Ecological Indicators
January 2017, Volume 72 Pages 33-46
http://dx.doi.org/10.1016/j.ecolind.2016.07.037
http://archimer.ifremer.fr/doc/00347/45843/

Benthic and fish aggregation inside an offshore wind farm: Which effects on the trophic web functioning?

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Abstract :

As part of the energy transition, the French government is planning the construction of three offshore wind farms in Normandy (Bay of Seine and eastern part of the English Channel, north-western France) in the next years. These offshore wind farms will be integrated into an ecosystem already facing multiple anthropogenic disturbances such as maritime transport, fisheries, oyster and mussel farming, and sediment dredging. Currently no integrated, ecosystem-based study on the effects of the construction and exploitation of offshore wind farms exists, where biological approaches generally focused on the conservation of some valuable species or groups of species. Complementary trophic web modelling tools were applied to the Bay of Seine ecosystem (to the 50 km2 area covered by the wind farm) to analyse the potential impacts of benthos and fish aggregation caused by the introduction of additional hard substrates from the piles and the turbine scour protections. An Ecopath ecosystem model composed of 37 compartments, from phytoplankton to seabirds, was built to describe the situation "before" the construction of the wind farm. Then, an Ecosim projection over 30 years was performed after increasing the biomass of targeted benthic and fish compartments. Ecological Network Analysis (ENA) indices were calculated for the two periods, "before" and "after", to compare network functioning and the overall structural properties of the food web. Our main results showed (1) that the total ecosystem activity, the overall system omnivory (proportion of generalist feeders), and the recycling increased after the construction of the wind farm; (2) that higher trophic levels such as piscivorous fish species, marine mammals, and seabirds responded positively to the aggregation of biomass on piles and turbine scour protections; and (3) a change in keystone groups after the construction towards more structuring and dominant compartments. Nonetheless, these changes could be considered as limited impacts of the wind farm installation on this coastal trophic web structure and functioning.

Highlights

► Ecopath models before/after an offshore wind farm were built. ► Possible reef effect would increase total system biomass by 55%. ► Bivalves build-up would lead to a food web dominated by detritivory. ► Benthos and keystone fish biomass increases attracted apex predators.

Keywords : Marine renewable energies, Reef effect, Wind farm, Ecopath with Ecosim, Ecosystem-based approach

1. INTRODUCTION

Humanity's ever growing energy demands have translated into an increase in fossil fuel combustion and greenhouse gases emissions and, consequently, into global climate changes (OSPAR, 2008; IPCC, 2014). A new focus on renewable energy source research and development arose during the last decades to counter this trend. The European Union (EU) has set a target of 20% of energetic consumption derived from renewable energy sources by 2020 (Directive 2009/28/EC). With more than 11 million km^2 of waters under its jurisdiction, France holds a huge natural potential for marine renewable energy (MEDDE 2011). Currently, the construction of six offshore wind farms is planned in metropolitan France. Among them, three should be built in the central-eastern part of the English Channel: the Courseulles-sur-mer (~50 km^2, 75 wind turbines), the Fécamp (~65 km^2, 83 wind turbines) and the Tréport (~67 km^2, 62 wind turbines) offshore wind farms. The implementation of this type of infrastructure is a challenge for developers from technical, legal, social, and environmental points of view. Indeed, these offshore wind farms will be integrated into ecosystems already subjected to a growing number of anthropogenic disturbances such as pollution, transport, fishing, aquaculture, aggregate extraction, or sediment dredging and deposit.

Concern about the potential environmental impacts generated by these new structures on marine ecosystems arose from this development (Lindeboom et al., 2011; Bailey et al., 2014). The exploration, construction, operation, and decommissioning of offshore wind farms can indeed be responsible for temporary and/or permanent impacts on marine ecosystems such as the destruction of seabed or the disturbance of fish and marine mammal populations (Shields et al., 2014; OSPAR, 2008; Mueller-Blenkle et al., 2010). During the construction phase, if special care is taken to protect rare habitats and spatial and temporal habitat use by sensitive species, effects can be kept relatively small or negligible (e.g. Wilhelmsson et al. 2010). During the operational phase, the anticipated and recorded disturbances caused by noise, vibrations and the electromagnetic fields are also in most cases considered to be of minor importance to the marine environment, at least to date (Westerberg et al., 2008; Petersen and Malm, 2006, Wilhelmsson et al. 2010). However, a noteworthy effect of the introduction of turbines with their associated scour protection is the creation of new habitats and shelters that will be immediately colonized by several marine species resulting in an additional source of food for higher trophic levels (Bergström et al., 2013). This effect, generally known as the "reef effect", is considered as one of the most important effect on the marine environment generated by the construction of offshore wind farms (Peterson and Malm, 2006; Langhamer, 2012; De Mesel et al., 2015). The reef effect has been described for epibenthic and demersal fauna as well as on bentho-pelagic fish (including commercial species) in the direct proximity of wind farm foundations (Wilhelmsson et al., 2006; Tougard et al., 2006; Wilhelmsson and Malm, 2008; Maar et al., 2009; Reubens et al., 2011; Leonhard et al., 2011; Lindeboom et al., 2011; Bergström et al., 2013; Reubens et al., 2013; Reubens et al., 2014; Degraer et al., 2014). The reef effect has also been demonstrated for other anthropogenic structures such as shipwrecks and oil platforms (Wolfson et al., 1979; Love et al., 1994, 1999; Wilhelmsson et al., 2006). The choice of material and the shape of the structures introduced in the marine environment both play an important role during the colonization process (e.g. Andersson et al., 2010). All these previous studies provide a vast amount of data on environmental effects at the species or community scales. However, the propagation of the reef effect at the ecosystem scale, impacting the structure and functioning of food webs remains unclear (Boehlert and Gill, 2010).

Until now, there is no holistic study on the effects of the construction and operation of offshore wind farms on an ecosystem taken as a whole. Here, we propose to develop a holistic view of offshore wind farm impacts on ecosystems functioning through the use of trophic web modelling tools. Our work will provide information on the food web change in response to the construction and operation of marine energy infrastructures, information which is essential to the sustainable development and management of renewable energy sources. The main feature of this work will be to propose a methodology that is complementary to what it is currently applied in Environmental Impact Assessments by using: (1) a holistic approach in which the ecosystem represents the management unit, (2) a functional perspective based on flows of energy circulating between ecosystem components, and (3) a high level of functional diversity to describe the food web.

Among the different existing modelling approaches, Ecopath with Ecosim (EwE) has been intensively developed and used over the last three decades and was applied on hundreds of aquatic ecosystems throughout the world (Polovina, 1984; Christensen and Walters, 2004; Christensen et al., 2008). This approach, in which all biotic components of the system are considered at the same time, provides measures of the ecosystem emergent properties through the calculation of Ecological Network Analysis (ENA) indices (Ulanowicz, 1986). These joint analyses have been frequently applied to coastal and marine systems to assess changes in their functioning in response to environmental perturbations (Ortiz and Wolff 2002, Rybarczyk et al., 2003; Patricio et al., 2006; Niquil et al., 2012; Tecchio et al., 2013, 2015). Some ENA indices, such as the redundancy, have also been linked to notions of stability (Christensen et al., 2005) such as the resilience of trophic webs to perturbations (Heymans et al., 2007). Finally, ENA indices have also been proposed as trophic descriptors of ecosystem health for the EU Marine Strategy Framework Directive (Dame and Christian 2007; Niquil et al., 2012; Rombouts et al., 2013; Niquil et al., 2014).

The objective of the present study was to model the potential impacts of the construction and operation of the Courseulles-sur-mer (southern part of the Bay of Seine along the Calvados coast) offshore wind farm on the local trophic-web functioning. Special attention was paid on how benthos and fish aggregation caused by the introduction of additional hard substrates from the piles and the scour protections might lead to the development of an artificial reef system, and also what the consequences on the food-web functioning could be. To analyse the impact of additionally available hard substrates, an Ecopath model was first built to describe the food web before the construction of the Courseulles-sur-mer offshore wind farm and then an Ecosim model was derived to project over the next 30 years the ecosystem evolution after the forced increase in biomass of some targeted benthic and fish compartments in relation to the wind farm construction. For this, observations of species changes in wind farm areas obtained through extensive literature searches were adapted to the Courseulles-sur-mer site based on expert knowledge. Two hypotheses regarding the food-web functioning were particularly investigated with Ecosim simulations: (i) a system dominated by mussels leads to a more detritivorous food web (Norling and Kautsky, 2008), and (ii) the increased biomass of benthic invertebrates and fish, as generated by the reef effect, would attract apex predators (Lindeboom et al., 2011; Henkel et al., 2014).This is, to our knowledge, the first attempt to study the potential impacts of the construction and operation of an offshore wind farm on the local trophic web structure and functioning using an integrated ecosystem modelling approach.

2. MATERIAL AND METHODS

2.1 Study area

The Bay of Seine, where the offshore wind farm will be built in the next years (from 2018) is located on the north-western French coast and opens onto the eastern English Channel (Fig. 1). The Bay of Seine forms an approximate quadrilateral of 5000 km², with a mean depth of about 20 m. The water depth never exceeds 35 m. The maximum tidal range is 7.5 m in the eastern part of the Bay near the mouth of the Seine estuary. Tidal currents average between 1 and 2 knots in the southern sector of the Bay, and their intensity gradually diminishes toward the eastern Bay of Seine (Salomon and Breton, 1991, 1993). The distribution of superficial sediments and benthic communities is strongly correlated to these currents (Gentil and Cabioch, 1997; Dauvin, 2015). There is an offshore-inshore gradient in the Bay, with the dominant sediment offshore generally consisting in pebbles, gravel and coarse sands and the sediment inshore in the coastal zones consisting mostly of fine sands and muddy fine sands (Dauvin et al., 2007, 2015). Benthic communities of the Bay of Seine are well described in terms of composition and spatial distribution (Dauvin and Ruellet, 2008) and were demonstrated to be good indicators of ecosystem health (Garcia, 2011). Coastal marine, estuarine and mixed systems along the French coasts are predicted to be high sensitive to climatic variations (Goberville et al., 2010). The Bay of Seine ecosystem is already submitted to multiple anthropogenic disturbances such as maritime traffic, fishing, and sediment dredging (Dauvin et al., 2004). All these features make it a system at the crossroad of various influences, central for studying cumulative impacts on the functioning of marine ecosystems.

