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

Jérôme Spitz[1,2], Vincent Ridoux[3,4] and Anik Brind'Amour[5]

[1]*Littoral Environnement & Sociétés, UMR 7266 Université de La Rochelle/CNRS, 17042, La Rochelle, France;* [2]*Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada;* [3]*Observatoire PELAGIS – Système d'Observation pour la Conservation des Mammifères et Oiseaux Marins, UMS 3462, CNRS/Université de La Rochelle, 17071, La Rochelle, France;* [4]*Centre d'études biologiques de Chizé – La Rochelle, UMR 7372, Université de La Rochelle/CNRS, 79360, Villiers en Bois, France; and* [5]*Ifremer, Département Écologie et Modèles pour l'Halieutique, Rue de l'île d'Yeu, BP 21105, 44311, Nantes, France*

Summary

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.

Key-words: 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 is among the most significant challenges facing ecologists. The growing development of functional approaches has been 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 for prey characteristics: 'which predator feeds on which species?' Thus, the study of foraging strategies tends to be too often limited to interpreting the species composition and richness of prey in the diet of predators – qualifying monotypic predators as specialized or selective predators and predators feeding on a large range of prey species as generalist or 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 there are functional aspects of the

*Correspondence author. E-mail: j.spitz@fisheries.ubc.ca

relationships between prey and predators. To achieve such an objective, methodological approaches focusing both on prey and predator characteristics are too often ignored, especially in marine ecosystems. Most of the previous studies investigating the diet of marine predators in a functional approach mainly focussed on predator–prey length relationships (Scharf, Juanes & Rountree 2000; Aljetlawi, Sparrevik & Leonardsson 2004), and only few studies attempted to group marine prey based on other characteristics regardless of taxonomy (Ridoux 1994). Size-based approaches have brought fundamental insights into community and ecosystem structures (Petchey & Belgrano 2010) or into 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, which is especially true for large marine predators (MacLeod *et al.* 2006; Spitz *et al.* 2012).

Changes in marine prey quality have revived interest in the functional relationships 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 contrast to prey quantity alone) in maintaining healthy populations of some marine top predators (Trites & Donnelly 2003; Spitz *et al.* 2012). This general hypothesis that prey characteristics are important for 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, the overall diet biomass and biodiversity could remain unchanged, while predator's nutritional fulfilments and energy requirements were jeopardized by a functional change of the 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 diets of common dolphins may exhibit spatial and/or temporal taxonomic variation, but they will always include a high proportion of lipid-rich fish (Meynier *et al.* 2008; Spitz *et al.* 2012). This leads to the conclusion that some prey species sharing common functional traits are interchangeable – while others are not. Identification of 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. The latter can be accomplished using three-matrix approaches, named the fourth-corner approach (Legendre, Galzin & Harmelin-Vivien 1997; Dray & Legendre 2008) and RLQ analysis (Dolédec *et al.* 1996). These multitable approaches consist of 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 (i) multiple traits and environmental variables can be assigned and tested (univariate analysis in fourth-corner method and multivariate analysis in RLQ) and (ii) 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, to our knowledge, such trait-based approaches have never been used 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 a trait-based approach in foraging ecology using a marine mammal community in the northeast Atlantic. Marine mammals are a particularly interesting group to conduct trait-based approaches because their morphological and physiological traits are extremely diversified, while they feed on a wide range of organisms. The outcome of a better understanding of marine mammal 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 carried out by focussing on the results of two main linkages: predators–prey morphological relationships and relationships involving costs of predation and prey profitability.

