



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

**Barbut, Leo; Vastenhoud, Berthe Maria Johanna; Vigin, Laurence; Degraer, Steven; Volckaert, Filip A. M.; Lacroix, Genevieve**

*Published in:*  
ICES Journal of Marine Science

*Link to article, DOI:*  
[10.1093/icesjms/fsz050](https://doi.org/10.1093/icesjms/fsz050)

*Publication date:*  
2020

*Document Version*  
Peer reviewed version

[Link back to DTU Orbit](#)

*Citation (APA):*  
Barbut, L., Vastenhoud, B. M. J., Vigin, L., Degraer, S., Volckaert, F. A. M., & Lacroix, G. (2020). The proportion of flatfish recruitment in the North Sea potentially affected by offshore windfarms. *ICES Journal of Marine Science*, 77(3), 1227-1237. <https://doi.org/10.1093/icesjms/fsz050>

---

### General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

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

2 **Léo Barbut<sup>1,2</sup>,**

3 **Berthe Vastenhou<sup>3</sup>,**

4 **Laurence Vigin<sup>1</sup>,**

5 **Steven Degraer<sup>1</sup>,**

6 **Filip A.M. Volckaert<sup>2</sup>,**

7 **Geneviève Lacroix<sup>1</sup>**

8

9 <sup>1</sup> Royal Belgian Institute of Natural Sciences (RBINS), Operational Directorate Natural Environment,  
10 Rue Vautier 29, B-1000 Brussels, Belgium

11 <sup>2</sup> Laboratory of Biodiversity and Evolutionary Genomics, KU Leuven, Ch. Deberiostraat 32, B-3000  
12 Leuven, Belgium

13 <sup>3</sup> National Institute of Aquatic Resources (DTU Aqua), Kemitorvet, DK-2800 Kgs. Lyngby, Denmark

14

15 **Corresponding author:**

16 Léo Barbut, phone: +32 2 7732100; email: leo.barbut@naturalsciences.be

17

18

19

20 **Abstract**

21 Understanding the influence of man-made infrastructures on fish population dynamics is an important  
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  
24 farms in place or planned for show a spatial overlap with their spawning grounds. This study focuses on  
25 six commercially important flatfish species in the North Sea: common sole (*Solea solea*), European  
26 plaice (*Pleuronectes platessa*), turbot (*Scophthalmus maximus*), brill (*Scophthalmus 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  
30 important overlap between planned areas of offshore wind farms and flatfish spawning grounds was  
31 detected, with a resulting proportion of settlers originating from those areas varying from 2 to 16%. Our  
32 study suggests that European plaice, common dab and brill could be the most affected flatfish species,  
33 yet with some important local disparities across the North Sea. Consequently, the study represents a first  
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  
48 needs covered by renewables by 2020 (Renewable Energy Directive 2009/28/EC). In this context, the  
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).

54 Several studies have highlighted the effects of OWFs during the construction, operation and  
55 decommissioning phases (Petersen and Malm, 2006; Bergström *et al.*, 2014). While impacts relating to  
56 the construction phase are significant, they occur over a relatively short time span (Vaissière *et al.*,  
57 2014). Given the short time span involved, Wilhelmsson (2010) suggested that the perturbation is most  
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  
61 local hydrodynamic conditions (Broström, 2008). Major effects are linked to the introduction of hard  
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  
65 activities. A reduction in the deployment of towed fishing gear decreases the disturbance of benthic  
66 communities and may facilitate the recovery of previously disturbed communities (Leonhard *et al.*,  
67 2011; Lindeboom *et al.*, 2011; Wilhelmsson and Langhammer, 2014), creating new opportunities for  
68 organisms such as fish.

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

72 Wilhelmsson and Langhammer, 2014) and an increase in food provision (Pike and Lindquist, 1994; Fabi  
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.*,  
80 2017) and illustrated by an apparent size increase of European plaice (*Pleuronectes platessa*) in Belgian  
81 OWFs (Vandendriessche *et al.*, 2015). Furthermore, general increases in flatfish density have been  
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).

85 Fisheries management requires an understanding of the present and prediction of the future state of the  
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  
89 spillover effect can be either positive as in the case of marine protected area (Stobart *et al.*, 2009;  
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  
94 species-specific population dynamics.