2.2 Courseulles-sur-mer offshore wind farm project

The project is owned by "Eoliennes Offshore du Calvados", a subsidiary of Éolien Maritime France and wpd Offshore. EMF was allowed to operate the offshore wind farm off from Courseulles-sur-mer by the Ministerial Order of April 18th 2012. The proposed wind farm will be located 10 to 16km offshore from the coast of Calvados – Normandy. The depth range is 22-31 m at Lowest Astronomical Tide (LAT to be checked). The wind farm will have a total area of approximately 50 km^2 (Fig. 1). The wind farm will comprise 75 6MW turbines giving a combinated nameplate capacity of 450MW. The wind farm turbines will be connected via an interarray network of 33 kV AC cables which will link at one offshore transformer substation located within the wind farm. From this station power will be exported via two 225 kV AC marine cables. The turbines are supported by 7 m of diameter monopiles driven into the sea bed. The foot print of the 75 turbines foundation and of the converter station will be 0.158 km^2 or 0.03% of the overall wind farm area. Our work hypothesis was that scour protections will be installed around the 75 turbines and the converter station and 33% of the cables will be rock-dumped, thus the total additional surface would amount to 0.342 km^2, or 0.72% of the offshore wind farm area when considered in two dimensions. In calculating the biomasses changes we took into account the actual "foot print" of the new structure: while in terms of surface it will be low, the colonization of the structure will happen in three dimensions including the whole pillar. The production generated by the wind park would cover the average annual electricity consumption of approximately 630,000 people, i.e. around 40% of the inhabitants of the surrounding region of Normandy.

<Figure 1>

2.3 Presentation of the trophic modelling approach

The *Ecopath with Ecosim* (EwE) software (Polovina, 1984; Christensen and Walters, 2004; Christensen et al., 2008) was used to model the food web at the site of the construction of the future Courseulles-sur-mer offshore wind farm. Among the different EwE modules, Ecopath is designed to build a snapshot of the ecosystem functioning while Ecosim allows simulating its dynamic evolution through time. Ecopath is a mass-balance (i.e. neglecting year-to-year changes in biomass compared to flows), single-solution model (i.e. returning only one value per flow), that estimates fluxes between a set of established trophic compartments. Each compartment corresponds to a single species or a group of species similar in terms of predators, preys and of metabolic rates (i.e. trophic group). It is parameterised with biomasses (B, gC.m^{-2}), production over biomass ratios (P/B, year^{-1}), consumption over biomass ratios (Q/B, year^{-1}) and a diet matrix (DC= diet composition) which establishes the interactions between predators and preys in the ecosystem.

The parameterization of an Ecopath model is based on satisfying two equations. The first one (Eq. 1) describes the production for each compartment in the system as a function of the consumption ratio (Q/B) of its predators (j), the fishing mortality (Yi, gC.m^{-2}), the net migration (Ei; emigration – immigration, year^{-1}), the biomass accumulation (BAi, year^{-1}), and its natural mortality (1—EEi). EE corresponds to the Ecotrophic Efficiency or the proportion of biomass consumed in the system for each compartment in the system.

$$B\left(\frac{P}{B}\right)_i = \sum_j B_j \left(\frac{Q}{B}\right)_j DC_{ij} + Y_i + E_i + BA_i + B_i\left(\frac{P}{B}\right)_i (1 - EE_i) \qquad \text{(Eq. 1)}$$

The second equation (Eq. 2) describes the energy balance within a compartment.

$$Q_i = P_i + R_i + U_i \qquad \text{(Eq. 2)}$$

The energy balance of each group in equation 2 is assured by making consumption of the *i^th^* group (Qi) equal to the sum of its production (Pi), respiration (Ri, gC.m^{-2}), and excretion of unassimilated food (Ui).

2.4 Parameterisation of the Ecopath model describing the situation before the wind farm

The selection and aggregation of functional groups included in the Ecopath model was based on biological and ecological characteristics of the species such as their food preference, size, and commercial importance as well as on data availability. On this basis, 37 groups were retained (Table 1, Fig. 2), two of which were seabirds, four marine mammals, eighteen fish, nine invertebrates, one zooplankton, one primary producers, one bacteria, and one detritus group.

<Table 1>

<Figure 2>

2.4.1 Seabirds

Abundance data were collected from the 41 boat surveys conducted by the Normandy Ornithological Group (GONm) on a monthly basis, from January 2008 to December 2010 (Morel, 2013). The Bay of Seine is on the migration route and wintering area for many marine birds. Consequently, the proportion of prey captured outside the area was considered as imports in seabird diets. The species observed inside the implantation area of the future Courseulles-sur-mer offshore wind farm were grouped into two categories according to their main feeding strategies. The "Plunge and pursuit divers" were composed of northern gannets (*Sula basana)*, loon (*Gavia* sp.), auks (common mures *Uria aalge*, razorbills *Alca torda)*, cormorant (*Phalacrocorax carbo*), and scoters (black scoter *Melanitta nigra*, White-winged scoter *Melanitta fusca).* The "surface feeders" were all gulls (herring gulls *Larus argentatus,* common gull *Larus canus,* lesser-backed gulls *Larus fuscus*, and great black-backed gulls *Larus marinus).*

The mean body mass of these species were derived from Hunt et al. (2005). Conversion factors of 0.3 and 0.4 were used to convert wet weights into dry weights and then into carbon contents, respectively (Lassalle et al., 2011).

Daily consumption ratios were calculated according to the following empirical equation (Nilsson and Nilsson, 1976):

$$\text{Log}(R_c) = -0.293 + 0.85 * \log_{10}(\text{body mass}) \qquad \text{(Eq. 3)}$$

This value was then multiplied by 365 days and divided by the mean weight of the taxon to provide annual Q/B ratio in year^{-1}. The P/B ratio for the two functional groups was based on estimates published in Nelson (1979). For these two groups, the diet compositions were retrieved from literature (Hunt et al., 2005). The proportion of prey captured outside the area was considered as imports in their diet (see Table 2 in Appendix A).

2.4.2 Marine mammals

Abundance data for bottlenose dolphins *(Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*) were collected from aerial surveys from November 2011 to August 2012 (Martinez et al., 2014). Abundance for harbour seals (*Phoca vitulina*) and grey seals *(Halichoerus grypus)* were derived from telemetric surveys from 2007 to 2013 (Martinez et al., 2014).

For each species, the mean body weight was calculated according to its maximum body length (Trites and Pauly, 1998). To convert wet weights into carbon contents, a conversion factor of 0.1 was used (Bradford Grieve et al., 2003). To estimate the Q/B ratio, we used the metabolic rates and the daily consumption according to the empirical equations of Boyd (2002) and Spitz et al. (2010). The P/B ratios for these four species were taken from Christensen et al. (2009). Their diet compositions were defined according to Spitz et al. (2006). Based on the aerial surveys, marine mammal distributions cover large spatial scales far beyond the Bay of Seine limits. Consequently, the proportion of prey captured outside the area was considered as imports in their diet (see Table 2 in Appendix A).

2.4.3 Fish compartments

Abundance data for fish were collected from the GOV (“Grande Ouverture Verticale”= high opening) bottom-trawl survey conducted annually in October by IFREMER in the eastern English Channel and the south of the North Sea since 1988 (Channel Ground Fish Survey, CGFS). Data were averaged over 3 years (from 2010 to 2013). Fish were grouped into 6 functional groups: sharks and rays, gurnards, piscivorous, planktivorous, benthos feeders, and other flatfish. Moreover, mackerel (*Scomber scombrus*), European sea bass (*Dicentrarchus labrax)*, Atlantic cod (*Gadus morhua)*, whiting (*Merlangius merlangus*), Atlantic horse mackerel (*Trachurus trachurus*), pouting (*Trisopterus luscus*), poor cod (*Trisopterus minutus*), European pilchard (*Sardina pilchardus*), European sprat (*Sprattus sprattus*) sea bream (*Spondyliosoma cantharus*), common sole (*Solea solea*), and European plaice (*Pleuronectes platessa*) formed 12 single-species compartments. These 12 species are either commercial species or species known to be attracted by the reef effect. Therefore, they were not aggregated with the other compartments in order to see more in details the potential impact of the MRE.

Fish wet body weights (originally in kg km^{-2}) were converted to carbon contents using a conversion factor of 0.11 (Oguz et al., 2008). Q/B and P/B ratios were taken from Mackinson and Daskalov (2007). The diet compositions were retrieved from the literature (Cachera 2013). Landings data were obtained from the Fisheries Information System of IFREMER (http://sih.ifremer.fr/).

2.4.5 Invertebrate compartments

Cephalopods

Abundance data (in kg.km^{-2}) for cephalopods were also collected from the GOV bottom-trawl survey CGFS and averaged over 3 years (from 2010 to 2013). Cephalopods were divided into 2 groups: “Bentho-pelagic cephalopods” composed of *Loligo* sp. and *Allotheuthis* sp*.,* and “Benthic cephalopods” composed of *Sepia officinalis.*, Conversion factors of 0.192 and 0.402 were used to convert wet weights into dry weights and then into carbon contents, respectively (Brey et al., 2010). Q/B and P/B ratios were taken from Sanchez and Olaso (2004). Landings data were taken from the Fisheries Information System of IFREMER (http://sih.ifremer.fr/). Diet compositions were retrieved from the literature (De Pierrepont et al., 2005; Daly et al., 2001).

Benthic invertebrates

Benthic invertebrates were sampled with a 0.1 m² Day grab in June 2009. Species were grouped into 4 compartments: “predators”, “filter feeders”, “bivalves” and “deposit feeders”. Bivalves were not aggregated with the filter feeders to investigate in more details their importance in the functioning of the trophic web as well as to test the hypothesis of Norling and Kaustky (2008). In addition the above 4 groups, king scallop (*Pecten maximus*) was included as a single-species compartment given its economic value. Ash-free dry weights were converted to carbon contents using a conversion factor of 0.518 (Salonen et al., 1976 in Brey, 2001). P/B and Q/B were taken from Le Loc’h (2004) and Brey (2001), and diet compositions were taken from Rybarczyk and Elkaim (2003).

Suprabenthos

The suprabenthos is defined as living organisms in the water layer immediately adjacent to the bottom that make daily vertical migrations and / or seasonal movements at varying distances from the bottom (Brunel et al., 1978) (e.g. gammarids, corophium). Abundance data were collected from Vallet (1997) that studied suprabenthos all across the English Channel. P/B and Q/B ratios were taken from Brey (2001) and Le Loc'h (2004), and the diet composition was obtained from Lobry et al. (2008). Ash-free dry weights were converted to carbon contents using a conversion factor of 0.518 (Salonen et al., 1976 in Brey 2001).

