Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context

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Abstract: Sperm whale (*Physeter macrocephalus* L., 1758 (= *Physeter catodon* L., 1758)) codas serve a communication function, but the message they carry remains unknown. Very few codas and extremely few coda types are available from males. For 7 years we studied the coda occurrence and the coda types produced by 15 males in different behavioural and encounter contexts. Of the 67 encounters, 615 codas were produced by nonsolitary males. Codas occurred in 60% of the nonsolitary encounters and 36% of the dive cycles. Four hundred and ninety codas have been categorized into 8 coda families and 25 distinctive coda types. Both the coda type used and the dive cycle phase in which codas occurred strongly depended on the behavioural context. This is the first time that coda types have been associated with particular behavioural contexts. The "Three plus" family coda types were mainly used by ascending or descending whales in feeding dive cycles. The "Regular" and "Progressive" families were used almost exclusively by interacting whales. The "Root" coda family was used exclusively at surface, mainly in altered dive cycles. The coda types used in these three behavioural contexts seem to carry different messages and are proposed to be named "dive cycle codas", "social codas", and "alarm codas", respectively.

Résumé : Les codas produites par les grands cachalots (*Physeter macrocephalus* L., 1758 (= *Physeter catodon* L., 1758)) jouent un rôle dans la communication, bien qu'on ne comprenne pas le message qu'elles véhiculent. Chez les mâles, on connaît très peu de codas et extrêmement peu de types de codas. Nous avons étudié pendant 7 ans la présence et les types de codas chez 15 mâles dans des contextes différents de comportement et de rencontre. Lors de 67 rencontres, nous avons noté 615 codas toutes produites par des mâles non solitaires. Des codas ont été produites lors de 60 % des rencontres de non solitaires et de 36 % des cycles de plongée. Quatre cent quatre-vingt-dix des codas ont été regroupées en 8 familles et 25 types distincts. Le type de coda utilisé et la phase du cycle de plongée pendant laquelle la coda est produite sont tous les deux associés à des contextes comportementaux particuliers; c'est la première fois qu'on établit une telle association. Les types de codas de la famille « trois plus » sont surtout utilisés par des cachalots qui plongent ou qui remontent durant un cycle de plongée alimentaire. Les familles « régulière » et « progressive » de codas sont utilisées presque exclusivement lors d'interactions entre les cachalots. La famille de codas « racine » sert exclusivement en surface, principalement lors de cycles de plongée altérés. Les types de codas utilisés dans ces trois contextes comportementaux semblent véhiculer des messages différents et nous proposons de les désigner respectivement les « codas du cycle de plongée », les « codas sociales » et les « codas d'alerte ».

[Traduit par la Rédaction]

Introduction

Male and female sperm whales (*Physeter macrocephalus* L., 1758 (= *Physeter catodon* L., 1758)) emit sharp, impulsive clicks with a variety of repetition rates, especially during their deep, foraging dives (Weilgart 1990; Jaquet et al. 2001; Madsen et al. 2002*b*). The presence of stereotyped "sequences of clicks which are repeated several times" among sperm whale vocalizations was first noted by Backus and Schevill (1966). Named codas, these sequences are composed of 3 (or possibly less) to about 20 clicks, last about 0.2–5 s, and constitute the most interesting click pattern of the sperm whale (Whitehead 2003).

Sperm whales have a complex social structure, with females being the core of relatively stable social units (Christal et al. 1998) and males dispersing from their natal units and living more solitary lives (Whitehead and Weilgart 2000). Codas have been studied mostly from groups of female and immature whales socializing at surface or close to it (Watkins and Schevill 1977; Whitehead and Weilgart 1991; Moore et al. 1993; Weilgart and Whitehead 1993, 1997; Rendell and Whitehead 2003*a*, 2003*b*; Drouot et al. 2004; Marcoux et al. 2006; but for an exception see Pavan et al. 2000) and are believed to serve a communication function (Watkins and Schevill 1977; Weilgart 1990; Whitehead and Weilgart 1991; Weilgart and Whitehead 1993). Recently, Marcoux et al. (2006) suggested that in the context of social units codas are actually produced almost exclusively by mature females, and may be important in

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forming and maintaining sperm whale associations between females.

Studies from different locations have reported 23 (Weilgart and Whitehead 1993), 28 (Moore et al. 1993), 47 (Weir 2003), 26 (Drouot et al. 2004), and 25 (Nuuttila 2004) coda types, although the number of coda types identified may depend on the methods used. The analysis of a large set of codas in two oceans revealed 70 coda types (Whitehead 2003). At the level of the ocean basin, sperm whale social units can be assigned to vocal clans with their own coda repertoires (Rendell and Whitehead 2003a). Vocal clans may share common coda types; however, the frequency of occurrence of each coda type differs among vocal clans. Based on the presumed matrilineal transmission of coda repertoires by one generation to the next within sperm whale social units, Rendell and Whitehead (2001) concluded that these "dialects" constitute nonhuman culture.

Despite the progress made, the message carried by codas remains unknown. Until now, no coda type (or group of coda types) has been associated with particular sperm whale behaviour, and it is unknown whether the distinctive coda types serve different communication needs. Furthermore, it is not known if the two sexes and their different age classes produce the same coda types or use codas in the same way. In this study, we followed photo-identified male sperm whales visually and acoustically. The frequency of occurrence and the codas types that they produced in various contexts have been analyzed with three objectives: (1) to understand when and how frequently males produce codas, (2) to examine if the coda repertoire of males is as rich in coda types as that of the social units, and (3) to investigate if the use of coda types depends on the behavioural context.

Materials and methods

Field data collection and data acquisition

Fieldwork was carried out from 1998 to 2004 (237 days at sea) as part of the long-term "Greek Sperm Whale Program". Encounters with sperm whales were made from a 13 m sailing vessel or a 16 m motor vessel along the Hellenic Trench, Greece. Fieldwork spanned two seasons (June–October), only during the daytime. Both males and social units were encountered (see Frantzis et al. 2003), but only encounters of males were studied in this work.

All the sightings of the same individual made during the same day were considered to be one encounter. While tracking the whales and during all encounters, the sea surface was continuously scanned by at least two experienced observers by naked eye and binoculars, 360° around the research vessel. The time of appearance at the surface (usually noticed by the first blow), the time of fluking (i.e., the act of raising the flukes above the surface before starting a deep, feeding dive), and all other distinctive visible or audible (such as the first and last regular echolocation clicks) behaviours of the whales were recorded in a log to the closest second. After surfacing, the focal whale was gradually approached and photos were taken to allow individual photo-identification. The approach followed a standard procedure (for guidelines on sperm whale watching see International Fund for Animal Welfare (IFAW) 1996), which minimizes any possible disturbance to the whales.

This consisted mainly in never positioning the vessel in front of the whale, never moving faster than 1–2 knot (1 knot = 1.852 km/h) at close distances (<300 m), minimizing the noise produced by the engine, never changing direction suddenly, approaching always from behind, and keeping a minimum distance of 100–150 m. The whales showed no signs of disturbance apart from a few cases where they shallow dived (i.e., they dived a few metres below the surface without fluking) to move a little bit farther away, or to approach and inspect the research vessel.

In >90% of cases, codas and dive cycles could be immediately assigned to a particular whale or pair of interacting whales because of their sound level. In these cases, the codas or the regular clicks heard or recorded were loud and clear; therefore, they could originate only from the focal animal or pair that was tens or few hundreds of metres away from our hydrophone. Any other whale present was more distant and was providing much lower signal level coming from few or several kilometres away. Furthermore, the combination of simultaneous visual and acoustic observations and three characteristics of the male sperm whale dive cycle facilitated the assignment of codas to particular whales. These characteristics are (i) the consistent pattern of the sperm whale's dive cycle, both visually and acoustically, allowing the prediction of the whales' arrival at and departure from the surface and of their first and last regular clicks; (ii) the fact that no codas are produced during the regular clicking phase of the dive cycle; and (iii) the independence, and therefore rarity, of synchrony in the dive cycles of male whales. When a doubt remained regarding the assignment of some codas, a detailed analysis was performed. This analysis was based either on (i) the bearing of the received signal through the two hydrophones, the vessel's course, and the whales' positions, or (ii) on the interpulse interval of the coda clicks, which correlate with the whale's size (see below). Coda recordings and dive cycles that could not be assigned with certainty to a known male whale were discarded.

