Let's go beyond taxonomy in diet description: testing a trait-based approach to prey–predator relationships

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Abstract:

1. Understanding 'Why a prey is a prey for a given predator?' can be facilitated through trait-based approaches that identify linkages between prey and predator morphological and ecological characteristics and highlight key functions involved in prey selection.
2. Enhanced understanding of the functional relationships between predators and their prey is now essential to go beyond the traditional taxonomic framework of dietary studies and to improve our knowledge of ecosystem functioning for wildlife conservation and management.
3. We test the relevance of a three-matrix approach in foraging ecology among a marine mammal community in the northeast Atlantic to identify the key functional traits shaping prey selection processes regardless of the taxonomy of both the predators and prey.
4. Our study reveals that prey found in the diet of marine mammals possess functional traits which are directly and significantly linked to predator characteristics, allowing the establishment of a functional typology of marine mammal–prey relationships. We found prey selection of marine mammals was primarily shaped by physiological and morphological traits of both predators and prey, confirming that energetic costs of foraging strategies and muscular performance are major drivers of prey selection in marine mammals.
5. We demonstrate that trait-based approaches can provide a new definition of the resource needs of predators. This framework can be used to anticipate bottom-up effects on marine predator population dynamics and to identify predators which are sensitive to the loss of key prey functional traits when prey availability is reduced.

Keywords: foraging strategy ; fourth-corner method ; functional ecology ; marine mammals ; prey selection ; RLQ analysis

Introduction

Understanding how ecosystems function and how they may change under natural or anthropogenic pressures are among the most significant challenges facing ecologists. The growing development of functional approaches marked an important step towards the understanding of ecosystem functioning. Hence, the use of trait-based frameworks greatly improved our knowledge of relationships between species and their environment (Luck *et al.* 2012). The major advances occurred in the linkage of species physiological or morphological traits to habitat characteristics (e.g. Barbaro & Van Halder 2009; Cleary *et al.* 2009; Hanspach *et al.* 2012). However, little attention has been given to the application of trait-based approaches in foraging ecology. Prey-predator relationships are often studied using a predominantly taxonomic approach without consideration on prey characteristics: "which predator feed on which species?". Thus, the study of foraging strategies tends to be too often limited to interpreting the species and richness of prey in the diet of predators, therefore qualifying monotypic predators as specialized or selective predators and predators feeding on a large range of prey species as generalist, or even opportunistic predators. A further step in foraging ecology is to go beyond the simple taxonomic description of the diet to understand and answer the question of "why a prey is a prey?". This, however, implies to assess the functional aspects of the relationships between prey and predators. To achieve such objective, methodological approaches focusing both on prey and predator characteristics are too often ignored, especially in marine ecosystems. Previous studies investigating the diet of marine predators in a functional approach most exclusively focussed on predator-prey length relationships (Scharf *et al.* 2000; Aljetlawi *et al.* 2004) and only few studies attempted to group marine preys based on other characteristics without regard on taxonomy (Ridoux 1994). Size-based approaches have brought fundamental insights in community and ecosystem structures (Petchey & Belgrano 2010) or in the study of energy metabolism for

instance (Kleiber 1975), suggesting that allometry can be used as a universal predictor in some processes from individual to ecosystem. However, theories of size spectra have generally failed to provide powerful predictions of prey selection and especially for large marine predators (MacLeod *et al.* 2006; Spitz *et al.* 2012).

Changes in marine prey quality have nevertheless contributed to revive functional considerations on relationship between marine top predators and their prey. Indeed, we now acknowledge functional diversity as being as important (if not more important) as taxonomic diversity to maintain a good ecosystem health and functioning (Flynn *et al.* 2009). In foraging ecology, recent studies have suggested the paramount importance of prey quality in comparison to prey quantity alone in maintaining healthy populations of some marine top predators (Trites & Donnelly 2003; Spitz *et al.* 2012). This hypothesis of importance of prey characteristics in sustaining healthy populations of marine top predators has been confirmed by the decline of several seabird and pinniped colonies impacted by a change of prey quality in their diet (Österblom *et al.* 2008). In such cases, overall biomass and biodiversity could remain unchanged while predator's nutritional fulfilments and energy requirements were jeopardized by a functional change of available prey. Consequently, prey selection should be more driven by prey characteristics than prey taxonomy, for instance common dolphins (*Delphinus delphis*) selected high energy density prey species and disregarded prey organisms of poor energy content even when the latter were more abundant in the environment (Spitz *et al.* 2010). Hence, the diet of common dolphin may exhibit spatial and/or temporal taxonomic variations but it always included a high proportion of fat fish (Meynier *et al.* 2008; Spitz *et al.* 2012). This lead to the conclusion that some prey species sharing common functional traits are interchangeable −while others are not. Identifying the common characteristics of prey species composing the diet of a predator should mark a breakthrough in animal foraging ecology.

Linking predator functional traits to species functional traits is methodologically similar to linking species traits to environmental characteristics. This latter can be accomplished by using three-matrix approaches, named the fourth-corner approach (Legendre *et al.* 1997; Dray & Legendre 2008) and RLQ analysis (Dolédec *et al.* 1996). These multiple-tables approaches consist in the analysis of three matrices of data (*R*, *L* and *Q*), composed of species abundance data (*L*), species trait data (*Q*) and environmental data (*R*). The fourth-corner approach yields correlation between *Q* and *R*, whereas the RLQ analysis provides a simultaneous ordination of *R*, *L* and *Q*. The main advantages of these methods are that -1- multiple traits and environmental variables can be assigned and tested (univariate analysis in fourth-corner method and multivariate analysis in RLQ) and -2- functional groups of traits can be identified and linked to key functions of ecosystems. Thus, these approaches have been applied to a wide range of species including plants, insects, fish, birds or bats in diverse ecosystems (Barbaro & Van Halder 2009; Brind'Amour *et al.* 2011; Hanspach *et al.* 2012; Ikin *et al.* 2012). However, such trait-based approach has never been used to our knowledge in a framework on prey-predator functional foraging.