Meiofauna

The values of mean annual biomass of meiofauna, the P/B ratio and Q/B were obtained from the literature (Ratsimbazafy, 1998; Chardy and Dauvin, 1992; Le Loc'h, 2004).

2.4.6 Zooplankton

Mean annual biomasses of zooplankton were collected from the Seine Aval I programme. P/B and P/C ratios were obtained from another study focused on the Eastern part of the Bay of Seine (Rybarczyk and Elkaim, 2003).

2.4.7 Bacteria

The benthic bacterial biomass, P/B, and Q/B ratios were taken from Chardy (1987), McIntyre (1978), and Mackinson and Daskalov (2007), respectively.

2.4.8 Phytoplankton

The phytoplankton biomass and P/B ratio were taken from data collected in the Bay of Seine by Baehr et al. (2014) and Souissi (2007).

2.4.9 *Detritus*

The mean annual biomass of dead organic matter was obtained from a study focused on the Eastern part of the Bay of Seine (Tecchio et al., 2015).

2.5 Balancing the Ecopath model

To obtain a mass-balanced model, inputs (i.e. B, P/B, Q/B, EE, and diets) were slightly and manually modified to satisfy the constraint of Ecotrophic Efficiency lower than 1. We also checked that physiological rates were within the known limits for each functional group: (i) P/Q of 0.1–0.3 for consumers, and (ii) respiration/biomass (R/B) ratios of 1–10 for fish groups. Biomass accumulation and net migration were both set to zero. The EwE pedigree routine was used to quantify the input parameter uncertainties (Christensen and Walters, 2004). It helped to identify the least certain parameters that should be modified first to achieve mass balance. The balancing approach that we used was top-down, starting with the top predator groups and moving down the food web to balance inconsistencies. When modifications of the data had to be performed, diet compositions (DC) were modified first, and then ratios of P/B and Q/B. Biomasses (B) were considered as less uncertain, and thus were modified the last during the balancing process.

Biomasses of the small pelagic fish and flatfish were left to be estimated by the model after setting their Ecotrophic Efficiency to 0.99 given their high exploitation rate. The estimated biomasses were higher than the input data first entered during model construction for those two groups. This can be partly explained by the fact that the GOV bottom-trawl deployed during the Channel Ground Fish Survey by IFREMER is not fully adapted to capture these species, the abundance of which is thus likely to be underestimated. In the same way, the deposit feeders and suprabenthos biomasses were also left to be estimated by the model assuming an Ecotrophic Efficiency to 0.99.

2.6 Simulating the "reef effect" due to the wind farm implantation using Ecosim simulations

The Ecosim module was used to analyse the potential impacts of biomass accumulation on hard substrates represented by the wind turbines and the scour protections on the structure and functioning of the local trophic web during the operational phase. The dynamic routine of the EwE package, Ecosim allows to describe temporal changes of the system variables (biomass, fishing, predation) starting from the initial Ecopath model (Walters et al., 1997; Christensen and Walters, 2004). The Ecosim equation that models the biomass growth rate for each group (i) is:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + E_i)B_i \qquad \text{(Eq. 4)}$$

Where I_i and E_i are the immigration and emigration rates, M_i is the natural mortality, and F_i is the fishing mortality (Walters et al., 1997, Christensen and Walters 2004). Calculations of the consumption rates (Q_{ij}) are based upon the 'foraging arena' theory, in which the biomass of *i* is divided between available prey (vulnerable fraction, V_i) and unavailable prey (non-vulnerable fraction, $B_i – V_i$). A low value of vulnerability will indicate a 'bottom-up' controlled interaction, while a high value of vulnerability will indicate that mortality of the prey is controlled by the predator biomass, as in a 'top-down' control (Ahrens et al., 2012).

Ecosim was used to build another Ecopath solution, derived from the initial Ecopath model described above. Biomasses of species that would presumably profit from the "reef effect" such as benthic invertebrates (filter feeders, bivalves, and predators), benthos feeders fishes, whiting, pouting, Atlantic cod, other flatfish, sole and surface feeders seabirds, were modelled based on data from the literature (Koller et al., 2006; Reubens et al., 2011; Lindebon et al., 2011, Krone et al., 2013a; Krone et al., 2013b; Reubens et al., 2013). These changes in biomass were the main variations taken into account to drive the evolution of the system through time. Species biomasses on the turbine foundations and scour protections were calculated by multiplying the average biomass per m² found in the literature by the surface area represented by the turbine foundations and scour protections and divided by the total wind farm area at Courseulles-sur-mer. Then, the estimated increase was added to the basal biomass for each functional group susceptible to profit from the implantation of the wind farm in 2018. Forcing time series over a period of 30 years were as such established for the biomass of the following groups: benthic invertebrates (filter feeders, bivalves, and predators), benthos feeders fish, whiting, pouting, Atlantic cod, other flatfish, sole, surface feeders seabirds. These forcing time series were responsible for a disruptive change in the biomass of the species cited above. Ecosim model were run with the new biomass values for the targeted groups listed above and the original biomass values for the other functional groups in the model. In this scenario, the biomass of groups that could presumably profit from a reef effect were simultaneously increased and vulnerability was set to 2 for all groups. In this scenario, we chose to take into account all the effects (direct and indirect), not only those directly propagating from prey-predator interactions. The biomass and production of the phytoplankton was blocked at the initial value. All other parameters and ratios remained unchanged. Then, a new Ecopath model was extracted at the end of the 30 years simulation to compare the situation before (BOWF (Before Offshore Wind Farm) model described above) and after the construction of the offshore wind farms (REEF scenario).

To test the robustness of our working hypotheses, four sensitivity analyses were also performed to analyse effects of fish and benthic aggregation on the trophic web functioning, inside an OWF. The methods included: (1) forcing biomass dynamics of only the bivalves and filters feeders compartments through time (forcing biomass); (2) starting to increase the biomass of benthic organisms and then one year later increase the biomass of fish that would presumably profit from the reef effect in order to take into account the different species time span (time lag); (3) and (4) changes in the vulnerability of the bivalve group. Vulnerability indicates the degree to which an increase in predator biomass will cause mortality for a prey (Christensen et al., 2008). In these two additional scenarios, we increased the vulnerability of bivalves to 5 and 10 respectively. These sensitivity analyses are presented in the Supplementary Material Appendix B.

2.7 Analysing ecosystem organisation, major interactions and emergent properties

For the two Ecopath models (BOWF model and REEF scenario), the trophic level of each functional group was calculated from its diet composition matrix. It is computed as the weighted average of the trophic levels of its prey, when primary producers and non-living material are set at a trophic level of 1:

$$TL_j = 1 + \sum_{i=1}^{N} DC_{ji} TL_j \qquad \text{(Eq. 5)}$$

where DC_{ji} is the fraction of the prey i in the diet of the predator j.

Ecological Network Analysis (ENA) indices were calculated using the network analysis plug-in included in *EwE* (Christensen and Walters, 2004). The following ENA indices were retained:

- Total System Throughflow (TST gC m^{-2} $year^{-1}$) was calculated as the sum of the flow balance (inflow = outflow) of all compartments (Latham, 2006).
- The Total System Throughput (T.., gC m^{-2} $year^{-1}$) was calculated as the sum of all the flows in the food web, characterising its overall activity and size (Latham, 2006).
- The Omnivory Index (OI) represents the trophic specialisation of the predator, assuming values close to zero when the consumer is fully specialized, feeding on a single trophic level, and higher values when the predator feeds on several trophic levels (Pauly et al., 1993).
- The System Omnivory Index (SOI) was calculated as the average of the OIs of the individual group, weighted by the logarithm of each consumer intake (Pauly et al., 1993; Christensen and Walters, 2004). It is both a measure of the predators trophic specialisation in terms of trophic levels and an indicator of the structure and complexity of a trophic network, assuming that high values of SOI correspond to a web-like structure and low values of SOI to a chain-like structure (Libralato, 2008). For instance, marine ecosystems of the northern Europe have a SOI ranging from 0.14 to 0.36 (Mackinson and Daskalov, 2007).
- The Finn’s Cycling Index (FCI) gives the percentage of all flows generated by cycling (i.e. the percentage of carbon flowing in circular pathways) (Finn, 1980).
    - The Ascendency (A) is a measure of the system activity (Total System Throughput) linked to its degree of organization (Average Mutual Information; AMI) (Ortiz and Wolff, 2002). This index was related to the developmental status or maturity of an ecosystem (Ulanowicz, 1986).
    - The Transfer Efficiency (TE) is the fraction of total flows of each discrete trophic level that throughputs into the next one (Lindeman, 1942). The ‘’Lindeman spine plot’’ is a representation of trophic transfers into a linear food chain. It includes the fraction of the biomass directed to detritus by each discrete trophic level (‘flow to detritus’) and the transfer efficiency from one level to the next one (TE).

The Mixed Trophic Impact (MTI) routine was applied to evaluate the impacts of direct and indirect interactions in the food web. This analysis shows the theoretical impact that a slight increase in the biomass of one group would have on the biomasses of all the other groups in the system (Ulanowicz and Puccia, 1990).

Although this is a static analysis that does not account for temporal scale changes, the MTI can be used as a sensitivity analysis to explore possible impacts of moderate biomass variations. The Keystoneness Index was calculated for each functional group, to identify which groups possess a high overall effect on the other groups compared to their relatively low biomass. Calculations were made according to the index defined by Libralato et al. (2006). This analysis uses the MTI matrix to calculate an index summarising the impact that a minimal variation of biomass of a particular group would have on the biomasses of the other groups in the system. The Detritivory/Herbivory ratio (D/H) is the ratio between values of detritivory flows (from detritus to trophic level II) and herbivory flows (from primary producers to trophic level II) (Ulanowicz, 1992). The proportion between biomass of fish groups and biomass of invertebrate groups was also calculated.

3. RESULTS

An Ecopath model (BOWF model) of the area was constructed using data from local sampling surveys or from similar ecosystems. Another Ecopath model (REEF scenario) was derived after simulating 30 years of dynamic evolution of the area following the construction of an offshore wind farm and the increase in hard substrates causing a reef effect (i.e. aggregation of biomass).

3.1 Compartments' ecological roles before the installation of the offshore wind farm

The overall pedigree index value calculated for the BOWF model before the implantation of the offshore wind farm was 0.523.

The functional group dominating biomass was "bivalves" (mostly composed of the clam *Polititapes rhomboides*), which represented 42% of the total living biomass of the system (Table 1). The functional groups contributing most to total throughflows were zooplankton, bacteria, and bivalves, with contributions of 36%, 15%, and 8%, respectively.