Sperm whales were tracked through a towed two-hydrohone array. High-pass-filtered (250 Hz filter break, –12 dB per octave roll off) signals from the array were recorded by a DAT recorder (Sony TCD-D8, 16 bits, 48 kHz sampling frequency) connected to the array. Recordings were played back on a desktop DAT (Sony PCM-R700) and digitally transferred to PC "wav" files. These files were then imported into Sound Forge version 4.5 software package, where codas were detected acoustically and visually using the waveform. If any of the clicks was not clearly visible because of the low signal to noise ratio, the presence of coda was noted but no further analysis was conducted.

The onset of each coda click was marked manually on the waveform according to the following procedure: after locating the click pulse, the first sample point (accuracy of 0.021 ms) with level exceeding the variability range of noise was detected and the marker was placed on the immediately previous sample point. The marker data were subsequently compiled to yield interclick intervals (ICIs), defined as the time difference between the onset markers of two successive clicks, and coda durations, defined as the time difference between onset of the first and last clicks of each coda.

Table 1. Sperm whale (*Physeter macrocephalus*) encounter contexts observed during the present study.

Code	Encounter context	Description
A	Solitary male	A single male with no other sperm whales visually or acoustically detectable around him for at least 2 h before and 2 h after the moment of observation
B	Pair of males	Pair of young and apparently maturing whales separated by a few tens or hundreds of metres; often with synchronized dive cycles and occasionally in visual contact or even physically interacting between dives
C, B+C	Loose aggregation	Two to five single males spread in a radius of up to 10 km, following independent dive cycles without approaching each other at approximately <2 km (in case of B+C, two of these whales formed a "pair of males")
D	Male and social unit	One mature male close to or among a social unit; usually absent or kilometres away the day before and after its presence among the social unit was noted

Gender determination

All coda data originated from 15 male individuals. Their gender was determined by one or more of the following methods: (*i*) genetic analysis of sloughed skin, (*ii*) video or photographs of the genital–anal area, and (*iii*) acoustic estimation of a total length that exceeded 12.5 m (no females are this long; Rice 1989).

Genetic analysis for gender determination was conducted in the Department of Biological Sciences, University of Durham, Durham, UK, by D. Engelhaupt. Skin samples were collected from eight photo-identified individuals and their gender was determined using the ZFX/ZFY technique described by Berubé and Pallsbøll (1996). Male and female stranded sperm whales from the Greek Seas were included as controls for polymerase chain reaction (PCR) amplifications and yielded the expected results (Engelhaupt 2004).

During encounters with five different individuals, we had the opportunity either to take underwater photos or video, or to have them very close to the research vessel while they turned upside down. These were clearly identified as males from the observation of their genital area.

Sperm whale clicks are known to have a multipulsed structure with constant time difference between pulses, called interpulse interval or IPI (Møhl 2001). IPIs are very apparent and clearly defined in most coda clicks (Madsen et al. 2002*a*), and can be used to estimate the total length of sperm whales (Gordon 1991). Coda recordings from 10 of the studied sperm whales had high enough signal to noise ratio to allow the appearance of the clear multipulsed structure in the waveform of coda clicks. All peaks of consecutive pulses that could be unambiguously defined within any coda click were marked to the nearest sample point (0.021 ms). The marker data were subsequently compiled to yield IPIs defined as the time difference between consecutive pulse peaks. This method was very accurate, since the IPI range was equal or smaller than 3 samples (0.063 ms) in 38 out of 45 recordings and constant in the rest of the cases. IPIs extracted from coda recordings of the same individual were pooled together and their median was used as the best estimate of the IPI (Table 1). Total length (TL) was estimated using the empirical equation $TL = 4.833 + 1.453 \cdot IPI - 0.001 \cdot IPI^2$ (Gordon 1991), which has been shown to give accurate results (Drouot 2003).

The use of the alternative equation in Rhinelander and Dawson (2004) for comparative reasons was unsuccessful, since it provides aberrant results for IPIs below 4.55 ms. Very different IPIs (e.g., 3.38 and 5.35 ms) result in equal total lengths (12.59 m), and depending on values, a smaller IPI (e.g., 3.50 and 4.55 ms) may result in larger total lengths (12.53 and 12.36, respectively).

Encounter contexts and behavioural contexts

To study the frequency of occurrence and the timing of codas during the sperm whale dive cycle, data were divided into acoustic "cycle samples" encompassing the period between the last regular click of a dive and the first regular click of the next dive just after fluking. No codas were recorded or are known to be produced during the remaining period of the dive cycle, i.e., the regular clicking phase. Each cycle sample was divided into three phases (i.e., ascending, surface, and descending) delimited by the first appearance of the whale at surface and the fluking, defined as the closest second to the disappearance of the flukes' trailing edge under the surface. During each cycle sample, an experienced observer was continuously listening through the hydrophone and noted any occurrence of codas. The acoustic presence and the number of other than the focal, distant sperm whales were also noted from the first detection of a whale until the end of each day's fieldwork. In most occasions, recordings were made on DAT tapes so that codas could be further analysed a posteriori (Table 2). Data from encounters with no complete cycle samples but with codas produced at a known time of the dive cycle have been retained only for the timing analysis of coda occurrence during the ascending and descending phases (Fig. 1) and the coda-type analysis.

Cycle samples were categorized to one of the five encounter contexts defined in Table 1 (A–D), according to the acoustic and (or) visual presence of other sperm whales. A few encounters that lasted several hours were divided in two periods, each one with cycle samples categorized in a different encounter context. At least four different individuals were sampled in each encounter context, except in the D encounter context. Because of the very small sample size, the D encounter context was marginal in this study and did not affect the main results.

According to the male sperm whale activity observed in the field, cycle samples, phases of dive cycles that were partly sampled (e.g., missing ascending phase), and the corresponding coda data were categorized into three distinct behavioural contexts: (1) regular feeding dive cycle (RFDC);

Table 2. Data regarding the 15 studied male sperm whales.

Whale ID	Total length (m)	No. of encounters	Year of encounter	Encounter context	No. of codas produced	No. of codas recorded	No. of codas analysed
Repro	14.63	2	2002	D	7	7	7
Antonis	13.58	19	2000, 2001	A, C	8	7	6
Zeus	13.52	10	1999, 2000, 2002	A, C	46	28	26
Trypos	12.99	8	1998, 1999, 2000	A, C	53	53	53
Aris	12.55	2	2003, 2004	A, C	5	3	3
Stelios	11.49	3	2000	B, B+C, C	35	22	22
Filaretos	11.44	3	2000	B, B+C, C	98	93	91
Elpidoforos	11.15	1	2003	C	100	85	85
Patroklos	9.74	4	2000	B, B+C, C	68	27	26
Achilleas	9.54	5	2000	B, B+C, C	23	14	11
Pantelis	12.70*	1	2000	A	0	0	0
Lefkotrypos	(12.50–13.50)[†]	1	2003	A	0	0	0
Pan	(12.50–13.50)[†]	4	2002, 2004	C	3	2	0
Nestor	(12.50–13.50)[†]	2	2004	A, C	0	0	0
Manolis	(11.50–12.50)[†]	2	2001	C	3	3	3
Pair 1	9.74 and 9.54	(3)[‡]	2000	B, B+C	126	126	122
Pair 2	11.49 and 11.44	(1)[‡]	2000	B+C	40	40	35
Total	9.54–14.63	67	1998–2004	A, B, B+C, C, D	615	510	490

Note: Total lengths were estimated through coda interpulse intervals (IPIs). See Table 1 for an explanation of the codes describing the encounter context. Pair 1 consists of Patroklos and Achilleas, whereas pair 2 consists of Stelios and Filaretos.

*Total length measured directly when this whale stranded.

[†]A rough visual estimation of the total length.

[‡]These numbers are included in the No. of encounters of each individual participating in the pair.

(2) dive cycle altered (ADC) by our presence or by unknown reasons during its surface phase (behaviour switched to shallow dives and (or) head out, side fluke, lateral swim, vessel approach for inspection, and a breaching once); and (3) interaction between whales (IBW), defined as a close encounter allowing visual contact (approximately <25 m) or physical contact while at surface or just under it, and (or) synchronized dive cycle. Pairs of sperm whales performing almost synchronized dives but separated by many tens or a few hundreds of metres while at the surface were categorized as performing RFDCs.

