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REGIONAL DIVERSITY IN THE SOCIAL VOCALIZATIONS OF SPERM WHALE IN THE MEDITERRANEAN SEA

Violaine DROUOT^{1,2,3}, John C. GOOLD² & Alexandre GANNIER^{1,3}

RÉSUMÉ

Récemment, les techniques acoustiques ont permis de mieux étudier la répartition et l'écologie du cachalot en mer Méditerranée. Parmi les vocalisations du cachalot, les « codas », composés de séries de 3 à 20 clics émis suivant un rythme constant, sont utilisés comme moyen de communication au sein des groupes. Un type de coda composé de 4 clics (« 3 + 1 » coda) a longtemps était considéré comme l'unique coda utilisé par les cachalots de Méditerranée. Cependant, les données recueillies lors d'études conduites dans différentes régions de Méditerranée de 1997 à 2001 nous ont permis de rejeter cette hypothèse. Au total, 751 codas ont été analysés, provenant de 13 groupes de cachalots détectés dans le Sud du bassin occidental, en mer Tyrrhénienne et mer Ionienne. Les codas ont été classés en catégories pré-définies, en se basant sur la mesure de l'intervalle de temps entre les clics formant le coda (ICI). Les codas comprenaient entre 3 et 11 clics, ceux incluant 4 clics étant les plus abondants. Les codas étaient en majorité construits sur une « racine » commune de 3 clics réguliers. Les résultats ont permis de décrire un répertoire de codas relativement diversifié et démontrent des variations régionales entre différents bassins de Méditerranée, suggérant une ségrégation des groupes. De plus, la différence entre le répertoire décrit dans cette étude et celui observé dans d'autres régions du monde conforte l'hypothèse d'un échange limité entre les cachalots de Méditerranée et ceux de l'océan Atlantique.

SUMMARY

Passive acoustic techniques combined with visual survey have been used to study Sperm Whale ecology in the Mediterranean Sea. Among Sperm Whale vocalizations, the "codas" consist of series of 3 to 20 clicks emitted in a distinctive temporal pattern and believed to have a communication function. It has been reported that coda repertoire of Mediterranean Sperm Whales was restricted to a "3 + 1" coda pattern. Results obtained during extensive acoustic surveys between 1997 and 2001 in different regions of the Mediterranean Sea let to rule out that assumption. 751 codas were analysed from 13 groups of Sperm Whales from the south-western basin, the Tyrrhenian Sea and the Ionian Sea. The temporal patterns of these codas were analysed by measuring the inter-click intervals, and codas were sorted into differ-

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ent pre-defined pattern categories. The codas ranged from 3 to 11 clicks, with the 4-click codas being the most common. The majority of codas embedded a "root" of 3 rapid and consistent clicks. Codas sharing this common root seemed to conserve a consistent click timing and differed only by the number of final clicks. These results evidence a more extensive coda repertoire than previously reported, and suggest some regional variations between different basins of the Mediterranean Sea. Although some similarities in the coda structure were observed with other parts of the world, in term of frequency of occurrence, the Mediterranean coda repertoire described here appears distinct from those reported from other oceans, suggesting limited exchange between the Mediterranean Sea and the Atlantic Ocean.

INTRODUCTION

The Sperm Whale (*Physeter macrocephalus*) is one of eight common cetacean species in the Mediterranean Sea (Duguy, 1991). Research has been carried out to map their distribution, using visual and passive acoustic techniques and regional variations in relative abundance have been evidenced (Gannier *et al.*, 2002). Among regions of high Sperm Whale abundance, some areas such as the north-western basin (the Gulf of Lions particularly) appear to be foraging grounds for the species while other areas such as the Balearic Islands, the central Tyrrhenian Sea and the Greek Islands appear to provide suitable conditions for breeding and rearing of young. A segregation of males and groups of females seem to take place in the Mediterranean Sea, with females and young likely to be restricted to higher temperature.

