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Diel variations of the striped dolphin distribution off the French Riviera (Northwestern Mediterranean Sea)

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Abstract

The striped dolphin is widely distributed in the Ligurian sea. Night acoustic sampling and day visual sampling where used to describe its distribution shift off the French Riviera in a region of 4836 km^2 extending to 83 km off-shore. A small boat was equiped with a dual-channel towed hydrophone and sampled the continental slope by night, during the summer of 1996 and 1997. The day sampling effort was taken from visual surveys made from 1989 to 1997. The area of study was divided into 4 strata: the near-shore, deep slope, offshore and open sea sectors. The daylight time was divided into 4 periods of 4 hours: the morning, the midday, the afternoon and the evening. A relative abundance index in 'dolphin per km of effort' was calculated for each stratum and each time period. The Pennington estimator was used for the mean and variance calculations. A total of 209 sightings of striped dolphins were obtained during a total effective effort of 5058 km. The night acoustic results show the presence and the intense activity of feeding of the striped dolphin close to the shelf break. The day distribution shows a marked preference of the striped dolphin for the open sea and the near-shore waters. The near-shore waters see a much fluctuating situation as the day passes: the relative abundance index of 2.01 dolphin per km in the morning falls to a minimum of 0.25 dolphin per km during the afternoon and then recovers to an evening level of 0.98 dolphin per km. The distribution shift is supported by the description of average movement pattern computed from 146 records: morning offshore and evening inshore movements are clearly shown. This study presents the scheme of an horizontal diel migration cycle, consistent with the nocturnal feeding of dolphins close to the shelf, and a diurnal offshore-inshore movement, whose motivation is not precisely known. The questions of prey availability and possible human disturbance effects are discussed.

Key words: striped dolphin, Mediterranean, distribution, movement, hydrophone, survey

Introduction

The striped dolphin (*Stenella coeruleoalba*, Meyen, 1833) is a cosmopolitan delphinid inhabiting tropical, subtropical and warm temperate waters worldwide (Perrin *et al*., 1994). Compared to other small sized oceanic dolphins, its distribution seems to be related to areas where some seasonal changes in thermocline depth occur, as shown in the Eastern Tropical Pacific by Reilly (1990) and Reilly and Fiedler (1993).

The striped dolphin is by far the most abundant species in the Western Mediterranean sea (Forcada *et al*., 1994). The highest summer densities have been estimated in the liguro-provencal basin (Forcada *et al*., 1995; Gannier, 1998*a*). *S. coeruleoalba* relies on a wide variety of fishes and cephalopods for its diet (Würz and Marrale, 1993); preferences are likely to depend on the local or seasonal availability of the different prey items. Visual surveys have shown that few other delphinid species are common in the Central Ligurian Sea (Duguy, 1991; Notarbartolo di Sciara *et al*., 1993; Gannier, 1998*a*; 1999): the bottlenose dolphin (*Tursiops truncatus*) is mainly restricted to Corsican coastal waters, and the common dolphin (*Delphinus delphis*) is rare. On the contrary, the long-finned pilot whale (*Globicephala melas*) and the Risso's dolphin (*Grampus griseus*) are regularly seen during surveys across the Ligurian Sea (Gannier, 1999). The striped dolphin is observed in the Ligurian Sea all year round, but with much lower relative abundances from winter to spring (Gannier and Gannier, 1997*a*; Gannier, 1998*b*). While it is primarily considered as an oceanic delphinid (Perrin *et al*., 1994), previous studies in the Northwestern Mediterranean Sea have shown that striped dolphins are well distributed from the continental shelf edge to the open sea, with a marked preference for

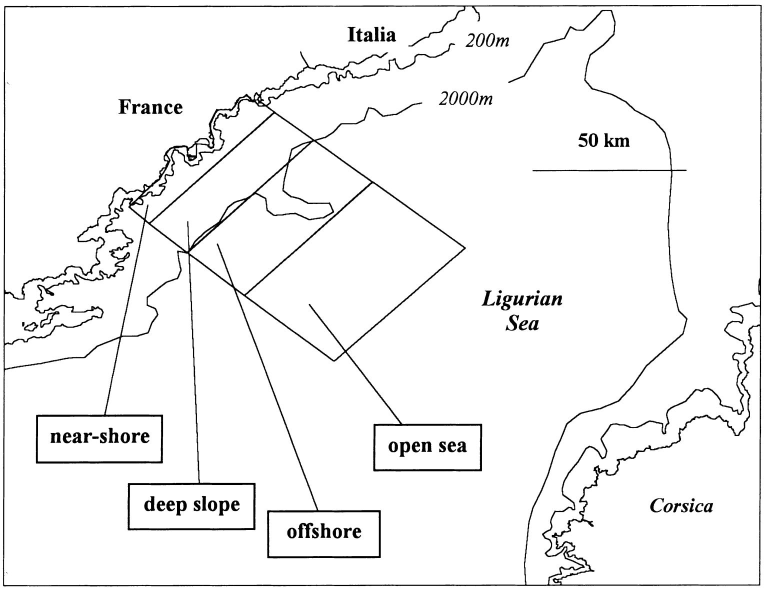

Figure 1. The area of study and the four geographical strata.

deep waters (Gannier, 1995; 1998*b*). Preliminary analysis of inshore waters data have shown a daily variation in its distribution: striped dolphins are found in inshore waters during the night and early morning and tend to move offshore later in the morning. The nocturnal feeding of striped dolphins in the vicinity of the shelf break is indicated by some preliminary acoustic sampling results (Gannier, 1996; Gannier and David, 1997).

