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Seasonal estimates of densities and predation rates of cetaceans in the Ligurian Sea, northwestern Mediterranean Sea: an initial examination

SOPHIE LARAN* CLAUDE JOIRIS+ ALEXANDRE GANNIER# AND ROBERT D. KENNEY^

Contact e-mail: sofy8@yahoo.com

ABSTRACT

The Ligurian Sea is one of the most attractive areas for cetaceans in the Mediterranean Sea, and is now included in a Marine Protected Area, the Pelagos Sanctuary. Despite a lower species diversity than in other parts of the world, because of their abundance, cetaceans are thought to represent significant consumers in this ecosystem. Surveys were conducted within the Pelagos Sanctuary from 2001 to 2004. Densities of five species: striped dolphin (*Stenella coeruleoalba*); fin whale (*Balaenoptera physalus*); sperm whale (*Physeter macrocephalus*); long-finned pilot whale (*Globicephala melas*); and Risso's dolphin (*Grampus griseus*), were estimated and converted to biomass. Total biomass density of cetaceans in the Ligurian Sea was estimated as 93kg km^{-2} (CV=28%) in winter (October to March) and 509kg km^{-2} (CV=16%) in summer (April to September). Daily predation rates by cetaceans were estimated as 2.9kg km^{-2} d^{-1} in winter, increasing to 10.4kg km^{-2} d^{-1} in summer, corresponding to a total annual ingestion of 2.4t km^{-2} y^{-1}. The annual primary production required for cetaceans was estimated to be 12.6gC m^{-2} y^{-1}, corresponding to 6-15% of the net primary production known for this area. Estimated cetacean predation on fish was similar to reported fisheries landings, nevertheless, management of artisanal fisheries and accurate quantification of the resources they exploit will be necessary for the responsible management of fisheries in this Mediterranean Marine Protected Area.

KEYWORDS: INDEX OF ABUNDANCE; NUTRITION; FOOD/PREY; SANCTUARIES; FEEDING GROUNDS; SURVEY - VESSEL; SURVEY – ACOUSTIC; STRIPED DOLPHIN; FIN WHALE; SPERM WHALE; LONG-FINNED PILOT WHALE; RISSO'S DOLPHIN; MEDITERRANEAN SEA; NORTHERN HEMISPHERE

INTRODUCTION

Marine mammals often play key roles within marine ecosystems, consequently their abundance and their distribution can have important effects on the structure and function of some ecosystems (Bowen, 1997; Estes *et al*., 2006). Nevertheless their role as top predators needs to be characterised and quantified in order to better understand their habitat use and identify the possible impacts of human activities. All cetaceans are carnivores and in many marine ecosystems they are among the top predators (Bowen, 1997; Trites, 2002). Their diet includes a wide variety of prey species from small crustaceans up to large squid (Barros and Clarke, 2002). They have a few predators of their own; these include large sharks, a small number of other cetaceans and humans. Given their large body sizes and relatively high metabolic rates, cetaceans can represent significant consumers in marine ecosystems.

Concerns about the interactions of fisheries with marine mammals in the Mediterranean Sea are probably as old as the first human attempts to catch fish with a net (Bearzi, 2002). In the Mediterranean, most commercial fish stocks are considered overexploited (Farrugio *et al*., 1993). This adds some degree of urgency to a need for estimates of cetacean consumption. Cetaceans may be affected by fisheries even when their prey species are not target species of commercial fisheries because of linkages though the food web (Trites *et al*., 1997). In addition, since 2002, the Ligurian Sea, located in the northwestern Mediterranean Sea, has been designated as a Marine Protected Area (MPA), called the Pelagos Sanctuary (Fig. 1).

In summer, the Ligurian Sea attracts large numbers of cetaceans (Forcada *et al*., 1996; Forcada and Hammond, 1998; Gannier, 2005), in particular striped dolphins (*Stenella coeruleoalba*) and fin whales (*Balaenoptera physalus*). In addition, six other species are known to inhabit this area: sperm whales (*Physeter macrocephalus*); Cuvier's beaked whales (*Ziphius cavirostris*); long-finned pilot whales (*Globicephala melas*); Risso's dolphins (*Grampus griseus*); bottlenose dolphins (*Tursiops truncatus*); and more rarely short-beaked common dolphins (*Delphinus delphis*). Summer densities have previously been reported for striped dolphins (Forcada and Hammond, 1998; Gannier, 1998) and fin whales (Forcada *et al*., 1996; Gannier, 1997), however those for other species and seasons have not been published yet.

For the Mediterranean Sea, the only previous estimates of cetacean prey consumption were by Viale (1985). This author estimated roughly the number of individuals for north of 40°N latitude from opportunistic surveys conducted on oceanographic vessels between 1972 and 1982. It was assumed that strip transect methodology could be considered and the effective strip half-width used was taken from other studies. With additional survey data to allow estimation of cetacean densities throughout the year, accurate estimates of consumption rates are now possible.

A single-species approach to estimating consumption rates or trophic relationships beginning from population size has a number of limitations when dealing with multiple species, especially in terms of ecological requirements of species that vary widely in body size. In this paper, an attempt was made to estimate annual prey consumption rates by cetaceans in the Ligurian Sea, and their overall trophic impacts as measured by primary production required to support that consumption. It has been assumed that cetaceans use the habitat for feeding purposes, as for the majority of species, feeding activity was observed or acoustically verified several times during surveys, except for pilot whales, which are known to feed at night (Baird *et al*., 2002).

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* *Centre de Recherche sur les Cétacés, Marineland-Parques Reunidos, 306 av Mozart, 06600 Antibes, France.*
+ *Laboratory for Polar Ecology (PolE), rue du Fodia 18, B-1367 Ramillies, Belgium.*
# *Groupe de Recherche sur les Cétacés, BP 715, 06633 Antibes, France.*
^ *Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA.*

