

Shallow food for deep divers: Dynamic foraging behavior of male sperm whales in a high latitude habitat

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Abstract

Groups of female and immature sperm whales live at low latitudes and show a stereotypical diving and foraging behavior with dives lasting about 45 min to depths of between 400 and 1200 m. In comparison, physically mature male sperm whales migrate to high latitudes where little is known about their foraging behavior and ecology. Here we use acoustic recording tags to study the diving and acoustic behavior of male sperm whales foraging off northern Norway. Sixty-five hours of tag data provide detailed information about the movements and sound repertoire of four male sperm whales performing 83 dives lasting between 6 and 60 min. Dives ranged in depth between 14 and 1860 m, with a median depth of 175 m, and 92% of the surfacings lasted less than 15 min. The four whales clicked for an average 91% (SD=10) of the dive duration, where the first usual click was produced at depths ranging between 4 and 218 m and the last usual click at depths ranging between 1 and 1114 m. Echolocation buzzes, which are used as an indication of prey capture attempts, were emitted at depths between 17 and 1860 m, during both the descent and ascent phase of deep dives. The foraging behavior varied markedly with depth, with the timing and duration of prey capture attempts during shallow dives suggesting that the whales target more sparsely distributed prey. In contrast, deep dives involve frequent prey capture attempts and seem to target more dense food layers. The evidence of exploitation of different food layers, including epipelagic prey, is consistent with the hypothesis that male sperm whales may migrate to high latitudes to access a productive, multi-layered foraging habitat.

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1. Introduction

As apex predators, marine mammals have evolved to target a wide range of aquatic food niches from shallow fresh water to bathypelagic depths in the open oceans. While most niche segregation occurs between species,

some marine mammals display marked temporal and spatial segregation between sexes in terms of foraging behavior and the trophic levels they target. Sexual dimorphism is exhibited in several marine mammal species, including pinnipeds (e.g. Lindenfors et al., 2002) and odontocetes (Best, 1981; Jefferson, 1990; Cranford, 1999; Clark and Odell, 1999). Dimorphic differences may include behavioral, morphological, and life history differences. The sperm whale (*Physeter*

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macrocephalus, L.) displays pronounced sexual dimorphism in body weight with mature males growing up to at least 57 t and females usually being less than 13 t (Best, 1979). The two sexes also differ in terms of social organization and geographical distribution. Mature females and immature males and females are normally limited to tropical and temperate waters between about 40°N and 40°S (Rice, 1989), where they are encountered in social cohesive groups (Whitehead et al., 1991). Contrary to females, males leave their matrilineal social unit at about age 10 when they are usually less than 9 m (Rice, 1989). With increasing age, male sperm whales are normally found in the higher latitudes of both hemispheres, usually by themselves or in small groups (Best, 1979; Caldwell et al., 1966; Rice, 1989).

Sexual segregation in migrating and foraging patterns occurs in a variety of taxa (Dingle, 1996), such as ungulates. Several hypotheses have been advanced to explain such sexual segregation (Main et al., 1996; Ruckstuhl and Neuhaus, 2000), including sexual differences in nutrient requirements and activity budgets, scramble competition, reproductive strategies and social preference. In the case of the sperm whale, one explanation for sexual segregation involves the possibility of different energetic requirements of the two sexes (e.g. Best, 1979).

Sperm whales are deep-diving predators (Papastavrou et al., 1989; Watkins et al., 1993; Watwood et al., 2006) that, based on stomach contents, primarily target cephalopods (Berzin, 1972; Okutani and Nemoto, 1964; Rice, 1989; Santos et al., 1999). Compared to other deep-diving species, like elephant seals and beaked whales, sperm whales feed on a wider variety of squid species (Whitehead et al., 2003) while in some regions, notably New Zealand and the northern parts of the Pacific and Atlantic oceans (Kawakami, 1980), fish are the predominant component of their diet (Berzin, 1972; Clarke and Macleod, 1976; Goshō et al., 1984, Martin and Clarke, 1986, Rice, 1989). Rice (1989) reported fish of up to 3 m being eaten by sperm whales. Male sperm whales seem to consume a greater range of food items and larger prey than females (Best, 1979; Clarke et al., 1988). They eat more fish (Kawakami, 1980; Martin and Clarke, 1986; Rice, 1989) and at low latitudes, they have been reported to feed on larger squids than females (Clarke, 1980; Rice, 1989; Clarke et al., 1993).