We propose here to describe the diel variation of the striped dolphin distribution off the French Riviera coast, in summer. We give distribution results from data obtained during night acoustic samplings and from conventional visual diurnal surveys. Moreover, we analyse average movement patterns of striped dolphins and we present examples of visual boat tracking experiments.

Material and methods

Area of study

The limits of the area of study are based on a radial segment used as a reference for numerous local oceanographical studies (Boucher *et al.*, 1987). A parallelogram was traced by extending this line to 45 milles offshore and by considering a direction parallel to the general coastline (Fig. 1). The total surface of the area is 4836 km^2; it encompasses a low extension continental shelf and a steep slope. For the purpose of this study, four geographical strata were considered: the sector extending from the shore to 5.5 km off the Cap d'Antibes is called 'near-shore' stratum, the sector extending 15 km farther offshore is called 'deep slope' stratum, the sector extending to 37 km is named 'offshore' stratum, and the sector extending from 37 to 83 km is called 'open sea' stratum (Fig. 1). The near-shore stratum is far from being a continental shelf area, the depth reaching 500 m to 1000 m within a few kilometers from the coast line. The mouth of the Var River is located in the north-east of the area, influencing part of the area by its downstream flow, during rain. The deep slope stratum sees the bottom depth increasing to between 1600 and 2100 m. From an oceanographic point of view, it is mostly influenced by the Ligurian current flowing to the southwest and featuring a thick superficial layer of oligotrophic waters in summer (Béthoux *et al.*, 1988). The offshore stratum is an area of deep waters, 1700 m to 2300 m, where the horizontal gradient of salinity is the highest. A complex pattern of vertical circulations takes place in this frontal area (Prieur, 1981). The frontal system located in this sector is known to enhance the primary and secondary production (Boucher *et al.*, 1987). The open sea stratum, where the depth reaches 2000 to 2600 m, ends approximately at the center of the Ligurian Sea, half-way to Corsica (Fig. 1). In this area, the summer pycnocline is quite shallow, restraining the superficial layer thickness to a minimum of 30–50 m (Gostan, 1968; Sournia *et al.*, 1990). The central part of the basin is favoured by several species of cetaceans, noticeably the striped dolphin and the fin whale, whose local abundance has been shown to be correlated with the availability of the euphausiid *Meganyctiphanes norvegica* (Orsi Relini *et al.*, 1994).

Material

All data were obtained from small boat surveys during the summer periods from 1989 to 1997. From 1989 to 1994, a 9.50 m auxiliary yacht was used with an average cruising speed of 9 km/hr and from 1995 onwards, a 12 m motorsailer was used with a mean speed of 11 km/hr. In both cases the boat cruised on engine during the sampling legs. Three observers were active onboard, searching the 180° frontal sector with naked eyes. Binoculars were used for species identification and sighting data collection. From 1993, binoculars with internal reticles were used for the measurement of the relative position of cetaceans (angle and radial distance). Positioning was achieved with a LORAN-C device up to 1993 and with a GPS navigator from 1994 onwards. From 1994 onwards, simultaneous acoustic monitoring was performed with a dual channel towed hydrophone of 200Hz–20 kHz effective bandwidth.

Night sampling

Nocturnal samplings took place during the summer of 1996 and 1997, as part of a distribution study for regional authorities. The night sampling segments were designed in relation to the local bottom topography, either along the outer shelf break (1996) or as zigzag legs from the 100 m isobath to the 2000 m isobath (1997). The acoustic sampling rate was set at 0.9 km (1996) and 1.85 km (1997): one minute of headphone listening was performed, with the speed slowly decreasing to below 3 knots after the propeller had been disengaged. If a very weak dolphin signal was suspected, a lower noise level was obtained by further decreasing the speed. The signal and overall noise were logged using a three levels scale (1996) or five levels scale (1997). The sound was recorded whenever cetaceans were heard. Dolphins signals often included echolocation clicks, but also whistles and other sounds as well. The recognition of striped dolphin signals is based on both previous visual and acoustic work (Gannier and Gannier, 1997*b*; Gannier, 1998*c*). Bottlenose dolphins and common dolphins were never sighted in the area of study during 10 years of surveys (Gannier, 1999). These studies indicated that none of the two other locally common delphinid species (the Risso's dolphin and the long-finned pilot whale) could be acoustically confused with the striped dolphin. Pilot whale clicks feature conspicuous rythmed sequences and longer inter-clicks intervals, and its vocalisations are louder, with broad band tonal calls. The Risso's dolphin is particular in producing few whistles but frequent pulses bursts of high repetition rate (Arnaud, 1995; Coquet, 1996; Richardson *et al.*, 1995). The assumption that striped dolphins are acoustically identifiable in the Ligurian Sea is also considered by Gordon *et al.* (in press). It was strenghtened by the visual sightings made during the course of the surveys, both in day and dusk periods. The results were plotted with *Oedipe* software (Massé and Cadiou, 1994).

