

The function of male sperm whale slow clicks in a high latitude habitat: Communication, echolocation, or prey debilitation?

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Sperm whales produce different click types for echolocation and communication. Usual clicks and buzzes appear to be used primarily in foraging while codas are thought to function in social communication. The function of slow clicks is less clear, but they appear to be produced by males at higher latitudes, where they primarily forage solitarily, and on the breeding grounds, where they roam between groups of females. Here the behavioral context in which these vocalizations are produced and the function they may serve was investigated. Ninety-nine hours of acoustic and diving data were analyzed from sound recording tags on six male sperm whales in Northern Norway. The 755 slow clicks detected were produced by tagged animals at the surface (52%), ascending from a dive (37%), and during the bottom phase (11%), but never during the descent. Slow clicks were not associated with the production of buzzes, other echolocation clicks, or fast maneuvering that would indicate foraging. Some slow clicks were emitted in seemingly repetitive temporal patterns supporting the hypothesis that the function for slow clicks on the feeding grounds is long range communication between males, possibly relaying information about individual identity or behavioral states.

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I. INTRODUCTION

The sperm whale (*Physeter macrocephalus*), the largest of the toothed whales, lives in matrifocal social systems where females, juveniles, and calves are found in social units limited to temperate and tropical waters. The males leave these social units at 10–20 years of age and migrate to higher latitudes to target food resources in colder waters, returning to warmer waters in search of females when they are physically and sexually mature (Best *et al.*, 1984; Rice, 1989). As the males get older they seem to be less social than the family units, whereas the bachelor groups, with younger males, apparently move with some degree of cohesion also at higher latitudes (Lettevall *et al.*, 2002). The cohesive distribution of male sperm whales at high latitudes may arise from patchy food resources or from a combination of reduced predation risk, benefits of practicing jousting with other males and cooperative behavior against other males (Connor, 2000).

The sperm whale has a hypertrophied nasal complex (up to 1/3 of the body length) which is used to produce clicks for echolocation and communication (Norris and Harvey 1972;

Møhl *et al.*, 2003; Madsen *et al.*, 2003, Zimmer *et al.*, 2005). Sperm whales are recognized to produce at least four types of clicks termed usual clicks, buzzes (also called “creaks”), codas, and so-called slow clicks (or clangs). All of these signals are sharp-onset broadband impulses with their main energy centered between 2 and 25 kHz (Madsen *et al.*, 2002a; Madsen *et al.*, 2002b). Although clicks comprise the large majority of their phonations, sperm whales also produce occasional tonal sounds described as trumpets, squeals, and pips (Goold, 1999; Whitehead, 2003; Teloni, 2005).

The high directionality and source levels of usual clicks (Møhl *et al.*, 2000) and their change in inter-click intervals (ICIs) with depth (Madsen *et al.*, 2002b; Thode *et al.*, 2002) strongly support the contention advanced by Norris and Harvey (1972) that these signals are used for long range echolocation (Madsen *et al.*, 2002b). Buzzes are rapid series of clicks with very short ICIs (15–100 ms) that occur in a foraging context and are associated with rapid maneuvering in prey capture attempts (Jaquet *et al.*, 2001; Miller *et al.*, 2004a). Codas, on the other hand, are stereotyped patterns of 3–20 clicks that may last 0.2–5 s (Watkins and Schevill, 1977). They are communicated between individuals within social units, probably to maintain social cohesion (Whitehead and Weilgart, 1991; Weilgart and Whitehead, 1993) with regional variation in coda types (Weilgart and Whitehead, 1997; Rendell and Whitehead, 2005).

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While the function of usual clicks, buzzes, and codas is somewhat understood, the use of slow clicks is still largely unresolved. Slow clicks, which are readily distinguished by their long ICI and distinctive metallic sound, are seemingly only produced by males (Mullins *et al.* 1988; Weilgart and Whitehead, 1988; Jaquet *et al.*, 2001; Madsen *et al.*, 2002b). The signals have a low frequency emphasis around 2–4 kHz, a longer duration, and they are probably more omnidirectional than usual clicks (Madsen *et al.*, 2002b). In previous studies, slow clicks have been detected in the breeding areas at lower latitudes (Gordon, 1987), as well as at higher latitudes (Weilgart and Whitehead, 1988; Douglas *et al.*, 2005) where only adult males are present (Best, 1979). Jaquet *et al.* (2001) reported that slow clicks (called surface clicks) from male sperm whales were produced mainly in the final part of the ascent phase of foraging dives, apparently at depths between 180 and 360 m.

The biological function of slow clicks has been attributed to either echolocation (Gordon, 1987; Mullins *et al.*, 1988; Goold, 1999; Tyack and Clark, 2000; Jaquet *et al.*, 2001) or communication (Gordon, 1987; Weilgart and Whitehead, 1988; Mullins *et al.*, 1988; Whitehead, 1993; Tyack and Clark, 2000; Madsen *et al.*, 2002b; Barlow and Taylor, 2005). Proposed communication functions include practicing of courtship displays at higher latitudes before migrating to the breeding grounds (Mullins *et al.*, 1988), where they may be used in vocal displays used in competition for females (Tyack and Clark, 2000; Weilgart and Whitehead, 1988). A related or possibly the same type of sperm whale signal referred to as a “gunshot” has been proposed to be used for prey debilitation (Gordon, 1987). In addition, Norris and Møhl (1983) and Cranford (1999) hypothesized that intense low frequency clicks from sperm whales might be used to debilitate prey to facilitate capture suggesting a possible foraging function for slow clicks. All of these hypothetical functions for slow clicks have been inferred from far-field acoustic recordings without any additional behavioral information. From the existing data it is therefore difficult to test which, if any, of these hypotheses reflects the true function of slow clicks.

