An ecosystem approach for the assessment of fisheries impacts on marine top predators: the Bay of Biscay case study

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A number of marine mammal populations is currently threatened by their interactions with fisheries. The present study aimed to provide insights into the severity of potential impacts of operational and biological interactions between top predators and fisheries, in the Bay of Biscay region. Our approach was to modify an Ecopath with Ecosim (EwE) model describing the overall structure and function of the ecosystem by including landings and discards of exploited stocks and estimations of the bycatch of non-target compartments. Second, a set of ecological indices and a trophic level (TL)-based model (EcoTroph, ET) were derived from the EwE model. ET was used to simulate the effects of increasing fishing pressure on the ecosystem and, more particularly, on top predators. The Bay of Biscay was demonstrated to be not far from overexploitation at the current fishing rate, this phenomenon being particularly noticeable for the highest TLs. Within the toothed cetacean community, bottlenose dolphins appeared the most sensitive to resource depletion, whereas common dolphins and harbour porpoises were most impacted by their incidental captures in fishing gears. This study provides a methodological framework to assess the impacts of fisheries on ecosystems for which EwE, or other ecosystem models, already exist.

Keywords: Ecopath, ecosystem modelling, EcoTroph, fisheries impacts, marine mammals, trophic level.

Introduction

Assessing the actual impact of a fishery on marine mammal populations has been achieved in only a very few cases. Fisheries can impact these top predators directly, through incidental captures in fishing gear and ship strikes (operational interaction; Lewison et al., 2004), but also indirectly, through modifications of prey abundance, size structure, and behaviour on those occasions when both top predators and fisheries occupy the same "niche-space" [biological interaction: DeMaster et al., 2001; see Northridge (1991) and Goñi (1998) for reviews of fisheries impacts]. Among the non-target organisms incidentally caught in fisheries, marine mammals have received the greatest public attention, with mortality due to fishery bycatch being considered the main anthropogenic threat for many cetacean populations in European waters (Tregenza et al., 1997; Morizur et al., 1999; López et al., 2003; ICES, 2011). Particular cases where fishery bycatch is considered to be unsustainable include the mortality of common dolphins (Delphinus delphis) in pelagic trawls targeting albacore tuna and sea bass in the Northeast Atlantic (Morizur et al., 1999) and the bycatch of harbour porpoises (Phocoena phocoena) in set-nets (Tregenza et al., 1997). To mitigate and monitor the level of bycatch taking place, the European Commission (EC) passed Council Regulation No. 812/2004 that specifically required Member States (MS) to implement on-board observer programmes to monitor bycatches in certain fisheries and to report annually on the results. Information

collected by each MS on the incidental captures and killing of cetacean in fisheries was made available from 2005 to 2008 (ICES, 2010a, b). However, to be able to assess the impact on a population of incidental mortality in fishing gear, the status and dynamics of the population need to be known with a level of detail that is not currently available for many marine mammals (Murphy *et al.*, 2009). Much effort has therefore been directed at obtaining unbiased abundance estimates of cetacean in European waters, and recent examples include SCANS-II (Small Cetaceans in the European Atlantic and North Sea in July 2005) and CODA (Cetacean Offshore Distribution and Abundance in July 2007).

Many species of fish and shellfish preyed upon by marine mammals are also exploited by fisheries. At a global scale, the resource overlap, defined as the extent to which both players exploit the same resources in the same areas, was demonstrated to be relatively moderate and to be essentially a problem of local concern (Kaschner *et al.*, 2001; Karpouzi *et al.*, 2007; Morissette, 2007). This exploitation of the same resources has led to growing concerns over potential competition between fisheries and these predators in both directions, i.e. the hypothesis of prey depletion as a result of fishing pressure (Bearzi *et al.*, 2008) and the "whales-eat-fish" conflict (Morissette *et al.*, 2010b). In the former case, because most marine mammals depend on an abundant supply of local food, fishing may negatively affect their survival by reducing the availability of prey or by inducing its dispersal. Adding to this, "fishing down the foodweb" is prevalent among marine ecosystems worldwide (Pauly *et al.*, 1998) and is most commonly caused not by serial replacement of fisheries as first thought, but rather by addition of new fisheries targeting lower trophic levels (*TLs*; Essington *et al.*, 2006). This phenomenon of "fishing through the foodweb" is symptomatic of increased impacts of fisheries on high-trophic-level species over recent decades.

Despite growing concern about this topic, previous studies that have tried to evaluate the impacts of interactions between fisheries and top predators in the Bay of Biscay have concentrated on either operational or biological interactions and have assessed them only partially. Goujon (1996) and Morizur *et al.* (1999) stated that the total number of by-caught cetaceans in fishing gear could be biologically significant in the area. When looking at biological interactions, Pusineri *et al.* (2004) identified diet overlap between fisheries and small delphinids in the neritic area of the Bay of Biscay. According to their results, only the common dolphin showed a quantitative impact of a similar order to that of the fisheries on their shared resources.

The main aim of this study was to analyse, for the continental shelf of the Bay of Biscay, the impact of the fisheries on toothed cetaceans while taking all other components of the ecosystem into account. A threefold approach was used: (i) a mass-balanced model describing the overall structure and function of the Bay of Biscay continental shelf ecosystem was developed, fishery landings and discards affecting the exploited and non-exploited compartments being detailed, (ii) a set of ecological indices derived from the ecosystem model was then used to evaluate the degree to which fisheries and top predators interact at steady state, and, finally, (iii) using a *TL*-based model also derived from the ecosystem model, various non-dynamic simulations were conducted with different levels of fishing effort targeting different *TLs*. This last step used EcoTroph (ET) software (http://sirs.agrocampus-ouest.fr/EcoTroph/), which has two key features. ET deals with the continuous distribution of the biomass in an ecosystem as a

function of continuous *TLs*. Second, the trophic functioning of marine ecosystems is modelled as a continuous flow of biomass surging up the foodweb, from lower to higher *TLs*, through predation and ontogenic processes (Gascuel and Pauly, 2009; Gascuel *et al.*, 2009).

Material and methods
Pre-existing Ecopath model
An Ecopath model (Polovina, 1984; Christensen and Pauly, 1992) was constructed for the Bay of Biscay continental shelf foodweb, specifically the part of this shelf extending between the 30- and 150-m isobaths and falling within French waters [Table 1; a full description of the model, including the diet composition matrix, can be found in Lassalle *et al.* (2011)]. A novel metric based on ecosystem production depicted an ecosystem not far from being over-exploited (L-index; Libralato *et al.*, 2008). This index relies on the assumption that the export of secondary production due to fisheries reduces the energy available for upper ecosystem levels, thus resulting in a loss of secondary production. This finding regarding the status of the Bay of Biscay was not entirely consistent across all indicators, demonstrating the need for further analyses based on simulations. The study area encompassed most of the ICES Subdivisions VIIIa and b (www.ices.dk; Figure 1). The model represented a typical year between 1994 and 2005, i.e. before the collapse of the European anchovy (*Engraulis encrasicolus*) and the subsequent 5-year closure of the fishery for this species. Biomasses came from scientific surveys covering the whole study area for top predators, demersal fish, anchovy, sardine (*Sardina pilchardus*), and sprat (*Sprattus sprattus*), and two categories of zooplankton. For other compartments, only a subset of the continental shelf was investigated.

For the two migratory species, mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*), estimates were derived from stock assessment results. As stock assessment extended beyond ICES Divisions VIIIa and b, a simple *pro rata* biomass allocation was applied based on landings. Values for the whole stock and for detailed ICES Divisions were required for this calculation (see Table 2 for a summary).

Ecotrophic efficiencies *EE* were preferentially fixed to 0.95 for both groups of cephalopods, as assessments of their abundance in the Bay were lacking, and for zooplanktonic compartments as existing estimations of their *P/B* were not accurate. *EE* corresponds to the fraction of the production of each group that is used in the foodweb. This value as high as 0.95 for cephalopods was justified by their commercial exploitation in the ecosystem. A sensitivity analysis revealed that the main results concerning the functioning of the ecosystem were not affected by the values of *EE* for zooplankton.