Materials and 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 the literature and unpublished data available from the French stranding network data base (see Appendix S5, Supporting information 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. Summarizing 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 recognized 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 summarize such species in a biological meaningful way is often impossible. For species with distinct ecotypes (e.g. *Tursiops truncatus*) or for species with extensive geographical variation, we retained characteristics corresponding to eastern North Atlantic populations, as sampled in our compilation of dietary studies instead of general or averaged 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 data base, and for full transparency, we provide all the values used for each functional traits and their sources (see Appendices 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 and body mass depth) have been discretized in several categories to conduct the statistical analyses. To limit arbitrary categories, we used literature and rapid clustering on our data to propose biologically meaningful categories. Such categorization 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 two to five 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 some of the 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 Appendices S3 and S4 in Supporting Information for complete species-traits assignments and Appendix S5 for sources of values for each functional trait).
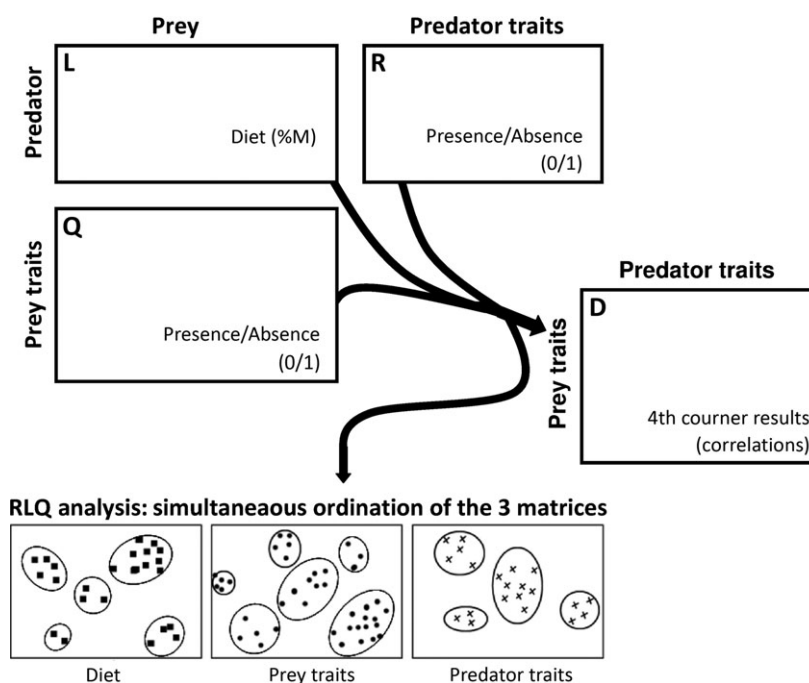
STATISTICAL ANALYSES

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*: $m \times p$) contains the percentage by mass of the *p* prey species in the diet of the *m* marine mammal species. The second matrix (*Q*: $p \times n$) describes the same *p* prey species according to the set of *n* functional traits (Table 1). The third matrix (*R*: $m \times k$) 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).

The analytical routine of the fourth-corner analysis was performed using R software (R Development Core Team. 2008) with the function 'fourthcorner' included in the 'ade4' package (Dray & Dufour 2007) and following methods recommended by Dray and 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* ($n \times k$) 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-step 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).

