



ORIGINAL ARTICLE

Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores

MÓNICA A. SILVA^{1,2*}, RUI PRIETO¹, IRMA CASCAÃO¹, MARIA INÊS SEABRA³, MIGUEL MACHETE¹, MARK F. BAUMGARTNER² & RICARDO S. SANTOS¹

¹Departamento de Oceanografia e Pescas, IMAR and LARSyS Associated Laboratory, Universidade dos Açores, Horta, Portugal, ²Biology Department, Woods Hole Oceanographic Institution, Woods Hole, USA, and ³Laboratório de Ciências do Mar, Universidade de Évora, Sines, Portugal

Abstract

Cetaceans living in offshore waters are under increasing pressure from anthropogenic activities. Yet, due to the lack of survey effort, relatively little is known about the demography or ecology of these populations. Spatial and temporal distribution of cetaceans in mid-Atlantic waters were investigated using a long term dataset collected from boat surveys and land-based observations around the Azores. From 1999 to 2009, 7307 cetacean schools were sighted during 271,717 km of survey effort. In 4944 h of land-based observations, 2,968 cetacean groups were detected. Twenty-four species were recorded: seven baleen whales, six beaked whales, eight dolphin species, *Physeter macrocephalus*, *Kogia breviceps* and *Kogia sima*. Overall, *Delphinus delphis* was the most frequently sighted species, but its encounter rate decreased in June–November, coinciding with the presence of *Stenella frontalis* in the region. *Tursiops truncatus*, *P. macrocephalus* and *Grampus griseus* were frequently encountered year-round, whereas large baleen whales showed a distinct peak in encounter rates in March–May. Mesoplodonts were fairly common and appear to be present throughout the year. These findings fill in a significant gap in the knowledge of cetaceans occurring in a poorly studied region of the North Atlantic, providing much needed data to inform management initiatives.

Key words: Cetaceans, spatial and temporal distribution, mid-Atlantic waters, sighting surveys

Introduction

Cetacean distribution and relative abundance in offshore waters of the North Atlantic remain largely unknown. Knowledge on the distribution and population size of cetaceans in European Atlantic waters comes mostly from a series of large-scale international surveys. The waters north of 52° were primarily covered by the North Atlantic Sighting Surveys (NASS 1985–2001; Lockyer & Pike 2009). In 1994 and 2005 the continental shelf waters of UK, Ireland, France and Spain were surveyed as part of the SCANS-I and SCANS-II projects (Hammond et al. 2002; SCANS-II 2008) and the area beyond the shelf to about 500 km was surveyed in 2007 by project CODA (CODA 2009). CODA was conducted in coordination with another multinational survey – the Trans North Atlantic Sightings Survey (TNASS) – extending from Norway to the

eastern Canadian seaboard (Lawson & Gosselin 2009). TNASS also took advantage of smaller surveys taking place in the same period in adjacent areas (ICES Redfish, Russian–Norwegian pelagic and ECOMAR surveys, called TNASS survey extensions), representing the largest area ever surveyed synoptically. Since 1992, NOAA periodically conducts broad-scale aerial and vessel surveys over the eastern US continental shelf and slope waters to provide abundance estimates of cetaceans (Waring et al. 2011). None of the aforementioned surveys covered the mid-Atlantic waters (Figure 1). In June–July 2004, the Mid-Atlantic Ridge Ecology Program (MAR-ECO) conducted a multidisciplinary single-leg survey along the Mid-Atlantic Ridge (MAR) from Reykjanes Ridge to north of the Azores, producing the first systematic survey information on cetacean distribution and density in this region (Waring et al. 2008). Despite its importance,

*Correspondence: Mónica A. Silva, Departamento de Oceanografia e Pescas, IMAR and LARSyS Associated Laboratory, Universidade dos Açores, Rua Prof. Doutor Frederico Machado, 9901-862 Horta, Portugal. E-mail: monica@uac.pt, msilva@whoi.edu

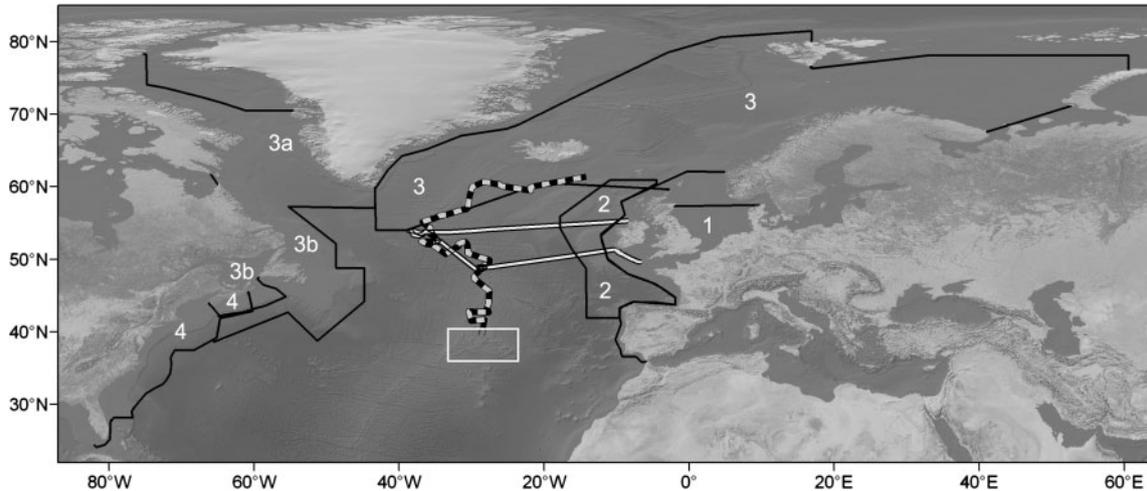


Figure 1. Location of the study area around the Archipelago of the Azores (white box) and geographic coverage of the main large-scale surveys conducted in the North Atlantic: 1, SCANS-II; 2, CODA; 3, TNASS survey (extensions 3a, western Greenland; 3b, Canada); 4, NOAA/NMFS. The single-leg surveys are shown as strips: black and white, MAR-ECO; white, ECOMAR.

this survey provided only a snapshot of cetacean distribution along the MAR in early summer.

The limited survey effort in mid-Atlantic waters, particularly outside summer months, severely restricts our knowledge of the full geographic range of most cetacean species within the North Atlantic and inhibits our understanding of their seasonal movements within this range. Nevertheless, surveys specifically designed to produce abundance estimates of cetaceans are costly and surveying vast areas of offshore waters is hampered by logistic and operational difficulties. The use of other long-term data sets constitutes a valuable alternative for investigating how cetaceans use these remote areas.

The Archipelago of the Azores is located in the middle of the North Atlantic, approximately 1500 km from Europe and 3000 km from the US. Apart from a sighting survey conducted in the summer–autumn of 1999–2000 (Silva et al. 2003) there have been no attempts to study the at-sea distribution of cetaceans around the Azores. At present, knowledge on their occurrence in the region comes mostly from strandings and incidental sightings. These data suggest the area holds a high diversity of cetaceans, with 28 species documented so far (reviewed in Prieto & Silva 2010; Silva et al. 2012). This article analyses 11 years of data collected during sighting surveys and nearly 5 years of data from land-based observations to provide the first assessment of the spatial and temporal distribution patterns of cetaceans around the Azores. In addition, we reviewed stranding records to document the occurrence of species that were rarely observed or those difficult to identify at sea. This information will contribute to fill in a major gap on our current knowledge of cetaceans occurring in an under-sampled region of the North Atlantic.