Quantitative information on diet composition was gathered from two main sources: stomach contents and stable isotope analyses performed on organisms captured/stranded in the area. Stable isotopes were mainly used to differentiate, among benthic organisms, those feeding on surface-layer particulate organic matter (POM) and those eating bottom POM (Le Loc'h and Hily, 2005; Le Loc'h *et al.*, 2008). Expert knowledge and data from similar ecosystems helped to fill gaps in data on birds' dietary regimes. Usually, *P/B* and *Q/B* estimates for higher *TLs* were derived from empirical equations, whereas estimates were obtained from literature sources for other compartments. When values obtained for one of these two parameters seemed doubtful,

Table 1. Input (regular) and output (bold) parameters for the ecosystem components used in the Bay of Biscay continental shelf model.

	TL	B	P/B	Q/B	EE	P/Q	U/Q	Landings	Discards	S_τ	Sigma
1. Plunge and pursuit divers seabirds	**4.36**	0.27	0.09	57.66	**0**	**0.002**	0.2	–	–	0	0.102
2. Surface feeders seabirds	**3.72**	0.07	0.09	69.96	**0**	**0.001**	0.2	–	–	0	0.091
3. Striped dolphins (*S. coeruleoalba*)	**4.73**	0.59	0.08	20.80	**0**	**0.004**	0.2	–	–	0	0.108
4. Bottlenose dolphins (*T. truncatus*)	**5.18**	2.18	0.08	21.67	**0**	**0.004**	0.2	–	–	0	0.114
5. Common dolphins (*D. delphis*)	**4.61**	1.44	0.08	26.11	0.875	**0.003**	0.2	–	*0.101*	0.4	0.106
6. Long-finned pilot whale (*G. melas*)	**4.64**	0.83	0.05	10.34	**0**	**0.005**	0.2	–	–	0	0.107
7. Harbour porpoise (*P. phocoena*)	**4.69**	0.12	0.08	40.69	0.833	**0.002**	0.2	–	*0.008*	0.4	0.107
8. Piscivorous demersal fish	**4.66**	48.45	0.63	2.03	0.991	**0.311**	0.2	10.42	–	0.75	0.107
9. Piscivorous and benthivorous demersal fish	**4.01**	130	0.66	3.42	0.981	**0.192**	0.2	10.68	13.82	0.3	0.096
10. Suprabenthivorous demersal fish	**3.49**	311.20	0.55	5.30	0.765	**0.104**	0.2	0.64	26.79	0.4	0.086
11. Benthivorous demersal fish	**3.41**	28.97	0.88	5.51	0.949	**0.159**	0.2	5	0.20	0.4	0.085
12. Mackerel (*S. scombrus*)	**3.73**	145.9	0.80	4.40	0.978	**0.181**	0.2	6.24	0.49	0.4	0.091
13. Horse mackerel (*T. trachurus*)	**3.69**	262.2	0.51	4.00	0.987	**0.128**	0.2	16.81	1.01	0.75	0.090
14. Anchovy (*E. encrasicolus*)	**3.67**	55.75	1.82	8.68	0.825	**0.210**	0.2	16.80	–	0.8	0.090
15. Sardine (*S. pilchardus*)	**3.44**	184.20	0.68	8.97	0.787	**0.076**	0.2	10.82	–	0.7	0.086
16. Sprat (*S. sprattus*)	**3.67**	49.78	1.34	11.59	0.679	**0.116**	0.2		–	0	0.090
17. Benthic cephalopods	**3.70**	**10.39**	2.75	7.00	0.950	**0.393**	0.2	3.53	–	0.5	0.091
18. Pelagic cephalopods	**4.44**	**14.11**	3.20	7.50	0.950	**0.427**	0.2	1.99	–	0.6	0.104
19. Carnivorous benthic invertebrates	**3.23**	116.8	2.30	**11.50**	0.999	0.200	0.2	2.91	1.09	0.08	0.081
20. Necrophagous benthic invertebrates	**2**	16.97	1.53	**15.30**	0.908	0.100	0.2	–	–	0	0.047
21. Subsurface deposit-feeders invertebrates	**2.34**	234.80	1.60	**8.00**	0.834	0.200	0.3	–	–	0	0.058
22. Surface suspension and deposit-feeders inv.	**2**	223.90	2.80	**14**	0.891	0.200	0.2	–	–	0	0.047
23. Benthic meiofauna	**2**	100	10	**50**	0.921	0.200	0.4	–	–	0	0.047
24. Suprabenthic invertebrates	**2.14**	38	20	**100**	0.936	0.200	0.2	–	–	0	0.052
25. Macrozooplankton (≥2 mm)	**2.57**	120	**6.13**	38	0.950	**0.161**	0.4	–	–	0	0.065
26. Mesozooplankton (0.2–2 mm)	**2.67**	638	**13.27**	80	0.950	**0.166**	0.4	–	–	0	0.067
27. Microzooplankton (≤0.2 mm)	**2.18**	894	**44.91**	316	0.950	**0.142**	0.4	–	–	0	0.053
28. Bacteria	**2**	394	115	**328.57**	0.811	0.350	0.5	–	–	0	0.047
29. Large phytoplankton (≥3 μm)	**1**	1 046	119	–	0.851	–	–	–	–	0	–
30. Small phytoplankton (<3 μm)	**1**	448	151	–	0.752	–	–	–	–	0	–
31. Discards	**1**	46.67	–	–	0.731	–	–	–	–	0	–
32. Pelagic detritus	**1**	2 800[a]	–	–	0.973	–	–	–	–	0	–

TL, trophic level; *B*, biomass (kg C km^{-2}); *P/B*, production/biomass ratio (year^{-1}); *Q/B*, consumption/biomass ratio (year^{-1}); *EE*, ecotrophic efficiency; *P/Q*, gross food conversion efficiency; *U/Q*, unassimilated consumption, landings, and discards expressed in kg C km^{-2} year^{-1}. Discards in italic corresponded to the bycatch of toothed cetaceans. S_τ or accessibility (the proportion of a species or a group that would be caught under the hypothesis of an infinite fishing effort) and sigma (*TL* variability within an ecological group) were supplementary information required to translate the content of an Ecopath model into an ET model. Biomass of detritus and bacteria were conventionally fixed to 1 kg C km^{-2} to run ET. Detritus imports to the system were estimated to be 454 kg C km^{-2} year^{-1}.
[a]Pelagic detritus biomass was entered preferentially in the model as its estimation was more precise compared with the one of benthic detritus.
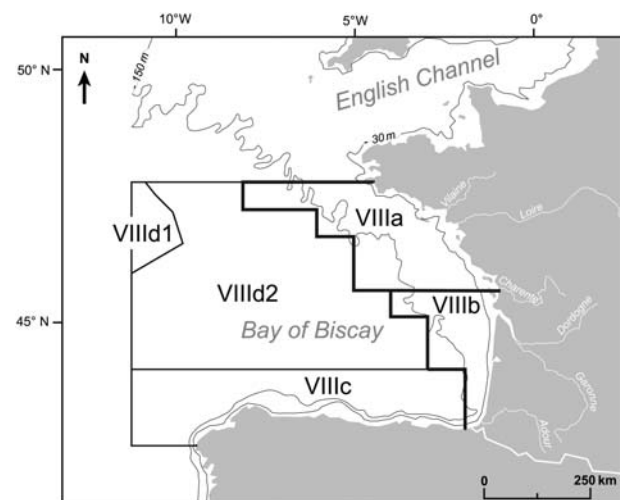
Figure 1. Study area of the Bay of Biscay continental shelf and locations of the main rivers flowing into it. For clarification, ICES Divisions VIIIa–d are also added. Boundaries of areas a and b are shown by a bold line.

P/Q when available or *EE* were preferentially entered into the model.

Marine mammals were included in the form of five monospecific groups representing the most frequently encountered small toothed cetaceans in the area. Small toothed cetaceans were represented by common dolphin, striped dolphin (*Stenella coeruleoalba*), bottlenose dolphin (*Tursiops truncatus*), long-finned pilot whale (*Globicephala melas*), and harbour porpoise (Certain *et al.*, 2008).