Passive acoustic techniques have also been used to relate Mediterranean Sperm Whale distribution to local topography, to assess the size of its distribution in the whole basin, and to study its main ecological and ethological aspects. In this paper, we focus on the social vocalizations of Sperm Whales to assess variations in the "dialect" used by Mediterranean populations.

Sperm Whales are known to emit different types of vocalizations which are made of series of clicks. These vocalizations have been termed "regular clicks", "slow clicks", "chirrups" and "codas" and differ mainly by the rate at which clicks are emitted. The codas are series of 3 to 20 clicks matching a distinctive and repetitive pattern (Watkins & Schevill, 1977). Codas have been identified as social vocalizations and are believed to play a major role in acoustic communication, although their function is not well understood. Extensive coda repertoires are usually emitted from group of socializing whales, generally when at the surface (Whitehead & Weilgart, 1991; Gordon, 1987; Watkins *et al.*, 1985), although codas have also been heard during prolonged dives.

In the Mediterranean Sea, a single coda pattern has been identified on several occasions (Borsani & Pavan, 1994; Pavan *et al*, 1996). This coda is constructed of 4 clicks and is described as a (3 + 1) coda, because the last click is emitted with substantial inter-click interval compared to the first three clicks. It has been hypothesized that this (3 + 1) coda pattern is the dominant pattern for Mediterranean Sperm Whales. For a long time one single coda pattern (3 + 1) had been thought to be the unique coda of the Mediterranean, although other codas were reported on few occasions (Pavan *et al*. 2000; Borsani & Pavan, 1994).

It has been suggested that the coda repertoire can be regionally specific (Watkins *et al.*, 1985; Gordon, 1987, Weilgart & Whitehead, 1997) and it has been demonstrated that genetically related individuals share similar coda dialects (Whi-

tehead *et al.*, 1998). Therefore, we might anticipate that group and/or region specific coda repertoire could reflect limited exchanges of Sperm Whale for generations.

We present a description of the codas recorded during summer surveys spanning over 5 consecutive years in different regions of the Mediterranean Sea in order to compare the coda repertoire of Mediterranean Sperm Whales with those described in other oceans and to assess any regional variations within the Mediterranean basin itself.

MATERIAL AND METHODS

SURVEY EQUIPMENT AND FIELD RECORDING

From the survey vessel, a 12 metre motor-sailer with a 80HP diesel engine, discrete acoustic recordings of Sperm Whale groups were performed during summer surveys between 1997 and 2001. Recordings were made with a stereo hydrophone (IFAW and MAGREC) during all surveys except for 1998, where a mono hydrophone of similar specification was used (HP 30MT, Magrec Ltd, England). The hydrophone sensitivity was about 89.10-6 mV per Pa and the frequency response was linear (+/– 2 dB) from 1 Hz to 25 kHz. The hydrophone was towed behind the vessel on a 100 m cable. A high-pass filter, generally set on 1 kHz, was used to improve the listening and recording quality. The output of the hydrophones was directly connected to a TCD-7 DAT recorder (or a Sony WMD6 analog tape recorder on some occasions).

LABORATORY DATA ACQUISITION

The DAT recordings were initially sorted aurally, through headphones, to locate on the tapes good quality recording sessions and the different types of vocalizations. Codas were distinguished from other sounds principally by their distinctive and repetitive click patterns. Sequences including codas were sampled onto a computer hard-disk using a Cambridge Electronic Design (CED) 1401 laboratory interface (Goold & Jones, 1995). The analog line output from the DAT recorder was connected to the sampler input and signals redigitized for storage on disk. A sampling frequency of 62.5 kHz was chosen. The recordings were sampled in sequences of 3 minutes, defined by memory and computer hard disk limitations. The sequences contaminated with low frequency background noise were filtered digitally with a 2 kHz, high-pass FIR filter to clarify the click signals.

