SUMMER DISTRIBUTION AND RELATIVE ABUNDANCE OF DELPHINIDS IN THE MEDITERRANEAN SEA

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RÉSUMÉ. — *Distribution estivale et abondance relative des Delphinidés en Méditerranée.* — Nous avons étudié la distribution et l'abondance relative des delphinidés de Méditerranée durant les périodes estivales de 1997 à 2001. Des prospections avec un bateau de 12 mètres ont été effectuées sur un espace compris entre Gibraltar et la Turquie, pour un échantillonnage effectif total de 16 008 kilomètres. Le protocole de terrain a été constant — échantillonnage aléatoire à 6 noeuds de moyenne — ainsi que la majorité de l'équipage scientifique : trois observateurs et un secrétaire étaient en permanence en poste et couvraient le secteur avant dès que les conditions d'observation étaient bonnes (vent faible, lumière suffisante). Nous avons testé la cohérence des performances de détection en fonction des conditions d'observation. Pour l'analyse, sept régions ont été délimitées : la mer d'Alboran, le bassin sud-occidental, le bassin nord-occidental, la mer Tyrrhénienne septentrionale et méridionale, la mer Ionienne et le bassin Levantin. Le Grand Dauphin a été observé 25 fois principalement en zone côtière, le Dauphin commun 33 fois dans des secteurs de profondeur modérée, le Dauphin de Risso 19 fois, souvent sur des secteurs de talus, et le Globicéphale noir n'a été détecté qu'à 8 reprises, uniquement dans le bassin occidental. L'espèce la plus commune a été le Dauphin bleu et blanc (294 observations) vu aussi bien en zone péri-côtière qu'au grand large, et dans toutes les régions. La diversité de peuplement a été plus élevée à l'Ouest qu'à l'Est. Les différentes espèces se rencontrent dans des habitats similaires pour les deux bassins de la Méditerranée. L'abondance relative a été minimale dans le bassin Levantin (0,14 dauphin/km), les autres régions faiblement ou moyennement peuplées étant la mer Ionienne, la mer Tyrrhénienne et le bassin sud-occidental (fourchette de 0,33 à 0,53 dauphin/km). Les abondances relatives élevées ont été obtenues dans le bassin nord-occidental (0,76 dauphin/km) et en mer d'Alboran (1,11 dauphin/km). L'abondance relative est cohérente avec les productions primaires calculées dans la littérature, à partir de donnéees satellitaires SeaWifs. Cette étude permet pour la première fois de disposer de résultats comparatifs sur les peuplements de dauphins à l'échelle de la mer Méditerranée.

SUMMARY. — The summer distribution and relative abundance of delphinids in the Mediterranean Sea was investigated. Field surveys took place in 1997, 1998, 1999, 2000 and 2001 between 19 June and 14 August in a 12 meter motor-sailer, at a mean speed of 6 knots on zig-zag lines. The effective sampling effort totalled 16 008 kilometers during which 379 on-effort delphinid sightings were obtained on five species. Seven regions were retained for analysis: the Levantine basin, the Ionian Sea, the southern and northern Tyrrhenian Sea, northwestern basin, the southwestern basin and the Alboran Sea. The consistency of detection width with different sighting conditions was tested. Comparative distribution was expressed as mean bottom depth and distance-to-shore. School sighting rates and sighting rates for individuals (SRI) were calculated for each region. The Bottlenose Dolphin (25 sightings) was found predominantly coastal, the Striped Dolphin (294 sight.) had a wide distribution in water deeper than 200 m, while the Common Dolphin (33 sight.) had a preference for waters shallower than 1,000 m. Both Risso's Dolphin (19 sight.) and Long-finned Pilot Whale (8 sight.) shared the slope and open sea areas. The sighting rates for individuals varied from a lowest value of 0.14 individual/km obtained in Levantine region, low to medium SRI in the Ionian, southern Tyrrhenian Sea, northern Tyrrhenian Sea and southwestern basin (range 0.33-0.53 ind./km). Higher SRI was observed in the northwestern basin (0.76 ind./km) and in the Alboran Sea (1.11 ind./km). Our results were in agreement with existing lite-

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rature and showed a consistency of species distribution across different regions of the western and eastern Mediterranean. The global delphinid relative abundance corresponded to the gradient in primary production, as shown in the literature from satellite data. This is the first study with comparative data on delphinids in the whole Mediterranean Sea.

From an oceanographic point of view, the Mediterranean Sea is formed by two main basins (Nielsen, 1912): the western basin (from Gibraltar to Sicily, including the Tyrrhenian Sea) and the eastern basin (regions east of Sicily). The Tyrrhenian Sea is commonly considered a distinct entity, because it is semi-enclosed between the islands of Corsica, Sardinia and Sicily, and mainland Italy (Fig. 1). Results from satellite data show the eastern basin features 30% less primary production than western basin regions, in particular the Alboran Sea and northwestern basin (Bosc *et al*., 2004).

Available survey results on cetaceans in the Mediterranean Sea mainly focused on the western basin, the immediate surroundings of Italy and, to a lesser extent, western Greece. A single basin-wide study enabled distribution and abundance estimates for the Striped Dolphin *Stenella coeruleoalba* and Short-beaked Common Dolphin *Delphinus delphis* (Forcada *et al.,* 1998) to be released for the western basin. The social distribution and behaviour of the Sperm Whale (*Physeter macrocephalus*) was studied in both eastern and western basins (Drouot *et al*., 2004). Researches in the northwestern basin mostly focused on the Striped Dolphin and the Fin Whale *Balaenoptera physalus* (Forcada *et al.,* 1995; Gannier, 1997a, 1998a), other « common » species such as the Risso's Dolphin (*Grampus griseus*), the Long-finned Pilot Whale (*Globicephala melas*), the Common Dolphin, the Bottlenose Dolphin (*Tursiops truncatus*), and the Cuvier's Beaked Whale (*Ziphius cavirostris*) receiving less attention (Duguy *et al*., 1983; Duguy, 1991). Those species remained poorly known in terms of global distribution and abundance, even in the western basin, some knowledge being gained on their respective habitat (Notarbartolo di Sciara *et al.,* 1993; Gannier, 1998b) in areas such as the northeastern Alboran Sea (Cañadas *et al*., 2002) or central Tyrrhenian Sea (Marini *et al.,* 1996). Large scale distribution studies were restricted to waters surrounding Italy (Notarbartolo di Sciara *et al.,* 1993) or in the western basin (Gannier, 1995), and were not carried out with systematic sampling protocoles. Some other sighting programs enabled data to be gained in areas such as the northeastern Ionian Sea (Politi *et al.,* 1994), the central Aegean Sea (Marini *et al.,* 1995) or the southern Tyrrhenian Sea (Mussi *et al.,* 1998), but did not provide effort-corrected results. So far, the only attempt to draw a general picture of cetacean occurrence in the Mediterranean Sea was based on sighting reports from various sources (Anonymous, 1995), but lacked reference to prospection effort.