95 In this context, North Sea flatfishes form an interesting group of species to model. In addition to their  
96 high economic value, flatfishes have a complex benthic-pelagic life cycle spanning broad geographical  
97 scales. There is high potential for interaction with OWFs during their different life stages, each of which  
98 involving spatially distinct habitats. During the adult phase, despite differences among species, most  
99 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  
101 and spawning grounds are located at different sites. Feeding grounds with increased macrobenthic  
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  
110 fish species (Houde, 2008; Cury *et al.*, 2014). Finally spawning grounds, due to their role in connectivity  
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  
113 recruitment constraints at the nursery grounds. In the present study, a model is used to investigate how  
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  
117 dynamics. The general aim of this study represents a first step to quantify the potential impact of OWFs  
118 on population dynamics. The specific aims are to assess (1) the proportion of overlap between spawning  
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 **Research strategy**

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

128 populations. The use of biophysical models is considered a valid methodology to study connectivity and  
129 settlement of early pelagic life stages in the open ocean for two reasons (Miller, 2007; Pineda *et al.*,  
130 2007; Cowen and Sponaugle, 2009). First, a direct observation of fish eggs and larvae trajectories is  
131 difficult in the open ocean and secondly, direct or indirect tagging such as genetics or otolith  
132 microchemistry have a limited power to spatially track fish recruits in a well-mixed sea such as the  
133 North Sea. For the present purpose, the Lagrangian larval transport model LARVAE&CO (Lacroix *et al.*,  
134 2013), resulting from the coupling between a hydrodynamical model and an Individual-Based Model  
135 (IBM), was used to simulate the dispersal of early life stages of flatfish. This model has shown to explain  
136 a significant part (31%) of recruitment variability of sole in the North Sea (Lacroix *et al.*, 2013). The  
137 simulations were carried out for a 10-year period (1997-2006), in order to span most of the year-to-year  
138 variability over the typical timescale of the North Atlantic Oscillation (NAO) cycle (Berglund *et al.*,  
139 2012).

140

#### 141 **Study area**

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

149

#### 150 **Species of interest**

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

154 Hereafter, common sole, common dab, European flounder and European plaice will be referred to as  
155 sole, 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  
158 2), which impact larval drift (Cowen *et al.*, 2007; Pineda *et al.*, 2007). Nursery grounds are mostly  
159 located in shallow coastal waters associated with soft sediments. Nursery grounds are species-specific,  
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  
162 geographically separated nurseries in the United Kingdom (Norfolk and Thames estuary). In addition,  
163 the Dogger Bank, which is an important offshore nursery for dab and plaice, was included in the Norfolk  
164 nursery ground (Figure 3). More details on spawning grounds and nursery grounds for the six species  
165 can be found in the supplementary material.

166

## 167 **Modelling of the early life stage**

### 168 *The hydrodynamic model*

169 The 3D hydrodynamic NOS (North Sea) model, based on the COHERENS model (Luyten *et al.*, 1999),  
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  $\sigma$ -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 20x20 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  
178 the Royal Meteorological Institute of Belgium based on the analyzed/forecast data of the UK Met Office  
179 Global Atmospheric Model (Hi\_Res; Walters *et al.*, 2017). Details about the model implementation can  
180 be found in Savina *et al.* (2010) and Lacroix *et al.* (2013).

181



182 *Individual-based model*

183 *xxx*

184 The Lagrangian larval transport model LARVAE&CO (Lacroix et al., 2013) was structured in four  
185 different stages representing flatfish life stages from eggs to metamorphosis (eggs, yolk-sac larvae, first-  
186 feeding larvae and metamorphosis larvae). Each stage has a species-specific parameterisation in terms  
187 of larval duration and behaviour (*in casu* vertical migration). Spawning grounds (Figure 2) and periods  
188 are also species-specific. The parameterisation 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  
198 spawning grounds and (planned and existing) OWFs is consequently expected to show a one to one  
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  
202 relative contribution of settlers originating from OWFs to the total number of settlers in a given  
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

208

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  
 219 grounds for the period 1997-2006 (Table 1 and Figure 4). Dab showed the highest proportion of settlers  
 220 originating from OWFs compared to the other species (16.1%). For brill and plaice this proportion was  
 221 lower while turbot, flounder and sole showed the lowest level of larval arrivals from OWFs (about 2%  
 222 of the settlers).

223

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

227

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

---

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  
233 from OWFs. The NI, Ge and No nurseries were also affected (2.6%, 1.4% and 3.9% from OWFs,  
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  
236 5% of the settlers coming from OWFs and less than 1.5% for other spawning grounds. For dab, OWF  
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 NI and Tha the number of settlers from OWFs  
241 was important (5% and 4%, respectively), but limited for Be and Fr (2% and <1%, respectively).  
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  
244 nursery in 1997 and 2001 (13% and 29% from OWFs, respectively). NI was the most affected nursery  
245 ground for this species (on average 6%).