The Trophic Level of functional groups ranged from TL=1 for primary producers and detritus, as imposed by construction, to a maximum of 4.8 for grey seals in the BOWF model (see Table 1 in Appendix A). Other marine mammals (i.e. bottlenose dolphins, harbour porpoises and harbour seals) ranked just below as top predators in the trophic webs. The omnivory of the functional groups, estimated by the omnivory index (OI), was low overall (0.001–0.474), except for Surface-feeding seabirds (OI=0.757) (see Table 1 in Appendix A). These low values indicate a general dietary specialisation of the fauna, each functional group feeding on a narrow range of trophic levels.

The MTI analysis highlighted that benthic invertebrate predators negatively affected benthic invertebrate filter feeders, bivalves, deposit feeders, suprabenthos and meiofauna (Fig. 3). Other predators (such as sea bream or flafish), also feeding on those benthic invertebrates and thus considered as competitors, responded negatively to an increase of benthic invertebrate predators' biomass. In fact, functional groups benefiting from an increase in benthic organisms' biomass (predators, filter feeders and bivalves) were some fish species (i.e. flat fish and sea bream), marine mammals and seabirds. Pouting exerted a widespread influence over the trophic web, due to its wide diversity of prey items (benthic invertebrate deposit feeders, filters feeders, and predators, pilchard, sprat, and planktivorous fish).

<Figure 3>

The keystoneness index was highest for pouting (0.095) and for benthic invertebrate predators (0.059), which also presented the maximum values of relative total impact (Fig. 4; see Table 1 in Appendix A). Another group with relatively high keystoneness and low biomass was the harbor porpoise.

<Figure 4>

3.2 Ecosystem structural features after the installation of the wind farm

Based on the simulation of the wind farm presence, REEF scenario, Ecosim generated a variation in biomass of the functional groups for which the biomass inputs were not set a priori.

An increase in substrates available for epibenthic sessile organisms and fish after the wind farm construction implied an increase of the total system biomass by 40%.

First, for those functional groups for which we calculated an accumulation of biomass on new substrates, the new biomass values increased by a factor of 6 for the surface feeders seabirds (dominated by *Larus* sp.), 3.5 for the Atlantic cod, 4 for whiting, 2 for pouting, 2 for fish benthos feeders (dominated by *Callionymus* sp.), 2 for sole, 4 for other flatfish (dominated by *Limanda limanda)*, 1.5 for benthic invertebrate predators (dominated by the omnivorous species *Psammechinus miliaris*), 1.5 for filter feeders (*Balanus* sp.), and 2 for bivalves (dominated by *Mytilus edulis*) (Table 1).

For groups whose biomass was not forced, the construction of the wind farm induced an increase in the biomass of top predators, except for "diving seabirds" (Table 1). The biomass of sea bream and plaice were higher in the REEF scenario than in the BOWF model (approximately 3 times higher, respectively; Table 1).

In contrast, Atlantic horse mackerel, poor cod, and piscivorous fish declined strongly with a 55%, 81%, and 97% diminution, respectively (Table 1). The biomass of benthic invertebrates, deposit feeders and suprabenthos also decreased in the REEF scenario (with a decrease of 17% and 15% respectively). The ratio of fish biomass over invertebrate biomass was reduced by approximately 34% between the two periods (BOWF model/REEF scenario). This was related to the strong increase in benthic invertebrate biomass that was multiplied by approximately 2 in the REEF scenario, while fish biomass was multiplied by 1.1 only. These

The keystoneness index varied between the two periods as biomasses changed (Fig. 4; see Table 1 in Appendix A). Pouting was the functional group with the highest keystoneness index in the two scenarios. In the BOWF model, benthic invertebrate predators occupied the second place followed by harbor porpoise whereas in the REEF scenario, zooplankton occupied the second place and was followed by benthic invertebrate predators.

The total ecosystem activity (T..), representing the sum of all flows in the system, increased between the two periods by approximately 13.96% (Table 2). The System Omnivory index (SOI) of the 2 trophic webs increased by 15.03% (from 0.173 to 0.199) between the two periods. This increase should be related to the variations of pouting omnivory (i.e. increased by a factor of 3). The Finn’s Cycling Index (FCI) increased by 40% between the two scenarios (Table 2). This result is in line with the increase of detritivory (mainly due to benthic invertebrate predators and filter feeders), which doubled. The ascendency (A) increased by 15% (Table 2). The transfer efficiencies (TE) showed a similar pattern in between the two periods, decreasing with TL in the 2 models (Fig. 5). However, values were slightly lower in the REEF scenario.

<Figure 5>

The comparison of compartment throughflows before and after the construction of the offshore wind farm showed that activity of top predators, except for “diving seabirds”, increased after the construction. The compartments sharks and rays, Atlantic cod, whiting, pouting, European sprat and sea bream strongly increased their activity after the construction as well (Fig.6). A similar pattern was observed with all flat fish groups (i.e. sole, plaice, and other flatfish). Activity strongly increased after the construction in some benthic groups, namely invertebrate predators, filter feeders and bivales. In contrast, other benthic groups such as king scallop, deposit feeders and suprabenthos, reduced their overall activity once the offshore wind farm was built.

<Figure 6>

The system overall EE (the percentage of production consumed by predators including fishing activities) increased by 5% between the two periods. For instance, the phytoplankton biomass and P/B remained unchanged in the REEF scenario but its EE increased by 32%. The biomasses and consumptions exerted by bivalves and benthic invertebrates filter feeders were higher in the REEF scenario than in the BOWF model; consuming/grazing more phytoplankton (e.g. until 4 times higher for filter feeders; Table 1). The EE of these species were also higher in the REEF scenario due to the fact that they were more consumed by fish such as cod, pouting and sea bream. The EE of these fish species were also higher as they were more consumed by marine mammals. For instance, Atlantic cod was consumed approximately 5 and 3.5 times more by cetaceans and seals, respectively, after the wind farm implantation. Again, after the construction, the consumption of detritus in the system increased by 68.5%.

In terms of flow analysis, the detritivory/herbivory ratio (D/H) increased by 18.8% between the two periods. The detritivory was multiplied by 1.5 and the herbivory was multiplied by 1.2 between the two situations.

3.3 Sensitivity analyses

The results of the four scenarios (presented in the Supplementary material, Appendix B) highlight that the choices made in the “REEF” scenario were robust as they show that even considering a possible range of variability, we obtained the same main results.

For instance, for groups without forced biomass at the start of the simulation, the construction of the wind farm induced an increase in biomass, especially for top predators, in the four additional scenarios (Table 1, in Supplementary Material, Appendix B). For instance, the biomass of sea bream after 30 years of simulations were higher in the four scenarios than in the “BOWF” Ecopath model (approximately 3 times higher in the “REEF Filter Feeders” and “time lag” scenarios and approximately 4 times higher in the “REEF Bivalve V5” and “V10” (Table 1, in Supplementary material, Appendix B)). On the same line, the biomass of plaice was higher in the four scenarios compared to the BOWF Ecopath model (approximately 3 times higher). This generalized increase in apex predators was congruent with the one highlighted under the “REEF” scenario. However, in the “REEF Filter feeders”, the biomass of predatory fish (cod, whiting) resulting from this simulation increased, but this increase was inferior to the input that we originally entered for the “REEF scenario”. The difference can be explained because EwE takes into account only prey-predator interactions and does not take into account other indirect effects such as the reserve effect that exist in the park where biomass sampling was performed.

In terms of flow analysis, we observed an increase in the Detritivory/Herbivory ratio (D/H) between the BOWF model and the different scenarios (Table 2, in Supplementary Material, Appendix B). For instance, the D/H increased by 11%, 17%, 20% in the “REEF filter feeders”, “REEF time lag”, “Reef mussel V5”, “Reef mussel V10”, respectively (Table 2, in Supplementary Material, Appendix B). Other ENA indices remained mostly unchanged under the different scenarios. Again, this change in D/H was in accordance with the conclusion drawn from the “Standard REEF” scenario.

4. Discussion

4.1 Food web control before the installation of the offshore wind farm

From a methodological point of view, the high value of the pedigree index indicated that the input data used in the reference Ecopath model (BOWF model) were of good quality when compared to the distribution of pedigree values for pre-existing models (Morissette, 2007). In fact, the pedigree index (0.523) was in the highest part of the range (0.164 to 0.676) reported in Morissette (2007). Indeed, biomass data were mainly obtained from local, highly replicated, and detailed samplings and the diet compositions of the main fish species came from stomach content studies performed in the eastern English Channel.

The Courseulles-sur-mer food web appeared to be mostly controlled by intermediate trophic levels. First, the MTI analysis revealed that benthic invertebrate predators and pouting, which occupied an intermediate trophic level (TL= 3 and TL=3.7 respectively), had a strong impact on numerous groups of both higher and lower trophic levels in the system. For instance, pouting supported a high diversity of predators (i.e. marine mammals, cephalopods, elasmobranch and teleosts) and fed mainly on benthic invertebrate predators (i.e. crustaceans), filter feeders, and suprabenthos. This result concurred with the high ranking of pouting in the keystoneness index (classification see Table 1 in Appendix A). A keystone group is defined as a group having a high structuring impact on the other groups, despite a relatively low biomass (Power et al., 1996). Since pouting biomass was high (i.e. 3.85 gC m^{-2} $year^{-1}$), this group was likely to be a key structuring group in the system rather than a keystone group *sensu* Power et al. (1996). These results suggest a possible “wasp-waist” control of the system by intermediate trophic levels (Cury et al., 2000). In “wasp-waist” systems, the flow of energy is controlled by the mid-trophic levels rather than the bottom or top organisms. The mid-trophic levels exert top-down control on zooplankton and benthic groups, and bottom-up control on top predators (Cury et al., 2000). This type of control has generally been demonstrated to be the norm for small plankton-feeding pelagic species, such as anchovies and sardines, in upwelling pelagic ecosystems around the world (Cury et al., 2000, 2004; Coll et al 2006; Bakun, 2006). The role played here by pouting, a demersal species, was hence an original feature of the Courseulles-sur-mer food web. Pouting could then be considered as a benthic equivalent of sardines but with a higher position in the food web compared to examples involving small pelagics. However, these results are only based on the MTI and Keystoneness analysis that are interrelated and must be taken with caution.

4.2 Potential impacts of the reef effect inside the offshore wind farm on the trophic web functioning

As the results show that even considering a possible range of variability through the 4 variants of the "REEF" scenario, we obtained the same main results, we choose to discuss only the results of the "REEF" scenario (Supplementary Material, Appendix B).