LABORATORY ACOUSTIC ANALYSIS

Coda analysis was based on the measurement of Inter-Click Intervals (ICI). Coda measurements were performed from the waveform display, using CED Spike 2 software V.4.70. The onset of each click in a coda was marked manually with a cursor in the waveform channel and the corresponding time values of each cursor position was logged into a file by the software. Inter-click intervals were

then calculated by simple subtraction as Δt between each click. This procedure also gave the complete coda length, as the difference between first click and last click. The *absolute* inter-click interval (ICI) was defined as the time interval between the onset of two consecutive clicks (Goold & Jones, 1995; Weilgart & Whitehead, 1992) and the *standardized* ICI was obtained by dividing each interval by the coda duration (Weilgart & Whitehead, 1993; Moore *et al.*, 1993). The standardized timing pattern — or rhythm — has been used in recent studies to discriminate different coda patterns (Weilgart & Whitehead, 1997; Pavan *et. al.* 2000).

CODA CLASSIFICATION

Assigning each coda to a particular pattern was difficult because variations appear in both the number of clicks forming the coda (coda type) and in the rhythm of the clicks (coda pattern). Codas have a degree of variation that makes it difficult to draw distinct boundaries between patterns. Thus different automated sorting methodologies were attempted. First, a standard k-mean analysis, in which coda types are treated separately and sorted into fixed number of cluster "k" was used, based on the work of Weilgart & Whitehead (1997). Secondly, based on the work of Rendell & Whitehead (2003) who evaluate different methods of comparing coda repertoire, the Variance Ratio Criterion method (Calinski & Harabasz, 1974) and the Duda & Hart's (1973) ratio criterion were used to help determining the number of clusters to be used in cluster analysis. However, these methods appeared to be inappropriate to sort the Mediterranean data, since no consistent clustering was obtained. It was therefore decided to base the coda classification on pre-defined pattern categories, as described below.

Codas were first sorted into regular and irregular codas. Codas were defined as regular when all ICI's were considered as equal, i.e.: neither 50% greater nor 50% smaller than the average ICI of the coda (Weilgart & Whitehead, 1993). In contrast, if one ICI was at least 50% greater than the mean ICI between the previous regular ICI of that coda, the clicks were considered as irregular. In the case of irregular codas, further analysis was carried out to better define the click pattern. Among the irregular codas, it was noticed that a majority were initiated by 3 consistent and relatively rapid and regularly spaced clicks, which was defined as a common root (Weilgart & Whitehead, 1993). Coda pattern classification was based on the presence/absence of a common root and on the relative proportion of the ICI of this root compared to the following ICI, as follows (Fig. 1):

- (1) Regular codas: all clicks evenly spaced (all ICI equal);
- (2) "3 +" codas: 3 first clicks evenly spaced ($ICI_1 = ICI_2$), forming a root, and the following clicks have greater ICI than the average ICI of the root (($ICI_1 + ICI_2$)/2):
- (3) "3 ++" codas: similar to "3 +" codas, but with the click following the root having ICI more than 3 times the length of the average ICI of the 3-click root;
- (4) *Undefined* codas: codas not falling into any of the three categories described above.

For this classification, *equal* ICIs refer to ICIs of length neither 50% greater or 50% smaller, otherwise, the ICI were considered as having different length.

Within each category, codas were discriminated into coda *types* (*i.e.* 3-click codas, 4-click codas, etc), according to the total number of clicks they include. Temporal changes associated with the addition of clicks within each coda pattern

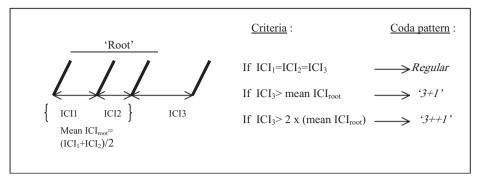


Figure 1. — Schematic illustration of the coda classification used, taking the 4-click coda as example. Each "/" represents a click.

were investigated. This classification enabled comparison of codas with different numbers of clicks, in contrast with the other methods where codas are primarily sorted into coda types.

REGIONAL CODA REPERTOIRE

For each region where codas were heard, the coda repertoire was determined using the relative frequency of each coda pattern and regional variations were assessed. Emphasis was given to the 4-click codas, which were the most frequent codas recorded. A ternary plot, which includes 3 axes for the 1st, 2nd and 3rd ICI of the codas (standardized ICI), was drawn in order to visualize regional clustering in the dataset.

