted three main groups of species in terms of proportion of settlers originating from OWFs, which are slightly different from the three former groups found in the overlap study. Dab had the highest proportion of settlers originating from OWFs, plaice and brill were at an intermediate level and turbot, sole and flounder showed the lower proportion of settlers of OWF origin. The comparison between species presented in this study revealed that the number of eggs spawned in potential OWFs and the number of settlers originating from those areas were different between species.

The proportion of recruits originating from OWFs was lower than the proportion of eggs spawned in OWF areas for all species, particularly for turbot (9.5% of eggs were spawned in OWFs and only 2.2% of the settlers came from OWF areas) and brill (15.3% of eggs were spawned in OWFs and only 6.9%

of the settlers originated from OWFs). The higher proportion of e percentage of overlap than settlement indicates that OWFs will impact mainly areas where the probability of reproductive success is low for the North Sea (i.e area where the probability of settlement is low for eggs and larvae).

Interannual variability and potential impact on the different nurseries

The model predicted high interannual variability in the proportion of settlers originating from OWFs. This variability suggests that the hydrodynamic regime plays an important role in the connectivity between OWFs and nurseries. Environmental conditions are known to affect larval transport and flatfish recruitment in the North Sea (van der Veer, 1986; van der Veer and Witte, 1999; Bolle *et al.*, 2009). In addition to the interannual variability at the regional scale, the model predicted strong variations at the local scale. The model helps to detect the nursery grounds that will most likely be impacted by the introduction of OWFs. The nursery grounds at the German Bight, Norfolk and Thames estuary might be particularly affected, while the number of settlers originating from OWFs would be more limited at the Belgian nursery. However, there is interannual variability in the connectivity between OWFs and nurseries, which can be substantial in some cases (e.g. flounder in the Belgian nursery, for which the settlement from OWFs is less than 5% on average but could be as high as 30% in some years). Recruitment of flatfish is known to present a high interannual variability at the scale of southern North Sea related to environmental conditions (Bolle *et al.*, 2009; Erftemeijer *et al.*, 2009; Lacroix *et al.*, 2013), this variability could even be higher when considering recruitment success in small areas, as OWFs, in comparison to the whole North Sea.

Specific effect of different offshore wind farms

Using the dispersal model, it is also possible to assess the impact of a single OWF group onto settlement. Despite their limited coverage, some OWF groups could largely contribute to the larval settlement across the North Sea given their coastal location. Due to the large size and specific position of OWFs located in the Eastern coast of UK, eggs spawned in this area spread throughout the North Sea, as well as to the

English coast, where the OWFs had the strongest influence among all species. Due to a more offshore position or location in the north of the study area, some OWFs had a limited impact on populations for which nurseries are mainly coastal. However, they strongly affected species such as plaice and dab that have more offshore nurseries in the central part of North Sea. It must be pointed out that the northern coast of Denmark and the Norwegian and Swedish coasts were not included in our analysis. Other studies on plaice indicate that most eggs spawned in the German Bight arrive in the northern part of the North Sea (e.g. Hufnagl *et al.*, 2013).

Biological implications

The implementation of OWFs could impact flatfish population owing to the expected increase of the number of eggs spawned inside, due to the cue that suggests an increase in size, biomass or density of fish in OWF areas (Walton, 1982; Bergström *et al.*, 2013; Stenberg *et al.*, 2015). For marine fish, the choice of spawning grounds is constrained both by ecological and evolutionary processes (Munk *et al.*, 2009; Ciannelli *et al.*, 2015). In addition to changes in the quantity of eggs produced in OWFs, spawning locations are also susceptible to change in response to environmental changes induced by OWFs.