The construction of the Courseulles-sur-mer offshore wind farm was suspected to increase detritivory in the food web. As expected, the D/H ratio changed positively between the two periods, underlying the importance of the trophic interactions involved in the detrital chain (Dame and Christian, 2007). This was related to the higher consumption of detritus by benthic organisms and might confirm the hypothesis of Norling and Kautsky (2007, 2008) by which blue mussels expansion could be responsible for a shift from primary producers and grazers dominated food chains towards a more detritus-feeding community. Sessile organisms, such as blue mussels colonizing the 75 turbines, are indeed expected to enhance the benthic production of food for fish and benthic organisms through the deposition of organic matter such as feces and dead organisms (Wilhemsson et al., 2006; Maar et al., 2009). Wind turbines and scour protections were identified as offering particularly favorable substrates and feeding conditions for blue mussels in field studies (Wilhelmsson, et al., 2006; Wilhelmsson and Malm, 2008; Maar et al., 2009; Krone et al., 2013). Bivalves can form dense belts and, in some cases, account for almost 97% of the total epibenthic biomass on foundations (Maar et al., 2009). According to Maar et al. (2009), wind turbines can support a mussel biomass ten times higher per unit area than the one observed on bridge pillings in the same region, and the growth of blue mussels on turbines can also double the biomass of filter feeders in a wind farm area as a whole compared to the situation before its construction. Another potential effect suggested in the litterature is an input of organic material from fish and crustaceans closely associated with the turbines as well as an entrapment of organic material by the turbines themselves, contributing to an enrichment of the seabed and enhancing the abundance of deposit-feeding organisms and their predators (Maar et al., 2009; Wilhelmsson et al., 2010). This material provided an additional source of food but, more importantly, a different "food quality" (Koller et al., 2006). In soft bottom communities, filters and detritus feeders feed on small particulate matter deposited on the seabed (Koller et al., 2006). Koller et al. (2006) stated that this different quality of food coming from the wind turbines was responsible for a "shortcut within the food web" because this resource was consumed by larger predators and scavengers. Other effects suggested in the literature, but that could not be demonstrated here as our flows were only in carbon currency, are that the increase in filter feeders biomass, and more particularly in blue mussels, could imply an increased excretion of ammonium and thus a clearer water (reduction of water turbidity), which in turn could lead to an increase in growth rates of phytoplankton and filamentous algae (Kautsky and Evans, 1987; Prins and Smaal, 1994; Norling and Kautsky, 2008).

The introduction of turbines with their associated scour protections generated an additional source of food in the ecosystem. Habitats created by the monopile foundations and the fauna they harbour were responsible for an increase in the system total biomass. Possibly due to the biomass modifications, EE values (the percentage of production consumed by predators) of the whole ecosystem showed an increase of 5%. This result can be explained by the increase in predation exerted by the species attracted by the reef effect. For instance, our model showed that the benthic invertebrates colonising the monopile foundations served in turn as food resources for other species such as poutings and sea breams. The related increases in pouting, cod and sea bream biomass was *in fine* beneficial to their predators, notably marine mammals. These results confirm the hypothesis enounced in the introduction of this study that the benthic biomass increase acts as an additional prey resource for higher trophic levels up to apex predators (Lindeboom et al., 2011; Scheidat et al., 2011; Russell et al., 2014). This result was also in line with the stomach content analyses of Reubens et al. (2011), who demonstrated that pouting fed on the macrobenthos produced on the Thornton bank wind turbines in the Belgian part of the North Sea. For instance, the amphipode, *Jassa herdmani*, presented a numerical abundance index of 84.6% and it was the most important prey species of the pouting dietary composition (Reubens et al., 2011). Moreover, it could be assumed that seabirds strongly profit from additional biomass of epifaunal bivalves on the 75 turbines as they would become easily available. These basic parameters estimates analysis was to some point consistent with the relatively low values of SOI indicating a chain-like structure both before and after the installation of the offshore wind farm.

According to our model, the “reef effect” generated by the construction of the Courseulles-sur-mer offshore wind farm was predicted to have a relatively limited impact on the structure and flow pattern of the local food web. The comparison of the ENA indices (total ecosystem activity (T..), system omnivory index (SOI), ascendency (A) and keystoneness) between the BOWF model and the REEF scenario showed small variations between the two periods. Furthermore, the transfer efficiencies (TE) decreased parallely with TL in the 2 models indicating that the compartments, although exposed to an increase in biomass of some specific groups, behaved functionally in a similar way under the two scenarios. Ecopath is a single solution model and so direct statistical comparisons were not possible. As network indices of Ascendency are scaled according to log values of combinations of flows, small changes expressed in percentages could reflect much larger disparities, and hence larger ecological changes (Ulanowicz 1986; Baird & Ulanowicz 1993). In addition, the ENA results from the BOWF model and the REEF scenario can be compared with other ecosystems studied with the same methodology (Ecopath) and located in the same biome such as the Bay of Somme (Rybarczyck et al., 2003), the Dublin Bay (Wilson and Parkes, 1998), and the Seine Estuary (Tecchio et al., 2015). Values of ENA indices in both situations for the Courseulles-sur-mer area remained in the range delimited by these similar ecosystems, suggesting no major trophic structural and functional shift due to the installation of an offshore wind farm (Table 2).

<Table 2>

4.3 Advantages and limitations of the EwE models

Conceptually, the main asset of this study was to lay the foundations defining an ecosystem-based approach to marine renewable energy management, in line with what has been done during the last 20 years in the Ecosystem Approach to Fisheries (Garcia et al., 2003). Previous studies have largely focused on the conservation of some groups of valuable species and their habitats only. The proposed model considered the full range of size classes of biota, from prokaryotes to apex predators, for a representative site of the eastern Bay of Seine basin: the Courseulles-sur-mer offshore future wind farm. The approach for this specific site can then be transposed to other wind farm projects in the English Channel and broadly to other shallow and macrotidal seas of temperate latitudes. Applying this modelling method can enrich the field of environmental impact studies on future offshore wind farms and, more generally, on marine renewable energy sites.

Models for offshore wind farms are by definition atypical due to their intrinsic small spatial scale (here, 50 km^2) with one on the main drawbacks being the fact that the population dynamics and home range of mobile species vastly exceed the limits of wind farm sites. Here, as a partial solution, we considered trophic transfers outside the area of the Courseulles-sur-mer offshore wind farm for marine mammals and seabirds by setting imports in the diet composition matrix. This limitation is common to all Ecopath small-scale models (e.g. marine protected areas (Albouy et al., 2010; Colléter et al., 2012; Valls et al., 2012). Regarding community changes, our choice here was to use estimates derived from the literature and expert knowledge and not from complex models. This option was relevant here as a lot of information coming from the offshore wind farms already in exploitation could be extracted and helped formulating meaningful hypotheses. Another possibility would have been to use these data for calibrating a community model predicting the changes in existing species and at the same time the arrival of new species around the turbines. Finally, the BOWF model and REEF scenario could not simulate all possible impacts generated by the increased biomass of mussels on biogeochemical process such as the excretion of ammonium as our model is based only on carbon flows.

5. Conclusions

This ecosystem-based approach of offshore wind farm impacts showed 1) an original control of the Courseulles-sur-mer site food web by pouting at the intermediate trophic levels, indicating a potentially “wasp-waist” controlled food web, 2) that the anticipated increase of mussel biomass after the offshore wind farm construction is predicted to lead to a food web dominated by detritivory, as hypothesized by Norling and Kautsky (2008), and (3) that the anticipated increase in benthic invertebrate and benthos feeding fish biomass, in response to the reef effect, is predicted to attract and benefit to apex predators, as hypothesized by Lindeboom et al. (2011) and Henkel et al. (2014).

By combining the data collected on various ecosystem components, we determine in this study how the local food web structure and function may change 30 years after the installation of the offshore wind farm. The

Ecopath models built in this study can then be useful to interpret how other threats, such as climate change or restrictions of fisheries activities within the offshore wind farm limits, can further affect the trophic web structure and functioning. This study could be considered as a first step in using food web models to assess offshore wind farm impacts on the whole ecosystem.

ACKNOWLEDGEMENTS

This work was co-funded by the Normandy Region and by the group “Eoliennes Offshore du Calvados” (EOC). We also acknowledge, for their help in compiling the datasets and for giving expert advices: Georges Safi and Jean-Paul Robin (UMR BOREA, Caen), Alexandrine Baffreau, Sandric Lesourd and Maxime Navon (UMR M2C, Caen), Ludivine Martinez, Jérôme Spitz and Charlotte Lambert (Observatoire PELAGIS, La Rochelle), Francis Gohin and Maria Ching Villanueva (IFREMER, Brest), Gregory Certain (Université de Suède des Sciences de l’Agriculture, Uppsala), James Jean Baptiste (Groupe Ornithologique Normand, Caen) and Nicolas Bacq (Groupement d’Intérêt Public “Seine-Aval”). This work was an introduction to the project Trophik (ANR/FEM EMR-ITE 2015).

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Figure Legends

Figure 1. Position of the Courseulles-sur-mer offshore wind farm in the Bay of Seine, north-western France.

Figure 2. Functional groups of the Courseulles-sur-mer ecosystem model arranged using trophic levels as y-axis and benthic/pelagic partitioning on the x-axis. Trophic levels are relative to the BOWF model, before the construction. Functional groups written in blue and bold identify the functional groups for which the biomasses have been set to their accumulated maximum during for the REEF scenario.

Figure 3. Mixed Trophic Impact (MTI) analysis performed on the BOWF model. Negative (red cells) and positive (blue cells) overall impacts are represented.

Figure 4. Keystoneness index calculated for the two Ecopath models (“before” and “after” the construction of the Courseulles-sur-mer offshore wind farm; BOWF model is in blue and REEF scenario is in green). The size of the circles is proportional to the functional group biomass.

Figure 5. Lindeman spine plot of flows and biomasses and transfer efficiencies by discrete trophic levels for the two Ecopath models.

Figure 6. Differences in compartment throughflows between the two Ecopath models. Note that the y-axis scale is log-transformed, and that this percentage analysis did not consider the difference in absolute values between functional groups. Grey bars identify functional groups for which the biomasses were set to their accumulated maximum during the Ecosim 30-years simulation of ‘Reef Effect’. Black bars represent groups for which variations in biomass were an output of the simulation.