RESULTS

CODA DATASET DESCRIPTION

Codas were recorded only from groups of Sperm Whales *i.e.* when more than 2 animals were detected acoustically or observed visually. No coda was heard from isolated animals. Codas were always heard together with other social vocalizations, such as "chirrups", "rapid clicks" and "squeals". The dataset counts 751 codas analysed. These codas came from thirteen distinct acoustic sequences among which eleven were associated with the observation of the whales at the surface (Table I). Each recording session was considered as a separate group encounter. As photo identification was not systematically undertaken, recordings from each sighting were treated separately and no attempt was made to assess between-group variations. However, on some occasions off the Balearic islands, the same group, or at least some individuals, were believed to have been sighted several times over a period of one week. The data come from different regions of the Mediterranean Sea: 60% of the codas were recorded from the Ionian Sea, 34% from the south-western basin and 6% from the Tyrrhenian Sea (Fig. 2). In the Ionian Sea, codas were recor-

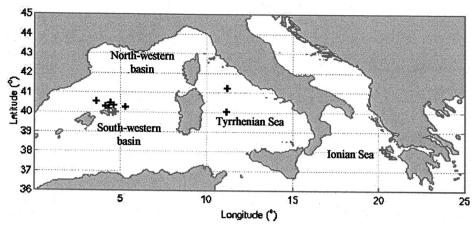


Figure 2. — Map of the Mediterranean Sea showing the position of the centre of the acoustic sequences, where codas were recorded.

Table I

Details of Sperm Whale acoustic recording sessions when codas were heard.

Tyr: Tyrrhenian Sea, Io: Ionian Sea, Sw: south-western basin

| Date Year . Aseq | Region | Latitude | Longitude | N codas | Frequency % | N animals | Comment | |
|------------------------|--------|----------|-----------|------------|-------------|--------------|-------------|--|
| 1998.02 | Tyr | 40°05'35 | 11°07'82 | 41 | 5.5 | 5 | sighting | |
| 1998.05 | Io | 37°54'49 | 20°25'53 | 167 | 22.2 | 7 | sighting | |
| 1999.11 | Sw | 40°23'95 | 3°48'06 | 17 | 2.3 | 7 | sighting | |
| 1999.12 | Sw | 40°08'33 | 4°17'54 | 6 | 0.8 | 4 | sighting | |
| 1999.14 | Sw | 40°15'07 | 5°09'05 | 58 | 7.7 | 7 | sighting | |
| 2000.01 | Tyr | 41°13'07 | 11°09'52 | 3 | 0.4 | 5 | No sighting | |
| 2000.02 | Io | 38°00'44 | 20°19'74 | 275 | 36.6 | 5 | sighting | |
| 2000.03 | Io | 37°49'07 | 20°34'22 | 7 | 0.9 | 3 | No sighting | |
| 2001.04 | Sw | 39°58'45 | 4°27'82 | 64 | 8.5 | 4 | sighting | |
| 2001.05 | Sw | 39°56'13 | 4°29'85 | 7 | 0.9 | 5 | sighting | |
| 2001.06 | Sw | 40°03'20 | 4°21'98 | 26 | 3.5 | 5 | sighting | |
| 2001.07 | Sw | 40°06'27 | 4°18'83 | 41 | 5 | 6 | sighting | |
| 2001.08 | Sw | 39°57'12 | 4°28'87 | 39 | 5.29 | 6 | sighting | |

ded from three groups during 1998 and 2000 surveys (Table I). Codas from the Tyrrhenian Sea were recorded from two groups during 1998 and 2000 surveys. In the south-western basin, groups producing codas were encountered in 8 occasions, mainly around the Balearic Islands, in 1999 and 2001.

The recorded codas contained between 3 to 11 clicks. Codas with many clicks were less common than those with a few clicks. The most common was the 4-click coda (66.8% of the data set), followed by the 5-click coda (14.1% of the data set) and the 3-click coda (8.4%). The 6-, 7- and 8-click codas contributed about 3.0% each. The 9-, 10- and 11-click codas were rare, accounting for just 1.7% of the data.