To establish the behavioral context of slow click production, we here employed archival, multisensor tags (Dtags; Johnson and Tyack, 2003) to record the sound production and movements of male sperm whales foraging in a high latitude habitat. We use these data to test the following predictions: if slow clicks are used for communication, they are expected to be audible at ranges commensurate with the separation distance of individuals. Alternatively, if the main function of slow clicks is to echolocate the sea floor or other bathymetric features, we expect them to be emitted mainly during the descent and bottom phases of the dives, so the whale can orient itself in relation to the bathymetry while searching for food. If slow clicks are used for prey debilitation, we predict them to be extremely powerful and to be associated with foraging phases of dives and with foraging indicators such as buzzes. We find that the combination of diving and acoustic data collected in this study indicates that slow clicks are likely used for long range acoustic communication and not for orientation or foraging.

II. MATERIAL AND METHODS

Fieldwork was conducted in July 2005 and May 2010 in or adjacent to the Andøya underwater canyon off Andenes, Northern Norway (69°25'N, 15°45'E). Adult and sub-adult male sperm whales that forage in this area are usually found several kilometers from each other with little or no apparent social interactions between them, except for rare occasions where two whales may rest for a period close together at the surface (Lettevall *et al.*, 2002).

Digital acoustic recording tags (Dtags) were attached to the dorsal surface of six whales with suction cups. Dtags have two hydrophones spaced 20 mm apart along with sensors for depth, temperature, and orientation (three-axis accelerometers and magnetometers; Johnson and Tyack, 2003). The two hydrophones were sampled at 96 kHz each using 16-bit sigma-delta analog-to-digital converters and stored as a stereo wav-format file. The inertial sensors were sampled using sigma-delta conversion at 50 Hz with 16-bit resolution, and subsequently decimated to 5 Hz for analysis. Acoustic data were recorded until 99% of the memory capacity was consumed, after which time only non-acoustic sensor data were recorded.

Sperm whales were approached at less than 3 knots from behind with a 7 m rigid-hulled inflatable boat. The tags were placed on the animal using a 15 m cantilevered carbon fiber pole mounted on the boat. The apparent responses of the sperm whales were minor (e.g., rolling and moving slowly away from the tag-boat). Once the suction cups detached from the whale, the tag floated to the surface and was recovered via tracking of its VHF radio beacon from a sailing boat (2005) or a 29 m research vessel (2010).

Both acoustic and non-acoustic sensor data were used in the analyses. Sound files were examined using custom spectrogram display functions in Matlab 7.0 (Mathworks, Inc.). The orientation of the tag on the animal was corrected using the method described in Miller *et al.* (2004b) This resulted in a time series representing the orientation of the whale in terms of the Euler angles pitch, roll and heading (Johnson and Tyack, 2003).

Sperm whales were named with a sequence that includes the year, Julian day, and order of tagging (e.g., Sw05_199a means that the sperm whale was tagged in 2005 on the 199th Julian day, and “a” means that it was the first tagged individual that day).

Audio files from all the tagged whales were examined by listening and by visual inspection of spectrograms to identify slow clicks, usual clicks, and buzzes. Slow clicks were distinguished from usual clicks by their ICI (minimum value was 2.2 s) and their metallic and reverberant timbre (see Fig. 1) as described by Gordon (1987) and Jaquet *et al.* (2001). Slow clicks produced by the tagged whale were distinguished from those of other whales in the vicinity by comparing their angle-of-arrival on the two tag hydrophones with that of usual clicks ascribed to the tagged whale. Based on this, clicks were ascribed to the tagged whale, from another whale, or to be of uncertain provenance. Only the clicks unequivocally attributed to the tagged whale were used in further analyses. In this study, it was not possible to

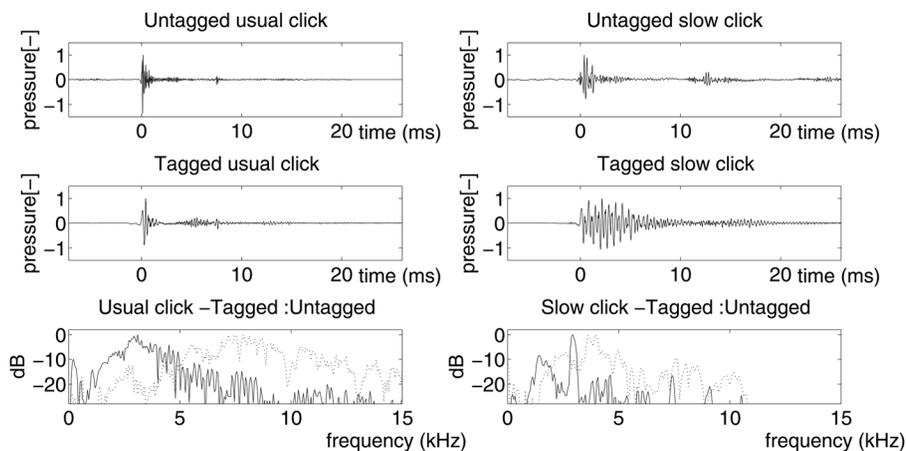


FIG. 1. Waveforms and spectra of untagged and tagged usual and slow clicks recorded from Dtags on sperm whales off Northern Norway (FFT size 1700, sampling rate 96 kHz, Hanning window).

compare acoustic individual differences (e.g., received levels, decay rate, root-mean-square bandwidth, etc.) because the slow clicks from the tagged whale were consistently clipped in the recordings.