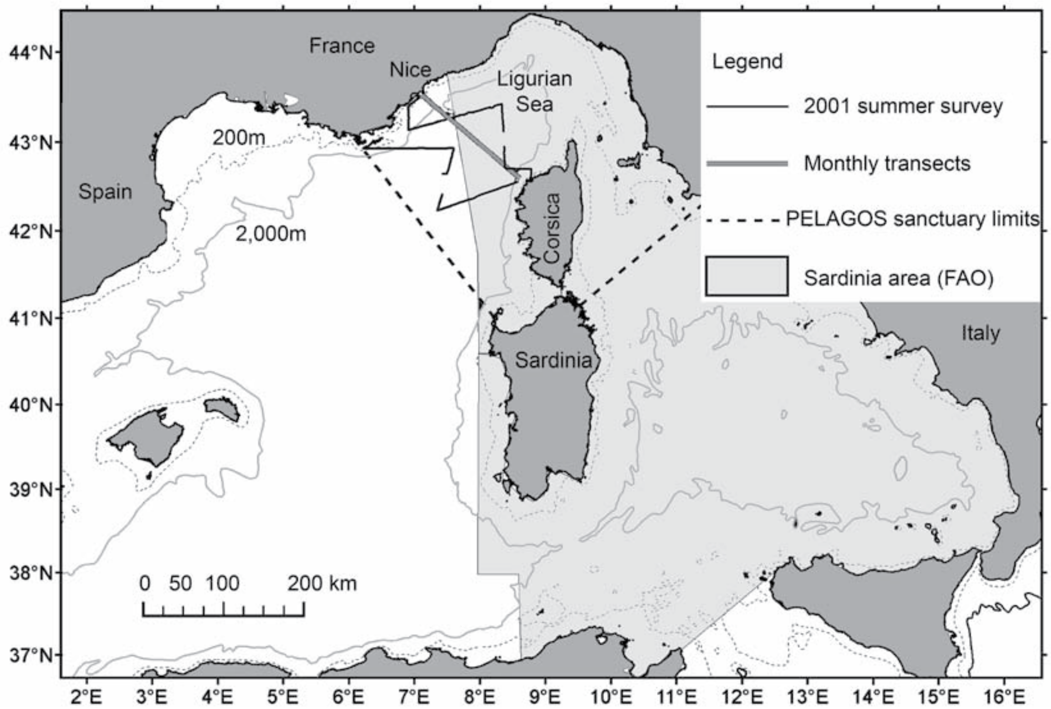

Fig. 1. Study area with transect locations (black and grey lines), PELAGOS Sanctuary borders (dashed lines) and Sardinia area (FAO).

MATERIALS AND METHODS

The Ligurian Sea is located north of the western Mediterranean basin (Fig. 1). This region includes large areas of deep water (>2,000m), with a narrow continental shelf. It is characterised by a frontal system, which provides a high level of primary production, peaking in March-April (Jacques *et al*., 1973; Nival *et al*., 1975). The Pelagos Sanctuary includes 87,500km^2, but the estimates used in this study only pertain to the northernmost portion (Fig. 1). In the absence of seasonal surveys of the whole MPA, cetacean density was estimated from transects conducted only in its northern part. It must be noted that environmental conditions in the corridor do not represent those of the entire MPA and that some cetaceans (e.g. fin whales) are known to aggregate near the northern frontal region in summer. Nevertheless it was considered that even rough estimates of biomass, densities and predation could be useful in term of management. For all estimates, the year was divided into two equal periods, April-September and October-March, which are referred to as ‘summer’ and ‘winter’ respectively, for convenience.

Density estimates

Data were collected between February 2001 and February 2004 from 30 dedicated line-transect surveys, conducted monthly along the same 160km track between the French mainland and Corsica (Fig. 1) and part of the return transect. The standard sampling design was to survey from France to Corsica at a speed of about 22km h^{-1} (12knots). In this analysis only effort conducted between 18km h^{-1} and 23km h^{-1} under sea conditions of Beaufort 3 or lower was considered. The return trip on the next day followed a parallel transect offset 11km north-east from the southbound track. A shorter (74km) section of the northbound transect was surveyed at lower speeds (13km h^{-1}) to try to estimate the probability of seeing a whale on the trackline, $g(0)$, for the most common species. Only sections of the northbound transect conducted at 18-23km h^{-1}, before and after the lower-speed segment, were included in the analysis. There was one additional survey conducted in summer 2001 within the same general area in the sanctuary (Gannier, 2006) (Fig. 1). All surveys were conducted with the same dedicated platform, a 13m vessel powered by two 350HP inboard engines, and a consistent crew. Three experienced observers, seated with their eyes 4m above the water surface, searched the forward sector (-90° to +90° relative to the bow) with the naked eye and were rotated every hour (see Laran and Drouot-Dulau, 2007).

The survey data were grouped by six-month seasons across the three years of sampling and analysed applying standard line-transect methods (Buckland *et al*., 2001). Transects selected for analysis varied from 10 to 158km (mean=81.7km) depending the length of segment conducted with good sighting conditions. The effective strip half-width (*esw*) was estimated for each species using *Distance 5.0* (Thomas *et al*., 2006); as the numbers of sightings were too low to reliably estimate *esw* for Risso’s dolphins and pilot whales, additional detections of the same species, recorded in the northwestern Mediterranean Sea from the same platform were included. For fin whales and striped dolphins, sightings were truncated prior to analysis to exclude 5% of the groups detected at the largest distances following Buckland *et al*. (2001). The density of species *i* during period *j* (in individuals per km^2) was estimated by:

$$D_{ij} = \frac{n_{ij} \; s_{ij}}{2 \; L_j \; esw} \tag{1}$$

where s_{ij} is the mean school size of species *i* during period *j*; n_{ij} is the number of primary sightings (after truncation) of species *i* during period *j* and L_j is the total transect length (km) surveyed during period *j*. The variance of D was estimated using *Distance 5.0*, by the delta method (Buckland *et al*., 2001). Replicate transects weighted by transect length were considered to estimate var(n). The annual variance or groups of species variances were estimated as the sum of variances of the different components (Buckland *et al*., 2001).

For sperm whales, a strip-transect method was applied to combined visual and acoustic detections. Two-minute recording sessions (with the vessel propeller de-clutched) were performed, each 18.5km of the southbound transect, with a monaural hydrophone (Magrec, HP 60MT). As the exact number of whales could not be reliably determined when more than three whales were vocally active in the area, three was the maximum school size allocated by acoustic sampling alone (Gannier *et al*., 2002). Two consecutive positive stations or a positive station following/preceding a sighting were considered as distinct whales when the recorded click-level index was equal or greater than 3 (on a scale varying from 0 to 5; see Laran and Drouot-Dulau, 2007). As sperm whales do not usually produce regular clicks at the surface (Drouot *et al*., 2004), the school size of each sighting was estimated by combining visual and acoustic information. With the same monaural hydrophone, Gannier *et al*. (2002) observed a click-level index of 0 for a sperm whale located at 14.8km and a level of 2 at 9.4km; from their results it is estimated that whales were heard up to 13km away (see fig. 3, plot for mono-hydrophone, in Gannier *et al*. 2002). Therefore an arbitrary distance of 13km was assumed to be acoustically scanned on each side of the transect line (equivalent to *esw*), considering the detection capability of the hydrophone. The calculation of sperm whale density was equivalent to Eqn. (1).

