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New trophic indicators and target values for an ecosystem-based management of fisheries

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Abstract :

In the present study, we tested five trophic indicators and we demonstrated their usefulness to assess the environmental status of marine ecosystems and to implement an ecosystem approach to fisheries management (EAFM). The tested indicators include the slope of the biomass spectrum, the mean trophic level (MTL), the marine trophic index (MTI) and two newly developed indicators, the high trophic level indicator (HTI) and the apex predator indicator (API). Indicators are compared between current state and potential reference situations, using as case studies: the Celtic Sea/Bay of Biscay, North Sea and English Channel ecosystems. Trophic spectra are obtained from Ecopath models while reference situations are estimated, simulating with EcoTroph and Ecosim different fishing pressures including three candidate scenarios for an EAFM. Inter-ecosystems assessments are done using Ecopath models, simulations outputs and scientific surveys data to assess the current states of the studied ecosystems, contrast the reference situations and analyze the responses of all indicators. Sensitivity analyses are also conducted on the main simulation parameters to test the robustness of the chosen indicators. Ecosystems specific targets for EAFM are proposed for the five trophic indicators estimated from whole-ecosystem models, while in the Celtic Sea/Bay of Biscay ecosystem targets are proposed for the MTL (=3.85) and HTI (48%) estimated from standard bottom-trawl surveys. The HTI is proposed to be relevant for survey data and the API is recommended using whole-ecosystem models. We conclude that HTI and API show trends in ecosystems health better than MTI.

Keywords : Environmental status, Trophic indicators, Ecosystem-based management, Ecopath with Ecosim, EcoTroph

1. Introduction

Among the different anthropic pressures, the most impacting on the structure and functioning of marine ecosystems is overexploitation (Dayton *et al*., 1995; Jackson *et al*., 2001; Ma *et al*., 2013; Worm et *al*., 2006). Its persistence is known to have consequences on individuals, populations and entire communities (Shin *et al*., 2005). Generally, long-lived and large species, which are the predators in the system, are the most impacted due to their intrinsically slow biological turnover (Pauly *et al*., 1998; Gascuel *et al*., 2008). Thus, increasing fishing pressures result in the size and mean trophic level of exploited fish assemblage gradually declining, as does the mean trophic level of catches. Such change in fish assemblage and in the catch, known as „fishing down the marine food web‟ process (Pauly *et al.* 1998), has been observed in many ecosystem worldwide (see www.fishingdown.org). In Europe, a decrease in the mean trophic level of landings has notably been observed in the Bay of Biscay (Guenette and Gascuel, 2012), the Celtic Sea (Pinnegar *et al*., 2002) or the North Sea (Heath, 2005; Jennings *et al*., 2002). More generally, Gascuel *et al*. (2015) observed a decrease in the mean trophic level within all European seas, from the North Sea to the Iberian coast, not only for landings but also for survey data.

In Europe, political authorities adopted in 2009, the Marine Strategy Framework Directive with the aim to achieve a „Good Environmental Status‟ (GES) of marine ecosystems by 2020. This directive reinforces the emergent need for simple indicators, which has recently became a major concern in marine ecology and fisheries (Greenstreet and Rogers, 2006; Jennings and Dulvy, 2005; Rice and Rochet, 2005; Rochet *et al.*, 2005). In particular, part of the good environmental status of marine ecosystems, as defined by the European directive, refers to food web (D4) and implies to define valid indicators of food web health. Besides the mean trophic level, other indicators based on changes in biomass distribution between different trophic levels could be used to meet the directive requirements. This proposal emerges from the evidence that repercussions of overexploitation occur on the shape of biomass trophic spectra (Gascuel *et al*., 2005), even if their evolution and resilience against fishing pressure just begin to be investigated (Branch *et* al., 2010; Rombouts *et al*., 2013; Shannon *et al*., 2014). In the present paper, we propose new trophic indicators and demonstrate their usefulness.

A good indicator must be concrete, have a theoretical basis, be easily understandable, inexpensive, accurate, available over a long period of time, sensitive and quickly responsive and specific to a type of pressure (Rice and Rochet, 2005). Usually, absolute values of indicators have no meaning and observed values must be compared to reference states, especially looking to a less-exploited state of the ecosystem when available (Ainsworth *et al*., 2002; Lotze and Worm, 2009 ; Mackinson, 2001; McClenachan *et al*., 2012) or by generating it by simulation (Jennings and Blanchard, 2004; Ravard *et al*., 2014).

Here, we explored reference states using simulations which are supposed to predict the effects of an ecosystem approach to fisheries management (EAFM). Two scenarios assumed to represent an EAFM, were simulated, one derived from Froese *et al*. (in press) and the other from Worm *et al*. (2009). In both cases, scenarios can be simulated and related trophic indicators calculated using ecosystem models such as Ecopath with Ecosim approach (Polovina, 1984; Christensen and Pauly, 1992; Walters *et al*., 1997) and the more recently developed EcoTroph model based on the concept that an ecosystem can be represented by its biomass distribution across trophic levels, the biomass trophic spectrum (Gascuel *et al*., 2005; Gascuel and Pauly, 2009).

Thus, the present study aims at testing five trophic indicators, including two new candidates, and at exploring the ability of tropho-dynamic models to define targets related to an EAFM. (1) Based on the Celtic Sea/Bay of Biscay case study and using EcoTroph, we assessed the sensitivity of each indicators to an increasing fishing pressure. (2) Using EcoTroph we simulated fisheries scenarios assumed to represent an EAFM in various European seas, including the North Sea, the Celtic Sea and the Bay of Biscay, and we quantified the related target values for each indicator. (3) Based on Ecosim simulations, we propose target values for indicators derived from bottom trawl surveys and we compared theses values with trends observed over the last 20 years. We also performed sensitivity analyses on a selection of parameters of the models to test the robustness of chosen indicators, which would represent an innovative task towards GES.

2. Material and Methods

2.1. Indicators

Five trophic indicators are tested in the simulations.

• **Slope**: the slope of size spectra is well-known to be a marine ecosystem state indicator, as it becomes steeper with increasing fishing pressure (Rice and Gislason, 1996; Bianchi *et al*., 2000). However it was never tested in trophic spectra. In our study, it is calculated by a linear regression of log (biomass) function of the trophic level, beginning at the trophic level from 2.5 representing the higher biomass to avoid the unaffected part of the ecosystem. This indicator is not calculated in survey data, where a large proportion of the species is missing, especially for low trophic levels.

• **Mean Trophic Level (MTL)**: this indicator is proposed to reflect the effect of fishing on the food web (Jiming, 1982; Pauly *et al*., 1998). It is calculated by

$$\mathrm{MTL}=\sum(B_{TL}*TL)/B \quad (1)$$

where B_{TL} is the biomass at the trophic level TL ($\mathrm{TL}\geq 2$) and B the total biomass of consumers. It is expected that its value should decrease with an increasing fishing pressure.

• **Marine Trophic Index (MTI)**: it reflects the trophic structure of the upper part of the food web (Pauly and Watson, 2005). It is calculated as MTL of species whose trophic level is higher than a predefined threshold. The chosen trophic level threshold is 3.25, excluding the planktivores whose high biomass tends to vary widely mainly in response to environmental factors.

• **High Trophic Indicator (HTI)**: this indicator has been developed for this study represents the percentage of consumers with a trophic level equal or higher than 4 in the ecosystems, which is a threshold for top predators, excluding small and intermediate pelagics (Essington *et al.*, 2006; Shannon *et al*., 2014). It is expected that its value should decrease with the depletion of large individuals caused by an increasing fishing pressure.

• **Apex Predator Indicator (API)**: this indicator has also been developed for this study and is calculated as HTI, except that it represents the percentage of top or apex predators (i.e. trophic level ≥ 4) on the total of predators excluding planktivores (i.e. trophic level ≤ 3.25). The values of this ratio are expected to decrease with the depletion of large individuals caused by an increasing fishing pressure and be less sensitive to annual biomass fluctuations compared to HTI.

2.2. Pre-existing models and scientific surveys

The study focuses on the Celtic/Biscay ecosystem and complementarily on the North Sea and the English Channel (Figure 1). For every area a pre-existing model was selected:

• The Celtic/Biscay 2012 model is based on the 1980 model built by Guénette and Gascuel (2009) and updated by Bentorcha *et al.* (in press). It was originally developed to assess the fishing impact on this ecosystem. An Ecosim model was fitted on time series of landings and fishing mortality (F) between 1980 and 2012. The model considers 38 trophic groups including 31 exploited groups.

• The Bay of Biscay continental shelf food web model of Lassalle *et al*. (2011, 2012) was originally developed for the structure and functioning understanding of this ecosystem, with emphasize on the ecological roles played by top predators and small pelagics. The model considers 32 trophic groups including 11 exploited groups and represents a typical year between 1994 and 2005.

• The North Sea model of Mackinson and Daskalov (2007) was built as a tool for ecosystem-based management. Its two principal aims are the quantitative description of the ecological and spatial structure of species assemblages in this ecosystem and to calibrate the dynamic responses of the modeled system by comparison with observed historical changes. It includes an Ecosim model and an Ecospace model. The model considers 68 trophic groups including 48 exploited groups and represents the ecosystem for the year 1991.

• The Western English Channel model of Araújo *et al*. (2008) was built to describe the properties and the trophic interactions in the ecosystem and to explore the effects of changes in phytoplankton production and fisheries. The model considers 52 trophic groups including 40 exploited groups and represents the ecosystem for the year 1994.

For the last part of the study, survey data from the different areas are used to assess ecosystem health states. They come from three demersal trawl surveys: EVHOE, IBTS and CGFS (Figure 1).

• EVHOE (Evaluating fisheries resources in Western Europe) survey data are divided in two subunits representing two covered areas according the Ecopath models we used. Thus, the first area covers the Bay of Biscay during the period 1987-2012, while the second covers also the Celtic Sea during the period 1997-2013. The surveys occur every year in autumn between 43.7°N and 47.9°N concerning the Bay of Biscay area and 43.7°N and 51.8°N concerning the Bay of Biscay and the Celtic Sea. Sampling follows a stratified random design in the study area. The bathymetric range is relatively wide (13-623 m for the Bay of Biscay; 13-587 m for the Celtic Sea / Bay of Biscay). The sampling gear was a GOV trawl 36/47 with 4 m vertical opening, 20 m horizontal opening and a mesh size of 20 mm in the codend.

