Prey consumption by cetaceans reveals the importance of energy-rich food webs in the Bay of Biscay

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ABSTRACT

Ecosystem-based management requires a clear understanding of marine ecosystem functioning, particularly the transfer of energy (consumption) to higher trophic levels. However, robust estimates of consumption are generally hampered by a dearth of data for predators (diet and abundance), and by methodological weaknesses. We undertook a comprehensive assessment of energy requirements and prey consumption for the 10 most abundant cetacean species in the Bay of Biscay (northeastern Atlantic Ocean, France) by combining recent data on their abundances from aerial surveys, and diets from stomach content analyses. We also incorporated functional considerations to group prey and address interspecific differences in the cost of living of cetaceans that are independent of body size. Species considered included harbour porpoise, common dolphins, striped dolphins, bottlenose dolphins, long-finned pilot whales, Risso's dolphins, sperm whales, Cuvier's beaked whales, minke whales and fin whales. We used Monte Carlo resampling methods to estimate annual and seasonal (winter and summer) consumption over the continental shelf and slope—and found that small toothed whale populations (which were much more abundant than other cetacean groups) required about twice as much resources as baleen whales and deep-diving toothed whales combined. Our results show that small energy-rich schooling fish are the key prey group sustaining a large part of the cetacean community in the Bay of Biscay. The biomass removal of small energy-rich schooling fish by cetaceans is 6 times higher than removals of all other prey groups. High quality nutritional resources appear to be crucial to sustaining cetaceans and maintaining ecosystem functions and services in the Bay of Biscay, and should be carefully monitored.

1. Introduction

Ecosystem-based management is promoted to protect ecosystem services, and maintain or restore marine biodiversity and the long-term economic sustainability of marine resources (e.g., Curtin and Prellezo, 2010; Pikitch et al., 2004). However, an essential prerequisite to implementing ecosystem-based management is having quantitative knowledge about predator-prey interactions—most notably about energy transfer and the consequences of removing prey species from the ecosystem.

Changes in the abundance or distribution of prey can result in food shortages and nutritional stress that negatively impact predator numbers (Österblom et al., 2008; Trites et al., 1999). Similarly, a change in the abundance or distribution of predators can shift the abundance and composition of prey communities, and cause major cascading effects on entire ecosystems (Baum and Worm, 2009; Pace et al., 1999). However, predicting such changes and implementing effective ecosystem-based

management policies requires synthesizing data on population abundances, prey-predator interactions, food-web structure and energy budgets.

Consumption by top predators—such as cetaceans—is often a major concern in marine ecosystem management because of the impact they can have on commercial species yield (Morissette et al., 2010; Trzcinski et al., 2006) as well as the impact that fishing can have on marine mammal conservation (Reynolds et al., 2009). Both concerns require assessing what prey are present and how much is consumed to elucidate the role of marine mammals in ecosystem, and their interactions with fisheries. Quantifying the amounts of prey consumed by marine top predators requires data on population abundance, structure and distribution, energetic requirements, diet and prey energy densities (Trites and Spitz, 2017); but robust consumption estimates are generally difficult to obtain due to the dearth of data on these predators.

In the northeastern Atlantic, the Bay of Biscay is a mid-latitude shelf ecosystem under intensive fishery pressures for human provisioning

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over the continental shelf and along the slope (Lorance et al., 2009). A multitude of crustaceans, shellfish, cephalopods, pelagic and demersal fish are heavily exploited from coastal waters to deep-sea areas. Over the last 30 years, the overexploitation of this ecosystem has caused stock collapses, decline of global biomass, severe truncation of fish lengths, and changes in population and community structures (Guénette and Gascuel, 2012; Lorance, 2010; Rochet et al., 2005). Such changes can significantly influence the population dynamics of top trophic level species in the Bay of Biscay continental food web through bottom-up processes (Lassalle et al., 2011), and may be particularly negative for cetacean populations (Lassalle et al., 2012).

Cetaceans in the Bay of Biscay are abundant and highly diversified with more than 20 species recorded from sightings and strandings (Laran et al., 2017; Savouré-Soubelet et al., 2017). Composition of the cetacean community varies with habitats, with 4 main species occurring on the continental shelf (common dolphin, *Delphinus delphis*; bottlenose dolphin, *Tursiops truncatus*; harbour porpoise, *Phocoena phocoena*; and minke whale, *Balaenoptera acutorostrata*), and 6 species dominating the slope (striped dolphin, *Stenella coeruleoalba*; long-finned pilot whale, *Globicephala melas*; Risso's dolphin, *Grampus griseus*; sperm whale, *Physeter macrocephalus*; Cuvier's beaked whale, *Ziphius cavirostris*; and fin whale, *B. physalus*). These 10 species forage on a wide diversity of prey species ranging from zooplankton to giant squids.

Significant amounts of commercial fish and cephalopod prey species are exploited by fisheries in the Bay of Biscay where cetaceans feed. Hence, trophic interactions between cetaceans and fisheries are regularly occurrences here (Lassalle et al., 2012). These interactions can lead to direct or indirect competition for the same resources, and can negatively affect the population dynamics of prey and predator populations.

Ecosystem models used to estimate the flow of energy within an ecosystem (and to assess the consequences of fishery removals) typically assume fixed proportions of biomass are consumed by different species occupying different trophic levels (Ainsworth et al., 2001; Lassalle et al., 2011; Trites, 2003). However, it appears that the risks incurred by cetaceans to changes in the availability of prey are more closely linked to the costs of living of the predator, and the dietary quality of the prey, than they are to the overall biomass of lower trophic species (Spitz et al., 2012).

Marine mammals appear to select prey based on prey functional traits (e.g., energy density, size, schooling behaviour, etc.) rather than prey taxonomy, which fails to accurately match the prey consumed by cetaceans (Spitz et al., 2014). For instance, the main prey species in the diet of common dolphin on the continental shelf of the Bay of Biscay are scads (*Trachurus* spp.), sardine (*Sardina pilchardus*), sprat (*Sprattus sprattus*), anchovy (*Engraulis encrasicolus*), and mackerels (*Scomber* spp.). The relative contribution of each of these species exhibit important temporal variations (Meynier et al., 2008); however, all these prey species share common functional traits and can be pooled in one functional group (i.e. small schooling fish with high energy content; Spitz et al., 2014). The relative contribution of this group to the diet of common dolphins is constantly high. Similarly, both bottlenose dolphin ecotypes (coastal and offshore) feed preferentially on large demersal fish (Louis et al., 2014), and sperm whales on oceanic pelagic squids (Spitz et al., 2011), irrespective of prey species. Taxonomy only failed to document accurately prey choice or prey consumption by cetaceans. Defining prey groups with respect to key functional traits to predators rather than mere taxonomy has the potential to yield better estimates of prey consumption.