We propose here to use the fourth-corner statistic and RLQ analysis to explore the functional relationship between prey traits and predator traits. These methods can be easily implemented in dietary studies of top predators using *predator traits* (matrix *R*) as equivalent to the *species traits*, the *prey traits* (matrix *Q*) substituting for *the environment*, and the predators *diet composition* (matrix *L*; quantitative measures) as the *abundance* data in the traditional use of fourth-corner and RLQ methods (Dolédec *et al.* 1996; Dray & Legendre 2008). Our first objective was to test the relevance of such trait-based approach in foraging ecology among a marine mammal community in the north-east Atlantic. Marine mammals are a particularly interesting group to conduct trait-based approaches because their morphological and physiological traits are extremely diversified, they feed on a wide range of organisms and the

outcome of a better understanding of their feeding ecology should benefit the conservation of marine ecosystems, and the management of human activities including fisheries. The second goal of the study was to identify the key functional traits shaping prey selection processes regardless of the taxonomy of both the predators and prey. This was done by focussing on the results of two main linkages: predators-prey morphological relationships and relationships involving costs of predation and prey profitability.

Materials & methods

DIETS OF MARINE MAMMALS: DATA ORIGIN

We compiled the diet composition of 16 species of marine mammals using 40 published stomach and scat content analyses composed of around 130 different prey species in European waters (see appendix S1 in Supporting Information for references and appendix S2 for data). Marine mammal species included dolphins, whales, porpoises and seals belonging to 7 families (Balaenopteridae, Phocoenidae, Delphinidae, Ziphiidae, Physeteridae, Kogiidae and Phocidae): minke whale (*Balaenoptera acutorostrata*), fin whale (*Balaenoptera physalus*), harbour porpoise (*Phocoena phocoena*), common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), bottlenose dolphin (*Tursiops truncatus*), long-finned pilot whale (*Globicephala melas*), Cuvier's beaked whale (*Ziphius cavirostris*), bottlenose beaked whale (*Hyperodoon ampullatus*), *Mesoplodon* beaked whales (*Mesoplodon europaeus*, *M. densirostris* and *M. bidens*), sperm whale (*Physeter macrocephalus*), pygmy sperm whale (*Kogia breviceps*), harbour seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*). Dietary data from the stomach content analyses included prey identified at the species level and their percentage by ingested biomass in the predator diet. Briefly described, stomach content analysis is based on the identification and quantification of prey remains including fish otoliths and bones, cephalopod beaks and crustacean carapaces following

standard analytical methods (e.g. Pierce & Boyle 1991; Spitz *et al.* 2011). Allometric relationships allow reconstructing individual prey body length and mass from remains to provide quantitative description of diets. Thus, the different studies used similar methodology and directly provided percentage by mass for each prey species to complete the matrix *L* (predator diets).

FUNCTIONAL TRAITS

Both marine mammals and their prey (fish, cephalopods and crustaceans) were categorized by morphological, physiological and ecological features called here functional traits. We collected data on traits of adult marine mammals and their prey from extensive searches in literature and unpublished data available from the French stranding network database (see appendix S5 for sources of values for each functional trait). We attempted to be as exhaustive as possible in the selection of functional traits; nevertheless, we mainly retained traits for their potential importance in prey-predator relationships. Moreover, we selected only traits which were well documented by quantitative data for all studied species, and we discarded poorly documented traits or traits defined on subjective judgements or interpretation such as some behavioural or physiological aspects. Summarising morphological, physiological and ecological features into distinct biologically relevant traits can be challenging both for prey and predator species. Some marine mammal species exhibit different populations, sometimes recognised as distinct ecotypes, with highly variable characteristics. Some prey species can also fall within different functional traits if their whole life history and distribution are considered. Hence, using a single set of functional traits to summarise such species in a biological meaningful way is often impossible. For species with distinct ecotypes (e.g. *Tursiops truncatus*) or for species with extensive geographic variation we retained characteristics corresponding to eastern North Atlantic populations, as sampled in our

compilation of dietary studies instead of general or average information on whole species. Similarly, prey characteristics refer mostly to stocks consumed by marine mammals in European waters. Thus, we acknowledge some limitations to the underlying trait database, and for full transparency we provide all the values used for each functional traits and their sources (see appendix S3 and S4 in Supporting Information for complete species-traits assignments and appendix S5 for sources of values for each functional trait).

Some continuous functional traits (*e.g.* body length, body mass depth) have been discretized in several categories to conduct the statistical analyses. In order to limit arbitrary categories, we used literature and rapid clustering on our data to propose biologically meaningful categories. Such categorisation allowed limiting the influence of ontogeny or sexual variation. For example with body size, all mature animals both male and female fall mostly in only one category for a given marine mammal species. Thus, prey species were described by 19 functional traits composed of 2 to 5 state categories for a total of 63 categories (Table 1). Marine mammals were described by 17 functional traits which organized in 2 to 5 state categories for a total of 68 categories (Table 1). It should also be pointed out that a species can fall in several categories for a given functional trait, in particular for continuous traits. Thus, we covered a part of inherent variability within each species from minimal to maximal values for a given trait rather than approximating a continuous trait by only one central or extreme value. For example with diving capacity, a given species will fall in all categories from the shallowest (0-200 m) to the deepest depth class including its maximum diving depth (see appendix S3 and S4 in Supporting Information for complete species-traits assignments and appendix S5 for sources of values for each functional trait).