• IBTS (International Bottom Trawl Survey) data cover the North Sea during the period 1983-2013. The surveys occur every year in the first trimester between 51.1°N and 61.4°N. The bathymetric range is 10-270 m. The sampling gear is a GOV trawl 36/47 with a wide vertical opening. Surveys are realized by four similar vessels (French, Belgium, Danish and German).

• CGFS (Channel Ground Fish Survey) data cover the Eastern English Channel during the period 1988-2013. The Surveys occur every year in the first trimester between 49.3°N and 51.3°N. The bathymetric range is 7-84 m. The sampling gear was a GOV trawl 36/47 with 3 m vertical opening, 10 m horizontal opening and a mesh size of 20 mm in the codend.

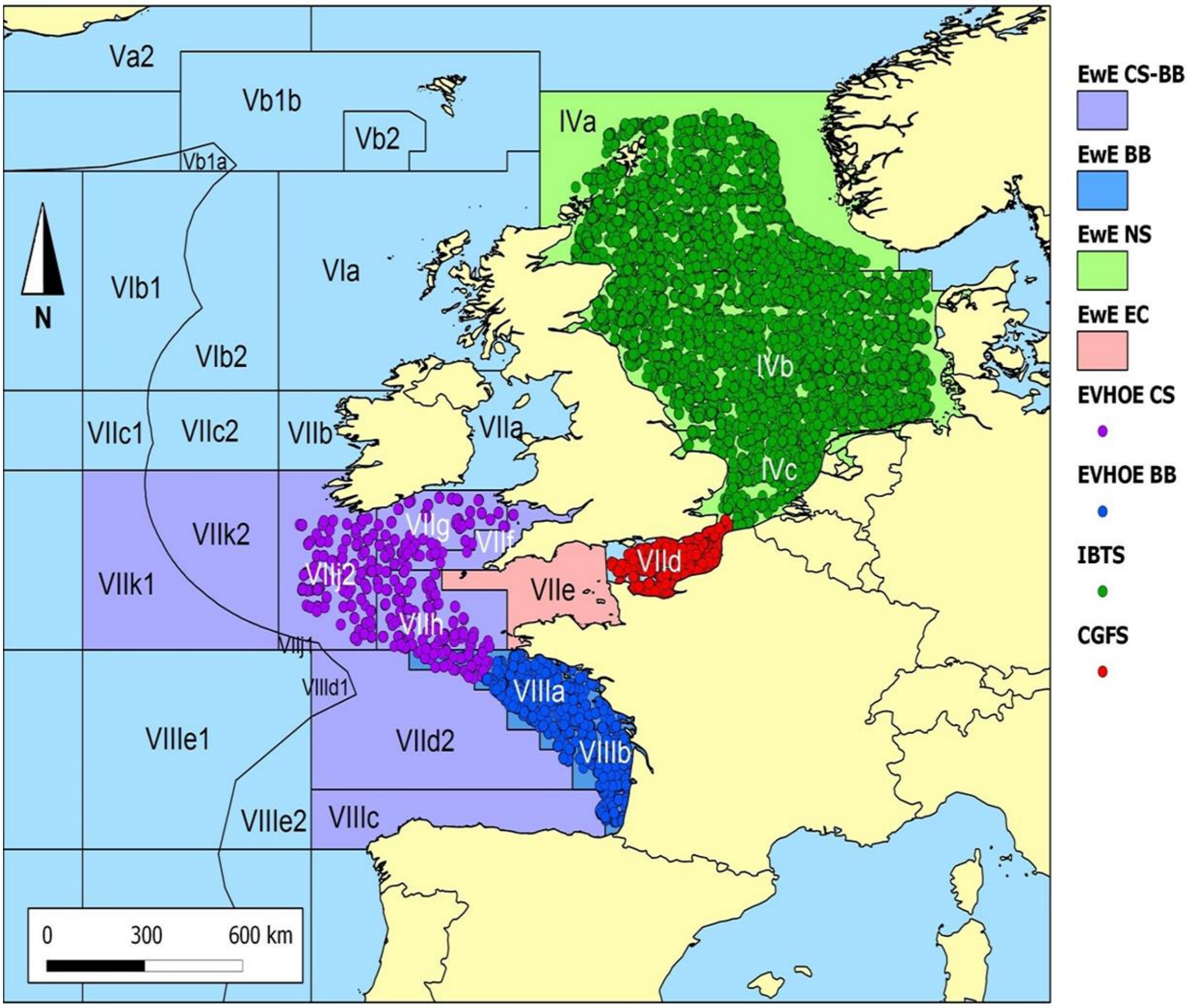

Figure 1. Coverage of studied areas for available models and survey. ICES divisions VIIe, VIIIa and VIIIb are also included in the Celtic Sea / Bay of Biscay model. CS/BB: Celtic Sea / Bay of Biscay; BB: Bay of Biscay; NS: North Sea; EC: English Channel.

2.3. EcoTroph simulations

Fishing-induced changes in the five indicators were simulated in the four ecosystems using EcoTroph (ET), a modeling approach complementary of Ecopath with Ecosim (EwE) (Gascuel and Pauly, 2009; Gascuel *et al*., 2011). In ET the functioning of the food web is represented as a biomass flow surging up from low to high trophic levels, due to predation and ontogeny. This flow suffers loss caused by respiration, excretion and natural mortality except predation and is characterized by a trophic kinetic, variable according to the trophic level and which defines the speed of biomass transfers within the food web. ET equations are fully detailed in Gascuel *et al*. (2011). Based on a pre-existing Ecopath model, resources required for the construction of an ET model are minimal. The „create.ETtranspose‟ function is used to represent an Ecopath model in trophic spectra of biomass, catches, fishing mortality, *etc*., while the „create.ETdiagnosis‟ function allows to simulate different fishing scenarios, by multiplying the current fishing effort (Gascuel *et al*., 2009). When the fishing effort is multiply by 0, a hypothetic virgin state is simulated.

For ecological and/or technological reasons, the entire biomass of an ecosystem is not accessible to fisheries. Therefore, an accessibility parameter has to be defined for all Ecopath trophic groups. In the four models used in the study, the accessibility value was given by authors only for the Celtic/Biscay and Bay of Biscay continental shelf models. For the North Sea and English Channel models, a conventional accessibility=0.8 is given to all exploited groups. The other values required to run ET are the names of the trophic groups, their biomass, their production rate and their catches (i.e. sum of landings and discards from the Ecopath model).

Within an Ecopath trophic group individuals do not have the same trophic level. Therefore, the „create.ETmain‟ routine builds trophic spectra by distributing the biomass of each group around its average trophic level to a lognormal distribution. In the study, default parameters of the „create.ETmain" function are used to specify the lognormal distribution of each group (Colléter *et al*., 2013).

The „create.ETdiagnosis" routine, devoted to the simulation of changes in the fishing mortalities, requires two additional user-defined parameters, the α TopD and the γ FormD coefficients. The former represents the fraction of the natural mortality depending on predator"s abundance, and expresses the intensity of top-down controls. It ranges between 0 (i.e. bottom-up dominated situation) and 1 (i.e. natural mortality of prey exclusively dependent on predators abundance), with a default value fixed at 0.4 (Gascuel *et al*., 2009). The γ FormD coefficient is a shape parameter which defines the functional relationship between prey and predators. It ranges between 0 and 1 (situation where predator abundance has a linear effect on the speed of the flow of their prey) with a default value fixed at 0.5 (Gascuel *et al*., 2009). In the current study, default values were used for α and γ, and we also performed sensitivity analyses on those two parameters.

2.4. Ecosim simulation and analysis of survey data

Trends in indicators for bottom trawl surveys were simulated in the Celtic/Biscay ecosystem using Ecosim and calculated from field data in the four ecosystems. Within Ecosim, predator-prey relationships are considered to explore temporal evolution of ecosystems based on the „foraging arena theory", which splits the prey biomass in two parts, the vulnerable prey and the invulnerable (Walters *et al*., 2009). The model can be adjusted on catches and biomass temporal series, especially available in stock assessment documents. By applying desired forcing parameters, Ecosim is able to become an exploration tool for the consequences of changes in the biomass or catches in a group over the others in a given year. Two major equations lead the predictions in Ecosim: the dynamic estimates of biomass over time and the amount of consumption by predators on their prey at a specific point of time. The latter is controlled by the vulnerability parameter which determines top down or bottom up control. The method and theory of Ecopath and Ecosim modeling are detailed in the EwE user guide (Christensen *et al.*, 2005). Ecosim was fitted to time series, and thus is available for simulations, in the Celtic/Biscay model only. It was used to simulate various scenarios related to EAMF, selecting functional groups in order to mimic the related trends which would be observed for demersal finfish in survey data.

Furthermore, current values of indicators were calculated in the four studied areas, based on survey data. Preliminarily, species caught in bottom trawl survey were selected to represent approximately 99% of the biomass of demersal fish community on the total of all years in each survey. The conger *Conger conger* was excluded from the selection as only a small fraction of the resident individuals were available to the survey at each hauls. Indeed this species inhabits the continental shelf and the rocky shelf-slope areas which offer many refuge opportunities (Xavier *et al*., 2010).

A length at which a species is considered to be correctly selected by the sampling gear of a survey (L_s) was determined for each species with the method used by Ravard *et al*., (2014) (Appendix 1). This survey selectivity is defined as a species catchability-availability. The potential case of large individuals not being covered by the survey (e.g. large *Merluccius merluccius* individuals) is not considered in the study.

Individual weights are calculated from the individual sizes available in the survey data using the length-weight relationship

$W(t)=aL(t)^b$ (2)

with values for the a and b coefficients from the literature (Appendix 2).

A trophic level was assigned to each species in the survey data. The trophic level values were taken from previous studies, ecosystem models, isotopic analysis, stomach contents or

Fishbase (www.fishbase.org) (Appendix 3). Because of the potential diversity of sources, the sequence to choose the "most confident" value for each species is as follow:

Local EwE estimate > close EwE estimate > local stomach contents estimate > nonlocal stomach contents estimate > local isotopic estimate > close isotopic estimate > Fishbase estimate.

Close estimate designate values from border ecosystems. The proportions of values pertaining to the three first "confidence" categories represented 45%. Furthermore only values corresponding to sexually mature individuals were kept to dampen any bias associated with diet changes due to ontogenic shifts.