The encounter contexts do not correspond to behavioural contexts, with the exception of the behavioural context IBW that can occur only within the framework of B or B+C contexts (Table 1). The behavioural contexts RFDC and ADC occurred in all encounter contexts. The numbers of individuals sampled in each behavioural context were 15 in RFDC, 9 in ADC, and 4 in IBC. The numbers of individuals that produced codas in each behavioural context were 12 in RFDC, 7 in ADC, and 4 in IBC.

Coda classification

Classifying codas and assigning each coda to a coda type are difficult tasks. Although promising methods have been recently proposed, tested, and applied (Rendell and Whitehead 2003*b*), there is no method that can classify codas in a fully automated, objective, and meaningful way independent of the data set (see Weir 2003; Drouot 2003; Nuuttila 2004). Because of (*i*) the relatively small data set in this study and (*ii*) the clear results that were obtained (see Fig. 5), we opted for an observer-based classification method.

Most studies base their coda classification and analysis on standardized codas (ICIs divided by the coda duration), since previous work has shown coda rhythm to be better preserved than tempo (Moore et al. 1993; Weilgart and Whitehead 1997). However, standardizing ICI data and discarding the information of coda duration has two weaknesses. It disguises the relatedness that may exist between codas containing different numbers of clicks, although they may originate one from the other through a deletion or an addition of one click (e.g., a 3+1 coda may arise by deleting the 4th click of a regular 5-click coda). More disturbingly, codas with very different durations can be pooled in one "artificial" coda type (for an example see Fig. 3B in Drouot et al. 2004 where 3+1 codas with similar rhythm are grouped together despite their very different durations of approximately 0.15 and 0.55 s). Standardization of the codas recorded during the present study grouped clearly different coda types (produced by the same individual in a single coda sequence) into a common coda type and separated codas that seem closely related. Therefore, no standardization and only absolute ICI data were used for coda analysis and classification.

Three criteria were used to classify codas: (1) the coda duration, (2) the pattern (or rhythm) of the click sequence within the coda, and (3) the number of the coda clicks. Codas were categorized into mutually exclusive "coda families" based on the first two criteria, and further classified into coda types according to their click number. The composite names given to each coda type consist of the family name (e.g., [Regular A]) and the "pattern name" (e.g., 5+1). For both the family and pattern names we followed existing definitions (Weilgart and Whitehead 1997; Nuuttila

Fig. 1. Timing of coda occurrence during the ascending and descending phases of regular feeding dive cycles of sperm whales (*Physeter macrocephalus*). The timing of codas is expressed as percentage of each phase duration, with the ascending phase usually eight times longer than the descending phase.
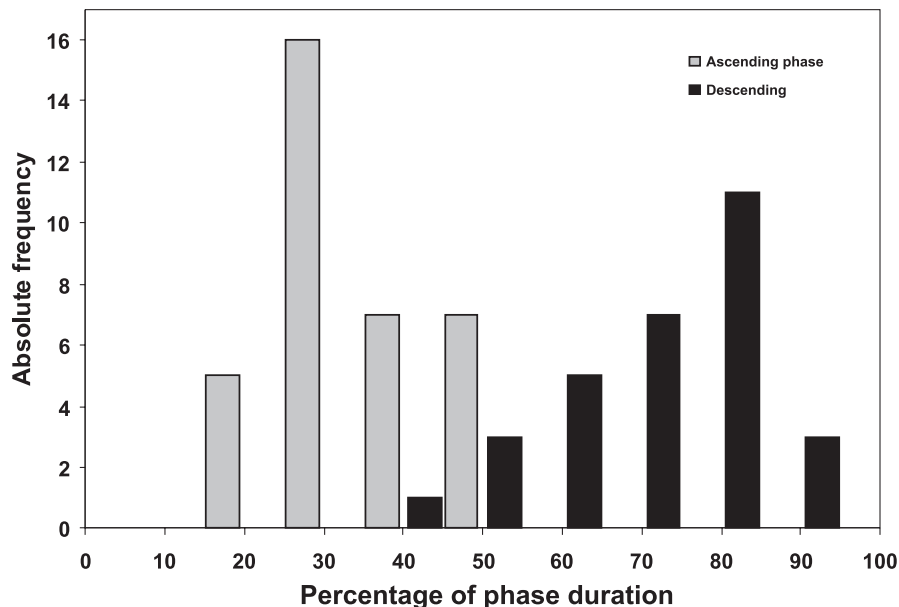
2004) slightly modified. The use of the "+" indicates a delay of one click from its expected, regular position in time. We use "+" once to indicate an ICI twice longer than the previous ICI, twice to indicate an ICI three times longer, and use an "→" to indicate an ICI four or more times longer than expected. Intermediate ICIs were assigned to the closest of the above categories. "Average coda types" (Fig. 2) were calculated by averaging the cumulative ICIs (equal to the time distance of each click from the first click) of all codas classified to the same coda type.

Codas composed of >12 clicks, hereinafter named "rapid codas" (because of their shorter average ICI than other codas), often have a high resemblance with chirrups. Since their click pattern is very rarely repeated, each one comes close to be a unique "coda type". Because of their high variety in tempo and pattern, it becomes meaningless to classify them into coda types. They seem to belong to a separate category of sperm whale sound commonly recorded from socializing social units of sperm whales (A. Frantzis and P. Alexiadou, unpublished data). Three "rapid codas" of 13 and 14 clicks recorded during this study were discarded from our coda analysis.

Results

Fifteen individual male sperm whales were identified during 67 encounters. A total of 615 codas were produced by 12 individuals of sizes ranging from 9.5 to 14.6 m. Among 510 codas recorded, 490 were of good enough quality to be further analysed and categorized into coda types. Detailed data regarding the sperm whales and the numbers of codas produced are given in Table 2.

Male sperm whales were encountered in five different encounter contexts described in Table 1, but also as young or immature members of social units (observations not included in this study). Two pairs of young males (Patroklos

and Achilleas, Stelios and Filaretos) were encountered three times and one time, respectively. The individuals forming each pair had similar total lengths (Table 2) and were also encountered as single whales being in acoustic contact (i.e., encounter context C) with their partner or with unidentified whales (who could be their partner) farther away.

### Frequency and timing of coda occurrence

While following the whales, 181 cycle samples were collected and categorized into 5 encounter contexts (Table 1) and three behavioural contexts (Table 3). In 49 cycle samples collected during 29 encounters, 434 codas were produced always when more than one whales were present. No codas were produced during any of the 66 cycle samples of "solitary males" (encounter context A) in 21 independent encounters.

The frequency of coda occurrence in cycle samples of RFDCs of all nonsolitary male encounter contexts (B, B+C, C, and D) was 36% ($N = 96$). However, when instead of cycle samples the entire encounter period was considered, the frequency of coda occurrence per encounter was 60% ($N = 40$). Furthermore, when the occurrence of codas was considered independently of the individuals who produced them, codas (by any of the whales present) occurred in 80% ($N = 40$) of nonsolitary male encounters.

To compare the frequency of coda occurrence between RFDCs and ADCs, cycle samples of encounter contexts B and C were grouped together. The frequency of coda occurrence was not independent of the behavioural context (χ^2 test: $\chi^2_{[1]} = 13.265$, $P = 0.0003$) and was much higher in ADCs (85%, $N = 13$) than in RFDCs (32%, $N = 85$). The number of cycle samples with interactions between whales was low and did not allow meaningful comparisons with the other behavioural contexts.