Slow clicks were divided into bouts using a log survival plot of slow click ICIs pooled from all animals (Slater and Lester, 1982; Sibly *et al.*, 1990). This analysis gave an upper limit for bout duration of 24.9 s (which is consistent with the sequences of 24 s found in Jaquet *et al.*, 2001). The log survival regression equation was: $\text{Log}_e(\text{frequency of ICIs}) = 2.5 e^{-0.063 \cdot \text{ICI class}}$ ($r^2 = 0.84$; $p < 0.0001$). The proportion of the duration of slow click periods was calculated as the percentage of total time of the slow click bouts in relation to the length of the whole recorded file.

Tagged whales spent their time either foraging at depth or resting at or near the sea surface (Miller *et al.*, 2008). Surface time was defined as the interval between dives in which the whale dove deeper than 20 m. Following Miller *et al.* (2004b), we defined descents as extending from when the whale left the surface until the pitch of the whale exceeded 0° (a positive pitch means that the animal is oriented upwards). Likewise, ascents started when the pitch was continuously greater than 0° . A few brief episodes (duration up to 11 s) of downward pitch angle during ascents were ignored. The ascent phase was considered to end when the whale reached the surface. The period between descent and ascent was called the bottom phase and the foraging phase was defined as the period between the first and last buzzes (Watwood *et al.*, 2006).

In foraging beaked whales, according to Johnson *et al.* (2004), it is often possible to detect an increase in the minimum specific acceleration (MSA) in the end of buzzes, indicating fast acceleration associated with prey capture. Consistent with that, Miller *et al.* (2004a) found spike changes in the roll and pointing angle in the end of buzzes produced by sperm whales. In our study, the three-axis accelerometer dataset was filtered to compare the MSA in the end of the buzzes with the MSA during slow clicks. The root-mean-square (rms) of the MSA within -5 to 5 s relative to the end of buzz and beginning of slow click, respectively, was compared with two control periods of -40 to -30 s and 30 to 40 s relative to the end of the buzz/beginning of the slow click. As this analysis computed 12 ANOVA tables, we

adjusted the significant p -value to 0.05/12 or 0.004 (a so-called Bonferroni correction; Legendre and Legendre, 1998).

The sound velocity profile in the study areas were calculated from CTD (ValePort MiniCTD, Serial Number 32956, Calibration Number 24319) measurements to a maximum depth of 470 m. The CTD data were collected within 2 days of the tag deployments in 2010 and in the same general location in the Andenes canyon.

III. RESULTS

Tags were attached to six sperm whales in 2005 and 2010, yielding a total of 98.8 h of recordings. A single animal was tagged each day except on the 18th of July 2005, when three whales were tagged and 11.6 h of simultaneous recordings were collected (Table I). The three whales were tagged with the following distances from each other: 3.4 km (sw05_199a to sw05_199b), 2.5 km (sw05_199a to sw05_199c), and 4.9 km (sw05_199b to sw05_199c).

All six whales produced usual clicks, buzzes, and slow clicks. The usual clicks and buzzes indicate that all the animals were involved in foraging during the major part of the tag recordings. Foraging behavior of the whales in the 2005 dataset has been reported in detail by Teloni *et al.* (2008). Clicks from other sperm whales in the area were also frequently audible in the recordings. The diving and foraging behavior of the whales was more diverse than that reported for female sperm whales (Watwood *et al.*, 2006), ranging from short, shallow dives to more typical long deep dives (Table I and Fig. 2; see also Teloni *et al.*, 2008).

The whales emitted slow clicks in the ascent (37%), bottom (11%), and surface (52%) phases of their dive cycles [Table I, Fig. 2, and Figs. 3(a) and 3(b)]. Although a total of 755 slow clicks were recorded, the whales spent only an average of 1% of their time producing bouts of slow clicks (Table II) compared to 61% producing usual clicks.

All slow clicks were emitted at depths < 300 m [Fig. 3(a)] with the majority (82%) occurring during ascent and surface phases. Only 11% of the slow clicks were emitted during the bottom phase and then predominantly in the second half of the bottom phase. No slow clicks were produced by tagged whales during the descent phase. Slow clicks were not produced during the bottom or foraging

TABLE I. Local time of tag deployment, total time of recording (h:min), number of dives, maximum depth, and dive duration (mean \pm 1 standard deviation), of the six tagged sperm whales.

Whale	Deployment Time	Total time	# of dives	Maximum depth (m)		Dive duration (min)
				Deepest dive	Shallowest dive	
sw05_196a	14:44	21:21	32	537	22	28 \pm 9
sw05_199a	13:06	18:05	28	1602	48	31 \pm 12
sw05_199b	14:43	13:50	17	1862	143	34 \pm 14
sw05_199c	16:57	13:24	14	1838	20	30 \pm 15
sw10_147a	13:03	15:53	26	684	34	25 \pm 7
sw10_149a	06:35	16:12	27	1122	141	27 \pm 8
Total		98:45	144			

phase of deeper (>300 m) dives and only 26 slow clicks (produced by two whales) of 755 slow clicks were produced in the foraging phase, between the first and last buzz, of any dive [Fig. 3(b)].