Knowing trophodynamic interactions within prey and predator functional groups is essential to understanding marine ecosystem functioning and furthering ecosystem-based management. Thus, our aims were to estimate the annual and seasonal (winter and summer) energy and biomass removals by the cetacean community of major prey groups from the ecosystem of the Bay of Biscay. In doing so, we paid particular attention to quantifying uncertainties around estimates to better inform decision-making for ecosystem-based management of the Bay of Biscay.

2. Material & methods

Calculating biomass consumption by cetaceans requires knowing relative proportions and energetic densities of ingested prey as well as cetacean energetic requirements and population sizes. Spatial distributions are required to determine where cetaceans extract prey biomass (Trites and Spitz, 2017).

2.1. Cetacean abundance

Estimates of cetacean abundance were derived from the SAMM aerial survey (*Suivi Aérien de la Mégafaune Marine*) conducted during winter (2011–2012) and summer (2012) in the Bay of Biscay (Laran et al., 2017). The sampling design used zigzag patterns to optimize searching effort, and visual observations of cetaceans were collected following a *Distance sampling* methodology (Buckland et al., 2001). Abundance estimates were available for two seasons (winter and summer) for two broad habitats in the Bay of Biscay: the continental shelf (< 200 m depth, $103,374 \text{km}^2$) and the continental slope (200–2000 m depth, $87,584 \text{ km}^2$) (Fig. 1). We took the average abundance of the two seasons for each area as an estimate of annual abundance (see detailed values in Supplementary Data S1). During aerial surveys, identification of two morphologically similar species—common and striped dolphins—could not be done with certainty from the air. As a result, abundance estimates were pooled for these two species of small-sized delphinids (Laran et al., 2017). We used the relative proportion of common to striped dolphin sightings observed during PELGAS boat survey between 2004 and 2014 over the continental shelf and slope in the Bay of Biscay (Authier et al., this issue) to split the aerial estimate of pooled abundance into species-specific abundance estimates (3:1 common to striped dolphin sightings on the slope, and 9:1 on the shelf area).

2.2. Diet

Relative contribution of each prey biomass in the diet of a given cetacean generally come from stomach analyses of stranded or by-caught animals. The diet composition of cetaceans used in our study came from published stomach content analysis from the Bay of Biscay (Meynier et al., 2008; Pusineri et al., 2007; Ringelstein et al., 2006; Spitz et al., 2011, 2006), except for fin and minke whales for which we used data from adjacent areas to estimate their Bay of Biscay diet (Lockyer, 2007; Pierce et al., 2004; Víkingsson, 1997) (see detailed values in Supplementary Data S1).

Functional groups of prey appear to be more consistent than solely taxonomy to describe cetacean-prey relationships and estimate prey consumption (Smith et al., 2015; Spitz et al., 2014, 2013). Hence, we allocated cetacean diet compositions to 12 prey groups that share similar key functional traits related to predatory characteristics of cetaceans (Spitz et al., 2014). We also used habitat to separate fish and squids types (*i.e.* oceanic for the slope or neritic for the shelf). The 12 prey groups were denoted as: (1) small neritic schooling energy-rich fish, (2) small neritic schooling energy-lean fish, (3) small oceanic schooling energy-rich fish, (4) small oceanic schooling energy-lean fish, (5) large demersal energy-rich fish, (6) large demersal energy-lean fish, (7) neritic pelagic squids, (8) oceanic pelagic squids, (9) bottom cephalopods, (10) crustaceans, (11) zooplankton, and (12) miscellaneous fish.

2.3. Energetic requirements and prey consumption

Several models have been developed to estimate the food requirements of cetaceans (e.g. Barlow et al., 2008; Santos et al., 2014; Smith
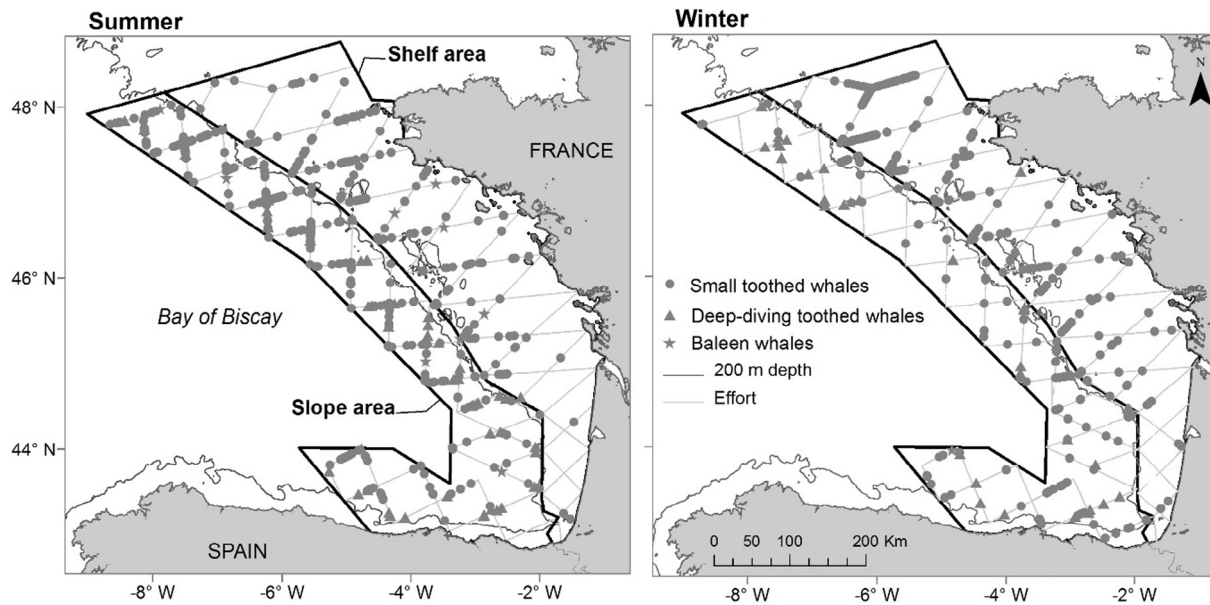
Fig. 1. Bay of Biscay continental slope and shelf with the SAMM survey blocks delimiting the areas where prey consumption by cetaceans was estimated: the continental shelf (< 200 m depth, 103,374 km²) and the continental slope (200–2000 m depth, 87,584 km²). Also shown are the distribution of sightings of small toothed whales (harbour porpoise, common, striped and bottlenose dolphins), deep-diving toothed whales (pilot whales, sperm and beaked whales) and baleen whales (fin and minke whales) in summer (left) and in winter (right).

et al., 2015). However, all of these specific bioenergetics models have assumptions and require parameter estimates that are difficult to obtain for most cetaceans. We therefore favored simplicity and used a generic model of basal metabolic rate (BMR; in kilojoules per day) to estimate energetic requirements at the population or community level:

$$BMR = 293.1 \times M^{0.75} \tag{1}$$

$$ADMR \approx FMR = \beta \times BMR \tag{2}$$

where *BMR* is a function of individual body mass (*M* in kg) according to Kleiber (1975) for a wide range of homeotherms, *ADMR* is the average daily metabolic requirement (in kJ·d⁻¹), *FMR* is the field metabolic rate (in kJ·d⁻¹), and β is a species-specific parameter accounting for activity costs.