Day Sampling

The diurnal samplings were randomly distributed and conducted from 1989 to 1997. They are either round trips from the port of Antibes, or initial (or final) radial segment of larger scale surveys departing from (or arriving to) Antibes. Sampling was conducted only with good environmental conditions: basically, only sea states corresponding to a wind speed equal of lower than Beaufort 3 were considered for analysis. Occasionally, in the absence of good luminosity or in the presence of a conspicuous swell, a Beaufort 2 cut-off was used. Each leg of effective effort is decomposed into samples consisting in linear segments of about 5 km length. When dolphins were detected visually, they were approached for a period of 5 to 10 min in order to record sighting data, such as the direction (estimated to the nearest 10°) and speed (estimated by comparison to the boat speed) of movement, the activity pattern, the occurrence of newborn calves, . . . The initial course of the boat was then resumed. A 'passing mode' was preferred to this 'closing' mode in 1996, in order to examine new sighting procedures. From 1994 onwards, the standard protocol includes a simultaneous acoustic sampling, the procedure being the same as that described for the night sampling, with sampling rates of one listening every 3.7 km.

Data recording

Sampling data were recorded on special forms and then entered into the 'logbook' database, from which all sampling variables were extracted: local time (UTC+2), date, position, detectability conditions, number of dolphins sighted during the sample (n), length of the sample (l), associated sighting rate (n/l), acoustic sample results (noise and signal levels). Sighting data were recorded on specific forms and then entered into the 'sighting' database, from which all relevant variables can be extracted. For this paper, extractions of the speed and direction of the dolphins movement were executed for every geographical stratum (near-shore, deep slope, offshore, open sea) and every time period.

Relative abundance index

Extractions of the databases were executed for every geographical stratum (near-shore, deep slope, offshore, open sea) and every time period. Four temporal strata were considered: the 6.00am–10.00am period (morning), the 10.00am–2.00pm period (midday), the 2.00pm–6.00pm period (afternoon) and the 6.00pm–10.00pm period (evening). The last period obviously ends around 8.30pm–9.30pm for reasons of visibility. The definition of the four time periods was influenced by ancillary data on the dolphins activity. A mean relative abundance index (y_p) was estimated from the sighting rate (n/l) data for every geographical stratum and every time stratum: this index is expressed in 'number of dolphins sighted per km sampled' (d/km). The data structure, and in particular the 3.7 km length of the samples, leads to a very high number of zero-values in the sighting rates data. Consequently, the arithmetic mean is not well suited for estimating the relative abundance indice. A Pennington estimator was preferred because it gives unbiased estimates of mean and variance when the data set includes many zero values, unlike the arithmetic estimator (Pennington and Berrien, 1984). This estimator is based on the log-normal distribution of the non-zero values of a serie of data, referred as delta distribution by Aitchison and Brown (1957). For a distribution of n samples with m non-zero values (m>1), with y_m the sample mean of the non-zero $\log_e$ values and s^2 a sample variance of the loge values, Aitchison and Brown (1957) give the estimate of the mean, y_p:

$$y_p = m/n \cdot \exp(y_m) \cdot G_m(s^2/2)$$

where $G_m(x)$ is defined by:

$$G_m(x) = 1 + (m-1/n) \cdot x + \Sigma_{2,\alpha(} [(m-1)^{2j-1} \cdot x^j] / [m^j (m+1)(m+3) \ldots (m+2j-3) \cdot j!]$$

Pennington (1983) gives the variance estimator, $\mathrm{var}(y_p)$:

$$\mathrm{var}(y_p) = m/n \cdot \exp(2 \cdot y_m) \cdot [m/n \cdot G_m^2(s^2/2) - (m-1/n-1)\ G_m((m-2/m-1) \cdot s^2)]$$

These estimates were obtained by processing sighting rate data with *Passtec* software (Ibanez and Etienne, 1994).

Dolphin movements

The average movement of the dolphins schools was computed for every geographical stratum and every time stratum: from the 'sighting' data base we extracted the estimated speed (in meter/second) and the movement direction of every school (when recorded). For this analysis, only records obtained with good sighting conditions (sea state <Beaufort 3) were conserved. Furthermore, records were excluded when the dolphins displayed an obvious response to the observers boat. The movement of each school was calculated as a vector and the average vector for every time-stratum case was computed. The time-variation of the movement is then described graphically.

Visual tracking of dolphin schools

In order to better describe the daily migration pattern, we attempted to follow schools of striped dolphins all day. Very calm sea conditions were needed to follow the dolphins without pertubating their 'natural' activity, i.e. to observe them from a certain distance. In a previous study (Gannier, 1998*a*), the response of striped dolphins to the same boat was found to be non significant at distances in excess of 150 m. The school was to be detected early in the morning, without to be seriously harassed by recreational boats cruising close to shore. Acoustic devices were used almost continuously to monitor the dolphin's activity during the tracking experiments.

Results

Day sampling and sighting results

The sampling amounts to a total of 5058 km, quite evenly distributed in every different strata with the exception of the southwestern coastal portion of the near-shore sector, poorly covered (Fig. 2). The effort amounts to 1267 km in the near-shore stratum, 1793 km in the deep slope stratum, 1151 km in the offshore stratum and 858 km in the open sea stratum.

Sampling took place with variable sighting conditions: 41–55% of the effort was obtained in good sighting conditions (Beaufort 3), 28–35% in very good sighting conditions (Beaufort 2) and 15–31% in excellent conditions (Beaufort 0–1). Some variations of the average sighting conditions are apparent between the different strata: the offshore and open sea strata display somewhat better conditions than the slope and near-shore sectors (Table 1). But these differences are not likely to alter seriously the consistency of our results, if we refer to a detailed analysis of this effect (Gannier, 1995).