Material and methods

Study area

Data analysed in this study were collected in an area of 258,228 km² around the Azores, between 36°30'N 24°30'W and 40°00'N 31°45'W (Figure 2). The archipelago is composed of nine volcanic islands divided into three groups (eastern, central and western) separated by deep waters (>2000 m). Shallow waters (<200 m) occur only at very short distances from the coast. The study area comprises a wide range of habitat types, including narrow island shelves, steep island slopes, shallow seamounts, submarine canyons, and vast areas of abyssal plain. The region is largely dominated by two eastward flows generating from the Gulf Stream: the cold southern branch of the North Atlantic Current that crosses the MAR to the north of the Azores (45–48°N), and the warm Azores Front/Current system, a quasi-permanent feature located south of the islands (34–36°N). Average sea surface temperature varies from 15 to 20°C in winter and 20–25°C in summer.

Data sources

Boat surveys. We analysed sighting and search effort data collected between 1999 and 2009 from dedicated cetacean surveys as well as platforms of opportunity. Details of the methodology of these surveys are given elsewhere (Silva et al. 2002, 2003, 2009). Surveys were classified into three categories according to the methodology and platforms used (Table I).

The Department of Oceanography and Fisheries of the University of the Azores (DOP/UAç) has

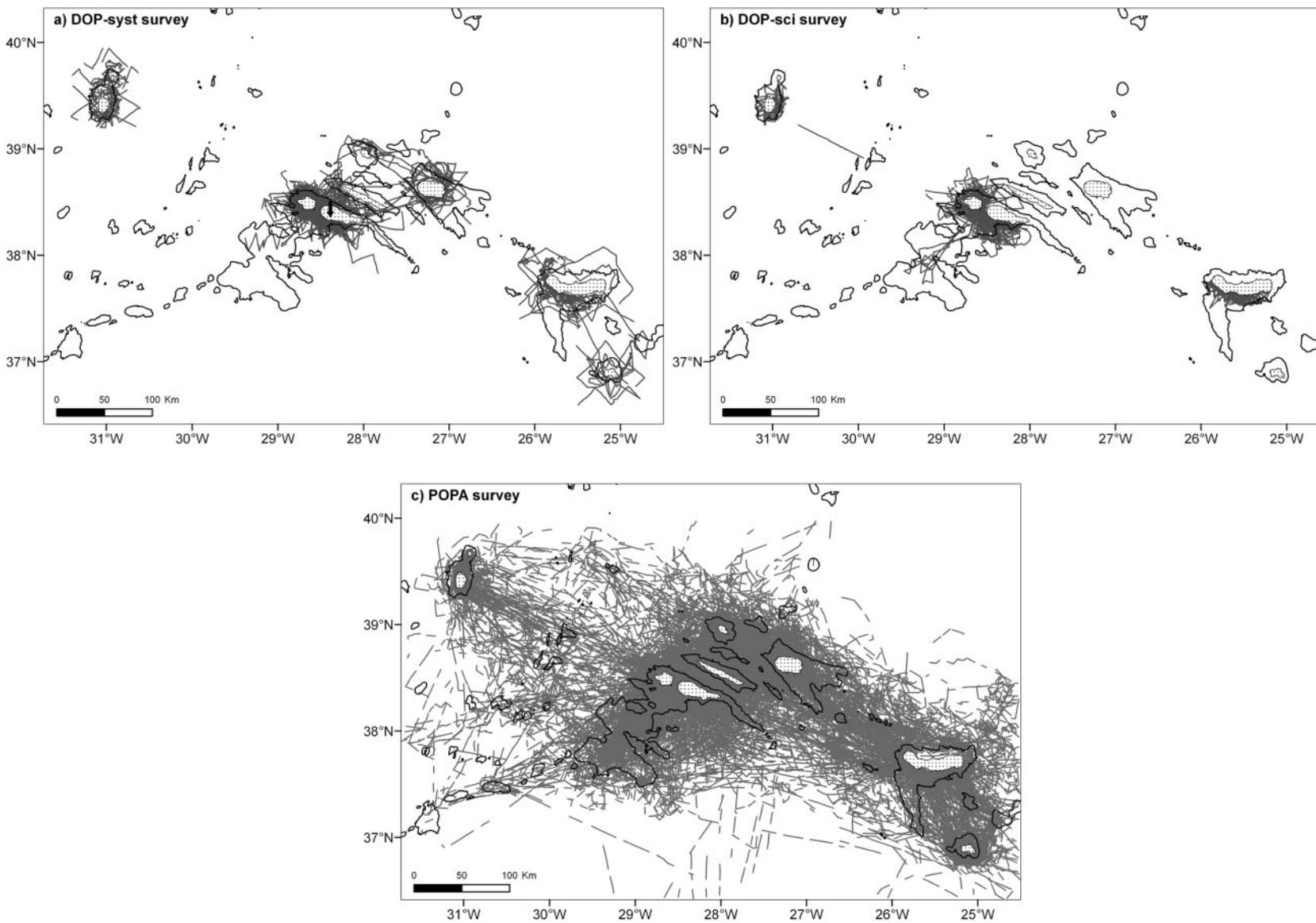


Figure 2. On-effort transect lines covered by: (a) DOP-syst survey (1999–2004); (b) DOP-sci survey (2005–2009); (c) POPA survey (2001–2009). The black arrow in (a) marks the location of the whaling lookout on Pico Island from where the land-based observations were made. The 1000-m isobath is shown as a solid line.

Table I. Methodology and design of boat surveys.

Survey name	Survey type	Survey design	Study period	Study area	Platform type	Observers
DOP-syst	Systematic survey for cetaceans	Zigzag transects up to 28 km of island/seamount	May–September 2000	All islands and nearby seamounts	12-m motor boat	3–4
		Alongshore at 1 km or zigzag transects up to 8 km of island/seamount	Year-round 1999–2004	Islands and seamounts in central group	12-m motor boat 5-m RHIB	3–4
DOP-sci	Scientific survey to study cetacean ecology	No predetermined track	February–October 2005–2009	All islands and nearby seamounts	12-m motor boat 5-m RHIB	2–4
POPA	Fisheries observer programme	No predetermined track	May–October 2001–2009	All islands and nearby seamounts	20-m fishing vessel	1

conducted systematic and opportunistic surveys for cetaceans in the scope of different research programmes. DOP systematic (hereafter called DOP-syst) surveys were carried out from 1999 to 2004 along fixed-line transects and were designed to ensure consistent coverage within the study area and to search in all types of habitat. Between 2005 and 2009, DOP/UAç conducted regular scientific surveys to study different aspects of the ecology of cetacean species. DOP scientific (DOP-sci) surveys used the same dedicated sighting protocols as DOP-syst surveys, but data were not collected along predetermined tracks.

The Azorean Fisheries Observer Program (POPA) places trained observers aboard tuna-fishing vessels to monitor and collect information on fishing operations and on the presence and behaviour of cetaceans, seabirds and turtles. Cetacean surveying is conducted only when the vessel is travelling or searching for tuna. The observer searches for cetaceans from the ship's flying bridge (8 m above the water) by naked eye and using binoculars.

We analysed only sightings from surveys collected during on-effort periods conducted in sea states on the Beaufort scale of ≤ 3 .