Our study attempted to assess the distribution and relative abundance of cetaceans in the western and eastern Mediterranean Sea from a series of five small boat summer surveys in an area ranging from Gibraltar (5˚W) to Rhodes (29˚E) and extending over 9˚ in latitude. This paper deals with visual sightings of delphinids only, large whales having been accounted for separately (Gannier *et al*., 2002; Gannier *et al*., in print).

MATERIAL AND METHODS

Study area

The surveys covered seven regions of the Mediterranean Sea encompassing a total area of 1,009,000 km^2: the northwestern basin (44˚ to 41˚ N and 3˚ to 9˚30 E), the southwestern basin (41˚ to 35˚ N and 0˚ to 9˚30 E), the Alboran Sea (0˚ to 5˚ W), the northern Tyrrhenian Sea (41˚ to 43˚ N and 9˚30 to 13˚E), the southern Tyrrhenian Sea (38˚ to 41˚ N and 9˚30 to 16˚ E), the Ionian Sea (38˚30' to 36˚ N and 15˚ to 21˚ E) and part of the Levantine basin (21˚ to 29˚ E). Lower primary production occurred in the eastern Mediterranean during the survey period, with levels of 121 gCm^{-2} year^{-1}, than in the western basin, 163 gCm^{-2} year^{-1} , where in particular the Alboran Sea (215 gCm^{-2} year^{-1}) and the northwestern basin (155-180 gCm^{-2} year^{-1}) were regions of higher productivity (Bosc *et al*., 2004). Northwestern and southwestern basins also feature different seasonal primary production patterns (Morel & André, 1991). The boundary between northwestern and southwestern areas was taken as the 41˚ parallel because the North Balearic Front is frequently located close to this latitude (Le Vourch *et al.,* 1992). The same latitude was chosen to separate the Tyrrhenian Sea into the shallower northern region and the deeper southern Tyrrhenian basin. The Ionian Sea and Levantine basin are very deep regions (more than 3,000 m depth) bordered on the north by shallower areas: the Adriatic and northern Aegean Sea, neither of which were sampled. Most sampled regions include three types of habitat: the oceanic or open sea habitat, the continental slope habitat and the neritic coastal habitat. Large oceanic areas (deeper than 2,000 m) are found in all regions, the northern Tyrrhenian Sea excepted. The open sea waters of the northern Tyrrhenian Sea and, to a lesser extent, those of the Levantine basin and Alboran Sea, are of intermediate depth (1,000 to 2,000 m). Continental slopes (200 to 2,000 m) are generally steep, but moderately deep areas (500 to 2,000 m) of some extension are found in the western Balearic Sea, the eastern Ligurian Sea, the Sicilian and Sardinian channels, and southern Aegean Sea (Fig. 1). Neritic areas (less than 200 m depth) are not extended and were not systematically sampled during the surveys.

Sampling strategy

The different regions were sampled during five consecutive summers, due to logistical constraints: data were collected during dedicated surveys from 7 July to 8 August 1997, 18 June to 13 August 1998, 24 June to 14 August 1999, 19 June to 4 August 2000 and from 3 to 24 July 2001. The different data sets were pooled to obtain an average picture, on the assumption that no large scale summer distribution shift occurred during the five year period. The 1997, 1999 and 2001 surveys covered the northwestern and southwestern basins, while 1998 and 2000 were mainly devoted to the Tyrrhenian and Ionian Seas, and the Levantine basin (in 2000). The sampling strategy was constrained by the survey vessel, a 12-meter motor-sailer with an 80 hp diesel engine allowing a mean speed of 11 km/h. The maximum endurance was 5 days with the nominal crew of five to seven persons. For practical reasons, surveys were organized as round trips from Antibes (France) to a remote area that had to be reached in about two-three weeks from departure (south Sardinia in 1997, Peloponese in 1998, Gibraltar in 1999, Rhodes in 2000 and Balearic islands in 2001). A sampling design with “survey boxes” in slope and open sea areas was designed prior to the survey beginning. These “survey boxes” were given a width of 28 km to 56 km and a variable length, according to the distance between harbours and to the vessel’s maximum range of 830 km. Within survey boxes, predetermined zig-zag tracks were aligned at 20-30° to the longitudinal axis to get a better coverage, compared to simple straight lines. Double counting was assumed to be very unlikely with this sampling technique, because delphinids were shown from past surveys to move at an average speed of less than 8 km/h (Gannier, 1998a). Cruises were continued during night-time, collecting passive acoustic data.

Table I

Sighting conditions index (good light applies to clear sky and sun ray incidence higher than 15°; swell applies to waves whose origin is away from sampling site)

Wind speed (knots) Beaufort scale	0,1 0	2-5 1-2	6-10 2-3	11-16 4	16-25 5-6	> 25 > 6	Over
Sighting condition index (swell < 0.5 m; good light)	6	5	4	3	2	1	0
Sighting condition index (swell < 0.5 m; low light)	5	5	4	2	2	1	0
Sighting condition index (swell > 0.5 m; good light)	5	4	3	3	2	1	0
Sighting condition index (swell > 0.5 m; low light)	5	4	3	2	2	1	0

Survey methods

Field protocol combined visual searching with systematic discrete acoustic sampling (in order to detect Sperm Whales). The visual survey consisted of continuous, naked eye observation by rotating shifts of three observers with an eye height of 3 m above the sea surface as in Gannier (1998a). One observer stood in front of the mast searching the +/– 45° sector ahead, two other observers scanned the 30° to 90° and – 30° to – 90° sectors either side of the line. Individual observers were rotated on a 2-hour basis. Visual searching took place from half an hour after sunrise to half an hour before sunset, when wind speed was lower than 12-13 knots (moderate Beaufort 4). Position and sighting conditions were recorded every 20 minutes: the sighting condition index varied from 0 (null) to 6 (excellent) and was derived from wind speed, sea-state, residual swell and light conditions (Gannier, 1997a). For example, with wind speed of 10 kts, good light conditions and no conspicuous swell, the sighting conditions index had a value of 4 (Table I). Upon detection, various sighting parameters were recorded (bearing and radial distance to the boat, school size, animal behaviour) and dolphins schools were approached whenever they were less than 500 m off the boat course; otherwise, school size was estimated with binoculars. Survey routine was interrupted for up to one hour when Sperm Whales were detected either visually or acoustically (in case of loud signal); those interruptions occurred 35 times.