Table 1. Biomass values, production over biomass (P/B) ratios, consumption over biomass (Q/B) ratios, and Ecotrophic Efficiencies (EE) in the two Ecopath models ("before" and "after" the construction of the Courseulles-sur-mer offshore wind farm in the Bay of Seine; BOWF model and REEF scenario, respectively). Functional groups for which biomasses were set to their accumulated maximum in the REEF scenario are marked in bold. Biomasses estimated in the BOWF model were indicated in grey and italic.

		Biomass gC m^{-2}		**P/B (year^{-1})**		**Q/B (year^{-1})**		**EE**	
		BOWF	**REEF**	**BOWF**	**REEF**	**BOWF**	**REEF**	**BOWF**	**REEF**
1	Bottlenose dolphins	1.87E-05	8.44E-05	0.08	0.06	23.64	23.15	0	0
2	Harbour porpoises	4.10E-04	1.43E-03	0.08	0.06	40.70	39.59	0	0
3	Harbour seals	6.73E-04	1.89E-03	0.04	0.02	15.90	18.45	0	0
4	Grey seals	2.68E-04	8.73E-04	0.04	0.02	13.23	16.01	0	0
5	Diving seabirds	1.50E-02	9.80E-03	0.09	0.09	55.00	55.01	0	0
6	**Surface feeders seabirds**	2.08E-03	**1.27E-02**	0.09	0.18	65.00	30.45	0	0
7	Benthopelagic cephalopods	1.36E-02	1.70E-02	2.80	2.78	15.00	14.64	0.43	0.626
8	Benthic cephalopods	6.22E-03	7.65E-03	3.50	3.50	15.00	14.60	0.918	0.948
9	Fish, mackerel	*2.39E-01*	2.30E-01	0.83	0.83	4.40	4.40	0.99	0.997
10	Fish, European seabass	1.86E-02	1.63E-02	0.54	0.53	3.20	3.09	0.431	0.439
11	Fish, sharks and rays	1.20E-01	1.64E-01	0.30	0.29	2.44	2.28	0.128	0.132
12	**Fish, Atlantic cod**	1.97E-02	**6.87E-02**	1.20	1.20	4.50	4.50	0.445	0.582
13	**Fish, whiting**	6.80E-03	**2.84E-02**	1.07	2.40	4.71	10.58	0.987	0.998
14	Fish, Atlantic horse mackerel	*1.41E-01*	6.36E-02	0.55	0.56	2.44	2.46	0.99	0.999
15	Fish, gurnard	6.30E-03	8.69E-03	0.55	0.54	4.75	4.50	0.001	0.001
16	**Fish, pouting**	1.66E+00	**3.85E+00**	1.32	1.32	8.97	8.97	0.037	0.098
17	Fish, poor cod	8.60E-03	1.64E-03	1.50	1.67	8.97	9.69	0.962	0.998
18	Fish, European pilchard	*4.76E+00*	3.68E+00	0.99	1.04	7.20	7.45	0.99	0.997
19	Fish, European sprat	*1.08E-01*	1.28E-01	1.34	1.33	11.59	11.39	0.99	0.999
20	Fish, piscivorous	*2.42E-01*	4.86E-03	0.87	1.03	5.11	5.54	0.99	0.995
21	Fish, planktivorous	*8.19E-01*	7.22E-01	1.04	1.09	8.38	8.62	0.99	0.995
22	**Fish, benthos feeders**	*1.21E+00*	**2.50E+00**	0.92	0.91	2.99	2.63	0.99	0.997
23	Fish, sea bream	2.98E-02	8.33E-02	0.58	0.57	4.47	4.29	0.298	0.319
24	**Fish, sole**	*5.07E-02*	**9.80E-02**	0.70	0.70	3.20	3.20	0.99	0.999
25	Fish, European plaice	*2.16E-02*	5.33E-02	0.85	0.85	3.42	3.33	0.99	0.997
26	**Fish, other flatfish**	*6.18E-03*	**2.70E-02**	0.82	1.09	4.48	3.35	0.99	0.99
27	**Benthic invertebrate, predators**	2.94E+00	**3.01E+00**	2.24	2.89	11.20	14.44	0.978	0.993
28	**Benthic invertebrate, filter feeders**	*3.12E+00*	**4.78E+00**	2.40	3.27	12.00	16.34	0.99	0.999
29	**Benthic invertebrate, bivalves**	1.95E+01	**4.29E+01**	0.60	1.20	3.00	6.00	0.013	0.014
30	King scallops	7.70E-01	7.43E-01	0.90	0.89	4.50	4.45	0.58	0.588
31	Benthic invertebrate, deposit feeders	*3.57E+00*	2.98E+00	2.90	3.05	14.50	15.23	0.99	0.994
32	Suprabenthos	*2.00E+00*	1.71E+00	5.66	5.82	28.30	29.10	0.99	0.994
33	Meiofauna	*9.70E-01*	1.06E+00	15.00	15.06	42.86	43.02	0.99	0.991
34	Zooplankton	1.72E+00	1.79E+00	50.00	47.45	150.00	141.80	0.882	0.998

35	Bacteria	7.50E-01	7.70E-01	72.80	72.34	145.60	144.68	0.219	0.246
36	Phytoplankton	3.24E+00	3.24E+00	150.00	150.00			0.758	0.997
37	Detritus	1.90E+01	1.92E+01						

Table 2. General system statistics and ENA indices for the BOWF model compared to values obtained for similar Northern European systems. The Total System Throughput (T.., gC m^{-2} year^{-1}) was calculated as the sum of all the flows in the food web. The Finn's Cycling Index (FCI) gives the percentage of all flows generated by cycling. The Ascendency (A) is a measure of the system activity (Total System Throughput) linked to its degree of organization (Average Mutual Information) and is given in gC m^{-2} year^{-1}.

Ecosystems	**T..**	**A**	**FCI**	**Biomass/Throughput**	**Total living biomass**	**Reference for Ecopath models**
Seine estuary	4584.92 - 1161.05	1442.6-6058.6	3.65 -20.65	0.07-0.022	10.23-40.40	Tecchio et al., 2015
Bay of Somme	2312.1	2401.6	12.2	0.01	27.44	Rybarczyck et al., 2003
BOWF model	1607.616	1869.1	9.16	0.030	48.12	
REEF scenario	1831,933	2156,9	12,86	0.041	74.73	
Dublin Bay	724.69	848.5	31.9			Wilson and Parkes, 1998

Figure 1

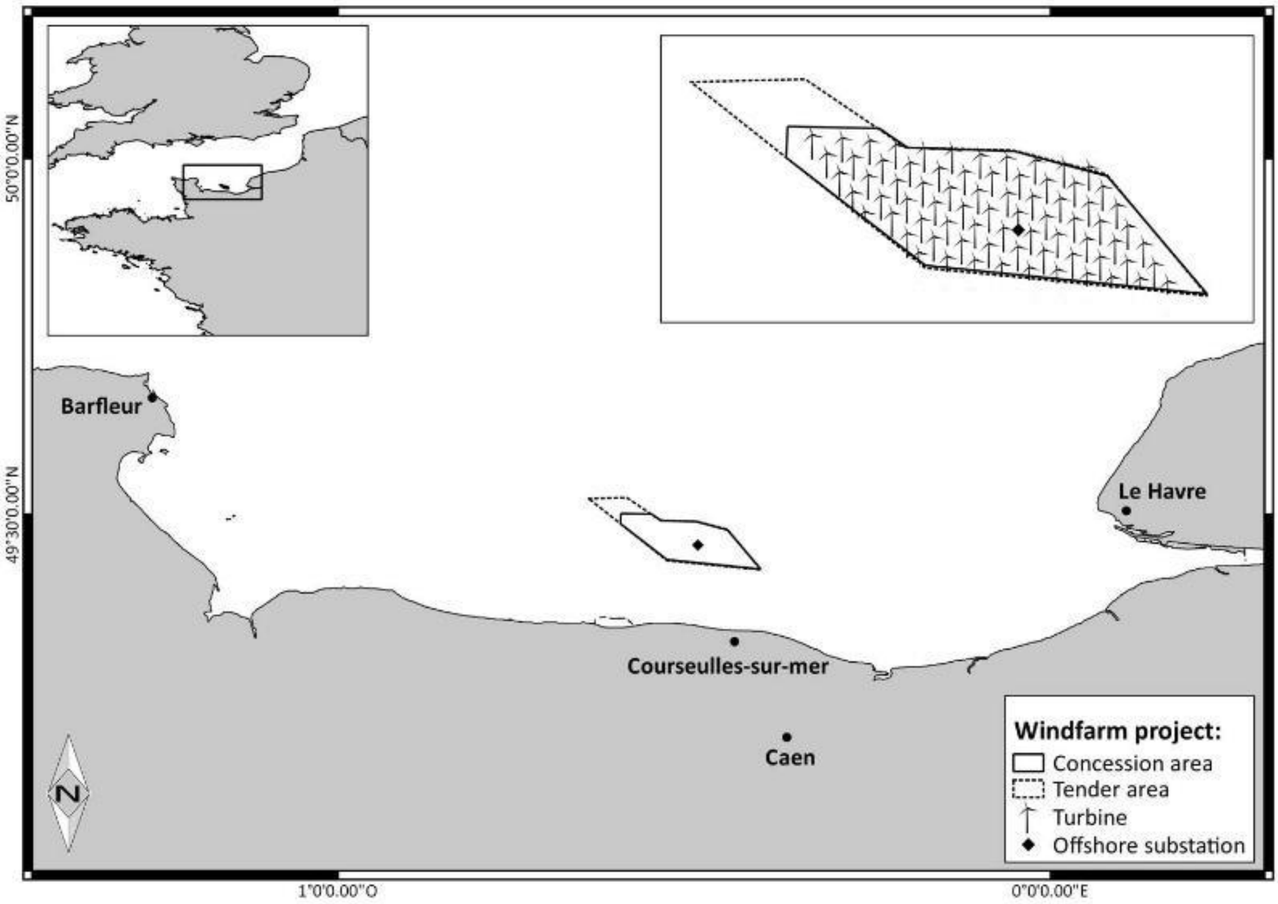

50°0'0.00"N
49°30'0.00"N
1°0'0.00"O
0°0'0.00"E
Barfleur
Le Havre
Courseulles-sur-mer
Caen
N
Windfarm project:
Concession area
Tender area
Turbine
Offshore substation