Mean body masses were required to estimate energetic requirements at the population level. Unfortunately field measured mean masses are unavailable for many cetacean populations. However, functional relationships exist between the maximum body length of a given species and the mean mass of all individuals in the population (Trites and Pauly, 1998). We therefore estimated mean body mass of all individuals for each population from maximum body length records using regression equations provided in Trites and Pauly (1998)—and obtained maximum body length data from stranded animals on the coasts of Bay of Biscay since 1990 (RNE Stranding database – Observatoire PELAGIS/University of La Rochelle – CNRS, France. www.observatoire-pelagis.cnrs.fr) (Table 1).

Different values of β (activity costs) have been used in previous studies on cetaceans, ranging from 1.2 to > 6 (e.g., Barlow et al., 2008; Santos et al., 2014). The parameter β incorporates the energetic costs of physiological and physical activities (e.g., cost of foraging, reproduction, thermoregulation, etc.). The sum of these costs, called the cost of living, may vary greatly among species, even for equivalent-sized cetaceans (Spitz et al., 2012). Here, we used different values for three functional groups of cetaceans (Spitz et al., 2012): β = 2, 3 or 4 for species with low, medium and high cost of living respectively (Table 1).

The average daily ration (*R*, in kg) of a predator can be estimated from *ADMR* by converting daily energy requirements to wet mass of ingested food using the mean energy content of diet for each prey species (E in kJ·kg⁻¹) corrected for assimilation efficiency (typically 80%; Barlow et al., 2008).

$$E = \sum (E_i \times p_i) \tag{3}$$

$$R = ADMR/(0.8 \times E) \tag{4}$$

where E_i is the energy density for prey species *i*, and p_i is the proportion of biomass of prey species *i* in the diet. Here, we used energy densities E_i of 78 forage species in the Bay of Biscay from 2002 to 2008 measured by direct calorimetry (Spitz et al., 2010).

Mean annual consumption estimates (*Q*) in tons for each prey group *i* by each cetacean species *j* in the Bay of Biscay were thus calculated:

$$Q_{i,j} = A_j \times R_j \times P_{i,j} \times (\text{nbdays})/1000 \tag{5}$$

where A_j is the mean annual abundance estimates of cetacean species *j*, $P_{i,j}$ is the proportion of biomass of prey group *i* in the diet of cetacean species *j*, and nb days is the number of days that cetacean species *j* spends in the Bay of Biscay. Calculations were done for each cetacean species, as well as for all cetacean species combined, and for the three cetacean groups (small toothed whales, deep-diving toothed whales and baleen whales as defined in the European Marine Strategy Framework Directive). Nb days was one-quarter of the year (91.25 days) for winter and summer estimates, and 365 days for annual estimates.

2.4. Uncertainty in prey biomass consumption

Each parameter required to calculate prey consumption comes with its own uncertainty. Uncertainty in diet composition can arise from sampling design, digestive processes, and methodological limitations. Parameter values for bioenergetics models are difficult to obtain for most marine mammals. However, the uncertainties in predator abundance generally have the greatest effect on consumption estimates at the population level (Smith et al., 2015; Vincent et al., 2016). One means of accounting for various uncertainties in the final estimates of biomass consumption is by using Monte Carlo simulation methods (Shelton et al., 1997; Smith et al., 2015; Warren et al., 1997).

Uncertainties in the estimates of prey consumption and energy requirements were performed with 100,000 Monte Carlo simulations using R v.3.3.1 (R Core Team, 2016). We assumed mean individual body masses had a 10% coefficient of variation, and used standard errors of ± 0.5 for the β parameter. For abundance, we used summer and winter estimates from Laran et al. (2017) for 3 functional groups of

Table 1
Estimates of daily food requirements for 10 species of cetaceans expressed as a daily ration and as a percent of body mass. Also shown for each species is mean body mass, mean diet quality and average daily metabolic rate (ADMR).

Species	Mean body mass (kg)	β	Mean diet quality (kJ/kg)	Daily requirements					
				ADMR (kJ/d)		Daily ration (kg)		% Body mass	
				Mean	95%CI	Mean	95%CI	Mean	95%CI
Small toothed whales									
Harbour porpoise	40	4	5100	18,636	[16,026–21,343]	4.6	[3.9–5.2]	11.4	[10–12.9]
Bottlenose dolphin	185	3	3800	44,065	[36,336–52,103]	14.5	[12–17.1]	7.8	[6.6–9.1]
Common dolphin	80	4	5700	31,353	[26,942–35,921]	6.9	[5.9–7.9]	8.6	[7.5–9.7]
Striped dolphin	80	3	4700	23,521	[19,370–27,820]	6.3	[5.2–7.4]	7.8	[6.5–9.1]
Deep-diving toothed whales									
Long-finned pilot whale	850	3	4700	138,420	[114,093–163,687]	36.8	[30.3–43.5]	4.3	[3.6–5]
Risso's dolphin	220	2	4500	33,474	[25,070–42,157]	9.3	[7–11.7]	4.2	[3.2–5.3]
Cuvier's beaked whale	800	2	2600	88,177	[65,911–111,055]	42.4	[31.7–53.4]	5.3	[4–6.6]
Sperm whale	17,000	2	3000	872,599	[651,504–1100,225]	363.6	[271.5–458.4]	2.1	[1.6–2.7]
Baleen whales									
Minke whale	6500	4	5600	848,049	[728,292–971,343]	189.3	[162.6–216.8]	2.9	[2.6–3.3]
Fin whale	55,000	3	3900	3155,657	[2600,605–3729,529]	1 011.4	[833.5–1195.4]	1.8	[1.5–2.1]

Box 1
Pseudo-code for Monte Carlo estimation of prey consumption by cetaceans.

For simulation k.

   From Kleiber equation.

Draw cost of living β_k from $\mathcal{N}(\overline{\beta},se_\beta)$.
Draw predator mass M_k from $\mathcal{N}(\overline{M},se_m)$.
Draw diet quality coefficient E_k from $\mathcal{N}(\overline{d},se_d)$.
Compute basal metabolic rate $BMR_k = 293.1 \times M_k^{0.75}$.
Compute average daily metabolic requirement $ADMR_k = \beta_k \times BMR_k$.
Compute daily ration $R_k = ADMR_k/0.8 \times E_k$.
Compute daily ration as a percentage of body mass $PDR_k = R_k/M_k$.