Large differences were observed among individual whales in both the frequency of coda occurrence and the number of

Fig. 2. Average coda types of all codas recorded by male sperm whales. The 25 coda types were classified in 8 coda families. The number of codas recorded from each coda type is in parentheses.
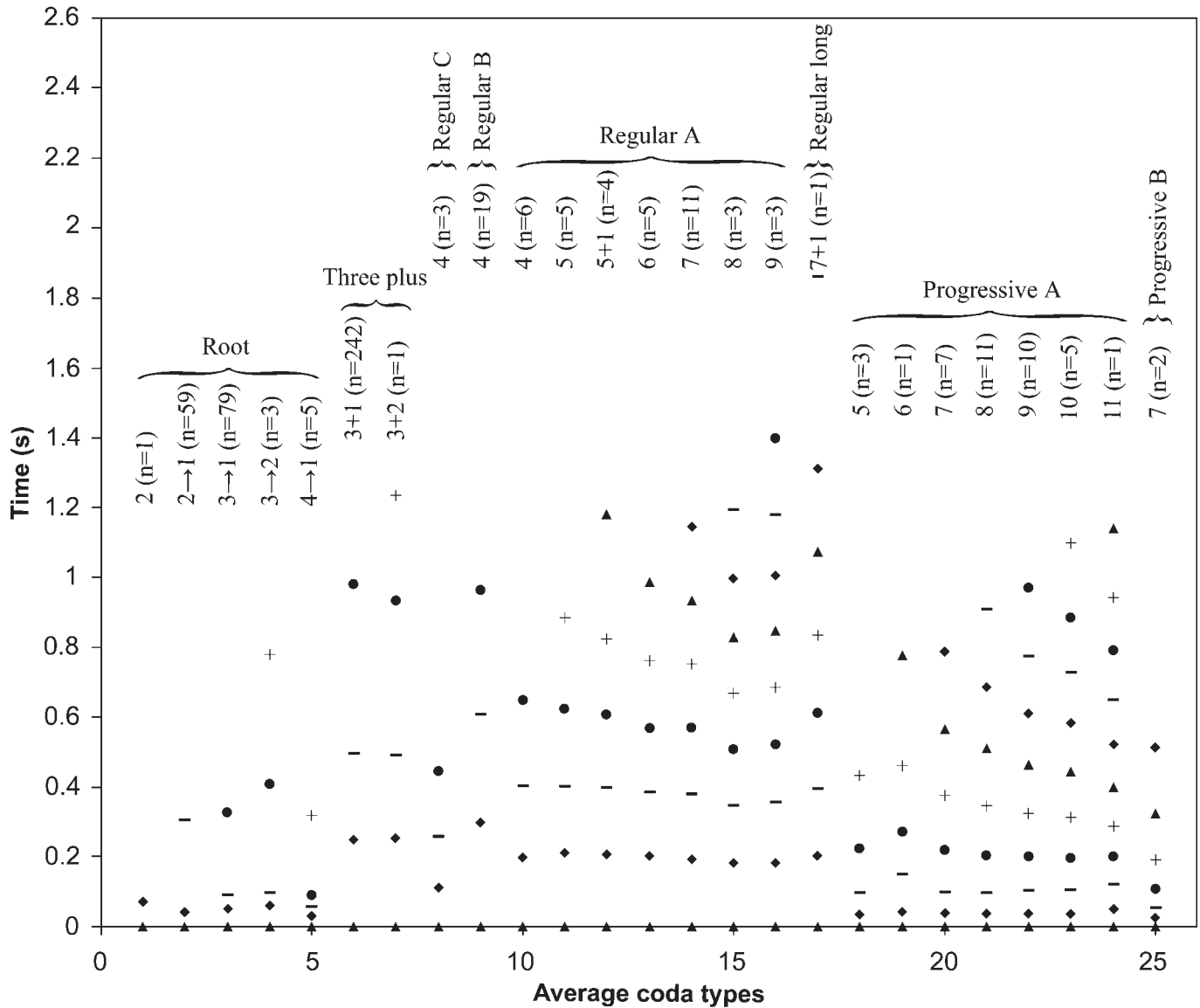
codas produced (Table 4). Considering only RFDCs and the three whales that were encountered more often, "Zeus" produced codas in 75% of its dive cycles when other whales were present around him, with an average of 2.7 codas per dive cycle. At the opposite extreme, "Antonis" produced codas only in 8% of its dive cycles, with an average of 0.2 codas per dive cycle.

Considering all behaviours and dive cycle phases together, the frequency of coda occurrence (Table 5) was not independent of the behavioural context and the phase of cycle sample (χ^2 test: $\chi^2_{[8]} = 46.861$, $P < 0.001$). In cycle samples of RFDCs, codas were almost exclusively produced during the ascending and descending phases. Codas occurred only once during the surface phase, in a cycle sample that was preceded and followed by ADCs. In a total of 35 cycle samples of RFDCs, codas occurred (*i*) either during the ascending phase or during the descending phase in 30 cases, (*ii*) during both the ascending and descending phases in 4

cases, and (*iii*) during both the ascending and surface phases in 1 case. Coda occurrence was not independent of the dive cycle phase (χ^2 test: $\chi^2_{[1]} = 9.785$, $P = 0.0018$), and was twice more frequent during the ascending phase (74%) than during the descending phase (37%).

In the behavioural contexts of ADCs or IBWs, codas were often produced during the surface phase (i.e., when interaction with our vessel or with another whale was taking place). During these behavioural contexts, the surface phase was almost always prolonged and the difference between the average surface phase of RFDCs (10.0 ± 0.4 min (mean ± SE), $N = 89$) and ADCs (19.9 ± 2.2 min (mean ± SE), $N = 11$) was highly significant.

When codas occurred in RFDCs, the average number of codas produced in the ascending phase (5.0 ± 4.3 (mean ± SD), $N = 26$) was significantly and almost twice as high as in the descending phase (2.6 ± 2.1 (mean ± SD), $N = 13$) of 35 cycle samples (Mann–Whitney U test: $U = 88.0$, $N_1 = 26$,

Table 3. Coda occurrence in cycle samples of male sperm whale collected during different encounter and behavioural contexts.

Encounter context	No. of encounters	Total no. of cycle samples	Behavioural context	No. of cycle samples per behavioural context	No. of cycle samples with codas	Percentage	No. of codas produced
A	21	66	RFDC	64	0	0	0
			ADC	2	0	—	0
B	2	12	RFDC	10	3	30	13 (4.3)
			ADC	2	2	—	10
B+C	4	15	RFDC	9	6	67	53 (8.8)
			IBW	6	3	50	42
C	36	86	RFDC	75	24	32	109 (4.5)
			ADC	11	9	82	202
D	1	2	RFDC	2	2	—	5 (2.5)
All	64	181	All	181	49	27	434

Note: Some encounters had periods belonging in different encounter contexts. For an explanation of the codes describing the encounter context see Table 1. RFDC, regular feeding dive cycle; ADC, altered dive cycle; IBW, interaction between whales. Numbers in parentheses represent the average of codas produced per cycle sample of RFDC. The average has no meaning for ADC and IBW, since the duration of the cycle sample varies a lot depending on the duration of the surface phase.

Table 4. Frequency of coda occurrence and number of codas produced by the three most often encountered male sperm whales, while one or more other whales were present.

Whale	Encounter context	No. of cycle samples	No. of cycle samples with codas	No. of codas	No. of codas per cycle sample
Antonis	C	26	2	4	0.2
Zeus	C	16	12	43	2.7
Trypos	C	4	1	18	4.5

Note: For an explanation of the codes of encounter context see Table 1.

Table 5. Frequency of coda occurrence during the three phases of cycle samples for the three different behavioural contexts of male sperm whales.

| Behavioural context	No. of cycle samples	Ascending		Surface		Descending	
		Coda occurrence	No. of codas	Coda occurrence	No. of codas	Coda occurrence	No. of codas
RFDC	35	26 (74)	130	1 (3)	16	13 (37)	34
ADC	11	6 (55)	83	8 (73)	93	7 (64)	36
IBW	3	0 (0)	0	1 (33)	4	2 (67)	38

Note: Coda occurrence is expressed in number of cycle samples, with percentages in parentheses. RFDC, regular feeding dive cycle; ADC, altered dive cycle; IBW, interaction between whales.