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	Predator traits	Categories	Codes	RLQ group
Body length	1–10 cm	L1	II	Body length	1–2 m	BL1	A
	10–30 cm	L2	IV		2–5 m	BL2	E
	30–100 cm	L3	IV		5–10 m	BL3	D
Body mass	1–10 g	W1	II		10–15 m	BL4	D
	10–100 g	W2	IV		15–30 m	BL5	B
	100–500 g	W3	IV	Body mass	10–100 kg	BM1	A
	500–1000 g	W4	IV		100–500 kg	BM2	E
	>1000 g	W5	IV		500–1000 kg	BM3	E
Body shape	Fusiform	F1	IV		1000–10 000 kg	BM4	D
	Compress	F2	II		10 000–50 000 kg	BM5	D
	Flat	F3	IV	Frontal surface	400–1000 cm^2	FF1	A
	Cylindric	F4	IV		1000–3000 cm^2	FF2	E
Spine	No	S1	IV		3000–5000 cm^2	FF3	E
	Few	S2	II		5000–10 000 cm^2	FF4	D
	Numerous	S3	IV		10 000–30 000 cm^2	FF5	D
Photophores	Absence	P1	IV	Fineness ratio	<5	FR1	E
	Presence	P2	I		>5	FR2	B
Colour	Cryptic	C1	IV	Rostrum	Presence	RO1	E
	Conspicuous	C2	IV		Absence	RO2	B
Skeleton	No	O1	III	Teeth on lower mandibular	0	TU1	B
	Exosquelette	O2	II		1–2	TU2	D
	Internal	O3	I		10–20	TU3	D
Mobility	Immobile	M1	IV		20–50	TU4	D
	Low escape ability	M2	IV		>50	TU5	A
	Swimmer	M3	I	Differentiated teeth	Presence	TD1	E
Water content	Low	WAT1	I		Absence	TD2	D
	Medium	WAT 2	II	Baleen plates	Presence	FA1	B
	High	WAT3	III		Absence	FA2	E
Protein content	Low	PRO1	III	Echolocation	Presence	EC1	D
	Medium	PRO2	I		Absence	EC2	B
	High	PRO3	IV	Vibrissae	Presence	VI1	E
Lipid content	Low	LIP1	III		Absence	VI2	D
	Medium	LIP2	I	School size	Isolated individual	GR1	E
	High	LIP3	I		Small	GR2	D
Ash content	Low	ASH1	IV		Large	GR3	A
	Medium	ASH2	II	Sustainable swimming speed	<2 km h^{-1}	SS1	D
	High	ASH3	IV		2–3 km h^{-1}	SS2	B
Energy density	Low	ED1	III		>3 km h^{-1}	SS3	E
	Medium	ED2	IV	Maximum swimming speed	<6 km h^{-1}	SM1	D
	High	ED3	I		6–10 km h^{-1}	SM2	B
School size	Isolated individual	B1	IV		>10 km h^{-1}	SM3	A
	Small	B2	IV	Diving capability	0–200 m	DD1	A
	Large	B3	I		200–500 m	DD2	B
Horizontal habitat	Coastal	H1	I		500–1000 m	DD3	E
	Shelf	H2	IV		1000–3000 m	DD4	C
	Slope	H3	IV	Muscle mitochondrial density	Low	IM1	C
	Oceanic area	H4	III		Medium	IM2	B
Vertical habitat	Surface	V1	IV		High	IM3	A
	Pelagic	V2	IV	Muscle lipid content	Low	LT1	C
	Demersal	V3	IV		Medium	LT2	A
	Benthic	V4	IV		High	LT3	A
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				

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.

Ter Braak, Cormont & Dray (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.* 2014). 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, Cormont & Dray (2012) and the Benjamini and Hochberg adjustment were used for ecological interpretation.

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, Chessel & Thioulouse 2003). It graphically summarizes and represents the main costructure 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 three or four different axes, and the groupings gave exactly the same results as those with two axes. Therefore, we kept the first 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 intracluster 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 carried out 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 a 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 the 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 (that is, muscle lipid content (LT) and mitochondrial density (IM)), and then the 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.
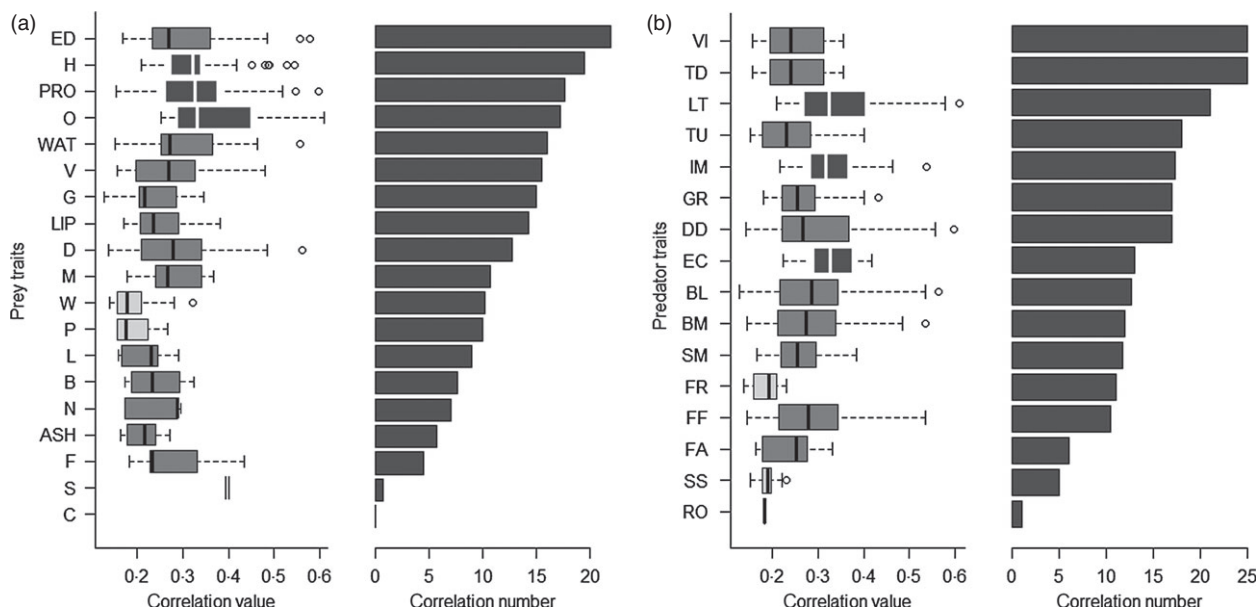
FOURTH-CORNER ANALYSIS OF PREDATOR TRAITS SHAPING PREY SELECTION