   Abundance equation.

Draw predator seasonal abundance A_k^s from $\log\mathcal{N}(\log(\overline{A^s}/\sqrt{1 + cv_A^s \times cv_A^s}),\sqrt{\log(1 + cv_A^s \times cv_A^s)})$.

   Consumption equation: scale up individual daily estimate to population- and season-level.

Compute consumption $C_k^s = A_k^s \times R_k \times$ (nb days).

   Store all computed quantities (BMR_k, $ADMR_k$, PDR_k, C_k^s) for inference (mean and confidence interval estimation).

   Notations:

$\overline{x}$ denotes an estimated parameter, se_x its standard error, and cv_x its coefficient of variation.
$\mathcal{N}(\mu,\sigma)$ denotes a normal distribution of location parameter μ and dispersion parameter σ.
$\log\mathcal{N}(\mu,\sigma)$ denotes a lognormal distribution of location parameter μ and dispersion parameter σ.

cetaceans (small toothed whales, deep-diving toothed whales, and baleen whales) for the shelf and slope areas. The pseudo-code used for Monte Carlo simulation is described in Box 1. Confidence intervals (CIs) of 80% from Monte Carlo simulations were preferred to 95% CIs to not give a misleading impression of accuracy (Overholtz, 2006; Smith et al., 2015).

3. Results

3.1. Energy and biomass requirements

Mean energy density of cetacean diets in the Bay of Biscay ranged from 2600 to 5700 kJ/kg of ingested prey. The energy-poorer diets consisted mostly of cephalopods whereas small pelagic fish supplied the energy-richer diets. Mean energy densities of diets varied considerably between species, even for cetacean species that look very similar to one another, such as common dolphins (5700 kJ/kg) and striped dolphins (4700 kJ/kg) (Table 1).

Mean individual daily requirements ranged from 4.6 to 14.5 kg/d for the small toothed-whale species, from 9.3 to 364 kg/d for the deep-diving toothed-whale species, and from 189 to 1012 kg/d for the two baleen whale species (Table 1). This broad range of individual daily requirements reflected the range of individual body masses from a 40 kg porpoise to a 55 ton fin whale. These daily per capita requirements accounted for 1.8–2.9% of the body mass for large cetaceans (individual body mass > 5 tons), 4.2–5.3% of the body mass for medium
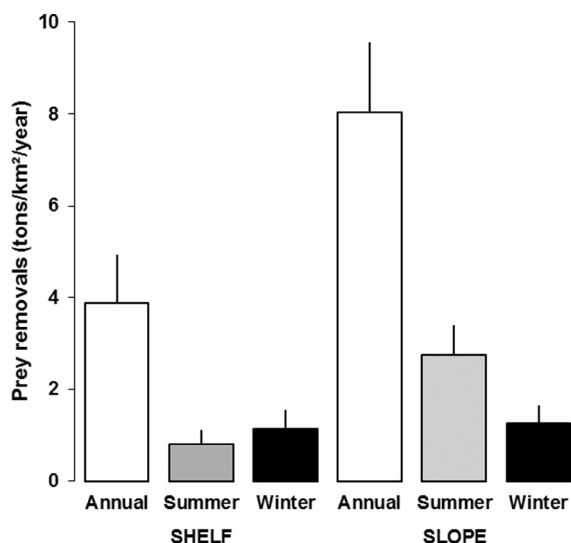
Fig. 2. Total annual, summer and winter prey consumption for all cetacean populations in the Bay of Biscay continental shelf and slope (tons/km²/year). Vertical bars represent the upper values of 80% CI. Each season corresponds to a period of 3 months.

cetaceans (200–1000 kg of individual body mass), and 7.8–1.4% of the body mass for small cetaceans (individual body mass < 200 kg).

Scaling up individual daily requirements with total abundance revealed that the whole cetacean community would remove ~700,000 tons/yr (80%CI: 579,873–837,897) from the slope and 400,000 tons/yr (80%CI: 303,991–509,737) from the shelf from the different prey groups over the year. This represents an annual removal of ~4 tons/km² on average from the shelf and ~8 tons/km² from the slope (Fig. 2). To sustain their needs, an average individual cetacean would thus require an average of 82,000 kJ/km²/d in energy or 22 kg/km²/d in biomass from the continental slope, and 47,000 kJ/km²/d or 11 kg/km²/d from the continental shelf.

Along the continental slope, cetacean density in the Bay of Biscay was higher in summer compared to winter. Energy and biomass removals by cetaceans differed accordingly through the year and were about two-times higher during the summer. Conversely, but to a lesser extent, prey consumption over the shelf was 1.4 times higher during winter compared to summer due to higher winter abundance of small cetaceans (Fig. 2). Among cetacean populations, baleen whales and deep-diving toothed whales exhibited similar mean energy and biomass requirements. However, small toothed whales populations were much more abundant in the Bay of Biscay than other cetacean groups. As a consequence, the small toothed whales required about twice as much resources as baleen whales and deep-diving toothed whales combined (Table 2).

3.2. Prey groups consumption

The small schooling energy-rich fish were the key prey group consumed by the cetacean community in the Bay of Biscay, both on the continental shelf and the slope, representing more than 50% of the total biomass of prey consumed (Fig. 3). Mean annual consumption of small schooling energy-rich fish reached 322,000 tons/yr in total on the shelf (8.5 kg/km²/d) and 285,000 tons/yr on the slope (8.9 kg/km²/d; Table 3). Minke whales and small toothed whales species (notably common dolphins) were the primary consumers of this prey group (Fig. 4). Seasonal variations of small schooling fish consumption occurred mainly on the slope due to variation that occurred here in the abundance of small delphinids (Table 2).

Deep-diving toothed whales are predominantly teutophageous and have large individual body sizes, which resulted in oceanic squids being the second most important prey group consumed by cetaceans (Fig. 4).

Table 2
Total annual, summer and winter consumption of 12 prey groups by 3 groups of cetacean in the Bay of Biscay feeding over the combined continental shelf and slope (thousands of tons/year). Each season corresponds to a period of 3 months. Bracketed values are 80% CI on the mean consumption estimates.

