

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

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20 Abstract

Understanding the influence of man-made infrastructures on fish population dynamics is an important 21 22 issue for fisheries management. This is particularly the case because of the steady proliferation of 23 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 24 25 six commercially important flatfish species in the North Sea: common sole (Solea solea), European 26 plaice (Pleuronectes platessa), turbot (Scophthalmus maximus), brill (Scophtalmus rhombus), European 27 flounder (Platichthys flesus) and common dab (Limanda limanda). We used a particle-tracking model 28 (LARVAE&CO) coupled to a 3D hydrodynamic model to assess the effects of spatial overlap of offshore 29 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 30 detected, with a resulting proportion of settlers originating from those areas varying from 2 to 16%. Our 31 32 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 33 34 step to quantify the potential impact of offshore wind farms on flatfish settlement, and hence on their 35 population dynamics.

36

37

38 Key words:

39 Coastal zone management, connectivity, dispersal, flatfish, individual based modelling, North Sea,

- 40 spawning ground, offshore wind farms
- 41

42 **Running title:**

43 Impact likelihood of offshore wind farms on flatfish settlement

44 Introduction

45 The capacity and number of offshore wind farms (OWFs) is increasing in European waters due to the 46 growing demand for renewable energy. Many are either operational, under construction or planned for 47 (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 48 49 recent widescale extension of OWFs in the southern and central North Sea is of particular significance 50 (Kalaydjian and Girard, 2017). However, the installation of thousands of turbines covering wide areas 51 of the central and southern North Sea (OSPAR Commission, 2014, see Figure 1) in the near future across 52 the entire North Sea raises questions about the environmental impact and the effects on the marine 53 ecosystem (Petersen and Malm, 2006; Bergström et al., 2013, 2014).

Several studies have highlighted the effects of OWFs during the construction, operation and 54 55 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., 56 2014). Given the short time span involved, Wilhelmsson (2010) suggested that the perturbation is most 57 58 likely to be of an acceptable level. Other impacts however persist throughout the lifespan of the OWFs. 59 These include underwater sound related to gearbox vibrations and shipping traffic (Nedwell and Howell, 60 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 61 62 substrates in sandy or muddy habitats, increasing the local habitat heterogeneity and providing substrates 63 for fouling organisms. This phenomenon is known as the 'artificial reef effect' (Petersen and Malm, 64 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 65 communities and may facilitate the recovery of previously disturbed communities (Leonhard et al., 66 67 2011; Lindeboom et al., 2011; Wilhelmsson and Langhammer, 2014), creating new opportunities for 68 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 72 73 et al., 2006; Leitão et al., 2007). This behaviour is known to fishermen who increase their fishing effort 74 in the vicinity of artificial hard structures such as oil and gas pipelines in the North Sea (Rouse et al., 75 2018). Several studies have indicated an increase in abundances of fish close to OWFs, including 76 commercially important species such as Atlantic cod (Gadus morhua) and pollock (Pollachius 77 pollachius) (Bergström et al., 2013; Stenberg et al., 2015). The concentration of adult fish around 78 windfarm could increase eggs production in OWF areas. OWFs are also known for their positive impact 79 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 80 OWFs (Vandendriessche et al., 2015). Furthermore, general increases in flatfish density have been 81 82 observed around artificial structures in the North West Atlantic (Walton, 1982). The closure of fishing 83 grounds, a general practice in OWFs, has had a positive impact on the egg production of turbot 84 (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 85 86 environment, including the future state of fish populations after the introduction of OWFs. Many studies 87 have addressed the question of the impact of OWFs on the ecosystem but most of them focus on local 88 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; 89 90 Abecasis et al., 2014) or negative in the case of nursery habitat degradation (Rochette et al., 2010). 91 From an ecosystem functioning perspective, these local studies must be extrapolated to the wider 92 environment, e.g. the North Sea at large. One route to achieve such spatial extrapolation is via a 93 modelling approach, which can provide valuable insights into the potential impact of OWFs onto species-specific population dynamics. 94

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 100 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 101 102 biomass, for example as a consequence of the presence of OWFs (Coates et al., 2016), could positively 103 impact the fish' condition, while spawning grounds may be strongly impacted by fisheries restrictions, 104 as it has been shown for temporal closure during spawning season (van Overzee and Rijnsdorp, 2014). 105 Indeed, the fishing pressure is higher for target species such as common sole (Solea solea) or European 106 plaice due to spawning aggregations. Flatfish produce a large number of eggs, with variable but 107 generally low chances of survival (Juanes, 2007; Le Pape and Bonhommeau, 2015). Large variations in 108 recruitment are at least partially due to the sensitivity of larval survival to environmental conditions and 109 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 110 111 and recruitment, can be considered a critical habitat for flatfish.