$N_2 = 13$, $P = 0.014$). This difference was even more accentuated in ADCs (ascending phase: 13.8 ± 8.4 (mean $\pm$ SD), $N = 6$; descending phase: 5.1 ± 4.2 (mean $\pm$ SD), $N = 7$; Mann–Whitney U test: $U = 4.5$, $N_1 = 6$, $N_2 = 7$, $P = 0.018$). However, it has to be noted that the descending phase (1.0 ± 0.1 min (mean $\pm$ 95% CI), $N = 86$) of a cycle sample is much shorter than the ascending phase (7.9 ± 0.3 min (mean $\pm$ 95% CI), $N = 86$), therefore the available time window for coda production is also much shorter. As a result, if coda production rates are compared, the picture is inversed and the descending phase (2.19 ± 1.10 codas/min (mean $\pm$ 95% CI), $N = 13$ and 2.51 ± 1.60 codas/min (mean $\pm$ 95% CI), $N = 6$) shows significantly higher rates than the ascending phase (0.67 ± 0.28 codas/min (mean $\pm$ 95% CI), $N = 19$ and 2.17 ± 1.39 codas/min (mean $\pm$ 95% CI), $N = 5$) for

RFDCs and ADCs, respectively (Student's t test). The number of codas produced during RFDCs ranged from 1 to 18 in the ascending phase ($N = 33$) and from 1 to 8 in the descending phase ($N = 19$). When all behavioural contexts are grouped, the maximum number of codas produced is 27 codas for the ascending phase and 13 codas for the descending phase.

Series of numerous codas produced by one whale were in most cases consisted of groups of codas separated by intervals of silence (see Pavan et al. 2000). This group pattern was observed mostly in the ascending phases and was not recorded in any surface phase. In most cases, codas were fairly regularly spaced within groups. This was also the case when a single group of codas was produced during ascending and descending phases. No pattern or regular spac-

Fig. 3. Spectrograms of two low-frequency moans from sperm whales. Many rapid clicks are visible in the first example. The sampling frequency was 48 kHz for both recordings. Fast Fourier transform size of 2048, Hanning window.
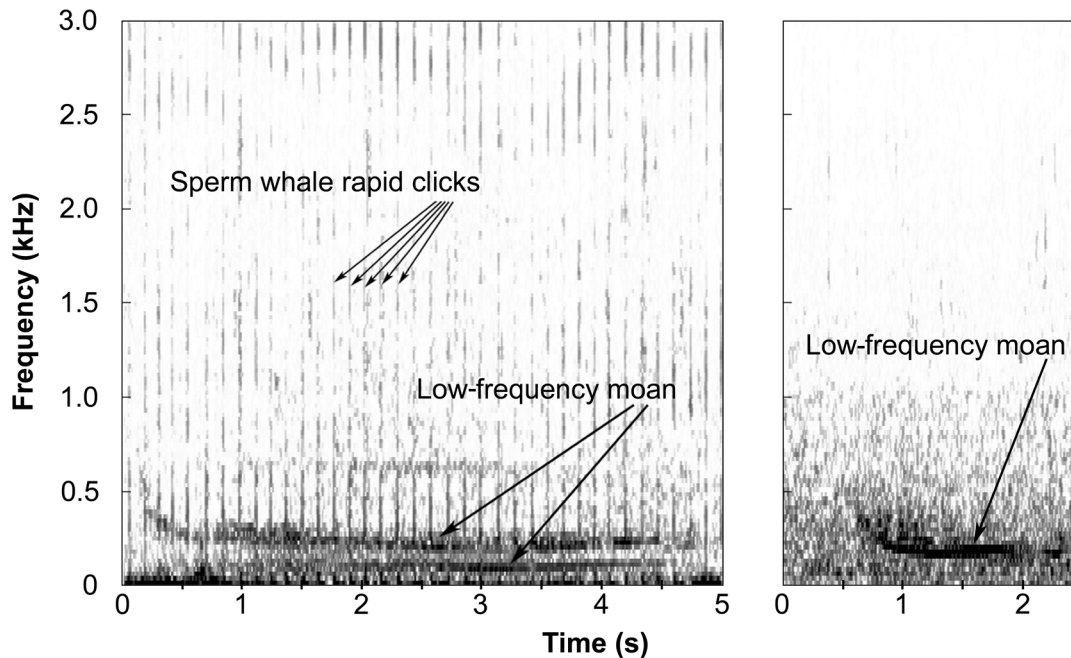
ing was observed in codas of the surface phase. In RFDCs, codas were mostly produced soon after and just before the regular click series, respectively, for the ascending and descending phases (Fig. 1). In the ascending phase, all codas occurred during the first 50% of the phase duration (soon after the last click). In the descending phase, codas occurred during the last 55% of the phase duration, and the majority of them just before the first click, between 80% and 90% of the phase duration (Fig. 1). In ADCs, the distribution of codas in time showed no apparent pattern for either the ascending phase or the descending phase, possibly because of the small sample size.

Occurrence of other sperm whale sounds

A total of 38 chirrups, 11 squeals (see Weir et al. 2007), 8 low-frequency moans, and 3 "rapid codas" were also recorded; all from subadult males (9.5–11.4 m long) during encounter contexts B, B+C, and C. All chirrups and squeals were produced by a pair of interacting whales (pair 1) on 2 different days, always in combination with codas. To our knowledge, low-frequency moans have not been reported before for sperm whales; however, we have recorded them repeatedly in the presence of socializing sperm whale social units (A. Frantzis and P. Alexiadou, unpublished data). Spectrograms of these sounds show that their frequency ranges mainly <300 Hz (Fig. 3). Moans were produced in 3 different days by the above-mentioned pair and independently by another whale, always a few seconds before or after a fluking. Finally, reverberating sounds very similar to slow clicks (as described by Madsen et al. 2002b) were recorded only once, in two sessions of 1.0 and 1.5 min separated by 5.5 min of silence and followed by silence. These clicks were produced by a distant whale (some 7 nautical miles away; 1 nautical mile = 1.852 km) that was reached and observed only 95 min later. A second whale became acoustically present (encounter context C) soon after the "slow

clicks". The average ICI of these clicks was 2.0 (range 0.8–7.8 s, N = 28) and 2.2 s (range 1.1–5.5 s, N = 41) for the two sessions, respectively. No trumpets were recorded in any of the 207 beginnings of deep dives, which is a surprising result when we consider the 49 occurrences of trumpet(s) in 279 dives studied by Teloni (2005) in the western Mediterranean.

Coda types and their use

All 490 analysed codas were classified into 25 coda types, subsequently grouped into 8 coda families (Fig. 2). Four coda families contained more than one coda types (from 2 to 7), and four families were represented by a single coda type. The [Root] family coda types had a starting "root" of two to four clicks separated by very short ICIs as a common characteristic. The root has a short duration almost always <0.15 s (usually <0.1 s) and is followed by one or rarely two last clicks separated from the root by ICIs 2–10 times longer than the root. In one coda type of this family, the [Root]2, no clicks follow the root. This coda type was produced only once, preceded and followed by [Root]2→1 codas, as if its last click was intentionally or mistakenly omitted by the whale. The [Three plus] family coda types start with three very regularly spaced clicks separated by about 0.25 s, which are followed by one click with a twice longer ICI. The four [Regular] families (A, B, C, long) consisted of codas of regularly spaced clicks, and the only difference among them is the tempo (the absolute ICIs). The [Progressive] families have codas that start with very short ICIs which gradually increase so that the last ICI is always the longest one (called "expanding" codas by Weir 2003 and Nuuttila 2004). Although this rule is valid for all average coda types of this family, some ICIs of a few codas may not have been longer than their previous ICI.

