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Original Article

Mapping the vulnerability of animal community to pressure in marine systems: disentangling pressure types and integrating their impact from the individual to the community level

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Assessing the vulnerability of biological communities to anthropic pressures in marine systems may be challenging because of the difficulty to properly model each species' response to the pressure due to lack of information. One solution is to apply factor-mediated vulnerability assessment which combines (i) information on species ecological traits and conservation status organized in a matrix of so-called "vulnerability factors", (ii) a conceptual model of how these factors affect species vulnerability, and (iii) data on the spatial distribution and abundance of each species issued from at-sea surveys. Such factor-mediated vulnerability assessment was originally introduced in the seabird – wind farm context by Garthe and Hüppop (2004. Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. Journal of Applied Ecology, 41: 724 – 734) and has since then been expanded to many case studies. However, the mathematical formulations that were proposed at that time are overly simplistic and may overlook critical components of the impact assessment. Our study briefly reviews the original approach and highlights its hidden assumptions and associated interpretation problems, for example, the overestimation of disturbance pressure to the detriment of collision, or the very high contribution of log abundances in vulnerability maps. Then, we propose a revised framework that solves these issues and permits easy transposition to other community-pressure case studies. To illustrate the usefulness and generality of the revised framework, we apply it to two case studies, one concerning the vulnerability assessment of a seabird community to offshore wind farms in the Bay of Biscay, and another focusing on the vulnerability assessment of the benthic megafauna community to trawling pressure in the Barents Sea.

Keywords: Barents Sea, Bay of Biscay, benthos, community, pressure, seabird, trawling, vulnerability assessment, wind farm.

Introduction

The gold standard for evaluating the vulnerability of biological communities to a specific pressure requires a combination of experimental and empirical approaches, in which the response of each species to the pressure is modelled and then predicted under different pressure

scenario, ideally integrating species interactions as well. In practice however, vulnerability assessments are more qualitative and pragmatic, especially when the communities under focus are hard to access or the pressures are hard to simulate or manipulate, a typical problem in many marine case studies. Many vulnerability

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assessments rely therefore on the *ad hoc* aggregation of factors related to species morphology, behaviour, demography, habitat, or conservation status (Feeley *et al.*, 2007; Lees and Peres, 2008; Wang *et al.*, 2009; Davidson *et al.*, 2012; Furness *et al.*, 2013; Ameca y Juárez *et al.*, 2014; Bradbury *et al.*, 2014; Jeppsson and Forslund, 2014). In these studies, factors are often scored between 0 and 1 and then aggregated, possibly to survey data, using *ad hoc* formulas such as weighted sums of terms. Classical outputs are a ranking of species according to their degree of vulnerability, and the production of vulnerability maps when survey data are employed.

The application of these factor-mediated vulnerability assessments is convenient when knowledge and data are limited. For example, benthic communities on the continental shelf, upper slope, and seamounts are submitted to trawling pressure (Clark and Tittensor, 2010; Puig et al., 2012), but estimating capture and survival rate following a trawl for each benthic species is very challenging because of the difficulty of accessing and manipulating these organisms. Another, well-documented example is the evaluation of the vulnerability of seabird community to the establishment of wind farms. There, extensive observations around existing wind farms, coupled to collection of behavioural data on flying patterns, behavioural response to wind farms, and how this ultimately affects reproductive and survival performances are needed (Camphuysen et al., 2012; Johnston et al., 2014; Miller et al., 2014). However, such information may be difficult to gather for every bird species in every site targeted by wind farm development.

The factor-mediated vulnerability assessment was actually pioneered by Garthe and Hüppop (2004) in the seabird—wind farm context, through the development of the wind farm sensitivity index (WSI). It is notable that their framework has already been transposed to other contexts (Noguera et al., 2010; Stelzenmüller et al., 2010; Sonntag et al., 2012), and that similar methods are currently being used in the context of cumulative impact assessments (Halpern et al., 2008; Coll et al., 2012; Maxwell et al., 2013). The framework uses very simple ad hoc mathematical formulations, often presented as an advantage. However, as we shall see, such overly simplistic formulation contains hidden assumptions that can lead to biased estimates of vulnerability as well as biased identification of concern areas.

In this study, we extend Garthe and Hüppop (2004)'s approach to place it in a broader context, allowing the factor-mediated examination of any community-pressure case study. First, we briefly review the original approach. Then, we provide a detailed description of the extended framework, based on clearly stated definitions, assumptions, and mathematical formulations that can easily be transposed to any case study. We demonstrate how to apply it in two case studies. The first one focuses on the assessment of the vulnerability of a seabird community to offshore wind farms in the Bay of Biscay, which allows comparison of the original approach and illustrates the improvements of the revised framework. The second case study concerns the assessment of the vulnerability of the benthos community to trawling pressure in the Barents Sea and demonstrates how the framework can be successfully implemented in a very different context.

Methods

The initial approach: a short review of Garthe and Hüppop (2004)

The wind farm sensitivity index (WSI) proposed by Garthe and Hüppop (2004) is still the current methodological tool

implemented to map the vulnerability of seabird community to wind farm establishment (Christensen-Dalsgaard *et al.*, 2010; Leopold and Dijkman, 2010; Bradbury *et al.*, 2014). It is based on a seabird sensitivity index (SSI) that documents the sensitivity of seabird species to wind farm based on nine factors noted $F_{1,...,9}$ for each species *i.* $F_{1,...,4}$ refers to collision, $F_{5,6}$ to disturbance, and $F_{7,...,9}$ to the overall sensitivity of the species, expressed in terms of demography and conservation status.