Biomass and prey consumption

Biomass densities for each species were estimated by multiplying calculated densities by average body mass (*W* in kg). The mean body mass values, for males and females separately, were taken from Trites and Pauly (1998) except for species where independent evidence suggested that individuals in the Mediterranean tended to be smaller than elsewhere in the world. In those cases, maximum lengths from the Mediterranean were used in the regression models from Trites and Pauly (1998) to compute mean weights for males and females. Maximum body lengths for Mediterranean specimens came from the long-term stranding database and were provided by F. Dhermain (Groupe d'Etude des Cétacés de Méditerranée) and O. Van Canneyt (CRMM - University of La Rochelle). For each species the male and female means were averaged with the sex ratio assumed to be 50%, except for the strongly dimorphic species (sperm whale and pilot whale), where the sex ratio was assumed to be 40% male and 60% female (following Barlow *et al*., 2008; Trites and Pauly, 1998). The CV of the biomass density estimate was assumed to be the same as that of the corresponding density, as no information on maximum length variability was available. Cumulative biomass densities for all odontocetes and total cetaceans were computed by summing the estimates for the individual species, and cumulative CV's were computed by summing the individual variances (following Buckland *et al*., 2001).

A variety of methods exist for estimating the consumption rates of cetaceans (see review by Leaper and Lavigne, 2007). Sergeant (1969), extrapolating from feeding rates of captive odontocetes ranging in size from harbour porpoises to killer whales, proposed that feeding rates of free-living cetaceans could be computed as a percentage of body weight, ranging from 3.5-4% in larger animals to 10-12% in the smallest individuals, but he did not fit a mathematical model. The available mathematical models are generally of two types: computing ingestion rate as a function of body weight; or computing metabolic rate as a function of body weight and scaling upward to ingestion rate for assimilation efficiency and activity. Innes *et al*. (1987) proposed that daily ration (*R*, in kg d^{-1}) could be estimated from body weight (W, in kg) by:

$$R_1 = 0.123\ W^{0.8} \tag{2}$$

Trites *et al*. (1997) modified that model by adjusting the multiplier slightly downward in an attempt to account for the difference between ingestion for growth and ingestion for maintenance:

$$R_2 = 0.1\ W^{0.8} \tag{3}$$

Kenney *et al*. (1997) used the model of Kleiber (1975) to estimate basal metabolic rate (BMR, in kcal d^{-1}):

$$BMR = 70\ W^{0.75} \tag{4}$$

and then applied a scaling factor to account for assimilation efficiency and activity:

$$R_3 = \frac{2.5\,BMR}{E} \tag{5}$$

where *E* is the energy density of the prey consumed, assumed to be 1,000kcal kg^{-1} for fish and crustaceans (Clarke and Prince, 1980; Sissenwine *et al*., 1984) and 830kcal kg^{-1} for squid (Croxall and Prince, 1982). Sigurjónsson and Víkingsson (1997) used Lockyer's (1981) model for near-basal metabolic rate:

$$M = 110\ W^{0.783} \tag{6}$$

which they then scaled upwards for 80% assimilation efficiency and a 1.5× activity factor. Incorporating the energy-to-biomass conversion, their model becomes:

$$R_4 = \frac{206.25\,W^{0.783}}{E} \tag{7}$$

All four models were used to estimate the daily rations of cetaceans ranging in size from 30kg to 100t (i.e. harbour porpoise to blue whale), presuming the same diet at 1,000kcal kg^{-1} (Fig. 2). The Sigurjónsson and Víkingsson (1997) method resulted in the highest estimates across the entire range, and the Trites *et al*. (1997) method generated the lowest values at all but the very largest body weights. The Innes *et al*. (1987) and Kenney *et al*. (1997) methods produced intermediate values, with the latter differing in slope. Barlow *et al*. (2008) tested an even broader range of consumption models, and settled on the same one used by Kenney *et al*. (1997). They also concluded that the same model using 3.0 as a multiplier rather than 2.5 (Fig. 2) and

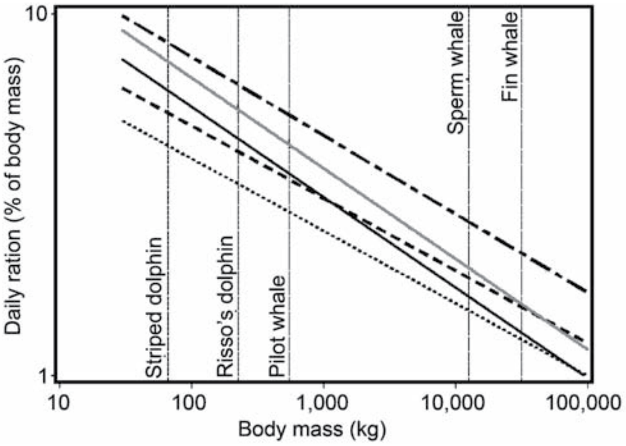

Fig. 2. Estimates of daily ration (as a percentage of body mass) from body mass for cetaceans from 30kg (e.g. an average male harbour porpoise) to 100 tonnes (e.g. a blue whale) from four different models: Trites *et al.* (1997) (dotted line); Kenney *et al.* (1997) (solid black line); Innes *et al.* (1987) (dashed line); and Sigurjónsson and Víkingsson (1997) (alternating long and short dashes). The solid grey line represents the Kenney *et al.* (1997) model using an activity multiplier of 3.0 instead of 2.5.

Table 1

Survey effort and on-effort total sightings after truncation (and number of individuals) collected between February 2001 and February 2004.

Seasonal period	No. of surveys	Effort (km)	Fin whale	Sperm* whale	Pilot whale	Risso's dolphin	Striped dolphin	Total
April-September	19	3,967	77 (126)	19 (29)	6 (171)	4 (39)	169 (3,520)	275
October-March	12	2,235	8 (9)	8 (24)	0	6 (68)	74 (959)	96
Total	31	6,202	85 (135)	27 (53)	6 (171)	10 (107)	243 (4,478)	371

*Both visual sightings and acoustic detections are included for sperm whales.

the Innes *et al.* (1987) model were also plausible. Similarly, the Kenney *et al.* (1997) model has been used for the principal analyses reported in this paper.