DIFFERENT CODA PATTERNS

From all codas, 7.5% showed a regular pattern of clicks with all coda types represented excepted the 9-click coda (Table II). The rest of the codas (92.5%) did not show equal click spacing, however, 72.2% of the codas tended to match the predefined "3 +" or "3 ++" patterns.

Table II

Frequency of the pre-defined coda pattern per coda type (codas with a given number of clicks), expressed as a percentage of the total number of codas of each type. N = number of codas

| Pattern | N | 3-click codas | 4-click codas | 5-click codas | 6-click codas | 7-click codas | 8-click codas | 9-click codas | 10- click codas | 11- click codas | Total |
|------------|-----|------------------|------------------|------------------|------------------|------------------|------------------|------------------|-----------------------|-----------------------|-------|
| Regular | 56 | 12.70 | 6.37 | 8.49 | 9.09 | 4.35 | 9.09 | 0 | 50.00 | 33.33 | 7.46 |
| "3 +" | 333 | 0 | 47.61 | 52.83 | 40.91 | 60.87 | 50.00 | 37.50 | 50.00 | 0 | 44.34 |
| "3 ++" | 209 | 0 | 40.44 | 4.72 | 4.55 | 0.00 | 0 | 0.00 | 0 | 0 | 27.83 |
| No pattern | 79 | 87.30 | 5.58 | 33.96 | 45.45 | 34.78 | 40.91 | 62.50 | 0 | 66.67 | 0.37 |

Of all the codas, 44.3% followed a "3 +" pattern (Table II) where the first 3 clicks were evenly spaced and the subsequent clicks showed ICI of twice the length of the initial regular ICI. The "3 +" root was predominant among the 4-, 5-, 6-, 7- and 8-click codas (Table II). Among these codas matching a "3 +" pattern, 71.8% were 4-click codas, with the last click occurring after an interval representing approximately half of the whole coda duration, i.e. matching a 1:1:2 click ratio and referred as a "3 + 1" codas. The "3 ++" pattern was found in 27.8% of all codas (Table II). Almost all codas of this category (97.1%) were 4-click codas ("3 ++ 1") where the three first clicks were rapid and usually emitted within about a quarter of

the total coda duration. This "3 ++" root was also found, to a lesser extent, in 5-click and 6-click codas. Of all codas analysed, 20.4% did not fall into the pre-defined categories.

The absolute click timing of the different patterns identified among the 4-click codas are shown in Figure 3 as they appeared to be the most abundant codas recorded in the survey and to allow comparisons to be undertaken with the "Mediterranean" 4-click codas reported in previous studies. Two main clusters were observed among the "3 + 1" codas: "short" (around 200ms duration) and "long" codas (around 600 ms duration) were clearly distinguishable. In contrast, the "3 ++ 1" codas showed a striking consistency in both the timing and total duration, particularly in the 3 first clicks forming the root.

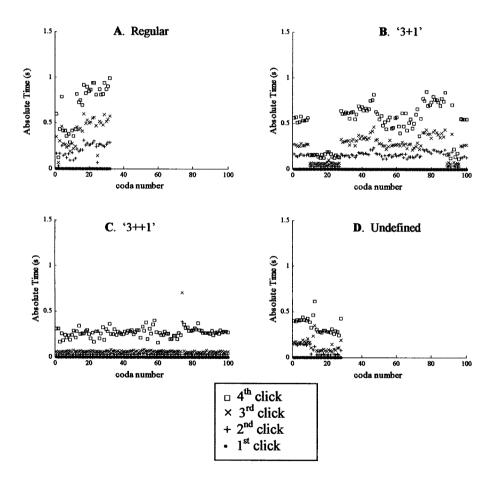


Figure 3. — Plot of the click timings of the 4-click codas recorded over the Mediterranean Sea, sorted by pattern: (A) Regular codas, (B) "3 + 1" codas, (C) "3 ++ 1" codas and (D) codas with undefined pattern.