Let us consider a study area divided in a succession of $j=1,\ldots,L$ locations and populated by a set of $i=1,\ldots,S$ seabird species. A_{ij} denotes the abundance of species i in location j. The WSI is defined as:

$$WSI_{j} = \sum_{i=1}^{S} \log(A_{ij} + 1) \times SSI_{i}$$
 (1)

$$SSI_i = \frac{F_{i1} + F_{i2} + F_{i3} + F_{i4}}{4} \times \frac{F_{i5} + F_{i6}}{2} \times \frac{F_{i7} + F_{i8} + F_{i9}}{3}$$
 (2)

Equation (2) integrates the vulnerability factors by making the following assumptions:

A1: The factors associated with collision, disturbance, and sensitivity are equally weighted, and their relationship is additive.

A2: Collision, disturbance, and sensitivity are equally weighted, and they interact multiplicatively.

Furthermore, a third assumption is made from Equation (1):

A3: The contribution of a given seabird species to the community vulnerability measure at a given location is proportional to its log abundance.

These assumptions can be called into question for a number of reasons. First, vulnerability factors related to the same pressure might not be independent and their relation may not be additive. For collision, for example, two factors (related to time spent flying and flight altitude) can be seen as primary factors for collision, while the two others (flight manoeuvrability and nocturnal activity) only matter if the species flies often at blade height. We can actually distinguish two categories of factors: primary factors that directly control the vulnerability, and aggravation factors that can increase a vulnerability that already exists. For seabirds, this hierarchy can be established not only for collision, but also for disturbance and sensitivity. For disturbance, two factors are being considered. One, ship and helicopter traffic, can be defined as a primary factor, while the second, habitat flexibility, only matters if the species is disturbed in the first place. Among factors related to overall sensitivity, those related to conservation status primarily determine the sensitivity of a species to any kind of pressure, while those related to demographic parameters (such as adult survival rate) correlate with a species capacity to replenish the population, and can therefore be seen as an aggravation factor (they only matter if the species suffers high mortality). If we recognize that vulnerability and sensitivity factors are not equal and they are subject to some hierarchy between primary and aggravation factors, then the mathematical formulation of SSI should be adapted therefore.

Assumption A2 is questionable as it states that different kinds of vulnerability are equally important and interact multiplicatively. In the seabird—wind farm example, collision and disturbance are two distinct pressure types, with different causes and consequences that might lead to different management measures (Drewitt and

Langston, 2006; Fox et al., 2006). However, since Equation (2) multiplies them in one single index, collision cannot be disentangled from disturbance. Moreover, the multiplicative link between collision, disturbance, and sensitivity can have another detrimental side effect: if one product term is close to zero then the whole product will also be close to zero and some important vulnerability could be missed. A much simpler alternative is to separate explicitly collision and disturbance, as advocated by Furness et al. (2013). It is therefore necessary to refine Equation (2) so that all pressure types can be explicitly disentangled and mapped separately.

Finally, assumption A3 gives more weight to areas where individuals concentrate. However, applying the weights at the species level, and using the log-abundance of species instead of simply the abundance introduces contradictions within the framework. For instance, rare species tend to be up-weighted by conservation status factors included in Equation (2). But when integrated spatially in Equation (1) rare species will be less abundant in the sea and then down-weighted in the final vulnerability assessment. The reverse effect is expected for abundant species. With the current formulation, there is no control on the magnitude of up-weight/down-weight of each species, which hinders interpretation of the spatio-temporal variations of the vulnerability maps. Besides, the use of log abundance assumes that the importance of a single individual in a location decreases exponentially as the total number of individuals in that location increases. A single individual in the middle of nowhere will have more weight than an individual located in a flock of 100 conspecifics. This assumption has neither ecological nor management support.

In the following section, we revise Garthe and Hüppop's methodology to take into account the caveats associated with assumptions A1, A2, and A3, and to allow a general transposition of the framework to different case studies.

Definitions

We focus on how to estimate the vulnerability of a given biological community to a specific, well-identified pressure, such as the establishment of new infrastructures, or the conducting of harvesting activity. These pressures may exert *impacts* on individuals. We understand impact as any detrimental effect an individual could suffer, should it be in the same location than the pressure under focus. The same pressure might affect this individual in different ways, that we will call *pressure types*, such as collision and disturbance in the seabird—wind farm example. The challenge is to establish how these pressure types, primarily exerted at the individual level, can be progressively integrated and quantified across individual, species, and community levels. Figure 1 provides a step-by-step summary of the method based on the seabird—wind farm example across these different levels of organization. Table 1 summarizes all mathematical notations used in this study.

First, we quantify the *individual vulnerability* to a given pressure type by combining together *vulnerability factors*, i.e. relative measures of elements controlling the probability of being impacted by a given pressure type. These vulnerability factors can relate to morphological, taxonomical, behavioural, or demographical traits.

Then, we will refer to *species sensitivity* as the strength of the impact that any pressure type may have on a species. Individuals from a given species can be vulnerable to a given pressure type, but if that species has a good regeneration capacity, then the impact is somewhat moderated. Conversely, a moderate pressure on a slow reproducing species may have stronger impact. In other words, individual vulnerability relates to the relative probability

that an individual from a given species is impacted by a given pressure type, while species sensitivity refers to the intrinsic vulnerability of the species to any pressure type. Species sensitivity is estimated by combining *sensitivity factors*, i.e. relative measures of elements describing species conservation status and their ability to recover from perturbations.

Species vulnerability will be the result of individual vulnerability weighted by species sensitivity, and finally, we will use *community vulnerability* when species vulnerability is integrated across several species.

In all vulnerability and sensitivity factors, we will establish a hierarchy between *primary* factors that directly control the vulnerability or the sensitivity, and *aggravation* factors that may not be important alone, but can increase an already existing vulnerability or sensitivity. All sensitivity and vulnerability factors will be scored between 0 and 1. A value of 0 indicates no sensitivity or vulnerability, and a value of 1 indicates maximum sensitivity or vulnerability. As these factors are all expressed on the same scale, they can be mathematically combined together.