Trends in indicators from field data are smoothed using a mobile average of five years to counteract the inter-annual variability and the small number of tows conducted yearly.

2.5. Testing fishing scenarios

In order to determine the trends in indicators values with the fishing pressure, simulations are realized with the EcoTroph R package (Colléter *et al*., 2013; http://sirs.agrocampus-ouest.fr/EcoTroph) with several fishing mortalities multipliers, from mF=1, the current state, to mF=5 with a splitting of mF=1. On the other hand a virgin state (i.e. mF=0) is simulated.

The fixed parameters of the „create.ETdiagnosis‟ function used for the simulations are: (*fleet.of.interest*=FALSE; *same.ME*=FALSE; *B.Input*=FALSE; *Beta*=0.2; *TopD*=0.4; *FormD*=0.5; *TLpred*=3.5).

In addition, two scenarios supposed to simulate an EAFM were considered, one derived from Froese *et al*. (in press), and the other from Worm *et al*. (2009). Froese *et al*. (in press) argue that three simple rules should characterize an EAFM, in order to minimize the impact of fishing: (1) according to Gulland (1971) and Shepherd (1981), the fishing mortality F has to be lower than the natural mortality M, (2) population size must be maintained above half of unexploited abundance to preserve the species functions in the ecosystem and (3) size at first capture has to be adjusted to let fish grow and reproduce. According to the first assumption, an exploitation rate F=M could be considered as a management target in accordance with an EAFM. Worm *et al*. (2009) have demonstrated that an exploitation rate of F=0.2 at community scale should permit obtaining at the same time: (1) catches equal to approximately 90% of their maximum, (2) a slightly reduced mean maximum length, (3) a total biomass comprised between 60% and 65% of its maximum, and (4) less than 5% of species collapse. Thus F=0.2 represents another potential target for an EAFM. The ET package did not allow to perform actually this kind of simulations and a modification of the „create.ETdiagnosis" function was thus operated. That modification enables to assign an accessible fishing mortality (*fish_mort_acc*) between 0 and 1 or equal to natural mortality of any trophic group. Two different interpretations of the management targets were tested. While F=M is only applied on the groups exploited over the fishing mortality target, F=0.2 is applied on the groups exploited over the fishing mortality target (F=0.2 scenario) in the first interpretation and on every groups exploited in the ecosystem (F=0.2* scenario) in the second one (Figure 2). The same simulations of EAFM scenarios were operated with the Ecosim model to estimate targets for the Celtic/Biscay ecosystem survey data.

If F is an indicator of trophic levels targeted by fisheries, the impact on the ecosystem should be brought to light by the fishing loss rate, which measures the proportion of production captured by year (Gasche *et al*., 2012). So both types of fishing responses are presented.

Sensitivity analyses have been performed on target values of indicators for Celtic/Biscay ecosystem model. Indicators sensitivity were tested for three user-defined parameters of ET, the top-down α and shape γ parameters, and the accessibility. These parameters are tested one by one for a range of values while all other parameters remained constant.

A summary of all analyses used is given in Figure 3.

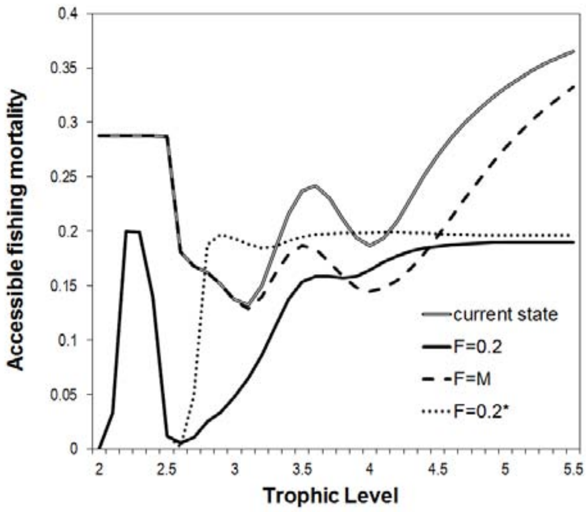

Figure 2. Accessible fishing mortality variability with trophic level in the current state and the EcoTroph simulations of three ecosystem-based management scenarios F=0.2, F=M and F=0.2* on the Celtic Sea / Bay of Biscay ecosystem model.

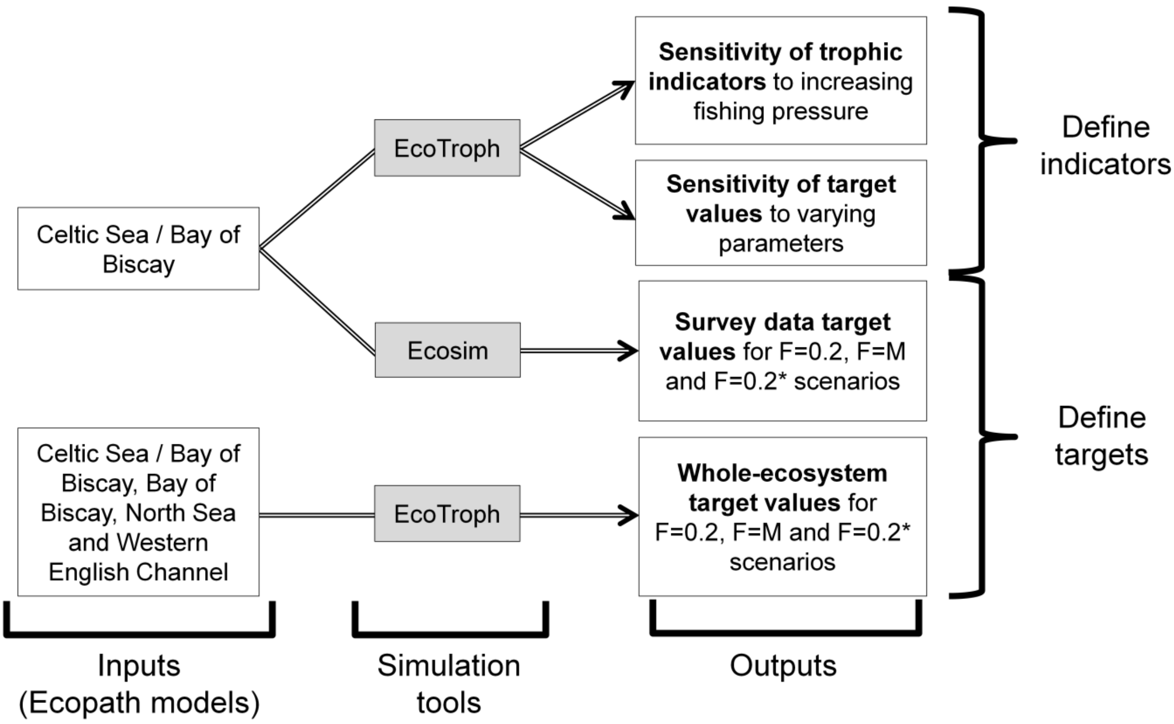

Figure 3. Summary of inputs used, simulation tools and outputs produced in the study.

3. Results

3.1. Indicators trends with increasing fishing pressure

In ET simulations for the Celtic/Biscay ecosystem the biomass of high trophic levels tend to decrease with an increasing fishing pressure (Figure 4). The slope of trophic spectra, the high trophic level indicator HTI and the apex predator indicator API present a stronger sensitivity to fishing pressure compared to the mean trophic level MTL and the marine trophic index MTI (Figure 5). It is worth mentioning that the slope comparison is permitted by the constancy of the modal value in each mF. In term of absolute values, MTL varies of more than 0.1 trophic level between virgin state and the highest fishing pressure, while MTI varies of 0.2 trophic level within these bounds. Concerning the two new candidate indicators, HTI and API, values are expressed in percentage, with higher differences in absolute values for API (i.e. from 32.9% to 15.8%) than for HTI (i.e. from 6.0% to 1.6%).

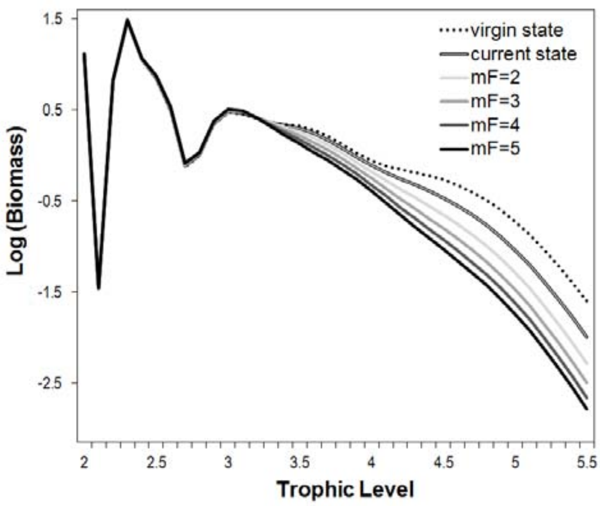

Figure 4. Biomass trophic spectrum changes with current state and simulations of virgin state and increasing fishing pressure on the Celtic Sea / Bay of Biscay ecosystem model.

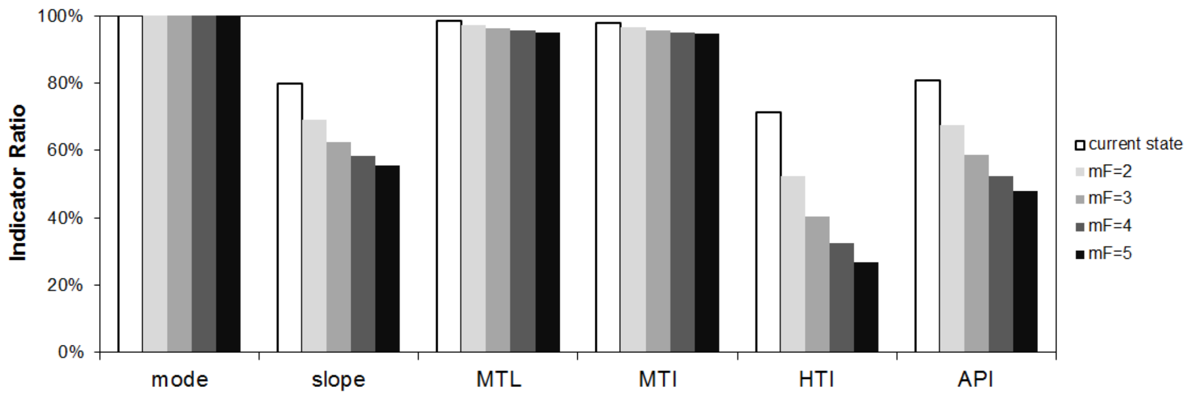

Figure 5. Indicators ratio changes of mode, slope, MTL, MTI, HTI and API with increasing fishing pressure simulations on the Celtic Sea / Bay of Biscay ecosystem model. The indicator ratio is the ratio of an indicator value on the virgin state indicator value.