Figure 2

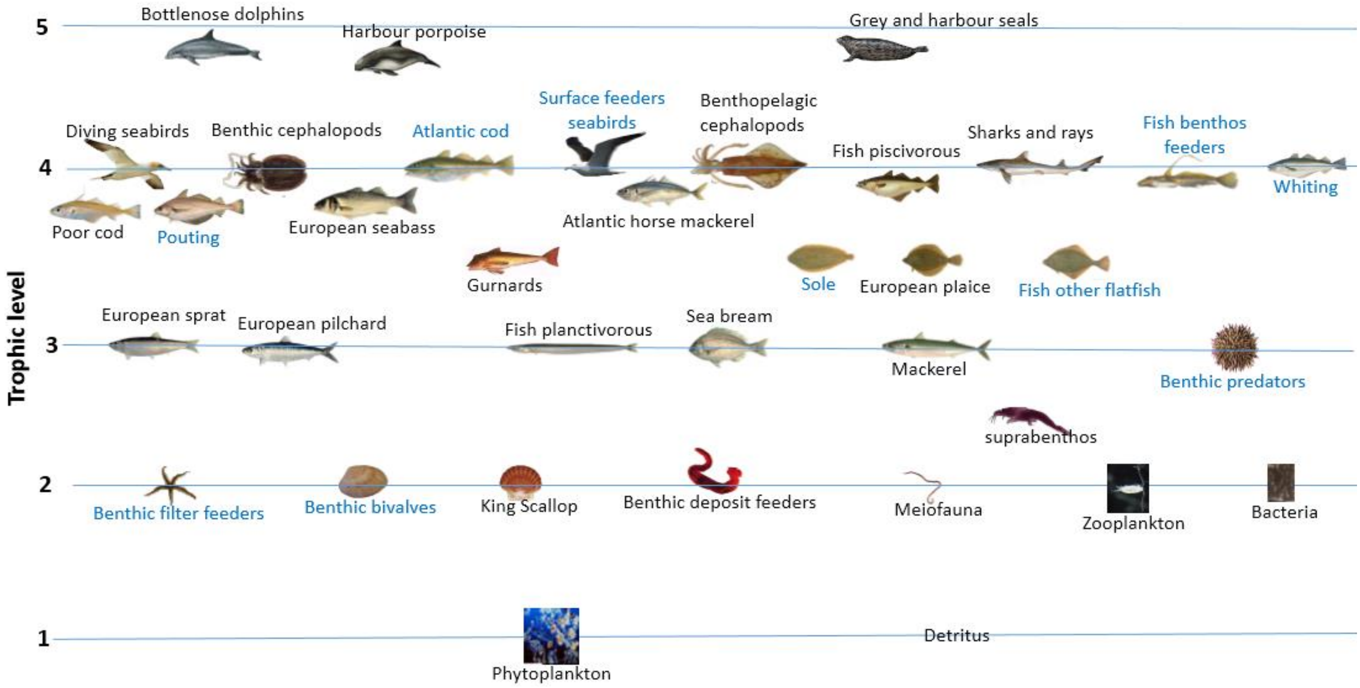

Trophic level
5
Bottlenose dolphins
Harbour porpoise
Grey and harbour seals
4
Diving seabirds
Benthic cephalopods
Atlantic cod
Surface feeders seabirds
Benthopelagic cephalopods
Fish piscivorous
Sharks and rays
Fish benthos feeders
Whiting
Poor cod
Pouting
European seabass
Atlantic horse mackerel
Gurnards
Sole
European plaice
Fish other flatfish
3
European sprat
European pilchard
Fish planctivorous
Sea bream
Mackerel
Benthic predators
suprabenthos
2
Benthic filter feeders
Benthic bivalves
King Scallop
Benthic deposit feeders
Meiofauna
Zooplankton
Bacteria
1
Phytoplankton
Detritus

Figure 3

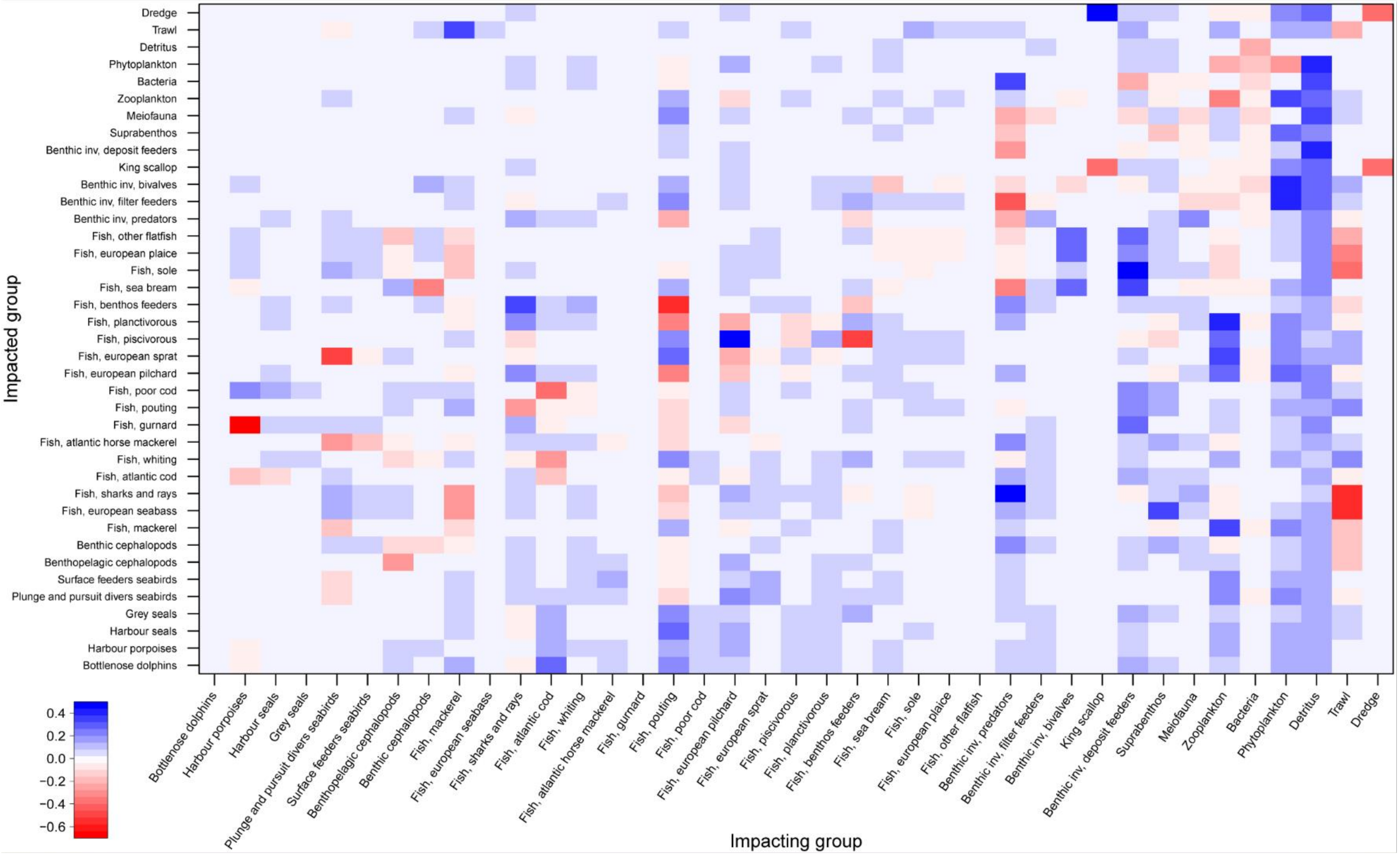

Impacted group
Dredge
Trawl
Detritus
Phytoplankton
Bacteria
Zooplankton
Meiofauna
Suprabenthos
Benthic inv, deposit feeders
King scallop
Benthic inv, bivalves
Benthic inv, filter feeders
Benthic inv, predators
Fish, other flatfish
Fish, european plaice
Fish, sole
Fish, sea bream
Fish, benthos feeders
Fish, planctivorous
Fish, piscivorous
Fish, european sprat
Fish, european pilchard
Fish, poor cod
Fish, pouting
Fish, gurnard
Fish, atlantic horse mackerel
Fish, whiting
Fish, atlantic cod
Fish, sharks and rays
Fish, european seabass
Fish, mackerel
Benthic cephalopods
Benthopelagic cephalopods
Surface feeders seabirds
Plunge and pursuit divers seabirds
Grey seals
Harbour seals
Harbour porpoises
Bottlenose dolphins
Bottlenose dolphins
Harbour porpoises
Harbour seals
Grey seals
Plunge and pursuit divers seabirds
Surface feeders seabirds
Benthopelagic cephalopods
Benthic cephalopods
Fish, mackerel
Fish, european seabass
Fish, sharks and rays
Fish, atlantic cod
Fish, whiting
Fish, atlantic horse mackerel
Fish, gurnard
Fish, pouting
Fish, poor cod
Fish, european pilchard
Fish, european sprat
Fish, piscivorous
Fish, planctivorous
Fish, benthos feeders
Fish, sea bream
Fish, sole
Fish, european plaice
Fish, other flatfish
Benthic inv, predators
Benthic inv, filter feeders
Benthic inv, bivalves
King scallop
Benthic inv, deposit feeders
Suprabenthos
Meiofauna
Zooplankton
Bacteria
Phytoplankton
Detritus
Trawl
Dredge
Impacting group
0.4
0.2
0.0
−0.2
−0.4
−0.6