Combining vulnerability and sensitivity factors

A simple way of combining factors is through either averaging or multiplication, as it was originally proposed by Garthe and Hüppop (2004). When averaging, compensation between factors is allowed, i.e. a low score for one factor can be balanced by a high score for another factor. This may be suitable when several factors of different nature are involved for a given pressure type. Another way of combining factors is multiplication, which may be convenient when factors are interacting, or when they are conditional to each other. Whether averaging or multiplication make sense depends on the factors considered, and has to be evaluated each time. As a default rule, however, we will use averaging when the factors are of different nature and compensation between them is a reasonable assumption, and we will use multiplication when factors are interacting or conditional to each other.

Averaging or multiplying factors does not recognize any hierarchy between factors though. Therefore, we propose a simple mathematical formulation that accounts for the hierarchy between primary and aggravation factors. Our suggestion is to use it as a default when no other model exists while hierarchy between primary and aggravation factors can be clearly argued for. The formula uses primary factors to determine the basic value of the vulnerability or sensitivity, while aggravation factors increase this basic value through an exponent. The relative importance of aggravation factors over primary factors is controlled by one parameter.

Let us denote the estimate of an individual vulnerability or species sensitivity as r, and let us assume that r is the combination of two factors: a primary factor, a, and an aggravation factor, g. We propose to link r to a and g through the following relationship:

$$r = a^{1-g/(g+\gamma)}$$
, where $a \in [0, 1], g \in [0, 1], \gamma \in [0.1, 1]$ (3)

Under this formulation, r=a when g=0, and then progressively increases as g increases. The parameter γ is a measure of the influence of g over r. The smaller the γ , the more influence g will have on r (Supplementary Appendix S1). We suggest to use $\gamma=0.5$ as a default, which means that $r=\sqrt[3]{a}$ when g=1. This choice is arbitrary, but ensures a balanced effect of aggravation factors over primary factors (Supplementary Appendix S1). In any case, we recommend using γ values between 0.1 and 1. Smaller values (i.e. $\gamma<0.1$) would lead to very strong effect of g, while larger γ values

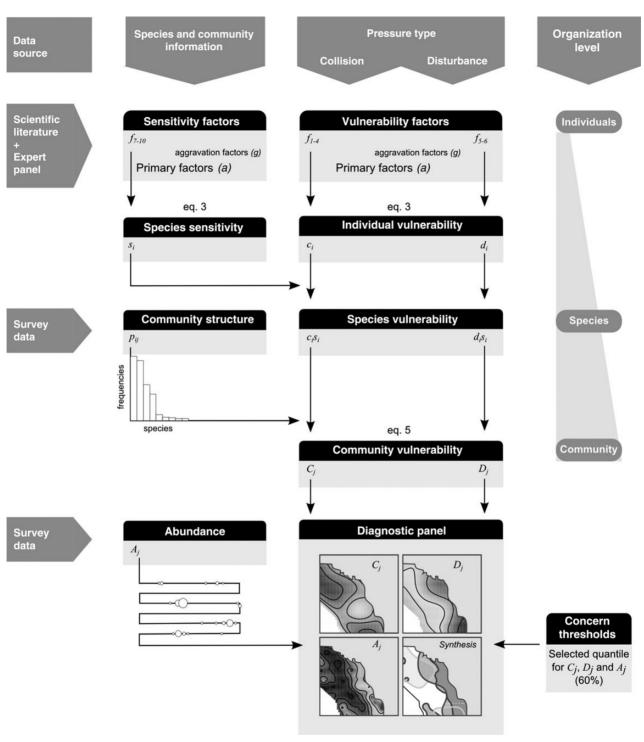


Figure 1. Summary of the method used to assess the impact of offshore wind farms on seabirds. The assessment keeps track of the different pressure types, and it is progressively integrated across individual, species, and community levels.

(i.e. $\gamma > 1$) would result in neglecting g. A sensitivity analysis on γ within this range of values further allows understanding the respective influence of primary and aggravation factors on the vulnerability assessment.

The vulnerability and sensitivity matrix F_{if}

Information on sensitivity and vulnerability factors for each species can be summarized in a matrix F_{if} of i = 1, ..., S rows and f = 1, ..., F

columns, where S stands for the number of species in the community and F the number of vulnerability and sensitivity factors identified as relevant to the vulnerability assessment. From F_{if} and Equation (3), specific formulae for estimating individual vulnerability and species sensitivity can be derived. This requires categorizing factors into either vulnerability or sensitivity factors, relating vulnerability factors to the different pressure types, and distinguishing primary from aggravation factors. Such categorization is

Table 1. Mathematical notations used in this study, together with definitions.

Notation	Definition	Can vary with
WSI	Wind farm sensitivity index	Location <i>j</i>
Α	Abundance	Species i at location j
SSI	Seabird sensitivity index	Species i
F	Vulnerability or sensitivity factor	Species i and factor f
r	Any individual vulnerability or species sensitivity	Species <i>i</i> and pressure type
g	Any group of aggravation factor	Species <i>i</i> and pressure type
а	Any group of primary factor	Species <i>i</i> and pressure type
γ	Parameter for the influence of aggravation over primary factors	Constant
С	Individual vulnerability to collision (seabird – wind farm case study)	Species i
d	Individual vulnerability to disturbance (seabird – wind farm case study)	Species i
S	Species sensitivity	Species i
$c \times s$	Species vulnerability to collision (seabird – wind farm case study)	Species i
$c \times d$	Species vulnerability to disturbance (seabird - wind farm case study)	Species i
р	Proportional abundance	Species i at location j
C	Community vulnerability to collision (seabird – wind farm case study)	Location <i>j</i>
D	Community vulnerability to disturbance (seabird - wind farm case study)	Location j
t	Individual vulnerability to trawling (benthos – trawling case study)	Species i
$t \times s$	Species vulnerability to trawling (benthos – trawling case study)	Species i
T	Community vulnerability to trawling (benthos - trawling case study)	Location j

Table 2. Vulnerability factors according to which species vulnerability has been assessed in both seabird – wind farm and benthos – trawling case study.