Since the intent is to provide a general overview of the impacts of fishing on this marine ecosystem, fisheries were not segmented by fishing gear types. Landings were obtained from the reports of the relevant ICES Working Groups for assessed stocks, i.e. WGMHSA for pelagic fish (ICES, 2005b), WGHMM for demersal fish and Norwegian lobster (ICES, 2008), and WGCEPH for cephalopods (ICES, 2005a). For multispecies fish groups, captures of species not covered by ICES reports were taken from the EuroStat/ICES database on catch statistics (ICES, 2010a, b, c—Copenhagen). For mackerel and horse mackerel, landings were estimated from the EuroStat/ICES database, which provided data by ICES Divisions, whereas stock assessment reports provided summed landings over the ICES Divisions VII and VIII. Landings

Table 2. Campaigns and years of the biomass data for each of the 32 compartments.

	Campaigns	Periods
1. Plunge and pursuit divers seabirds	ROMER/ATLANCET	2001–2004
2. Surface feeders seabirds		
3. Striped dolphins (S. coeruleoalba)	ROMER/ATLANCET	2001–2005
4. Bottlenose dolphins (T. truncatus)	SCAN	
5. Common dolphins (D. delphis)	PELGAS	
6. Long-finned pilot whale (G. melas)		
7. Harbour porpoise (P. phocoena)		
8. Piscivorous demersal fish	EVHOE	1998–2003
9. Piscivorous and benthivorous demersal fish		
10. Suprabenthivorous demersal fish		
11. Benthivorous demersal fish		
12. Mackerel (S. scombrus)	Stock assessment	1998–2003
13. Horse mackerel (T. trachurus)		
14. Anchovy (E. encrasicolus)	PELGAS	2000–2003
15. Sardine (S. pilchardus)		
16. Sprat (S. Sprattus)		
17. Benthic cephalopods	EE fixed to 0.95	
18. Pelagic cephalopods		
19. Carnivorous benthic invertebrates	INTRIGAS II	2001
20. Necrophagous benthic invertebrates		
21. Subsurface deposit-feeders invertebrates		
22. Surface suspension and deposit-feeders inv.		
23. Benthic meiofauna		
24. Suprabenthic invertebrates		
25. Macrozooplankton (≥2 mm)	BIOMAN	1999–2002
26. Mesozooplankton (0.2–2 mm)		
27. Microzooplankton (≤0.2 mm)	MICRODYN/PELGAS	2003–2005
28. Bacteria	PNOCAT	May 1994
29. Large phytoplankton (≥3 μm)	BIOMET 1	May 1995
30. Small phytoplankton (<3 μm)	BIOMET 2	January 1998
32. Pelagic detritus	BIOMET 3	March 1998
	PEGASE	June 1998
	PLAGIA 1	February 1999
	PLAGIA 2	April 1999
	PLAGIA 3	May 1999
	PLAGIA 4	June 1999
	PLAGIA 5	July 1999
	PLAGIA 6	October 1999
	GASPROD	April 2002
	PELGAS	May 2000
	PELGAS	May 2001
31. Discards	OBSMER programme (Nephrops trawlers)	1998

The 14 Ifremer campaigns used to estimate phytoplankton, bacteria, and detritus parameters in the Bay of Biscay continental shelf model were given in full. PNOCAT, BIOMET, and PLAGIA were localized in the Gironde plume, GASPROD in the Loire plume, and PELGAS over the continental shelf.

were averaged over the 1998–2003 period for all compartments (Table 1).

In pelagic fisheries, discarding occurs in a sporadic way compared with demersal fisheries. Discard estimates are still not available for sardine and anchovy; however, given their high economic value, discard levels are thought to be low. Discard data for cephalopods are still not homogeneously collected by EU Member Countries (Pierce *et al.*, 2010). For these compartments, discards were set to zero in the model. Discards for benthic and demersal species were obtained from direct observations on *Nephrops* trawlers operating in the Bay of Biscay, 69 hauls being sampled over the whole 1998 year (Tables 1 and 2; French ministry programme OBSMER).

Bycatch estimates for the common dolphin and the harbour porpoise derived from the most recently available observations of incidental captures of cetaceans and seabirds in European waters (data from National Reports on the implementation of Regulation 812/2004; ICES, 2010a, b) and were entered as discards in the model. The term "catches" when used in the manuscript refers to landings *plus* discards.

Mass-balanced ecosystem indices of fisheries–top predator interactions

To investigate the effects of fisheries on top predators, various ecological metrics can be directly derived from the Ecopath model constructed for the Bay of Biscay continental shelf. The primary production required to sustain the food intake by top predators (*PPR*) and the total catches were compared (after Pauly and Christensen, 1995).

Then, the extent of the overlap in terms of resource use between different top predator functional groups and fisheries (catches) was calculated using an ecological niche overlap index proposed by Morissette *et al.* (2010a). This index considers, at the same time, the similarity of resource utilization [first term of Equation (1)] and the relative importance of fisheries vs. top predators as consumers within a given ecosystem [second term of Equation (1)]. It ranges from 0 (no overlap) to 0.25 (identical resource) and is calculated as follows:

$$\alpha_{fm} = \left(\frac{2 \sum p_{mk} p_{fk}}{\sum p_{mk}^2 + \sum p_{fk}^2} \right) \times \left(\frac{Q_m}{Q_m + C_f} \times \frac{C_f}{Q_m + C_f} \right), \quad (1)$$

where α_{fm} is the quantitative overlap between a top predator group m and a fishery f in the ecosystem, with p_{mk} and p_{fk} representing the proportions of group k in the diet of top predator m or in the catch by fishery f, Q_m the proportion of total food consumption by top predator m, and C_f the proportion of total intake by fishery f.

Finally, the computation of the mixed trophic impact (MTI) matrix implemented as a routine in Ecopath indicates the effect that a small increase in the biomass of one (impacting) group will have on the biomass of other (impacted) groups, taking into account both direct and indirect trophic relationships (Ulanowicz and Puccia, 1990). In the present study, the analysis was performed with two versions of the same model that differed in their integration of toothed cetacean bycatch estimates. As a first step, only the effect of food depletion on apex predators was hypothesized to be the major factor in causing these variations. Then, both the reduction in prey numbers and the increase in incidental captures were considered to operate simultaneously.

ET model

ET is a modelling approach articulated around the idea that an ecosystem can be represented by its biomass distribution across *TL*s (Gascuel and Pauly, 2009; Gascuel *et al.*, 2009). Such an approach, wherein species as such disappear, may be regarded as the ultimate stage in the use of the *TL* metric for ecosystem modelling. By concentrating on biomass flow as a quasi-physical process, it allows aspects of ecosystem functioning to be explored that are complementary to Ecopath with Ecosim (EwE). It provides users with simple tools to quantify the impacts of fishing at an ecosystem scale and a new way of looking at ecosystems. To apply ET to specific ecosystems, an observed biomass trophic spectrum and a biomass flow trophic spectrum have to be built. In this context, a spectrum can be defined as the continuous distribution of ecological properties over *TL*s. One obvious way this can be done is when an Ecopath model has already been built for the ecosystem under consideration. In such cases, resources required for the construction of an ET model are minimal. As such, ET may be seen as a complementary module of EwE, enabling a quick and simple exploration of various fishing scenarios (including the estimation of the biomass spectrum of the unexploited state; Gascuel *et al.*, 2009). ET is now freely available as a plug-in module for EwE version 6 (Christensen *et al.*, 2008) and as an R package (ET version 1.0). The increasing complementary between the versions of Ecopath and ET has led to successful applications of the *TL*-based approach to various case studies including the Port-Cros national park in France (Valls, 2009), the Bamboung marine protected area in Senegal (Colleter, 2010), the Southern

Benguela upwelling system in Southern Africa (Gasche *et al.*, 2012), the Guinean shelf (Gascuel *et al.*, 2011), and the worldwide ocean (Tremblay-Boyer *et al.*, 2011).

In the present study, analyses were performed with R 2.12.0 (R Foundation Core Team, 2011). The ET-Transpose subroutine allows translation of the content of an Ecopath model into an ET model to produce biomass and catch trophic spectra, the outputs being stored in the format required for simulations. The ET-Diagnosis subroutine is used to simulate the effects of (i) increasing (or decreasing) fishing pressures on ecosystem functioning or (ii) preferentially targeting different *TL*s. This provides a global diagnosis of ecosystem state, as well as simple forecasts of total catches and biomass for a range of fishing effort multipliers. The corresponding R functions were, respectively, "create.ETmain" and "create.ETdiagnosis", as well as their companion "plot" functions.