Consumption rates were estimated using Eqns (4) and (5), and partitioned into three prey categories: fish; cephalopod; and zooplankton (crustaceans). In the absence of knowledge on variation of the ingestion rate, the CVs were propagated from biomass densities estimates through to the consumption estimates, whilst aware that the CV value would be underestimated by an unknown and maybe important amount. For the group of species, the sum of variances of the different components were estimated. The estimated percentages of each species' diet comprising the three categories were based upon previous reviews (Kenney *et al.*, 1985; Kenney *et al.*, 1997; Pauly *et al.*, 1998) as modified by literature and data specific to the Mediterranean Sea. The food of fin whales in summer was assumed to be 100% crustaceans, as the euphausiid *Meganyctiphanes norvegica* is considered as its only food resource (Astruc, 2005; Orsi Relini and Giordano, 1992). Since fin whales are present in the Mediterranean Sea in winter and there is evidence of winter feeding, at least close to Sicily (Canese *et al.*, 2006), no scaling factor was applied to increase summer feeding rate to account for winter fasting. Based on information for other areas (Lockyer, 2007; Sigurjónsson and Víkingsson, 1997; Viale, 1985), it was assumed that during winter, fin whales feed mainly on euphausiids (90%) but occasionally on fish when available (10%). For sperm whales, there have been reports on two stomach contents from the Mediterranean Sea (Astruc, 2005; Roberts, 2003); both included only cephalopods, mainly *Histioteuthis bonnellii*. However, to account for possible consumption of fish, as is reported in the Atlantic Ocean (Clarke *et al.*, 1993), it was assumed that 90% of the diet is cephalopods and 10% is fish. For pilot whales and Risso's dolphins, based on a small sample in the Mediterranean Sea (Astruc, 2005; Orsi Relini and Garibaldi, 1992) and the earlier reviews, diets of 95% cephalopods and 5% fish were assumed. The food of striped dolphins in the Ligurian Sea is comprised of 49.3% fish, 49.7% cephalopods and 1% crustaceans (Würtz and Marrale, 1993).

The daily prey consumption rate for each species in each six-month season (in kg km^{-2} d^{-1}) was then estimated by multiplying seasonal density by daily ration. Seasonal consumption was calculated by multiplying daily rates by the number of days in each six-month period (182.5), and the annual consumption rate per species (Q, in kg km^{-2} y^{-1}) was then the sum of the winter and summer values, with the variance calculated as the sum of the seasonal variances.

Primary production required

The role of cetaceans within the food web of their ecosystem was also examined by estimating the proportion of net primary production required to sustain the prey that they consumed. This was estimated using a constant transfer efficiency of 10% between successive trophic levels, *TL* (Pauly and Christensen, 1995). The primary production required (PPR$_p$, gC m^{-2} y^{-1}) to support consumption of any prey type *p* was calculated from consumption of that prey (Q_p) using a factor 10^k, with *k* being the number of trophic steps between phytoplankton (*TL* = 1) and the given prey category:

$$PPR_p = \frac{(Q_p \cdot E_p) \times 10^{(TL-1)}}{13.3 kcal\ gC^{-1} \times 10^6 m^2\ km^{-2}} \tag{8}$$

where E_p is the energy density of the prey. *TL* is the trophic level of the prey category and assumed to be 2.2 for crustaceans, 3.2 for cephalopods, and 3.0 for fish (Pauly and Christensen, 1995). The terms in the denominator convert from energy to carbon units (Platt, 1969) and from km^2 to m^2. The primary production required was then compared to total net primary production as reported in the literature.

Comparison with fisheries

Annual global capture production estimates were extracted with *FishStat Plus*[1] and the time series of the Food and Agriculture Organisation of the United Nations (FAO), available from the area. Results were averaged from 2000 to 2005 for two different areas: (1) the total Mediterranean Sea plus Black Sea global dataset of Capture Production (1950-2006); (2) total fishery production (1950-2006) considering commercial, industrial, recreational captures and aquaculture and other kinds of fish farming (FAO, 2008); and (3) the Sardinia region alone (Tyrrhenian Sea to east of Sardinia and Corsica; Fig. 1) extracted from GFCM (Mediterranean and Black Sea) Capture Production (1970-2005) (FAO, 2008). Total fisheries production values were converted to rates by dividing by the respective surface area. Surface area for the Mediterranean and Black Sea is 2,966,000km^2 (Aubouin and Durand-Delga, 2002). Surface area for the Sardinia region was estimated with *ArcView 9.2* as 288,750km^2.

RESULTS

Density, biomass and prey consumption

During these surveys, 371 sightings (or acoustic detections in the case of sperm whales) were recorded (Table 1). Five cetacean species were recorded on-effort. Striped dolphins were the most frequently observed (*n*=243 sightings), followed by fin whales (85), sperm whales (27), Risso's dolphins (10) and finally pilot whales (6), the only species that was encountered in summer only. Total survey effort was 2,235km during October-March and 3,967km during April-September.

Striped dolphin

An *esw* of 489m (CV=8.4%) was estimated for striped dolphins using a hazard-rate model without adjustment, after truncation at 1,400m. Mean school size was 19.9

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[1] http://www.fao.org/fishery/statistics/programme/3,1,2/en

Table 2

Mean body masses (*W*, in kg) for males, females, and both sexes averaged, for five cetacean species in the Ligurian Sea, and mean daily ration per individual (kg d^{-1}, and as % of body mass in parentheses) estimated from four different models: (1) Innes *et al.* (1987); (2) Trites *et al.* (1997); (3) Kenney *et al.* (1997); (4) Sigurjónsson and Víkingsson (1997). Model 3 (in bold) was selected for use in the analysis reported in this paper. Mean body masses were taken from Trites and Pauly (1998) or estimated using their regression models from maximum lengths (L_{max}, in cm) from Mediterranean specimens (F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.).

	L_{max}		*W*			Daily ration			
Species	♂	♀	♂	♀	Mean	(1)	(2)	**(3)**	(4)
Fin whale	2,000	2,000	31,429	30,832	31,131	484 (1.6)	393 (1.3)	**410 (1.3)**	680 (2.2)
Sperm whale	1,500	na	16,083	10,098	12,492	233 (1.9)	189 (1.5)	**244 (2.0)**	393 (3.1)
Pilot whale	600	500	689	450	546	19.0 (3.5)	15.5 (2.8)	**23.6 (4.3)**	34.2 (6.3)
Risso's dolphin	na	na	236	211	224	9.3 (4.2)	7.6 (3.4)	**12.1 (5.4)**	17.0 (7.6)
Striped dolphin	227	225	68	65	66	3.5 (5.3)	2.9 (4.3)	**4.4 (6.7)**	6.0 (9.1)

(CV=9.4%) in April-September and 10.9 (CV=13.5%) in October-March. The maximum density was observed in April-September with 0.87 individuals km^{-2} (CV=15.2%). The density in winter was somewhat less than half of the summer density at 0.37 (CV=21.7%), with a significant difference (Z-test=3.23, $p<0.005$).

Maximum lengths of stranded striped dolphins from the Mediterranean were 227cm for males and 225cm for females (from 406 males and 327 females; F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.). The average weights computed from the Trites and Pauly (1998) regressions were 68kg and 65kg, respectively, and the average for the species was 66kg (Table 2).