3.2. Effects of ecosystem-based management scenarios on trophic spectra

Effects of the different management scenarios simulated in the Celtic/Biscay ecosystem on fishing loss rate, catches and biomass are observed using trophic spectra (Figure 6). The fishing loss rate is reduced in all scenarios compared to the current state, with exception for between TL=2.6 and TL=3.3 for the F=0.2* scenario, where a fishing mortality equal to 0.2 is applied to all exploited groups. High trophic levels are less exploited with F=0.2 and F=0.2* than with F=M and exploitation is kept at the same level as in current state in low trophic levels with F=M but not in the others. Compared to the current state, the various simulated scenarios lead to slight changes or to a decrease in the catches in almost all trophic levels, with the exception in intermediate trophic levels with F=0.2* and in the surrounding of TL=4 with F=0.2 and F=0.2*. For every scenarios the biomass increases in high trophic levels, from TL=4 to TL=5.5, in comparison to the current state. We also observe that biomass is slightly reduced with the F=0.2* scenario for intermediate TLs (i.e. between TL=3.5 and TL=4).

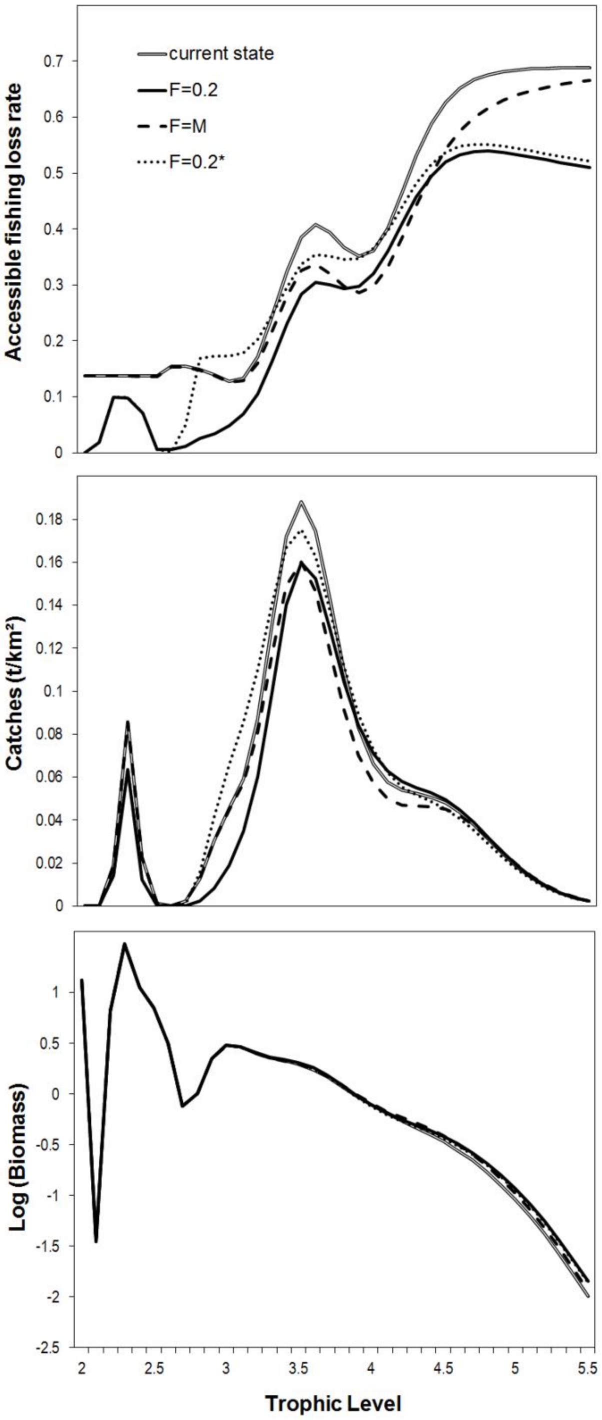

Figure 6. Accessible fishing loss rate, catch trophic spectrum and biomass trophic spectrum with of the current state with simulations of three ecosystem-based management scenarios F=0.2, F=M and F=0.2* on the Celtic Sea / Bay of Biscay ecosystem model.

3.3. Target values of indicators and inter-ecosystems assessment

In all studied ecosystems, target values of indicators are relatively close regardless of the simulated scenario and values of the current state are always equal or lower than any scenarios including the virgin state (Figure 7; Table 1). In the Celtic/Biscay, the North Sea and the English Channel ecosystems notably, only thin differences are observed (e.g. less than 1% for the API). In the Bay of Biscay the F=M scenario diverges a little more compared to the others, especially in MTI, HTI and API indicators.

Table 1. Values of current state and ecosystem-based management targets of slope, MTL, MTI, HTI and API for three different scenarios in the different ecosystems. The ecosystem-based management targets are obtained by EcoTroph simulations.

		slope	MTL	MTI	HTI (%)	API (%)
Celtic Sea / Bay of Biscay	current state	-1,67	2,61	3,76	4,27	26,78
	F=0,2	-1,56	2,62	3,78	4,63	27,89
	F=M	-1,60	2,62	3,78	4,64	28,32
	F=0,2*	-1,57	2,62	3,78	4,44	27,57
Bay of Biscay	current state	-1,73	2,69	3,68	4,91	17,18
	F=0,2	-1,64	2,70	3,70	5,34	18,51
	F=M	-1,73	2,69	3,68	4,83	16,93
	F=0,2*	-1,65	2,69	3,70	5,23	18,53
North Sea	current state	-3,35	2,90	3,53	1,16	9,29
	F=0,2	-3,11	2,91	3,55	1,37	10,68
	F=M	-3,21	2,90	3,54	1,25	9,91
	F=0,2*	-3,16	2,90	3,54	1,22	10,70
English Channel	current state	-3,29	2,33	3,53	0,58	7,74
	F=0,2	-3,07	2,34	3,55	0,73	9,39
	F=M	-3,09	2,34	3,55	0,70	8,99
	F=0,2*	-3,08	2,33	3,55	0,73	9,44

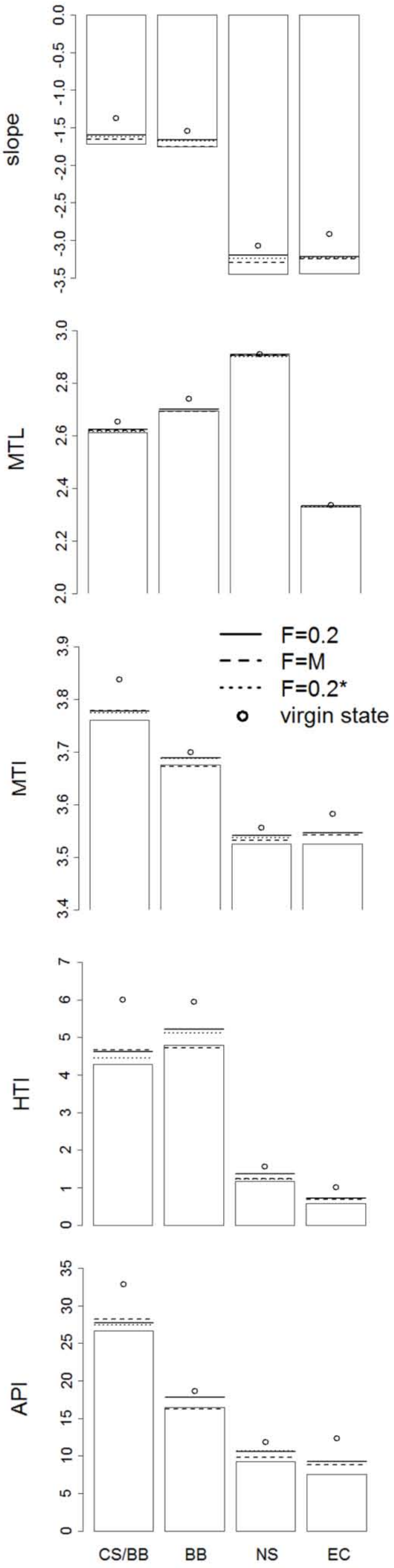
slope
MTL
MTI
HTI
API
F=0.2
F=M
F=0.2*
virgin state
CS/BB
BB
NS
EC

Figure 7. Raw indicator values of slope, MTL, MTI, HTI and API for current state and three ecosystem-based management scenarios F=0.2, F=M and F=0.2* in the different ecosystems. CS/BB: Celtic Sea / Bay of Biscay; BB: Bay of Biscay; NS: North Sea; EC: English Channel.

The TL difference across highest and lowest values in ecosystems is 0.3 for the MTL while it is slightly lower (0.2) for the MTI. The percentage difference is approximately 4% for the HTI and nearly 20% for the API. In almost every cases the target values simulated using EAFM suggest a better health of the ecosystem than the current state, with exception for MTL using F=0.2* in the North Sea and for almost all indicators using F=M in the Bay of Biscay. Current and target values of slope, MTL and MTI are almost equal, while HTI and API allow discerning ecosystems. The raw values of slope, MTI, HTI and API in models are the highest based on the Celtic/Biscay and the Bay of Biscay models. The same pattern is displayed concerning indicator ratio (current/target) (Figure 8). In the survey indicators, the slope of trophic spectra, conventionally calculated between TL=2.5 and TL=5.5, cannot be estimated because low trophic levels are absent due to the bottom trawl selectivity. For MTI, HTI and API, Bay of Biscay ecosystem exhibit high values, while Celtic/Biscay has clearly the lowest for HTI and API (almost 20% less predators than other ecosystems in both cases) (Figure 9). The North Sea exhibits lower raw values in models than the Bay of Biscay, except for MTL, higher compared to the others ecosystems. The values of indicator ratios of the North Sea are medium, and values of MTI, HTI and API in survey indicators are among the highest. The English Channel values remain the lowest for all the raw values of indicators in models, HTI and API in indicators ratios and among the lowest in survey indicators. These results suggest too that the Bay of Biscay and in a lesser extent the North Sea would be healthier compared to others while the English Channel would be the most degraded ecosystem.