Table 1. *Functional traits and categories for prey and predator species considered in the analyses with results of RLQ group assignment.*

PREY TRAITS	CATEGORIES	CODES	RLQ GROUP
Body length	1-10 cm	L1	II
	10-30 cm	L2	IV
	30-100 cm	L3	IV
Body mass	1-10 g	W1	II
	10-100 g	W2	IV
	100-500 g	W3	IV
	500-1000 g	W4	IV
	>1000 g	W5	IV
Body shape	Fusiform	F1	IV
	Compress	F2	II
	Flat	F3	IV
	Cylindric	F4	IV
Spine	No	S1	IV
	Few	S2	II
	Numerous	S3	IV
Photophores	Absence	P1	IV
	Presence	P2	I
Color	Cryptic	C1	IV
	Conspisius	C2	IV
Skeleton	No	O1	III
	Exosquelette	O2	II
	Internal	O3	I
Mobility	Immobile	M1	IV
	Low escape ability	M2	IV
	Swimmer	M3	I
Water content	Low	WAT1	I
	Medium	WAT2	II
	High	WAT3	III
Protein content	Low	PRO1	III
	Medium	PRO2	I
	High	PRO3	IV
Lipid content	Low	LIP1	III
	Medium	LIP2	I
	High	LIP3	I
Ash content	Low	ASH1	IV
	Medium	ASH2	II
	High	ASH3	IV
Energy density	Low	ED1	III
	Medium	ED2	IV
	High	ED3	I
School size	Isolated individual	B1	IV
	Small	B2	IV
	Large	B3	I
Horizontal habitat	Coastal	H1	I
	Shelf	H2	IV
	Slope	H3	IV
	Oceanic area	H4	III
Vertical habitat	Surface	V1	IV
	Pelagic	V2	IV
	Demersal	V3	IV
	Benthic	V4	IV
Diel migration	Absence	N1	III
	Presence	N2	I
Seasonal migration	Absence	G1	I
	Presence	G2	III
Depth	0-30 m	D1	I
	30-200 m	D2	I
	200-500 m	D3	IV
	500-1000 m	D4	IV
	1000-3000 m	D5	IV

PREDATOR TRAITS	CATEGORIES	CODES	RLQ GROUP
Body length	1-2 m	BL1	A
	2-5 m	BL2	E
	5-10 m	BL3	D
	10-15 m	BL4	D
	15-30 m	BL5	B
Body mass	10-100 kg	BM1	A
	100-500 kg	BM2	E
	500-1000 kg	BM3	E
	1000-10000 kg	BM4	D
	10000-50000 kg	BM5	D
Frontal surface	400-1000 cm²	FF1	A
	1000-3000 cm²	FF2	E
	3000-5000 cm²	FF3	E
	5000-10000 cm²	FF4	D
	10000-30000 cm²	FF5	D
Fineness ratio	<5	FR1	E
	>5	FR2	B
Rostrum	Presence	RO1	E
	Absence	RO2	B
Teeth on lower mandibular	0	TU1	B
	1-2	TU2	D
	10-20	TU3	D
	20-50	TU4	D
	>50	TU5	A
Differentiated teeth	Presence	TD1	E
	Absence	TD2	D
Baleen plates	Presence	FA1	B
	Absence	FA2	E
Echolocation	Presence	EC1	D
	Absence	EC2	B
Vibrissae	Presence	VI1	E
	Absence	VI2	D
School size	Isolated individual	GR1	E
	Small	GR2	D
	Large	GR3	A
Sustainable swimming speed	<2 km.h-1	SS1	D
	2-3 km.h-1	SS2	B
	>3 km.h-1	SS3	E
Maximum swimming speed	<6 km.h-1	SM1	D
	6-10 km.h-1	SM2	B
	>10 km.h-1	SM3	A
Diving capability	0-200 m	DD1	A
	200-500 m	DD2	B
	500-1000 m	DD3	E
	1000-3000 m	DD4	C
Muscle mitochondrial density	Low	IM1	C
	Medium	IM2	B
	High	IM3	A
Muscle lipid content	Low	LT1	C
	Medium	LT2	A
	High	LT3	A

STATISTICAL ANALYSES

The hypothesis tested here is that prey species composition of marine mammal diets results from the selection of prey traits driven by predator physiological and morphological characteristics. We used (as mentioned in the Introduction) three-matrix approaches to test that hypothesis. These approaches require three input matrices, R, L and Q (Fig. 1). The first matrix (L: m x p) contains the percentage by mass of the p prey species in the diet of the m marine mammal species. The second matrix (Q: p x n) describes the same p prey species according to the set of n functional traits (Table 1). The third matrix (R: m x k) described the same m marine mammal species according to the set of k functional traits (Table 1). Data in matrices Q and R were coded as 1 or 0 (presence or absence respectively of the considered trait).
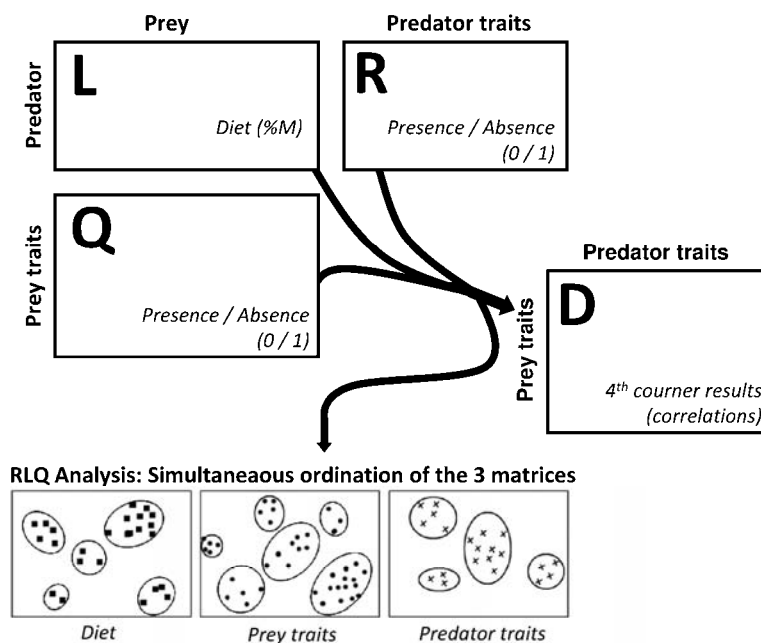