For ecological or technological reasons, only a fraction of the ecosystem biomass is usually accessible to fisheries. As a consequence, an accessibility parameter (S_τ) expressing, for each Ecopath group, the fraction of the biomass that can be caught supposing an infinite fishing effort was added manually by the user to the table returned by the Ecopath routine (Table 1). This table, used as the basis for the "create.ETmain" function, contains the group name, *TL*, biomass, production rates, and catches. The accessibility of each group was fixed according to two main criteria: the ratio between the species distribution area and the study area, and the presence of sheltering habitats in the study area. When necessary, values were corrected according to the proportion of species that are caught and by-caught in the group. This parameter, also known as selectivity, was fixed to zero for species or groups of species that are not by-caught or targeted by fisheries and to 0.4 for top predators that are accidentally captured during fishing operations, the maximum value being 1. Information was taken from the available literature (mostly ICES Working Group publications for species distribution and exploitation levels) and expert knowledge. Moreover, converting data pertaining to specific taxa or functional groups into data by trophic classes requires an estimation of *TL* variability within each group. The underlying assumption is that all individuals in a trophic group are not identical and therefore do not share the same *TL* but on the contrary occupy a range of *TL*s around the group's mean *TL*. This information was specified in the "create.ETmain" function via the "sigmaLN" argument that defines the shape of the group's distribution. In the present study, we assumed that *TL* variability within an ecological group increases log-linearly with the mean *TL* of the group (Gascuel *et al.*, 2009):

$$sigma(TL) = smooth \times \ln(TL - 0.05) \quad (2)$$

where *TL* is the mean trophic level of the group and the *smooth* parameter representing the slope of this increase, fixed to the default value of 0.07 (Table 1). In addition, a set of three coefficients, all varying between 0 and 1 and the first two being related to a top–down effect, must be entered into the "create.ETdiagnosis" function. The *TopD* coefficient expresses the top–down control, i.e. the fraction of the natural mortality which depends on predator abundance. A value of zero pertains to a situation dominated by bottom–up processes, and where changes in predator abundances have no effects on their prey. The *FormD* coefficient defines the functional relationship

between prey and predators. The value 1 relates to a situation where predator abundance has a linear effect on the speed of the flow of their prey and therefore on prey abundance. The *Beta* coefficient refers to the origin of the secondary production. The value zero relates to an ecosystem where all secondary production originates from grazing on primary producers and the value 1 to a major contribution of detritus and recruitment. Default values for *TopD*, *FormD*, and *Beta* were fixed in ET to 0.4, 0.5, and 0, respectively, for all *TL*s. The Ecopath network analysis of the Bay of Biscay continental shelf model strongly indicated a mature, bottom–up regulated, and detritus-based foodweb (Lassalle *et al.*, 2011). According to Odum (1969), ecosystems tend to increase the control of, or homeostasis with, the physical environment, in the sense of achieving maximum protection from its perturbation. ET gives the opportunity to convert this valuable information regarding the functioning of marine ecosystems into model parameters. The *TopD* coefficient was derived from the top–down effects contributing to the keystoneness index (*KS*) of mesozooplankton, identified as the compartment with the highest *KS* value. As no information exists for the *FormD* coefficient, it was fixed to its default value. The *Beta* coefficient was set equal to the system herbivory to detritivory ratio that quantifies the flow along grazing and detrital foodwebs. As such, these three coefficients characterizing the ecosystem functioning were set to 0.2, 0.5, and 0.76 for this continental shelf ecosystem.

Testing scenarios of increasing fishing pressures

In ET, two parameters provide a synthetic overview of the ecosystem exploitation at the current state: fishing mortality (*F*) and fishing loss rate (Φ). Fishing mortality measures the probability of one fish being caught and the fishing mortality spectrum reflects which *TL*s are currently exploited in the ecosystem. The fishing loss rate measures the proportion of the production caught each year and the corresponding trophic spectrum reflects the level of impact of fishing on the ecosystem.

Then, in the table obtained from the Ecopath routine, official landings and discards were summed together (Table 1). As for the MTI analysis, simulations of the effects of increasing fishing pressure on the system were performed with (targeted) catch only, then with the catch and bycatch of common dolphins and harbour porpoises, to finally compare the simulation results. In the "create.ETdiagnosis" function, the reference fishing effort was multiplied by values within the 0 to 3 range, with smaller intervals in the range 0–1, and ecosystem properties for each new fishing state were recalculated. Values between 0 and 1 correspond to decreases in the fishing mortality and values above 1 increases in the fishing mortality. Along the trophic continuum, predators in ET conventionally refer to species with *TL*s ≥3.5. In the present study, focusing the analysis of fisheries impacts on *TL*s of ≥4.5 allows us, to some extent, to focus on marine mammals. Indeed, six compartments of the Ecopath model had a mean *TL* above this value; this included the five toothed cetacean boxes.

Sensitivity analyses have been performed on both the current state of the ecosystem and on the simulated states using both versions of the model, i.e. with and without bycatches of toothed cetaceans. The tested parameters are modified one by one, within the realistic ranges of values, and all other parameters remaining constant. The effects of these changes on the simulated biomass and catch trophic spectra were investigated for *TL* 4.7, which corresponds to the mean *TL* of the marine mammal community. The

Table 3. Details on sensitivity analysis of biomass and catch to parametrization and model used as input.

				S_τ	
	TopD	*Beta*	*Smooth*	**Marine mammals**	**Global**
Range	0–1	0–0.9	0.05–0.1	−50, −20, −10, 0, +10, +20, +50	
Increment	0.1	0.1	0.01		
Model values	0.2	0.76	0.07	0.4	see Table 1

For example, *TopD* varied from 0 to 1 with a step increment of 0.1; this parameter being originally set in the model to 0.2. Regarding the smooth parameter, the realistic range of variation that was tested during sensitivity analysis was determined by judging the ecological relevance of the biomass trophic spectrum obtained for marine mammals' compartments only.

effects of varying the *TopD*, *Beta*, and *smooth* (S_τ) parameters were tested. The accessibility of by-caught marine mammals (common dolphins and harbour porpoises) was modified and then the accessibility of all compartments in the model (see Table 3 for details of values applied during sensitivity analysis).

Values presented were those extracted from the model version including by-caught toothed cetaceans, except when the contrary was stipulated.

Results
Steady-state ecological indices of fishery–marine mammal interactions

Total prey biomass consumed annually by toothed cetaceans (consumption matrix in EwE) was of a similar magnitude to catches by fisheries (fishery matrix in EwE), i.e. 110.4 vs. 129.4 kg C km^{-2}, respectively. Consumption of the two forage fish species by common dolphins was similar in magnitude to the fishery catches for these two species, i.e. 25.4 and 27.6 kg C km^{-2}, respectively. Demersal fish were the most important component of fishery catches and of estimated total prey biomass consumed annually by the local bottlenose dolphin population, i.e. 33.5 and 67.6 kg C km^{-2}, respectively.

Values for primary production required to sustain marine mammal consumption, and fisheries catches were also similar, at 16.8 and 19.7%, respectively. In terms of the percentage of the *PPR* required by the toothed cetacean community, bottlenose dolphins required the most primary production (65.5%), followed by common dolphins (21.3%; Table 4). For fishery catches, the value can be decomposed by taxonomic categories as follows: 59.6% for demersal fish, 18.8% for pelagic fish, 18.6% for toothed cetaceans, 2.7% for cephalopods, and 0.5% for crustaceans.

The calculated resource overlap α_{fm} between toothed cetaceans and fishery catches varied among species and could be summarized into two broad categories: (i) no direct overlap, as was the case with striped dolphins, harbour porpoises, and long-finned pilot whales, and (ii) direct overlap, as was the case with bottlenose and common dolphins (both with a medium to low degree of direct overlap with fisheries). When toothed cetaceans were considered as a single category, the mean overlap index, weighted by the biomass of each species, was equal to 30% of the maximum value [α_{fm} (%); Table 4].