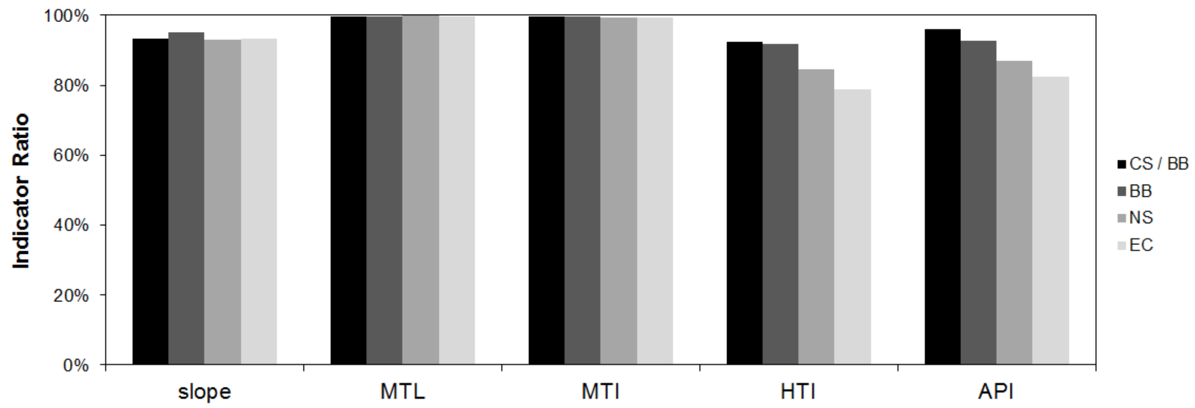

Figure 8. Indicator ratio values of slope, MTL, MTI, HTI and API for current state of the different ecosystems. CS/BB: Celtic Sea / Bay of Biscay; BB: Bay of Biscay; NS: North Sea; EC: English Channel. The indicator ratio is the ratio of an indicator value on the virgin state indicator value.

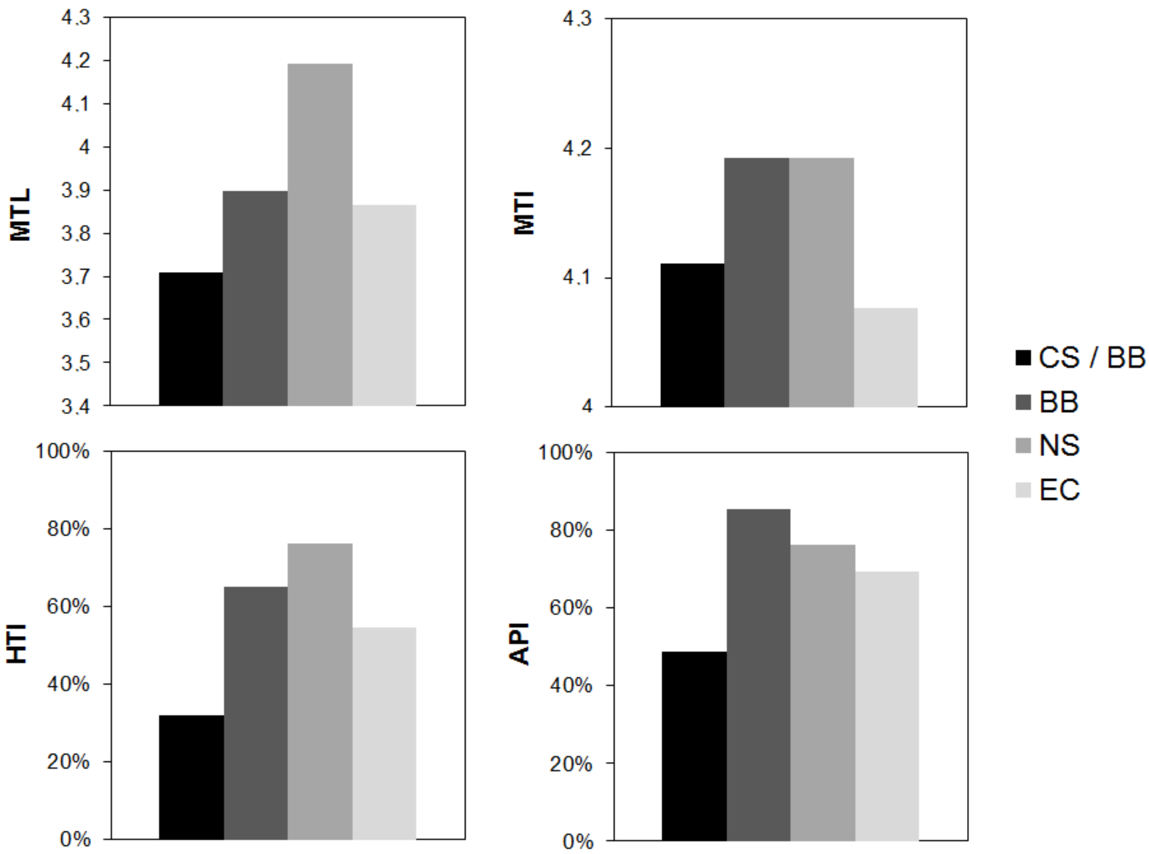

Figure 9. Raw indicator values of slope, MTL, MTI, HTI and API for current state in survey data for different ecosystems. CS/BB: Celtic Sea / Bay of Biscay; BB: Bay of Biscay; NS: North Sea; EC: English Channel.

3.4. Estimate of target values from bottom trawl surveys

Time series of indicators assessed from the Ecosim Celtic/Biscay model and target values estimated for EAFM scenarios are compared with temporal trends observed in EVHOE survey for the demersal community (Figure 10). Values estimated for the survey data lay within or close to the Ecosim estimates for MTL and HTI. These two indicators, related to the whole trophic spectrum, are both increasing after 2006 in Ecosim series, and successively increasing and decreasing in survey data, reaching a maximum value between 2004 and 2006. Regarding MTI and API, which are indicators related to the highest part of the trophic spectrum, estimates from the survey data are widely above those estimated from the Ecosim time series or simulated scenarios. Such a result suggests that selecting the demersal finfish within the Ecopath trophic groups is not a sufficient restriction to mimic what happens in survey data that is in the highest part of the trophic spectrum. Nevertheless, trends in indicators are consistent between survey and Ecosim estimates.

Target values related to the three ecosystem-based management scenarios are very close one to another in the survey data, with a target value equal to 3.85 for MTL and 48% for HTI. Time series of these two indicators estimated from Ecosim never reached the target values, while values observed from survey data were equal to or higher than targets in the mid-2000s. Due to inconsistencies between survey and Ecosim estimates, target values are not specified for MTL and API.

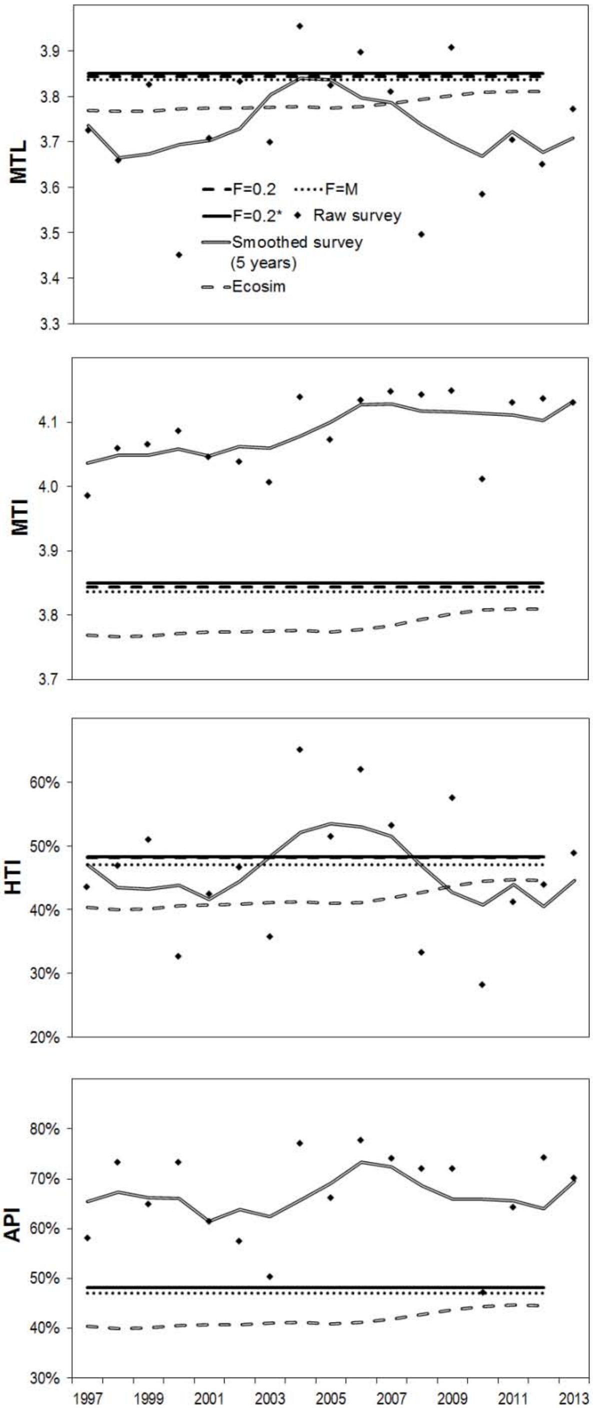

Figure 10. Survey data Ecosim indicators trends of MTL, MTI, HTI and API compared to three ecosystem-based management scenarios F=0.2, F=M and F=0.2* in the Celtic Sea / Bay of Biscay ecosystem.