Given the Kleiber-scaling of metabolic rates (Kleiber, 1975), the absolute food requirements of a male sperm whale with this size ratio will be almost 3 times greater than for a female with a body weight of $\frac{1}{4}$ that of the male. However, the mass-specific food requirements (J/kg body weight) for a male sperm whale will be some 30% smaller than for a female. Sexual dimorphism in sperm whales

may have evolved through sexual selection, both intra- and inter-sexually (Harvey and Bradbury, 1991), with larger males being favored when competing for females (Whitehead, 1994). In order to attain and maintain great size, it follows that male sperm whales, need to catch either many more prey items of the same size or select larger and/or more calorific prey species than would females. Such foraging requirements are likely reflected in different diving and foraging patterns of males compared to females. However, at latitudes where mature males and females are together, males apparently have lower feeding success than females as determined by defecation rates (Whitehead, 1993) and stomach contents (Clarke et al., 1988; Best, 1999). It is unclear if this reflects less success in finding prey or if males dedicate more time to mating vs. foraging when associating with females.

The foraging behavior of sperm whales, although inherently difficult to observe, has been studied in different areas of the world with a variety of methods (Whitehead, 1996; Jaquet and Whitehead, 1999; Jaquet et al., 2001; Madsen et al., 2002b; Miller et al., 2004a; Rendell et al., 2004; Drouot et al., 2004; Ruiz-Cooley et al., 2004; Watwood et al., 2006). However, field studies have mainly focused on groups of females and sub-adults of both sexes at low latitude (e.g. Gordon, 1987; Whitehead and Weilgart, 1991; Watwood et al., 2006). Male sperm whales away from the breeding ground have been studied off Kaikoura in New Zealand (e.g. Jaquet et al., 2000; Douglas et al., 2005), off Nova Scotia in Canada (Whitehead et al., 1992; Mullins et al., 1988) and off Andenes in Norway (Lettevall et al., 2002; Madsen et al., 2002b), but very little is known about how and at what depths the males forage at high latitudes.

This paper presents novel data on the foraging behavior of male sperm whales in a high latitude habitat. Detailed information about the movements and echolocation behavior of four mature male sperm whales was collected with non-invasive multi-sensor tags, called Dtags (Johnson and Tyack, 2003). We demonstrate that male sperm whales in this habitat display a different and more plastic foraging behavior than female and immature sperm whales studied at lower latitudes. We show that these male sperm whales forage over a wide depth range and display a bimodal foraging behavior consisting of shallow and deep dives, which indicates exploitation of a broad range of prey types.

2. Materials and methods

2.1. The study area

Field work took place in the Andøya Canyon, 15–30 km northwest of Andenes (northern Norway 69°25′

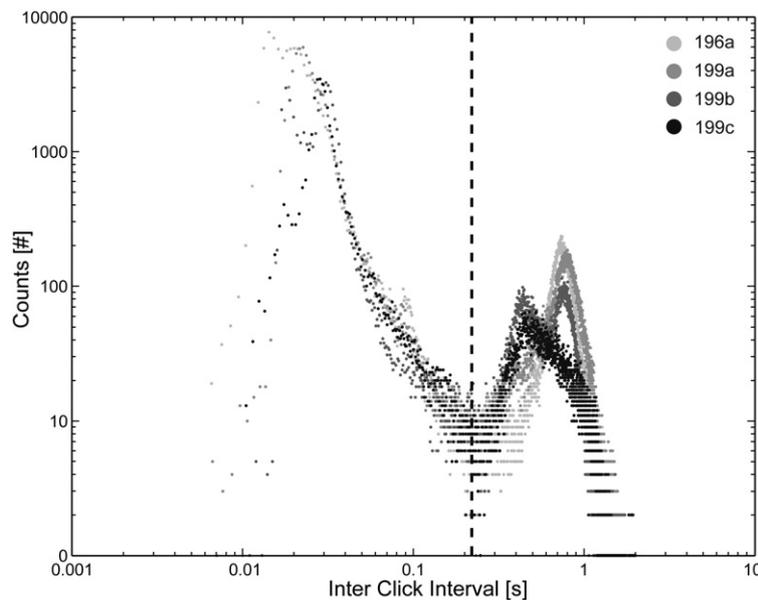


Fig. 1. Log–log plot of distribution of inter-click intervals (ICI) using all detected clicks ($ICI < 2$ s) from each of the tagged whales (196a $n = 158217$, 199a $n = 128153$, 199b $n = 88222$, 199c $n = 61546$). Bin width is 1 ms. The peaks centered on around 0.02 s mark the dominant ICI for buzz clicks. The peaks between 0.4 and 0.8 s mark the dominant ICI range for usual clicks. The vertical dashed line at 0.22 s marks the higher limit of ICI used to define buzz clicks.