246

247

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

249 The inflow of settlers originating from OWFs varied between years (Table 1). In addition to the  
250 year-to-year variability, the model also predicted spatial heterogeneity (Figure 5). All nursery  
251 grounds were predicted to be prone to OWFs influences, but the impact is likely to differ among

252 the nursery grounds, the species, and the origin of settlers. For the French nursery ground, two  
253 species presented more than 0.5% of arrivals from OWFs: dab from South UK OWFs (8.5%)  
254 and turbot from French OWFs (0.5%). The proportion of arrivals from OWFs at the Belgian  
255 nursery ground was limited compared to the other nurseries (less than 0.5% for all species,  
256 except for flounder and plaice, for which the proportion reached 4.5% and less than 2%  
257 respectively) and mainly from local OWFs (BE\_NL). In the Dutch nursery ground, brill and  
258 flounder are likely to be most prone to OWFs influence, with 8% and 6%, respectively. The  
259 settlement of dab was limited. For most species, the main treat of impact comes from the  
260 Belgian and Dutch OWFs, except for flounder for which Dutch OWFs imported the majority  
261 of larvae originating from an OWF. The German nursery ground displayed a relatively high  
262 proportion of settlers from OWFs (more than 5% for brill, dab and plaice). The origin of the  
263 settlers also revealed a strong disparity between species in terms of OWFs contribution.  
264 Germany 1 OWFs was the major contributor for sole, turbot, brill and dab, and to a lesser extent  
265 a contributor for plaice. In the case of dab, there was also more than 1% of input from East UK,  
266 NL and Belgium-Netherlands OWFs. For plaice, most of the arrivals was due to East UK,  
267 Germany 1 and NL OWFs, with Belgium-Netherlands OWFs playing an important role. In the  
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  
270 to a lesser extent for plaice. Brill, sole, turbot and plaice were strongly influenced by East UK  
271 OWFs. Finally, the predicted arrivals from OWFs at the Norfolk nursery ground were  
272 considerable for dab (more than 30%), and relatively important for plaice (about 10%). East  
273 UK OWFs was the main contributor for brill, sole and turbot. North-East UK 1 OWFs played  
274 an important role in the case of dab and plaice. OWFs located further offshore or close to the  
275 North boundary of the domain (North-East UK 1, North-East UK 2 and Germany 2) had a  
276 limited impact in the Southern North Sea at the notable exception of Norfolk for East UK 1.

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

282

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

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

283

284

## 285 **Discussion**

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

293

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  
308 overlap is not directly related to recruitment as there is no linear relation between spawning and  
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.

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

320 of the settlers originated from OWFs). The higher proportion of e percentage of overlap than settlement  
321 indicates that OWFs will impact mainly areas where the probability of reproductive success is low for  
322 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  
329 addition to the interannual variability at the regional scale, the model predicted strong variations at the  
330 local scale. The model helps to detect the nursery grounds that will most likely be impacted by the  
331 introduction of OWFs. The nursery grounds at the German Bight, Norfolk and Thames estuary might  
332 be particularly affected, while the number of settlers originating from OWFs would be more limited at  
333 the Belgian nursery. However, there is interannual variability in the connectivity between OWFs and  
334 nurseries, which can be substantial in some cases (e.g. flounder in the Belgian nursery, for which the  
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; Erfteimeijer *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*

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

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

353

### 354 *Biological implications*

355 The implementation of OWFs could impact flatfish population owing to the expected increase of the  
356 number of eggs spawned inside, due to the cue that suggests an increase in size, biomass or density of  
357 fish in OWF areas (Walton, 1982; Bergström *et al.*, 2013; Stenberg *et al.*, 2015). For marine fish, the  
358 choice of spawning grounds is constrained both by ecological and evolutionary processes (Munk *et al.*,  
359 2009; Ciannelli *et al.*, 2015). In addition to changes in the quantity of eggs produced in OWFs, spawning  
360 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,  
362 the length of the spawning season, fertilisation rate, and (post)larval survival (e.g. Chambers and  
363 Leggett, 1992; Rijnsdorp and Vingerhoed, 1994; Butts and Litvak, 2007; Donelson *et al.*, 2009; Morais  
364 *et al.*, 2014). Adult condition might be influenced by altered environmental quality consecutive to the  
365 implementation of OWFs due to the change in species distribution and introduction of hard substrate,  
366 which could affect food availability or carrying capacity, and so eggs production and recruitment  
367 (Marshall *et al.*, 1999; van der Veer *et al.*, 2003, 2015). Thus, it may be also interesting to focus on the  
368 impact of OWFs on the feeding grounds, as they may have an impact on fish condition, and hence  
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.