Land-based observations. Data from boat-based surveys were insufficient to characterize the occurrence of some species during winter; therefore, we analysed information collected year-round from a vantage point by an experienced lookout that worked for whale-watching companies. The vantage point is situated on the southern coast of Pico Island (Figure 2a). The lookout searched an area of approximately 800 km², extending from the shoreline to 22 km offshore and to a water depth of 1650 m, using 15 × 80 mm binoculars. Observations were carried out from May 1999 to March 2001, and January 2008 to September 2009. Data on sighting effort and environmental conditions were collected for each period of continuous observation (ranging from 1 to 3 h) and whenever conditions changed. For each sighting

the initial time and approximate location, species, estimated number of individuals, behaviour and composition of the school were recorded. Data collected in Beaufort wind speed > 3 were excluded from the analysis.

Stranding records

We reviewed the stranding database maintained by the Regional Environment Directorate to document the occurrence of species that were infrequently sighted or difficult to identify at sea and complement information on temporal patterns of occurrence of other species. The stranding database contains records from 1990 onwards, although information from early years (until 1998) was not recorded systematically.

Data analysis

Due to the methodological differences outlined above, data from different sources were analysed separately to avoid introducing further bias. For each type of boat survey, species encounter rates were computed as the number of sightings divided by the number of kilometres searched in Beaufort scale ≤ 3 , yielding the number of schools sighted/100 km surveyed. Fishing vessels occasionally operated together, resulting in a duplication of POPA survey tracks in the same area and day. When this happened, only data from the longest survey track were analysed. For land-based observations, species encounter rates were estimated as the number of schools sighted divided by the number of hours searched (scaled by 100). Days with < 1 h of effort were excluded, as this was the minimum time required to scan the observation area.

Spatial and temporal variation in encounter rates, depth conditions associated with species occurrence and school size statistics were examined in detail only for the most common species. Spatial distribution was investigated by dividing the study area into

Table II. Mean, standard deviation (SD) and range of school size of cetaceans recorded during DOP-syst and DOP-sci surveys.

Species	Mean	SD	Range
<i>Megaptera novaeangliae</i>	1.0	0	1
<i>Balaenoptera acutorostrata</i>	1.0	0	1
<i>Balaenoptera edeni</i>	2.0	0	2
<i>Balaenoptera borealis</i>	3.1	1.5	1–7
<i>Balaenoptera physalus</i>	2.5	1.6	1–7
<i>Balaenoptera musculus</i>	1.7	0.7	1–3
<i>Physeter macrocephalus</i>	4.4	3.6	1–17
<i>Kogia</i> spp.	1.0	0	1
<i>Ziphius cavirostris</i>	2.1	0.9	1–4
<i>Hyperoodon ampullatus</i>	5.7	2.0	1–13
<i>Mesoplodon</i> spp.	3.9	1.9	1–8
<i>Tursiops truncatus</i>	18.3	23.5	1–250
<i>Stenella frontalis</i>	41.7	55.9	1–500
<i>Stenella coeruleoalba</i>	43.3	31.4	3–150
<i>Delphinus delphis</i>	27.2	35.9	1–500
<i>Grampus griseus</i>	10.3	7.9	1–45
<i>Pseudorca crassidens</i>	10.4	6.1	3–20
<i>Globicephala macrorhynchus</i>	9.4	5.1	3–18

a 10-min grid and calculating an encounter rate for each square. Encounter rate maps were obtained using information from POPA surveys as these provided the widest distribution of search effort within the study area and the longest time span. A Digital Terrain Model of seabed, generated from a

bathymetric data set with a resolution of 1-min, was used to extract water depth at each POPA sighting. Monthly encounter rates were calculated using data from year-round DOP-syst surveys and land-based observations. Information from DOP-syst and DOP-sci surveys was used to estimate mean and range of school sizes for 18 cetaceans (Table II).

Results

Effort and sightings by data source

The tracks of DOP-syst, DOP-sci and POPA surveys are shown in Figure 2. DOP-syst surveys covered the entire study area, but effort was mostly concentrated around islands and seamounts on the central group of islands (Figure 2a). A total of 1021 sightings of 16 species and 2 genera (*Kogia* and *Mesoplodon*) were recorded for 25,930 km of effort (Table III). *Delphinus delphis* Linnaeus, 1758, *Tursiops truncatus* Montagu, 1821, *Stenella frontalis* Cuvier, 1829, *Grampus griseus* G. Cuvier, 1812 and *Physeter macrocephalus* Linnaeus, 1758 were frequently sighted during DOP-syst surveys.

Fourteen species and one genus were identified during 15,145 km of search effort conducted during DOP-sci surveys (Figure 2b). Delphinids were the

Table III. Number of on-effort sightings and estimated encounter rates (ER) for cetaceans observed during boat surveys (DOP-syst (1999–2004), DOP-sci (2005–2009), POPA (2001–2009)) and land-based observations (1999–2000, 2008–2009). Species encounter rates were obtained by dividing the number of schools sighted by the survey effort (100 km for boat surveys and 100 h for land-based observations).

Species	DOP-syst		DOP-sci		POPA		Land-based	
	N	ER	N	ER	N	ER	N	ER
<i>Eubalaena glacialis</i> (Müller, 1776)							1	0.02
<i>Megaptera novaeangliae</i> (Borowski, 1781)	3	0.01			7	0.00	7	0.14
<i>Balaenoptera acutorostrata</i> Lacépède, 1804	3	0.01	2	0.01	28	0.01	9	0.18
<i>Balaenoptera edeni</i> Anderson, 1878	2	0.01						
<i>Balaenoptera borealis</i> Lesson, 1828	3	0.01	24	0.16	86	0.04	73	1.48
<i>Balaenoptera physalus</i> (Linnaeus, 1758)	11	0.04	8	0.05	115	0.05	56	1.13
<i>Balaenoptera musculus</i> (Linnaeus, 1758)	2	0.01	16	0.11	37	0.02	108	2.18
<i>Physeter macrocephalus</i> Linnaeus, 1758	90	0.35	67	0.44	503	0.22	460	9.30
<i>Kogia</i> spp.	1	0.00			1	0.00		
<i>Ziphius cavirostris</i> Cuvier, 1823	6	0.02	5	0.03	28	0.01	4	0.08
<i>Hyperoodon ampullatus</i> (Forster, 1770)	9	0.03	7	0.05	79	0.03	40	0.81
<i>Mesoplodon</i> spp.	37	0.14	20	0.13	153	0.07	100	2.02
<i>Tursiops truncatus</i> (Montagu, 1821)	160	0.62	88	0.58	433	0.19	376	7.60
<i>Stenella frontalis</i> (Cuvier, 1829)	143	0.55	127	0.84	1076	0.47	53	1.07
<i>Stenella coeruleoalba</i> (Meyen, 1833)	45	0.17	26	0.17	108	0.05	15	0.30
<i>Delphinus delphis</i> Linnaeus, 1758	317	1.22	121	0.80	2253	0.98	243	4.91
<i>Grampus griseus</i> (G. Cuvier, 1812)	105	0.40	44	0.29	244	0.11	329	6.65
<i>Pseudorca crassidens</i> (Owen, 1846)	3	0.01	2	0.01	43	0.02	30	0.61
<i>Orcinus orca</i> (Linnaeus, 1758)					17	0.01	10	0.20
<i>Globicephala macrorhynchus</i> Gray, 1846	9	0.03	4	0.03				
<i>Globicephala</i> spp.					101	0.04	113	2.29
Unidentified baleen whale	2	0.01	2	0.01	106	0.05	179	3.62
Unidentified beaked whale	9	0.03	8	0.05	3	0.00	71	1.44
Unidentified dolphin	41	0.16	21	0.14	246	0.11	682	13.79
Unidentified cetacean	20	0.08	8	0.05	19	0.01	9	0.18
Total	1021	3.94	600	3.96	5686	2.47	2968	60.03