Species	Small toothed whales			Deep-diving toothed whales			Baleen whales		
	Summer	Winter	Annual	Summer	Winter	Annual	Summer	Winter	Annual
Small neritic schooling energy-rich fish	37.3 [25.1–51.6]	91.8 [59.2–130]	258.1 [185.8–341.2]	0.3 [0.2–0.4]	0.3 [0.1–0.4]	1 [0.7–1.5]	52.2 [28.3–81.6]		104.4 [56.5–163.1]
Small neritic schooling energy-lean fish	7 [5.6–8.6]	11.9 [9–15.2]	37.9 [31–45.4]	0.1 [0–0.1]	0.1 [0–0.1]	0.2 [0.1–0.3]	0.5 [0.3–0.8]		1.1 [0.6–1.6]
Large demersal energy-rich fish	2 [1.3–2.7]	3.7 [2.3–5.3]	11.3 [8.1–14.9]						
Large demersal energy-lean fish	4.2 [3.1–5.6]	8.3 [5.7–11.4]	25.1 [19.1–32]	0 [0–0.1]	0 [0–0.1]	0.1 [0.1–0.2]			
Neritic pelagic squids	2.9 [2.3–3.5]	6.3 [4.8–7.9]	18.3 [15.1–21.9]	2.1 [1.3–3.1]	2.2 [1.2–3.3]	8.5 [5.8–11.7]			
Bottom cephalopods	1.3 [0.8–1.8]	3.3 [2.1–4.7]	9.1 [6.5–12.1]	5.2 [3.4–7.4]	4.4 [2.4–6.9]	19.3 [13.4–26.2]			
Zooplankton				0.8 [0.4–1.1]	0.8 [0.4–1.2]	3 [2–4.2]	13.2 [5.8–22.7]	10.8 [3.5–20.7]	48 [24.6–76.6]
Small oceanic schooling energy-rich fish	100.1 [70.2–134.5]	22.3 [14.5–31.4]	244.7 [181.2–316.7]						
Small oceanic schooling energy-lean fish	21.2 [15.3–27.8]	4.7 [3.2–6.5]	51.7 [39.4–65.5]						
Oceanic pelagic squids	27.1 [20.4–34.5]	7.9 [5.9–10.1]	69.9 [55.6–85.6]	0.1 [0–0.1]	0.1 [0–0.1]	0.2 [0.1–0.3]			
Crustaceans	5.9 [4.3–7.6]	1.3 [0.9–1.8]	14.3 [11.1–17.9]	36 [20.8–54.6]	46 [24.7–72.4]	163.8 [106.8–231.2]			
Miscellanous fish	5 [3.4–6.9]	1.6 [1.2–2.2]	13.4 [9.8–17.3]						

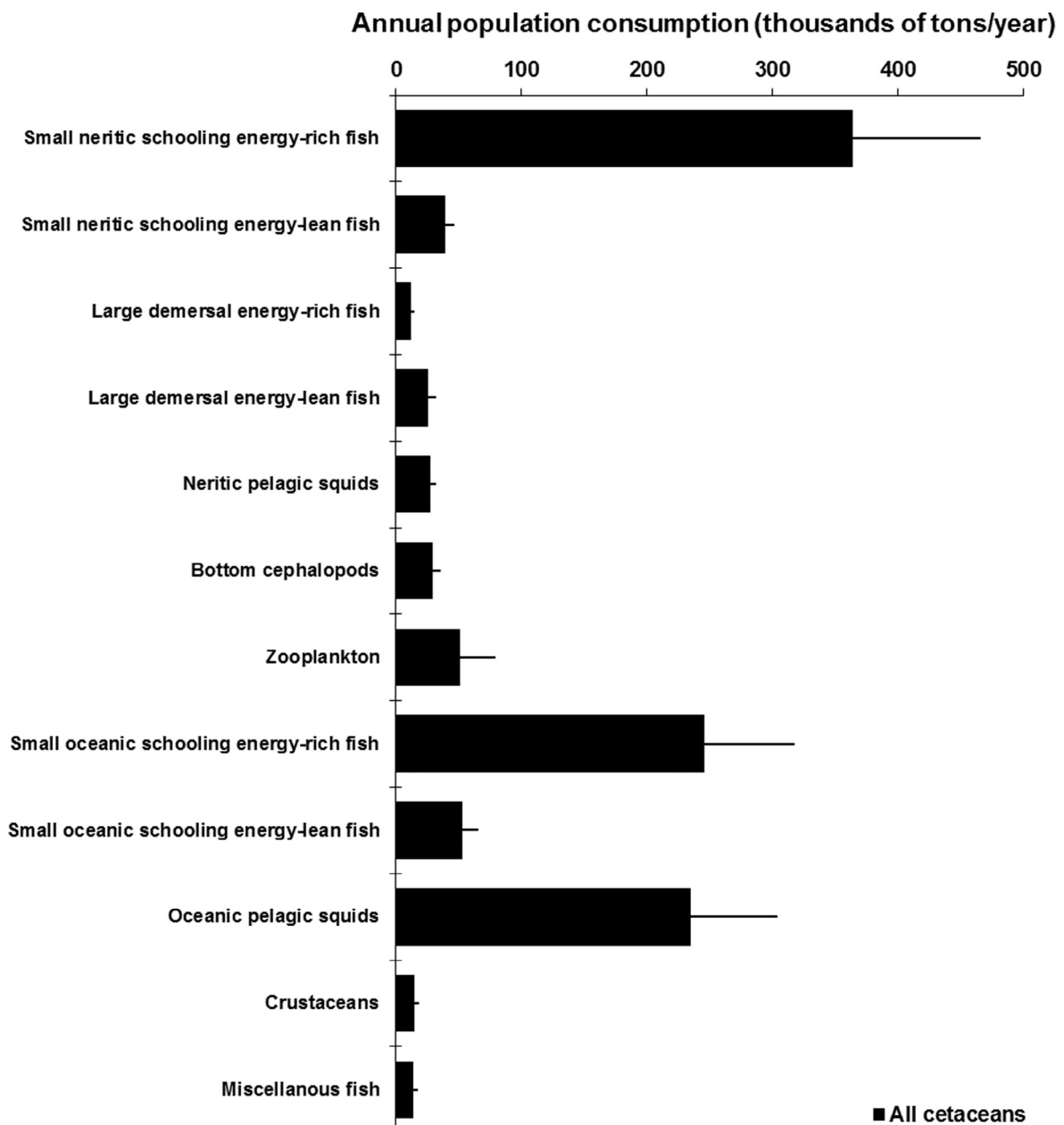## Annual population consumption (thousands of tons/year)

Fig. 3. Annual consumption of prey groups for all cetacean populations feeding over the slope and continental shelf of the Bay of Biscay (thousands of tons/year). Vertical bars represent the upper 80% CI values.

Mean annual consumption of oceanic squids reached 235,000 tons/yr (7.4 kg/km²/d Table 3). Cuvier's beaked whales were the primary consumers of oceanic squids (110,000 tons/yr), followed by sperm whales (35,000 tons/y), common dolphins (31,000 tons/yr) and striped dolphins (40,000 tons/yr). Seasonal variations of small delphinids abundance on the slope explained seasonal variations of oceanic squid consumption (Table 3).