Seabird	windfarm	case study

	Short description	Factor type	Pressure type	Factor hierarchy
F ₁	Proportion of time spent flying	Vulnerability	Collision	Primary
F_2	Proportion of time spent at blade height	Vulnerability	Collision	Primary
F ₃	Flight manoeuvrability	Vulnerability	Collision	Aggravation
F_4	Nocturnal flight activity	Vulnerability	Collision	Aggravation
F ₅	Disturbance by ship and helicopter traffic	Vulnerability	Disturbance	Primary
F ₆	Habitat flexibility	Vulnerability	Disturbance	Aggravation
F_7	Species status in the international red list	Sensitivity	None	Primary
F ₈	Species status in the bird directive	Sensitivity	None	Primary
F ₉	Species status in the national red list	Sensitivity	None	Primary
F ₁₀	Adult survival rate	Sensitivity	None	Aggravation
Benthos-tr	awling case study			
F_1	Size	Vulnerability	Trawling mortality	Primary
F_2	Habitat relative to the sediment	Vulnerability	Trawling mortality	Primary
F_3	Mobility	Vulnerability	Trawling mortality	Primary
F ₄	Degree of vertical complexity	Vulnerability	Trawling mortality	Aggravation
F ₅	Softness of the external shell	Vulnerability	Trawling mortality	Aggravation

case-study-specific. It corresponds to the conceptual model linking the factors to vulnerability and sensitivity and is therefore a critical part of the vulnerability assessment. Table 2 summarizes the categorizations we used for our two case studies, which are detailed in the sections below.

Individual vulnerability and species sensitivity for seabird and wind farms

To estimate the vulnerability of seabird to wind farms, Furness *et al.* (2013) suggested the use of ten factors listed in Table 2 and detailed in Supplementary Appendix 2a. For each of the 30 seabird species in our study area, these factors have been scored between 1 (low vulnerability) and 5 (high vulnerability) and then divided by 5 to be comprised between 0.2 and 1 (all values given in Supplementary Appendix 2b). The factor classification we consider is detailed in

Table 2, and includes two pressure types, collision and disturbance. Therefore, for assessing the vulnerability of the seabird community to wind farms, the two individual vulnerabilities to these two pressure types need to be estimated, as well as species sensitivity.

Individual vulnerability to collision c_i can be estimated by using factors F_{i1} to F_{i4} (Table 2). Proportion of time spent flying (F_{i1}) and proportion of time at blade height when flying (F_{i2}) are naturally seen as primary factors. Flight manoeuvrability (F_{i3}) and nocturnal activity (F_{i4}) are seen as aggravation factors because they only matter if the bird actually flies at blade height. Individual vulnerability to collision c_i is therefore obtained by applying Equation (3) with $a_i = F_{i1} \times F_{i2}$ and $g_i = (F_{i3} + F_{i4})/2$. Spending time flying at blade height can be viewed as F_{2i} conditional on F_{1i} and therefore we use a multiplicative relationship between them. Conversely, we have no reason of assuming dependence between flight

manoeuvrability and nocturnal activity, at least concerning their contribution to the vulnerability of colliding with a wind farm. Therefore, we use an additive relationship between F_{i3} and F_{i4} .

Individual vulnerability to disturbance d_i is the combination of a primary factor, the intensity of the behavioural response to anthropic activity (F_{i5}) , and an aggravation factor, the flexibility of habitat use (F_{i6}) . Therefore, d_i is obtained by applying Equation (3) with $a_i = F_{i5}$ and $g_i = F_{i6}$.

The species sensitivity s_i results from the combination of the four last factors, three related to species conservation status at different scales, F_{i7} to F_{i9} , and the natural survival rate of the species (F_{i10}). Here, the primary sensitivity factors are the average conservation status over the three national, European, and international scales, while the natural survival rate of the species can be seen as an aggravation factor. Therefore, s_i is obtained by applying Equation (3) with $a_i = (F_{i7} + F_{i8} + F_{i9})/3$ and $g_i = F_{i10}$. Finally, species vulnerability to a given pressure type is computed simply by multiplying individual vulnerability to species sensitivity. Therefore, $c_i s_i$ represents species vulnerability to collision, and $d_i s_i$ species vulnerability to disturbance.

Individual vulnerability and species sensitivity for benthos and trawling

For the benthos-trawl case study, the structure of the vulnerability assessment was simpler. Five factors were considered, listed in Table 2 and detailed in Supplementary Appendix 3a. They all related to one pressure type: trawling-induced mortality. Three of them are primary factors, and two are aggravation factors. For each of the 355 benthos species in our study area, they have been scored between 1 (low vulnerability) and 3 (high vulnerability) and then divided by 3 to be comprised between 0.33 and 1. We used a rougher numerical scale for the benthos (1–3 compared with 1–5 for seabirds) because of the lower level of ecological information available for many species. Supplementary Appendix 3b shows the factor values for all the benthos species. No sensitivity factors were available for these benthic species, neither in the form of demographic parameters nor in terms of conservation status, simply because these organisms are poorly known.

The vulnerability factors for the benthos relate to morphological and ecological traits, namely size, habitat, speed, shape, and texture. These five traits are thought to affect the probability of a given benthic individual of suffering trawl-induced mortality in the following way: slow and larger animals living at the sea surface are likely to be caught if a trawl is carried out at their location, while quick and small animals living into the sediment will most likely escape. When caught, individuals with complex shapes and soft texture will more likely be damaged than ball or worm-shaped individuals with hard shells. Therefore, the estimate of trawling-induced individual vulnerability t_i is made using Equation (3) with size F_{i1} , habitat F_{i2} , and speed F_{i3} seen as primary factors as they directly control the probability of being caught in a trawl. On the other hand, shape F_{i4} and texture F_{i5} are seen as aggravation factors because they affect the probability of suffering damage once being caught. None of them is assumed to interact and, therefore, t_i is obtained by applying Equation (3) with $a_i = (F_{i1} + F_{i2} + F_{i3})/3$ and $g_i = (F_{i4} + F_{i5})/2$. As no measure of species sensitivity is available at the moment for the benthic community, we assumed that individual vulnerability to trawling equals species vulnerability to trawling.