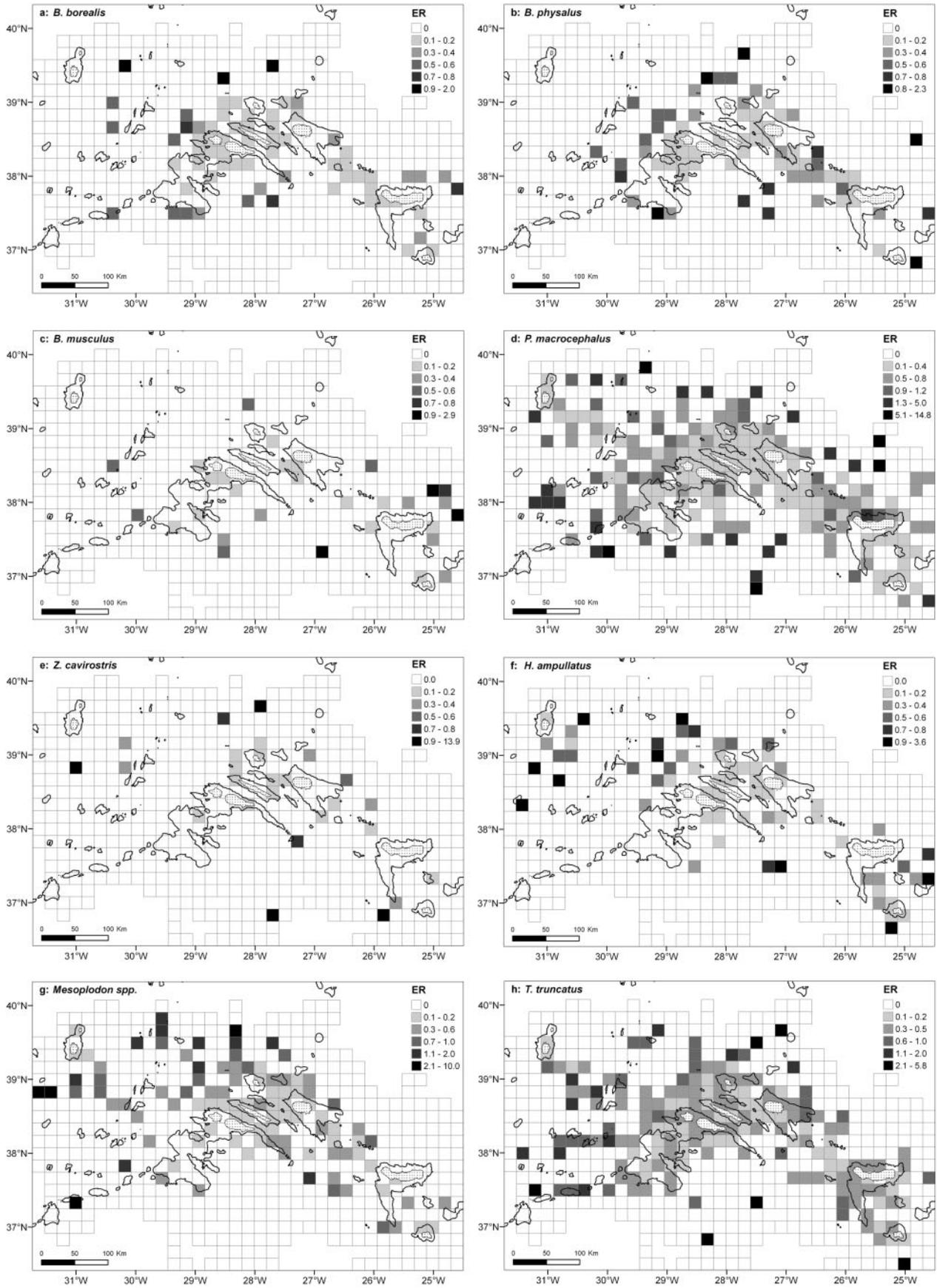


Figure 3. Encounter rates (sightings/100 km) of cetaceans calculated from data collected during POPA survey (2001–2009). The 1000-m isobath is shown as a solid line.

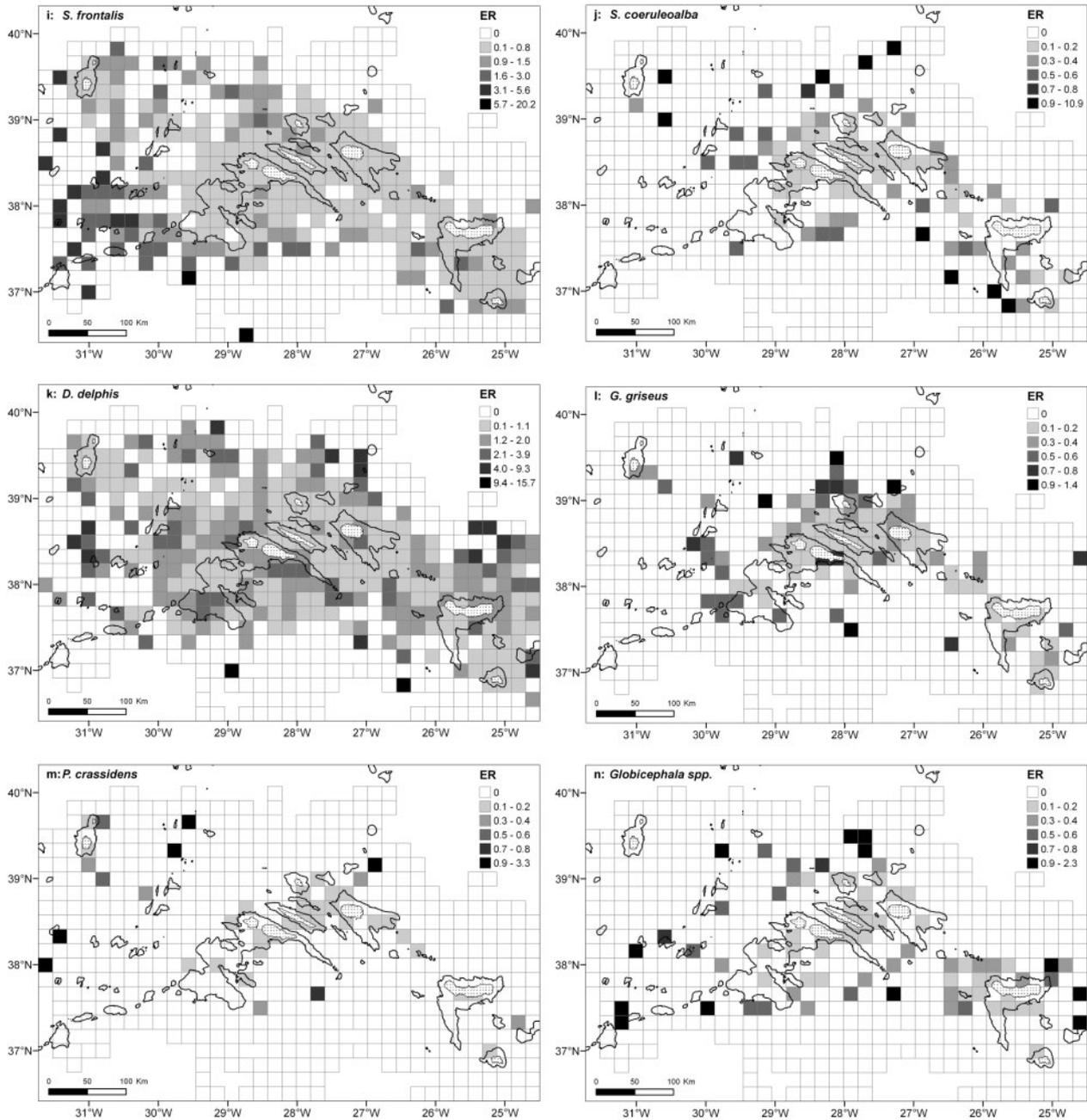


Figure 3. (continued)

most frequently encountered group (72% of total sightings), followed by *P. macrocephalus* (11%), baleen whales (9%) and beaked whales (8%) (Table III).