Fig. 1. *Schematic flow diagram of the three-matrix approaches. The fourth-corner method was used to test statistically each combination of prey traits and predator traits. RLQ analysis was used to facilitate ecological grouping and interpretation of the results.*

The analytical routine of the fourth-corner analysis was performed using R software (R Development Core Team 2012) with the function "fourthcorner" included in the "ade4" package (Dray & Dufour 2007) and following methods recommended by Dray & Legendre (2008). The fourth-corner approach computes predator–prey correlations in a fourth matrix (*D*) using the three matrices *R*, *L* and *Q*. Therefore, matrix *D* (*n* x *k*) contains the correlation values α of the *n* prey functional traits crossed with the *k* predator functional traits. The null hypothesis (H_0) tested in the fourth-corner approach, is that prey functional traits are unrelated to functional traits of their predators. According to Dray and Legendre (2008), this hypothesis cannot be tested directly. They suggested a two-steps strategy in which rejection of H_0 requires the rejection of two secondary hypotheses (H_{01} and H_{02}) associated with two permutation models. H_{01} tests for the absence of a link between prey composition in the predators' diets and prey functional traits (L → Q). This is the underlying hypothesis when one is permuting the entire rows (permutation model 2). Whereas, H_{02} tests the absence of a link between the prey composition in the predators' diets and predator functional traits (L → R). This hypothesis is used when the entire columns are permuted (permutation model 4).

Ter Braak *et al.* (2012) showed that H_0 can be correctly rejected at significant level $\alpha=0.05$ by reporting the maximum of the individual *p*-values obtained under the two hypotheses (H_{01} and H_{02}) as the final one. This is what the function "fourthcorner" does in the default permutation model as of "ade4" version 1.6. (Dray *et al.* 2013). As multiple correlations are being tested in matrix *D*, the False Discovery Rate (FDR) adjustment for multiple testing (Benjamini & Hochberg 1995) was also applied on the *p*-values from the matrix *D*. Thus, only the correlations that remained significant at the 0.05 level after the correction of Ter Braak *et al.* (2012) and the Benjamini & Hochberg adjustment were used for ecological interpretation. Hence, at most 5% of the entries are falsely listed in the lists of significant correlations.

RLQ analyses (Dolédec *et al.* 1996) were performed using the "rlq" function of the "ade4" package. RLQ is an extension of co-inertia analysis that simultaneously finds linear combinations of the variables of matrix R and linear combinations of the variables of matrix Q of maximal covariance weighted by the data in matrix L (Dray *et al.* 2003). It graphically summarizes and represents the main co-structure in the three matrices R, L and Q. The RLQ and fourth-corner analyses were jointly used to identify the groups of prey or predator traits. Graphical representations of the outputs of RLQ analysis (e.g. scores of the prey traits and predator traits) were used for interpretation purposes.

Groups of predator and prey traits were obtained by K-means partitioning (Hartigan & Wong 1979) computed on the first two axes of the R and Q scores. We also computed K-means partitioning on 3 or 4 different axes and the groupings gave exactly the same results as those with two axes. Therefore, we kept the firsts two axes just as we did for visualization. K-means partitioning searches for the groups that minimize the total within-group (or "error") sum of squares or, equivalently, the total intra-cluster variation. It was applied in cascade on several numbers of groups. For each number of groups identified by the K-means partitioning, the simple structure index (SSI, Dolnicar *et al.* 1999) criterion was computed. The partition displaying the highest SSI value was used to assess the best number of groups corresponding to the most condensed set of traits. The K-means partitioning was done using the *cascadeKM* function in the *vegan* package.

RESULTS

FOURTH-CORNER ANALYSIS OF TRAITS INVOLVED IN PREY – PREDATORS RELATIONSHIPS

The multivariate statistic of the fourth-corner analysis, inertia of matrix D, revealed an overall significant link between the prey and the predator functional traits (permutation test *p-value* =

0.001). The null hypothesis H_0 was thus rejected at the global scale of the analysis, and specifically, a high number of significant relationships between the prey and predator functional traits were detected and analysed (see appendix S6 in Supporting Information for the entire matrix *D*).

The prey functional traits most involved in prey selection by predators are those reaching both high number of significant relationships with predator functional traits and high correlation values. These traits should be interpreted as the key functional traits targeted by predators. Here these key functional traits were energy density (ED), horizontal habitat (H), protein content (PRO), skeleton structure (O), and water content (WAT). In contrast, some traits such as colour (C), body mass (W) or presence of photophores (P) appeared not to be strongly involved in selection by predators (Fig. 2a).