Community vulnerability

The final step is to integrate species vulnerabilities into a measure for the whole community. To do so, we build upon the recent development of Leinster and Cobbold (2012) that modifies the classical estimate of Hill's diversity (Hill, 1973) to take into account species similarity:

$${}^{q}D^{Z}(p) = \left(\sum_{i=1}^{S} p_{i}(Z_{p})_{i}^{q-1}\right)^{1/(1-q)} \text{ where } q \in [0, +\infty].$$
 (4)

Where p_i is the proportional abundance of the ith species, and $(Z_p)_i$ a measure of the similarity between an individual of the ith species and an individual taken at random in the community. $(Z_p)_i$ is expressed between 0 (completely dissimilar) and 1 (identical) and it is usually measured through a set of traits for each species, as in classical functional diversity studies (Leinster and Cobbold, 2012). This index produces a diversity measure in effective species number, i.e. the number of equally abundant species required to obtain the same diversity measure. This is a recommended practice as it greatly eases the interpretation of the index (Tuomisto, 2010; Leinster and Cobbold, 2012). The introduction of the term $(Z_p)_i$ gives more weight to the highly dissimilar species.

Replacing $(Z_p)_i$ by (1-species vulnerability) in Equation (4) leads to a diversity measure that gives more weight to the most vulnerable species, that we interpret as a community vulnerability measure. In the formulations of Hill (1973) and of Leinster and Cobbold (2012), there is a parameter, q, which controls the sensitivity of the diversity metric to the weighting parameter, i.e. $(Z_p)_i$ for Leinster and Cobbold (2012). The lower q is, the higher the weight of dissimilar species over similar ones. As we precisely wish to give maximum weight to the most vulnerable species, we simply set q=0. After replacing these parameters in the original formulation and setting a spatial context where community data are available over $j=1,\ldots,L$ locations, the community vulnerability to a pressure type, collision for instance, is written as follows:

$$C_j = \sum_{i=1}^{S} \frac{p_{ij}}{1 - c_i s_i}.$$
 (5)

 C_j provides an estimate of the vulnerability of a community to a given pressure type in effective species number. It can be interpreted as the number of equally abundant and fully vulnerable species that compose the community in a particular location. This measure can be obtained for every pressure type, and we will in the following denote C_j the vulnerability of the seabird community to collision with wind farm, D_j the vulnerability of the seabird community to disturbance with wind farm, and T_j the vulnerability of the benthic community to trawl-induced mortality.

Presenting the output of community vulnerability assessment

The output of our framework is primarily constituted of a set of maps presenting the community vulnerability to each pressure type, C_j and D_j in the seabird—wind farm case; T_j in the benthos—trawling case. These community vulnerability measures are based on the species proportional abundance at each location p_{ij} . They fully account for species composition but leave total abundance aside. Total community abundance A_j at each location is therefore a natural complement to the community vulnerability measure which can easily be computed from survey data.

Therefore, we suggest the presentation of a diagnostic panel composed of (i) maps dedicated to the community vulnerability for each

pressure type, (ii) a map for total community abundance, and (iii) a synthesis map displaying this information jointly. In their pioneering work, Garthe and Hüppop (2004) proposed to use the 60% quantile to designate areas of concern. Based on this recommendation, we built concern thresholds map where only the 60% quantile isolines are presented. Such a map will quickly identify overlapping areas of high vulnerability and high abundances. The maps presented in this study were made by geostatistical interpolation based on spherical variogram models (Cressie, 1993; Pebesma and Wesseling, 1998) and ordinary kriging to ease the representation and interpretation of the spatial patterns. The interpolations were carried out on a 5 \times 5 km grid in the Bay of Biscay, and on a 20 \times 20 km grid in the Barents Sea.

Data collection and analysis for the seabird community, Bay of Biscay

Seabird populations on the French continental shelf of the Bay of Biscay have been extensively sampled through a series of aerial ("ROMER") and ship-based ("PELGAS") surveys extensively described in Bretagnolle et al. (2004), Certain et al. (2007), Certain and Bretagnolle (2008), and Certain et al. (2011). During ROMER surveys, strip-transect aerial surveys repeatedly covered the Bay of Biscay in the wintering period, from October 2001 to March 2002, offering a first exhaustive snapshot of the extent and abundance of the wintering population of seabirds in the Bay of Biscay. From 2003 onward, observers recorded top predator data from the RV-THALASSA during the PELGAS cruises that are carried out each spring in the Bay of Biscay. In the aerial and the boat surveys, the sampling scheme was systematic with perpendicular transects separated by ca. 20 km of each other. Seabird observations were collected continuously along each transect, including species identification and number of individuals. The sampling design homogeneously covered the entire study area (ca. 100 000 km²). For data processing, the transects were sliced into segments of 20 km, and in the discussion below the location subscript i stands for any such segment. The relative abundance of each species, i.e. number of counted individuals, was reported for each segment. To ease the comparison with previous studies, we use the whole ROMER dataset and the PELGAS dataset from 2003 to 2008. Individual vulnerabilities c_i , d_i , and species sensitivity s_i were computed for the 30 species and 7 groups within which unidentified sightings could be placed. For these, the factor value was computed as averages from the different species in the corresponding group, weighted by their respective proportions.

For the sake of comparison, we also applied Garthe and Hüppop's framework (2004) to our seabird dataset. We first used regression analysis to model the relationships between our c_i , d_i , s_i and their counterpart the SSI_i . We produced the WSI_j maps, and looked at the relationships between WSI_j and summed log abundance across species.