N 15°45'E) in July 2005. The canyon is north of the Arctic Circle and the sun was continuously visible 24 h a day during the field work. Adult male sperm whales are normally found year round in this area (Ciano and Huele, 2001; Lettevall et al., 2002), and during the summer season whale-watching trips from Andenes occur on a daily basis. Due to adverse weather, tagging was only attempted on two days.

The Andøya Canyon is about 2000 m deep, and the maximum width at the canyon floor and between its shoulders is 2 and 12 km, respectively (Laberg et al., 2000). The coastal current that flows northwards along the Norwegian coast is episodically altered by northerly winds, generating upwelling (Sundby, 1984; Skarðhamar, 2004).

2.2. The tagging operation

Sperm whales were tagged with high-resolution digital archival tags (Dtag), which include a hydrophone, a depth sensor, a temperature sensor, and 3-axis accelerometers and magnetometers (Johnson and Tyack, 2003). Sounds were sampled at 96 kHz with a 16 bit sigma-delta analog-to-digital converter while non-acoustic sensors were sampled at 50 Hz, also with 16 bit resolution. The tags were programmed to record acoustic data until 99% of the memory capacity was consumed after which time only non-acoustic sensor data were recorded for the remainder

of the attachment. Surfacing whales were approached slowly from behind with a 7 m rigid-hull inflatable boat. Tags were deployed using a 15 m pole and attached with suction cups (for details of tag attachment, see Miller et al., 2004b). The tagging procedure, monitored with a handheld video camera, did not appear to provoke strong or sustained reactions from the whales. Minor reactions, such as rolling and moving slowly away from the tag-boat, were observed after tagging, but the whales resumed breathing at the surface in a normal fashion within tens of seconds of tag attachment. Tagged whales were followed from a 12 m

Table 1
Description of each tag deployment

TagID	Date tag ON	Time (UTC) tag ON	Hours of recording	# of foraging dives	Length and weight (m)
196a	July 15	14:43:40	21.1	29	16.3 (51 MT)
199a	July 18	13:05:47	17.7	25	15.3 (43 MT)
199b	July 18	14:43:15	13.6	17	16.0 (49 MT)
199c	July 18	16:57:12	13.1	12	14.3 (36 MT)

The hours of tagging and the number of foraging dives refer to the period when both acoustic data and motion sensors data were collected. Each whale was given a code according to the day of tagging (Julian day) and the order of tagging. Visual length measurements were made by calibrated video recordings at measured ranges when the whales were resting at the surface (Miller et al., 2004b). The animal mass in metric tons (10^3 kg, MT) was estimated using the equation $1.25 \times 0.0196 \times \text{length (m)}^{2.74}$ (Lockyer, 1976; Rice, 1989).

sailing boat, and a VHF radio beacon in the Dtag facilitated tracking and recovery of the tag from the sea surface after detachment. The lengths of tagged whales were measured using calibrated video recordings at measured ranges when the whales were resting at the surface (Miller et al., 2004b). The animal mass in metric tons (10^3 kg, MT) was estimated using the equation $1.25 \times 0.0196 \times \text{length (m)}^{2.74}$ (Lockyer, 1976; Rice, 1989).

2.3. Data analysis

Analysis was limited to periods in which both acoustic and non-acoustic sensor data were collected. The

duration of each dive (time from the fluke-up to the following surfacing) and the surface duration (time the whale was at the surface in between dives) were measured from the pressure sensor recording. Sounds produced by the tagged whale were detected using a custom click detector written in MATLAB 6.0 (MathWorks). Clicks from non-tagged conspecific whales were not individually detected but their presence was noted. Following Watwood et al. (2006), the search phase was defined as the time from the first usual click to the last click in a dive, a period ascribed to the active search for prey given the potential of usual clicks for long-range echolocation (Møhl et al., 2003; Madsen, 2002; Madsen