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, that is, maximum swimming speed (SM), diving capability (DD), muscle mitochondrial density (IM) and muscle lipid content (LT); and prey traits associated with the prey profitability for predators, that is, lipid content (LIP) and energy density (ED). Fourth-corner analysis revealed that predator traits illustrating high activity levels (SM3, IM3, LT3) were strongly correlated with high-quality prey (LIP3, ED3). Conversely, low activity levels (SM1, IM1, LT1) and high diving capability (DD4) were correlated with 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 (2–5 m, 100–500 kg) appeared to target a particular prey size (large preys >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.

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 also exhibited 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

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 indicates no significant correlation; light grey boxes indicate values of positive correlations <0·2; dark grey boxes indicate values of positive correlations from 0·2 to 0·3; and black boxes indicate 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.

Table 2. Extract from matrix *D* representing the fourth-corner correlations involving the functional traits associated with costs of predation, prey traits associated with the prey profitability for predators and body size and body mass both for prey and predator. White box indicates no significant correlation; light grey boxes indicate values of positive correlations <0·2; dark grey boxes indicate values of positive correlations from 0·2 to 0·3; and black boxes indicate values of positive correlations >0·3

Shading key used in cells below: L = light grey (<0·2); D = dark grey (0·2–0·3); B = black (>0·3); blank = no significant correlation.

| PREDATOR TRAITS		Lipid content			Energy density			Prey body length			Prey body mass				
		LIP1 (Low)	LIP2 (Medium)	LIP3 (High)	ED1 (Low)	ED2 (Medium)	ED3 (High)	L1 (1–10 cm)	L2 (10–30 cm)	L3 (30–100 cm)	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		L			L										
SM2 6-10 km.h-1															
SM3 >10 km.h-1				L			D								
Diving capability DD1 0-200 m						D	L			L	B				
DD2 200-500 m						L									
DD3 500-1000 m										L			L		
DD4 1000-3000 m		D			D										
Muscle mitochondrial density IM1 Low		L			D										
IM2 Medium															
IM3 High		D			B										
Muscle lipid content LT1 Low		L			D								L		
LT2 Medium						L									
LT3 High		B			B										
Predator body length BL1 1-2 m					D	D									
BL2 2-5 m												L	D	D	
BL3 5-10 m															
BL4 10-15 m		D													
BL5 15-30 m															
Predator body mass BM1 10-100 kg					L	D									
BM2 100-500 kg								L				D	D	D	
BM3 500-1000 kg			L					L				D			
BM4 1000-10000 kg					B						L				
BM5 10000-50000 kg		L			D										

on the first axis. Regarding predator traits, the ordination represented a gradient from species with low muscular performances, that is, 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, that is, 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 the 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.