371 Nurseries play an important role in population dynamics of flatfish (Nash and Geffen, 2000). After  
372 metamorphosis, most larvae settle in shallow coastal nurseries, which most likely limits the direct impact



373 of OWFs on juveniles. However, the interspecific difference in the number of settlers could also affect  
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  
376 Leeuwen 1992; Van Der Veer *et al.* 2000; Le Pape and Bonhommeau 2015). In addition, environmental  
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  
385 the establishment of marine protected areas (Shipp, 2003). However, some studies showed that spatial  
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  
389 species could be dependent of their exploitation level, which means that target species in the North Sea  
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*

398 The model excluded several sources of variability in larval survival related to trophodynamics, such as  
399 prey abundance and predation (Peck and Hufnagl, 2012). The observed increase in abundance of filter

400 feeders in OWFs could lead to additional uncertainty in larval survival. In addition, a previous study  
401 (Lacroix *et al.*, 2018) based on the same model as the one used here, showed how climate change could  
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  
404 OWFs on fish density and distribution should be studied *in situ* due to expected knock-on effects in  
405 settlement at nurseries and at population level. Once the magnitude of OWF impact on egg production  
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  
412 European plaice, common dab and brill could be the most affected flatfish species, yet with some  
413 important local disparities across the North Sea. Our results predicted interspecific differences resulting  
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  
416 to be affected differently across the North Sea. Survey to assess the specific effect of OWFs on the  
417 different species, especially on eggs production, would help to further understand the potential impact  
418 of the presence of OWFs on flatfish population. Overall, our study represents a first step towards the  
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 Willstead *et al.* (2017).

422

423

## 424 **Acknowledgements**

425 This research was funded by the B-FishConnect research project (G.0702.13N) and the  
426 Scientific Research Network ‘Eco-evolutionary dynamics in natural and anthropogenic  
427 communities’ (grant W0.037.10N), both funded by the Research Fund - Flanders (Belgium).  
428 We thank two anonymous reviewers for their constructive comments.

429

430

431

## 432 **References**

433 Abecasis, D., Afonso, P., and Erzini, K. 2014. Can small MPAs protect local populations of a coastal  
434 flatfish, *Solea senegalensis*? *Fisheries Management and Ecology*, 21: 175–185.

435 Ashley, M. C. C., Mangi, S. C. C., and Rodwell, L. D. D. 2014. The potential of offshore windfarms to  
436 act as marine protected areas – A systematic review of current evidence. *Marine Policy*, 45: 301–  
437 309.

438 Berglund, M., Nilsson Jacobi, M., and Jonsson, P. R. 2012. Optimal selection of marine protected  
439 areas based on connectivity and habitat quality. *Ecological Modelling*, 240: 105–112.

440 Bergström, L., Sundqvist, F., and Bergström, U. 2013. Effects of an offshore wind farm on temporal  
441 and spatial patterns in the demersal fish community. *Marine Ecology Progress Series*, 485: 199–  
442 210.

443 Bergström, L., Kautsky, L., Malm, T., Rosenberg, R., Wahlberg, M., Åstrand Capetillo, N., and  
444 Wilhelmsson, D. 2014. Effects of offshore wind farms on marine wildlife—a generalized impact  
445 assessment. *Environmental Research Letters*, 9: 034012. IOP Publishing.

446 Bohnsack, J. A. 1989. Are high densities of fishes at artificial reefs the results of habitat limitation or  
447 behavioural preference? *Bulletin of Marine Science*, 44: 631–645.

448 Bolle, L. J., Dickey-Collas, M., Van Beek, J. K. L., Erfemeijer, P. L. A., Witte, J. I., Van Der Veer,  
449 H. W., and Rijnsdorp, A. D. 2009. Variability in transport of fish eggs and larvae. III. Effects of

450 hydrodynamics and larval behaviour on recruitment in plaice. *Marine Ecology Progress Series*,  
451 390: 195–211.

452 Broström, G. 2008. On the influence of large wind farms on the upper ocean circulation. *Journal of*  
453 *Marine Systems*, 74: 585–591. Elsevier.

454 Butts, I. A. E., and Litvak, M. K. 2007. Parental and stock effects on larval growth and survival to  
455 metamorphosis in winter flounder (*Pseudopleuronectes americanus*). *Aquaculture*, 269: 339–  
456 348. Elsevier.