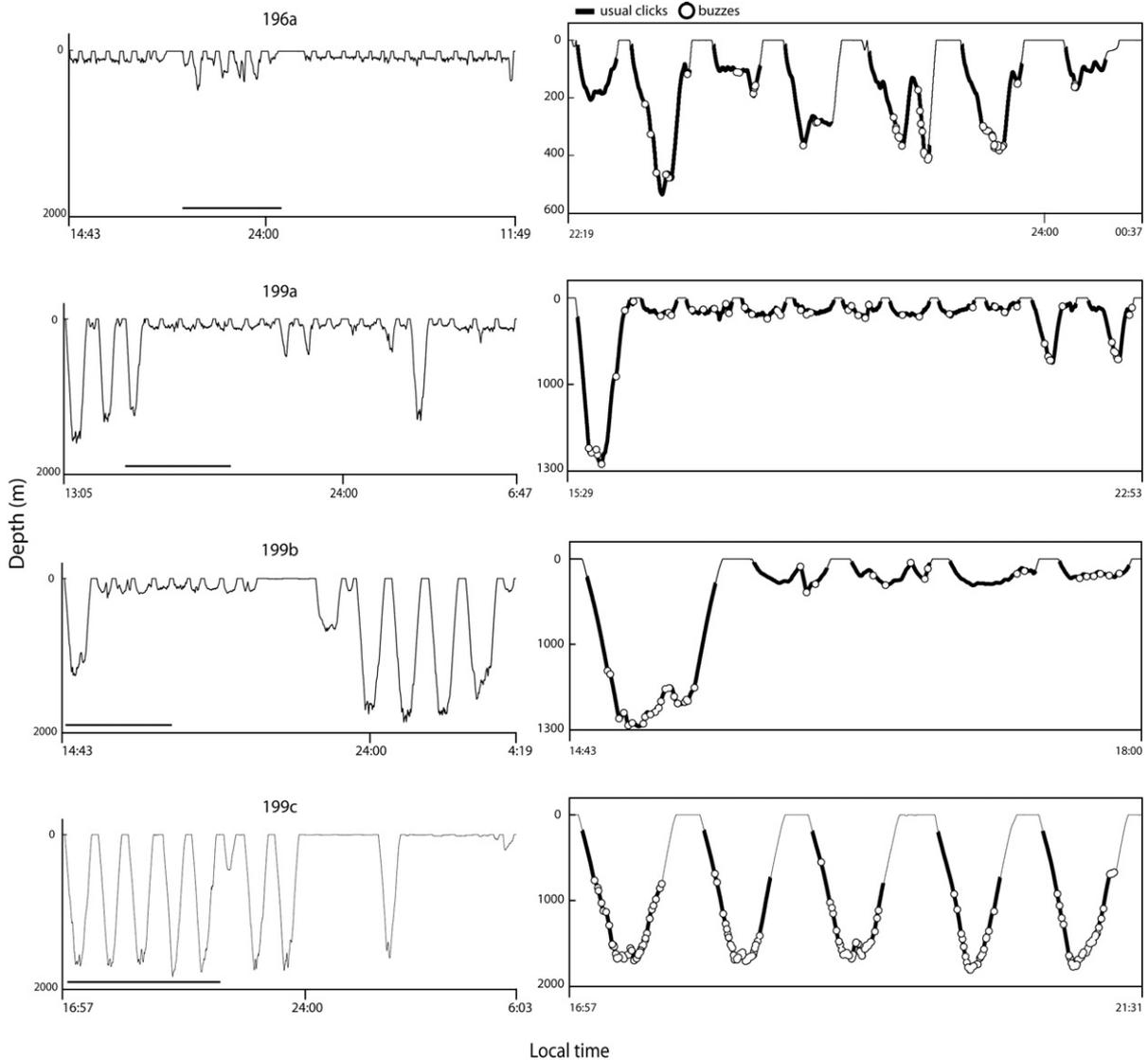


Fig. 2. Dive profile and sound production for each of the tagged whales. X-axes on the left-hand panels show the hour of day during which acoustic data were recorded. The right-hand panels are a magnification of time periods marked with horizontal black lines in the left-hand panels.