RLQ ANALYSIS OF GROUPS OF TRAITS

The cluster analyses applied to RLQ results identified four groups of prey traits and five 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
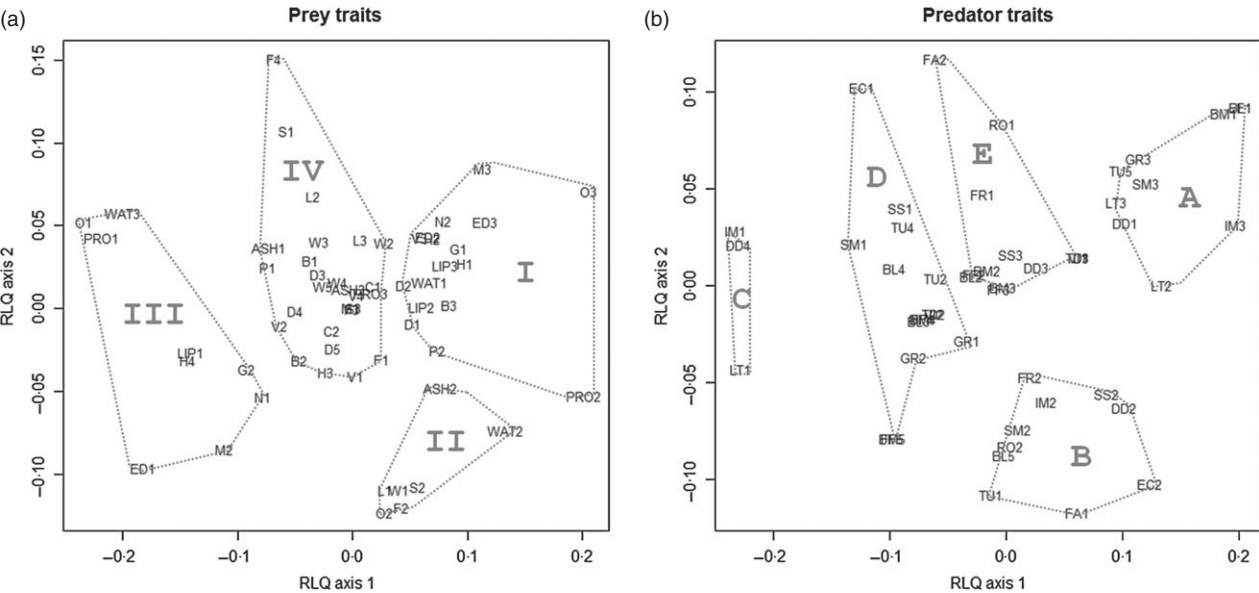
Fig. 3. RLQ ordination of prey traits (a) and predator traits (b) along the first two axes. Polygons represent trait grouping provided by cluster analysis (I to IV: groups of prey traits; A to C: groups of predator traits). Trait codes are available in Table 1.

Table 3. Extract from matrix *D* representing the fourth-corner correlations obtained between main traits of each group identified by RLQ analysis. White box indicates no significant correlation; light grey boxes indicate values of positive correlations <0·2; dark grey boxes indicate values of positive correlations from 0·2 to 0·3; and black boxes indicate values of positive correlations >0·3

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

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 with 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), the 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 with 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.

Discussion

IDENTIFY FUNCTIONAL RELATIONSHIPS BETWEEN PREY AND PREDATORS

We investigated for the first time the functional foraging ecology of predators using fourth-corner statistics and RLQ analysis to relate prey traits to marine mammal traits. We showed that such a trait-based approach allows the identification and grouping of key traits involved in prey selection processes among a predator community, as demonstrated here with marine mammals. The combination of the fourth-corner method and RLQ analyses is currently the most sophisticated approach for analysing linkages between species trait and environmental characteristics (Dray & Legendre 2008; Lacourse 2009; Oldeland, Wesuls & Jürgens 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

approaches in foraging ecology and reinforcing 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 wide taxonomic prey diversity in the diet implies opportunistic foraging (e.g. Hall-Aspland, Hall & Rogers 2005; Bearzi, Fortuna & Reeves 2009). Nevertheless, an increasing number of studies have shown 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 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 help dispel the common wisdom that cetaceans and pinnipeds are opportunistic or random feeders (i.e. feeding without selection) and strengthen the hypothesis of a functional prey selection (primarily shaped by predator physiological constraints).