112 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 113 114 OWFs throughout the southern and central North Sea, whatever their stage (operational, under 115 construction or planned), may spatially interfere with the population dynamics of flatfish. The study 116 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 117 on population dynamics. The specific aims are to assess (1) the proportion of overlap between spawning 118 119 grounds and OWFs, (2) the proportion of settlers originating from (realised and planned) OWFs, (3) the 120 potential connectivity between OWFs and nursery grounds, and (4) how the expansion of OWFs across 121 the North Sea may spatially affect flatfish nursery grounds.

122 123

124 Materials and Methods

125 <u>Research strategy</u>

126 The spatial overlap in spawning grounds and the consequent arrival of settlers from (realised and 127 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 128 settlement of early pelagic life stages in the open ocean for two reasons (Miller, 2007; Pineda et al., 129 130 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 131 microchemistry have a limited power to spatially track fish recruits in a well-mixed sea such as the 132 North Sea. For the present purpose, the Lagrangian larval transport model LARVAE&CO (Lacroix et al., 133 2013), resulting from the coupling between a hydrodynamical model and an Individual-Based Model 134 135 (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 136 simulations were carried out for a 10-year period (1997-2006), in order to span most of the year-to-year 137 variability over the typical timescale of the North Atlantic Oscillation (NAO) cycle (Berglund et al., 138 2012). 139

140

141 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).

149

150 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 assole, dab, flounder and plaice, respectively.

156 The six flatfish species display a wide range of life history traits related to growth (e.g. pelagic larval 157 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 158 located in shallow coastal waters associated with soft sediments. Nursery grounds are species-specific, 159 160 based on bathymetry and sediment type (see in supplementary material) and further divided in six areas 161 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, 162 the Dogger Bank, which is an important offshore nursery for dab and plaice, was included in the Norfolk 163 nursery ground (Figure 3). More details on spawning grounds and nursery grounds for the six species 164 165 can be found in the supplementary material.

166

167 Modelling of the early life stage

168 *The hydrodynamic model*

The3D hydrodynamic NOS (North Sea) model, based on the COHERENS model (Luyten et al., 1999), 169 170 has been implemented in the Eastern English Channel and the southern and central part of the North 171 Sea, between 48.5°N and 57°N and 4°W and 9°E in latitude and longitude respectively (Figure 1). The 172 model domain contains a 157 x 205 horizontal grid with a resolution of 5' in longitude and 2.5' in 173 latitude and 20 σ -coordinate vertical layers. The boundaries are formed by the northern and western 174 open boundaries (at 4°W and 57°N) and included daily river discharges of 14 rivers (Figure S1). The 175 model is forced by weekly sea surface temperature (SST) data on a 20×20 km grid interpolated in space 176 and time according to the model resolution (Bundesamt für Seeschifffahrt und Hydrographie, BSH, 177 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 178 179 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). 180

183 *xxx*

184 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-185 feeding larvae and metamorphosis larvae). Each stage has a species-specific parameterisation in terms 186 187 of larval duration and behaviour (in casu vertical migration). Spawning grounds (Figure 2) and periods 188 are also species-specific. The parametrisation details for the six flatfish species can be found in the 189 supplementary material. Larval trajectories were calculated online using the particle tracking model. 190 The vertical diffusion was modelled by the random walk technique following Visser (1997). Because in 191 the North Sea vertical turbulent diffusion is considered to be the dominant horizontal dispersal 192 mechanism (Christensen et al., 2007), explicit representation of horizontal diffusion was neglected. 193 Specific details on the implementation can be found in Lacroix et al. (2013).

194

195 Analysis

196 We assume that the production of eggs has a one to one relationship with the spawning ground surface 197 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 198 199 relationship with the proportion of eggs spawned in areas with OWFs. The dispersal model was used to 200 assess how much the dispersal and settlement success of flatfish are likely to be affected by OWFs over 201 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 202 203 spawning ground. Finally, to assess the eventual repercussion of a change in egg production inside OWF 204 areas on settlement, four scenarios were tested. These scenarios consider an hypothetical change of egg 205 production of -20%, +10%, +25% and +50% inside the OWFs and an absence of change outside. No 206 change in the spatial distribution of eggs was considered in these scenarios.