The predator traits showing high number of significant correlations and high correlation values with prey traits were the echolocation ability (EC), muscular performance, *i.e* muscle lipid content (LT) and mitochondrial density (IM), then presence of differentiated true teeth (TD) or vibrissae (VI) and diving capacities (DD) (Fig. 2b). These traits should be interpreted here as the key functional traits driving the predator foraging strategies.
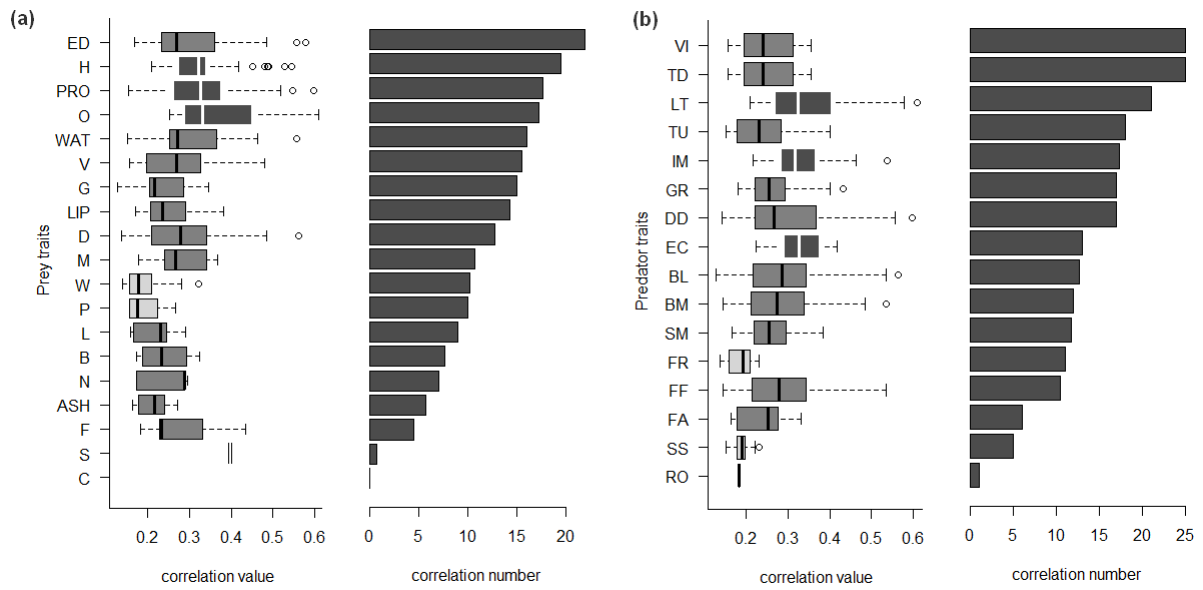
Fig. 2. *Values (boxplot on the left of each panel) and number (barplot on the right of each panel) of significant correlations found for each prey (a) and predator traits (b) obtained by the fourth-corner analysis. The bold solid line within each box is the median, and the bottom and top of each box represent the 25th and 75th percentiles; the whiskers represent the 10th and 90th percentiles and values outside this range are plotted as individual outliers; white box indicate no significant correlation, light-grey boxes indicative values of positive correlations <0.2, dark-grey boxes indicative values of positive correlations from 0.2 to 0.3 and black boxes indicative values of positive correlations >0.3. As the number of categories varies among traits, the number of correlations has been corrected (i.e. the total number of correlations divided by the number of categories for each trait). Trait codes are available in table 1.*

FOURTH-CORNER ANALYSIS OF PREDATOR TRAITS SHAPING PREY SELECTION

To verify the hypothesis of an energetically-based foraging strategy, we selected from the matrix of predator-prey traits correlations (matrix *D*) the functional traits associated with costs of predation, *i.e.* maximum swimming speed (SM), diving capability (DD), muscle

mitochondrial density (IM) and muscle lipid content (LT), and prey traits associated to the prey profitability for predators, *i.e.* lipid content (LIP) and energy density (ED). Fourth-corner analysis revealed that predator traits illustrating high activity levels (SM3, IM3, LT3) were strongly correlated to high-quality prey (LIP3, ED3). Conversely low activity levels (SM1, IM1, LT1) and high diving capability (DD4) were correlated to low-quality prey (LIP1, ED1) (Table 2). The values of these correlations were among the highest values across the entire matrix *D*. In the same way, we selected the functional traits associated with size characteristics for both marine mammals and prey. In general, we observed only few correlations and these correlations displayed low values. No allometric relationship was detected between prey body length or mass (L and W) and predator body length or mass (BL and BW), meaning that size of prey was not correlated with size of predators at an interspecific scale (Table 2). Only, medium-sized predators (2 to 5 m, 100 to 500 kg) appeared to target particular prey size (large preys greater than 30 cm and 500 g), whereas both smaller and larger marine mammal species appeared to be more plastic on the size of prey they consume.

Table 2. *Extract from matrix D representing the fourth-corner correlations involving the functional traits associated with costs of predation, prey traits associated to the prey profitability for predators and body size and body mass both for prey and predator. White box indicate no significant correlation, light-grey boxes indicative values of positive correlations <0.2, dark-grey boxes indicative values of positive correlations from 0.2 to 0.3 and black boxes indicative values of positive correlations >0.3.*

PREY TRAITS

Legend for shading: LG = light-grey (correlation <0.2); DG = dark-grey (0.2–0.3); BK = black (>0.3); blank = no significant correlation.

PREDATOR TRAITS			Lipid content LIP1 (Low)	LIP2 (Medium)	LIP3 (High)	Energy density ED1 (Low)	ED2 (Medium)	ED3 (High)	Prey body length L1 (1-10 cm)	L2 (10-30 cm)	L3 (30-100 cm)	Prey body mass W1 (1-10 g)	W2 (10-100 g)	W3 (100-500 g)	W4 (500-1000 g)	W5 (>1000 g)
Maximum swimming speed	SM1	<6 km.h-1	DG			DG										
	SM2	6-10 km.h-1														
	SM3	>10 km.h-1			LG			BK								
Diving capability	DD1	0-200 m					LG			LG		BK				
	DD2	200-500 m			LG											
	DD3	500-1000 m									LG			LG	LG	LG
	DD4	1000-3000 m	BK			BK										
Muscle mitochondrial density	IM1	Low	LG			BK										
	IM2	Medium														
	IM3	High				BK		BK								
Muscle lipid content	LT1	Low	LG			BK							DG			
	LT2	Medium					DG									
	LT3	High				BK		BK								
Predator body length	BL1	1-2 m					DG									
	BL2	2-5 m												LG	DG	DG
	BL3	5-10 m														
	BL4	10-15 m	DG													
	BL5	15-30 m														
Predator body mass	BM1	10-100 kg					DG		DG							
	BM2	100-500 kg							DG					DG	DG	DG
	BM3	500-1000 kg		LG										LG		
	BM4	1000-10000 kg				BK									LG	
	BM5	10000-50000 kg	DG			BK										