On the interspecific scale, no allometric relationships and a low number of correlations were found between prey size and predator size, or between prey and predator morphological traits in our trait-based approach. In fact, size seemed to be an effective driver of prey selection for small marine predators with mechanistic constraints such as invertebrate filters (Fenchel, Kofoed & Lappalainen 1975); some predictive relationships may also exist between the length of some fish species and the length of their prey (Scharf, Juanes & Rountree 2000). However, attempts to establish scaling relationships between the length of large predators such as marine mammals and the size of their prey generally fail (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 with prey traits. Such morphological relationships were previously suggested in cetaceans with respect to prey size and jaws or skull adaptations, and scaling relationships between predator and prey lengths can also occur at an intraspecific

scale (MacLeod *et al.* 2006, 2007). For instance, differences in the size of prey consumed 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 roughly describe four main types of predators and prey characterized by different key functional traits; moreover, groups of predators can be associated with groups of prey based on this structure. For instance, predators characterized by high muscular performance that live in large schools and have a small body size appear to select gregarious, high-quality prey that swim actively and having an internal skeleton. Thus, our 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); species groups 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 allowed for revisiting and identifying guilds of predators based on similarities in key functional traits that shape their prey selection. Here, muscular performance and diving capability appeared to be the key functions that delineate guilds of marine mammals in a functional predation perspective.

The concept of functional groups was initially defined based on similarities in ecosystem function (Blondel 2003); in this case, species contributing to the same ecosystem process were aggregated. Contrary to guilds, functional groups can also refer to an infinite number of ecosystem functions, such as those found in marine ecosystem nutrient cycling, primary production, climate regulation or biological control (Levin *et al.* 2001). Here, functional groups of prey indicated 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 provides functional groups of prey defined by similarities in key functional traits targeted by predators. This grouping strategy offers a new perspective on the food and habitat needs of predator species.

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, Wursig & Thewissen 2009). In spatial ecology, relationships between environmental characteristics and cetacean sightings are used to provide predictive maps of cetacean distribution in areas not covered by surveys (e.g. Gregr & Trites 2001; Laran & Gannier 2008; Mannocci *et al.* 2013). In foraging ecology, relationships between prey and predator traits could similarly be used to predict diets or at least prey preferences of marine mammals in undocumented areas or for undocumented species. The relevance of such a 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 geographical and species ranges of the present study. Regarding predator functional traits, these two species fall in our predator group characterized by high muscular performance, 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 abundant forage species characterized by large schools, high energy density, active swimming and internal skeleton. The prediction coincides with observations of diet for these species: 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 Sulu sea, Philippines (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. For example, bottlenose dolphin and killer whales exhibit contrasting ecotypes that may fall within different predator types. Here, we propose predictions based on eastern North Atlantic populations; the accuracy of these general predictions for other populations may be limited to species which fall into one of the dominant ecotypes 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 will respond to biodiversity changes. Trait-based approaches have proved useful in providing predictive frameworks to assess terrestrial species response to environmental change (Webb *et al.* 2010; Hanspach *et al.* 2012). Such studies point out that the sensitivity to environmental changes varies across species

and can be predicted by analysing 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 'junk-food' emergence in marine ecosystems which particularly affect 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 predict which type of predators will be particularly sensitive to the loss of prey key functional traits resulting from a shift in prey availability.

Acknowledgements

References

Ainley, D.G. & Siniff, D.B. (2009) The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. *Antarctic Science*, **21**, 317.

Aljetlawi, A.A., Sparrevik, E. & Leonardsson, K. (2004) Prey-predator size-dependent functional response: derivation and rescaling to the real world. *Journal of Animal Ecology*, **73**, 239–252.

Barbaro, L. & Van Halder, I. (2009) Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography*, **32**, 321–333.

Bearzi, G., Fortuna, C.M. & Reeves, R.R. (2009) Ecology and conservation of common bottlenose dolphins *Tursiops truncatus* in the Mediterranean Sea. *Mammal Review*, **39**, 92–123.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B*, **28**, 9–300.

Blondel, J. (2003) Guilds or functional groups: does it matter? *Oikos*, **100**, 223–231.

Brind'Amour, A., Boisclair, D., Dray, S. & Legendre, P. (2011) Relationships between species feeding traits and environmental conditions in fish communities: a three-matrix approach. *Ecological Applications*, **21**, 363–377.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. & Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, **10**, 235–251.

Cleary, D.F., Genner, M.J., Koh, L.P., Boyle, T.J., Setyawati, T., de Jong, R. *et al.* (2009) Butterfly species and traits associated with selectively logged forest in Borneo. *Basic and Applied Ecology*, **10**, 237–245.