Survey effort

The survey totalled 16,008 km of effective sampling, including 13,447 km with a sighting condition index over 4 (Fig. 1). The sampling effort was obtained with medium (index 3: 16.0%), good (index 4: 42.4%), or very good conditions (index 5: 22.8% and index 6: 18.7%). The northwestern basin received the maximum coverage in good or very good sighting conditions (4,824 km), while it was of 580 km in the Levantine basin (Table II). In other regions, the effective effort varied between 663 km in the northern Tyrrhenian Sea, 1,583 km in the southern Tyrrhenian Sea, 1,065 km in the Alboran Sea and higher values of 2,156 km in the southwestern basin and 2,576 km in Ionian Sea (Table II). The global effective effort distribution favoured the continental slope, with 67.3% of effort against 32.7% for the open sea (depth > 2,000 m). In the northern and southern Tyrrhenian Sea, the northwestern basin and Alboran Sea, sampling effort and respective proportions of oceanic and slope habitat were similar (Table II). But the effort favoured the continental slopes in the Ionian Sea (57.1% of effort against 37.0% of the surface), the southwestern basin (81.1% of effort against 42.3% of surface) and the Levantine basin (96.8% of effort against 77.1% of the surface).

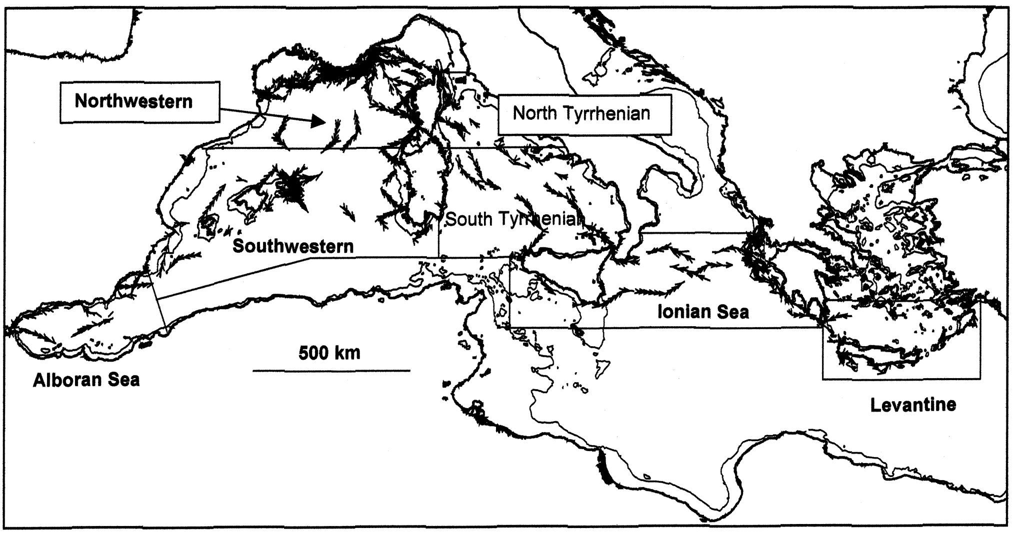

Figure 1. — Study area and effective sampling effort 1997-2001 (200 m isobath is drawn).

Table II

Description of study area and effective effort (area of seven regions and proportion of open sea (depth > 2000 m) and slope waters (z < 2000 m) in each region. Effective sampling effort, and proportion of effort in open sea and slope waters

Region	Area (km^2)	Slope area %	Open sea area %	Effective effort (km)	Effort % slope	Effort % open sea
Northwestern basin	155,600	44.1	55.9	4,824	60.0	40.0
Southwestern basin	268,600	42.3	57.7	2,156	81.1	18.9
Alboran Sea	81,200	79.3	20.7	1,065	94.6	5.4
Northern Tyrrhenian Sea	45,700	99.8	0.2	663	98.6	1.4
Southern Tyrrhenian Sea	163,700	50.0	50.0	1,583	45.0	55.0
Ionian Sea	195,000	37.0	63.0	2,576	57.1	42.9
Levantine basin	99,500	77.1	22.9	580	96.8	3.2

Data analysis

The geographic software *Oedipe* (Massé & Cadiou, 1994) was used for mapping the survey track and sightings and determining effective effort distribution in all regions in both continental slope (200-2,000 m depth) and open sea (> 2,000 m depth) strata. For every sighting, the water depth value was interpolated from the closest data found on nautical charts (*Service Hydrographique et Océanographique de la Marine*), and the distance to shore was measured on computer maps. A mean distance-to-shore and a mean water depth were calculated for each species by including all on-effort sightings. Both variables are known to be related to the sampling effort (*i.e.* are not robust habitat indicators), but were expressed to enable comparisons with previous papers (Notarbatolo di Sciara *et al.*, 1993). The mean distance to the 200 m isobath (D200) was also computed, as it was considered more useful for interspecific comparisons than distance-to-shore variable (Mangion & Gannier, 2002). Regional populations were expressed as sighting frequencies (SF) for every species observed:

$$SF_k = n_{jk}/n_k$$

where $\mathbf{n_{jk}}$ is the number of sightings of species **j** in region **k** and $\mathbf{n_k}$ is the number of on-effort sightings in region **k** (including sightings obtained with a sighting condition index of 3, or Beaufort 4 sea state). Delphinid diversity was then evaluated with the Shannon-Weaver index (Frontier & Pichod-Viale, 1995). We used number of sightings rather than number of individuals, because school sizes may be unaccurately estimated under Beaufort 4 sea state conditions:

$$H = -\Sigma\,(n_{jk}/n_k)\,\mathrm{Log}_2\,(n_{jk}/n_k)$$

A sighting rate of individuals (SRI), defined as the number of delphinids observed per kilometer, was calculated with *Distance 2.2* software (Laake *et al.,* 1994). The SRI was preferred to a simple sighting rate (SR), in sightings per kilometer, because our study involves comparisons between different — in the ecological sense — marine regions where delphinid school sizes may vary with biotic and abiotic factors (Wells *et al.*, 1980; Forcada & Hammond, 1998). Sampling heterogeneities in each region were accounted for by pooling estimates obtained for each habitat (slope and open sea) with area-weighting:

$$(SRI)_k = (A_{slope}\,(n_k \times S_k/L_k)_{slope} + A_{open\ sea}\,(n_k \times S_k/L_k)_{open\ sea})/(A_{slope} + A_{open\ sea})$$

where $\mathbf{n_k}$ is the number of on-effort sightings (sighting conditions of 4 or better), $\mathbf{S_k}$ is the mean school size, $\mathbf{L_k}$ is the sampling effort. $\mathbf{A_{slope}}$ and $\mathbf{A_{open\ sea}}$ are the areas of every habitat in each region. In fact, SRI could be derived from the density estimator in the line transect method (Buckland *et al.,* 1993), assuming that effective search half-width (esw) were constant across regions. This hypothesis may hold for a given type of survey (same platform and observers, same sighting protocole) carried out with similar sighting conditions (weather and sea state) in the different regions. Variance, SE and CV were obtained for each region with the delta method:

$$var(SRI)/SRI^2 = var(n)/n^2 + var(S)/S^2$$

Confidence intervals were estimated by *Distance* on the basis of a log-normal distribution of the SRI (Buckland *et al.*,1993), because this relative abundance index is a product of estimates and tend to have a skewed distribution.