3.5. Sensitivity analyses

Sensitivity analyses underline that relative values (i.e. current/target) globally show little sensitivity to α TopD and γ FormD parameters (Figure 11). Whatever the value of the tested parameter, and for all EAFM scenarios, current values of indicators are estimated below the target for slope, HTI and API, while once again sensitivity of MTL and MTI appears very low. The F=M management target is the less impacting scenario for almost all the indicators as its variation remains either constant (especially for slope and API, with values equal to 93% and 90% respectively) or lies with 4% of variation (for HTI, from 90% to 94%). For the two other scenarios (F=0.2 and F=0.2*), an increase in the assumed strength of top-down controls decreases the values of the targets, and thus leads to a more optimistic diagnostic (i.e. current/target ratio closer to 100%).

Sensitivity of the accessibility parameter in the estimation of the indicators is a little more pronounced than the α TopD and γ FormD parameters. For instance the wider changes occur in the F=0.2* scenario whereas in F=M the indicators are nearly constant. When increasing the accessibility parameter (i.e. proportion of biomass which is exploitable) the target value of the F=0.2* scenario become lower than the current state value, leading to an opposite diagnosis of the ecosystem health, from below to above the target.

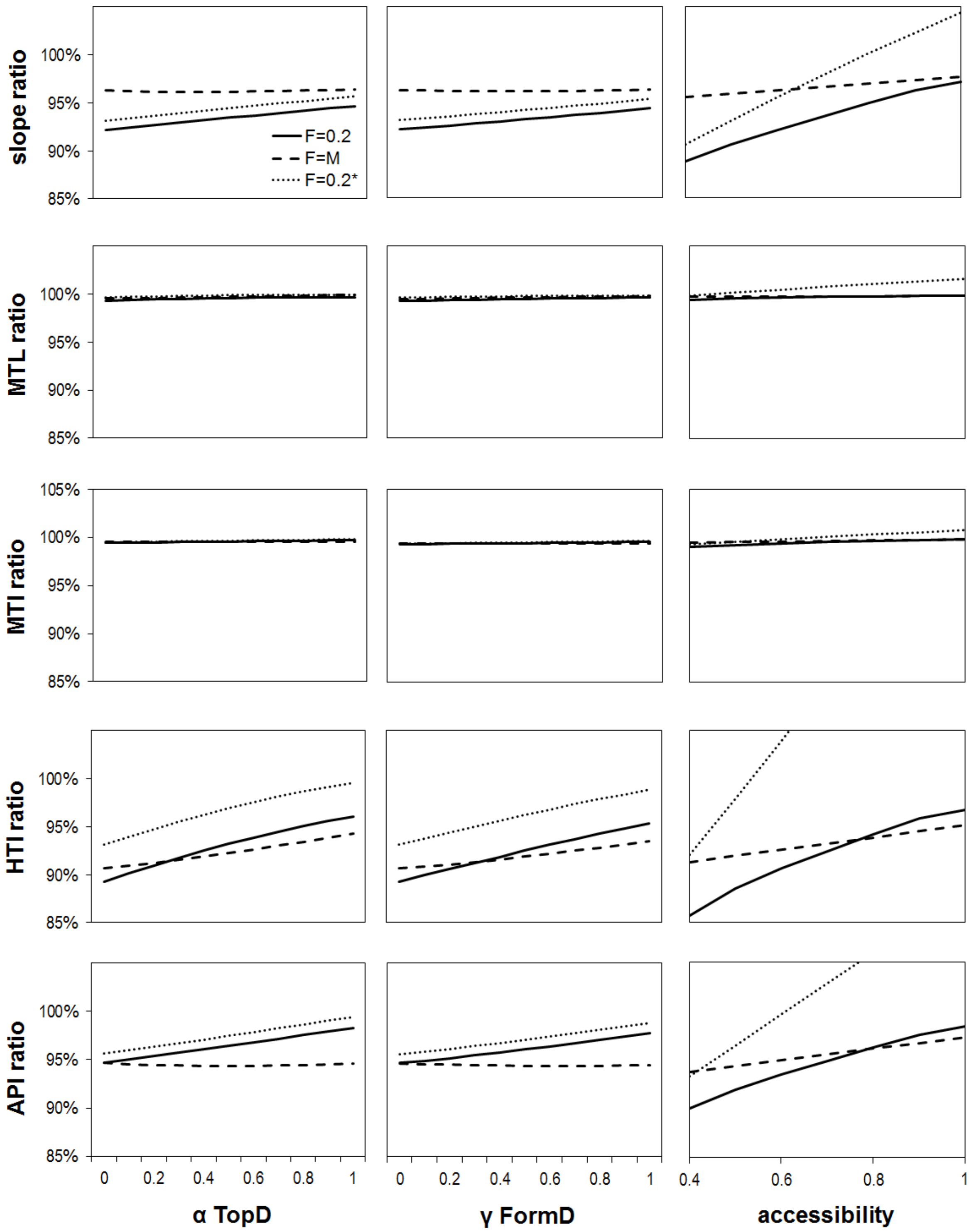

Figure 11. Sensitivity analysis of indicators ratios for variable α TopD parameter, γ FormD parameter and accessibility parameter in the Celtic Sea / Bay of Biscay ecosystem. The indicator ratio is here the ratio of an indicator value on the target indicator value.

4. Discussion

4.1. Changes in trophic levels: an ecosystem effect of fisheries

Pauly *et al.* (1998) first introduced MTL as a trophic indicator to observe changes in ecosystems health due to the impact of fishing, highlighting the now „fishing down the marine food web" process. In order to avoid environmental induced fluctuations and to focus on changes occurring within predators Pauly and Watson (2005) proposed the use of MTI. However Essington *et al*. (2006) in their „fishing through the food web" process reported that changes occurring in fishing strategies can bias the trophic indicators estimated from landings. This was further confirmed in several cases when catches trophic indicators were compared with survey-based indicators (Branch *et al*., 2010; Gascuel *et al*., 2015). Trophic level-based indicators have been much criticized since their first proposal (Caddy *et al*., 1998; Stergiou and Christensen, 2011), yet appear to be useful as they highlight clear trends in many ecosystems (see for instance a collection of examples on www.fishingdown.org, based on both catch and survey data). More generally the greater sensitivity of high trophic levels to fishing is due to their globally smaller productivity and turn-over (Gascuel *et al*., 2015). Our results confirm that trophic indicators are efficient tools to assess ecosystem impact of fishing, with clear fishing-induced decreases, at least for some of the tested indicators, in the four studied ecosystems and using model-based as well as survey-based estimates. In that context supplementary research is urgently needed to assess the spatial and temporal variability of trophic level estimations and furthermore species diet. This is of prime importance when one is using trophic level data in the computation of trophic indicators as it will likely frame the methodological limits of using a single trophic level value and increase the relevancy and strength of the indicator.

4.2. Defining some new trophic indicators

Among the indicators properties claimed by Rice and Rochet (2005), sensitivity is one of the most important when precautionary measures are needed. In our study, five trophic indicators were tested by assessing their trends under different fishing efforts. Each indicator behaved in line with the tested hypotheses but the slope, HTI and API showed clearer responses (i.e. sensitivity to fishing efforts) than MTL and MTI.

Disentangling the environmental effect from the predation release in the interpretation of MTL or other indicators (e.g. mean length of individuals) is not straightforward (Stergiou and Tsikliras, 2011; Rochet and Trenkel, 2003). A 3.25 threshold value was proposed for MTI to exclude high variability of biomasses due to environmental factors. As demonstrated in our study, the biomass trophic spectrum is stable in lower trophic levels with high biomass, partly because exploitation is often directed on higher trophic levels, and because low or intermediate TLs tend to have faster turn-over rates. Top-down compensation effects, induced by the release of predation resulting from the predator‟s overexploitation can also explain high biomasses in lower TLs. Therefore, stability in biomasses lead to stability in MTI and notably MTL, while the few observed changes are conducted by higher trophic levels.

By removing in their calculation the effect of „insensitive‟ lower trophic levels, HTI, trophic equivalent of the Large Fish Indicator (LFI) widely used in Europe (Greenstreet *et al*., 2011; Shephard *et al*., 2011; Gascuel *et al*., 2015), and API focus on the most impacted parts of the ecosystems (the higher TLs) and represent in a sense a best precautionary approach than does for instance the MTI (Stergiou and Tsikliras, 2011). To some extent this is also the case for the slope, as its value is widely influenced by high trophic levels.

At the first glance HTI and API seem to focus only on a small part of the ecosystem, unlike MTL or slope. However the abundance of predators within an ecosystem is characteristic of the good functioning of the whole food web. In a way, high trophic levels represent functional „information‟ which reveals the energetic efficiency of ecosystems and improves their

stability (Jørgensen *et al.*, 2000; Odum, 1969). On the other hand, the slope, HTI and API will respond to changes occurring not in the whole food web but in high trophic levels only, especially under high selective fishing efforts. In situations where targeted species are exclusively of intermediate or low trophic levels, such as anchovy or sardine, these indicators may not be appropriate and demonstrate a misleading improvement of the global ecosystem health (Sweeting *et al*., 2009). In EcoTroph API has technically the advantage against HTI to provide more consistent percentage values that can be further used to compare among different states of an ecosystem. In survey data from the Celtic/Biscay ecosystem both API and MTI were able to avoid the large fluctuations in the abundance of middle trophic levels organisms (e.g. the boarfish *Capros aper*; Shephard *et al*., 2011). As opposed to the slope could reflect better the trends by giving the same weight to every trophic level, as in size spectra (Jennings *et al*., 2002). Given all the above considerations, API seems to be the best indicator but HTI has the advantage of being easier to understand by a large audience (including fisheries managers) and to be computed using a single threshold (i.e. TL>=4).
As specified by Pauly and Watson (2005) concerning the TL=3.25 threshold for MTI, the various thresholds used in the HTI and API could also vary among ecosystems such as the LFI (Modica *et al.* 2014). In that case however selected threshold values should be carefully and thoroughly justified by watching trophic levels of functional groups, fisheries targets and proportions of these groups in the total biomass in the ecosystem. Colléter *et al*. (2014) demonstrate for example that top predators in the Bamboung estuary (Senegal) ecosystems reach rarely trophic levels higher than 4 and thus should have a reduced threshold.
Another limitation to trophic indicators is the relevance of assigning a single TL value to every species, given that TL varies with size, age, space, and time (Jennings *et al.*, 2002; Vinagre *et al*., 2012). Furthermore, the data used in assigning species TL were of multiple sources, including those from stable isotopes (Piet and Jennings, 2005). Our results show that

for HTI, one may claim that either less than a quarter or over half of the species present in an ecosystem is of high trophic levels depending on the chosen TL. Nevertheless, it is important to keep in mind that the uttermost caution must be taken when assigning a TL value to a species, when using the same TL values to compare the states of an ecosystem using different data sources, or when estimating targets using models. Indeed the reliability of diet composition matrix used in EwE are paramount in estimating trustworthy TL.