POPA survey tracks extended farther offshore, providing a more complete coverage of the study area (Figure 2c). POPA surveys totalled 230,642 km of on-effort segments, during which 5686 sightings of 15 species and 3 genera (*Kogia*, *Mesoplodon* and *Globicephala*) were made (Table III). *Delphinus delphis*, *S. frontalis* and *P. macrocephalus* accounted for 67% of all sightings, whereas the sum of sightings of *Kogia* spp., *Megaptera novaeangliae* Borowski,

1781, *Orcinus orca* Linnaeus, 1758, *Balaenoptera acutorostrata* Lacépède, 1804 and *Ziphius cavirostris* Cuvier, 1823 did not reach 2%.

The lookout made 948 days of observations, representing 70% of the days during the study period. In 4944 h of monitoring 2968 cetacean schools were detected, yielding 60 sightings per 100 observation hours (Table III). A large number ($n = 682$) of sightings were classified as 'unidentified dolphin' due to the difficulty in distinguishing between delphinids of similar size. About 85% of these sightings corresponded to one of the smallest dolphins (*S. frontalis*, *Stenella coeruleoalba* Meyen,

1833 or *D. delphis*) and 6% were either of *T. truncatus* or *G. griseus*. In addition to the former species, *P. macrocephalus*, *Balaenoptera musculus* Linnaeus, 1758, and the genera *Globicephala* and *Mesoplodon* were commonly recorded during land-based observations (Table III).

Spatial patterns of occurrence

Encounter rate maps and distribution in relation to water depth of species frequently sighted during POPA surveys are presented in Figures 3 and 4, respectively.

Large baleen whales (*Balaenoptera borealis* Lesson, 1828, *B. physalus* Linnaeus, 1758 and *B. musculus*) were never encountered in the western-most part of the study area and the highest encounter rates occurred along the banks off the central islands and in open waters between groups of islands (Figure 3a–c). Sightings of large whales generally occurred seaward of the 1000-m isobath, but compared to the other species *B. musculus* tended to be seen over deeper waters (Figure 4). Sperm whales were found in all groups of islands, but seemed more abundant in the deep waters (mean = 1472 m) between the western and central islands and north of the eastern islands (Figures 3d and 4). *Ziphius cavirostris*, *Hyperoodon ampullatus* Forster, 1770 and *Mesoplodon* spp. were also commonly recorded over deep open waters located to the north and west of

the central islands (Figures 3e–g and 4). Delphinids were widely distributed in the study area and occupied a broad range of habitat types, but there were some differences with respect to water depth preferences (Figures 3h–m and 4). *Tursiops truncatus* tended to be seen over shallower waters (median = 673 m), whereas *Stenella coeruleoalba* and *Globicephala* spp. were mainly encountered in waters deeper than 1000 m. Sightings of other delphinids tended to occur at intermediate water depths (Figure 4).

Seasonality

Figure 5 shows the monthly effort from DOP-syst surveys and land-based observations and the seasonal patterns of the most commonly sighted cetaceans. Stranding data presented in Table IV complement information on cetaceans' temporal distribution provided by the sighting surveys and land-based observations, and adds to the number of species reported in Table III.

Balaenoptera borealis and *Balaenoptera musculus* were frequently sighted during boat surveys and land-based observations from spring to early summer, but reports of their presence after August were rare. Encounter rates of *Balaenoptera physalus* calculated from DOP-syst surveys were also higher in May and June, but land-based records showed a wider period of occurrence spanning from January to

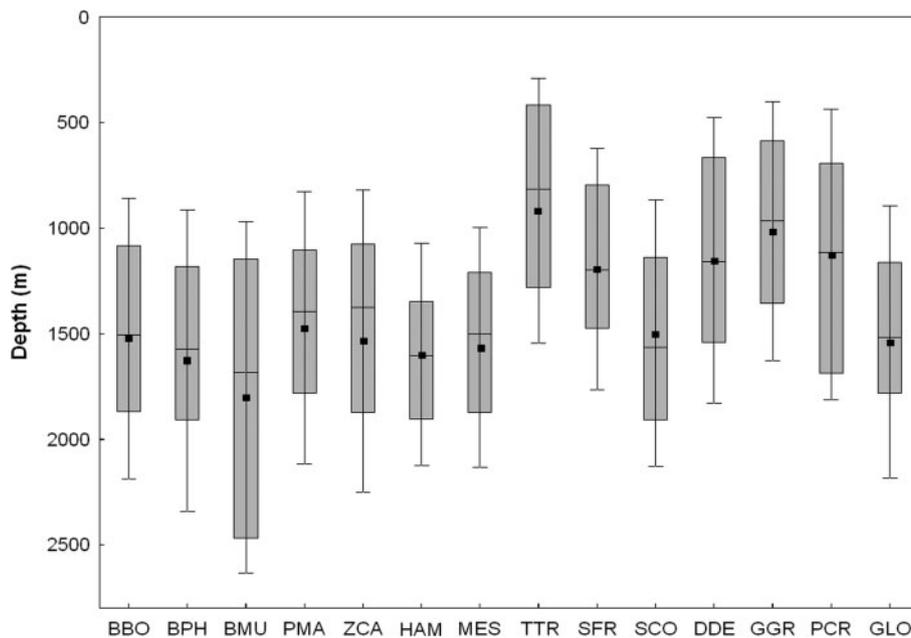


Figure 4. Mean (dot), median (line), interquartile range (grey box) and standard deviation (whiskers) of depth for each species, based on sightings recorded during POPA survey (2001–2009). BBO, *Balaenoptera borealis*; BPH, *Balaenoptera physalus*; BMU, *Balaenoptera musculus*; PMA, *Physeter macrocephalus*; ZCA, *Ziphius cavirostris*; HAM, *Hyperoodon ampullatus*; MES, *Mesoplodon* spp.; TTR, *Tursiops truncatus*; SFR, *Stenella frontalis*; SCO, *Stenella coeruleoalba*; DDE, *Delphinus delphis*; GGR, *Grampus griseus*; PCR, *Pseudorca crassidens*; GLO, *Globicephala* spp.