The effect of sighting condition index on mean school sizes and sighting rates was assessed by a stratified analysis (Table III) and differences between categories for each component were tested by means of z-tests (Buckland *et al.*, 1993). For reasons of sample size, this analysis was done only for Striped Dolphins. Mean school size obtained under sighting condition index of 3 were significantly lower than under better sighting conditions (Table 3). Similarly, a sharp significant decrease in sighting rate, from 0.403 to 0.192 sight./100 km, was observed when the condition index was lower than 4 (Table 3). The stratified analysis showed that wind in excess of Beaufort 3 had adverse effects on the detection on delphinids, a statement made by other authors (Buckland *et al.*, 1993; Hammond *et al.*, 1995), and whales during our study. Hence, we only retained data obtained with sighting index equal or higher than 4 for estimating relative abundance.

Table III

Mean school sizes and sighting rates for different sighting conditions (standard errors in parentheses, values in the same column with the same superscript character are significantly different p < 0,05)

	Number of sightings n	Mean school size S	Sighting rate (n/100 km)
Sighting condition index 3	17	13.50^a (3.20)	0.192^a (0.056)
Sighting condition index 4	111	25.95^a (4.11)	0.403^a (0.049)
Sighting condition index 5	87	29.03^a (3.89)	0.383^a (0.052)
Sighting condition index 6	69	26.47^a (3.69)	0.508^a (0.068)

RESULTS

Species occurrence

A total of 510 on-effort sightings were obtained with sighting condition index higher than 3 including Fin Whales (83 sight.), Sperm Whales (37 sight.), Cuvier's Beaked Whales (8 occasions) and 379 delphinid sightings of five species, from which 326 with a sighting condition index higher than 4 (Table IV). The most frequent delphinid species was by far the Striped Dolphin with 294 sightings (Fig. 2) in schools ranging from 1 to 400 individuals

TABLE IV

Sighting and school sizes for different regions and species (1997-2001). Number in parentheses in the first column refers to sightings obtained with sighting conditions index higher than 4. Mean school size and SE are given for Striped Dolphin, and school size range for other species

Region	On-effort delphinid sightings	Striped Dolphin	Common Dolphin	Bottlenose Dolphin	Risso's Dolphin	Long-finned Pilot Whale
Northwestern basin	192 (163)	23.9 (2.4; n = 174)	25 n = 1	9-40 n = 4	3-35 n = 6	4-80 n = 7
Southwestern basin	48 (39)	23.9 (2.7; n = 33)	12-25 n = 6	2-15 n = 5	11-28 n = 4	0
Alboran Sea	52 (44)	58.2 (24.8; n = 20)	2-90 n = 21	9-11 n = 3	2-8 n = 7	11 n = 1
North. Tyrrhenian Sea	16 (13)	37.4 (13.8; n = 10)	15 n = 1	1-7 n = 4	2 n = 1	0
South.Tyrrhenian Sea	31 (31)	26.6 (5.3; n = 26)	28-90 n = 2	8-12 n = 3	0	0
Ionian Sea	32 (29)	35.0 (9.6; n = 26)	2-15 n = 2	2-8 n = 3	35 n = 1	0
Levantine basin	8 (7)	23.3 (8.3; n = 5)	0	4-7 n = 3	0	0
Total	379 (326)	294	33	25	19	8

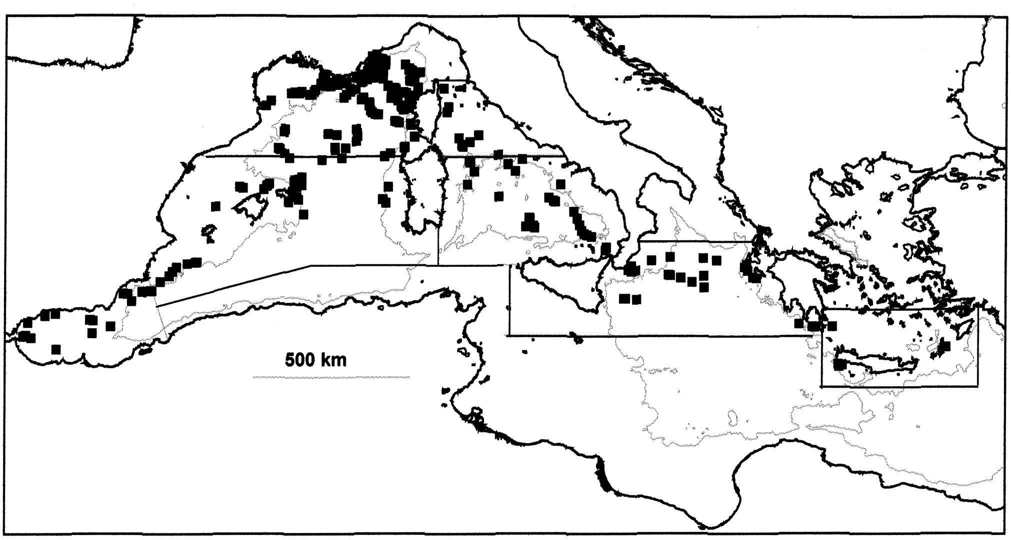

Figure 2. — Sightings of Striped Dolphin (2,000 m isobath is drawn).

(mean school size S = 28.3). The second species in terms of frequency was the Short-beaked Common Dolphin with 33 sight. (S = 16.3), followed by the Bottlenose Dolphin with 25 sight. (S = 7.4). Risso's Dolphin was sighted on 19 occasions (S = 12.5) and the Long-finned Pilot Whale 8 times with a mean school size of 21.7 (Fig. 3).

Striped and Bottlenose Dolphins were sighted troughout the area of study (Figs. 2 and 3), when Common Dolphin was observed in six regions (*i.e* not the Levantine basin) with much variable frequency, and the Risso's Dolphin was sighted in five regions (the Ionian and Alboran Sea, the northwestern and southwestern basin and the southern Tyrrhenian Sea). On the contrary, the Long-finned Pilot Whale was only observed in two regions (Fig. 3): the northwestern basin and the Alboran Sea (one off-effort sighting was recorded in the southwestern basin).