Data collection and analysis for the benthic community, Barents Sea

The Barents Sea is submitted to an intense fishing activity carried out through bottom trawling (Jakobsen and Ozhigin, 2011). Therefore, identifying areas where benthic communities will be most sensitive to trawling is important for the management of this marine ecosystem and the conservation of the benthic community. In 2011, an exhaustive snapshot of the Benthic community over the whole Barents Sea was gathered through a series of 391 bottom trawl stations during the Barents Sea Ecosystem Survey (Michalsen et al.,

2013). These trawl stations are placed according to a regular sampling grid every 50 km, and cover homogeneously the whole Barents Sea continental shelf (1 600 000 km²). All benthic invertebrates caught in the trawl were identified to the species level and weighted, resulting in a unique inventory of the distribution and abundance of 355 benthic species. These taxonomic categories are the result of an intense cooperation between Norwegian and Russian taxonomists on board of the survey vessels. This process, along with the data and the benthic community structure, is extensively described in Anisimova *et al.* (2010) and Jørgensen *et al.* (2015). For visualization purpose, we applied a cubic root transformation on the relative biomass of benthos per trawl (in kg).

Results

Diagnostic panels for seabirds in the Bay of Biscay

Values of c_i , d_i , s_i , and SSI_i can be viewed in Supplementary Appendix 2c, with a correlation analysis between them in Supplementary Appendix 2d that demonstrates that SSI_i is in fact much more influenced by disturbance and sensitivity than by collision. Figures 2 and 3 present diagnostic panels for seabirds in the Bay of Biscay based on winter aerial (ROMER) and spring boat surveys (PELGAS), respectively.

The ROMER-based panel clearly shows that during the wintering period, the Bay of Biscay is composed of different communities whose vulnerability to wind farms differs in space. East coastal communities are composed of species vulnerable to disturbance, while a large area in the Northwest of the Bay of Biscay is populated by species vulnerable to collision. The abundance map indicates that high abundances can be found both in areas of high collision vulnerability and high disturbance vulnerability, and this is clearly shown in the synthesis map of the diagnostic panel (Figure 2). Supplementary Appendix 4 furthermore shows that the synthesis map is robust to changes in the values of the parameter γ in Equation (3), using ROMER example.

The PELGAS-based panel shows that the spring situation differs from the wintering season. At that time, seabird abundances in the Bay of Biscay are reduced because several species have migrated northward for breeding. As a consequence, the seabird populations are either concentrated in the North of the Bay or in a coastal band, and vulnerability to collision and disturbance overlap.

Supplementary Appendix 2e shows that the assessment based on the original WSI and the 60% isoline would miss the collision-vulnerable community identified by the refined assessment in the Northwest of the Bay during the wintering period (ROMER). In spring (PELGAS), the results obtained by the original and the refined method are fairly in agreement. The correlation between WSI_j and summed log abundance is very high (Pearson's r=0.99 with ROMER data, and 0.98 with PELGAS data, p-value <0.01 in both cases, see Supplementary Appendix 2f), which means that conclusions drawn from WSI_j are in fact primarily drawn from summed log abundances and are not affected by SSI_j .

Diagnostic panel for benthos in the Barents Sea

Figure 4 shows the diagnostic panel for benthic organisms in the Barents Sea, which clearly highlights strong contrasts between the central Barents Sea and the surrounding area. Communities vulnerable to trawling are mostly localized on the Southern and western part of the Barents Sea, but also important vulnerability patches are observed in the North. Biomasses have almost a reverse pattern, being much higher in the whole northernmost areas. Two

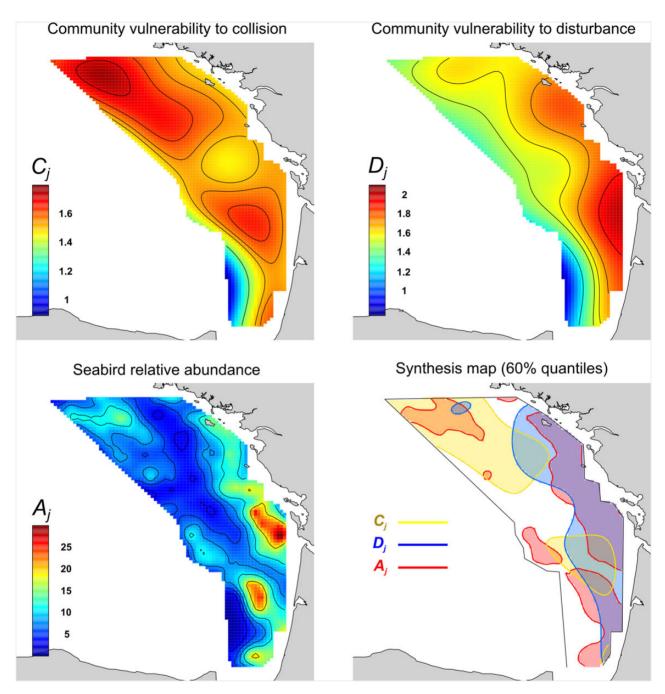


Figure 2. Diagnostic panel for ROMER data (wintering period: October 2001 – March 2002). The unit of A_j is the number of bird observed per 20 km of transect.

main areas where high vulnerability and high biomasses overlap can be observed in the Southwest and Northeast of the Barents Sea, and constitute a potentially critical area for the conservation of benthic organisms.

Discussion

Usefulness of the refined framework

The approach originally developed by Garthe and Hüppop (2004) has several useful features. The clear identification of species-specific vulnerability factors and the method for scaling them is

undoubtedly useful to synthesize quantitative and qualitative ecological information for impact assessment. It allows identifying which species are more likely to suffer which impacts, it is a catalyst for expert meeting groups, and it is a major methodological tool to reach a consensus between scientists and managers. However, the way this information is integrated and combined with survey data [Equations (1) and (2)] is not optimal, and critical information could be lost during this integration, as we demonstrate with the collision risk in the seabird—wind farm case study.