The seasonal biomass densities were 57.6kg km^{-2} (CV=15.2%) in April-September and 24.5kg km^{-2} (CV=21.7%) in October-March (Fig. 3). The average daily ration for a striped dolphin was estimated from the four different models to range from 2.9 to 6.0kg d^{-1} (4.3-9.1% of body mass, Table 2), with 4.4kg d^{-1} estimated from Kenney *et al.* (1997) model. The striped dolphin annual consumption rate was estimated to be 999kg km^{-2} y^{-1} (CV=17.7%): 492kg of fish; 497kg of cephalopods; and 10kg of crustaceans (Table 3).

Risso's dolphin

Risso's dolphin sightings were truncated at 600m and an *esw* of 430m (CV=8.9%) was estimated using a half-normal model. Mean school size was 9.8 (CV=43.2%) in April-September and 11.3 (CV=41.2%) in October-March. These results lead to an extrapolated winter density of 0.035 individuals km^{-2} (CV=58.2%), decreasing to 0.011 (CV=58.9%) during summer. Risso's dolphins were the only species with a substantially higher density in winter than in summer, differing by a factor of about three, but with no significant difference due to large CVs (Z-test=1.10, $p>0.30$).

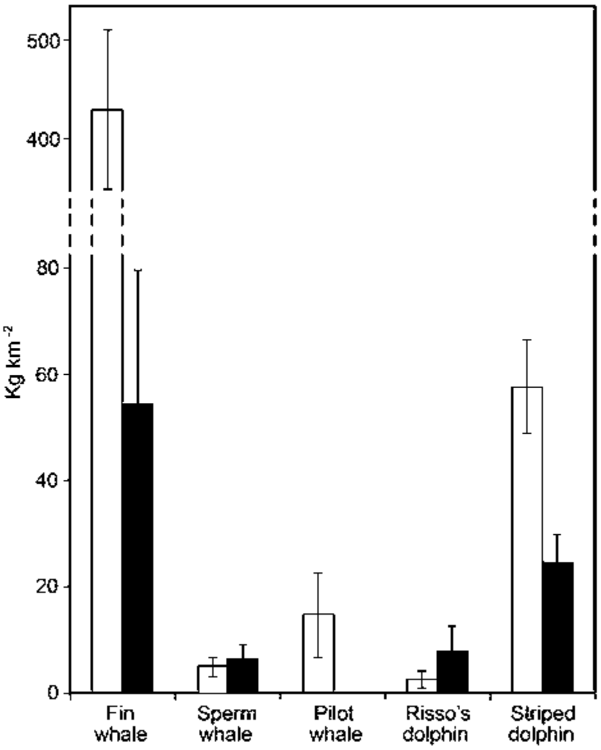

Fig. 3. Estimated biomass density (in kg km^{-2}) for each species for April-September (open bars) and October-March (filled bars) periods. Error bars represent the standard errors.

Table 3

Seasonal (kg km^{-2} d^{-1}) and annual (kg km^{-2} y^{-1}) estimates of consumption of three categories of prey by five species of cetaceans in the Ligurian Sea.

		Season		
Species	Prey	Apr.-Sep.	Mar.-Oct.	Annual
Sperm whale	Fish	0.01	0.01	4
	Cephalopods	0.09	0.12	37
Pilot whale	Fish	0.03	0.00	6
	Cephalopods	0.60	0.00	110
Risso's dolphin	Fish	0.01	0.02	5
	Cephalopods	0.13	0.41	98
Striped dolphin	Fish	1.89	0.80	492
	Cephalopods	1.91	0.81	497
	Crustaceans	0.04	0.02	10
All odontocetes	Fish	1.94	0.84	507
	Cephalopods	2.73	1.33	742
	Crustaceans	0.04	0.02	10
Fin whale	Fish	0.00	0.07	13
	Crustaceans	5.66	0.65	1,150
All species	Fish	1.94	0.91	521
	Cephalopods	2.73	1.33	742
	Crustaceans	5.69	0.66	1,160
	Total	10.4	2.9	2,422

Maximum lengths of Risso's dolphin from the French Mediterranean stranding network differed by only 20cm from the global values of 380cm for males and 360cm for females reported by Trites and Pauly (1998) and were based on small sample sizes ($n<20$ for both males and females). Therefore average weights were used for males and females as in Trites and Pauly (1998); 236kg and 211kg, respectively. The average for the species was 224kg (Table 2).

The seasonal biomass densities were 7.9kg km^{-2} (CV=58.2%) in October-March and 2.6kg km^{-2} (CV=58.9%) in April-September (Fig. 3). The average daily ration for Risso's dolphin was estimated to range from 7.6 to 17.0kg d^{-1} (3.4-7.6% of body mass, Table 2). From the selected model (Kenney *et al*., 1997) a value of 12.1kg d^{-1} was obtained. The annual consumption rate was estimated to be 103kg km^{-2} (CV=65.3%): 5kg of fish; and 98kg of cephalopods (Table 3).

Pilot whale

Most of the sightings of pilot whales occurred at perpendicular distances of less than 800m; therefore a uniform model was adopted, considering that all animals were detected up to 800m from the transect. The species was encountered in summer only, with a mean school size of 28.4 (CV=28.0%). The density was estimated as 0.027 individuals km^{-2} (CV=49.1%).

Maximum lengths of Mediterranean pilot whales were 600cm from 31 males and undetermined individuals and 500cm from 20 females (F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.). The average weights computed from the Trites and Pauly (1998) regressions were 689kg and 451kg, respectively, and the average for the species was 546kg (Table 2).

The summer biomass density was 14.7kg km^{-2} (CV=49.1%) (Fig. 3). The average daily ration for pilot whales was estimated from the four models to range from 15.5 to 34.2kg d^{-1} (2.8-6.3% of body mass, Table 2), with an estimate from the selected model of 23.6kg d^{-1}. The annual consumption rate was estimated to be 116kg km^{-2} (CV=69.4%): 110kg of cephalopods; and 6kg of fish (Table 3).

Sperm whale

Sperm whale visual sightings and distinct acoustic sequences represented a total of 27 encounters, including 20 detected only acoustically and 7 using both methods. Mean school size was 1.5 (CV=10.5%) in summer and 3.0 (CV=29.6%) in winter. Their extrapolated density varied between 3.9x10^{-4} individuals km^{2} (CV=39.1%) in April-September and 5.2x10^{-4} (CV=38.6%) in October-March, the smallest seasonal difference of any of the five species, with no significant difference (Z-test=0.52, *p*>0.60).

The maximum length of sperm whales stranded along the French Mediterranean coast was 15m from 18 males and undetermined individuals (F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.). This length was also greater than 30 length estimates based on inter-pulse interval measurements from acoustic recordings in the northwestern Mediterranean Sea (Drouot *et al*., 2004). The average male weight computed from the Trites and Pauly (1998) regression was 16.1t. As only one female length was available, the average female weight of 10.1t reported by Trites and Pauly (1998) was used. The average for the species was 12.5t (Table 2).