There was no apparent causal link between slow clicks and buzzes (Table III). The minimum interval between a

slow click and the closest subsequent or previous buzz was 30 s, and the median interval ranged between 194 and 1496 s. Linear regressions were made to evaluate if there was any linear relationship between the number of buzzes and the number of slow clicks per dive for each of the tagged whales. Significant negative linear regressions were found

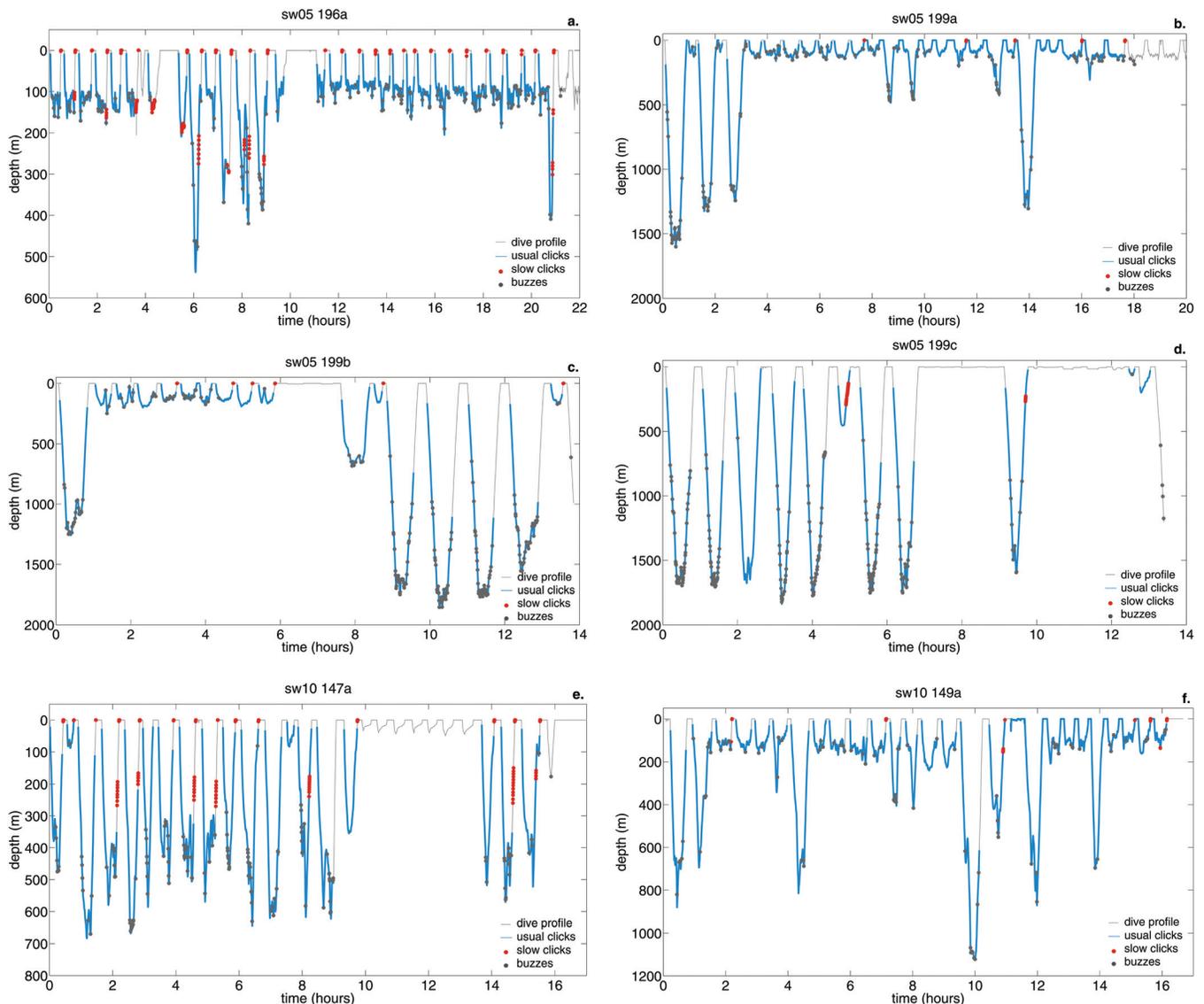


FIG. 2. Dive profiles, usual clicks, slow clicks and buzzes of the six tagged sperm whales off Northern Norway, (a) sw05_196a, (b) sw05_199a, (c) sw05_199b, (d) sw05_199c, (e) sw10_147a, (f) sw10_149a. In sw05_199c there is a gap in the sound file from time 2:00:46 to 2:29:36 due to an error in the original sound file.