Cetaceans consumed considerably less of other prey groups in the Bay of Biscay. Zooplankton, crustaceans, large fish and others cephalopods combined accounted for ∼15% of the total annual prey consumption. Nevertheless, some of these other prey groups were important for certain cetacean species. Unsurprisingly, zooplankton consumption (48,100 tons/yr) was exclusively due to fin whales. The 36,500 tons of large fish consumed per year by the cetacean community was due almost entirely to bottlenose dolphins, while Risso's dolphins and long-finned pilot whales combined consumed almost 70% of all the bottom cephalopods (Table 4).

4. Discussion

We collated a comprehensive dataset to estimate the annual and seasonal energy requirements and prey consumption of 10 cetacean species at the scale of an ecosystem. Combining recent data on cetacean abundance from the SAMM dedicated surveys, diet from stomach content analyses, as well as functional considerations related to cetacean cost of living and prey grouping revealed that small energy-rich schooling fish are the key prey group sustaining a large part of the cetacean community in the Bay of Biscay. Although our estimates are subject to biases and limitations inherent to the input data, our results highlight the importance of energy-rich resources for the functioning of the Bay of Biscay ecosystem.

4.1. Estimates and uncertainties

Our estimates of prey consumption relied on assumptions and

Table 3
Total annual, summer and winter consumption of prey groups by 10 cetacean populations in the Bay of Biscay feeding over the continental shelf and slope (thousands of tons/year). Each season corresponds to a period of 3 months. Bracketed values are 80% CI on the mean consumption estimates.

Species	Annual			Summer			Winter		
	Slope	Shelf	Total	Slope	Shelf	Total	Slope	Shelf	Total
Small neritic schooling energy-rich fish	41.2 [21.2–67.3]	322.1 [235.6–420.3]	363.2 [272.9–465.3]	18.1 [8.2–31.1]	71.4 [46.7–100.8]	89.5 [61.6–122.5]	2.5 [1.4–3.8]	89.6 [57.2–127.6]	92.1 [59.7–130]
Small neritic schooling energy-lean fish	4.7 [3.4–6.1]	34.5 [27.8–41.8]	39.2 [32.3–46.6]	1.5 [1 – 2]	6.1 [4.7–7.7]	7.6 [6.1–9.3]	0.9 [0.5–1.3]	11.1 [8.2–14.4]	12 [9–15.3]
Large demersal energy-rich fish	8.3 [5.5–11.6]	3 [1.8–4.5]	11.3 [8.1–14.9]	1.6 [1.1–2.3]	0.3 [0.2–0.5]	2 [1.3–2.7]	2.5 [1.3–3.9]	1.2 [0.6–1.9]	3.7 [2.3–5.3]
Large demersal energy-lean fish	15.3 [10.2–21.3]	9.9 [7.2–13.1]	25.2 [19.2–32.1]	3.1 [2–4.3]	1.2 [0.8–1.7]	4.3 [3.1–5.6]	4.6 [2.4–7.2]	3.8 [2.5–5.3]	8.4 [5.7–11.4]
Neritic pelagic squids	12.7 [9.6–16.1]	14.2 [11.2–17.5]	26.9 [22.5–31.6]	3.1 [2.2–4.1]	1.9 [1.4–2.5]	5 [4–6.1]	3.3 [2.1–4.6]	5.2 [3.9–6.7]	8.5 [6.6–10.5]
Bottom cephalopods	18.6 [12.7–25.4]	9.8 [7.1–12.9]	28.5 [21.8–35.9]	4.9 [3.1–7.1]	1.6 [1–2.2]	6.5 [4.6–8.7]	4.4 [2.3–6.8]	3.4 [2.2–4.8]	7.7 [5.3–10.6]
Zooplankton	51 [27.6–79.6]		51 [27.6–79.6]	13.9 [6.5–23.5]		14 [6.5–23.5]	11.5 [4.3–21.3]		11.5 [4.3–21.3]
Small oceanic schooling energy-rich fish	244.9 [181.3–317]		244.9 [181.3–317]	100.2 [70.1–134.5]		100.2 [70.1–134.5]	22.3 [14.5–31.3]		22.3 [14.5–31.3]
Small oceanic schooling energy-lean fish	52 [39.6–65.9]		52 [39.6–65.9]	21.2 [15.4–27.9]		21.2 [15.4–27.9]	4.8 [3.2–6.5]		4.8 [3.2–6.5]
Oceanic pelagic squids	228.5 [169–298]	5.6 [3.9–7.6]	234.1 [174.6–303.7]	62.3 [45.3–82.5]	0.8 [0.5–1.1]	63.1 [46–83.3]	51.9 [30.5–78.6]	2 [1.3–2.9]	54 [32.5–80.6]
Crustaceans	14.3 [11–18]		14.3 [11–18]	5.9 [4.3–7.6]		5.9 [4.3–7.6]	1.3 [0.9–1.8]		1.3 [0.9–1.8]
Miscellanous fish	11.9 [8.4–15.8]	1.5 [1.1–1.9]	13.4 [9.8–17.4]	4.8 [3.2–6.7]	0.2 [0.1–0.3]	5 [3.4–6.9]	1.1 [0.7–1.6]	0.5 [0.4–0.7]	1.6 [1.2–2.2]

previously estimated parameters that each had their own limits and uncertainties (see detailed discussion in Santos et al., 2014). Sensitivity analyses of similar models to ours have shown that estimates of marine mammal abundance have the strongest influence on uncertainty of prey biomass consumption (Smith et al., 2015; Vincent et al., 2016). The relatively high coefficient of variation associated with abundance estimates and relatively high population sizes dominates the other sources of uncertainties when individual daily consumptions are scaled up to annual estimates of consumption for entire populations. To obtain the best possible estimates, we used absolute cetacean abundance corrected for availability bias (due to different diving behaviours of species) from the dedicated SAMM surveys carried out in 2011–2012 in the studied area. Other studies that have estimated annual prey consumption have generally been limited to only a single month of cetacean abundances without having information on seasonal changes in distribution and abundance (e.g., Santos et al., 2014; Smith et al., 2015). In our case, we knew the abundances of cetaceans in both habitats (slope and shelf), and had data for two seasons (summer and winter), which allowed us to integrate seasonal and spatial variability of cetacean abundance over the Bay of Biscay.

Estimates of energetic requirements have the second strongest influence on uncertainty in amounts of prey consumed (after population size). Accurate estimates of daily individual needs requires detailed bioenergetics models that are difficult to parameterize for most cetacean species (see for example Rechsteiner et al., 2013). As a result, we used a simple and commonly used energetic model based on body mass, but applied a range of values for activity costs (β ± 0.5) using Monte Carlo simulations that address uncertainties in daily requirements and account for energy requirements that do not scale with body mass across all cetacean species (Barlow et al., 2008; Spitz et al., 2012). This approach allowed us to address interspecific variabilities in the cost of living for the entire cetacean community (*i.e.*, including small cetaceans, deep-diving odontocetes and baleen whales). The daily per capita requirements we calculated (expressed in kJ or in % of body mass) were consistent with published values of energetic requirements and food consumption (Kastelein et al., 2000; Lockyer, 2007; Markussen et al., 1992; Young and Phillips, 2002).