Two hundred and nine groups of striped dolphins were observed in the area of study, with the selected sighting conditions (Fig. 3). The distribution of small schools (less than 5 individuals), medium schools (6 to 20 individuals), large schools (21 to 50 animals) and very large schools (more than 51 animals) does not show any spatial trend. The mean school size is 18.1 individuals (n=45, SE=16.9) for the near-shore stratum and 16.7 individuals for the deep slope stratum (n=48, SE=15.8). School sizes appear slightly higher in the offshore stratum, with 22.1 individuals (n=61, SE=22.6), and the open sea

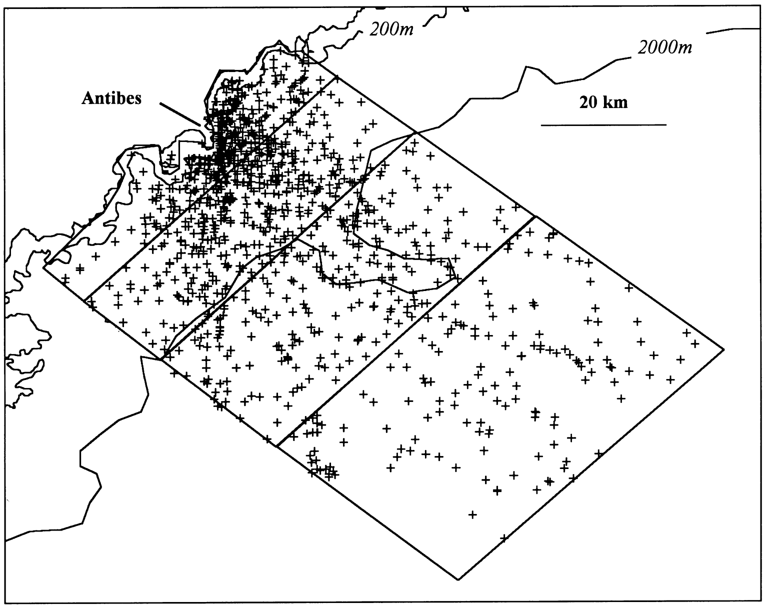

Figure 2. The sampling effort in the area of study (plots indicate the end of a 3–5km sampling bout).

Table 1. Sampling effort and sighting conditions for every stratum. (effort (in km) and proportion of effort spent with the different sighting conditions)

Effort/Stratum	Near-shore	Slope	Offshore	Open sea
Beaufort 0-1	194 (15%)	337 (19%)	252 (22%)	264 (31%)
Beaufort 2	381 (30%)	511 (28%)	403 (35%)	237 (28%)
Beaufort 3	692 (55%)	945 (53%)	496 (43%)	357 (41%)
Total	1267 (100%)	1793 (100%)	1151 (100%)	858 (100%)

stratum, with 22.2 individuals (n=55, SE=23.9). The mean school size estimates are not significantly different one from each other, when compared with paired t-tests.

Night sampling results

The nocturnal acoustic results are first given for the nights of 14–15 and 20–21 August 1996 (Fig. 4a). The nocturnal survey protocol was continued until 8.00 am in both cases, with the visual sighting conditions becoming good around 7.00 am.

On 15 August, the sampling was conducted from 3.35am southward from the port of Antibes, some distance off the shelf break, then southwestward, and then northward into a submarine canyon (Fig. 4a). The canyon's head was reached at 6.15am and a reverse path was followed until 7.50am. Striped dolphins were often heard along the path, east of the Cap d'Antibes and around the shelf break of the Lerins Islands: 69% of the 32 acoustic samples were positive. A group of 6 striped dolphins was visually observed at 7.40 am.

On 21 August, the sampling was conducted from 3.45 am northeastward across the continental slope, then southwestward to the shelf break off the Cap d'Antibes and then to the 500 m isobath (Fig. 4a). Striped dolphins were heard discontinuously along the path: 45% of the 43 samples being positive. A group of 4 striped dolphins was observed at 6.56 am. It is worth noting that Risso's dolphins were also detected acoustically, and subsequently sighted.

The other set of data was obtained during the night of 3–4 July 1997 (Fig. 4b), when zig-zag sampling started at 9.20 pm from the 2000 m isobath and reached the 500 m isobath, northeast of the canyon sector, at 0.48 am. None of the 19 acoustic samples was positive during that first part

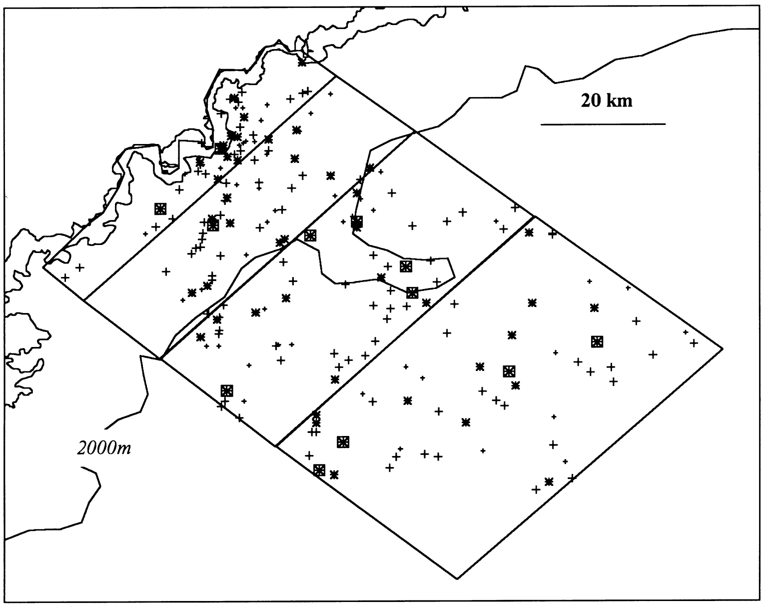

Figure 3. Sightings of striped dolphins (1–5 individuals: small cross; 6–20 ind.: large cross; 21–50 ind.: star; over 50 ind.: dark square).