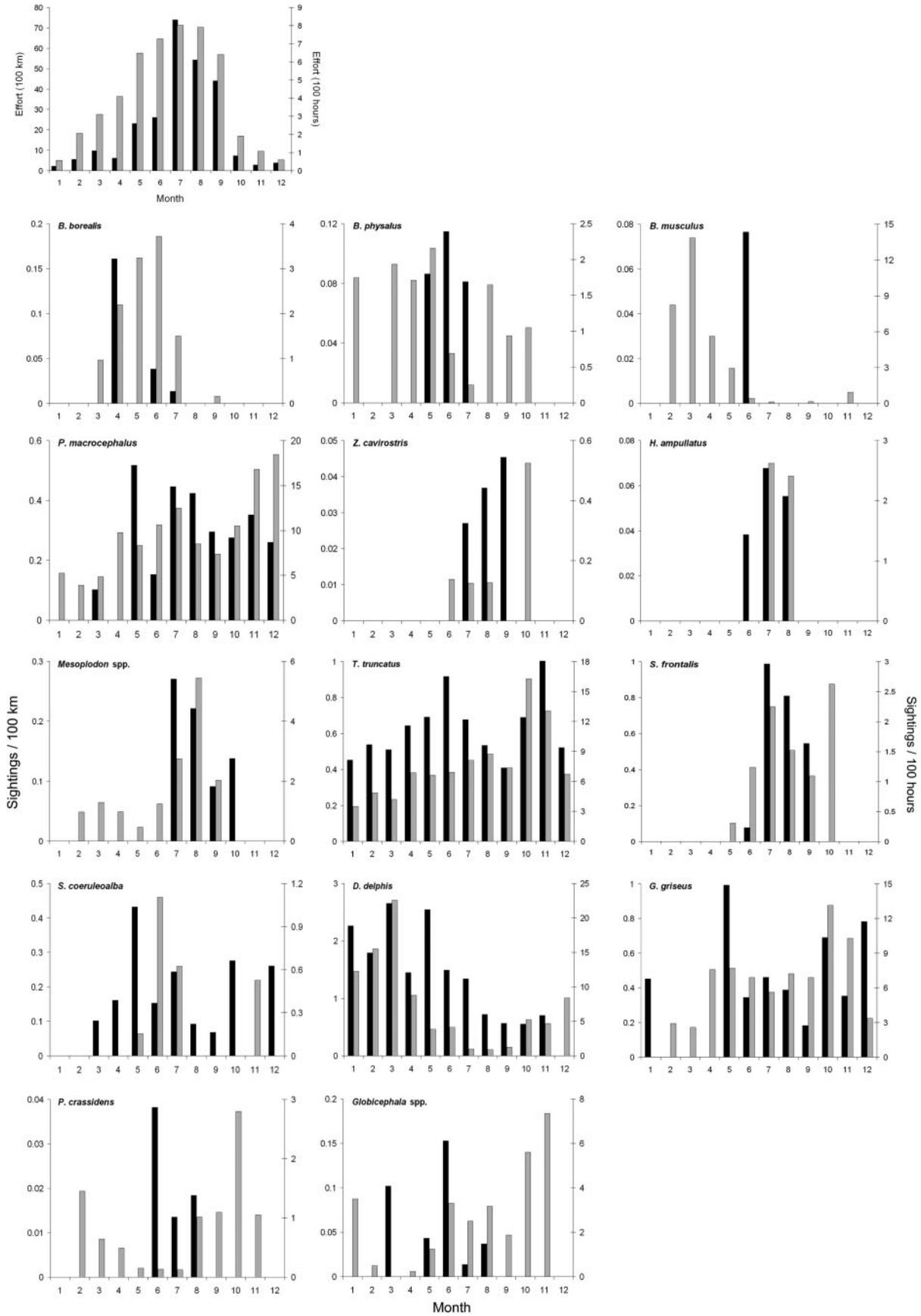


Figure 5. Observation effort (uppermost graph) and mean encounter rate (all other graphs) per month of cetaceans from DOP-syst survey (1999–2004; black bars) and land-based observations (1999–2000, 2008–2009; grey bars).

Table IV. Cetaceans stranded per month from 1990 to 2010.

Species	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Megaptera novaeangliae</i>			1									
<i>Balaenoptera acutorostrata</i>		2		1	1			1	1	1		
<i>Balaenoptera borealis</i>		1										
<i>Balaenoptera physalus</i>			1		1	1	1					
<i>Physeter macrocephalus</i>	8	5	1	5	1	3	5	10	3	2	1	1
<i>Kogia breviceps</i>							1	1		1		1
<i>Kogia sima</i>						1			1			
<i>Kogia</i> spp.	1	1	1			1			1		1	
<i>Ziphius cavirostris</i>	1	1	1			1			1		1	
<i>Mesoplodon densirostris</i>			2									
<i>Mesoplodon bidens</i>						4	12	2				
<i>Mesoplodon europaeus</i>								1				
<i>Mesoplodon mirus</i>							1					
<i>Mesoplodon</i> spp.			1				2	1				
<i>Tursiops truncatus</i>	1	1	2		1	2		1	3	1		
<i>Stenella frontalis</i>		1				1		2	1			
<i>Stenella coeruleoalba</i>	3		3	4		4	2	2	1	1	1	
<i>Delphinus delphis</i>	8	10	12	7	6	2	5	4	1		1	1
<i>Grampus griseus</i>		3						1			1	
<i>Pseudorca crassidens</i>			1									
<i>Orcinus orca</i>				1	1		1		1			1
<i>Globicephala macrorhynchus</i>									1			1
<i>Globicephala</i> sp.			1									

October. *Physeter macrocephalus* were recorded during land-based observations from January throughout December. About 76% of the sightings of the species made during DOP-syst surveys comprised groups of adult females, subadults and calves, and 8% were of adult males, observed singly or in aggregations of up to seven individuals. The remaining sightings consisted of both female groups and adult males. All population segments and types of aggregation occurred year-round. Calves were frequently observed throughout the year, but the proportion of sightings with calves was much higher in August and September. Newborns (<5 m length) were only observed in August and March. Sightings of *Ziphius cavirostris* and *Hyperoodon ampullatus* were restricted to summer and early autumn. A few strandings of *Z. cavirostris* in November, January and March suggest the species may occur year-round. Combining lookout records and survey data, *Mesoplodon* whales were present from February to October, with higher encounter rates in July and August for both data sources.

With the exception of *Stenella frontalis*, the remaining dolphin species were recorded every month either from boat surveys, land observations, or stranded. Their monthly encounter rates varied, but for most species the seasonal pattern was not consistent between years. In *Delphinus delphis*, however, the seasonality trend was evident across years and data sources. This species was recorded year-round but encounter rates decreased significantly

during the summer and autumn months (DOP-syst surveys: $F_{(11,345)} = 4.281$, $P < 0.0001$; land-based observations: $F_{(11,936)} = 13.493$, $P < 0.0001$) (Figure 5). The seasonality of *S. frontalis* was also very noticeable: first sightings dated from early May; highest relative abundance was reached in July/August, depending on year (the peak in land-based encounter rates in October resulted from an unusual number of sightings recorded by the lookout in 2008; exclusion of this year resulted in a peak in sighting rates in July), and by October the species disappeared.

Discussion

Using a combination of data collected during dedicated and opportunistic sighting surveys, land-based monitoring and stranding records, we provide novel information on the spatial and temporal occurrence of cetaceans in mid-Atlantic waters. Care should be taken, however, because methods used in this study are subject to various limitations and biases that may have influenced the patterns of cetacean occurrence described.

Depending on the type of survey and of data collected – incidental sightings, effort-related sightings, or distances and angles to sightings made during on-effort periods – one can determine presence and seasonality of cetaceans, assess their relative abundance, or obtain an estimate of the size of the population in the study area. Evans &

Hammond (2004) provide a useful overview of techniques commonly employed to monitor cetaceans and a critical appraisal of the applicability and limitations of each type of survey data. Here we concentrate on issues which specifically relate to the problems of our survey design and data.