et al., 2002b; Zimmer et al., 2005). As we focused on the foraging activity of sperm whales, we therefore removed from the analysis dives during which the whales were not clicking and likely not foraging. Silent and shallow dives occasionally occurred during prolonged periods at the surface and were usually less than 25 m deep. One whale (196a) made a silent dive to a depth of 115 m. Echolocation buzzes were used as a proxy for feeding attempts (Madsen et al., 2002b; Miller et al., 2004a). Accordingly, the time from the first to the last buzz in a dive was designated as the foraging phase, i.e. the period when the whale was actively attempting to capture prey items (Watwood et al., 2006). This proxy is based on the assumption that sperm whales use echolocation to locate and capture prey. Source parameters and behavioral observations (Møhl et al., 2003; Jaquet et al., 2001; Madsen et al., 2002b; Miller et al., 2004a) strongly support the hypothesis that usual clicks are used to locate prey and buzzes are used in the terminal phase of prey capture foraging, as seen in bats (Griffin et al., 1960) and smaller toothed whale (Johnson et al., 2004; Madsen et al., 2005). However, we cannot say that every buzz leads to a successful prey capture or that the whale does not ingest a prey without emitting a buzz, but we argue that it is a good measure of the foraging attempts made by the whale. The duration of each buzz was measured as the time from the first to the last click in a

buzz having an inter-click interval (ICI) shorter than 0.22 s. This value was chosen from the distribution of ICIs of all whales (Fig. 1) as the ICI corresponding to the marked dip in the bimodal distribution. The interval between consecutive buzzes was measured as the time from the last click of a buzz to the time of the first click of the subsequent buzz.

Clicks emitted by a diving sperm whale normally generate echoes from surface and bottom reflections (e.g. Thode et al., 2002; Zimmer et al., 2005). Bottom reflections can be used to determine the distance of the whale from the sea floor, by measuring the delay between the emitted click and the returning echo. The delay equals the two-way-travel time of the click to and from the reflecting surface and can thus be converted to bottom range if the sound velocity is known. Echo delays were detected and measured with custom-written software in MATLAB 6.0 (MathWorks). A sound velocity of 1475 m s^{-1} was used, as this was the average sound velocity measured with a conductivity–temperature–depth probe (XCTD, Sippican Inc.) from surface to 1000 m depth on location. Surface and bottom reflections could be detected in recordings from all tagged whales, although reflections from the bottom were not detectable in all dives. This may be explained by the whale not pointing its sonar beam towards the bottom all the time or changes in reflectivity of different bottom

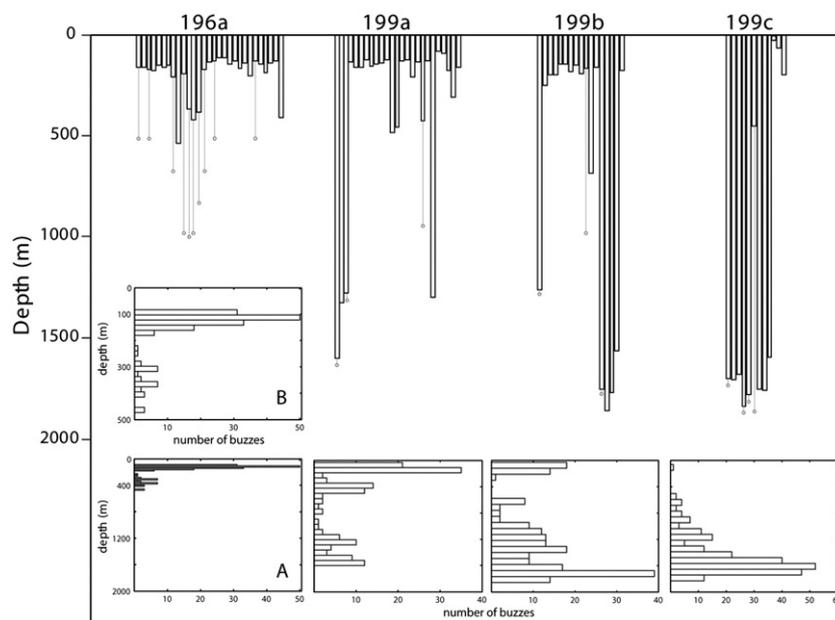


Fig. 3. Depths of consecutive dives for each whale (196a $n=29$, 199a $n=25$, 199b $n=17$ and 199c $n=12$). Bottom panels: histograms of buzz depth (196a $n=167$, 199a $n=142$, 199b $n=200$ and 199c $n=239$). Panel B is a magnification of panel A for whale 196a. Grey lines indicate the bottom depth at the corresponding dive (196a $n=11$, 199a $n=4$, 199b $n=3$ and 199c $n=4$), obtained by measuring the time delay between the emitted click and the returning echo from the bottom (see explanation in the text).

substrates. Bottom reflections could be detected in 10 dives for whale 196a, four dives for whale 199c and three dives for whales 199a and 199b.