of the survey. Then a series of parallel legs were sampled inside the semi-enclosed shape of the shelf break, ending at 7.55am. From these 31 acoustic samples, 26% revealed the presence of striped dolphins, which were briefly sighted bow-riding at 4.58 am and 5.06 am, close to the Cap de Nice. A school of 18 dolphins was observed at 6.55 am off the 200 m isobath near the mouth of the Var river, displaying a behavior typical of feeding activity, and echolocating.

In spite of the limited amount of data, the nocturnal presence of the striped dolphins close to the continental shelf is clearly shown in the area of study. Further nocturnal samplings conducted in other sites largely confirms this picture (Gannier, 1996; 1997*a*). The absence of positive listenings in the outer part sampling of the 3–4 July 1997 is striking. If we exclude the possibility of the dolphins remaining silent (or undetected), this might indicate either that striped dolphins had already moved to nearshore waters during the first half of the night, or that dolphins were still farther offshore when the sampling started.

The night acoustic cues were generally a continuous series of echolocating clicks ('clicks forest'), but whistles and other sounds were sometimes audible as well. Underwater noise was sometimes a major problem in the areas closest to shore, where anthropogenic noise may sometimes have overrun weak dolphin signals.

Spatio-temporal variation of relative abundances

The overall distribution picture is obtained by pooling the data across all four time periods: the relative abondance index (dolphin/km) is expressed for the four geographical strata (Table 2). The open sea stratum appears to be the most favourable stratum with an index of 2.32 dolphin/km (SE=0.60), while 1.43 dolphin/km (SE=0.35) are observed in the off-shore area, 0.73 dolphin/km (SE=0.20) in the slope area, and 1.46 dolphin/km (SE=0.47) in the near-shore stratum. The differences between results in adjacent areas are statistically significant (t-test, $P<0.01$).

The temporal variation of the distribution is then investigated by comparing the relative abundance indices obtained in each stratum for the successive time periods (Table 3).

In the near-shore stratum, there is a substantial decrease from the morning index (2.01 d/km, CV=42%), when it is the highest value among the four strata, to the midday index (1.27 d/km, CV=45%), and then to the lowest value found in the afternoon (0.25 d/km, CV=79%). Then, a relative increase is found from the afternoon to the evening index (0.98 d/km, CV=67%). This temporal variation seems statistically significant, when successive values are compared (t-test, $P<0.01$). A further nocturnal increase of the striped dolphin presence can be deduced from the differing evening and morning estimates (Fig. 5).

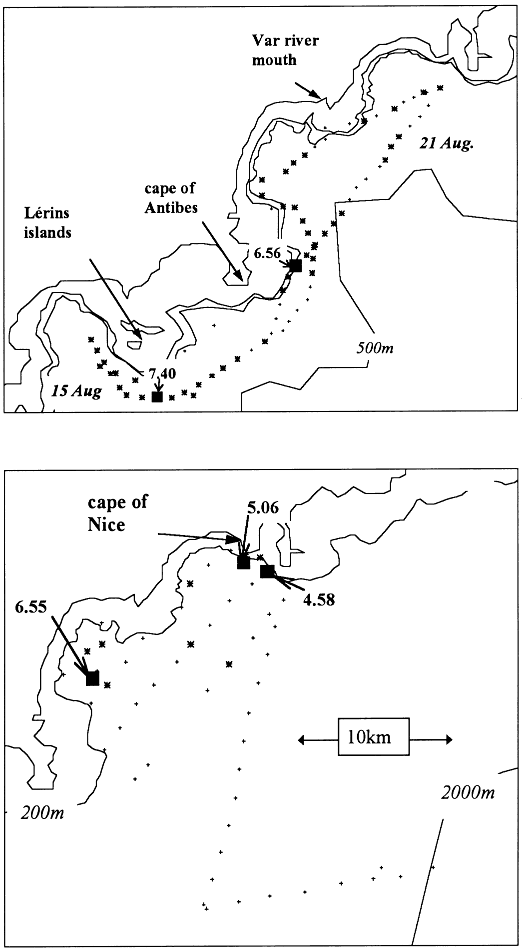

Figure 4. Night sampling results in August 1996 (top) and in July 1997 (bottom) (negative acoustic samples are figured by small crosses and positive contacts by stars; black squares are visual sightings).

Table 2. Spatial variation of the relative abundance. (the mean is expressed in dolphin per km, mean and SE are 'Pennington' estimates)

Stratum	N Samples	N no. 0	Mean (P)	S.E. (P)
Near-shore	394	45	1.46	0.47
Deep slope	377	48	0.73	0.20
Offshore	254	61	1.43	0.35
Open sea	159	55	2.32	0.60

In the deep slope stratum, the lowest relative abundance index is obtained in the morning (0.50 d/km, CV=47%) and midday (0.49 d/km, CV=37%). A slight, but significant increase (t-test, $P<0.02$) is then apparent during the afternoon (0.71 d/km, CV=46%), and more substantially from the afternoon to the evening (1.10 d/km, CV=61%), when the presence of dolphins in this stratum is at the highest (Fig. 5).