Dolar, M., Walker, W.A., Kooyman, G.L. & Perrin, W.F. (2003) Comparative feeding ecology of spinner dolphins (*Stenella longirostris*) and Fraser's dolphins (*Lagenodelphis hosei*) in the Sulu Sea. *Marine Mammal Science*, **19**, 1–19.

Dolédec, S., Chessel, D., Ter Braak, C.J.F. & Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics*, **3**, 143–166.

Dolnicar, S., Grabler, K., Mazanec, J.A., Woodside, A.G., Crouch, G.I., Oppermann, M. *et al.* (1999) *A Tale of Three Cities: Perceptual Charting for Analysing Destination Images*. CAB International, London, UK.

Dray, S., Chessel, D. & Thioulouse, J. (2003) Co-inertia analysis and the linking of ecological data tables. *Ecology*, **84**, 3078–3089.

Dray, S. & Dufour, A.-B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.

Dray, S. & Legendre, P. (2008) Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology*, **89**, 3400–3412.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S. *et al.* (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, **95**, 14–21. http://dx.doi.org/10.1890/13-0196.1

Feinsinger, P. (1976) Organization of a tropical guild of nectarivorous birds. *Ecological Monographs*, **46**, 257–291.

Fenchel, T., Kofoed, L.H. & Lappalainen, A. (1975) Particle size-selection of two deposit feeders: the amphipod *Corophium volutator* and the prosobranch *Hydrobia ulvae*. *Marine Biology*, **30**, 119–128.

Flynn, D.F., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B. *et al.* (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, **12**, 22–33.

Ford, J.K., Ellis, G.M., Olesiuk, P.F. & Balcomb, K.C. (2010) Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biology Letters*, **6**, 139–142.

Gregr, E.J. & Trites, A.W. (2001) Predictions of critical habitat for five whale species in the waters of coastal British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1265–1285.

Hall-Aspland, S.A., Hall, A.P. & Rogers, T.L. (2005) A new approach to the solution of the linear mixing model for a single isotope: application to the case of an opportunistic predator. *Oecologia*, **143**, 143–147.

Hanspach, J., Fischer, J., Ikin, K., Stott, J. & Law, B.S. (2012) Using trait-based filtering as a predictive framework for conservation: a case study of bats on farms in southeastern Australia. *Journal of Applied Ecology*, **49**, 842–850.

Hartigan, J.A. & Wong, M.A. (1979) Algorithm AS 136: a k-means clustering algorithm.. *Journal of the Royal Statistical Society Series C (Applied Statistics)*, **28**, 100–108.

Ikin, K., Knight, E., Lindenmayer, D.B., Fischer, J. & Manning, A.D. (2012) Linking bird species traits to vegetation characteristics in a future urban development zone: implications for urban planning. *Urban Ecosystems*, **15**, 961–977.

Kleiber, M. (1975) *The Fire of Life: An Introduction to Animal Energetics*. Kreigern, Huntington, NY.

Lacourse, T. (2009) Environmental change controls postglacial forest dynamics through interspecific differences in life-history traits. *Ecology*, **90**, 2149–2160.

Laran, S. & Gannier, A. (2008) Spatial and temporal prediction of fin whale distribution in the northwestern Mediterranean Sea. *ICES Journal of Marine Science*, **65**, 1260–1269.

Legendre, P., Galzin, R. & Harmelin-Vivien, M.L. (1997) Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology*, **78**, 547–562.

Levin, L.A., Boesch, D.F., Covich, A., Dahm, C., Erséus, C., Ewel, K.C. *et al.* (2001) The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems*, **4**, 430–451.

Luck, G.W., Lavorel, S., McIntyre, S. & Lumb, K. (2012) Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology*, **81**, 1065–1076.

MacLeod, C.D., Santos, M.B., Lopez, A. & Pierce, G.J. (2006) Relative prey size consumption in toothed whales: implications for prey selection and level of specialisation. *Marine Ecology Progress Series*, **326**, 295–307.

MacLeod, C.D., Reidenberg, J.S., Weller, M., Santos, M.B., Herman, J., Goold, J. *et al.* (2007) Breaking symmetry: the marine environment, prey size, and the evolution of asymmetry in cetacean skulls. *The Anatomical Record*, **290**, 539–545.