RLQ ANALYSIS OF PREY AND PREDATOR TRAIT ORDINATIONS

The first two axes of the RLQ analysis explained respectively 63 % and 22 % of the total variance. The first RLQ axis was strongly correlated with physiological traits both for prey and predators. Thus, the ordination of prey traits appeared to represent a gradient from low quality prey to high quality prey; low lipid content (LIP1), low protein content (PRO1), high water content (WAT3) and low energy density (ED1) exhibited among the lowest values on the first axis whereas moderate protein content (PRO2), high lipid content (LIP3) and high energy density (ED3) exhibited among the highest values on the same axis (Fig. 3a). The skeleton structure exhibited also a high correlation; the absence of internal skeleton (O1) contributed to explain the negative part of the first RLQ axis, whereas the presence of an internal skeleton (O2) characterized the positive part of the same axis. Finally, some ecological traits, such as habitat (H) or migrations (N and G), completed the explanation of the variance observed on the first axis. Regarding predator traits, the ordination represented a gradient from species with low muscular performances, *i.e.* low mitochondrial (IM1) and lipid contents in the muscle (LT1), low swimming speed (SM1) and high diving capability (DD4) to species with high muscular performances, *i.e.* high mitochondrial (IM3) and lipid contents in the muscle (LT3), high swimming speed (SM3) (Fig. 3b).

The second RLQ axis was correlated with morphological traits (Fig. 3). The ordination of prey trait was here mainly explained by body shape (F), body size (L) or presence of spines (S) for instance. The negative part showed also a high correlation with the presence of exoskeleton (O2). Regarding the predator traits, morphological adaption of the mouth such as the presence of baleen plates (FA) or the presence of a distinct rostrum (RO) appeared to mostly explain the second axis. The contribution of the predator body size (BL and BM) seemed shared between the two axes.
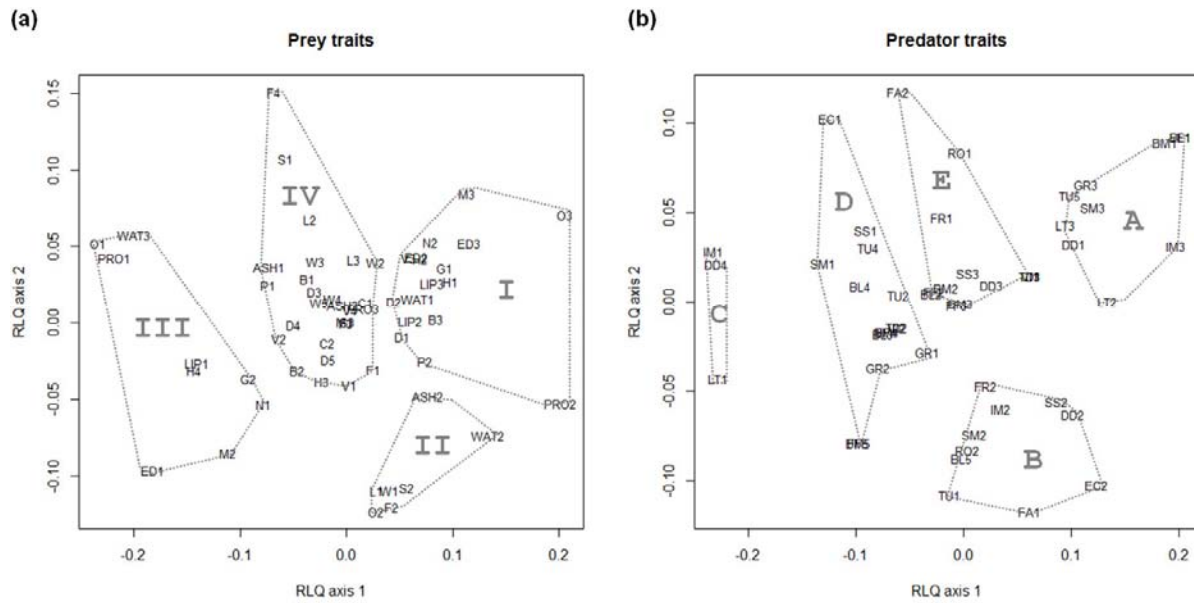
Fig. 3. *RLQ ordination of prey traits (a) and predator traits (b) along the first two axes. Polygons represent trait grouping provided by cluster analysis (I to IV: groups of prey traits; A to C: groups of predator traits). Trait codes are available in table 1.*