The frequency of occurrence was very variable for both the coda types (Fig. 2) and the coda families (Fig. 4). The

Fig. 4. Number of analysed codas for each of the eight coda families of male sperm whales.
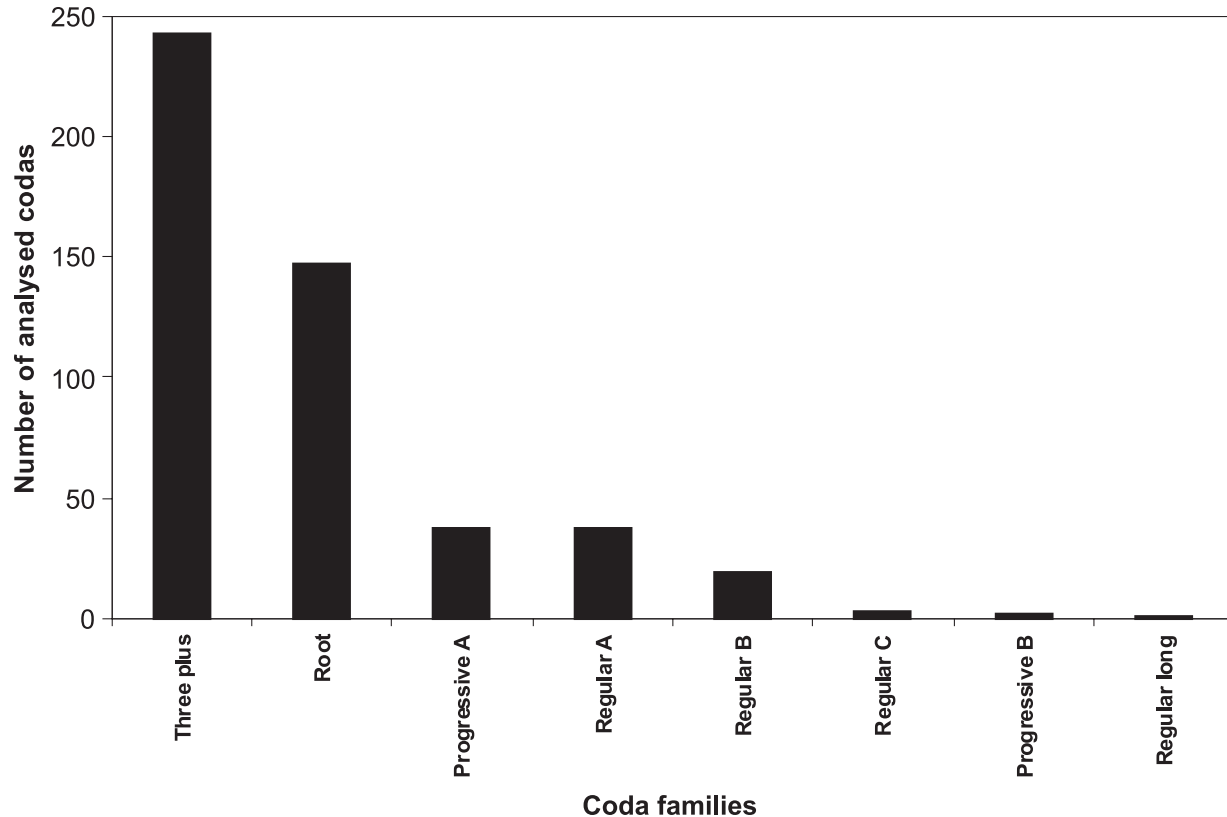
[Three plus]3+1 coda type and the [Three plus] coda family were by far the most commonly used by male sperm whales, constituting half of all the analysed codas (243 out of 490). All 11 whales from which codas were analysed produced the [Three plus]3+1 coda several times.

The use of coda families was not independent of the behavioural context or the dive cycle phase in which they were produced (Table 6). Chi-square analyses for both variables were highly significant (behavioural context: $\chi^2_{[6]}$ = 418.548, $P < 0.0000$; dive cycle phase: $\chi^2_{[6]}$ = 570.183, $P < 0.0000$). Figure 5 illustrates how the behavioural context clearly affected the use of the different coda families and Fig. 6 shows the dive cycle phase in which each coda family was used.

The repertoire of male sperm whales during RFDCs was dominated (at 85%) by one coda family, the [Three plus] family, consisting exclusively of [Three plus]3+1 codas. Codas of the [Root] family were also recorded during RFDCs on two occasions; however, all of them were recorded from two whales that were at surface, i.e., a phase in which no other codas were recorded during RFDCs. In addition, although in both cases the behavioural context corresponded to RFDC according to our definitions, special conditions occurred. The first case concerned two synchronized whales (pair 2) that were close to one another (approximately 100 m), but not close enough to be considered to be interacting (no visual contact); the research vessel was positioned almost between them and slightly behind. In the second case, the codas were recorded during a RFDC in between two ADCs. Finally, on one occasion, two codas of the [Reg-

ular A] family (one 4-click coda and one 5-click coda) were recorded by one whale during the descending phase of a RFDC behavioural context.

During ADCs, male sperm whales used mostly the five coda types of the [Root] family. All these codas were produced while the whale was at surface, i.e., near the research vessel, which altered the whale's behaviour. A number of codas of the [Three plus] family was recorded also during ADCs. These were 93 [Three plus]3+1 codas and 1 [Three plus]3+2 coda. However, 67 of them (71%) were recorded during the ascending phase, i.e., before any interaction with the research vessel (which subsequently altered the whale's behaviour) had occurred.

The [Three plus] and the [Root] coda families occupied only a small proportion of the repertoire of interacting male sperm whales (5% and 17%, respectively). The [Three plus] family was recorded only once by one of the whales of pair 1 in a sequence of six [Three plus]3+1 codas that initiated a rich coda exchange between the two whales just after they both fluked in a synchronized way. The four [Regular] and the two [Progressive] coda families dominated the repertoire of interacting male sperm whales. All but two codas of these six families were recorded only during the behavioural context of interaction between the whales. Also all chirrups and squeals occurred exclusively in the behavioural context of interaction.

Codas were used in different phases of the diving cycle depending on the coda family to which they belonged (Fig. 6). The differences were so clear that most coda families seemed to be used only in one or two phases while

Table 6. Summary of the contexts in which each coda family was used by the studied male sperm whales.

Coda families	Coda family usage
[Three plus]	Used mainly during RFDCs while ascending or descending and never at surface; occurred also in ADCs (four times less than the [Root] family) mainly while descending and very rarely at surface; used rarely during interaction of two whales at surface
[Root]	Used exclusively at surface, in between the end of a deep dive (first blow) and the start of a new one (fluking), by whales that altered their behaviour owing to the presence of the research vessel. Used also by interacting whales, although much less than other coda families. Its rare use at surface by whales performing RFDC was considered indicative of unnoticed "disturbance"
[Regular] and [Progressive]	Used almost exclusively during interaction of two whales at surface, or following such interaction after fluking, while starting a deep dive. An exception of one single occurrence at the descending phase of a RFDC was recorded

Note: RFDC, regular feeding dive cycle; ADC, altered dive cycle; IBW, interaction between whales.

Fig. 5. Use of the different coda families by male sperm whales during three different behavioural contexts: regular feeding dive cycle (RFDC); altered dive cycle (ADC); and interaction between whales (IBW). Values within the bars indicate the number of codas produced in each of the three phases (ascending phase (Asc); surface phase (Sur); descending phase (Des)) of the dive cycle.
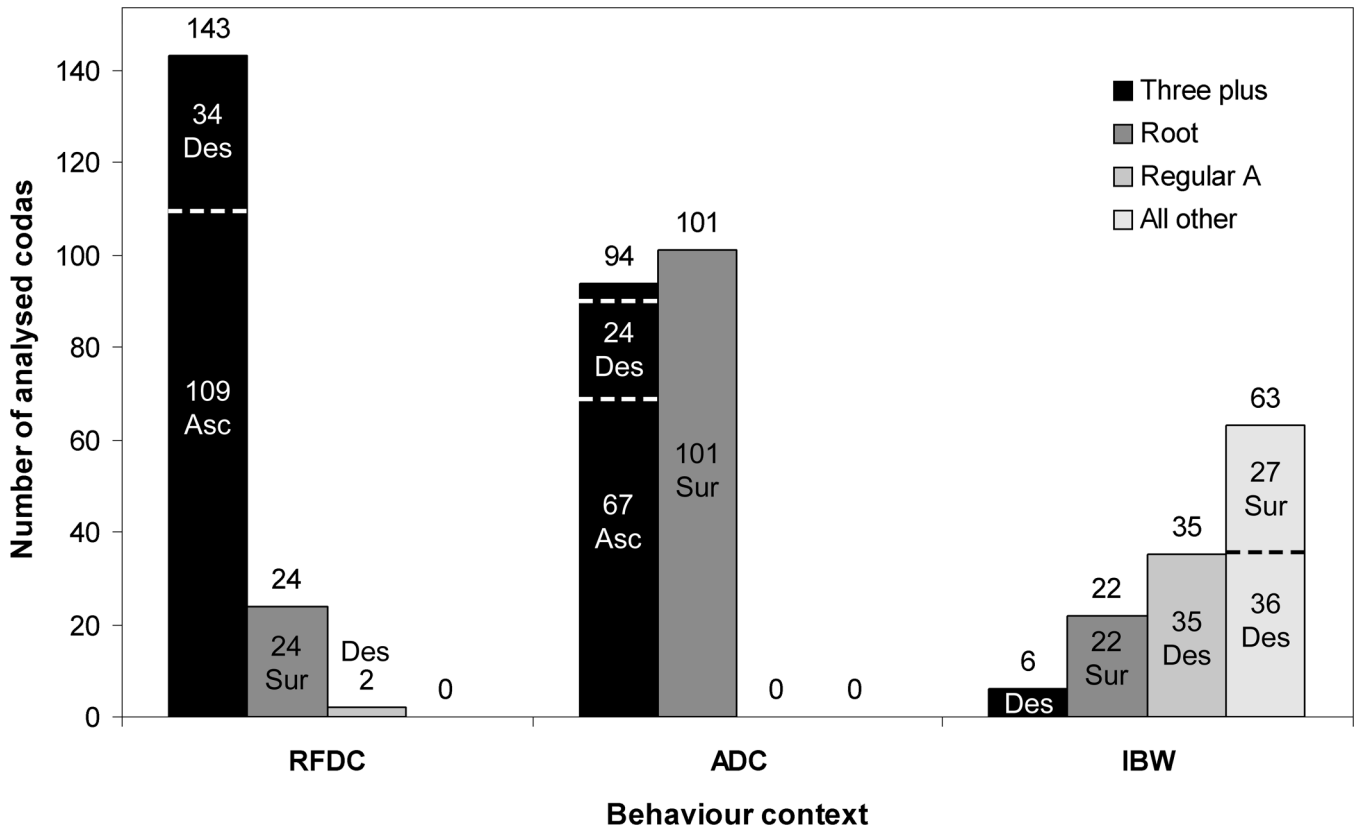
being completely absent in the remaining phase(s). The [Three plus] family occurred mainly in the ascending phase, during which 73% of the [Three plus] codas were produced, and also in the descending phase (26%). Only in one occasion did a sequence of three codas of this family (1%) occur while the vocalizing whale was at surface. The [Root] family codas were produced exclusively during the surface phase. Finally, the codas of the six [Regular] and [Progressive] families were produced either at surface or while descending, but never in the ascending phase, as no interaction between whales was observed or suspected to occur during this phase.