In conventional line-transect sampling, transects must be placed so every point in the study area has the same probability of being sampled (Hammond 2010). The boat surveys used in this work were not designed for the purpose of estimating cetacean abundance and none aimed for equal coverage probability of the area. Even DOP-syst surveys, in which transect lines were placed to sample across all habitats within a fixed distance from the islands, failed to achieve equal coverage probability of the whole research area. Thus, the estimated encounter rates may not be representative for the entire study area and the patterns observed in the encounter rate maps may be an artifact from the uneven distribution of effort, although this was partially dealt with when sightings were divided by line length.

In addition, estimates of encounter rate from each data source were not corrected for factors thought to affect cetacean detectability. The probability of detecting cetaceans is known to decline as a function of distance from the observation platform and to be influenced by species behaviour, school size, vessel characteristics (e.g. platform height and speed), number and experience of observers, and environmental conditions. In line-transect sampling, measurements of the perpendicular distance to observed animals are used to fit a detection function (using factors known to affect detectability as covariates), which is then used to adjust the estimated encounter rates (Hammond 2010). Distance to sightings was not available for any data source used in this study, making it impossible to quantify detection probability and therefore to draw conclusions about species' overall density in the area. For the same reason, encounter rates cannot be used to compare relative abundance among different species. Factors influencing detectability are also likely to vary among surveys, affecting the comparison of encounter rates of a given species across seasons and geographic areas. By using only data collected under Beaufort scale 4 (a threshold commonly used in cetacean sighting surveys) and analysing data from each survey type separately, we were able to reduce some of the bias introduced by variability in sighting conditions within and between surveys. The characteristics of the observation platforms, number of observers or their training did not differ consistently between months or areas. We did not detect, nor are we aware of, substantial changes in species' behaviour or school size over time or space that

might have affected estimates of encounter rate. We're thus convinced that bias arising from differences in detectability among surveys was minimized by the large data set analysed here and did not invalidate the comparison of species' encounter rates among months and areas.

Lack of distance data also hindered application of density surface models that would allow overcoming the problem of unequal coverage probability of survey effort (Hammond 2010). Despite these caveats, the survey data presented here provide important insights into the seasonality and distribution of several cetacean species that would hardly be revealed by a snapshot survey.

We report the occurrence of 24 cetacean species in Azorean waters, including 7 baleen whales, 6 beaked whales, 8 dolphins, *Physeter macrocephalus*, *Kogia breviceps* de Blainville, 1838 and *Kogia sima* Owen, 1866. Habitat heterogeneity is known to be one of the drivers of species diversity and the varied physiography of the region creates a wide range of habitats that allow for the presence of species with distinct preferences. *Tursiops truncatus* was typically found over the island shelves and slopes and around shallow banks, in areas < 700 m deep. In contrast, *Globicephala* spp., *Stenella coeruleoalba*, the large baleen and beaked whales were rarely encountered in water depths < 500 m and were mostly sighted within the 1000–2000 m isobaths. *Grampus griseus*, *Delphinus delphis* and *Pseudorca crassidens* Owen, 1846 were well represented in coastal and offshore waters with intermediate water depths. Future work will examine the habitat preferences of these species in relation to a number of physiographic and oceanographic variables.

Besides increasing habitat diversity, complex seabed topography is also known to enhance biological productivity by upwelling nutrient-rich waters into the photic zone, or by accumulating primary and secondary producers through mechanisms such as topographic blockage, convergence of surface waters, horizontal advection and mixing (Genin 2004). Amid the oligotrophic waters of the central North Atlantic, the greater biological productivity in the vicinity of the Azores likely increases foraging opportunities for cetaceans, thus explaining the diversity of species encountered.

Delphinus delphis was the most frequently sighted species during DOP-syst and POPA surveys. The species was widely distributed in the region, occurring in coastal and offshore waters over a large range of water depths. Although *D. delphis* was present all year round, sightings declined significantly from June to November. Seasonal changes in *D. delphis* abundance and distribution have been reported in the Northwest and Northeast Atlantic, with dolphins

being more northerly and offshore distributed in summer, possibly as a result of a shift in prey distribution (ICES 2009).

Interestingly, *D. delphis* displacement generally coincided with the short period of occurrence of *Stenella frontalis* in the Azores, when sightings of the latter species generally outnumbered those of *D. delphis*. The same phenomenon was reported in Florida and Madeira, where *D. delphis* left the area in summer once *S. frontalis* showed up (Moore 1953; Freitas et al. 2004). The succession of the two species may be related to the warming of water and to its effect on prey distribution. This would mean that *D. delphis* and *S. frontalis* have distinct prey preferences and the former does not feed on whatever prey are available for *S. frontalis* during summer. Temporal segregation of *D. delphis* and *S. frontalis* could also represent a form of ecological separation to reduce competition for limited prey resources. The niche segregation hypothesis cannot be confirmed with the available data and requires further investigation.

Tursiops truncatus and *Grampus griseus* were among the most frequently sighted species in all data sets, occurring primarily in near-shore waters. Both species were observed year-round, but encounter rates varied greatly between months. Photo-identification data showed that in addition to resident populations of both species, a few hundred non-resident dolphins are identified each year in the Azores (Silva et al. 2008; Hartman et al. 2009). Although we cannot rule out the potential effects of variability in survey effort, temporary immigration of a large number of non-resident dolphins into the study area could help to explain fluctuations in the number of sightings per month.

Not surprisingly, the region around the Azores seems to be an important habitat for several species that typically inhabit deep waters. *Physeter macrocephalus* was the third most frequently sighted species during POPA surveys and the fifth during DOP-syst surveys. Groups of females accompanied by juveniles and calves were observed foraging in the area every month. Although each female group remains on average 14.7 days in the Azores (Silva et al. 2006), groups often concentrated in relatively small areas forming feeding aggregations of up to 50 animals. Matthews et al. (2001) estimated that from 1988 to 1994, 400–2200 female and immature *P. macrocephalus* visited the central group of islands every year in spring and summer. Lagged identification rate models applied to more recent data collected in the same area produced an annual estimate of 700 whales (Silva et al. 2006). No data are available from the other islands, but given their widespread distribution, a few thousand sperm

whales might forage in the Azores every year. Our work also gives some support to earlier suggestions that the area is a calving and possibly mating ground for *P. macrocephalus* (Clarke 1956). Although less common than adult females and immature whales, adult males visited the area regularly and were often seen interacting with female groups, suggesting mating may also take place in the Azores. Assuming a gestation of 14–16 months (Best et al. 1984), the highest number of newborns in August points to a peak in breeding activity in April–June, consistent with inferences from whaling data (Clarke 1956).