Mannocci, L., Laran, S., Monestiez, P., Dorémus, G., Van Canneyt, O., Watremez, P. *et al.* (2013) Predicting top predator habitats in the Southwest Indian Ocean. *Ecography*, **37**, 261–278.

McCabe, E.J.B., Gannon, D.P., Barros, N.B. & Wells, R.S. (2010) Prey selection by resident common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine biology*, **157**, 931–942.

Meynier, L., Pusineri, C., Spitz, J., Santos, M.B., Pierce, G.J. & Ridoux, V. (2008) Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: importance of fat fish. *Marine Ecology Progress Series*, **354**, 277–287.

Morton, A. (2000) Occurrence, photo-identification and prey of Pacific white-sided dolphins (*Lagenorhyncus obliquidens*) in the Broughton Archipelago, Canada 1984–1998. *Marine Mammal Science*, **16**, 80–93.

Oldeland, J., Wesuls, D. & Jürgens, N. (2012) RLQ and fourth-corner analysis of plant species traits and spectral indices derived from HyMap and CHRIS-PROBA imagery. *International Journal of Remote Sensing*, **33**, 6459–6479.

Österblom, H., Olsson, O., Blenckner, T. & Furness, R.W. (2008) Junk-food in marine ecosystems. *Oikos*, **117**, 967–977.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P., Fernandez-Manjarrés, J.F. et al. (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496.

Perrin, W.F., Wursig, B. & Thewissen, J.G.M.(2009). *Encyclopedia of Marine Mammals*, 2nd edn. Academic Press, San Diego.

Petchey, O.L. & Belgrano, A. (2010) Body-size distributions and size-spectra: universal indicators of ecological status? *Biology Letters*, **6**, 434–437.

Pierce, G.J. & Boyle, P.R. (1991) A review of methods for diet analysis in piscivorous marine mammals. *Oceanography and Marine Biology: an annual review*, **29**, 409–486.

Pusineri, C., Chancollon, O., Ringelstein, J. & Ridoux, V. (2008) Feeding niche segregation among the Northeast Atlantic community of oceanic top predators. *Marine Ecology Progress Series*, **361**, 21–34.

R Development Core Team.(2008). *R: A language and environment for statistical computing*, R Foundation for Statistical Computing Vienna Austria, ISBN 3-900051-07-0n.

Ridoux, V. (1994) The diets and dietary segregation of seabirds at the sub-antarctic Crozet Islands. *Marine Ornithology*, **22**, 1–192.

Root, R.B. (1967) The niche exploitation pattern of the blue-gray gnat-catcher. *Ecological Monographs*, **37**, 317–350.

Scharf, F.S., Juanes, F. & Rountree, R.A. (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*, **208**, 229–248.

Spitz, J., Mourocq, E., Leauté, J.-P., Quéro, J.-C. & Ridoux, V. (2010) Prey selection by the common dolphin: fulfilling high energy requirements with high quality food. *Journal of Experimental Marine Biology and Ecology*, **390**, 73–77.

Spitz, J., Cherel, Y., Bertin, S., Kiszka, J., Dewez, A. & Ridoux, V. (2011) Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers*, **58**, 273–282.

Spitz, J., Trites, A.W., Becquet, V., Brind'Amour, A., Cherel, Y., Galois, R. et al. (2012) Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. *PLoS ONE*, **7**, e50096.

Ter Braak, C.J., Cormont, A. & Dray, S. (2012) Improved testing of species traits-environment relationships in the fourth-corner problem. *Ecology*, **93**, 1525–1526.

Trites, A.W. & Donnelly, C.P. (2003) The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Review*, **33**, 3–28.

Vitt, L.J. & de Carvalho, C.M. (1995) Niche partitioning in a tropical wet season: lizards in the lavrado area of northern Brazil. *Copeia*, **1995**, 305–329.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I. & LeRoy Poff, N. (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, **13**, 267–283.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. References of dietary studies.

Appendix S2. Predator diet composition in percentage by mass (matrix L).

Appendix S3. Predator trait values (matrix R).

Appendix S4. Prey trait values (matrix Q).

Appendix S5. References of trait values.

Appendix S6. Correlation values of 4th corner analysis (matrix D).