Considering only landings and discards of exploited stocks, the fishery had an overall negative MTI on the upper trophic foodweb (arithmetic sum of impacts = −0.9), particularly marked for the piscivorous demersal fish, the bottlenose dolphin, and the

piscivorous and benthivorous demersal fish (Figure 2a). The whole toothed cetacean category responded negatively to even a small increase in fishing pressure.

Table 4. Ecological metrics relevant to the evaluation of fisheries impacts on top predators.

| Functional groups	α_{fm}	α_{fm} (%)	TotQ	PPR
1. Plunge and pursuit divers seabirds	0.05	19	15.45	1.36
2. Surface feeders seabirds	0.01	4	5.11	0.26
3. Striped dolphins (S. coeruleoalba)	0.05	21	12.17	1.24
4. Bottlenose dolphins (T. truncatus)	0.10	41	47.24	10.99
5. Common dolphins (D. delphis)	0.08	30	37.68	3.57
6. Long-finned pilot whale (G. melas)	0.02	7	8.57	0.35
7. Harbour porpoise (P. phocoena)	0.03	11	4.76	0.63
8. Piscivorous demersal fish	0.23	91	98.28	10.89
9. Piscivorous and benthivorous demersal fish	0.07	26	444.67	17.79
Toothed cetacean community	0.07	30	110.42	16.78
Fisheries (catches)			129.35	19.70

They were derived from the Ecopath model of the Bay of Biscay continental shelf (Lassalle *et al.*, 2011). α_{fm}, resource overlap index between food intakes by top predators and catches, values were also expressed as a percentage of the maximum possible value for this index (0.25); *TotQ*, food intake expressed in kg C km^{-2} year^{-1}; *PPR*, primary production required to sustain the top predator consumption or catches (% of total primary production). Values given are those calculated with incidental captures of toothed cetaceans (common dolphins and harbour porpoises) included in the model.

Incorporating the bycatch of toothed cetaceans into the analysis, the overall negative effect of fishing on toothed cetacean increased substantially (Figure 2b; arithmetic sum of impacts = −2.3). In this case, commercial fisheries showed markedly greater negative impact on common dolphins and harbour porpoises (ratio of impacts = 26 and 15, respectively; Figure 2b). The negative impact of fisheries related to marine mammal bycatches appeared to be the most important effect constraining these two species and the community in general. Regarding the groups impacting marine mammals, toothed cetacean species were predominantly and positively influenced by their dominant prey.

ET biomass and catch trophic spectra

According to the biomass distribution by Ecopath groups and *TLs*, more than 75% of toothed cetacean biomass corresponds to very high *TLs* of ≥4.5. In the range 4.5−6, they represented 7.7% of the summed biomass (the values obtained for all boxes were summed over *TLs*). The remaining biomass in these very high *TLs* was made up of demersal fish and cephalopods.

Total biomass (across all *TLs* excluding *TL* 1 and bacteria) decreased, when increasing exploitation effort from 1 (baseline scenario; current state) to 3, by around 20%. Predator biomass (which conventionally refers to *TLs* of ≥3.5) was reduced by 34%, whereas for predators with a *TL* of ≥4.5, biomass was reduced by 55%. The higher the *TL*, the more strongly biomass decreases when fishing mortality increases. Increasing fishing effort by threefold led to total yields reaching the maximum value of 229 kg C km^{-2}, within which predator catches
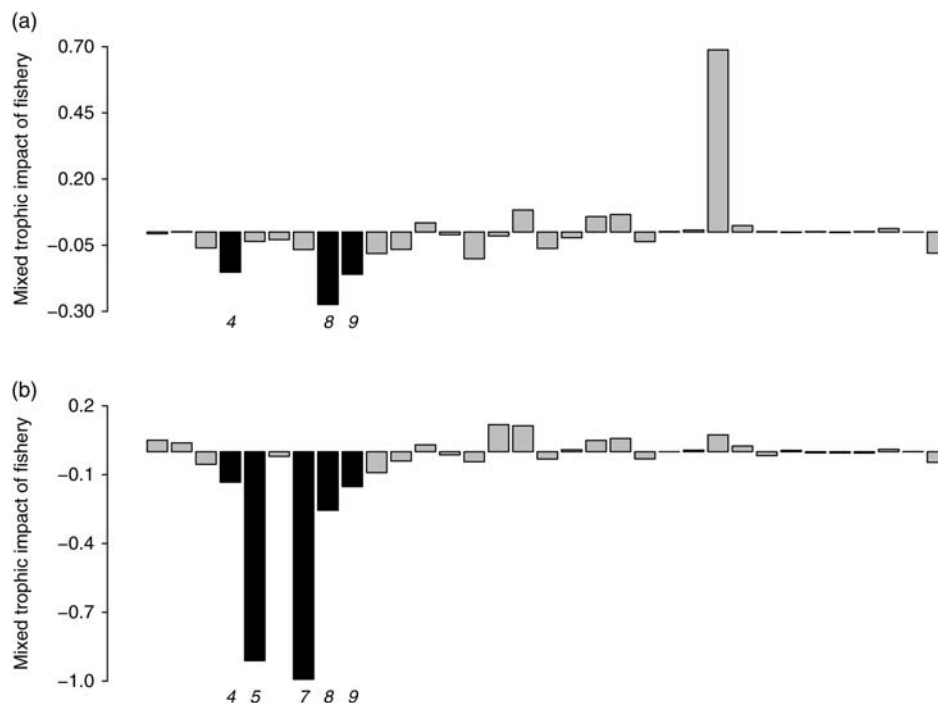
Figure 2. Mixed trophic impacts of fisheries in the different trophic groups of the Bay of Biscay continental shelf. Analysis was performed with (a) landings and discards of exploited compartments and later (b) by incorporating bycatches of toothed cetaceans (common dolphins and harbour porpoises). The bars pointing upwards indicate positive impacts, and the bars pointing downwards show negative impacts. Compartments detailed in the results section were highlighted in black (4, bottlenose dolphin; 5, common dolphin; 7, harbour porpoise; 8, piscivorous demersal fish; 9, piscivorous and benthivorous demersal fish; the functional group number is the same as the one provided in Table 1).

Table 5. Summary statistics for the ecosystem (i.e. summed over $TLs > 1$ and without bacteria), for each fishing effort multiplier, including the absolute and relative values compared with the baseline scenario ($mE = 1$).

mE	TotB	PredB	Y	R_TotB	R_PredB	R_Y	TL_TotB	TL_Y
0.2	4 112	1 540	54	1.13	1.22	0.32	2.82	3.74
0.4	3 977	1 461	95	1.10	1.16	0.57	2.80	3.72
0.6	3 853	1 388	126	1.06	1.10	0.75	2.79	3.70
0.8	3 737	1 321	149	1.03	1.05	0.89	2.78	3.69
1	3 630	1 258	167	1	1	1	2.77	3.68
2	3 198	1 008	214	0.88	0.80	1.28	2.72	3.64
3	2 894	832	229	0.80	0.66	1.37	2.68	3.61

TotB and R_TotB, total biomass and relative total biomass in kg C km^{-2}; PredB and R_PredB, predator biomass and relative predator biomass ($TL \geq$ 3.5) in kg C km^{-2}; Y and R_Y, catches and relative catches in kg C km^{-2} year^{-1}; TL_TotB and TL_Y, mean trophic level of the total biomass and the catch. Relative values were expressed by regarding the current state as the reference. Values given are those calculated with incidental captures of toothed cetaceans (common dolphins and harbour porpoises) included in the model.

corresponded to 95.3% of total catch on average. The mean TLs of the total biomass and catch were reduced by around 0.1 when compared with those calculated for the current effort values (from 2.77 to 2.68 and from 3.68 to 3.61, respectively; Table 5), this value of 0.1 being generally considered as not negligible in studies of fishing down marine foodwebs.