Beaked whales, especially some *Mesoplodon* species and *Hyperoodon ampullatus*, appear to be fairly common in the Azores. The four *Mesoplodon* species known from the North Atlantic – *M. bidens* Sowerby, 1804, *M. densirostris* de Blainville, 1817, *M. europaeus* Gervais, 1855 and *M. mirus* True, 1913 – were recorded, either by sightings or strandings. Mesoplodonts, unlike *H. ampullatus*, appear to occur all year round in Azorean waters. However, because we chose to group all sightings into a single category, probable species-specific distribution patterns could not be discerned. Still, *M. bidens* was found in greater numbers in the stranding records and was the most frequently encountered *Mesoplodon* at sea. This species is rarely observed off Madeira (Freitas et al. 2004) or in Canary waters (Carrillo et al. 2010) and the Azores may well represent a critical habitat for *M. bidens* at the southern part of its range. The Azores are also located at the southern edge of the distribution of *H. ampullatus*, an inhabitant of North Atlantic subpolar and cold temperate waters (Whitehead & Hooker 2012). Little is known about their movements within this range, but whaling data suggest that *H. ampullatus* summers off Iceland, Greenland and Norway and migrates south in the autumn, returning to higher latitudes in spring (Benjaminsen & Christensen 1972). Further evidence of north–south migratory movements comes from strandings in European waters (MacLeod et al. 2004). *Hyperoodon ampullatus* are seasonal visitors to the Azores, but our results do not support the hypothesis of a general migration to these southerly latitudes in late autumn. Instead, we found a noticeable peak in sightings in July and August and no records after September, which overlaps the known period of occurrence of *H. ampullatus* at higher latitudes (MacLeod et al. 2004). Whitehead & Hooker (2012) recently suggested that rather than a north–south seasonal migration, *H. ampullatus* may make inshore–offshore movements following their prey. This would help explain the discrepancy between our findings and what has been previously suggested. Our study also suggests the Azores may be an area of concentration for this species during

the summer that has not yet been recognized (Whitehead & Hooker 2012).

Balaenopterid whales were never taken by Azorean open-boat whaling in over 150 years of operations and until recently they were considered rare in the region (Clarke 1981; Gordon et al. 1990, 1995). Here we show that *Balaenoptera physalus*, *B. borealis* and *B. musculus* are frequently sighted every year, especially in spring and summer. Land-based observations indicate that these species also occur in the region in late autumn and winter, as has been recently shown for *B. physalus* using passive acoustic data (Silva et al. 2011; Nieukirk et al. 2012), and contradicting previous reports (Visser et al. 2011). Baleen whales are thought to undertake annual migrations between low-latitude wintering grounds and high-latitude summer feeding areas. The timing of their presence at middle latitudes around the Azores is consistent with the notion of a spring migration towards feeding grounds. This is further supported by satellite telemetry studies that showed that *B. borealis* and *B. physalus* travel northwards after leaving the Azores, with sei whales heading to the Labrador Sea (Prieto et al. 2012), and fin whales travelling to eastern Greenland (Silva et al. 2011).

For other cetaceans, the pattern of occurrence was less obvious, either because they only make sporadic or rare incursions to the area, or because of their cryptic habits that makes it difficult to find them at sea. *Stenella coeruleoalba*, *Pseudorca crassidens* and *Globicephala* sp. were regular visitors to the Azores, as shown by the multiple sightings or strandings recorded each year. Yet, encounter rates of these species estimated from land and DOP-syst data varied greatly across months and years, consistent with their transitory presence in the area. Such a pattern of occurrence is in agreement with the oceanic, generally nomadic habits of the three species. Sightings of *Ziphius cavirostris* and *Kogia* spp. at sea were very infrequent, but strandings suggest both taxa are present year-round in the Azores and possibly in higher numbers than revealed by the sighting information. *Balaenoptera acutorostrata*, *Megaptera novaeangliae* and *Orcinus orca* were observed a few times every year, with no apparent seasonal pattern. The sighting database also included a record of an adult female of *Eubalaena glacialis* Müller, 1776 from the western Atlantic population (Silva et al. 2012), and two sightings of a mother–calf pair of *Balaenoptera edeni* Anderson, 1878.

Four species previously reported in the Azores were not recorded in this study. A single *Phocoena phocoena* Linnaeus, 1758 found stranded in 2004 led to the conjecture that a small population would exist in Azorean waters (Barreiros et al. 2006). However,

there is no other record of the species despite years of monitoring in coastal and offshore waters and of a regular whale-watching industry on several islands. Furthermore, *P. phocoena* inhabits coastal waters of cool temperate and subpolar regions and it is unlikely that the Azores are part of its normal range. Conversely, the expected distribution of *Globicephala melas* Traill, 1809 in the Atlantic includes the Azores, even though there are only two confirmed sightings in recent years (Prieto & Fernandes 2007). It remains unclear whether these sightings represent abnormal movements or if the species occurs regularly in the area, having been misidentified as *Globicephala macrorhynchus*. The Azores is located near or at the marginal distribution of some species that may venture into the area sporadically, possibly as a result of temporary oceanographic events. *Steno bredanensis* Lesson, 1828 and *Lagenodelphis hosei* Fraser, 1956 were observed twice in the summers of 1995 and 2008, respectively (Steiner 1995; J.N. Pereira, pers. commun.). Both species are found primarily in open waters and around oceanic islands in tropical to warm temperate waters. Although the Azores are slightly north of their usual range, their presence in this region in summertime when water temperatures reach 25°C is not totally surprising.

Relatively little is known about the stock structure of cetaceans in offshore areas, but limited data on the movements of some species suggest that cetaceans from both sides of the Atlantic may range to the Azores. At least part of the population of *B. borealis* that forages in the Labrador Sea migrates through the archipelago during spring (Prieto et al. 2012); the *E. glacialis* sighted in the Azores belonged to the western population (Silva et al. 2012); also, an *O. orca* was tracked from eastern Canada to near the Azores (Matthews et al. 2011). On the other hand, *P. macrocephalus* are known to move between the Azores and Iceland, Norway or the Canary islands (Steiner et al. 2012); *M. novaeangliae* have been matched to whales photographed in Cape Verde (Wenzel et al. 2009) and *B. physalus* fitted with satellite tags travelled to eastern Greenland (Silva et al. 2011). Thus, our findings are relevant not only at a regional level, but fill in data gaps in the knowledge of the movements and ecology of several wide-ranging species.

Conclusions

Notwithstanding potential bias limiting an unambiguous interpretation of distribution patterns here depicted, our work indicates that the waters around the Azores provide important habitats for a wide diversity of cetacean species. *Delphinus delphis*, *Tursiops truncatus*, *Physeter macrocephalus* and *Grampus*

griseus were the most commonly encountered species and are year-round inhabitants. Others, like *Stenella frontalis*, *Balaenoptera borealis*, *B. physalus* and *B. musculus*, are seasonal but regular visitors. The deep waters around the archipelago may be of particular significance for beaked whales, especially *Mesoplodon* whales. With a few exceptions (e.g. Bay of Biscay and the Canaries), *Mesoplodon* are rarely sighted at sea in most areas of the North Atlantic (MacLeod & Mitchell 2006). The compiled sighting data place *Mesoplodon* spp. among the most frequently observed cetaceans in the Azores.

Cetaceans living in offshore waters of the North Atlantic are under increasing pressure from several potential stressors, including intense shipping traffic, military exercises and seismic surveys for oil and gas exploration and for marine research. Information on population size and habitat use of cetaceans is urgently needed for assessing the potential adverse effects of human activities and for proposing appropriate measures to manage these activities.

Our study illustrates the potential of using alternative sources of information to obtain meaningful population and ecological data, when data from systematic surveys are not available. Fisheries observer programmes are a cost-effective means to monitor cetaceans over wide areas on a long-term basis. With a few changes in the sampling protocol, POPA surveys might yield abundance estimates for cetaceans in the Azores. If data on distances are available, estimates of cetacean density along transects calculated through line-transect methods can be modelled as a function of spatial and environmental covariates to predict density for the entire survey area. Moreover, detection functions derived from future surveys might be used to estimate detection probability for POPA surveys without distance data, based on values of covariates (Paxton et al. 2011).

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