207

209 **Results**

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

211 The proportion of eggs spawned in the areas with OWFs varies among species (Table 1). Dab, which 212 has the largest spawning ground (see Figure 2) of the six selected species, present the highest level of 213 overlap: 16.7% of the eggs produced in the model domain by this species will be derived from an area 214 where OWFs are or will be present in the near future. Plaice has a large spawning ground but showed a 215 lower level of overlap with OWFs (about 9%). The spawning distribution of brill showed likewise a 216 15% of overlap with OWF areas whereas turbot presented a lower level. Flounder and sole, which 217 spawn in more coastal waters, present the lowest level of spatial overlap with OWFs (around 3%). 218 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).

223

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.

	Proportion of	Proportion	n of settlemen	t from OWFs (%)
Species	spawning in 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

228

229 The inflow of settlers originating from OWFs varied between the years (Table 1). The difference 230 between the maximum and minimum proportion of settlers coming from OWFs drew attention (about 231 30%-60%). In addition to year-to-year variability, the model also predicted spatial heterogeneity (Figure 232 4). For turbot, the Thames nursery was the most affected, with an average of 7.8% of settlers coming from OWFs. The NI, Ge and No nurseries were also affected (2.6%, 1.4% and 3.9% from OWFs, 233 234 respectively), while Fr and Be received less than 1% of settlers from OWFs. For brill, NI, Ge and No 235 were the most impacted nursery grounds. For sole, the most impacted nursery ground was NI, with about 5% of the settlers coming from OWFs and less than 1.5% for other spawning grounds. For dab, OWF 236 237 arrivals were important in No, Tha and Ge (30%, 14% and 13%, respectively), while for the French 238 nursery 8% of the settlers on average came from OWFs, with high interannual variability (from 42% in 239 1999 to low input in 2001 or 2002). For plaice, No and Ge nursery grounds presented the highest number 240 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). 241 242 Flounder displayed the same interannual variability than dab. While overall, Fr, Tha and Be were the 243 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). NI was the most affected nursery 244 245 ground for this species (on average 6%).

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- 247

248 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 252 253 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 254 nursery ground was limited compared to the other nurseries (less than 0.5% for all species, 255 except for flounder and plaice, for which the proportion reached 4.5% and less than 2% 256 respectively) and mainly from local OWFs (BE_NL). In the Dutch nursery ground, brill and 257 258 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 259 Belgian and Dutch OWFs, except for flounder for which Dutch OWFs imported the majority 260 261 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 262 settlers also revealed a strong disparity between species in terms of OWFs contribution. 263 264 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, 265 NL and Belgium-Netherlands OWFs. For plaice, most of the arrivals was due to East UK, 266 Germany 1 and NL OWFs, with Belgium-Netherlands OWFs playing an important role. In the 267 268 Thames nursery the origin of settlers predicted by the model indicated that 14% for dab and 8% 269 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 270 OWFs. Finally, the predicted arrivals from OWFs at the Norfolk nursery ground were 271 272 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 273 274 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 275 limited impact in the Southern North Sea at the notable exception of Norfolk for East UK 1. 276

277 XX

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.

282

Table 2: Expected change of settlement (in percent) under different scenarios of altered eggproduction 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

283

284

285 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.

294 Spatial overlap between spawning grounds and offshore wind farms

295 From an ecological and evolutionary perspective the location of spawning areas of marine fish results 296 from a large number of constraints including fertilisation, survival from eggs to juveniles, reduced 297 predation and transport toward suitable nursery (Ciannelli et al., 2015). Also, the spawning grounds 298 show a large variability among the six species due to the wide range of life history traits of the selected 299 species and, hence, different levels of overlap with OWFs. These differences are explained by the 300 species-specific reproductive strategy, spawning ground location, either coastal (e.g. sole) or more 301 offshore (e.g. dab), and the position of spawning hotspots (higher egg densities, Figure 2). Three groups 302 emerged: dab and brill which present the highest level of overlap with OWFs of the species studied, sole 303 and flounder which present a lower level of overlap and turbot and plaice that exhibit an intermediate 304 level of overlap.