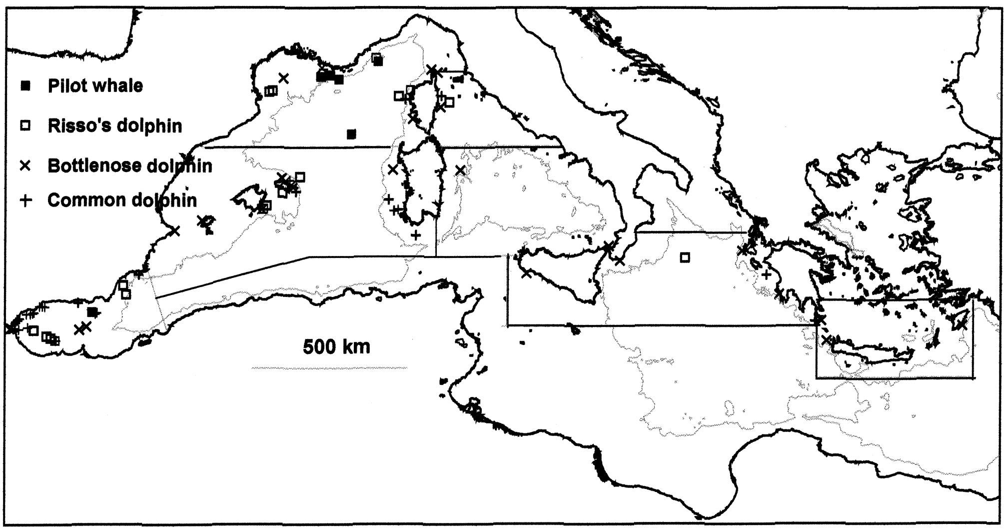

Figure 3. — Sightings of Bottlenose, Common and Risso's Dolphins, and Long-finned Pilot Whales (black square = Pilot Whale, white square = Risso's Dolphin, cross = Bottlenose Dolphin, oblique cross = Common Dolphin) (2,000 m isobath is drawn).

Species distribution in relation to topography

Sighting frequencies over four bottom depth strata, the continental shelf (depth **z** < 200 m), upper slope (200 m < **z** < 1,000 m), deep slope (1,000 m < **z** < 2,000 m) and open sea (**z** > 2,000 m), were shown to compare two pairs of species: the Striped and Common Dolphins, and the Risso's Dolphin and Pilot Whale. Striped and Common Dolphins were observed in all four strata, but the former was found more frequently in open sea (50.0%) and deep slope (32.1%) when the latter was more common in the coastal (26.7%) and upper slope (56.7%) (Fig. 4). This result was confirmed by the mean bottom depth, 1,759 m for Striped Dolphin and 479 m for Common Dolphin, as well as by mean distances to shore (Table V) and mean distances to 200 m isobath: Common Dolphin had a much lower D200 (6.7 km) than Striped Dolphin (45.6 km). Our results showed that *S. coeruleoalba* is a wide ranging oceanic and slope species in the Mediterranean, when *D. delphis* is rather linked to the shallower part of the continental slope and also to shelf areas in part of its distribution range.

Both Risso's Dolphin and Pilot Whale were found to share the slope and open sea strata (Fig. 4), however the former was more frequent in upper and deep slope strata (37.5% each)

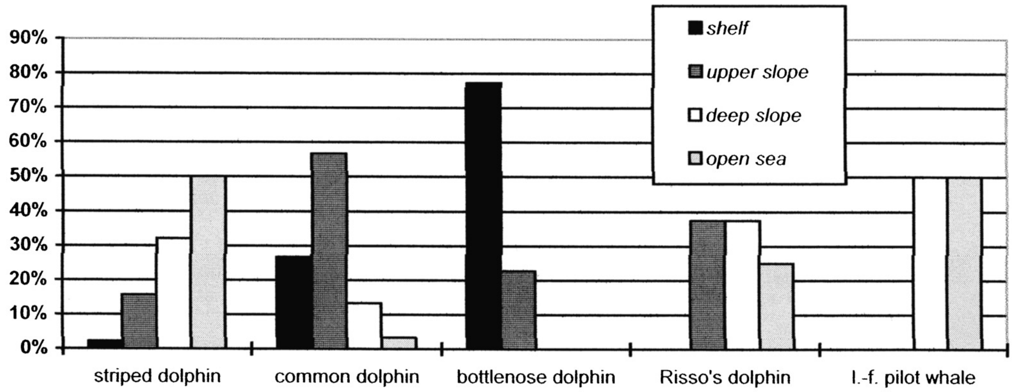

Figure 4. — Comparative distribution of the delphinids for 4 depth strata.

TABLE V

Comparison of habitats for five delphinids

	Striped Dolphin	Common Dolphin	Risso's Dolphin	Pilot Whale	Bottlenose Dolphin
Mean bottom depth of sightings (SD)	1,759 m (751)	479 m (469)	1,280 m (640)	2,056 m (403)	147 m (97)
Mean distance from sighting to shore (SD)	49 km (42.3)	15.3 km (20.2)	44 km (32.7)	47 km (40.1)	15.7 km (13.5)
Mean distance from sighting to 200m isobath (SD)	46 km (43.4)	6.7 km (10.7)	23.9 km (31.0)	32.1 km (35.5)	-2.1 km (5.9)

than in open sea waters (25%), when the latter was observed equally within and off the 2,000 m contour (50% each). Mean bottom depth of 1,280 m for *G. griseus* and 2,056 m for *G. melas* reflected that, and Risso's Dolphin was also found closer to the shelf edge than Pilot Whale, with respective D200 of 23.9 km and 32.1 km (Table 5). Hence, *G. griseus* preference for slope areas was globally confirmed, despite one record farther than 100 km from shore in the Ionian Sea, when *G. melas* was also regularly found in deep oceanic areas.

Bottlenose Dolphin was mainly observed over the shelf stratum (77.6% of sightings), other sightings being recorded in upper slope waters (mean depth 147 m). Sightings were also obtained over a remote (50 km from shore) sea-mount in the southern Tyrrhenian Sea and off the Gulf of Lion extended continental shelf. Bottlenose Dolphins had almost the same mean shore-distance as common dolphins (15.7 km) and a negative D200 of – 2.1 km (Table V). In the Mediterranean Sea, our results showed the Bottlenose Dolphin to be a fully neritic species.

Regional sighting frequencies by species

The Striped Dolphin was a dominant delphinid species in all areas, with sighting frequencies ranging from 90.6% (northwestern basin), to 83.9% (southern Tyrrhenian Sea), 68.7% (southwestern basin) and 62.5% (Levantine basin and northern Tyrrhenian Sea), except in the Alboran Sea where it represented 38.4% of sightings, ranking second after Common Dolphin. Mean school sizes did not differ significantly between regions (ANOVA F test, p = 0.056), but a large difference was noted between then highest value in the Alboran Sea (S = 58.2) and lowest (S = 23.3) in the Levantine basin (Table IV). Common Dolphin was well represented in the Alboran Sea (SF = 40.4%), southwestern basin (12.5% of sightings), and had a SF of about 6% in three other regions (northern and southern Tyrrhenian Sea, Ionian Sea). Risso's Dolphin was moderately frequent in the Ionian Sea and northwestern basin (sighting frequencies of about 3%) and more frequently seen in the southwestern basin (SF = 8.3%) and the Alboran Sea (13.5% of sightings). The Long-finned Pilot Whale SF were quite low with 3.9% of sightings in the northwestern basin and 1.9% in the Alboran Sea. Bottlenose Dolphin had much variable SF ranging from higher values of 37.5% (Levantine basin) or 25% (northern Tyrrhenian Sea) to a lowest value of 2.3% in the northwestern basin.