Compared with uncertainties in population size and energetic requirements, uncertainty in diet has less effect on estimates of annual prey consumption (Pierce et al., 2007; Vincent et al., 2016). Limitations associated with reconstructing diets from stomach content analysis are well understood and generally considered minor (Pierce et al., 2007; Pierce and Boyle, 1991; Santos et al., 2001). We took the species identified in stomach contents and grouped them by prey types to reduce temporal variability and gain greater stability in diet composition (Meynier et al., 2008; Spitz et al., 2014)—thereby yielding more consistent and realistic global estimates of prey consumption.

Overall, our Monte Carlo simulations integrated uncertainties around body mass, activity costs and population size—and provided confidence intervals for energy requirements and prey consumption of cetaceans in the Bay of Biscay. Resulting uncertainties were in the same order of magnitude as studies of cetacean consumption in other regions of the world (Overholtz and Link, 2007; Santos et al., 2014; Smith et al., 2015).

4.2. Spatio-temporal variation of prey consumption

Prey consumption were generally estimated as annual means, and prey removals were considered uniform throughout the studied area. It should be kept in mind that such annual estimates for the Bay of Biscay hide important differences in where and when prey are consumed at finer spatial and temporal scales. Cetaceans tend to be highly mobile and vary their distributions even between day and night. This is particularly true for small cetaceans in the northeastern Atlantic (Certain et al., 2008; Laran et al., 2017; Scheidat et al., 2012). Spatio-temporal
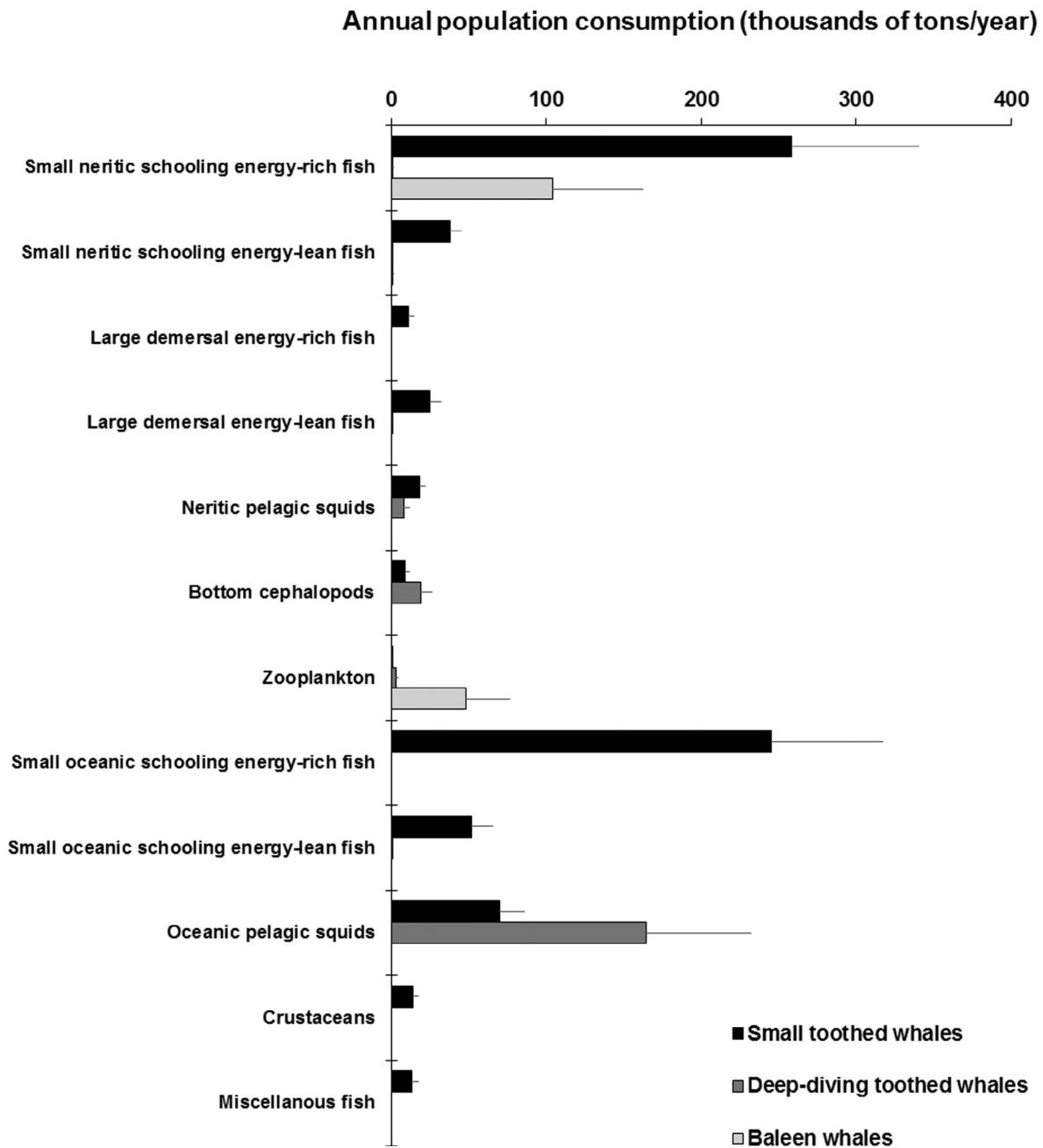
Annual population consumption (thousands of tons/year)

Fig. 4. Annual consumption of 12 prey groups by 3 groups of cetaceans in the Bay of Biscay over the continental shelf and slope (thousands of tons/year). Vertical bars represent the upper 80% CI values.

changes in the abundances and distributions of cetaceans affect trophodynamic interactions that may in turn have differing outcomes.

The SAMM aerial surveys allowed us to explore how seasonal variation in abundance of cetacean populations affects seasonal prey consumption. We found the biggest seasonal difference in consumption occurred over the slope where prey removal was twice as high in summer compared to winter. This seasonal difference is likely driven by higher productivity and availability of prey during spring and summer compared to winter along the slope (Pingree and Garcia-Soto, 2014). We also found greater predation pressure on small-energy rich fish and oceanic cephalopods during summer compared to winter on the slope of the Bay of Biscay.