In the marine environment, maternal effects may affect recruitment, egg quality, the number of batches, the length of the spawning season, fertilisation rate, and (post)larval survival (e.g. Chambers and Leggett, 1992; Rijnsdorp and Vingerhoed, 1994; Butts and Litvak, 2007; Donelson *et al.*, 2009; Morais *et al.*, 2014). Adult condition might be influenced by altered environmental quality consecutive to the implementation of OWFs due to the change in species distribution and introduction of hard substrate, which could affect food availability or carrying capacity, and so eggs production and recruitment (Marshall *et al.*, 1999; van der Veer *et al.*, 2003, 2015). Thus, it may be also interesting to focus on the impact of OWFs on the feeding grounds, as they may have an impact on fish condition, and hence fecundity and migration success of fish larvae. Similarly, the behaviour and movement of fish which overlap with OWFs may be another topic of interest.

Nurseries play an important role in population dynamics of flatfish (Nash and Geffen, 2000). After metamorphosis, most larvae settle in shallow coastal nurseries, which most likely limits the direct impact of OWFs on juveniles. However, the interspecific difference in the number of settlers could also affect the juvenile life stage by changing the species composition of the nurseries. Indeed, many processes occurring at the nursery grounds are density-dependent (e.g. Van Der Veer 1986; Rijnsdorp and Van Leeuwen 1992; Van Der Veer *et al*. 2000; Le Pape and Bonhommeau 2015). In addition, environmental conditions in nurseries are important for young flatfish (Rijnsdorp *et al.*, 1992b; Cabral *et al.*, 2007). Overlap between OWFs and nurseries could change both the quality and capacity of the nursery grounds (due to a change in species composition, a reduction of surface due to the implementation of hard structures…) and influence the whole population, as in the case of habitat degradation for sole in Western English Channel (Rochette *et al.*, 2010)..

Management perspectives

Due to their specific life history, flatfish have not been identified as having the potential to benefit from the establishment of marine protected areas (Shipp, 2003). However, some studies showed that spatial restriction of fisheries or implementation of OWFs increase flatfish population size (Walton, 1982; Florin *et al.*, 2013) whereas others reported a limited impact (e.g. Ashley *et al.*, 2014). This study represents a baseline to test the potential impact of planned OWFs. The specific effect on the different species could be dependent of their exploitation level, which means that target species in the North Sea (especially sole and plaice) could be strongly affected by the overlap between OWFs and spawning grounds. This impact can be both positive and negative, depending on the real impact on OWFs on these species. The different scenarios in eggs production effects suggest that dab is the species more prone to OWFs influence. In the North Sea, dab is also the most common species (Rogers *et al.*, 1998). Despite potentially being the most impacted species, dab is not a target species for the fishing industry, so the effect of fishing restrictions could be more limited for this species than for other fished species.

Perspectives

The model excluded several sources of variability in larval survival related to trophodynamics, such as prey abundance and predation (Peck and Hufnagl, 2012). The observed increase in abundance of filter feeders in OWFs could lead to additional uncertainty in larval survival. In addition, a previous study (Lacroix *et al.*, 2018) based on the same model as the one used here, showed how climate change could affect recruitment and the connectivity pattern of sole in the North Sea. Climate change could also affect fish distribution (Perry *et al.*, 2005) and so the overlap between fish and OWFs. The real impact of OWFs on fish density and distribution should be studied *in situ* due to expected knock-on effects in settlement at nurseries and at population level. Once the magnitude of OWF impact on egg production is known, it will be possible to assess the impact on population dynamics from the likelihood of impact by OWFs based on the overlap computed in this study.

Conclusions

An important overlap between future OWF areas and flatfish spawning grounds was estimated, with a proportion of settlers originating from OWF areas varying from 2 to 16%. This study suggests that European plaice, common dab and brill could be the most affected flatfish species, yet with some important local disparities across the North Sea. Our results predicted interspecific differences resulting from the interaction between life history traits (such as pelagic larval duration, spawning period and distribution) and the environmental conditions (such as temperature and currents). Overall, species seem to be affected differently across the North Sea. Survey to assess the specific effect of OWFs on the different species, especially on eggs production, would help to further understand the potential impact of the presence of OWFs on flatfish population. Overall, our study represents a first step towards the understanding of the effects of OWFs on marine ecosystems. As the effects are many and varied, the results should be integrated into a larger study to assess the cumulative impact of OWFs as proposed by Willsteed *et al*. (2017).

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