The lowest diversity index was found for the northwestern basin (0.62), in agreement with the high dominance of Striped Dolphins in this area. Higher indices were obtained in the northern Tyrrhenian Sea (1.42), the southwestern basin (1.38) and the Alboran Sea (1.79), where four species scored each more than 10% in sighting frequency. Moderate values of Shannon-Weaver indices were obtained for the Levantine basin (0.95), the southern Tyrrhenian Sea (0.79), the Ionian Sea (0.97).

Relative abundance indices by region

Sighting rates for individuals varied widely in the area of study, from 0.143 ind./km in the Levantine basin and 0.334 in the Ionian Sea, to 1.107 ind./km in the Alboran Sea. A high SRI was also observed in the northwestern basin (0.756 ind./km). Regions with medium SRI were the Ionian Sea (0.334 ind./km), southwestern basin (0.369 ind./km), southern Tyrrhenian Sea (0.402 ind./km), and northern Tyrrhenian Sea (0.528 ind./km). The Levantine basin lowest SRI was partly due to a low sighting rate ($1.07\ 10^{-2}$ group/km) and a low mean school size (13.3). At the opposite, the Alboran Sea highest SRI reflected both a high sighting rate and a mean school size of 30.2 ind./school (Table VI). The Ionian Sea offered a contrasting example with a low sighting rate ($1.09\ 10^{-2}$ group/km) and the highest mean school size (30.7 ind./school). Otherwise, regional variability could be mostly attributed to changes in sighting rate estimates, with school sizes variation restricted to the 19.8-29.2 range, respectively for the southwestern basin and northern Tyrrhenian Sea (Table VI).When 95% confidence intervals were considered (Fig. 5), it could be observed

Table VI

Relative abundance indices for all delphinid pooled (numbers in parentheses refer to coefficient of variation (CV%))

Region	Sighting rate group/10^2 km	mean S ind./grp	Sighting rate for individuals ind./km	95% Confidence Interval on SRI
Northwestern	3.24 (17.2)	23.3 (9.3)	0.756 (19.6)	0.514-1.104
Southwestern	1.87 (41)	19.8 (10.1)	0.369 (42.3)	0.162-0.826
Alboran Sea	3.66 (19.7)	30.2 (35.4)	1.107 (40.5)	0.501-2.422
N.Tyrrhenian	1.81 (24.2)	29.2 (54.0)	0.528 (59.2)	0.164-0.813
S.Tyrrhenian	1.58 (18.5)	25.4 (18.0)	0.402 (25.8)	0.255-0.705
Ionian Sea	1.09 (29.7)	30.7 (26.1)	0.334 (39.6)	0.154-0.727
Levantine	1.07 (40.2)	13.3 (43.7)	0.143 (59.4)	0.043-0.472

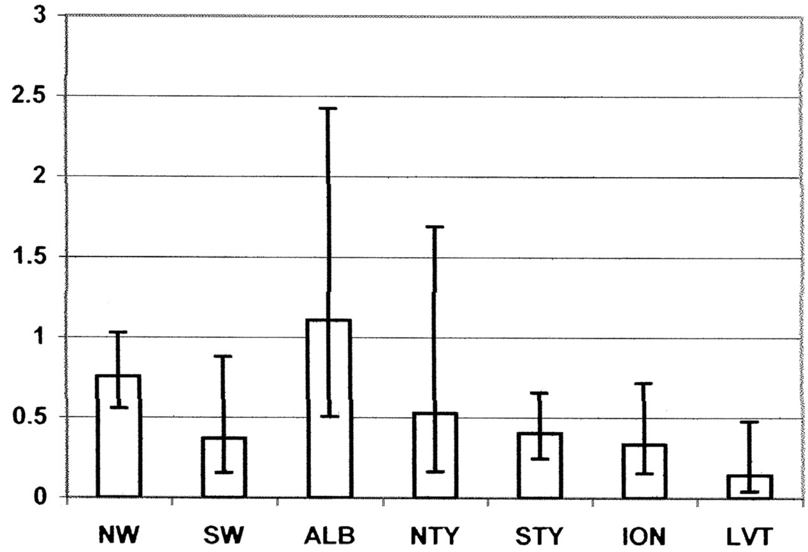

Figure 5. — Regional relative abundance indices and confidence intervals.

that SRI estimates for the southwestern, southern Tyrrhenian, Ionian and Levantine regions did not intercept the confidence intervals of Alboran and northwestern regions, the latter's confidence intervals overlapping. Hence, our results outlined two main groups of regions: those with a high delphinid relative abundance, and those with moderate or low delphinid relative abundance; the northern Tyrrhenian region was intermediate, and featuring a wide confidence interval.

DISCUSSION

This study showed that species occurrence, diversity and relative abundance indices varied greatly in the seven regions of the Mediterranean Sea that we investigated. These regions could be sorted into three groups: areas whith low or moderate SRI and low diversity index (the Levantine basin, southern Tyrrhenian, Ionian Sea), areas of medium SRI and high diversity (the northern Tyrrhenian and southwestern basin), and regions with high SRI (the Alboran Sea and to a lesser extent, the northwestern basin) further divided into one high diversity sector (Alboran) and one low diversity sector (northwestern).

METHODOLOGY

The results could be affected by a sampling strategy resulting in non-homogeneous coverages of habitats in regions (Fig. 1). To account for sampling biases, slope and open sea regions were post-stratified in the analysis, with the option of area-weighting and pooling, including for the mean school size component of the estimate (Buckland *et al.*, 1993). In most regions (the Levantine basin excepted), our survey included substantial open sea areas and, once stratified and pooled, could be used for an inter-regional description of relative abundance and species sighting frequency. Obviously, our description did not aim at the same level of accuracy as large international surveys with systematic sampling that were carried out, for example in the North Sea (Hammond *et al.*, 1995). But such surveys were not carried out in the Mediterranean Sea. Our survey platform was not specifically adapted to abundance surveys: biasing effects such as « response to the platform » and unknown « probability of detection on the line » (Hiby & Hammond, 1989; Buckland *et al.*, 1993) could affect abundance estimates, either absolute or relative. These effects were not adressed here, because they were assumed to be constant across years. Both biasing effects are likely to be severe with mediocre sighting conditions (*i.e.* when observer sighting efficiency decrease and animals are detected at shorter distances), as was examplified by our stratification of mean school size and sighting rate (Table III). Hence, only data obtained in sighting conditions equivalent to Beaufort 3 or less were used for relative abundance estimates.