One should keep in mind that accessibility parameters have to be defined by experts when estimating targets through an EcoTroph model, particularly when simulating scenarios increase the fishing effort in lower trophic levels (e.g. F=0.2*).

4.3. Management scenarios and target values of indicators

An ecosystem-based management aims to restore and maintain the health, productivity and biodiversity of ecosystems while allowing men to keep an appreciable quality of life by integrating the acquisition of natural resources to social and economic needs (Szaro *et al*., 1998). It must preserve the health of the ecosystem, particularly its function, organization and resilience (Arreguín-Sánchez and Ruiz-Barreiro, 2014; Costanza and Mageau, 1999; Ulanowicz, 1980). In this study we tested only the fishing mortality proposition argued by Froese *et al*. (in press). The concerns about population size and size at first capture were not explored. We are aware that our representation of an EAFM state is indeed partial as it simply includes intra-population and intra-specific needs. It has to be understood as a first attempt to characterize the effect of various management targets on ecosystems. In fact, the main result of our approach is to demonstrate that targets for trophic indicators can be estimated by food web models, simulating a given scenario representing an EAFM. In such approach, EAFM is not defined by the achievement of predefined targets. It is an adaptive process where stakeholders have to agree on (acceptable) measures of management, which define reachable and desirable targets for a set of indicators. Estimating targets through simulations is thus a key step to assessing various management options. In other words, the targets reflect time-based assessment of the good environmental status of an ecosystem. Just as for gas emissions by cars, where targets are regularly revised according to technological innovations, the targets used for fisheries management should be pragmatically set with reachable objectives, meant to improve the current status of marine ecosystems. In such approach, new assessments are required to gradually improve/adapt the management and confirm that the estimated state of the ecosystem and associated values of indicators are in line with the society needs or wills. When comparing global health of ecosystems with our selection of trophic indicators, the impacts of the tested management-based scenarios are relatively similar (see Figure 7). However when looking at the trophic level scale, pressures strongly diverge. Among the three scenarios F=0.2 (i.e. only for species whose F is currently above F=0.2) causes the major reduction of fishing impact. In comparison F=M keeps high fishing impact, notably on low and intermediate trophic levels which tend to have high natural mortality potentially above 0.2. For the lowest trophic levels, the current F is below M and thus is not reduced in our management scenario. It is worth mentioning that both F=0.2 and F=M tend to reduce total catches, by 14% and 10% respectively, but a slight increase in high trophic level biomass captured can be observed with F=0.2. This is probably due to a bottom-up effect with the enhancement of potential prey. It is also interesting to note that the F=M scenario, which minimize the total catches losses compared to F=0.2, tends towards the „balanced harvest" concept (Zhou *et al*., 2010; Jacobsen *et al*., 2014).

The scenario F=0.2* (i.e. for all fishable species) provides the same amount of global catches as the current fishing effort, but with a shift towards the low-middle trophic levels (i.e. 2.7≤TL≤3.3). This scenario, characterized by increased fishing mortalities on some low TLs, is in the continuity of the „fishing through the marine food web" process (Essington *et al*., 2006). Our comparison between F=0.2* and its alternative would have been more realistic if the proportion of edible species and energetic values would have been taken into account. Theoretically the choice between the two scenarios, an F=0.2* and F=0.2 would likely depend on the will of societies to either manage for the long-term economic performance by restricting the impact of fishing on high trophic levels or to convert lower trophic levels into commercial sources of protein. It appears that European societies tend more towards the first objective and therefore to a rather conservative approach (Pinnegar *et al*., 2002).

We estimate target values for the five tested indicators based on whole-ecosystem models, and for MTL and HTI based on survey data for the Celtic/Biscay demersal community. Regarding models, our results demonstrate that model-specific target values can be estimate for all indicators, and within each ecosystem, as long as a management scenario has been agreed as the operational enforcement of an EAFM. F=M incoherent target values for the Bay of Biscay model are likely due to the structure of the model, which groups a number of demersal exploited species together. That grouping is certainly not the most adapted when one is dealing with fishing effort. It is worth mentioning that this type of incongruity is absent in the three other models as they differ in their structure.

Concerning survey data, Ecosim simulations did not provide good estimations of targets for MTI and API, for two major reasons. Firstly because trophic levels are given to species but great disparities are often found among species composing the trophic groups. Thus, Rogers *et al.* (2010) advocate that the efficiency of trophic indicators is conditional to the TL precision being used in the estimations. Secondly, because species observed in surveys are mostly included in intermediate trophic levels. Therefore, great care must be taken when dealing with different sources of TL as they can be underestimated in EwE due to the parameterization of the model (Deehr *et al*., 2014; Lassalle *et al*., 2014).

4.4. Inter-ecosystems assessment

Results from our study suggest that the Bay of Biscay is the healthiest ecosystem, while the North Sea and the English Channel seems to be the most degraded. Raw and ratio values of indicators emphasized that ecosystem structures differ (i.e. proportion of low, intermediate and high trophic levels) and may vary according to the type of values used (raw vs relative). The Celtic/Biscay has the highest current raw and ratio values of slope, MTI and API. On the contrary the North Sea ecosystem ranks very low raw values but is healthier than the English Channel with ratio values. This sensitivity to the values used to assess the status of an ecosystem is somehow disturbing but has been observed with other indicators (Rombouts *et al*., 2013) suggesting that this is not unique to trophic indicators. We may add that trophic indicators are most likely relevant in the comparison of an ecosystem with itself through tome or under different management scenarios than in the comparison among different ecosystems. Comparison between trophic indicators trends estimated using models and survey data is nonsense when the two datasets encompass different geographic areas or include different part or compartments of the ecosystem. In other cases, the comparison may be informative and/or useful. It would be for instance hazardous to compare the trends from Araújo *et al.* (2008) model in the English Channel with the CGFS survey data as the model includes the Western English Channel while trawling is conducted in the Eastern English Channel: two areas of highly dissimilar biogeographic features (Dauvin, 2012). On the other hand, the patterns between models and surveys differ for the Celtic/Biscay and the North Sea ecosystems. North Sea indicators values are higher in survey data than in models. This difference can be explained by the wider proportion of pelagics in the North Sea model in comparison to IBTS survey data.

The Celtic/Biscay is a major fishing area in the European Union in terms of landings. Its lower health compared to the Bay of Biscay considered alone could be partially explained by the intensive fishing operated in the Celtic Sea since a fairly recent period, the late 1980s

(Blanchard *et al*., 2005; Pinnegar *et al*., 2002). Fishing effort reduction measures have been effectively applied since 2000, leading to a significant decrease in the mean fishing mortality applied to major stocks (Gascuel *et al.*, 2015). Jennings and Blanchard (2004) have highlighted that the North Sea fish community biomass was 38% lower than the virgin state. Yet fishing effort is decreasing after having reached its highest value in the middle of 1980s (Daan *et al*., 2005). In the English Channel catches have increased in the late 1970s and remain relatively stable since the peak of 1982, which caused a sharp decline in the abundance of large species of high trophic levels exhibit in the MTL of landings (Molfese *et al*., 2014). Otherwise, Araújo *et al*. (2008) has pointed that the Western English Channel was a relatively immature ecosystem using Finn‟s index and Primary Production/Respiration ratio, which is confirmed by our results concerning the proportion of top predators. Potential differences between ecosystem states could thus be explain by the intensity of fishing effort and the response quickness of the ecosystem to suitable management measures.

Jennings *et al*. (2002) highlighted that the North Sea has been trawled since 1900, whereas much of the Celtic Sea was not fished until the 1970s. We would thus expect the North Sea community to be extremely degraded compared to the Celtic/Biscay ecosystem. However in the non-equilibrium thermodynamic paradigm (Nicolis and Prigogine, 1977; Prigogine and Stengers, 1984; Ulanowicz, 2007), ecosystems „jump‟ through attractors and the almost healthy state of the North Sea suggested in our results would be a repercussion of scenarios simulated on a new mode of ecosystem behavior (probably less stable) than it was before 1900, prior to the collapses of houting, sturgeon or angelshark, and this could explain the minor raw values of indicators in the North Sea. Therefore one interesting direction of the health examination of ecosystems would be to connect their ancient and current states to observe their trends in terms of dissipative structures, for example with thermodynamic-based indicators, better linked to maturity and resilience (Marques *et al.*, 1997; Jørgensen *et al*., 2000; Fath *et al*., 2004). In this direction, Bentorcha *et al*. (in press) found that the Respiration/Biomass ratio of the sum of groups with TL>3.4 has increased of 20% from 1980 to 2012 in the Celtic/Biscay ecosystem. Furthermore, instead of being mainly a direct link with management, EcoTroph could be used as a theoretical Ecology tool (e.g. Colléter, 2014) to explore and improve the relationships between Conservation Ecology and Statistical Physics works such as those of Alonso Chávez and Michaelian (2011) or the domain of ecological network analysis indices (Saint-Béat *et al*., 2015).

One assessment that could slightly counteract the complexity of ecosystem maturity in a trophic questioning would be to create indicators not only based on the TL but on the TL weighted by the Respiration/Biomass ratio of species or groups. Knowing the correlation between biological rates, body size and thermoregulation characteristics (Peters, 1983), these additional „TL by Respiration" indicators would exhibit increasing values in more mature systems along with maximum eco-exergy hypothesis (e.g. higher contribution of marine mammals in the system; Marques *et al.*, 1997; Molozzi *et al*., 2013).

5. Conclusion

Trophic indicators responsiveness to various management scenarios is estimated by simulations corresponding to an EAFM. All the tested trophic indicators respond to fishing pressure, but the two candidates HTI and API and the slope display wider variations than the MTL and MTI. Although the ecosystem-based management scenarios F=0.2, F=M and F=0.2* showed similar estimated targets, their impact on fishing mortality and catches differed, notably for F=0.2*. Targets were proposed for the five indicators in models using EcoTroph and for MTL and HTI in survey data using Ecosim simulations. If the influence of input parameters is relatively stable on targets in models, the trophic levels ascribed to species in survey data induce strong fluctuations on yearly estimates of the indicators, underlining the paramount importance of the choice and the precision of trophic level values. Taking together the results from both our simulations and sensitivity analyses, HTI and API are the most two relevant trophic indicators to assess ecosystems health.