457 Cabral, H. N., Vasconcelos, R., Vinagre, C., França, S., Fonseca, V., Maia, A., Reis-Santos, P., *et al.*  
458 2007. Relative importance of estuarine flatfish nurseries along the Portuguese coast. *Journal of*  
459 *Sea Research*, 57: 209–217. Elsevier.

460 Chambers, R. C., and Leggett, W. C. 1992. Possible causes and consequences of variation in age and  
461 size at metamorphosis in flatfishes (pleuronectiformes): An analysis at the individual, population,  
462 and species levels. *Netherlands Journal of Sea Research*, 29: 7–24. Elsevier.

463 Christensen, A., Daewel, U., Jensen, H., Mosegaard, H., St John, M., and Schrum, C. 2007.  
464 Hydrodynamic backtracking of fish larvae by individual-based modelling. *Marine Ecology*  
465 *Progress Series*, 347: 221–232.

466 Ciannelli, L., Bailey, K., and Olsen, E. M. 2015. Evolutionary and ecological constraints of fish  
467 spawning habitats. *ICES Journal of Marine Science*, 72: 285–296. Oxford University Press.

468 Coates, D. A., Kapasakali, D.-A. A., Vincx, M., and Vanaverbeke, J. 2016. Short-term effects of  
469 fishery exclusion in offshore wind farms on macrofaunal communities in the Belgian part of the  
470 North Sea. *Fisheries Research*, 179: 131–138. Elsevier.

471 Cowen, R. K., and Sponaugle, S. 2009. Larval Dispersal and Marine Population Connectivity. *Annual*  
472 *Review of Marine Science*, 1: 443–466. Annual Reviews .

473 Cowen, R. K. R. K. G., Gawarkiewicz, G., Pineda, J., Thorrold, S. R., and Werner, F. E. 2007.  
474 Population Connectivity in Marine Systems: An Overview. *Oceanography*, 20: 14–21.

- 475 Cury, P., Fromentin, J.-M., Figuet, S., and Bonhommeau, S. 2014. Resolving Hjort's Dilemma: How  
476 Is Recruitment Related to Spawning Stock Biomass in Marine Fish? *Oceanography*, 27: 42–47.
- 477 De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., and Degraer, S. 2015. Succession and seasonal  
478 dynamics of the epifauna community on offshore wind farm foundations and their role as  
479 stepping stones for non-indigenous species. *Hydrobiologia*, 756: 37–50. Springer International  
480 Publishing.
- 481 Donelson, J. M., Munday, P. L., and McCormick, M. I. 2009. Parental effects on offspring life  
482 histories: when are they important? *Biology letters*, 5: 262–5. The Royal Society.
- 483 Erftemeijer, P. L. A., Van Beek, J. K. L., Bolle, L. J., Dickey-Collas, M., and Los, H. F. J. 2009.  
484 Variability in transport of fish eggs and larvae. I. Modelling the effects of coastal reclamation.  
485 *Marine Ecology Progress Series*, 390: 167–181.
- 486 Fabi, G., Manoukian, S., and Spagnolo, A. 2006. Feeding behaviour of three common fishes at an  
487 artificial reef in the northern Adriatic Sea. *Bulletin of Marine Science*, 78: 39–56. University of  
488 Miami - Rosenstiel School of Marine and Atmospheric Science.
- 489 Florin, A. B., Bergström, U., Ustups, D., Lundström, K., and Jonsson, P. R. 2013. Effects of a large  
490 northern European no-take zone on flatfish populationsa. *Journal of Fish Biology*, 83: 939–962.  
491 Blackwell Publishing Ltd.
- 492 Gibson, R. N. 1997. Behaviour and the distribution of flatfishes. *In Journal of Sea Research*, pp. 241–  
493 256. Elsevier.
- 494 Gill, A. B., Bartlett, M., and Thomsen, F. 2012. Potential interactions between diadromous fishes of  
495 U.K. conservation importance and the electromagnetic fields and subsea noise from marine  
496 renewable energy developments. *Journal of Fish Biology*, 81: 664–695.
- 497 Houde, E. D. 2008. Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science*,  
498 41: 53–70.
- 499 Hufnagl, M., Peck, M. A., Nash, R. D. M., Pohlmann, T., and Rijnsdorp, A. D. 2013. Changes in

500 potential North Sea spawning grounds of plaice (*Pleuronectes platessa* L.) based on early life  
501 stage connectivity to nursery habitats. *Journal of Sea Research*, 84: 26–39.

502 Hunter, E., Metcalfe, J. D., and Reynolds, J. D. 2003. Migration route and spawning area fidelity by  
503 North Sea plaice. *Proceedings. Biological sciences / The Royal Society*, 270: 2097–2103.