From the variation of the mean click timing it can be observed that codas with different number of clicks but constructed on either the "3 +" or the "3 ++" pattern showed a striking timing conformity (Fig. 4 B&C). In fact, within each pattern category, codas were nearly identical in click spacing and differed only by the number of additional clicks.

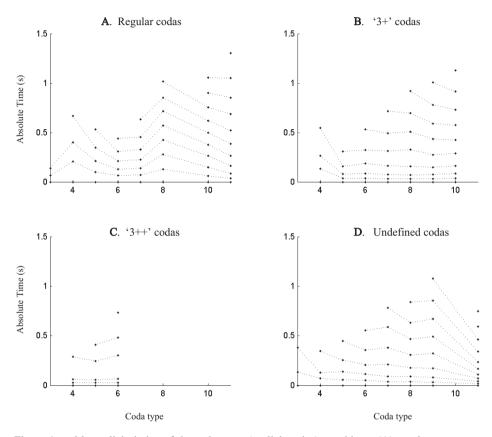
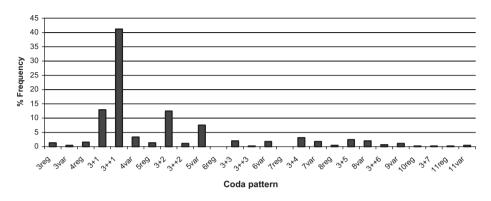


Figure 4. — Mean click timing of the coda types (n-click codas) matching a (A) regular pattern, (B) "3 +" pattern, (C) "3 ++" pattern and (D) undefined pattern.

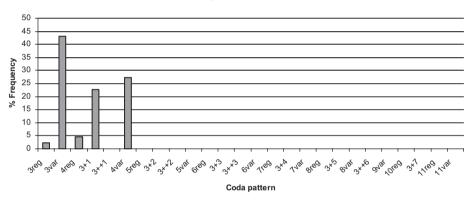
REGIONAL VARIATION IN CODA REPERTOIRE

Overall, groups recorded in the Ionian Sea displayed the greatest variability in their coda repertoire, with 24 categories of coda patterns identified (Fig. 5A). Codas recorded from the Ionian Sea varied from 3 to 11 clicks. The most common pattern observed in this region was the "3 ++ 1"coda which represented 41.2% of the codas analysed. Two other patterns were also well represented: the "3 + 1" codas (12.9%) and the 5-click codas embedding the "3 +" root (12.5%). The codas recorded in the Tyrrhenian Sea accounted for 5.3% of the codas analysed. The coda

A. Ionian Sea



B. Tyrrhenian Sea



C. South-western basin

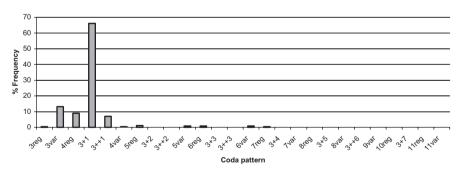


Figure 5. — Distribution of coda patterns in the 3 regions where codas were recorded: (A) Ionian Sea, (B) Tyrrhenian Sea and (C) south-western basin. Nreg refers to regular coda, with N number of clicks, Nvar refers to N-click codas with undefined pattern. "3 + n" and "3 ++ n" refer to codas embedding a "3 +" root, followed by n clicks.

repertoire was less diverse and included five defined coda patterns among the 3-click and 4-click codas which were the only coda type observed in this region (Fig. 5B). The most common codas were those matching an irregular 3-click pattern (43.2% of the codas recorded in this region), followed by the "3 + 1" codas (22.7%). In the south-western basin, where 34.3% of all our codas were recorded, the coda repertoire was also quite rich, with 11 categories of coda pattern recognized (Fig. 5C). Codas had a maximum of 7 clicks, although those containing more than 4 clicks were relatively rare (3.9% of the codas) in this region. The majority (82.5%) of the codas recorded in the south-western basin were 4-click codas, and 66.3% matched a "3 + 1" pattern. The second most frequent codas were the irregular 3-click codas, which accounted for 13.2% of all codas recorded in this region. The 5-click, 6-click and 7-click codas were present although relatively rare, and all included some regular form (other patterns were undetermined).