305 Settlement of larvae originating from offshore wind farms

306 The overlap between spawning grounds and OWFs is an important aspect to understand the potential 307 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 308 309 settlement (Cury et al., 2014). In this context, using hydrodynamic models coupled to individual-based 310 model was useful to understand how spawning grounds and nursery grounds are connected (Pineda et 311 al., 2007). The model predicted three main groups of species in terms of proportion of settlers originating 312 from OWFs, which are slightly different from the three former groups found in the overlap study. Dab 313 had the highest proportion of settlers originating from OWFs, plaice and brill were at an intermediate 314 level and turbot, sole and flounder showed the lower proportion of settlers of OWF origin. The 315 comparison between species presented in this study revealed that the number of eggs spawned in 316 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).

323

324 Interannual variability and potential impact on the different nurseries

325 The model predicted high interannual variability in the proportion of settlers originating from OWFs. 326 This variability suggests that the hydrodynamic regime plays an important role in the connectivity 327 between OWFs and nurseries. Environmental conditions are known to affect larval transport and flatfish 328 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 329 330 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 331 332 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 333 nurseries, which can be substantial in some cases (e.g. flounder in the Belgian nursery, for which the 334 335 settlement from OWFs is less than 5% on average but could be as high as 30% in some years). 336 Recruitment of flatfish is known to present a high interannual variability at the scale of southern North 337 Sea related to environmental conditions (Bolle et al., 2009; Erftemeijer et al., 2009; Lacroix et al., 2013), 338 this variability could even be higher when considering recruitment success in small areas, as OWFs, in 339 comparison to the whole North Sea.

340

341 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).

353

354 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.

361 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 362 Leggett, 1992; Rijnsdorp and Vingerhoed, 1994; Butts and Litvak, 2007; Donelson et al., 2009; Morais 363 et al., 2014). Adult condition might be influenced by altered environmental quality consecutive to the 364 365 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 366 367 (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 368 369 fecundity and migration success of fish larvae. Similarly, the behaviour and movement of fish which 370 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 373 374 the juvenile life stage by changing the species composition of the nurseries. Indeed, many processes 375 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 376 377 conditions in nurseries are important for young flatfish (Rijnsdorp et al., 1992b; Cabral et al., 2007). 378 Overlap between OWFs and nurseries could change both the quality and capacity of the nursery grounds 379 (due to a change in species composition, a reduction of surface due to the implementation of hard 380 structures...) and influence the whole population, as in the case of habitat degradation for sole in 381 Western English Channel (Rochette et al., 2010)..

382

383 Management perspectives

384 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 385 386 restriction of fisheries or implementation of OWFs increase flatfish population size (Walton, 1982; 387 Florin et al., 2013) whereas others reported a limited impact (e.g. Ashley et al., 2014). This study 388 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 389 390 (especially sole and plaice) could be strongly affected by the overlap between OWFs and spawning 391 grounds. This impact can be both positive and negative, depending on the real impact on OWFs on these 392 species. The different scenarios in eggs production effects suggest that dab is the species more prone to 393 OWFs influence. In the North Sea, dab is also the most common species (Rogers et al., 1998). Despite 394 potentially being the most impacted species, dab is not a target species for the fishing industry, so the 395 effect of fishing restrictions could be more limited for this species than for other fished species.

396

397 *Perspectives*

The model excluded several sources of variability in larval survival related to trophodynamics, such asprey 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 400 (Lacroix et al., 2018) based on the same model as the one used here, showed how climate change could 401 402 affect recruitment and the connectivity pattern of sole in the North Sea. Climate change could also affect 403 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 404 settlement at nurseries and at population level. Once the magnitude of OWF impact on egg production 405 406 is known, it will be possible to assess the impact on population dynamics from the likelihood of impact 407 by OWFs based on the overlap computed in this study.

408

409 **Conclusions**

410 An important overlap between future OWF areas and flatfish spawning grounds was estimated, with a 411 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 412 important local disparities across the North Sea. Our results predicted interspecific differences resulting 413 414 from the interaction between life history traits (such as pelagic larval duration, spawning period and 415 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 416 417 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 418 419 understanding of the effects of OWFs on marine ecosystems. As the effects are many and varied, the 420 results should be integrated into a larger study to assess the cumulative impact of OWFs as proposed by 421 Willsteed et al. (2017).

422

423

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