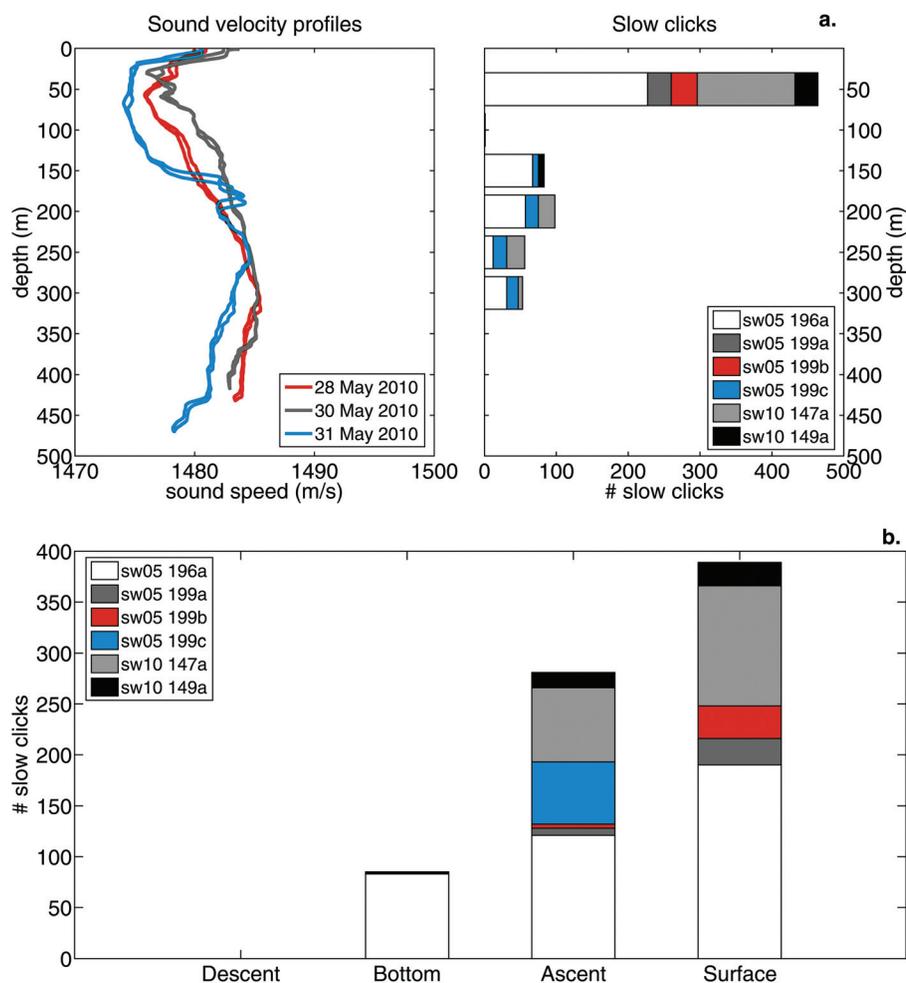


FIG. 3. (a). Sound velocity profiles on the 28, 30, and 31 of May 2010 and depth distribution of slow clicks produced by six tagged sperm whales in 50 m depth bins, (b) Slow click production in six tagged sperm whales as a function of the phase of the dive cycle.

for sw05_199a, sw05_199b, and sw10_149a, indicating that slow clicks production was higher when buzz production was lower in these samples. For the remaining sperm whales, the buzz-slow click data had non-significant negative linear regressions (Table III). There is thus no positive correlation and therefore no apparent functional link between buzz production and slow clicks.

The average ICI in bouts of slow clicks produced by the six animals ranged from 4 to 10 s (Table II). Although the ICI in bouts was often variable, some possible temporal patterns were visually observed in the ICI of slow clicks produced by sw05_199c [Fig. 4(a)]. However, there is insufficient data to establish definitively whether that slow clicks were produced in rhythmic patterns.

We detected one possible exchange of slow clicks between sw05_196a and an untagged sperm whale, with some overlap of the bouts produced by the two animals [Fig. 4(b)]. This occurred when sw05_196a was approaching the surface (2–20 m depth). Other slow clicks from untagged whales may have been missed if they occurred when the tagged whale, and therefore the tag, was at the surface where splashing sounds may mask sounds from distant whales. Such sounds would likely be heard by the tagged whale, having its lower jaw well underwater when surfaced.

One of the key sources of evidence relating buzzes with prey capture attempts in beaked and sperm whales is an increase in movement of tagged animals during buzzes compared to other similar-length intervals (Johnson *et al.*, 2004;

TABLE II. Inter-click interval (ICI), total number of slow clicks from each whale (N), the number of slow click bouts, and the proportion of the duration of the slow click bouts and total recorded duration.

Whale	Mean \pm 1 s.d.	ICI(s)		N	No. slow click bouts	Proportion of slow click bouts (%)
		Min	Max			
sw05_196a	8.0 \pm 4.5	2.5	24.1	394	43	3.17
sw05_199a	10.0 \pm 5.2	6.1	20.6	33	5	0.31
sw05_199b	9.2 \pm 4.4	6.6	20.0	36	6	0.41
sw05_199c	4.0 \pm 2.2	2.2	9.0	61	3	0.47
sw10_147a	6.0 \pm 2.6	3.3	16.8	191	21	1.77
sw10_149a	5.0 \pm 2.5	2.2	12.4	40	6	0.27

TABLE III. Median, minimum, and maximum interval from a slow click and a buzz recorded on the tagged sperm whales. The buzz may have preceded or followed the slow click, whichever appeared within the shortest time interval. N is the total number of slow clicks analyzed from each whale. Nr periods: the number of distinct periods with buzzes and slow clicks counts. Slope L. reg.: slope of the linear regression equation for the number of slow clicks as a function of the number of buzzes, r^2 : regression coefficient of determination, p : ANOVA probability that the regression slope is different than 0.

Whale	Median (s)	Min (s)	Max (s)	N	Nr periods	Slope		
						L. reg.	r^2	p
sw05_196a	359	29.9	1558	394	57	-0.55	0.05	0.10
sw05_199a	194	114	605	33	31	-0.14	0.17	0.02
sw05_199b	662	263	1416	36	23	-0.08	0.20	0.03
sw05_199c	1496	328	1652	61	11	-0.41	0.17	0.20
sw10_147a	445	98.6	2802	191	33	-0.20	0.04	0.29
sw10_149a	358	75.6	1067	40	30	-0.33	0.15	0.03
Total				755				

Miller *et al.*, 2004a). This increase in movement is consistent with the last-second maneuvering needed to acquire agile prey. Similar results were obtained for the MSA of buzzes recorded in the present study (Fig. 5). Repeating the analysis with slow clicks instead of buzzes, we found no clear peak in acceleration associated with slow clicks (Fig. 5). There was a significant ($p < 0.004$; corresponding to $p = 0.05$ after Bonferroni correction; Legendre and Legendre, 1998) increase in acceleration in the interval -5 to 5 s from the end of the buzz compared to a chosen control period from 30 to 40 s after the end of the buzz, except for sw05_199c with $p > 0.5$ (Table IV). For slow clicks, there was no significant

difference between the MSA during the chosen control period 30 – 40 s after the beginning of the slow click and the interval from -5 to 5 s relative to the time of the slow click, for five of the six whales (Table IV). There were significant changes in MSA during slow clicks when comparing to another chosen control period lasting from -40 to 30 s relative the onset of the slow click (Table IV). This may however often be attributed to the change in the whales' position when it approaches the surface, as more than 61% of the slow clicks were produced between 50 m depth and the surface.