Table 3. Temporal variation of the relative abundance (mean is in dolphin/km, mean and SE are 'Pennington' estimates)

Stratum	N samples	Mean (P) dolphin/km	S.E. (P) dolphin/km
Near-shore morning	114	2.01	0.84
Near-shore midday	147	1.53	0.58
Near-shore afternoon	69	0.25	0.20
Near-shore evening	64	0.98	0.66
Deep slope morning	75	0.50	0.23
Deep slope midday	133	0.49	0.18
Deep slope afternoon	116	0.71	0.33
Deep slope evening	53	1.10	0.67
Offshore morning	21	1.19	0.82
Offshore midday	116	1.10	0.24
Offshore afternoon	100	2.34	0.72
Offshore evening	17	0.73	0.45
Open sea morning	16	1.05	0.46
Open sea midday	38	1.53	0.79
Open sea afternoon	65	1.82	0.74
Open sea evening	40	4.07	1.76

In the offshore stratum, moderate and not significantly different indices are obtained for the morning (1.19 dolphin/km, CV=69%) and midday periods (1.10 d/km, CV=22%). The relative abundance reaches its highest level during the afternoon period, with an index of 2.34 dolphin/km (CV=31%), and seems then to decrease steeply during the evening (0.73 d/km, CV=62%). The successive variations from the midday period to the evening are statistically significant (t-test, ($P<0.01$) Fig. 5).

In the open sea stratum (Fig. 5), the index increases significantly from the morning (1.05 dolphin/km, CV=44%) to the midday (1.53 dolphin/km, CV=51%), and then to the afternoon value (1.82 dolphin/km, CV=41%). A still higher relative abundance is found during the evening, when the index is very high (4.07 d/km, CV=43%).

This period by period analysis shows a quite coherent picture of the habitat use:

—the near-shore stratum is apparently a nocturnal concentration area, where striped dolphins feed, and is progressively deserted by the animals from the morning to the afternoon,

—the deep slope stratum can be regarded as a transit area, crossed by the dolphins during the course of the day (when they go farther offshore)

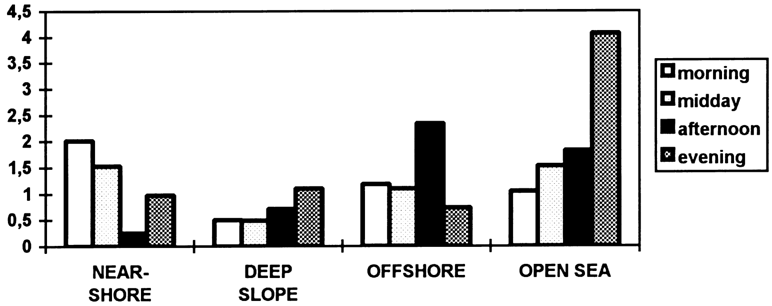

Figure 5. Temporal variation of the distribution in the four strata (relative abundance indices in dolphin per km).

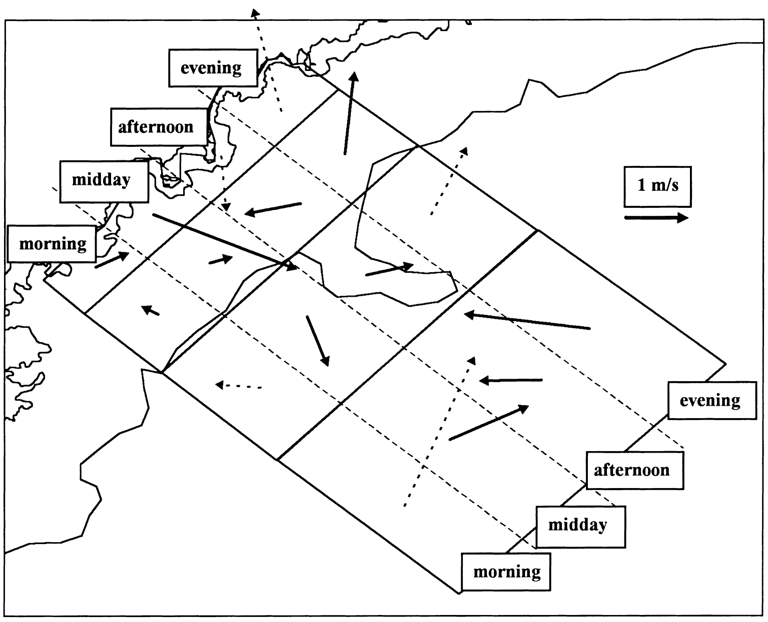

Figure 6. Description of the movement patterns for the four periods of the day (average vectors are figured for every spatial stratum and every time period and drawn in solid line when the number of records exceeds 6).

and, supposedly, from the evening to the middle of the night,
—the offshore stratum always shelters numerous striped dolphins, but apparently receives additional schools, proceeding from inshore areas, during the afternoon,
—the open sea stratum is always an area favoured by striped dolphins, the increase of occurrence during the evening is not clearly explained by our scheme.

This habitat use description is quite consistent with the results of the nocturnal acoustic samplings: the nocturnal feeding in near-shore waters is indicated by the high proportion of positive acoustic samples in this stratum, mostly signaling echolocation activity. The negative acoustic samples in the deep-slope stratum may corroborate the opinion that dolphins are mainly using this area for transiting between the near-shore and the offshore strata.