Non-dynamic ET simulations of increasing fishing pressure

Here, fishing mortality exhibited a bell-shaped curve, starting at TL 2.8 and reaching a maximum of 0.19 year^{-1} at TL 4.8; 67% of the total biomass at this TL being composed of piscivorous demersal fish (Figure 3a). This curve showed that fisheries mainly target predatory species (conventionally referred to species with $TLs \geq 3.5$ in ET) and can remove every year as much as about one-fifth of the total biomass of these species. The fishing loss rate followed a monotonic increasing curve, reaching a value of 0.26 year^{-1} at TL 5.5, 71% of the biomass at this TL being piscivorous demersal fish. In other words, at the 1994–2005 level of fishing, a quarter of the production of TL 5.5 is fished yearly. This confirms that high TLs are the most impacted by the fishery. Representing the biomass trophic spectrum for each fishing effort multiplier confirmed that the decrease in biomass was especially pronounced for the highest TLs (space between lines increased throughout the continuum; Figure 3b). When plotting the relative change in biomass (B/B_{ref}) according to the fishing effort for several exploited trophic classes ($TL = 3, 3.5, 4,$ 4.5, and 5), steepest slopes were observed between the current state ($mE = 1$) and a doubling of the fishing rate ($mE = 2$), and the decline in biomass was especially strong for the highest trophic classes (Figure 3c). Relative catches (Y/Y_{ref}) increased with fishing effort for trophic classes 3 and 3.5 and tended towards a maximum value for trophic class 4. Full exploitation was, however, reached for TL 4.5 with $mE = 2$ and for TL 5 with $mE = 1$; the values of Y/Y_{ref} then decreased in a trend of increasing fishing effort (Figure 3d). These trophic classes are exhibiting signs of overexploitation at the current fishing mortality or would do so after a realistic increase in fishing pressure. Along the gradient of increasing fishing effort, total catches represented between 5 and

8% of the total biomass, excluding TL 1 and bacteria, and between 13 and 28% of the predator biomass ($TL \geq 3.5$; Table 5).

Sensitivity analysis on ET parameters

The intra-group variability in TLs is the only parameter tested to which biomass and catch of TL 4.7 were shown to be sensitive (Figure 4). Changes were investigated for TL 4.7 because it corresponds to the mean TL of the marine mammal community. For each value of this parameter between 0.05 and 0.1, the biomass along the increasing gradient of fishing pressure declined monotonously; absolute values being modified by as much as 25%. In relation to catches at TL 4.7, the shape of the curve and the diagnosis varied markedly with the smoothing parameter. Values above the default setting of 0.07 led to an early decrease in catches with increasing fishing effort, depicting a more severe exploitation status of the ecosystem. The response of catches to variations of the smoothing parameter must be put in the context of the biomass distribution across TLs, which influences the proportion of biomass accessible to fisheries.

Inclusion of the bycatch of common dolphins and harbour porpoises did not modify the results at the ecosystem scale presented above.

Discussion
Bycatch estimates and population structure
For the Bay of Biscay continental shelf ecosystem, significant negative effects of fisheries appeared for the common dolphin and the harbour porpoise, when the MTI analysis included the bycatch of toothed cetaceans. The estimated ecotrophic efficiency of 0.833 for the harbour porpoise indicates that a large proportion of the production is used in the system. In the model, given the fact that the mortality caused by predators is null for this upper trophic-level species, the mortality is as such non-natural and due to incidental captures. In reality, probably a very few porpoises may be eaten by sharks, or even killer whales, and there may also be other kinds of anthropogenic mortality. In the past, concern has been expressed over the level of negative operational interactions between fisheries and the harbour porpoise in the northern part of its distribution range (Tregenza *et al.*, 1997; Rogan and Mackey, 2007). However, the deleterious impact of bycatch for this species in the present model must be interpreted with caution for two main reasons. The Bay of Biscay is at the southern margin of the harbour porpoise distribution in European waters. There are harbour porpoises also in Galicia (Northwest Spain) and northern Portuguese waters, but these are considered to be a separate population differing from the Northeast Atlantic stock. An isolated population also exists in the Black Sea (Fontaine *et al.*, 2010). The same authors demonstrated that porpoises in the central and eastern North Atlantic probably represent a single continuous population that extends thousands of kilometres from the French coasts of the Bay of Biscay northwards to the Arctic waters of Norway and Iceland. Second, the absolute abundance estimates in this area were lacking until recently, and the best estimate for the number of individuals present has changed markedly over the last two decades from a number below the limit of detectability based on aerial surveys to thousands of individuals as estimated during the first SCANS survey in 1994 (Hammond *et al.*, 2002; Marine Mammal Research Centre, http://crmm.univ-lr.fr/, unpublished data). Data from the SCANS-II survey in 2005 suggest an absolute abundance estimate of 386 000 individuals for the
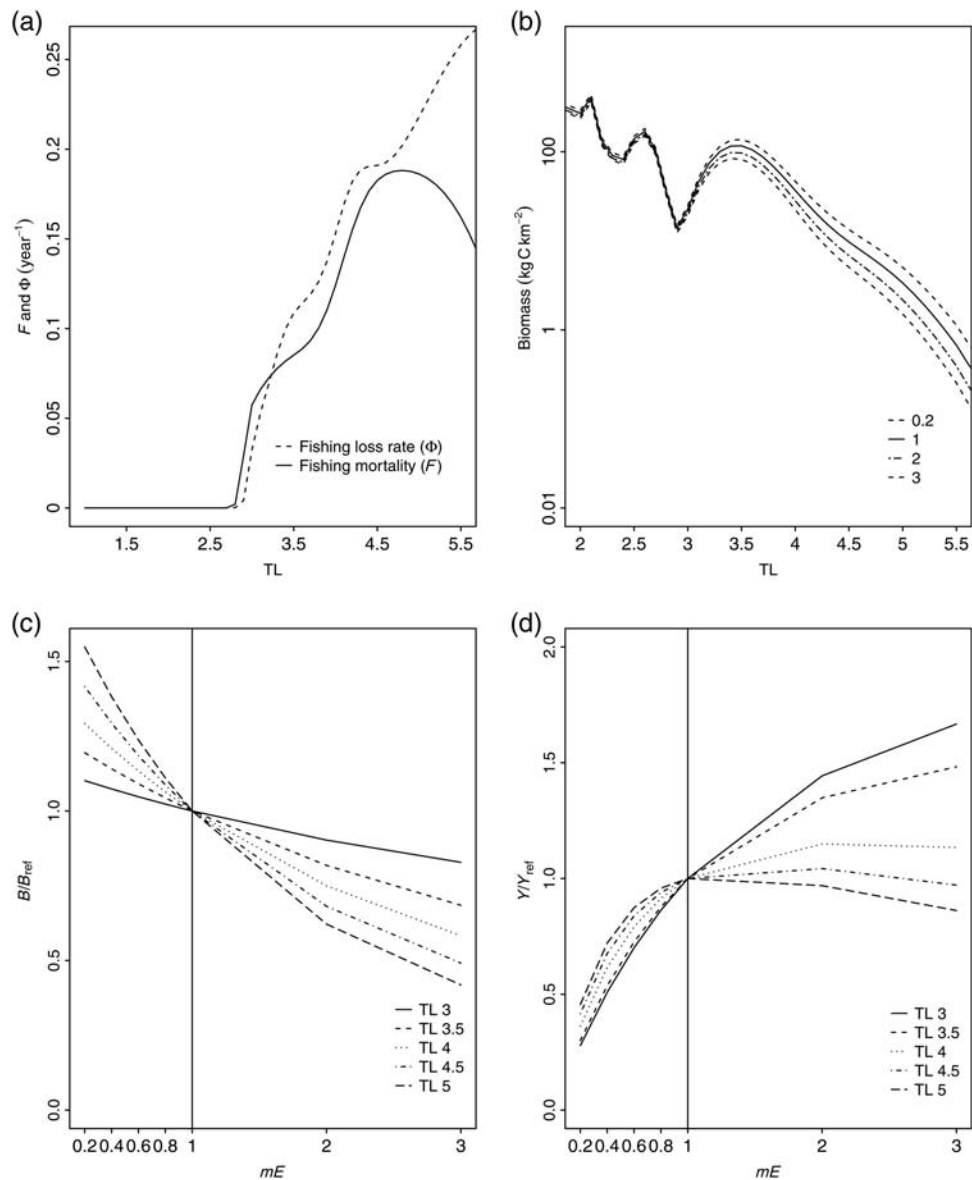
Figure 3. (a) Exploitation pattern at the current state of the ecosystem: fishing loss rate (Φ) and fishing mortality (F) for the total biomass; (b) for the simulated ecosystem, biomass trophic spectrum (biomass distribution over *TL*s); (c) relative biomass (B/B_{ref}) for trophic classes expressed as a function of the multiplier of the current fishing mortality ($mE = 1$); and (d) relative catch (Y/Y_{ref}) for trophic classes expressed as a function of the multiplier of the current fishing mortality calculated for different effort multipliers [from an unexploited state ($mE = 0$) to a threefold increase in fishing pressure ($mE = 3$)]. The solid line represents the current situation. Values given are those calculated with incidental captures of toothed cetaceans (common dolphins and harbour porpoises) included in the model.

entire European Atlantic and North Sea area, with ∼2646 individuals frequenting the survey block that comprises waters around southwestern France, Spain, and Portugal (http://biology.st-and.ac.uk/scans2/; SCANS-II final report). Allowable bycatch limits simulated under a series of management procedures and under the conservation objective of allowing the populations to recover to and/or maintain 80% of carrying capacity in the long term, based solely on the SCANS-II estimates, never exceeded ten individuals per year in the waters around southwestern France, Portugal, and Spain. This figure is far lower than the value estimated from observations and entered into the current model (ICES, 2010a, b).