IV. DISCUSSION

All six whales tagged in this study produced occasional bouts of slow clicks resulting in an average rate of 7.6 slow clicks per hour. Thus, slow clicks represent a very small portion of the total vocal output of sperm whales but their production by apparently solitary males in Arctic feeding grounds nevertheless raises questions as to the possible function of these sounds. Possible functions suggested in the literature include communication, echolocation, orientation, or prey debilitation—or a combination of several of these.

The distinctive metallic sound of slow clicks, whether recorded by a tag on the vocalizing animal or in the far-field, make these clicks easy to distinguish from usual clicks, and therefore few mis-classified clicks are likely to occur. It can be more challenging to determine if a click is produced by the tagged whale or a nearby conspecific. The angle-of-arrival of clicks at the tag is usually a strong indicator but this method breaks down when a vocalizing conspecific is directly in front or behind the tagged whale. However, very few (27 out of 782) clicks could not be conclusively allocated to either the tagged whale or another animal. These ambiguous vocalizations were excluded from the analyses but, even if the excluded clicks were actually produced by the tagged whales, they represent around 3% of the slow clicks and so would have little impact on our results.

If slow clicks are used for prey debilitation, we expect the signals to occur during the parts of the dives where the whales are involved in foraging. However, slow clicks were most prevalent in normally otherwise silent dive phases, i.e., during ascents from foraging dives and at the surface. Critically, no slow clicks were produced by whales at depths >370 m in foraging dives even though five of six whales performed deep dives (Table III and Fig. 2). Although some of the sperm whales were also foraging during shallow dives (Teloni *et al.*, 2008), only 26 of 755 slow clicks were produced by tagged whales during the foraging phase of any dive. Thus, if slow clicks indeed signify prey debilitation attempts, their low production rate is difficult to reconcile with the number of prey it takes to meet the energy demands of a 40–60 ton predator (Lockyer, 1981). The weak overlap of slow clicks with echolocation sounds does not eliminate the possibility that slow clicks are used primarily to debilitate prey that is hunted visually. This would be consistent with the typically shallow production depth of slow clicks. However, there are no indications that whales maneuver rapidly while producing slow clicks as is the case during foraging buzzes (Fig. 5, Table IV, Miller *et al.*, 2004a).

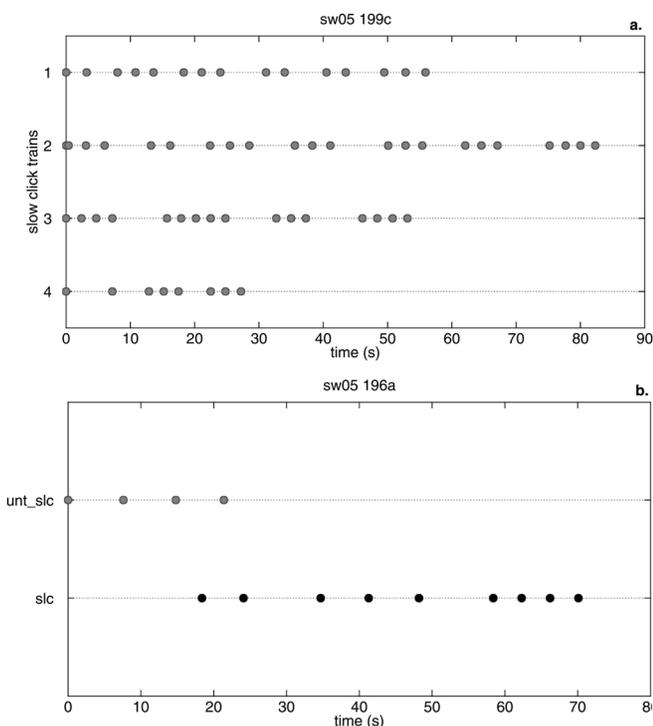


FIG. 4. (a). Example of slow clicks produced in regular temporal patterns by sw05_199c. (b) Example of a possible slow click exchange from the tagged sw05_196a. Slow clicks from the tagged whale (slc) and an untagged whale (unt_slc) are displayed as a function of time (s).