Daily variation of the dolphins movements
Relevant information on movements were obtained in a total of 146 cases: 32 in the near-shore stratum, 42 in the deep slope area, 43 in the offshore stratum and 29 in the open sea area. In a number of cases,

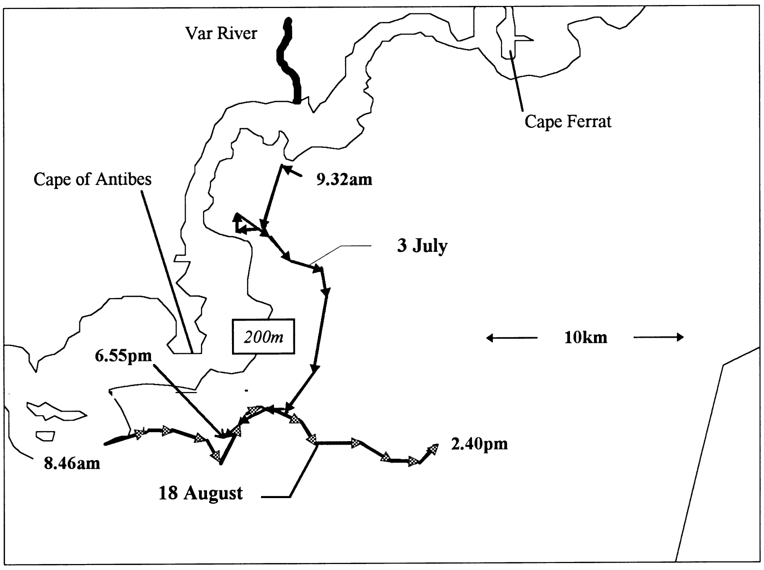

Figure 7. Results of two visual tracking experiments (3 July, from 9.32am to 6.55pm; 18 August from 8.46am to 2.40pm).

the average movements are of low amplitude, indicating that different groups of dolphins were moving in various directions. This is noticeably the case for the morning period (6.00 am–10.00 am), when the only high amplitude movement is found for the open sea area, but results from only 6 records (Fig. 6). During the midday period (10.00 am–2.00 pm), the average movement in the near-shore stratum is definitely towards offshore areas (with a mean speed of 1.45 m/s), while the movement is weak in the deep slope stratum, and moderate and parallel to the coast line in the open sea (Fig. 6). During the afternoon (2.00 pm–6.00 pm), average movements are of moderate amplitudes and variable directions in every stratum. However, none of the average vectors have a strong radial component relative to the general coastline (Fig. 6). During the evening (6.00 pm–10.00 pm), the average movements show a strong inshore component in three of the strata, the highest amplitude being found in the open sea stratum (Fig. 6). This descriptive analysis of movement patterns is in agreement with the main features of the temporal variation of the distribution, which shows an offshore shift of the population from the morning to midday, and an inshore shift starting during the afternoon.

Visual tracking of striped dolphin schools
In 1997, three boat tracking attempts occurred, two of which being considered successful (Fig. 7). On 3 July, a school was detected at 9.32 am, well in the near-shore stratum, apparently in feeding activity close to the 200 m isobath. The school was followed until 6.45 pm, when it was lost close to the deep slope stratum, moving to the southwest, along side the continental slope. The school was not disturbed by any boat traffic. On 17 August, a school was detected at 7.17am in the near-shore stratum, but the tracking was interrupted at 12.30 am, after the dolphins suffered repeated harassment from several recreational boats. At that time, the dolphins were heading offshore. On 18 August, a school was detected at 8.48 am in the near-shore stratum, the dolphins apparently feeding. They were followed up until 2.40 pm, when the dolphins were visually lost, while in the deep slope stratum and heading offshore.

Two of these observations confirm the basic trend shown above: after the feeding activity ceases during the morning, the school heads offshore. On two occasions, the dolphins were successfully followed until they reached the deep slope stratum, when the visual (and acoustic) contact was interrupted. The amplitude of the offshore movement could not be verified with these experiments. It is possible, however, that the school which we followed on 3 July had already completed its offshore movement at the time of losing contact.

In summary, the distribution of striped dolphins off of the French Riviera displays a clear temporal shift: from the morning to the afternoon period, the relative abundance index in the near-shore stratum falls steeply, and that in the offshore stratum increases (Fig. 5). The analysis of movement patterns confirms this trend and the visual tracking of a few schools supports this scheme (Fig. 7). During the evening, an increase of the near-shore frequentation is observed, consistent with an average inshore movement. The nocturnal acoustic sampling indicates that feeding activity takes place in the near-shore stratum, particularly along the shelf break. The deep slope area appears to be more like a transit area, with a relative abundance peaking in the afternoon. The offshore stratum appears like an afternoon resting area, while the open sea always shelters numerous schools of dolphins.

Discussion

Most distribution studies in the Northwestern Mediterranean have so far been large scale (Notarbartolo di Sciara *et al*., 1993; Gannier, 1999). The distribution has previously been expressed in relation to the bathymetry: when the bottom depth was sorted into four categories (0–500 m, 500–1000 m, 1000–2000 m, over 2000 m), the relative abundance was found to be considerably higher in deep offshore sectors than in shallower inshore areas the depth (Gannier, 1998*b*). The high relative abundance presently found in the open sea stratum is well in agreement with this previous analysis. In that early study, the '0–500 m' stratum was not found to be favoured by striped dolphins (Gannier, 1998*b*), but the present results in the near-shore stratum applies for a deeper area, with depth ranging from 200 m to 1300 m (Fig. 1). Furthermore, the former results were obtained for a wider part of the Liguro-Provencal Basin, area in which topographic features such as canyons and steep slopes are sometimes absent. A large increase of coverage and data was gained in 1995–96–97 before obtaining the present result, particularly in the near-shore stratum.