The relative abundance indices were obtained in different regions by pooling survey results over a five-year period. The same boat was used throughout the study, with the same basic observer team, including the author (100% of the survey duration) and four other skilled observers who each participated to four of the five surveys (see Acknowledgement Section). It was shown by modeling the effective search half width that no significant change in detection efficiency occurred along the five-year period of this study (Gannier, unpubl. report). Furthermore, all regions, except the Alboran Sea and Levantine basin, were covered twice: the Ionian and Tyrrhenian Seas were sampled in 1998 and 2000 and the southwestern basin in 1999 and 2001. Hence, eventual heterogeneity in detection efficiency, a consequence of multiple vessel or long term surveys, were eventually damped. The same reason stands to allow an « average » situation to be delivered by our five-year survey period, in spite of eventual interannual large scale distribution changes. Mesoscale variability was shown to affect Fin Whale distribution in the northwestern basin (Gannier, 2002; Gannier *et al.*, in print), probably as a result of large annual fluctuations in primary biomass (Littaye *et al.,* 2004; Bosc *et al.*, 2004). In the eastern tropical Pacific, Reilly & Fiedler (1994) have observed that open sea delphinid populations were affected by large scale interannual variability in environmental variables, but their data covered a region of the Pacific Ocean and a period affected by 1987 ENSO episodes (Enfield, 1989). In the western Mediterranean basin, the annual primary production — obtained from Seawifs data, showed a notable 15% increase in 1999, compared to other years in the 1997-2001 period, when the only significant change for the eastern basin was a 9% decrease in 2001 (Bosc *et al.*, 2004). Our surveys did not cover the eastern basin in 2001, and both northwestern, southwestern and Alboran Sea regions were covered in 1999, year of higher primary production in the western basin. Among five taxa investigated by Reilly & Fiedler (1994), the Common Dolphin had the strongest response to habitat changes, and the Striped Dolphin, the weakest. Furthermore interannual variability was not apparent for the Striped Dolphin in the Ligurian Sea during the period 1989-1997 (Gannier, 1997b). In summary, available informations support our assumption that the average situation provided by our multi-year sampling was not biased by interannual distribution changes.

Comparative distribution

A discussion on basin-wide comparative distribution is heavily constrained by the availability of literature including suitable information on species occurrence and sampling effort, such as Notarbartolo di Sciara *et al.* (1993), Forcada *et al.* (1994), or Gannier (1998a). More local studies such as in the Alboran Sea (Cañadas *et al.*, 2002), Ligurian Sea (Forcada *et al.,* 1995; Gannier, 1998b) or central Tyrrhenian Sea (Marini *et al.,* 1996) provide useful results on regional species sighting frequencies SF, but are of limited interest on a global comparative point of view because of the heterogeneity between local survey protocols.

Our study showed that Striped Dolphins are wide ranging animals, although they have a marked preference for waters deeper than 1,000 m in the Mediterranean, including slope and open sea regions. On the contrary, Common Dolphins are often observed in shallower waters (less than 1,000 m), including in areas where the continental slope is not steep. This is also detailed by Cañadas *et al.* (2002) in the northeastern Alboran Sea, who determined optimal slope values of less than 40 m/km for Common Dolphin and 20 to 80 m/km for Striped Dolphin. Notarbartolo di Sciara *et al.* (1993) determined a mean bottom depth of

1,490 m for *S. coeruleoalba* and 785 m for *D. delphis*, when we obtained respectively 1,759 m and 479 m. Our study showed that Risso's Dolphin is more frequent in slope areas than the more pelagic Pilot Whale (Fig. 4 and Table IV), as also expressed in Mangion & Gannier (2002). Cañadas *et al*. (2002) determined favourable slope values of more than 40 m/km for Risso's Dolphin and stated that Pilot Whale is a widespread pelagic species. Notarbartolo di Sciara *et al*. (1993) obtained a mean bottom depth of 958 m for *G. griseus* and 2,063 m for *G. melas* when we obtained respectively 1,280 m and 2,056 m, both set of results are remarkably close in spite of sampling heterogeneities. Distribution results were globally convergent for the essentially neritic *T. truncatus*, although Cañadas *et al*. (2002) showed Bottlenose Dolphin in the Alboran Sea to prefer slope waters between 200 and 400 m depth.

Our results confirmed existing papers on interspecific comparative distribution, but an important achievement of this study was the consistency of species topographic preferences across different regions of the eastern and western basins, either oligotrophic or mesotrophic.

Regional delphinid diversity and sighting frequencies

The Alboran Sea is the only Mediterranean region where Striped and Common Dolphins are observed with comparable frequencies (Forcada & Hammond, 1998; Franco *et al.,* 1993; Sagarminaga & Cañadas, 1996). Our sighting frequencies for the Striped (38.5%) and Common Dolphins (40.4%) were similar to those provided by Sagarminaga & Cañadas (1998) and Franco *et al*. (1993) (Table VII). Our Pilot Whale SF (1.9%) is less than those of same authors, but Cañadas & Sagarminaga (2000) showed the Long-finned Pilot Whale local occurrence could vary considerably with time. Our Risso's Dolphin sighting frequency (13.5%) was higher than figures reported by Franco *et al*. (1993); *G. griseus* is a wide ranging species which can be locally present or absent from an area at a given time (Kruse *et al.,* 1999). Finally, our sighting frequency for *T. truncatus* (5.8%) is close to the SF obtained by Sagarminaga & Cañadas (1996) (Table VII).

In the southwestern basin, we found a high diversity index and Striped Dolphin dominance was moderate (SF = 68.7%), compared to 18.2% for *D. delphis*, 15.1% for *T. truncatus* and 12.1% for *G. griseus*. Absence of Pilot Whale from our records may be incidental, since one off-effort sighting was obtained in the southwestern part of this region. Only two sightings of Common Dolphin were recorded by Forcada & Hammond (1998). The Algerian region has been shown from strandings to shelter the five delphinid species (Boutiba *et al*., 1996).

Table VII

Delphinid populations reported in the literature (in % of sightings)

Region	Striped Dolphin (%)	Common Dolphin (%)	Risso's Dolphin (%)	Pilot Whale (%)	Bottlenose Dolphin (%)	References
Northwestern basin	88.2	2.6	7.9	1.3	0.0	Forcada *et al*., 1995
	91.3	0.4	3.5	3.6	1.2	Gannier, 1998
N. Tyrrhenian Sea	41.5	0.0	17.5	1.7	39.2	Notar. *et al*., 1993
	86.9	1.1	3.6	0.0	8.4	Marini *et al*., 1996
S. Tyrrhenian Sea	66.8	2.2	1.5	2.6	24.8	Mussi *et al*., 1998
Ionian Sea	55.4	4.5	14.4	0.0	25.7	Notarbartolo di Sciara *et al*., 1993
Alboran Sea	37.8	26.2	8.9	6.0	7.4	Sag. & Caña., 1996
	23.0	31.1	1.6	26.2	18.0	Franco *et al*., 1993

In the northwestern basin, our diversity index was low in spite of five species observed. Striped Dolphin was a dominant species (SF = 90.6%) and Common Dolphin was rare (0.6%), as also apparent from past surveys results (Table VII): in this region *D. delphis* range is apparently limited to northwestern Sardinia and southwestern Corsica (Gannier, 1998b; Gannier *et al*., 2001). Our sighting frequencies for *G. griseus* (3.0%) and *G. melas* (3.9%) are within the range of results reported by Gannier (1998b), but quite different to SF derived from Forcada *et al*. (1995) in the Ligurian Sea, who suggested a lower SF for Pilot Whale (Table VII): this is perhaps an indication that Pilot Whale is more frequent in western waters of this region (Gannier, 1998b). Bottlenose Dolphin (2.1% of sightings in our study) scored low and variable frequencies in the literature: the species is common in neritic waters of Corsica and the Gulf of Lion (Bompar *et al.,* 1994; Dhermain *et al.,* 1999).