Our methodological approach solves these issues and extends the framework applicability to many case studies, as exemplified with

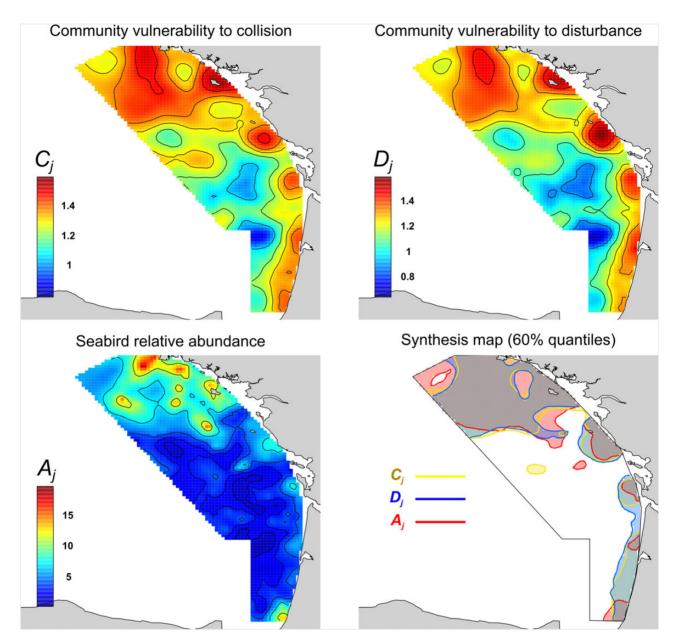


Figure 3. Diagnostic panel for PELGAS data (spring period: 2003 - 2008). The unit of A_i is the number of bird observed per 20 km of transect.

the benthos-trawling example. We introduce the hierarchy between primary and aggravation factors, and a way to combine them mathematically [Equation (3)], which permits a more accurate estimate of species vulnerability and sensitivity. In the seabird-wind farm case study, for example, SSI_i value for common guillemot Uria aalge and northern gannet Morus bassanus, two of the most abundant seabird species in the Bay of Biscay (Certain, 2007), are 18.00 and 12.38, respectively, making the guillemot much more vulnerable to wind farms than the gannet. With the new approach, the guillemot has $c_i = 0.23$, $d_i = 0.79$, and $s_i = 0.79$ while the gannet displays $c_i = 0.69$, $d_i = 0.52$, and $s_i = 0.74$. With these numbers, the vulnerability to disturbance and the sensitivity of the guillemot is clearly highlighted, but high collision risk for the gannet is also clearly emphasized. This is a fundamentally different interpretation with clear management implications. Using solely the SSI_i, all the attention would have been focused on a species that would not suffer collision, while the one actually experiencing greater mortality would have been disregarded.

Aggregating multiplicatively different pressure types as proposed in Equation (2) had undesired effects. As vulnerability to collision was averaged over four factors while vulnerability to disturbance was averaged over two factors only, vulnerability to disturbance was more likely to vary between species. Because of the multiplicative relationships, this increased variability was propagated to the SSI_i which therefore tended to over-represent disturbance over collision, which explains the correlation patterns observed in Supplementary Appendix 2d. This problem is now solved as we explicitly disentangle the different pressure types and assess them separately. The over-representation of one pressure type is a clear problem when different communities, vulnerable to different pressure types (collision and disturbance), are spatially separated, as it is the case in the Bay of Biscay during the wintering period.

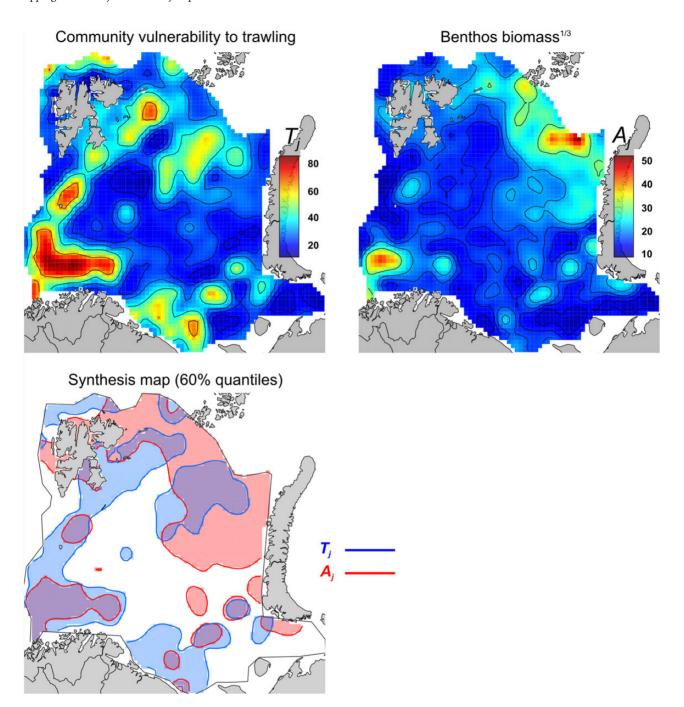


Figure 4. Diagnostic panel for the Barents Sea data (summer 2009). The unit of A_i is the cubic root of the benthic biomass in kilogramme per trawl.

Multiplying SSI_i by spatial log abundances to get WSI_j [Equation (1)] resulted in making a decision based on summed log-abundance patterns only (Supplementary Appendix 2f), instead of accounting for the additional information provided by the thorough documentation of all the vulnerability and sensitivity factors and the computation of the SSI_i . This was because the numerical differences in abundances of the different species in a location were much higher than their differences in sensitivity and vulnerability, even when abundances were log-transformed. Therefore, the product of SSI_i with summed log-abundance mostly depended on the latter, and as a side effect, all the efforts previously made to distinguish species based on vulnerability factors were unfortunately

dismissed in the WSI_j maps. Bradbury *et al.* (2014) recently proposed an assessment for sea areas around the UK using the WSI methodology. They separated collision from disturbance, but multiplied both by log abundances. Their maps of collision and disturbance pressure are very similar, which might well be an artefact of the log abundance multiplication. This problem is now solved by integrating vulnerability measures sequentially first at the species level and then at the community level in a way that is mathematically grounded in biodiversity statistics [Equations (4) and (5)], and by explicitly differentiating community composition from abundance.