RLQ ANALYSIS OF GROUPS OF TRAITS

The cluster analyses applied to RLQ results identified 4 groups of prey traits and 5 groups of predator traits. The simultaneous ordination on the first two RLQ axes showed the association between certain groups of functional prey traits with traits of their predators; the associations suggested here by RLQ analyses were congruent with the correlations obtained in fourth-corner analysis (Table 3). The first group of prey traits (Fig. 3a; group I) was mainly characterized by high-quality species (ED3, LIP3, PRO2), living in schools (B3), swimming actively (M3) and having an internal skeleton (O3). These prey traits were associated to the first group of predator traits including species with high muscular performances (IM3, LT3), living in large schools (GR3), and having a small body size (BM1, BL1) (Fig. 3b; group A). The second group of prey traits (Fig. 3a; group II) included small species (L1) characterized by the presence of an exoskeleton (O2) and a compressed body shape (F2). These prey traits

were associated with the second group of predator traits including the presence of baleen plates (FA1), absence of echolocation (EC2), moderate muscular performances (IM2) and diving capability (DD2) (Fig. 3b; group B). The third group of prey traits (Fig. 3a; group III) encompassed low-quality species (PRO1, LIP1, ED3, WAT3), without skeleton structure (O1) and living in the deep-sea (H4). This type of prey was associated to the third and fourth group of predator traits (Fig. 3b; groups C, D) characterized respectively by low muscular performances (IM1, LT1), high diving capabilities (DD4), low swimming speeds (SM1), relatively low number of teeth on the lower mandibular (TU) and large body size (BL4, BM5). The other prey and predator groups of traits (Fig. 3; respectively group E and group IV) were mainly composed by traits exhibiting values close to 0 both on the two first RLQ axes; consequently these groups gathered traits having a limited role on dietary selection processes and were disregarded from ecological interpretation.

Table 3. *Extract from matrix D representing the fourth-corner correlations obtained between main traits of each group identified by RLQ analysis. White box indicate no significant correlation, light-grey boxes indicative values of positive correlations <0.2, dark-grey boxes indicative values of positive correlations from 0.2 to 0.3 and black boxes indicative values of positive correlations >0.3.*

GROUPS OF PREDATOR TRAITS

			A				B				C-D				
			IM3 — High muscle mitochondrial density	SM3 — High swimming speed	GR3 — Large school size	BM1 — Low body mass	FA1 — Baleen plates	EC2 — No echolocation	DD2 — Medium diving capability	BL5 — Large body mass	IM1 — Low muscle mitochondrial density	LT1 — Low musclelipid content	DD4 — High diving capability	SM1 — Low swimming speed	BL4 — Medium body mass
I	O3	Internal skeleton	black		light-grey	black		dark-grey							
	M3	Swimmer													
	ED3	High energy density	black	black	light-grey										
II	W1	Low body mass								black					
	F2	Compress body							black						
	O2	Exosquelette								black					
III	ED1	Low energy density									black	black	black	light-grey	black
	O1	No skeleton									black	black	black		
	H4	Oceanic habitat									light-grey	black	black	white	light-grey
	PRO1	Low protein content									black	black	black	black	black

GROUPS OF PREY TRAITS

Discussion

IDENTIFY FUNCTIONAL RELATIONSHIPS BETWEEN PREY AND PREDATORS

We investigated for the first time functional foraging ecology of predators using fourth-corner statistic and RLQ analysis to relate prey traits to marine mammal traits. We showed that such a trait-based approach allows the identification and the grouping of key traits involved in prey selection processes among a predator community, as demonstrated here with marine mammals. The combination of fourth-corner statistic and RLQ analyses is currently the most

sophisticated approach for analysing linkages between species trait and environmental characteristics (Dray & Legendre 2008; Lacourse 2009; Oldeland *et al.* 2012); we assume that the use of these methods in foraging ecology will open new avenues to investigate predator-prey relationships in a functional perspective.

Specifically for marine mammals, our trait-based approach provided evidence that prey found in the diet of marine mammals possessed functional traits which were directly and clearly linked to predator characteristics. Significant correlations have been found for instance between predators with baleen plates and prey with exoskeleton, predators with high diving capacities and prey living in the depth or else predators with vibrissae and prey living close to the bottom. Obviously, such relationships were intuitive but they have here been statistically demonstrated and quantified for the first time, thereby supporting the use of trait-based approach in foraging ecology and reassuring on the interpretation of other significant correlations provided by the fourth-corner statistics.

Taxonomic interpretations of diets have had misleading effects on the perception of marine mammal foraging strategies suggesting that a wide taxonomic prey diversity in the diet implied opportunistic foraging (e.g. Hall-Aspland *et al.* 2005; Bearzi *et al.* 2009). Nevertheless, an increasing number of studies showed that some marine mammals consume prey species disproportionately to their availability in the environment, hence suggesting prey selection (McCabe *et al.* 2010; Spitz *et al.* 2010). However, mechanisms underlying prey selection remain often unknown. The hypothesis tested in here was that prey selection of marine mammals was primarily shaped by physiological traits and then by morphological traits of both predators and prey. Indeed, a high proportion of significant correlations in matrix *D* and the first RLQ axis were associated with physiological traits involving costs of predation and prey profitability, thus confirming that energetic costs of foraging strategies and muscular performance are major drivers of prey selection in marine mammals. This result is

consistent with the recent assumption that some marine mammal species (e.g. common dolphin, Steller sea lion) exhibiting high cost of living select high-quality prey and may not be able to thrive on low-energy prey, whereas others (e.g. phocids and deep-diving cetaceans) may be less constrained by the quality of food they consume (Trites & Donnelly 2003; Österblom *et al.* 2008; Spitz *et al.* 2012). Hence, our results contributed to dispel the common wisdom that cetaceans and pinnipeds are opportunistic or random feeders (i.e. feeding without selection) and strengthened the hypothesis of a functional prey selection primarily shaped by predator physiological constraints.