Thus the greatest variability in coda repertoire was observed in recordings from the Ionian Sea and the south-western basin, while the coda repertoire identified from the Tyrrhenian Sea groups was relatively restricted. Within these three regions, the 4-click codas were the most common although considerable variations were observed within this coda type. The "3 + 1" pattern was being the most common in the Tyrrhenian Sea and south-western basin while the "3 ++ 1" pattern was dominant in the Ionian Sea.

When assessing the variations in the standardized click timing of these 4-click codas without taking any classification into account, a clustering appeared clearly between the 4-click codas obtained from the south-western basin and those recorded in the Ionian Sea (Fig. 6). In the south-western basin, the 4-click codas mainly matched a 1:1:2 ratio, corresponding to the "3 + 1" pre-defined pattern, whereas in the Ionian Sea most of the 4-click codas had a first and a second ICI representing each 10% and the third ICI 80% of the all coda duration, thus matching the "3 ++ 1" pattern.

DISCUSSION

During this study, most recordings were associated with the observation of the animals at the surface. The recorded groups showed surface behaviour identified as socializing activity, as opposed to prolonged dives related to feeding activity. This is consistent with other studies, although codas from diving animals have also been reported (Gordon, 1987; Whitehead & Weilgart, 1991; Pavan *et al.*, 1996).

Previous studies suggest a single coda pattern to predominate in the Mediterranean Sea. Pavan *et al.* (2000) measured 136 codas from dispersed locations in the Mediterranean Sea (Ligurian, Tyrrhenian and western Ionian Seas) over a 12 year period: nearly all codas matched a "3 + 1" click pattern such as the one described in this study and two "miscellaneous" codas matched a 5-click pattern. Our data suggest a much wider coda repertoire than previously suspected in the Mediterranean Sea, including the "3 + 1" pattern, typically considered as the "Mediterranean" coda pattern. However, this "Mediterranean" pattern, while predominant in coda repertoires of the Tyrrhenian Sea and south-western basin, was poorly represented in the recordings from the Ionian Sea. Borsani & Pavan (1994) first described a "3 + 1" coda pattern from diving Sperm Whales in the Mediterranean Sea, which had a mean duration of 1,051 ms (SD = 42.6, N = 44). Pavan *et al.* (1996)

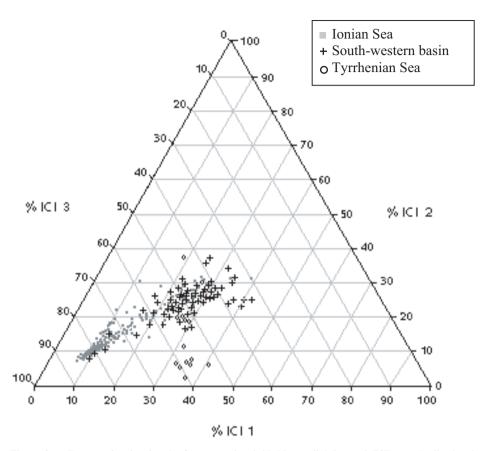


Figure 6. — Ternary plot showing the first, second and third Inter-click Interval (ICI), standardized and expressed as a percentage of the total coda duration, of all 4-click codas analysed, with coda of each region plotted with a different symbol.

recorded a similar "3 + 1" coda pattern with variations in the coda length, including "short codas" of 486 ms (SD = 15.6) duration. The "3 + 1" codas we recognized in most recording sequences (from 200 ms to 600 ms duration) were similar to the "short coda" previously recorded by Pavan *et al.* (1996), although a great deal of variation was observed.

Although the "3 + 1" pattern constitutes a major component of the Mediterranean coda repertoire, the notion of a single, restricted coda pattern in the Mediterranean Sea is not supported by our results. The coda diversity revealed here is in sharp contrast to previously documented studies in the Mediterranean Sea. The increased diversity observed might be due to the conditions when codas were recorded between the different studies. Previous studies were dealing with data recorded during long dive of Sperm Whales (Borsani & Pavan, 1994; Pavan *et al.*, 2000), while the recordings used in this study were performed from social groups. The difference in recording context might well be of significance if Sperm Whales might use a more complex coda repertoire during these "socializing" periods. Whitehead

& Weilgart (1991) have shown that an extensive coda repertoire was associated with the presence of tight groups at the surface.