As with temporal variations, predation pressure was not evenly distributed throughout the Bay of Biscay. Most notably, prey removals per km² were much higher on the slope compared to the shelf. In terms of continental shelf foraging locations, large concentrations of

delphinids off Brittany (northern coastal region of the Bay of Biscay) suggest that some cetacean populations might exploit the northern part of the continental shelf more intensively than southern regions. This is consistent with habitat model predictions showing variability in cetacean densities across the continental shelf (Lambert et al., 2017). In general, however, predation pressure should correlate with cetacean densities such that prey removals are lower in coastal waters (< 50 m depth) and become higher as water depth increases in the Bay of Biscay.

Long-term sighting data collected during integrated surveys such as the PELGAS survey (Doray et al., this issue) provide information on relative abundance and habitat preferences for cetaceans (Authier et al., this issue; Lambert et al., this issue), and should contribute to distinguishing foraging areas from traveling or resting areas. Such data has the potential to provide finer spatial scale insights into where cetaceans remove prey in the Bay of Biscay. Moreover, abundances of prey and cetaceans are typically estimated by independent surveys, which means

Table 4
Total annual consumption of 12 prey groups by 10 species of cetaceans feeding in the Bay of Biscay over the continental shelf and slope (thousands of tons/year). Bracketed values are 80% CI on the mean consumption estimates.

Species	Harbour porpoise	Bottlenose dolphin	Common dolphin	Striped dolphin	Long-finned pilot whale	Risso's dolphin	Cuvier's beaked whale	Sperm whale	Minke whale	Fin whale
Small neritic schooling energy-rich fish	6.7 [4.7–9]	9.4 [6.6–12.6]	242.1 [170.3–324.3]	0.1 [0–0.1]	1 [0.7–1.5]				103.9 [56–162.5]	
Small neritic schooling energy-lean fish	6.3 [4.4–8.4]	3.5 [2.4–4.7]	11 [7.7–14.7]	17.2 [11.9–23.2]	0.1 [0.1–0.1]		0.1 [0.1–0.2]		1 [0.6–1.6]	
Large demersal energy-rich fish		10.6 [7.5–14.2]		0.7 [0.5–0.9]						
Large demersal energy-lean fish	0.2 [0.1–0.3]	19.4 [13.7–26.1]	4.9 [3.5–6.6]	0.5 [0.4–0.7]	0.1 [0.1–0.2]					
Neritic pelagic squids	0.1 [0.1–0.1]	4.4 [3.1–5.9]	6.9 [4.8–9.2]	7 [5–9.2]	7.6 [4.9–10.7]					
Bottom cephalopods	0.1 [0.1–0.2]		8.8 [6.2–11.8]	0.2 [0.1–0.3]	15.8 [10.3–22.3]	3.5 [1.8–5.6]	0.8 [0.4–1.2]	0.1 [0.1–0.2]		
Zooplankton			210.5 [148–281.7]	34.4 [24–46.3]	3 [2–4.2]					48.1 [24.7–77.2]
Small oceanic schooling energy-rich fish			38.9 [27.3–52.1]	12.9 [9–17.3]						
Small oceanic schooling energy-lean fish							0.2 [0.1–0.3]			
Oceanic pelagic squids			30.5 [21.4–40.8]	39.5 [29–51.4]			108 [58.2–168.3]	34.2 [14.4–60]		
Crustaceans			9.7 [6.8–12.9]	4.7 [3.3–6.3]						
Miscellanous fish	0.2 [0.1–0.2]		12.9 [9.4–16.9]	0.3 [0.2–0.5]						

there are usually spatial and temporal inconstancies between predator and prey data sets. Integrated surveys that concurrently assess prey and predator abundances would address many of the spatio-temporal limitations of prey consumption studies and thus provide the data needed to ensure effective ecosystem-based management of the Bay of Biscay.

4.3. Energy-rich resources in food-web functioning

The transfer of energy to higher trophic species plays a central role in ecosystem functioning. In highly productive pelagic ecosystem, such as sub-polar seas or upwelling regions that have relatively short and lipid-rich food chains (Falk-Petersen et al., 2009; Trites, 2003), herbivorous zooplankton rapidly convert nutrients into large lipid stores (Lee et al., 2006). These are in turn consumed by carnivorous zooplankton and some forage fish species that constitute the dense energy-rich schools required to sustain top predators with high costs of living, such as fur seals, sea lions, small delphinids and some seabird species (Jodice et al., 2006; Rosen and Trites, 2000; Spitz et al., 2010).

In the Bay of Biscay, small energy-rich pelagic schooling fish appear to be crucial to transfer lipids from plankton to cetaceans, and sustain the cetacean populations. During plankton blooms, mesozooplankton species accumulate large amounts of lipids (such as *Calanus helgolandicus* or *Labidocera wollastoni*). This results in high energy densities and represents a major energy pathway for small pelagic schooling fish, such as sardine or anchovy (Dessier et al., this issue). Such small pelagic fish species collectively constitute a key functional group of prey in the Bay of Biscay for many top predators over the continental shelf, which includes cetaceans as well as large fish (such as seabass or meagre) (Spitz et al., 2013; Hubans et al., 2017).

Our models indicate that biomass removals of small energy-rich schooling fish by cetaceans is 6 times higher than removals of other prey groups in the Bay of Biscay. They further indicate that most cetacean populations in the Bay of Biscay depend on having an energy-rich food web. Reducing the availability of such energy-rich resources would dramatically affect the population dynamics of cetacean populations living here because alternative resources are generally not equally profitable to them.

Prey species are not always interchangeable for predator populations, as observed following dietary shifts in a number of top predator populations. Examples include declines of bluefin tuna in the Gulf of Maine (Golet et al., 2015), declines of Steller sea lions in Northwestern Pacific (Trites and Donnelly, 2003), and reproductive failures of seabirds in the North Sea (Wanless et al., 2005). All of these negative changes occurred in the presence of abundant prey. However, the abundant prey present were not the right ones to be eating (Österblom et al., 2008; Rosen and Trites, 2000).

Energy-rich food webs appear to be particularly sensitive to climate or human pressures due to a low functional redundancy at key trophic levels (Murphy et al., 2016). Moreover, changes that affect nutrient cycles or primary production can have rapid cascading effects in short food webs of high-energy prey species. As a consequence, ecosystem-based management in the Bay of Biscay—or more widely in similar productive ecosystems that are based on short energy-rich food webs—must consider the quality of prey (i.e., energy densities) required by predators, rather than overall prey abundance alone. Considering that energy-rich fish often have high commercial fishery interest and include species subject to quotas, explicit allocations of fishery quotas for predators may be an appropriate policy solution (Williams et al., 2011) to limit the risk of top predators facing shortages of high-quality food. Given the importance of energy-rich prey species to humans and cetaceans, it would also be prudent to implement a rigorous monitoring program of energy-rich food chains (from nutrients to the energetically costly predators) to ensure the long-term productivity and sustainability of the Bay of Biscay.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2017.09.013.

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