504 Juanes, F. 2007. Role of habitat in mediating mortality during the post-settlement transition phase of  
505 temperate marine fishes. Blackwell Publishing Ltd.

506 Kalaydjian, R., and Girard, S. 2017. Données économiques maritimes françaises 2016. Brest, France :  
507 Ifremer.

508 Lacroix, G., Maes, G. E., Bolle, L. J., and Volckaert, F. A. M. 2013. Modelling dispersal dynamics of  
509 the early life stages of a marine flatfish (*Solea solea* L.). *Journal of Sea Research*, 84: 13–25.

510 Lacroix, G., Barbut, L., and Volckaert, F. A. M. 2018. Complex effect of projected sea temperature  
511 and wind change on flatfish dispersal. *Global Change Biology*, 24: 85–100.

512 Langhamer, O. 2012. Artificial Reef Effect in relation to Offshore Renewable Energy Conversion:  
513 State of the Art. *The Scientific World Journal*, 2012: 1–8. Hindawi.

514 Le Pape, O., and Bonhommeau, S. 2015. The food limitation hypothesis for juvenile marine fish. *Fish  
515 and Fisheries*, 16: 373–398.

516 Leitão, F., Santos, M. N., and Monteiro, C. C. 2007. Contribution of artificial reefs to the diet of the  
517 white sea bream (*Diplodus sargus*). *ICES Journal of Marine Science*, 64: 473–478.

518 Leitão, F., Santos, M. N., Erzini, K., and Monteiro, C. C. 2008. Fish assemblages and rapid  
519 colonization after enlargement of an artificial reef off the Algarve coast (Southern Portugal).  
520 *Marine Ecology*, 29: 435–448. Wiley/Blackwell (10.1111).

521 Leitão, F., Santos, M. N., Erzini, K., and Monteiro, C. C. 2009. *Diplodus* spp. assemblages on  
522 artificial reefs: Importance for near shore fisheries. *Fisheries Management and Ecology*, 16: 88–  
523 99.

524 Leonhard, S., Stenberg, C., and Støttrup, J. 2011. Effect of the Horns Rev 1 Offshore Wind Farm on  
525 Fish Communities Follow-up Seven Years after Construction. DTU Aqua Report: 99 p.

526 Lindeboom, H., Degraer, S., Dannheim, J., Gill, A. B., and Wilhelmsson, D. 2015. Offshore wind park  
527 monitoring programmes, lessons learned and recommendations for the future. *Hydrobiologia*,  
528 756: 169–180. Springer International Publishing.

529 Lindeboom, H. J., Kouwenhoven, H. J., Bergman, M. J. N., Bouma, S., Brasseur, S., Daan, R., Fijn, R.  
530 C., *et al.* 2011. Short-term ecological effects of an offshore wind farm in the Dutch coastal zone;  
531 A compilation. *Environmental Research Letters*, 6: 035101. IOP Publishing.

532 Loewe, P. 2003. Weekly North Sea SST Analyses since 1968, in: *Hydrographie*, O.d.a.h.b.f.S.u.  
533 (Ed.), D-20305 Hamburg, P.O. Box 301220, Germany.

534 Luyten, P. J., Jones, J. E., Proctor, R., Tabor, A., Tett, P., and Wild-Allen, K. 1999. COHERENS a  
535 coupled hydrodynamical–ecological model for regional and shelf seas: user documentation.  
536 Belgium. 911 pp pp.

537 Marshall, C. T., Yaragina, N. A., Lambert, Y., and Kjesbu, O. S. 1999. Total lipid energy as a proxy  
538 for total egg production by fish stocks. *Nature*, 402: 288–290. Nature Publishing Group.

539 Miller, T. J. 2007. Contribution of individual-based coupled physical-biological models to  
540 understanding recruitment in marine fish populations. *Marine Ecology Progress Series*, 347:  
541 127–138.

542 Morais, S., Mendes, A. C., Castanheira, M. F., Coutinho, J., Bandarra, N., Dias, J., Conceição, L. E.  
543 C., *et al.* 2014. New formulated diets for *Solea senegalensis* broodstock: Effects of parental  
544 nutrition on biosynthesis of long-chain polyunsaturated fatty acids and performance of early  
545 larval stages and juvenile fish. *Aquaculture*, 432: 374–382. Elsevier.

546 Munk, P., Fox, C. J., Bolle, L. J., Van Damme, C. J. G., Fossum, P., and Kraus, G. 2009. Spawning of  
547 North Sea fishes linked to hydrographic features. *Fisheries Oceanography*, 18: 458–469.