One the interspecific scale, no allometric relations and a low number of correlations have been found between prey size and predator size and between prey and predator morphological traits in our trait-based approach. Actually, size seemed to be an effective driver of prey selection for small marine predators with mechanistic constraints such as invertebrate filters (Fenchel *et al.* 1975); some predictive relationships may also exist between the length of some fish species and the length of their prey (Scharf *et al.* 2000). However, attempts to establish scaling relationships between the length of large predators such as marine mammals and the size of their prey generally failed (MacLeod *et al.* 2006; Meynier *et al.* 2008), suggesting that size and morphology of prey species are of secondary importance in the establishment of marine mammal foraging strategies. Nevertheless, some specific adaptations to locate, capture and swallow prey appeared to be correlated to prey traits. Such morphological relationships were previously suggested in cetaceans as regarding prey size and jaws or skull adaptations, and scaling relationships between predator and prey lengths can also occur at intraspecific scale (MacLeod *et al.* 2006, 2007). For instance, difference of prey size have been related to the mode of prey capture; predators with jaws containing a large number of teeth and using pincer-like movement feed on larger prey than predators with reduced dentition and using suction to capture their prey (MacLeod *et al.* 2006).

TOWARDS A FUNCTIONAL TYPOLOGY OF MARINE MAMMALS PREDATOR-PREY RELATIONSHIPS

Several trait-based groups emerged from RLQ analysis both for prey and marine mammal species. These groups allowed roughly describing four main types of predators and prey characterized by different key functional traits; moreover groups of predators can be associated to groups of prey. For instance, predators characterized by high muscular performances, living in large schools and having a small body size appeared to select gregarious, high-quality prey, swimming actively and having an internal skeleton. Thus, trait-based approach provided an innovative way to classify prey and predator species into functional groups. Indeed, grouping species according to their ecological or morphological similarities rather than their phylogeny has been widely attempted in animal ecology. The guild concept applied to animals was born in the middle of twentieth century (Root 1967); groups of species were then based on similarities in resources sharing or foraging tactics without regard to taxonomy such as granivorous species or nectar-feeding species. The guild approach has been mainly used in community ecology to investigate overlap and segregation of feeding niches (Feinsinger 1976; Ridoux 1994; Vitt & de Carvalho 1995; Pusineri *et al.* 2008). The three-matrix approaches originally allow revisiting and identifying guilds of predator based on similarities in key functional traits shaping their prey selection. Here, muscular performance and diving capability appeared to be the key functions to constitute guilds of marine mammals in a functional predation perspective.

The concept of functional groups was initially defined on similarities in ecosystem function (Blondel 2003); in this case, species contributing to the same ecosystem process were gathered. Contrary to guilds, functional groups can so refer to an infinite number of ecosystems functions such as in marine ecosystem nutrient cycling, primary production,

climate regulation or biological control (Levin *et al.* 2001). Here, functional groups of prey provided here by RLQ analysis can be viewed as clusters of prey species which are interchangeable in terms of predation costs and energy intake for a predator guild. Thus, our trait-based approach provided functional groups of prey defined on similarities in key functional traits targeted by predators; such grouping propose a new definition of predator needs.

PREDICTIVE FRAMEWORKS FOR FORAGING ECOLOGY

Dietary data are central in ecology but the diets of predators may be difficult to obtain in certain ecosystem. For instance, diets of marine mammals are relatively well described in numerous temperate ecosystems but little is known in tropical ecosystems where collecting samples is often too difficult to provide robust data (Perrin *et al.* 2009). In spatial ecology, relationships between environmental characteristics and cetacean sightings are used to provide predictive map of cetacean distribution in areas not being covered by any survey (e.g. Gregr & Trites 2001; Laran & Gannier 2008; Mannocci *et al.* 2013). In foraging ecology, relationships between prey and predator traits could be similarly used to predict diets or at least prey preferences of marine mammals in undocumented areas or for undocumented species. The relevance of such predictive framework can be illustrated by empirical examples from the literature; for instance, Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and spinner dolphins (*Stenella longirostris*) are two cetacean species outside the geographic and species range of the present study. Regarding predator functional traits, these two species fall in our type of predators characterized by high muscular performances, living in large schools and having a small body size. Consequently, our results predict that pacific white-sided dolphins and spinner dolphins should feed on locally most abundant forage species characterized by large schools, high energy density, active swimming and internal skeleton,

and they do it. Pacific white-sided dolphins feed on herring (*Clupea harengus*), capelin (*Mallotus villosus*) and Pacific sardine (*Sardinops sagax*) in British Columbia, Canada (Morton 2000) while spinner dolphins feed on lanternfish (mainly *Ceratoscopelus warmingi, Diaphus* spp. and *Myctophum asperum*) in the Sula sea, Phillipines (Dolar *et al.* 2003). Nevertheless, we need to keep in mind that some species are highly variable and different populations of the same species can differ in morphology, physiology and ecological strategies such as bottlenose dolphin or killer whale, which show contrasted ecotypes that may fall in different predator types. Here, we propose predictions based on eastern North Atlantic populations; the accuracy of these general predictions to other populations may be limited for such species to the dominant ecotype present in the eastern North Atlantic.

Finally, climatic shifts and anthropogenic pressures of global warming and overfishing deeply affect marine ecosystems (Cheung *et al.* 2009; Pereira *et al.* 2010). An important challenge in ecology and conservation biology is to predict how species would respond to biodiversity changes. Trait-based approaches has proved useful in providing predictive frameworks to assess terrestrial species response to environmental change (Webb *et al.* 2010; Hanspach *et al.* 2012b). Such studies pointed out that the sensitivity to environmental changes varied across species and could be predicted by using different functional traits. Trait-based studies such as ours provide an appealing framework to anticipate bottom-up effects on marine predator population dynamics (Ainley & Siniff 2009; Ford *et al.* 2010). This is essential for the assessment of predator risk exposure such as the "junk-food" emergence in marine ecosystem which particularly affects predators exhibiting high cost of living (Österblom *et al.* 2008). Thus, as all prey are not equal for all predators, the knowledge of predator functional needs defined by trait-based approaches will help to predicting which type of predators will be particularly sensitive to the loss of prey key functional traits resulting from a shift in prey availability.

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