The seasonal biomass densities were 4.9kg km^{-2} (CV=39.1%) and 6.6kg km^{-2} (CV=38.6%), in April-September and October-March respectively (Fig. 3). The average daily ration for sperm whales was estimated to range from 189 to 393kg d^{-1} (1.5-3.1% of body mass, Table 2). The daily ration estimated from Kenney *et al*. (1997) model was 244kg d^{-1}. The annual consumption rate was estimated to be 41kg km^{-2} (CV=39.2%): 37kg of cephalopods; and 4kg of fish (Table 3).

Fin whale

An *esw* of 1,152m (CV=10.3%) was estimated for fin whales, using a hazard-rate model without adjustment and after truncation at 2,000m. Mean school size was 1.6 (CV=8.1%) in April-September and 1.1 (CV=11.1%) in October-March. The maximum density was observed in summer with 0.014 individuals km^{-2} (CV=19.2%), against 0.002 (CV=46.3%) in winter. The 8-fold difference between seasonal densities was the highest of any of the four species that were present in both seasons and was significant (Z-test=4.35, *p*<0.0001).

The maximum length of Mediterranean fin whales was 20m, with no clear difference between males and females (from 68 stranded individuals; F. Dhermain, GECEM and O. Van Canneyt, CRMM - University of La Rochelle, pers. comm.). The average weights computed from the Trites and Pauly (1998) regressions were 31.4t for males and 30.8t for females, and the average for the species was 31.1t (Table 2).

The seasonal biomass densities correspond to 429kg km^{-2} (CV=19.2%) in April-September and 54kg km^{-2} (CV=46.3%) in October-March (Fig. 3). The average daily ration for a fin whale was estimated to range from 393 to 680kg d^{-1} (1.3-2.2% of body mass; Table 2) and computed to be 410kg d^{-1} from the selected model. The annual consumption rate was estimated to be 1,163kg km^{-2} (CV=25.2%): 1,150kg of crustaceans; and 13kg of fish (Table 3).

All cetacean species

For all odontocetes combined, the biomass densities varied between 38.9kg km^{-2} (CV=19.2%) in winter and 79.8kg km^{-2} (CV=14.5%) in summer. The total cetacean biomass densities were 93.4kg km^{-2} (CV=28.2%) in winter and 509.0kg km^{-2} (CV=16.3%) in summer. These seasonal values were significantly different (Z-test=4.9, *p*<0.0001).

The combined daily food consumption of all cetaceans was estimated to be 2.9kg km^{-2} d^{-1} (CV=28.2%) in winter (Table 3), dominated by cephalopods (45.9%), followed by fish (31.3%) and crustaceans (22.8%). In summer, daily consumption increased to 10.4kg km^{-2} d^{-1} (CV=16.3%), strongly dominated by crustaceans (54.9%) and followed by cephalopods (26.3%) and fish (18.7%). The seasonal difference in prey types is driven by the different densities of fin whales. Annual food requirement represents 2.4t km^{-2} (CV=20%) (Table 3, Fig. 4).

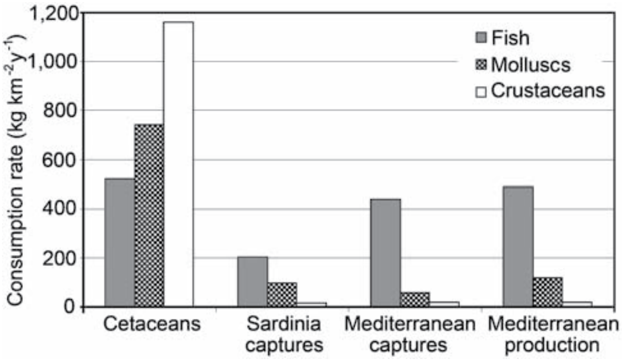

Fig. 4. Annual consumption rate (kg km^{-2} y^{-1}) by cetaceans in the Ligurian Sea compared to 2000-2005 average fishery landings and production reported for Sardinia (FAO area 1.3) and the entire Mediterranean and Black Sea.

Compared to reported fishery landings from either the whole Mediterranean Sea or only the Sardinia region, cetacean predation rates on crustaceans and molluscs are much larger than fishery harvest rates (Fig. 4). Competition for molluscs between cetaceans and humans is even lower than apparent from the data because most of the species consumed by teuthophageous odontocetes, particularly large ones (Astruc, 2005), are not commercial species. Cetacean consumption of fish is much closer to fish (including sharks) harvest rates reported for the Sardinia area (202kg km^{-2}) or for the entire Mediterranean and Black Sea (437kg km^{-2} or 487 considering aquaculture).

Primary production required

The primary production required to support total prey consumption by cetaceans was estimated to be 12.6gC m^{-2} y^{-1}. In the Ligurian Sea, the mean primary production has been estimated at 165gC m^{-2} y^{-1}, from SeaWiFS remotely sensed imagery from 1998 to 2001 (Bosc *et al*., 2004). *PPR* for cetaceans is 7.6% of that value. Total annual productivity estimates from *in situ* ^{14}C methods have varied from 86 to 226gC m^{-2} y^{-1} (Marty and Chiavérini, 1999), of which the primary production requirement for cetaceans represents between 5.6 and 14.7%.

DISCUSSION

This study estimates for the first time the seasonal variability of density and biomass of cetaceans in the Ligurian Sea, as well as their rates of prey consumption and trophic effects. Although the results are sensitive to many input parameters and assumptions, these results allow basic comparisons in order of magnitude with reported fishery landings and phytoplankton production. A recent document from the European Community (COM, 2003) concluded that despite an increase of the fishing effort in the Mediterranean Sea overall production and rates have been steadily decreased compared to the past. The approach allows better quantification of the trophic importance of cetaceans in the area and their fish demand than has been available in the past.