548 Nash, R. D. M., and Geffen, A. J. 2000. The influence of nursery ground processes in the

549 determination of year-class strength in juvenile plaice *Pleuronectes platessa* L. in Port Erin Bay,  
550 Irish Sea. *Journal of Sea Research*, 44: 101–110.

551 Nedwell, J., and Howell, D. 2004. A review of offshore windfarm related underwater noise sources.  
552 Cowrie Rep: 1–63.

553 OECD. 2016. *The Ocean Economy in 2030*. OECD Publishing.

554 OSPAR Commission. 2014. OSPAR database on offshore windfarms. 2013 UPDATE (revised in  
555 2014). OSPAR Biodiversity Series: 17 pp.

556 Peck, M. A., and Hufnagl, M. 2012. Can IBMs tell us why most larvae die in the sea? Model  
557 sensitivities and scenarios reveal research needs. *Journal of Marine Systems*, 93: 77–93.

558 Perry, A. L., Low, P. J., Ellis, J. R., Reynolds, J. D., Allison L. Perry, Low, P. J., Ellis, J. R., *et al.*  
559 2005. Climate Change and Distribution Shifts in Marine Fishes. *Science*, 308: 1912–1915.

560 Petersen, J. K., and Malm, T. 2006. Offshore Windmill Farms: Threats to or Possibilities for the  
561 Marine Environment. *AMBIO: A Journal of the Human Environment*, 35: 75–80.

562 Pickering, H., and Whitmarsh, D. 1997. Artificial reefs and fisheries exploitation: A review of the  
563 ‘attraction versus production’ debate, the influence of design and its significance for policy.  
564 *Fisheries Research*, 31: 39–59. Elsevier.

565 Pike, L. A., and Lindquist, D. G. 1994. Feeding Ecology of Spottail Pinfish (*Diplodus holbrooki*)  
566 from an Artificial and Natural Reef in Onslow Bay, North-Carolina. *Bulletin of Marine Science*,  
567 55: 363–374. University of Miami - Rosenstiel School of Marine and Atmospheric Science.

568 Pineda, J., Hare, J., and Sponaugle, S. 2007. Larval Transport and Dispersal in the Coastal Ocean and  
569 Consequences for Population Connectivity. *Oceanography*, 20: 22–39.

570 Raoux, A., Tecchio, S., Pezy, J. P., Lassalle, G., Degraer, S., Wilhelmsson, D., Cachera, M., *et al.*  
571 2017. Benthic and fish aggregation inside an offshore wind farm: Which effects on the trophic  
572 web functioning? *Ecological Indicators*, 72: 33–46. Elsevier.



573 Reubens, J. T., De Rijcke, M., Degraer, S., and Vincx, M. 2014. Diel variation in feeding and  
574 movement patterns of juvenile Atlantic cod at offshore wind farms. *Journal of Sea Research*, 85:  
575 214–221. Elsevier.

576 Rijnsdorp, A. D., Van Leeuwen, P. I., and Leeuwen, P. I. van. 1992a. Density-dependent and  
577 independent changes in somatic growth of female North Sea plaice *Pleuronectes platessa*  
578 between 1930 and 1985 as revealed by back-calculation of otoliths. Inter-Research Science  
579 Center.

580 Rijnsdorp, A. D., and Vingerhoed, B. 1994. The ecological significance of geographical and seasonal  
581 differences in egg size in sole *Solea solea* (L.). *Netherlands Journal of Sea Research*, 32: 255–  
582 270.

583 Rijnsdorp, A. D. D., Van Beek, F. A. A., Flatman, S., Millner, R. M. M., Riley, J. D. D., Giret, M.,  
584 and De Clerck, R. 1992b. Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic.  
585 *Netherlands Journal of Sea Research*, 29: 173–192. Elsevier.

586 Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., and Le Pape, O. 2010. Effect of nursery  
587 habitat degradation on flatfish population: Application to *Solea solea* in the Eastern Channel  
588 (Western Europe). *Journal of Sea Research*, 64: 34–44. Elsevier.

589 Rogers, S. I., Rijnsdorp, A. D., Damm, U., and Vanhee, W. 1998. Demersal fish populations in the  
590 coastal waters of the UK and continental NW Europe from beam trawl survey data collected  
591 from 1990 to 1995. *Journal of Sea Research*, 39: 79–102.

592 Rouse, S., Kafas, A., Catarino, R., and Peter, H. 2018. Commercial fisheries interactions with oil and  
593 gas pipelines in the North Sea: Considerations for decommissioning. *ICES Journal of Marine*  
594 *Science*, 75: 279–286.