Whale-watching boats frequented the canyon during the field work and on one occasion three boats were within 100 m of a tagged whale. This whale was observed visually to move away from the boats and a subsequent inspection of the tag recording revealed strong ship noise at this time. We therefore excluded data collected during this close approach from the analyses (three dives from whale 199a).

3. Results

Four mature male sperm whales were tagged in the Andøya Canyon at locations with water depths between 400 and 2000 m. The lengths of the whales were estimated by photogrammetry to be between 14 and 16 m long (Table 1). Motion and acoustic data were collected for 21.1, 17.7, 13.6 and 13.1 h, during which the four whales performed 29, 28, 17 and 12 foraging dives, respectively (Table 1, Figs. 2 and 3). The whales were followed visually for 26, 20, 8 and 1 surfacings, respectively. All whales were tagged when alone at the surface and they remained alone for the period of time they were visually tracked, except in one case when two whales (199a and 199b) were sighted within a few hundred meters of each other during a single surfacing. The maximum dive depth varied between 14 and nearly 1900 m with a median depth

of 175 m ($n=83$, Table 2). One of the whales (196a) did not dive deeper than 540 m and 76% of its dives were shallower than 200 m (Table 2, Figs. 2 and 3). Overall, the dive duration was on average 32 min \pm 10 (range 6.2–56.7, $n=83$, see Table 2 for individual statistics). Based on the analysis of bottom reflection delays, whales foraged on average 146 m from the bottom (range 23–348) during deep dives (depth > 500 m, $n=8$), searching for food in 90% (SD 6) of the water column on average. During shallow dives (depth < 500 m, $n=12$), whales foraged on average 690 m from the bottom (range 340–1630) exploiting 22% (SD 12) of the water column on average (Fig. 3). Although three of the whales made prolonged surfacings, sometimes exceeding 2 h (Table 2), 92% of the surfacings lasted less than 15 min. Extended periods at the surface were interspersed with shallow dives around 5–20 m, which were silent and therefore not considered for the current analysis.

The acoustic repertoire of the tagged whales included usual clicks (Weilgart and Whitehead, 1988), buzzes (“creaks” in Gordon, 1987; Madsen et al., 2002b; Miller et al., 2004a) and slow clicks (Weilgart and Whitehead, 1988; Madsen et al., 2002b). Slow clicks are thought to function as communication signals within mating systems on the breeding grounds (Weilgart and Whitehead, 1988), but may have a different role in high latitude habitats where only males are present. For the current work, we focused on usual clicks and buzzes which appear to serve primarily as echolocation signals in the context of

Table 2
Basic statistics for the diving parameters

	196a	199a	199b	199c	All
<i>Diving parameters</i>					
Number of dives	29	25	17	12	83
Dive duration (min)	19.9–37.9 (30.1) 30.0 \pm 4.8	15.4–50.5 (32.2) 33.6 \pm 9.0	14.1–56.7 (27.6) 34.1 \pm 14.1	6.2–46.7 (40.0) 32.7 \pm 14.4	6.2–56.7 (31.2) 32.3 \pm 10.1
Surface duration (min)	5.5–74.0 (9.4) 12.9 \pm 13.9	5.3–16.3 (7.2) 7.4 \pm 2.2	4.9–105.3 (6.6) 13.8 \pm 23.7	6.4–161.3 (11.2) 34.0 \pm 54.1	4.9–161.3 (8.3) 14.5 \pm 25.4
Max. dive depth (m)	116–537 (163) 202 \pm 109	82–1600 (159) 383 \pm 459	143–1861 (197) 639 \pm 689	14–1837 (1691) 1212 \pm 768	14–1861 (175) 492 \pm 593
<i>Search phase parameters</i>					
Number of dives	29	25	17	12	83
Search duration (min)	9.8–36.7 (28.4) 27.2 \pm 6.2	15.2–45.9 (32.2) 32.5 \pm 8.4	12.4–44.7 (26.3) 29.9 \pm 10.4	6.1–37.7 (32.2) 26.5 \pm 11.1	6.1–45.9 (29.8) 29.2 \pm 8.8
% of dive in search phase	90 \pm 12	97 \pm 2	90 \pm 8	83 \pm 7	91 \pm 10
Depth first click (m)	5–33 (8) 9 \pm 6	4–218 (5) 20 \pm 50	6–204 (12) 62 \pm 77	4–207 (194) 163 \pm 72	4–218 (8) 46 \pm 73
Depth last click (m)	47–348 (83) 105 \pm 69	1–148 (20) 36 \pm 40	1–1114 (80) 286 \pm 410	1–820 (697) 442 \pm 375	1–1114 (68) 170 \pm 273