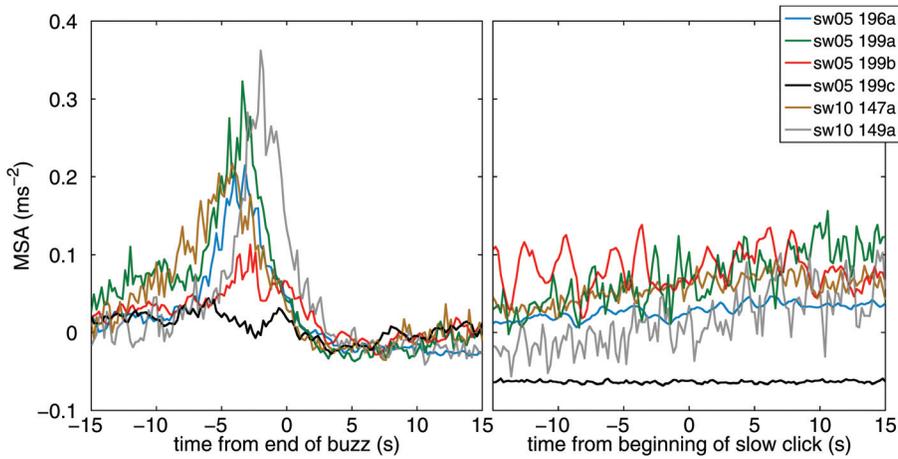


FIG. 5. Mean of the minimum specific acceleration (MSA) relative the end of buzzes (left panel) and the start of slow clicks (right panel) of the six tagged whales. Buzzes and slow clicks numbers are, respectively: 169 and 394 for sw05_196a, 151 and 33 for sw05_199a, 201 and 36 for sw05_199b, 210 and 61 for sw05_199c, 142 and 191 for sw10_147a, and 92 and 40 for sw10_149a.

Further, the acoustic debilitation of prey would demand sound pulses of extremely high levels. Debilitation of potential sperm whale prey species using high intensity transient signals has not been achieved in the laboratory despite considerable efforts (Benoit-Bird *et al.*, 2006) and it has proven difficult to affect the behavior of some fish and squid species at all even with received sound pressure levels beyond 210 dB re 1 μ Pa (pp) (Wilson *et al.*, 2007, Schack *et al.*, 2008). Measurements made by Madsen *et al.* (2002b) indicate that slow clicks have source levels of 200 dB re μ Pa (pp), more than 30 dB lower than the source level of on-axis usual clicks. The lower frequency emphasis of slow clicks (Madsen *et al.*, 2002b) suggests that they are also less directional than usual clicks, although little is known about the sound emission beam pattern of these sounds. Taken together, these considerations make it very unlikely that slow clicks are used for prey debilitation.

Whether or not slow clicks are used for echolocation is more difficult to test. The acoustical properties of slow clicks (i.e., their low frequency emphasis, probable low directionality, and their low and mostly irregular ICIs) are atypical for

signals specifically evolved for biosonar in any echolocating animal whether bat or toothed whale. If slow clicks are used to echolocate prey, these phonations should be associated with the descent or foraging phase of dives (Miller *et al.*, 2004a). We find weak negative correlations between the number of slow clicks and the number of buzzes in a dive (Table III and Fig. 2) counter to the hypothesis that slow clicks function with echolocation-based foraging of individual prey.

If slow clicks are used for any form of echolocation, their frequency content (around 2 kHz peak frequency, Madsen *et al.*, 2002b) suggests echolocation of large targets such as scattering layers, conspecifics or hydrographical and bathymetry features (Gordon, 1987; Weilgart and Whitehead, 1988; Mullins *et al.*, 1988; Whitehead, 1993; Goold, 1999). It is difficult to discount such a function, as the reverberation pattern produced by any signal provides information about the large scale composition of the environment. However, the predominance of slow clicks during the ascent phase of dives as well as near or at the surface is inconsistent with the idea that these sounds could help in locating prey layers or bathymetric features while foraging. Such information would presumably be most useful in the early part of foraging dives, where few if any slow clicks are produced, rather than in the final parts of the dive or at the surface.

Given that there is no strong support in the data for slow clicks being used for either prey debilitation or echolocation, the most plausible function is communication. The parts of the dives where slow clicks are most prevalent (ascent and surface phases) are also the parts where there is little or no production of usual clicks or buzzes (Teloni *et al.* 2008). These otherwise silent phases could therefore be appropriate to produce signals to communicate with conspecifics, as is the case for at least part of female sperm whale coda production (Whitehead and Weilgart, 1991; Weilgart and Whitehead, 1993). The finding of a negative correlation between slow click and buzz production is consistent with a communication function that largely takes place in time not allocated to foraging, i.e., less time may be available for communication in more successful foraging dives.

If slow clicks do serve for communication, the question arises as to what messages would male sperm whales wish to communicate to other males? The actual function of these

TABLE IV. Results from ANOVA and Tukey's range tests for rms values of the minimum specific acceleration for two control groups and one test group, defined relative to the end of the buzz or the beginning of the slow click. Control groups C_1 : -40 to -30 s, and C_2 : 30-40 s; test group T: -5 to 5 s. * indicates statistically significant p values (Bonferroni-corrected $p < 0.05$ to $p < 0.004$ from 12 tests; see Legendre and Legendre, 1998).

		ANOVA		Tukey's range test, p		
		$F_{df,df}$	p	C_1 vs T	C_2 vs T	C_1 vs C_2
sw05_196a	buzz	$F_{2,504} = 173$	<0.001*	<0.001*	<0.001*	<0.01
	slow click	$F_{2,1179} = 46$	<0.001*	<0.001*	0.613	<0.001*
sw05_199a	buzz	$F_{2,450} = 39$	<0.001*	<0.001*	<0.001*	0.100
	slow click	$F_{2,96} = 48$	<0.001*	<0.001*	0.061	<0.001*
sw05_199b	buzz	$F_{2,600} = 37$	<0.001*	<0.001*	<0.001*	0.400
	slow click	$F_{2,105} = 20$	<0.001*	<0.001*	0.535	<0.001*
sw05_199c	buzz	$F_{2,626} = 0.5$	0.604	0.593	0.764	0.960
	slow click	$F_{2,180} = 5.5$	<0.01	0.023	0.900	<0.01
sw10_147a	buzz	$F_{2,421} = 23$	<0.001*	<0.001*	<0.001*	0.985
	slow click	$F_{2,570} = 44$	<0.001*	<0.001*	0.964	<0.001*
sw10_149a	buzz	$F_{2,270} = 106$	<0.001*	<0.001*	<0.001*	0.918
	slow click	$F_{2,117} = 30$	<0.001*	<0.001*	0.262	<0.001*

vocalizations may depend on whether they are used on the feeding grounds (as the ones studied here) or on the breeding grounds.