595 Savina, M., Lacroix, G., and Ruddick, K. 2010. Modelling the transport of common sole larvae in the  
596 southern North Sea: Influence of hydrodynamics and larval vertical movements. *Journal of*  
597 *Marine Systems*, 81: 86–98.

598 Shipp, R. L. 2003. A Perspective on Marine Reserves as a Fishery Management Tool. *Fisheries*, 28:  
599 10–21.

600 Stenberg, C., Støttrup, J. G., Van Deurs, M., Berg, C. W., Dinesen, G. E., Mosegaard, H., Grome, T.  
601 M., *et al.* 2015. Long-term effects of an offshore wind farm in the North Sea on fish  
602 communities. *Marine Ecology Progress Series*, 528: 257–265.

603 Stobart, B., Warwick, R., González, C., Mallol, S., Díaz, D., Reñones, O., and Goñi, R. 2009. Long-  
604 term and spillover effects of a marine protected area on an exploited fish community. *Marine*  
605 *Ecology Progress Series*, 384: 47–60.

606 Turrell, W. R. 1992. New hypotheses concerning the circulation of the northern north sea and its  
607 relation to north sea fish stock recruitment. *ICES Journal of Marine Science*, 49: 107–123.  
608 Oxford University Press.

609 Vaissière, A. C., Levrel, H., Pioch, S., and Carlier, A. 2014. Biodiversity offsets for offshore wind  
610 farm projects: The current situation in Europe. *Marine Policy*, 48: 172–183. Pergamon.

611 van der Veer, H. W. 1986. Immigration, settlement, and density-dependent mortality of a larval and  
612 early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea.  
613 *Marine Ecology Progress Series*, 29: 223–236.

614 van der Veer, H. W., and Witte, J. 1999. Year-class strength of plaice *Pleuronectes platessa* in the  
615 southern bight of the North Sea: A validation and analysis of the inverse relationship with winter  
616 seawater temperature. *Marine Ecology Progress Series*, 184: 245–257.

617 van der Veer, H. W., Berghahn, R., Miller, J. M., and Rijnsdorp, A. D. 2000. Recruitment in flatfish,  
618 with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia. *ICES*  
619 *Journal of Marine Science*, 57: 202–215. Oxford University Press.

620 van der Veer, H. W., Kooijman, S. A. L. ., and van der Meer, J. 2003. Body size scaling relationships  
621 in flatfish as predicted by Dynamic Energy Budgets (DEB theory): implications for recruitment.  
622 *Journal of Sea Research*, 50: 257–272. Elsevier.

623 van der Veer, H. W., Freitas, V., and Leggett, W. C. 2015. Recruitment level and variability. *In*  
624 Flatfishes: Biology and Exploitation: Second Edition, pp. 185–206. John Wiley & Sons, Ltd,  
625 Chichester, UK.

626 van Overzee, H. M. J., and Rijnsdorp, A. D. 2014, March 29. Effects of fishing during the spawning  
627 period: implications for sustainable management. Springer International Publishing.

628 Vandendriessche, S., Derweduwen, J., and Hostens, K. 2015. Equivocal effects of offshore wind farms  
629 in Belgium on soft substrate epibenthos and fish assemblages. *Hydrobiologia*, 756: 19–35.  
630 Springer International Publishing.

631 Visser, A. W. 1997. Using random walk models to simulate the vertical distribution of particles in a  
632 turbulent water column. *Marine Ecology Progress Series*, 158: 275–281.

633 Wahlberg, M., and Westerberg, H. 2005. Hearing in fish and their reactions to sound from offshore  
634 wind farms. *Mar. Ecol. Prog. Ser.*, 288: 295–309. Inter-Research Science Center.

635 Walton, J. M. 1982. the Effects of an Artificial Reef on Resident Flatfish Populations. *Marine*  
636 *Fisheries Review*, 44: 45–48.

637 Wilhelmsson, D. 2010. Greening Blue Energy: Identifying and managing the biodiversity risks and  
638 opportunities of off shore renewable energy. IUCN. 1-104 pp.

639 Wilhelmsson, D., and Langhammer, O. 2014. The influence of fisheries exclusion and addition of hard  
640 substrata on fish and crustaceans. *In* *Humanity and the Seas: Marine Renewable Energy and*  
641 *Environmental Interactions*, pp. 49–60. Springer, Dordrecht.

642 Willstead, E., Gill, A. B., Birchenough, S. N. R., and Jude, S. 2017. Assessing the cumulative  
643 environmental effects of marine renewable energy developments: Establishing common ground.  
644 Elsevier.

645