Dive duration is the time from fluke-up to following surfacing. Surface duration is the time from surfacing to following fluke-up. The search phase is the time from the first to the last usual click in a dive. Dive duration, surface duration, max. diving depth, search phase duration, depth first click and depth last click show range (median) and mean \pm SD. The percentage of dive in search phase shows mean \pm SD.

foraging dives (Madsen et al., 2002b; Miller et al., 2004a). The four whales clicked for an average of $29.2 \text{ min} \pm 8.8$ (range 6.1–45.9, $n=83$) per dive, the first usual click being produced at depths ranging between 4 and 218 m and the last usual click at depths ranging between 1 and 1114 m ($n=83$, Table 2). The search phase accounted for an average 91% (SD=10) of the dive duration (Table 2). The depth of the first usual click was correlated with the maximum dive depth for the three whales that performed deep dives (196a $r=0.10$, $p=0.62$, $n=29$; 199a $r=0.75$, $p<0.01$, $n=25$; 199b $r=0.95$, $p<0.01$, $n=17$; 199c $r=0.79$, $p<0.01$, $n=12$). The depth of the last click was correlated with the maximum dive depth for two of the whales that performed deep dives (196a $r=0.53$, $p<0.01$, $n=29$; 199a $r=0.23$, $p=0.26$, $n=25$; 199b $r=0.92$, $p<0.01$, $n=17$; 199c $r=0.85$, $p<0.01$, $n=12$). The last usual click was produced at depths ranging between 1 and 1114 m (Table 2). Buzzes were heard in 74 of 83 dives, at depths between 17 and 1860 m, and were emitted during both the descent and ascent phase of deep dives (Table 3, Fig. 2). The number of buzzes per dive ranged from 1 to 45 (Table 3). A total of nine dives between 14 and 450 m deep contained usual clicks but no buzzes (196a=1, 199a=3, 199b=2, 199c=3). The duration of buzzes (Fig. 4) was negatively correlated with dive depth for the three deep-diving whales and positively correlated with dive depth for the shallow-diving whale (196a $r=0.47$, $p<0.01$, $n=167$; 199a $r=-0.49$, $p<0.01$, $n=142$; 199b $r=-0.85$, $p<0.01$, $n=200$; 199c $r=-0.65$, $p<0.01$, $n=239$). The time interval between consecutive buzzes (Fig. 4) was also negatively correlated with the dive depth for all the whales (196a $r=-0.25$, $p<0.01$, $n=139$; 199a $r=-0.47$, $p<0.01$, $n=142$; 199b $r=-0.67$, $p<0.01$, $n=185$; 199c $r=-0.41$, $p<0.01$, $n=230$). The number

of buzzes per dive was correlated with the maximum dive depth for the same three whales (196a $r=0.31$, $p=0.10$, $n=28$; 199a $r=0.76$, $p<0.01$, $n=22$; 199b $r=0.97$, $p<0.01$, $n=15$; 199c $r=0.73$, $p<0.05$, $n=9$).

4. Discussion

This study investigated the foraging behavior of sperm whales in a high latitude habitat. The use of non-invasive archival tags allowed us to quantify for the first time details of the diving and acoustic behavior of large, adult male sperm whales for many consecutive dive cycles. The bimodal distribution of short and long dives of sperm whales in this habitat has been noted in previous studies (Sarvas, 1999), so while the presented data are from a limited period and from only four whales, the overall diving and foraging behavior is most likely not uncommon in this habitat. Sperm whales off Andenes are usually widely separated when visible at the surface (Lettevall et al., 2002). However, clicks from non-tagged conspecifics were audible in the tag recordings on several occasions, demonstrating a strong potential for acoustic contact between these apparently non-social males (Madsen et al., 2002b).