Density

Both seasonal sampling periods were covered by more than 2,000km of survey effort, including at least 12 surveys over the 4 years. The estimated densities for the two most common species, striped dolphin and fin whale, should be considered as reliable, which is supported by CVs of <22% except for fin whales in winter. The estimate of summer fin whale density (0.014 individuals km^{-2}; CV=19.2%) is in agreement with previous results, which vary from 0.015 individuals km^{-2} (CV=15.9%; Gannier, 1997) in the Liguro-Provençal area to 0.024 individuals km^{-2} (CV=27.0%; Forcada *et al*., 1996; Gannier, 1997) in the western Mediterranean Sea. Fin whale density in the Ligurian Sea is also similar to other regions of the North Atlantic, with 0.021 individuals km^{-2} to 0.053 (Buckland *et al*., 1992; Kenney *et al*., 1985) Previous estimates of the summer density of striped dolphins in the area ranged between 0.30 individuals km^{-2} (CV=35%) and 0.75 (Forcada and Hammond, 1998; Gannier, 2006), with the minimum estimated just after an epizootic mortality event. The estimate of 0.87 individuals per km^{-2} (CV=15.2%) in April-September period is in agreement, considering that previous estimates were conducted in July and/or August, while in the data set used in this study surveys were also carried out in September, which corresponds to the maximum occurrence of striped dolphins in the area (Laran and Drouot-Dulau, 2007). In the central Spanish Mediterranean Sea, a maximum seasonal abundance of 0.60 individuals per km^{-2} (CV=26.0%) was recorded in Autumn (Gómez de Segura *et al*., 2006) – this is a well-known productivity area (e.g. Cañadas and Hammond, 2006). These estimates are higher than the maximum density estimate for any sampling stratum in the northwest Atlantic (0.37 individuals per km^{-2}; Kenney *et al*., 1985) or for small delphinids in the Bay of Biscay (0.55 individuals per km^{-2}, CV=29%; Certain *et al*., 2008), however both studies were based on aerial surveys and for the northwest Atlantic a much higher proportion of small delphinid sightings was not identified to species. In addition, striped dolphins in the northwest Atlantic are known to be most abundant in waters of the continental slope and farther offshore (Waring *et al*., 2008), but the surveys reported by Kenney *et al*. (1985) were almost entirely inshore of the shelf break.

The estimated densities for the less common species (sperm whales, pilot whales and Risso's dolphins) must be considered with some caution, and the CVs are substantially larger in most cases. For sperm whales, the annual encounter rate of individuals was estimated to be 0.012 individuals km^{-1} (CV=55.0%), close to previous values; 0.006 individuals per km (CV=44.0%; Gannier, 2006) or 0.007 (CV=21.7%; Gannier *et al*., 2002) estimated in the same area. The estimated densities of 5.2×10^{-4} individuals km^{-2} (CV=38.6%) in winter and 3.9×10^{-4} (CV=39.1%) in summer obtained in this study could only be compared with the rough estimate of 10×10^{-4} by Gannier (1995), which considered visual sightings only. The wide arbitrary distance (13km), on both sides of the transect, to account for hydrophone efficiency may have led to an underestimate of sperm whale density and is a factor that must be better quantified for future work. For Risso's dolphins, the few existing estimates vary over the year from 0.015 individuals km^{-2} (CV=60.6%) for the central Spanish Mediterranean (Gómez de Segura *et al*., 2006) to 0.021 (CV=37.1%) for the northwestern Mediterranean Sea (Gannier, 1995). An estimated annual average of 0.023 individuals km^{-2} (CV=65.3%) was obtained in this study, which is similar. There was a strong seasonal variation, with winter density three times summer density, showing the migratory behaviour of Risso's dolphin in the area. For pilot whales, the obtained sighting rate of 0.043 individuals km^{-1} (CV=49.1%) between April and September is quite low when compared to the value of 0.14 whales km^{-1} (CV=69.3%) obtained in the area in July-August 2001 (Gannier, 2006). However the latter result was based on only a single sighting, and both estimates have large variances. The estimated summer density (0.027 individuals km^{-2}; CV=49.1%) is almost identical to the 0.028 (CV=62.3%) value computed from the results of Gannier (1995).

Biomass and food consumption

Prior to the first dedicated surveys for cetaceans in the Mediterranean Sea in the 1990s, biomasses of the eight most common species were roughly estimated for the area between 40°N and European coasts (300,000km^2) (table 13 in Viale, 1985). Interestingly, beginning from mean body mass estimates that varied substantially from the values used in this study and approximate numbers of animals in the area (with no clear details available on those estimates), the author calculated a total cetacean biomass of 86,950t, representing a biomass density of 290kg km^{-2}, very close to the estimate obtained in this study (300kg km^{-2}). In addition, Viale (1985) estimated fish consumption of 58,100t, corresponding to 194kg km^{-2}, while a value of 522 kg km^{-2} was obtained in this study. For cephalopods her results corresponded to 763kg km^{-2}, and for macro- and microzooplankton, 1,100kg km^{-2}, while estimates of 739 and 1,160kg km^{-2} respectively were obtained here. Since the methods and input parameters were completely independent, this level of agreement is somewhat encouraging. The better-supported estimates obtained through this study, using better density values, also identify variations between warm and cold seasons.

Comparisons with different studies and locations

The Mediterranean Sea, a semi-enclosed sea, has a lower cetacean diversity than many other areas. Along the US western coast, for example, about twenty cetacean species are observed in the Californian Current ecosystem (Barlow *et al*., 2008). Thirty-five species of cetaceans are known to occur along the eastern coast of the US (Waring *et al.*, 2008). Estimates of biomass densities and prey consumption rates allow for more informative comparisons with other areas than is possible using only species abundances or densities. The estimate of annual average biomass density obtained in this study (301kg km^{-2}) is intermediate between 143kg km^{-2} for marine mammals in the entire Pacific Ocean (Trites *et al.*, 1997) and 729kg km^{-2} for cetaceans only in the northeastern US continental shelf system (Kenney *et al.*, 1997). During summer and autumn, Barlow *et al.* (2008) estimated a value of 282kg km^{-2} for cetacean biomass density in the California current ecosystem, with a proportion of Balaenopteridae (70%) similar to the observations noted in this paper. Seasonal variability was somewhat stronger in the Ligurian Sea than in the NE US shelf; the results detailed here differ by a factor of five between six-month winter and summer seasons, while Kenney *et al.* (1997) reported a maximum ratio of 3.8 between winter and spring. In agreement with the results of the study presented here and those of Barlow *et al.* (2008), Kenney *et al.* (1997) showed a cetacean community dominated by balaenopterids, at 72-78% of the total standing stock, but their dominance continued through all four seasons of the year.

The point estimate of food intake by cetaceans (2.4t km^{-2} y^{-1} in this study) is much greater than results for northern European seas, ranging between 0.25t km^{-2} y^{-1} in Atlantic waters to 0.75 around Spitsbergen and in polar waters (Joiris, 1992; 1996; 2000). Prey consumption estimates from the studies discussed immediately above, as expected, follow the same order as the estimates of biomass density. Barlow *et al.* (2008) reported consumption of 1.5-2.4t km^{-2} y^{-1} in the California current, the most similar value to that of this study; the minimum was 0.84t km^{-2} y^{-1} in Pacific Ocean (Trites *et al.*, 1997) and the maximum was 6.7t km^{-2} y^{-1} on the northeastern US continental shelf (Kenney *et al.*, 1997). Estimates of fish consumption by marine mammals vary from 0.10t km^{-2} y^{-1} in the North Sea to 5.4t km^{-2} on Georges Bank (Bax, 1991), and the point estimate obtained here of 0.48t km^{-2} y^{-1} of fish consumed corresponds to the lower end of that range. Kenney *et al.* (1997) estimated fish consumption to be an order of magnitude higher at 4.6t km^{-2} y^{-1} because the diet of fin, humpback and minke whales off the northeastern US is primarily fish rather than crustaceans.