Figure 4

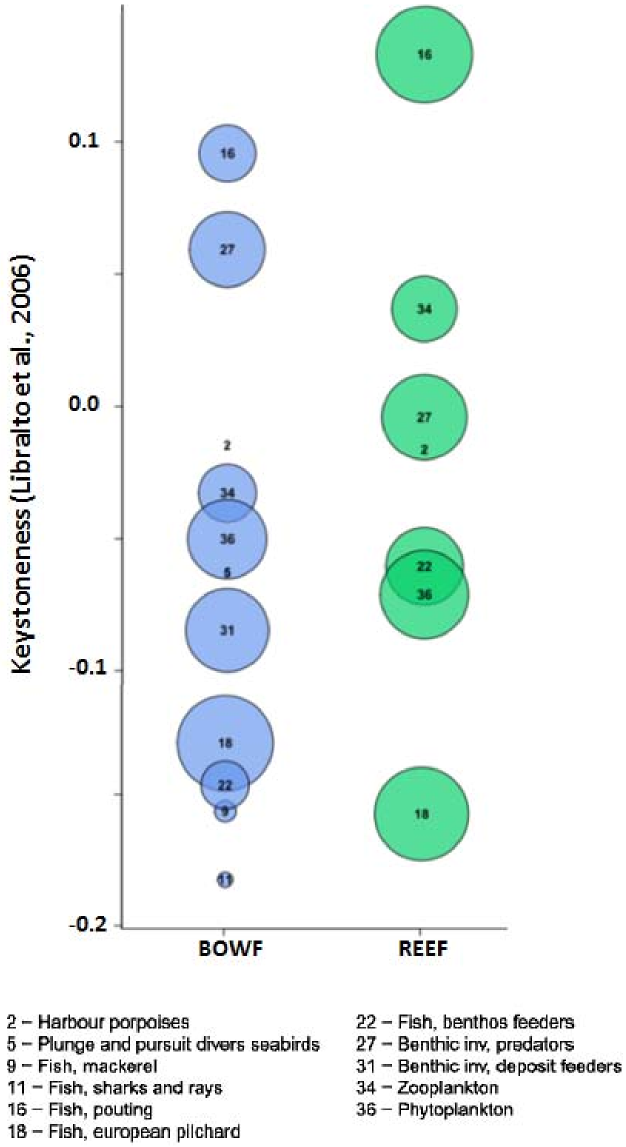

Keystoneness (Libralto et al., 2006)
0.1
0.0
-0.1
-0.2
BOWF
REEF
16
27
2
34
36
5
31
18
22
9
11
16
34
27
2
22
36
18
2 – Harbour porpoises
5 – Plunge and pursuit divers seabirds
9 – Fish, mackerel
11 – Fish, sharks and rays
16 – Fish, pouting
18 – Fish, european pilchard
22 – Fish, benthos feeders
27 – Benthic inv, predators
31 – Benthic inv, deposit feeders
34 – Zooplankton
36 – Phytoplankton

Figure 5

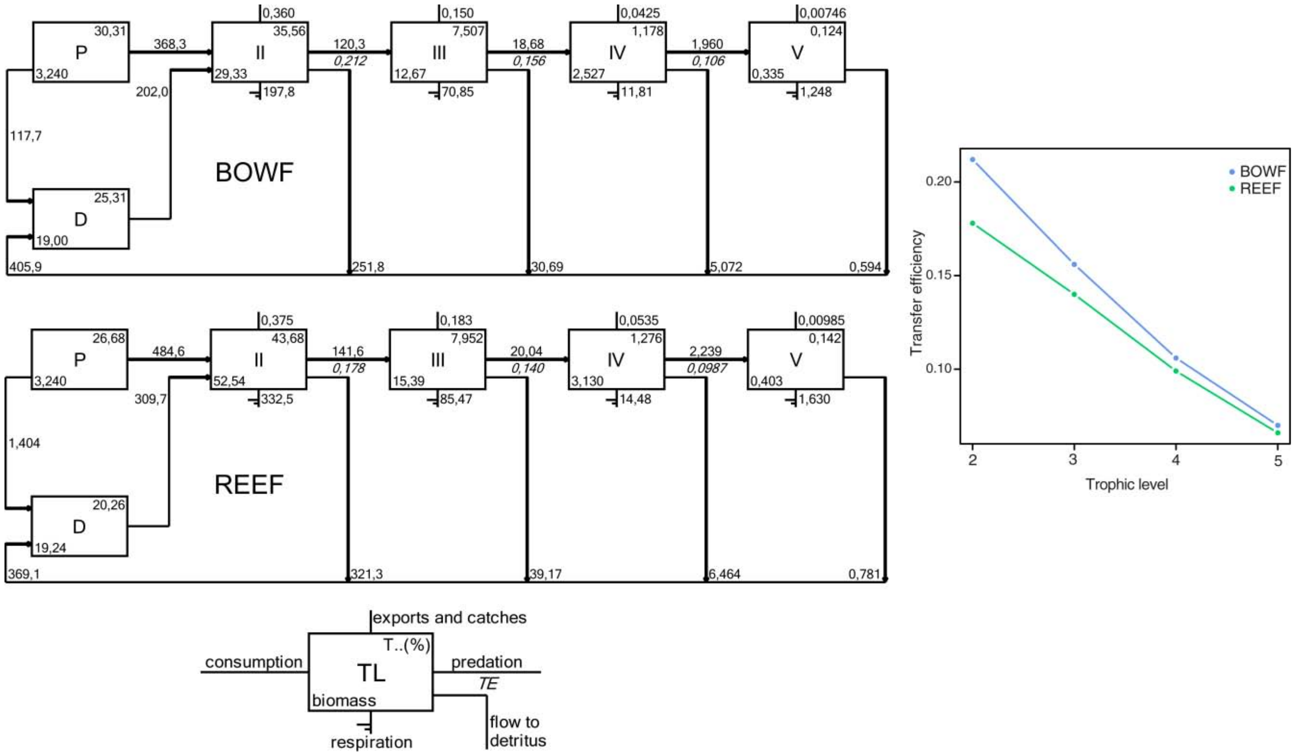
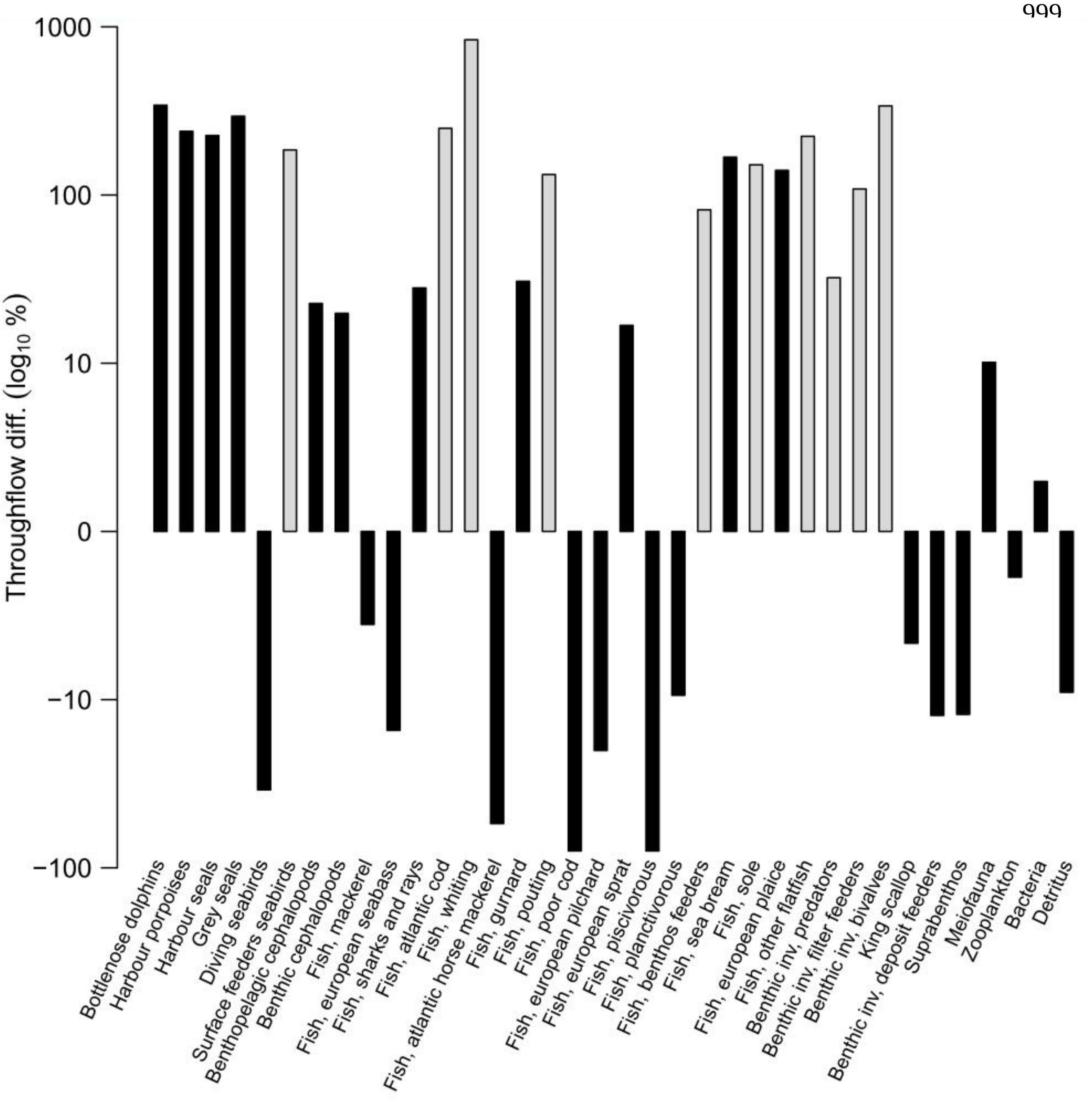

BOWF
P
30,31
3,240
368,3
202,0
117,7
D
25,31
19,00
405,9
II
0,360
35,56
29,33
197,8
120,3
0,212
251,8
III
0,150
7,507
12,67
70,85
18,68
0,156
30,69
IV
0,0425
1,178
2,527
11,81
1,960
0,106
5,072
V
0,00746
0,124
0,335
1,248
0,594
REEF
P
26,68
3,240
484,6
309,7
1,404
D
20,26
19,24
369,1
II
0,375
43,68
52,54
332,5
141,6
0,178
321,3
III
0,183
7,952
15,39
85,47
20,04
0,140
39,17
IV
0,0535
1,276
3,130
14,48
2,239
0,0987
6,464
V
0,00985
0,142
0,403
1,630
0,781
exports and catches
T..(%)
consumption
TL
predation
TE
biomass
respiration
flow to detritus
Transfer efficiency
0.20
0.15
0.10
Trophic level
2
3
4
5
BOWF
REEF

Figure 6


Throughflow diff. (log$_{10}$ %)
1000
100
10
0
−10
−100
Bottlenose dolphins
Harbour porpoises
Harbour seals
Grey seals
Diving seabirds
Surface feeders seabirds
Benthopelagic cephalopods
Benthic cephalopods
Fish, mackerel
Fish, european seabass
Fish, sharks and rays
Fish, atlantic cod
Fish, whiting
Fish, atlantic horse mackerel
Fish, gurnard
Fish, pouting
Fish, poor cod
Fish, european pilchard
Fish, european sprat
Fish, piscivorous
Fish, planctivorous
Fish, benthos feeders
Fish, sea bream
Fish, sole
Fish, european plaice
Fish, other flatfish
Benthic inv. predators
Benthic inv. filter feeders
Benthic inv. bivalves
King scallop
Benthic inv. deposit feeders
Suprabenthos
Meiofauna
Zooplankton
Bacteria
Detritus