In the northern Tyrrhenian Sea, we obtained a high diversity index with sighting frequencies of 62.5% for Striped Dolphin against 6.2% for Common and Risso's Dolphins, and 25% for Bottlenose Dolphin. The Striped Dolphin dominance was also apparent in Marini *et al*. (1996) for all seasons combined (Table VII). Notarbartolo di Sciara *et al*. (1993) found a lower SF for Striped Dolphin and a higher value for *T. truncatus*, in agreement with the more coastal nature of their sampling.

In the southern Tyrrhenian Sea, the dominance of Striped Dolphin (SF = 83.9%) was high compared to other species (Common Dolphin, 6.4% and Bottlenose, 9.7%). Local surveys off the Pontino Archipelago (northeastern part of the region) showed sightings frequencies of 66.8% for Striped Dolphin and 24.8% for Bottlenose Dolphin (Mussi *et al.,* 1998), the three other delphinid species being observed with low SF (Table VII). We observed *D. delphis* off western Sicilia (Fig. 3), a region adjacent to southern Sardinia waters where we also scored several sightings. These data support the existence of a Common Dolphin sub-population in a region encompassing moderate depth waters around Sicily, Sardinia and Tunisia, in complement to other regional stocks suggested by Bearzi *et al*. (2003).

The delphinid population in the waters surrounding Greece relies mainly on the four species which we observed during our study (Frantzis *et al*., 2003). In the Ionian Sea, we obtained a medium diversity, with a dominance of Striped Dolphin (SF = 81.2%), compared to other species (Risso's Dolphin, 3.1%, Common dolphin, 6.2% and Bottlenose, 9.4%), which is different from sighting frequencies extracted from Notarbartolo di Sciara *et al*. (1993) (Table VII), probably due to the more coastal coverage of these authors. In the Levantine basin, our diversity index was very low, with only two species sighted, but our sampling coverage was reduced. Marini *et al*. (1995) issued results from 52 delphinid sightings obtained during summer opportunistic surveys: Bottlenose Dolphin represented 53.8% of the sightings, Striped Dolphin had a SF of 32.7% and other species included Risso's (SF = 9.6%) and Common Dolphins (SF = 3.8%), which were recorded in the northeastern Aegean Sea.

In summary, our sighting frequencies were mostly confirmed by existing litterature, despite the diversity of sources. An eastwards decreasing trend in delphinid diversity is observed, mainly due to the Long-finned Pilot near absence in the eastern Mediterranean, at least in summer.

Regional variation in relative abundance

Few studies deal with abundance, either relative or absolute, of delphinids in the Mediterranean Sea. Forcada & Hammond (1998) released summer density estimates for Striped and Common Dolphins in part of the western basin: they obtained the highest abundance in the Alboran Sea (0.36 ind./km^2, for both species pooled). Ranking second was the northwestern basin with a Striped Dolphin density of 0.24 ind./km^2 (almost no Common Dolphin sightings) and estimates for the southwestern basin were far below, 0.08-0.09 ind./km^2. Keeping in mind that we dealt with five species, instead of two for Forcada & Hammond (1998), both studies are in agreement. Notarbartolo di Sciara *et al*. (1993) provided sighting rates for different regions around Italy, although they expressed sightings per hour of effort pooled from different boats, and their results included data on Fin and Sperm Whales. The Ligurian-Corsican region (eastern part of the northwestern basin) was credited with a mean sighting rate of 0.27 sighting/hour, against 0.12 for the Ionian Sea and 0.07 for the

Tyrrhenian Sea, when we obtained higher sighting rates in the northern and southern Tyrrhenian Sea (1.81-1.58 group/100 km) than in the Ionian Sea (1.09 group/100 km). Given that Notarbartolo di Sciara *et al*. (1993) analysis was not corrected for sampling heterogeneity among habitats, their results are quite similar to those presented here.

Our sea-wide relative abundance indices also allow us to compare delphinid populations and primary biomass. We obtained a higher delphinid relative abundance in the Alboran Sea (SRI = 1.11 ind./km) than in all other regions, including the northwestern basin (Table VI). Both papers give useful cues on interspecific comparative distribution, although the latter figures are sampling-dependent. Relative abundance were medium (0.4-0.5 ind./km) in all regions not affected by a permanent primary production process (*i.e*. the Alboran and Ligurian Seas). Bosc *et al*. (2004) obtained annual primary productions from four years of Seawifs data: average level was 30% higher in the western than in the eastern basin. They partitioned the Mediterranean Sea in 13 regions: annual production amounted to 215 g/C/m^2 in the Alboran Sea, 155-180 g/C/m^2 in the northwestern region, 145-153 g/C/m^2 in the southwestern region, 135 g/C/m^2 in the central-southern Tyrrhenian Sea, 128 g/C/m^2 in the northern Ionian Sea and only 104 g/C/m^2 in the northern Levantine basin. This primary production ranking resembles that obtained here for delphinid relative abundances: even if dolphins are high level predators, they are generally more abundant in mesotrophic areas than in oligotrophic regions, at least in the Mediterranean. Such a result might also be meaningful in large oceanic areas.

CONCLUSION

Our study described regional delphinid populations from 379 sightings on five species obtained during 13,447 km of surveys in the major basins of the Mediterranean Sea. All species had fairly consistent habitat across the whole study area: beside the wide ranging pelagic Striped Dolphin, the Common Dolphin associated to moderate depths and slopes, Risso's Dolphin was mostly distributed along slope areas when Pilot Whale was familiar with deeper regions and Bottlenose Dolphin was constrained to shallow waters. Delphinid diversity is probably depending on habitat in terms of both production and topographic features: beside the opportunistic Striped Dolphin, the Pilot Whale seems to be dependent on the availability of large amounts of pelagic preys, when the presence of Bottlenose, Common and Risso's Dolphins is more linked to specific habitat features. A variable topography also contributes to global delphinid abundance, such as in the Alboran Sea, by allowing more than one species to have an abundant population. Relative abundance was high in the northwestern basin, but the diversity was lower perhaps due to a stronger seasonal variability in production and temperature. Relative abundance showed a southwards and eastwards decreasing trend, in agreement with lower primary biomass, and despite the presence of diverse topographic situations (shelf extensions, variable slopes, canyons ...). Pending to the availability of extensive results obtained with sea-wide multiple vessel cetacean surveys, this study brings much improved knowledge on dolphin distribution in the Mediterranean Sea.

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