World fishery catch rates vary between 10 and 22.2t km^{-2} y^{-1} (from oligotrophic open-ocean systems to highly productive upwellings) representing 1.8-35% of the total net primary production (Pauly and Christensen, 1995). Compared with commercial fisheries, the point estimate of the relative proportion of fish consumed by marine mammals represents some 2% of the fisheries in the North Sea (Bax, 1991), 167% in the Barents Sea (Bax, 1991) and 171% in the northeastern US shelf (Kenney *et al.*, 1997). About 150% was estimated for herring only in the Gulf of Maine (Overholtz and Link, 2006). In the Ligurian Sea, the point estimate of the proportion of fish consumed by cetaceans represents 257% of the reported fishery if only the Sardinia area is considered and 107% compared to global production of fisheries (i.e. catches and aquaculture combined) from the entire Mediterranean Sea. Since a large proportion of the fish harvested remains unrecorded, relative percentages of cetacean consumption should probably be reduced compared to actual catches. In the Pacific Ocean, Trites *et al.* (1997) estimated that fisheries target only 35% of the prey items sought by marine mammals. However this ratio could vary between predator species; for example 70% of the total prey species of striped and Risso's dolphins in the Mediterranean are commercial species (Würtz *et al.*, 1992).

The primary production required for cetaceans was estimated as 20-30gC m^{-2} y^{-1} in the Pacific Ocean (Trites *et al.*, 1997), 31.4gC m^{-2} y^{-1} in the California Current ecosystem (Barlow *et al.*, 2008) and 47.5gC m^{-2} y^{-1} in the northeastern US shelf ecosystem (Kenney *et al.*, 1997), all higher than the estimate of 12.6 obtained here. The mathematical model used to estimate *PPR* (Eqn. 8) includes a power function, so the *PPR* estimates are especially sensitive to the trophic level of the prey species and the most difficult result to compare between ecosystems. Following Barlow *et al.* (2008), who conducted sensitivity analysis in a similar study in the California area, the main effect on approximation of result is the energy transfer across the food web.

Potential sources of variability and error

In the area used in this study, further investigation is necessary to derive more reliable density estimates for less common species such as sperm whales, pilot whales and Risso's dolphins, in addition to the rarer or coastal species that were not sampled at all during the surveys. In addition, there is a negative bias caused by not considering $g(0)$. For the fin whale, no decrease in detection probability on the line was recorded between fast and reduced-speed sampling (22 and 13km h^{-1}), in contrast with the striped dolphin for which a decrease of 12% was estimated at 22km h^{-1} (Laran, 2005). Therefore there was probably an underestimation of striped dolphin density. For the sperm whale, acoustic sampling allowed detection of clicks during almost all their dive durations (Mullins *et al.*, 1988), but the efficiency of the hydrophone likely varies with water column conditions, instead of remaining constant at the arbitrary sampling width of 13km. In addition, the sampling protocol allowed monthly effort to be maintained during three years, but was not suited to estimation of cetacean abundance in the entire Pelagos Sanctuary. Additional field campaigns over broader areas of the Sanctuary, dedicated to abundance estimation, should be carried out in summer and winter to obtain accurate estimates.

Previous studies of this type (Kenney *et al.*, 1985; Kenney *et al.*, 1997; Sigurjónsson and Víkingsson, 1997; Trites and Pauly, 1998) generally have relied on relatively imprecise estimates of body mass available from the literature as the starting point for bioenergetic models. Kenney *et al.* (1985) had reliable data from their own study area for only one species, using a set of photogrammetric length measurements of fin whales and a published weight-length equation to derive a mean weight for the study region. Trites and Pauly (1998) have assisted researchers developing marine mammal energetic models by presenting estimates of average body weights for all species, although they did not provide estimates of variability. Finally, using maximum lengths observed within a particular area, when available, enables the modelling results to better represent the local or regional system. Large datasets of body weights from a particular region would allow direct estimation of mean weights and variability, although it becomes more difficult with increasing body size and there are concerns over bias if the data are obtained from strandings.

Another important source of uncertainty in the results is prey consumption rate. The mean daily rations estimated as percentages of an individual's body mass (1.3-6.7% using the selected model and 1.3-9.1% across all four models) are consistent with general approximations of 3 to 5% for marine mammals (Trites, 2003). The model used here was intermediate in value, and was the model proposed by Barlow *et al.* (2008) to be the most realistic. Fin whale daily intake has been estimated as 1.3-3.3% of body mass from various methods (Lockyer, 1981; 2007), but the estimates generally are based on very low or no feeding during winter and higher rates in summer to compensate. The rate of 1.3% obtained during the study described here represents the lower end of the range, but increased feeding in summer to account for lower consumption during winter was not considered. Although fin whales have been observed feeding in winter in the Mediterranean (Canese *et al*., 2006), it is believed that they feed very little or not at all and therefore must increase their summer feeding rate.

For many marine mammal species, Pauly *et al.* (1998) estimated proportions of their diets comprised of eight different prey categories (benthic invertebrates, large zooplankton, small squid, large squid, small pelagic fishes, mesopelagic fishes, miscellaneous fishes and higher invertebrates). However their estimates represent worldwide averages, do not includes estimates of variability and are themselves based on relatively sparse data. Additional detailed information on diet composition specific to the Ligurian Sea is required to improve consumption estimates for individual prey categories and to better assess variability. For pilot whales and Risso's dolphins only a few results are available for the Mediterranean Sea, and we recognise that our conclusions could vary greatly based on new and better information. Striped dolphins feed on a variety of pelagic and benthopelagic fish and squid (Archer, 2002). Pauly *et al.* (1998) described their diet as 5% benthic invertebrates, 20% small squid, 15% large squid, 5% small pelagics, 30% mesopelagics and 25% miscellaneous or 60% fish, 35% squid and 5% invertebrates, as compared with the values used in this study of 49.3% fish, 49.7% squid and 1% crustaceans. In the Ligurian Sea they exploit many mid-water species (Würtz and Marrale, 1993). The few winter samples analysed from the Ligurian Sea suggest that they may feed at times in winter on cephalopods alone (G. Astruc and D. Agati, pers. comm.). The stable-isotope analyses developed for several species in the area could also help to better quantify and refine cetacean diets and interannual variability in diet, and stable-isotope studies on particular prey species would enable more precise estimates of the trophic levels of prey for *PPR* calculations. Meanwhile accurate estimate of numerous parameters in the area and better quantification of their variability is important to better quantify CVs associated with cetacean consumption estimated in the area.

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