Because our framework is clearly mathematically defined and all the assumptions are stated and written, we provide scientists with a

transparent and tractable method to transpose the factor-mediated vulnerability assessment methodology into many different case studies. For transposition purpose, some general guidelines can be phrased regarding the identification of vulnerability and sensitivity factors. Sensitivity factors should include demographical parameters, when possible, as they often play a critical role in the likelihood of suffering from pressure (Davidson et al., 2012). Gathering several vulnerability factors for each pressure type ensures that the result will not be too dependent on a single vulnerability factor, whose estimate can be uncertain for some species. The use of multiplication has stronger numerical consequences than averaging and therefore clear reasons should be advocated when deciding to use it. Multiplying vulnerability scores by abundances results in information loss in the context of vulnerability assessment. Both patterns should be kept separated.

A relevant characteristic of our approach, that in our opinion should be an important aspect of any vulnerability assessment, is that we do not attempt to synthesize all the information into one single map. Rather, we try to disentangle the different basic components of the assessment to present it in an integrated way to the managers. This is a key aspect of communication between scientists and managers. While scientists usually try to identify all the aspects of a problem, managers seek simple answers and synthetic visualizations. Our work illustrates well that, indeed, complex information related to the spatial distribution of hundreds of species can be synthesized in a few set of maps. However, information reduction has to be carefully designed and firmly theoretically grounded. Reducing complex problems to a single formula may result in an intractable mixing of information that becomes difficult to interpret and may overlook crucial aspects of the problem. The proposed diagnostic panel provides managers with all the pieces of information required to make informed decision without implicitly masking any component of the pressure. It is all the more important that, based on this method, management action may differ according to the pressure type. The summary map allows presenting this information in an even simpler way, while keeping track of the distinct pieces of information.

Lastly, the development we presented here, though focusing on one pressure over a given community, could be conveniently transposed within the context of cumulative impact assessment (Halpern et al., 2008; Coll et al., 2012; Maxwell et al., 2013). In these studies, the effects of multiple pressures on multiple ecosystems are being summarized through a weighted sum of terms where the weights reflect the expected effect of a given pressure on a given ecosystem. Instead of using these multiplicative weights, our formula for linking numerically primary and aggravation factor [Equation (3)] could be applied at the pressure level, allowing the explicit distinction between primary and aggravation pressures for each ecosystem. Furthermore, these cumulative impact assessments tend to focus on presence-absence data or presence probability estimates for ecosystems or species at a given site. Should they be extended to community data, then the use of the community vulnerability index we propose here [Equation (5)] would be appropriate as well.

Wind farm impact assessment in the Bay of Biscay

Our study clearly identifies areas of high and low expected impact on seabirds for the establishment of offshore wind farms, and it also provides a qualitative assessment of the type of pressure to be expected. However, the reader should be aware that the quality of such an evaluation depends not only on the consistency of the method, but also on the quality of the data. We have no doubt

that ROMER and PELGAS surveys provided state-of-the-art data on seabird populations. However, these surveys have spatiotemporal limitations that need to be clearly stated. First, both surveys focused on the continental shelf and therefore they do not document with detail the strictly coastal community, which is the reason we do not map abundance or vulnerabilities near the coast. Second, the timing of the surveys also limits the interpretation of our results. The ROMER surveys focused on the wintering period, which is the period during which the seabird community reaches the largest numbers in the Bay of Biscay (Certain, 2007). PELGAS surveys offer the spring perspective, when some of the main seabird taxa present in winter have left the area for breeding (e.g. auks). Therefore, the maps presented in this study can only serve for impact assessment during these periods. Further surveys and analyses should be carried out to provide a more complete picture for the whole year and the nearshore community. Finally, we would like to warn readers against comparison of seabird relative abundance between the two ROMER and PELGAS datasets. As the ship and aerial survey protocols differ, the relative abundances derived from the two datasets cannot be directly compared.

Trawling impact assessment in the Barents Sea

The application of our method for benthos vulnerability shows how to use benthos survey data at regional scale, and therefore complement and extend past vulnerability assessment based on qualitative information at global scale (Clark and Tittensor, 2010). Again, as for the seabird—wind farm case study, limitations in the benthos dataset need to be clearly stated. One problem is that we used community data issued from trawl bycatch, and therefore, our description of the benthic community composition is biased towards species that are actually caught. As a result, our vulnerability assessment is likely to overemphasize vulnerable communities. This has to be kept in mind when interpreting the vulnerability maps. Alternative sampling methods less subject to this problem, such as grabs or video recording (Beazley et al., 2013), exist, but they have not been implemented extensively at the scale of the entire Barents Sea vet.

The high trawling vulnerability recorded on the Southwestern Barents Sea is partly attributable to the abundance of several sponge species in this area (Jørgensen et al., 2015). Bottom trawling might have a severe impact on these slow-growing sponges, most likely requiring many years to re-establish themselves in a degraded area. The identification of large biomasses of highly vulnerable communities in the Northeastern part of the Barents Sea is an important result, as these areas were until now either not or only slightly impacted by the fishing activity. However, with a warming climate and the potential migration of several fish species of commercial interest (Hollowed et al., 2013), it is likely that some of these areas will be more and more targeted by fisheries. Therefore, the clear identification of these highly vulnerable communities can serve as guidelines for protecting some of these previously undisturbed communities from the potential impact of fisheries development.

Conclusion

As reviewed in the introduction, Garthe and Hüppop's method has already been adapted to evaluate other types of hazards in different taxa. By improving the method formulation and including the explicit link between an identified pressure and a biodiversity-related metric at the community level, we aim to contribute these numerous situations where community vulnerability assessments are needed. Indeed, our adaptation of the work of Leinster and Cobbold

(2012) can be applied to estimate the vulnerability of any kind of community to any kind of pressure. If a species-specific vulnerability parameter (such as c_i) is available and community distribution and abundance data have been collected, the application of Equation (5) is straightforward.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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