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Appendix 1 : L_s (cm) given to species in the four areas of study.

	Celtic Sea / Bay of Biscay	**Bay of Biscay**	**North Sea**	**Eastern English Channel**
Ammodytes tobianus		14		
Argentina silus	27	25	13	
Argentina sphyraena	15	15	15	
Arnoglossus imperialis	9	10		
Callionymus lyra	14	12		12
Capros aper	7	7		
Cepola macrophthalma	22	22		
Chelidonichthys cuculus	15	17	15	20
Dicentrarchus labrax	30	30	30	30
Dicologlossa cuneata	14	14		
Etmopterus spinax	31	14		
Eutrigla gurnardus	15	15	15	21
Gadus morhua			25	33
Galeus melastomus	19	19		
Helicolenus dactylopterus	15	14		
Hippoglossoides platessoides	11		13	
Lepidorhombus boscii	12	12		
Lepidorhombus whiffiagonis	15	15	23	
Leucoraja naevus	26	26	30	
Limanda limanda	15		15	15
Liza ramada		31		
Lophius budegassa	7	7		
Lophius piscatorius	13	13	13	
Melanogrammus aeglefinus	15	16	13	
Merlangius merlangus	12	9	10	9
Merluccius merluccius	9	9	23	
Microchirus variegatus	10	10		
Microstomus kitt	19		17	21
Mullus surmuletus	10	9	12	9
Mustelus asterias				55
Phycis blennoides	12	12		
Platichthys flesus			23	20
Pleuronectes platessa	22		17	21
Pollachius virens			35	
Raja clavata			31	29

Scyliorhinus canicula	26	26	18	47
Solea solea	17	17	7	19
Spondyliosoma cantharus	7	6		6
Trachinus draco	17	17		
Trisopterus esmarkii	10		10	
Trisopterus luscus	9	8	15	11
Trisopterus minutus	8	8	9	8
Zeus faber	19	15		25

Appendix 2 : α et β parameters estimates given to species for the length-weight relationship in the four areas of study.

Celtic Sea / Bay of Biscay	α	β
Argentina silus	0,0039	3,203
Argentina sphyraena	0,0017	3,378
Arnoglossus imperialis	0,00284	3,34
Callionymus lyra	0,014	2,709
Capros aper	0,0305	2,791
Cepola macrophthalma	0,0128	2,169
Chelidonichthys cuculus	0,00325	3,31963
Dicentrarchus labrax	0,01248	2,94846
Dicologlossa cuneata	0,0066	3
Etmopterus spinax	0,0018	3,24
Eutrigla gurnardus	0,00671	3,06235
Galeus melastomus	0,0025	3,02
Helicolenus dactylopterus	0,0061145	3,2738
Hippoglossoides platessoides	0,0044	3,204
Lepidorhombus boscii	0,004311	3,19043
Lepidorhombus whiffiagonis	0,00307	3,2446
Leucoraja naevus	0,00236	3,233
Limanda limanda	0,008513	3,09066
Lophius budegassa	0,015	3,004
Lophius piscatorius	0,02457	2,85612
Melanogrammus aeglefinus	0,0132404	2,9008
Merlangius merlangus	0,00455	3,1669
Merluccius merluccius	0,00438	3,113
Microchirus variegatus	0,008393	3,05663
Microstomus kitt	0,0051448	3,2420508
Mullus surmuletus	0,00512	3,29558
Phycis blennoides	0,213006	2,103422
Pleuronectes platessa	0,005015	3,23905
Scyliorhinus canicula	0,00342	2,99468
Solea solea	0,00475	3,18094
Spondyliosoma cantharus	0,0093059	3,162883
Trachinus draco	0,01312	2,76555
Trisopterus esmarkii	0,0066	3

Trisopterus luscus	0,00738	3,15608
Trisopterus minutus	0,0086	2,98
Zeus faber	0,01809	2,9827

Bay of Biscay	***α***	***β***
Ammodytes tobianus	0,0015	3,169
Argentina silus	0,0039	3,203
Argentina sphyraena	0,0017	3,378
Arnoglossus imperialis	0,00284	3,34
Callionymus lyra	0,014	2,709
Capros aper	0,0305	2,791
Cepola macrophthalma	0,0128	2,169
Chelidonichthys cuculus	0,00325	3,31963
Dicentrarchus labrax	0,01248	2,94846
Dicologlossa cuneata	0,0066	3
Etmopterus spinax	0,0018	3,24
Eutrigla gurnardus	0,00671	3,06235
Galeus melastomus	0,0025	3,02
Helicolenus dactylopterus	0,00611445	3,2738
Lepidorhombus boscii	0,004311	3,19043
Lepidorhombus whiffiagonis	0,00307	3,2446
Leucoraja naevus	0,00236	3,233
Lophius budegassa	0,015	3,004
Lophius piscatorius	0,02457	2,85612
Melanogrammus aeglefinus	0,0132404	2,9008
Merlangius merlangus	0,00455	3,1669
Merluccius merluccius	0,00438	3,113
Microchirus variegatus	0,008393	3,05663
Mullus surmuletus	0,00512	3,29558
Phycis blennoides	0,213006	2,103422
Scyliorhinus canicula	0,00342	2,99468
Solea solea	0,00475	3,18094
Spondyliosoma cantharus	0,0093059	3,162883
Trachinus draco	0,01312	2,76555
Trisopterus luscus	0,00738	3,15608
Trisopterus minutus	0,0086	2,98
Zeus faber	0,01809	2,9827

North Sea	***α***	***β***
Argentina silus	0,0039	3,203
Argentina sphyraena	0,0053	3,053
Chelidonichthys cuculus	0,0045	3,223
Dicentrarchus labrax	0,0074	3,096
Eutrigla gurnardus	0,0037968	3,2247
Gadus morhua	0,0104	3
Hippoglossoides platessoides	0,0044	3,204
Lepidorhombus whiffiagonis	0,00245	3,321
Leucoraja naevus	0,00089	3,486
Limanda limanda	0,00492	3,20388
Lophius piscatorius	0,0153	2,998
Melanogrammus aeglefinus	0,00519	3,15534
Merlangius merlangus	0,00984	2,926
Merluccius merluccius	0,0047	3,099
Microstomus kitt	0,00611	3,15626
Mullus surmuletus	0,0047	3,309
Platichthys flesus	0,00867	3,06
Pleuronectes platessa	0,0215	2,7901
Pollachius virens	0,0104	2,97172
Raja clavata	0,0031778	3,193812
Scyliorhinus canicula	0,003204	3,017954
Solea solea	0,00497	3,2
Trisopterus esmarkii	0,0066	3
Trisopterus luscus	0,0038	3,3665
Trisopterus minutus	0,0092	3,026

Eastern English Channel	***α***	***β***
Callionymus lyra	0,0022	2,591
Chelidonichthys cuculus	0,005599	3,1681
Dicentrarchus labrax	0,01379698	2,92394
Eutrigla gurnardus	0,005315	3,179638
Gadus morhua	0,005315	3,179638
Limanda limanda	0,005498	3,21827

Merlangius merlangus	0,007555	3,0431
Microstomus kitt	0,00756	3,142
Mullus surmuletus	0,00772236	3,174146
Mustelus asterias	0,002	3,16
Platichthys flesus	0,011379	2,9679
Pleuronectes platessa	0,011571	2,98144
Raja clavata	0,0031778	3,193812
Scyliorhinus canicula	0,003204	3,017954
Solea solea	0,006214	3,112853
Spondyliosoma cantharus	0,012575	3,065911
Trisopterus luscus	0,0066	3,085816
Trisopterus minutus	0,0092	3,026
Zeus faber	0,021757	2,9304

Appendix 3 : Trophic level values given to species in scientific surveys in the four areas of study.

	Celtic Sea / Bay of Biscay	Bay of Biscay	North sea	Eastern English Channel
Ammodytes tobianus		3,7		
Argentina silus	3,6	3,6	3,6	
Argentina sphyraena	3,8	3,8	3,8	
Arnoglossus imperialis	3	3		
Callionymus lyra	3,5	3,5		3,5
Capros aper	2,94	2,94		
Cepola macrophthalma	4,1	4,1		
Chelidonichthys cuculus	3,9	3,9	3,9	3,9
Dicentrarchus labrax	4,2	4,2	3,47	3,47
Dicologlossa cuneata	3,8	3,8		
Etmopterus spinax	4,7	4,7		
Eutrigla gurnardus	3,9	3,9	3,8	3,9
Gadus morhua			4,83	4,12
Galeus melastomus	4,4	4,4		
Helicolenus dactylopterus	4,1	4,1		
Hippoglossoides platessoides	4,03		4,18	
Lepidorhombus boscii	3,38	3,38		
Lepidorhombus whiffiagonis	4,03	4,03	4,46	
Leucoraja naevus	3,8	3,8	3,8	
Limanda limanda	4,2		4,01	3,19
Lophius budegassa	4,3	4,3		
Lophius piscatorius	4,1	4,1	4,85	
Melanogrammus aeglefinus	3,88	3,88	4,28	
Merlangius merlangus	4,4	4,4	4,4	4,07
Merluccius merluccius	4,34	4,34	4,91	
Microchirus variegatus	3,8	3,8		
Microstomus kitt	3,67		3,94	3,14
Mullus surmuletus	4,38	4,38	3,3	3,3
Mustelus asterias				3,8
Phycis blennoides	4	4		
Platichthys flesus			4,38	3,95
Pleuronectes platessa	3,07		3,99	3
Pollachius virens			4,36	
Raja clavata			4	3,7
Scyliorhinus canicula	4,5	4,5	4,3	4,5
Solea solea	3,16	3,16	4	3,01
Spondyliosoma cantharus	4,3	4,3		4,3
Trachinus draco	3,8	3,8		
Trisopterus esmarkii	3,91		3,59	
Trisopterus luscus	4	4	4,2	4

Trisopterus minutus	3,9	3,9	4	3,9
Zeus faber	4,1	4,1		4,22