Despite little evident social interactions at high latitudes, slow clicks perhaps serve to maintain group cohesion (Whitehead *et al.*, 1992). A possible exchange of slow clicks [Fig. 4(b)] and potential temporal patterning in slow click bouts [Fig. 4(a)] observed here provide intriguing hints of a complex social function of slow communication. However, the fact that only one such exchange was found from a total of 755 slow clicks in this study indicates that slow click production at high latitudes is not necessarily induced by hearing other slow-clicking animals. Thus, a chorusing function of the slow clicks is unlikely.

Killer whales (*Orcinus orca*) are known to sometimes attack groups of sperm whales, albeit usually groups of females and calves, and coordinated social responses to predation have been observed (Ambom, 1987; Pitman, 2001). Slow clicks were emitted frequently by a bachelor group of sperm whales trapped in the Scapa Flow (Goold, 1999) which may indicate a function of cohesion calls during danger or stress. Social cohesion may also be important during bachelor group migrations in which individuals are known to travel together towards higher latitudes (Best *et al.*, 1984; Rice, 1989; Lettevall *et al.*, 2002). Aggressive signaling is used by other species of toothed whales, as well as other marine animals. Clausen *et al.* (2010) report acoustic aggressive behavior between captive female and male harbor porpoises (*Phocoena phocoena*) during competition for fish, involving up-sweeping high repetition rate click trains. Slow clicks may serve analogous functions in competitively foraging sperm whales. The idea that slow clicks are used to maintain a foraging space free from other males fits well with the fact that slow clicks are produced during ascent periods, after presumably successful foraging events.

Irrespective of their social function it has previously been speculated that slow clicks convey information on the presence, location, identity, size and age of the clicking whale (Gordon, 1987; Weilgart and Whitehead, 1988; Tyack and Clark, 2000; Madsen *et al.*, 2002b; Whitehead, 2003). While presence and location are inevitably revealed by any phonation, the other information could conceivably be encoded in the waveform or in the ICI of the clicks. In this study, clicks produced by tagged whales were consistently clipped in the recordings and therefore not available for spectral analysis, while clicks from untagged whales could not be allocated to individuals making encoding via spectral features untestable. The inter-pulse-intervals within sperm whale clicks are known to provide information about the size, and therefore age, of the vocalizer (Gordon, 1991; Rhineland and Dawson, 2004). On the breeding grounds, this could be important information when reproductive competitors are present, or when males try to get the attention of females (Gordon, 1987; Weilgart and Whitehead, 1988; Tyack and Clark, 2000; Madsen *et al.*, 2002b; Whitehead, 2003). However, the multi-pulse structure often seen in usual and coda clicks is rarely, if ever, seen in slow clicks (Madsen *et al.*, 2002b). The possible temporal patterns of slow clicks within bouts [Fig. 4(a)] detected in this study

may be speculated to reflect some degree of individual identity or characteristics although Jaquet *et al.* (2001) argue that slow click ICIs vary widely within each individual, and are therefore unlikely to identify individuals. If information is indeed relayed via the ICI patterns over many clicks, it is an example of a very slow way of communicating, but one that offers a potentially large active space both because of the high source levels of sperm whale clicks and because ICIs are more resilient to distortion from propagation that are within click information.

Madsen *et al.* (2002b) estimated that other whales may be able to hear slow clicks at ranges up to 60 km. Such an estimate is critically dependent on the sound velocity profile, which will cause the sound paths to refract over long ranges. Depending on the depth of the caller and the receiver, the actual detection distance may therefore be much shorter or longer than when assuming spherical spreading conditions. In Fig. 3(a), we have plotted the sound velocity profiles taken within a maximum of two days from the tag deployments to evaluate if the whales produce slow clicks at depths with the lowest sound speeds to maximize their active space. Although the sound speed minimum is shallow as expected for cold high latitude waters, many slow clicks are produced even shallower, at or near the surface [Fig. 3(b)], where a downwards refracting sound velocity profile will preclude long range communication to other surfaced animals. However, the active space of slow clicks will, even when produced by surfaced callers, still be probably many kilometers when addressing listeners at depths closer to the sound speed channel.

V. CONCLUSION

Among the previously hypothesized functions of slow clicks, prey debilitation can be ruled out due to a lack of any relationship between slow click production and buzzes, and also because there is no indication of rapid maneuvers while producing slow clicks. Likewise, even though echoes from slow clicks may provide bathymetric information, the context in which they are produced (mainly at the surface and during ascents from foraging dives) is inconsistent with a primary echolocation function. The signal structure reported in earlier studies as well as the behavioral context of the signals as described here all point towards a communicative function for slow clicks. The click interval and conceivably the waveform of slow clicks could carry individual information, making these sounds a possible long-range communication signal provided that both sender and receiver are at depths at which such propagation is supported. The fact that slow clicks are produced both among foraging males in the Arctic as well as by males encountering females on the breeding grounds in warmer waters indicate that the communicative function of slow clicks may vary depending on the behavioral context in which they are produced.

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