The same reservation should be applied to conclusions regarding the common dolphin. Although results from genetic studies (Amaral *et al.*, 2007; Luca *et al.*, 2009) and skull morphometric analysis (Murphy *et al.*, 2006) support the existence of a single common dolphin population in the Northeast Atlantic, ranging from waters off Scotland to Portugal, three separate management units were proposed by Caurant *et al.* (2009) based on the analysis of several ecological tracers. Each methodology has its own time-scale: generation to evolutionary time-scale for genetic and morphometric studies and day to lifetime for ecological tracers. As such, in the northeastern Atlantic, ecological tracers were presented as useful to refine management units on a finer time-scale
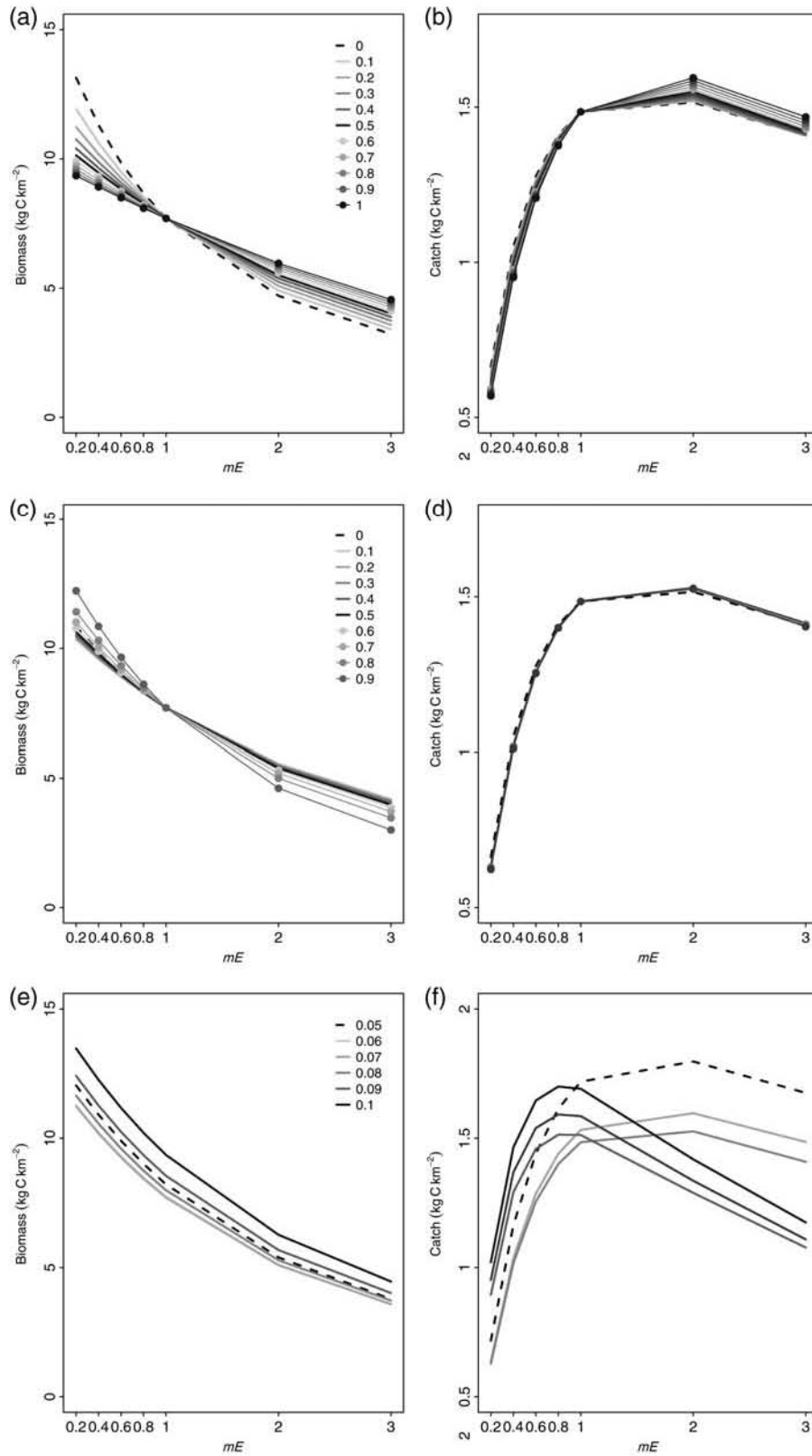
Figure 4. Sensitivity analysis of biomass (left) and catch (right) of the [4.7 – 4.8[trophic class to the main ET parameters: (a and b) top – down control (*TopD*), (c and d) biomass recycling (*Beta*), (e and f) width of the curves in the smoothing function (*smooth*), (g and h) accessibility to fisheries of by-caught marine mammals, and (i and j) accessibility to fisheries of all exploited and non-targeted compartments. The effects of these changes were investigated on *TL* 4.7 that corresponds to the mean *TL* of the marine mammal community (see Table 3 for details of values applied during sensitivity analysis). Values given are those calculated with incidental captures of toothed cetaceans (common dolphins and harbour porpoises) included in the model.
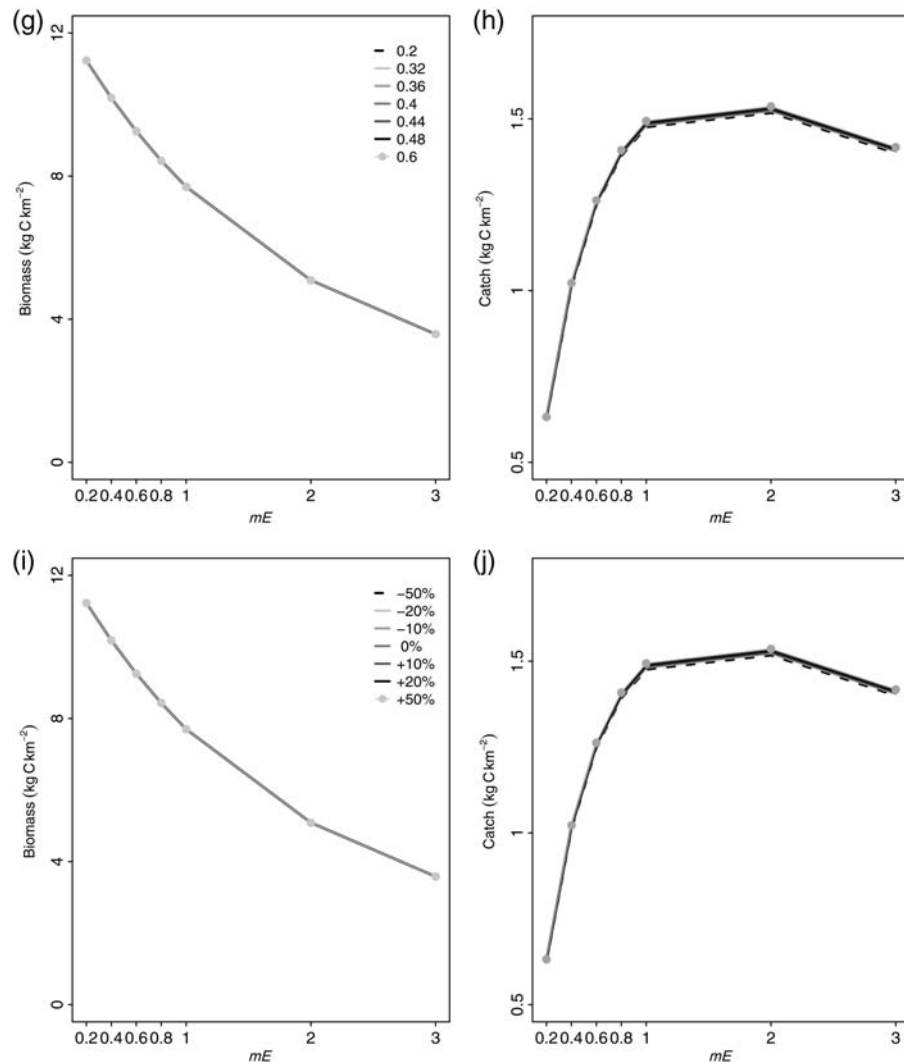
Figure 4. Continued