Some similarities were observed between the Mediterranean codas and the codas recorded from Sperm Whales off the Galapagos Islands (Weilgart & Whitehead, 1993). First, the intervals between the final clicks were always longer than the intervals between the initial clicks (either twice or four times the length). The reverse trend was observed by Moore *et al.* (1993) in the south-eastern Caribbean, where longer ICI intervals occurred generally at the beginning of the coda. Second, some of the codas contained a consistent sequence of regular clicks, that could be seen as a common "root". In our recordings, this common root was the 3 rapid clicks upon which the "3 +" and "3 ++" patterns were constructed. Hence, our analysis of Sperm Whale codas in the Mediterranean Sea displays a structural complexity similar to that demonstrated in at least one other geographical area (Weilgart & Whitehead, 1993).

In general within each coda type, the clicks forming the root showed little variation from one coda to the other, while the final clicks were much more variable. It could be suggested that different type of information might be coded in the root and the final clicks. When considering all coda types, the codas embedding the same root differed mainly by the number of clicks added after the root, which tends to support the hypothesis that information contained in the coda is coded in both the rhythm and the number of clicks.

Some of the coda patterns described in this study are similar to those reported in other oceans such as the "3 + 1" coda and the regular 5-click codas obtained in the Galapagos (Weilgart & Whitehead, 1993). The regularly-spaced five-click coda was relatively rare in our recordings but seems to be common to different areas of the world ocean, such as the West Indies (Moore et al., 1993), where it represents a dominant pattern, the Galapagos (Weilgart & Whitehead, 1993), and the northwestern Atlantic (Watkins & Schevill, 1977). In contrast, the "3 + 1" pattern dominant in the Mediterranean Sea, has been rarely reported in world oceans (e.g. 1.5% of the Pacific codas reported by Weilgart & Whitehead, 1997). Although some coda patterns are common to those of Sperm Whales in other oceans, it is suggested that Mediterranean Sperm Whales have a coda repertoire, in terms of frequency, that is fairly distinct from other regions. Several authors have suggested that geographically variations might exist in coda repertoire (Gordon, 1987; Borsani & Pavan, 1994), whereas genetic studies supported that similarities in coda repertoire might result from maternal transmission of the coda repertoire through generations (Whitehead et al., 1998). Differentiation in the Mediterranean dialect might reveal a restricted exchange between groups of females and their offspring living in the Mediterranean Sea and those of the adjacent ocean. Genetic studies tend to confirm this hypothesis as Sperm Whales living in the Mediterranean Sea appear to constitute a distinct maternal entity from those of the adjacent North Atlantic Ocean (Drouot et al., in prep.).

Furthermore, the study suggests some regional variation in coda repertoire between different basins of the Mediterranean Sea. In particular, the coda repertoire from the Ionian Sea appears to differ from the Tyrrhenian sea and the south-western basin, displaying a higher proportion of a specific pattern (*i.e.* "3 ++ 1" codas). This is consistent with the gregarious behaviour of female Sperm Whales and the topography of the Mediterranean Sea, where the shallow (400m) Strait of Sicily effectively divides the region into two distinct eastern and western basins. However, since regional comparisons were based on relatively few groups within each region, these

data need to be complemented to confirm any discrimination within the Mediterranean Sea. These results should be regarded as preliminary. For a regional comparison to be meaningful, one has to be confident that (i) codas were representative of the whole group (and not biased by a single individual emitting codas), (ii) that the groups sampled in each region had the same probability of emitting codas, and (iii) that the entire coda repertoire was adequately sampled (similar recording conditions/whale activity). Our data are unlikely to fulfil adequately these criteria, thence further research is encouraged to test the hypotheses brought up in this study.

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