Effort heterogeneities may still affect our results, as it is true that our sampling is not as reliable as a dedicated stratified zig-zag pattern. But in the case of our study, pre-designed strata were difficult to determine successfully, because the distribution picture comes from a post-stratification process whose strata limits were unknown *a priori*. Zig-zag patterns can be successfully designed in future studies.

Our distribution results outline two main concentration areas: the near-shore and the open sea. It is clear from acoustic data that feeding occurs intensively in both areas, echolocating signals being overwhelming from 1–3 h before sunset to 1–3 h after sunrise. Stomach contents studies in the Ligurian Sea show that the striped dolphin feeds opportunistically, some preys items being of greater importance (Würz and Marrale, 1993): this is the case of the gadoid fish *Micromesistius poutassou* and of the ommastrephid squid *Todarotes sagittatus*. Other important prey in the Mediterranean Sea include epipelagic and mesopelagic fishes (Viale, 1985; Würz and Marrale, 1993), as well as oceanic squids of the genus *Histioteuthis* (Pulcini *et al*., 1992), or numerous other squid species (Blanco *et al*., 1994).

On one hand, the continental shelf break is a favoured area for several species of cephalopods, since they perform seasonal migrations across the slope during their reproductive cycle (Sanchez, 1986). It is also an area favoured by medium sized predator fishes such as gadoid (Fisher *et al*., 1987). On the other hand, the open sea area of the Ligurian Sea is known to shelter an abondant biomass of the euphausiid *Meganyctiphanes norvegica* (Casanova, 1974; Orsi Relini *et al*., 1994) and the diet of the *Histioteuthis* oceanic squids includes euphausiid crustaceans (Clarke, 1966).

Andersen and Sardou (1992) and Andersen *et al*. (1992) have shown that vertical distributions of many micronecton and macroplankton species feature a diel migration cycle, with many organisms undertaking a 100–500 m vertical migration to spend the night in the superficial layers. This vertical distribution shift is apparently exploited by the striped dolphin community during the night feeding sessions (Gannier, 1996; 1997*b*): the nocturnal increase of the striped dolphin acoustic activity (Gordon *et al*., in press) is well in agreement with the simultaneous increase of biomass availability.

The sharp decrease of the striped dolphin relative abundance which occurs in the near-shore stratum from the morning to the afternoon is linked to an off-shore movement as shown from the descriptive analysis of movement patterns (Fig. 6). Movements at speeds of 6–10 km/hr to distances of 8 to 15 kilometers off the Cap d'Antibes (*i.e.* in the deep slope stratum) were observed before trackings were interrupted, in the afternoon (Fig. 7). Interactions with the recreational boat activity were also observed, apparently interfering with the normal behavior of the dolphins. Can we attribute the daily distribution shift of striped dolphins to some kind of anthropogenic activity avoidance? Much quieter areas can usually be found by the dolphins some 5–10 km off the capes, even in summer. However, the extent of the apparent shift (Fig. 5) is much larger than necessary for such a purpose.

There are at least two other possibilities to explain the distribution change. A first option involves dolphins leaving the open sea during the evening for the 'near-shore night feeding ground', on an opportunistic mode, and moving back offshore the next morning to join the rest of the community. The other option involves several particular schools of dolphins performing the inshore-offshore migration cycle, and implies a degree of site fidelity. Both options are equally consistent with the observed distribution shift. The second one appears more likely, since the efficient exploitation of near-shore resources by dolphins might be favoured by site fidelity, due to their useful experience of local topographic and hydrologic features. A 2–3 h daily migration scheme is compatible with the 8 h of time available between the morning and the evening. It must be motivated by some serious reason, because of the energetic cost involved. The quest for additional food resources available offshore cannot be ruled out. But, the daily migration might also be performed by striped dolphins feeding in the near-shore waters in order to meet and socialize with the striped dolphins feeding in the open sea: furthermore, two distinct population components may exist. This rather speculative hypothesis makes some sense if one remembers that only a fraction of the striped dolphins population winters in the area of study (Gannier and Gannier, 1997*a*). The wintering animals are regularly observed in near-shore waters (Gannier, 1998*b*). The possibility of a division of the striped dolphin population into two components may therefore be forwarded: one component would be mainly feeding inshore and be yearly resident in the area, and the second one would be mainly feeding offshore and migratory. This hypothesis will remain speculative until suitable investigations, such as photo-identification studies, are conducted.

Conclusion

This study describes an important aspect of the striped dolphins habitat use off the French Riviera: the shelf edge is intensively used by dolphins during nocturnal feeding. The daily offshore migration is also well apparent, with a distribution shift of about 20 km between the morning and the afternoon, and is in agreement with the described movement patterns. Several questions are rised on the motivation of this diel distribution cycle and its eventual link with anthropogenic activities. The distribution results also call the nature of the population in question: the possibility of two distinct population components cannot be discarded. Complementary studies with other methodologies, either proven, such as photo-identification studies, or advanced, such as radio tracking, may be necessary to address these questions.

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