that may be more relevant to management issues (ICES, 2010c). These ecological tracers indicated a segregation with restricted interchange of individuals between oceanic, northern neritic, and southern neritic regions (the Bay of Biscay and the north-eastern Iberian Peninsula), which implies that effective population sizes are smaller than previously thought, and the impact of bycatch on individual populations consequently greater (Caurant *et al.*, 2009).

Competition for food and resource overlap

The present study and that of Pusineri *et al.* (2004) provided evidence for a significant direct overlap between the diet composition of the two commonest dolphin species in the region (in number of individuals and biomass) and fishery catches. Pusineri *et al.* (2004) studied the dietary overlap between fisheries and small delphinids in the Bay of Biscay by applying the original Pianka niche overlap index (Pianka, 1973) to data quite similar in their origin to those presented in the current study (stomachs of stranded dolphins collected along the coasts of the Bay). In the neritic area of the Bay, the Pianka index value for overlap with fisheries was found to be high for common dolphins, low for striped dolphins, and

intermediate for both bottlenose dolphins and harbour porpoises. In the present study, the index proposed by Morissette *et al.* (2010a), which differed from the Pianka index by the inclusion of a weighting factor accounting for the total quantity of resource consumed, was used. As the total food intake of marine mammals was low compared with the biomass removed by the fisheries, the calculated degree of common resource utilization was tempered and appeared as such to be medium to low. It should be acknowledged as well that overlap estimates for the toothed cetacean community were probably smoothed by the inclusion of fisheries as a single average fleet and were likely to have been slightly underestimated. Adding to this, the MTI analysis including direct and indirect trophic linkages provided the strongest evidence of competition between bottlenose dolphins and fisheries, as dietary overlap alone does not prove competition given the fact that resources could be adequate to support both species. The increase in landings and discards of exploited compartments in the MTI routine resulted in a significant direct decrease in food available to bottlenose dolphins.

At the community scale, overlap "hot spots" in the North Atlantic (calculated using an index similar to the one used here)

occurred mainly on, or along, the edges of shelves in the North Sea and adjacent waters but with almost no overlap between toothed whales (sperm and beaked whales, porpoises and dolphins) and fisheries detected (Kaschner *et al.*, 2001). Specific results for the community of the Bay of Biscay tended in the same direction (global $\alpha_{fm} = 0.07$), meaning that the availability of food is not constrained much by competition, but food could theoretically still be scarce in absolute terms.

Ecosystem models are useful for generating hypotheses about potential impacts of fisheries on marine ecosystems but conclusions can be biased by the uncertainty in input parameters and influenced by the model structure. Indeed, foodwebs with lower complexity in the community structure (fewer trophic links) tend to have higher overlap values (Hall and Raffaelli, 1993; Morissette, 2007). In the present study, the global omnivory value of 0.20 (*SOI*) is a relatively "intermediate" value when compared with those obtained for other shelf ecosystems in the world and with outputs from previous Bay of Biscay models (Lassalle *et al.*, 2011), but it is a relatively "high" value when the comparison extends to a broader set of marine ecosystems (Morissette *et al.*, 2010b). So, the low level of prey aggregation in our model, which is made up of several mono-specific boxes, could be part of the explanation for the restricted community overlap found in the system.

A *TL*-based assessment of fisheries impacts

Results from the simulations of fishery impacts on the Bay of Biscay continental shelf ecosystem presented the same patterns to catches and ecosystem biomass obtained with virtual ecosystems submitted to increasing fishing pressure (Gascuel *et al.*, 2011). The ecosystem under study combined three characteristics that, according to these theoretical simulations, amplify sensitivity to fishing activities, i.e. bottom−up regulation, biomass input control (detritus-based), and high transfer efficiencies (mean transfer efficiency was 15.7%). In this direction, signs of overexploitation, i.e. decreasing catches for the highest exploitation rates, rapidly appeared for predator classes during simulations. Further evidence of overexploitation at ecosystem scale, i.e. declining mean *TL* of the catch with increased fishing effort, was nonetheless moderate. This picture of an ecosystem not far from being overexploited at the current level of fishing pressure strengthened previous findings derived from trophodynamic indicators (L-index; Libralato *et al.*, 2008) in this area (Lassalle *et al.*, 2011). However, in the present work, the biomass decomposition did not allow us to associate a specific trophic class with marine mammals (other species occupy the same levels as dolphins), as we first thought might be possible. This highlights the fact that some targeted fishes also play a top predator role within the ecosystem. As a consequence, the response of marine mammals to fisheries could not be isolated. Similarly, inclusion of the bycatch of toothed cetaceans did not change the diagnosis produced by ET. Indeed, the related additional bycatch mortality is low and only impacts a small fraction of the high *TLs*' biomass. Therefore, the potential effects of fisheries bycatch on marine mammals were masked by the response to increasing fishing pressure of other biological elements that composed the trophic class 4.5. Nevertheless, this *TL*-based analysis of fisheries impacts was useful to supply a general context to more species-specific results presented in the two previous sections and to provide important novel insights on the ecosystem functioning.

From a methodological point of view, the sensitivity analyses showed that the key ET parameter, impacting our diagnosis, is the estimation of the sigma of the lognormal function. This parameter is critical to produce continuous distributions of biomass, production, and catch (Gascuel and Pauly, 2009; Gascuel *et al.*, 2009). The omnivory index (*OI*) estimated from Ecopath models at first appeared to be the candidate measure of dispersion to use in ET. However, its values refer in fact to the variability between the different prey of a given predator and not necessarily to the variability between various predators constituting a model compartment. Additionally, these values can be underestimated by the inclusion of "imports" and "discards" in the diet of functional groups, as it was the case here. Adding to this, Libralato and Solidoro (2010) who presented various methods for the construction of trophic spectra concluded that *OI* was a weak measure of the distribution of energy flow. According to these authors, *OI* does not integrate the cascade propagation of the dispersion of prey items along the ecological network. ET developers are currently working on the definition of a reference smoother with a unique and fixed value [see Equation (2), M. Colleter, pers. comm.]. Ultimately, the theoretical model with the default parametrization was used as the best compromise in the present study.

Conclusions

To our knowledge, this is the first extensive study of fisheries− marine mammal interactions at the ecosystem scale in the Bay of Biscay. Fisheries, in addition to causing significant bycatch mortalities on the common dolphin and harbour porpoise (operational interactions), were demonstrated to affect the bottlenose dolphin through direct, and most probably indirect, competition for food (biological interactions). Adding to this, the exploitation status of this ecosystem as a whole was determined through non-dynamic simulations performed with ET, a new statistical technique. The Bay of Biscay continental shelf appeared not far from being overexploited, this view being consistent with previous but partial conclusions obtained from ecological network analysis. This phenomenon seemed even more pronounced when focusing on high *TL* organisms. This paper provides a concrete illustration of how the joint utilization of Ecopath and ET allowed an easy-to-implement assessment of fisheries impacts at the ecosystem scale, and more particularly, on compartments which are biologically and culturally important and reinforced the importance of durably gathering long-term series on marine mammal bycatch.

Acknowledgements

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