Discussion

Very few reports of codas from male sperm whales are available in the literature, from any of the male feeding or breeding grounds that have been studied. Codas are very seldom heard in northern Norway (Madsen and Møhl 2000). Wahlberg (2002) and Madsen et al. (2002*b*) detected no codas, but only a few slow clicks from the same area. In long-term studies off Kaikoura in New Zealand, no codas have been reported, but slow clicks ("surface clicks") were very commonly produced (Jaquet et al. 2001). Gordon et al. (1992) heard some codas during 2 out of 40 days of contin-

Fig. 6. Use of the different coda families by male sperm whales during the three phases of the dive cycle.
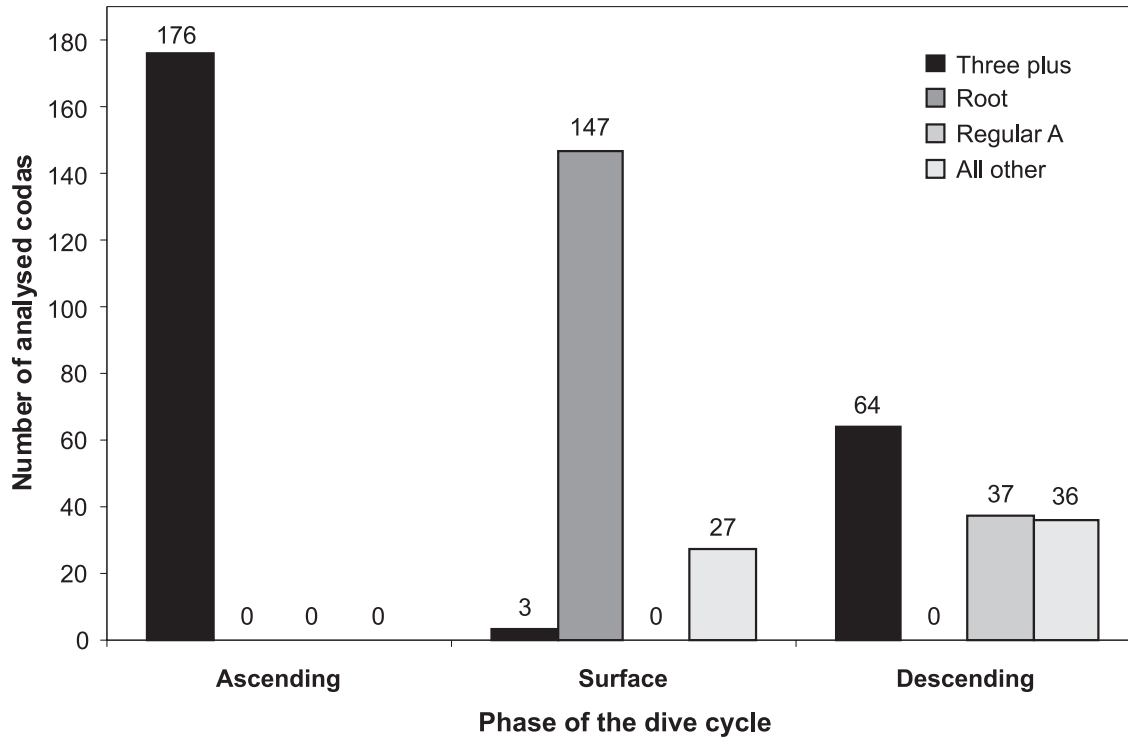
uous survey in the same area. Mullins et al. (1988) tracked two single sperm whales off Nova Scotia and recorded no codas, but heard codas at other times when more than one sperm whale was present. Slow clicks were recorded repeatedly from the two single whales. Goold (1999) reported no codas from a group of six, supposedly subadult male, sperm whales that entered the Scapa Flow, Orkney Islands, but recorded numerous slow clicks ("clangs") during a shepherding operation to rescue the whales. No codas were heard by Christal and Whitehead (1997) while studying aggregations of mature males in the Galápagos Islands. Once more, slow clicks were recorded both in the absence and presence of social units in the area.

The only exception so far to this scarcity of male codas occurs in the Mediterranean Sea. Studies in both the western and eastern basins commonly recorded codas from single, supposed or confirmed male, sperm whales (Frantzis et al. 2000; Pavan et al. 2000; Teloni 2005). In the present study, codas were commonly produced when more than one whales were present (60% of the encounters and 36% of their RFDCs). During RFDCs, codas were very likely to be produced (80% of the time) by at least one of the whales. Apparently, the acoustic behaviour of Mediterranean male sperm whales is different from male conspecifics in both the Atlantic and Pacific oceans, and codas seem to play a particular role at least during their deep feeding dives.

As it was suggested previously (Pavan et al. 2000; Teloni 2005) and shown in this study, no codas are produced by solitary male sperm whales. Therefore, no doubt should remain regarding their communicative role, which is in agreement with their click characteristics: narrow-band nature, low directionality, long pulse duration, and low decay rate (Madsen et al. 2002a). A long-range communicative role

has also been proposed for slow clicks occurring in male feeding habitats (Madsen et al. 2002b). Off Kaikoura, where they have been studied extensively, slow clicks are heard mainly from ascending whales shortly before surfacing or in a lesser degree shortly after the start of a deep dive (Jaquet et al. 2001). This corresponds exactly to what we have observed for codas produced during RFDCs (73% ascending, 26% descending), and is in agreement with Teloni's (2005) observations (82% ascending, 18% descending). Slow clicks are very rare in the Mediterranean Sea (they were recorded only once during this study; see also Teloni 2005), in contrast with their common presence in most areas where male codas are absent or very rare. It is therefore tempting to suggest that codas produced during RFDCs in the Mediterranean Sea may play the role of slow clicks produced in the same context in other geographical areas. We propose these codas be called "dive cycle codas" and be defined as codas produced by sperm whales (either males or members of a social unit) after the start or before the end of a regular deep feeding dive, with no interruption of the dive cycle sequence. Dive cycle codas have already been recorded from female or immature whales of social units (A. Frantzis and P. Alexiadou, unpublished data).

The exact message that is communicated through the dive cycle codas remains unknown. The slow clicks, which may have an equivalent role, have been proposed to be used for long-range acoustic display in competition for food while in aggregations (Madsen et al. 2002b), to actively avoid each other on the breeding grounds (Weilgart and Whitehead 1988; Christal and Whitehead 1997), or to maintain the apparent cohesion among males during migrations (Goold 1999). Mediterranean male sperm whales produce codas when they already know that another whale is in their vicin-

ity through its regular clicks. This indicates that dive cycle codas carry different or more complete information than just presence. Through the specific characteristics of their clicks (Madsen et al. 2002*a*), dive cycle codas may help males identify one another and remain in close contact, or display their size, assess one another, and define the limits of their moving feeding territory acoustically. Therefore, they may serve competition, co-ordination, or both depending on the conspecific to whom they are addressed.

Dive cycle codas occur much more often and are more numerous in the ascending phase than in the descending phase. Possible explanations might be (*i*) the available time window (free of regular clicks) for coda production is at least eight times longer while ascending and (*ii*) a descending whale has constraints related to the production of echolocation clicks soon after the fluking and coda production may require an additional effort which is best avoided, unless absolutely necessary. The timing of dive cycle codas (usually occurring just after or just before the last and first regular click, respectively) indicates that the whale may have to send a message as close as possible in time to a feeding session, during which no coda messages can be sent. This timing is reminiscent of the dawn and dusk choruses of bird songs (Armstrong 1973) before and after their nocturnal silence. Such choruses are explained as a daily announcement of the male territory occupancy and a keep-out signal to other males (Kacelnik and Krebs 1983; Staicer et al. 1996); a function that is also plausible for male sperm whale codas.

Codas have mostly been associated with groups of sperm whales socializing at surface or close to it (Whitehead and Weilgart 1991; Marcoux et al. 2006), and seemed to occur particularly as exchanges or "conversations" between whales that are close together and often manoeuvring about one another (Watkins and Schevill 1977; Weilgart and Whitehead 1993). To our knowledge, this behaviour had not been previously reported for males and no codas were recorded in such a context. Although the members of both pairs encountered during the present study had visual contact with one another in several occasions, only pair 1 was observed in physical contact on 2 different days. Seven sessions of coda exchanges or "conversations" were recorded in this context. These coda exchanges presented no apparent difference in duration, speed of exchange, number of coda types produced, or coda overlap to those recorded by socializing sperm whale groups (Watkins and Schevill 1977; Weilgart and Whitehead 1993; A. Frantzis and P. Alexiadou, unpublished data). We propose these codas be called "social codas" and be defined as codas produced by two or more sperm whales (either males or members of a social unit) that are near one another and sometimes manoeuvre about one another.

Single male (but also female) sperm whales when alone are usually silent while at surface between dives (Madsen et al. 2002*b*; Whitehead 2003). No codas had been previously reported by supposed or confirmed male sperm whales while resting at the surface in between deep dives (Pavan et al. 2000; Teloni 2005). We recorded 128 codas from male sperm whales at surface on 10 occasions. Although originally surprising, this result strongly correlated with the behavioural context. In eight cases the whale's behaviour had

been altered by our presence, and in the two remaining cases we strongly suspect that the whale had been disturbed, although there were no observable changes in its swimming behaviour. We conclude that surface codas were the response of the whale to our presence. These codas could be an alarm, rather than an intimidating sound toward us, since they were never produced by disturbed solitary whales. We propose these codas be called "alarm codas" and be defined as codas produced by single whales or nonsocializing small groups at surface when they are disturbed and often alter their usual surface behaviour. Dive cycles with altered behaviour of the whale while at surface presented a significantly higher frequency of coda occurrence (85%) than RFDCs (32%). The average number of codas produced was also significantly higher in ADCs than in RFDCs. Both results indicate that disturbance may create an increased need to communicate information apparently related to our presence. These findings regarding "alarm codas" might contribute to controlling and mitigating the disturbance induced by human activities like whale-watching, although their significance may be only regional.

The recorded coda repertoire of the studied sperm whales consisted of 25 coda types. This is probably an underestimation of the total Mediterranean male sperm whale repertoire, because the occasions of long coda exchanges were relatively few. Even so, it is far more diverse than previously found, since it was thought to contain just one coda type in the Mediterranean Sea (Pavan et al. 2000; Teloni 2005). Furthermore, this repertoire is as rich as those recorded from socializing social units in both the eastern (Drouot 2003; A. Frantzis and P. Alexiadou, unpublished data) and the western (Drouot 2003; Nuuttila 2004) Mediterranean basins (24 and 25 coda types, respectively), or the oceans (for a review see Weir 2003). The dive cycle codas dominated the repertoire in number of codas produced, but were represented by almost only one coda type, the [Three plus]3+1. Both the "alarm" and "social" codas were much more varied in coda types (5 and 18, respectively). On one occasion, a particular individual used as "alarm codas" the [Root]2→1, 3→1 and 4→1 coda types in a sequence which showed no pattern, indicating that all these codas might have a similar or equivalent value. The pattern of some rare coda types like the [Root]2, [Root]3+2 or [Three plus]3+2 could be explained as derivative or by-product of other coda types. Produced either by mistake or intentionally, such coda types may contribute to the evolution of sperm whale coda repertoires.

Supposing that males leave their maternal social unit before reaching a length of 9 m, Marcoux et al. (2006) suggested that codas are not likely to be produced by immature males in the context of the social units, and that unlike the females, males may not need to use coda communication to the same extent. Pavan et al. (2000) speculated that males may have smaller repertoires than females, possibly reflecting their less social life once they leave their maternal groups. Eighteen of the recorded coda types originated from a pair of young males that apparently were at an intermediate stage of their life after they left their maternal social unit. Their coda repertoire was apparently acquired in the context of their maternal social unit. It remains unknown if males maintain such a rich repertoire in their solitary life,

during which they have limited occasions to use it. Coda recordings from mature males interacting with social units in a reproductive context and (or) aggressively interacting with other males (Kato 1984; Whitehead 2003) could provide the answer.

While using nonstandardized coda data, it has been possible to classify codas into coda types and then into coda families (i.e., descriptive categories). Coda types belonging to the same family often differ in duration, click number, or even pattern, but present an overall similarity in their structure, which may be impossible to discern through the currently available automated methods. It is not known which of the coda characteristics carry information that is important to sperm whales (Whitehead 2003; Nuuttila 2004). However, the most interesting result of the present study is that coda families are important to the whales, since they are not used randomly but correlate strongly with particular behavioural contexts and dive cycle phases. Despite the relatively small sample size (especially the number of whales in IBW), these results were surprisingly clearcut (Figs. 5 and 6, as well as the relevant statistical tests) for a complex behaviour such as coda-type production. They do not reflect individual differences, because if each whale was following its own rules, or no rules of coda-family use, the distribution of coda families in behavioural contexts and dive cycle phases would be more or less homogeneous.

Finally, the way that coda families were used further supports the concept of dividing codas in "dive cycle codas", "social codas", and "alarm codas": (*i*) the [Three plus] family was the unique dive cycle coda family, (*ii*) the [Root] family was used exclusively at surface and almost always as an "alarm coda", and (*iii*) the four [Regular] and the two [Progressive] families were used almost exclusively as "social codas". These results appear very promising; however, more data (especially coda conversations from interacting males) and additional contexts (e.g., interacting mature males and males among social units) are needed to further support our findings. Furthermore, alternative methods to investigate the information conveyed in coda types, such as playback experiments, should be explored. The only carefully designed attempt so far resulted in unclear or no reaction of the whales exposed to codas previously recorded from sperm whales (Rendell and Whitehead 2001). The authors concluded that playback studies will be crucial in elucidating the function of codas, but before this can be done, there is a need for more knowledge on coda usage in natural conditions, especially at the individual level.

In summary, this study showed that male sperm whales regularly produce codas along the Hellenic Trench, in contrast to the scarcity of coda production by males in the oceans. The coda-type repertoire of males is far more diverse than previously thought and is as rich as that of socializing females and immature sperm whales in the Mediterranean Sea. In agreement with their suggested communicative role, codas of male sperm whales occur only when other whales are present. Finally, according to the actual data set, coda types are not used randomly but correlate with behavioural contexts and dive cycle phases; therefore, they seem to have functional significance rather than being functionless epiphenomena.

Acknowledgements

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