Sperm whales are well-known for the deep dives they perform to reach foraging depths (Papastavrou et al., 1989; Watkins et al., 1993). Watwood et al. (2006) reported that female and immature sperm whales in subtropical habitats perform stereotypical foraging dives to depths of 400–1200 m. We have observed a radically different diving behavior for physically mature males in this high latitude habitat. While we recorded dives to depths of nearly 1900 m, comprising the deepest dives recorded with a calibrated onboard recorder on a sperm

Table 3
Basic statistics for the foraging parameters

	196a	199a	199b	199c	All
<i>Foraging phase parameters</i>					
Number of dives	28	22	15	9	74
Number of buzzes	167	142	200	239	748
Number of buzzes per dive	1–12 (5.5) 6.0±3.1	1–29 (4.5) 6.5±6.3	1–40 (6) 13.7±14.6	1–45 (33) 26.6±13.4	1–45 (6) 10.0±11.0
Foraging duration (min)	0.2–32.0 (17.4) 17.1±8.6	0.2–37.9 (16.5) 16.3±10.9	0.2–37.9 (17) 18.2±10.1	0.4–32.3 (21.9) 21.8±9.1	0.2–37.9 (19.2) 18.2±10.0
% of dive in foraging	55±24	47±24	49±23	52±19	51±24
Depth first buzz (m)	84–368 (119) 143±68	64–1126 (129) 276±317	45–986 (145) 373±350	61–931 (763) 699±282	45–1126 (128) 297±305
Depth last buzz (m)	84–410 (133) 151±83	28–1056 (118) 191±266	45–1334 (160) 473±500	64–1403 (1058) 919±389	28–1403 (129) 322±390
Buzz duration (s)	6.6–78.8 (13.5) 16.7±10.4	2–54.9 (11.6) 14.0±9.8	3.1–21.2 (6.7) 7.8±3.4	1.6–29.4 (5.1) 5.8±2.9	1.6–78.8 (7.3) 10.3±8.2

The foraging phase is the time from the first to the last buzz in a dive. Number of buzzes per dive, foraging duration, depth first buzz, depth last buzz and buzz duration show range (median) and mean±SD. Dives that did not contain buzzes were excluded from this statistics.

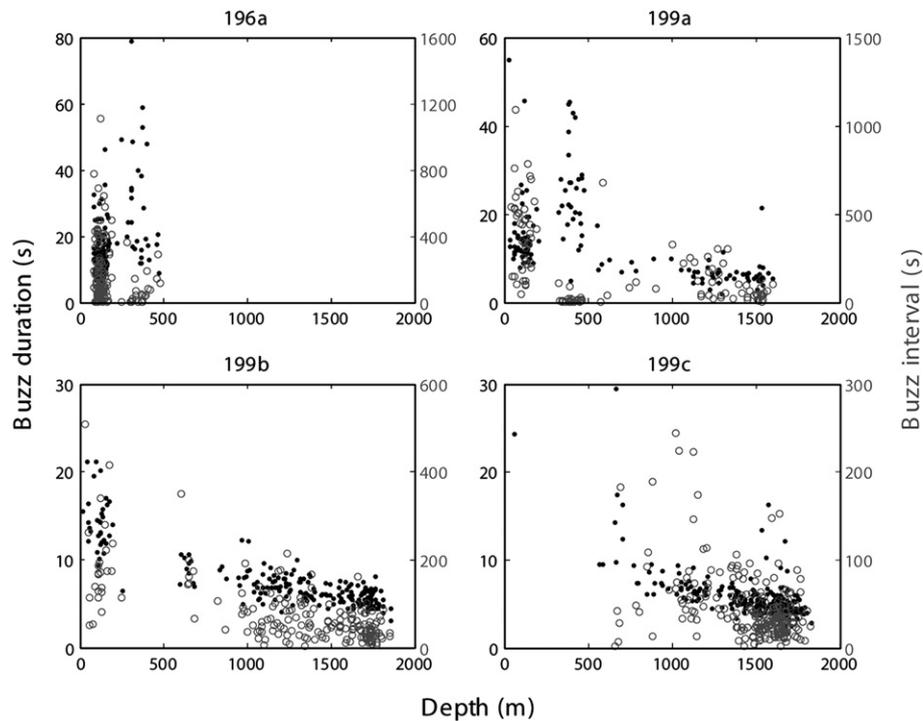


Fig. 4. Buzz duration (196a $n=167$, 199a $n=142$, 199b $n=200$ and 199c $n=239$), shown by black dots, and time interval between consecutive buzzes (196a $n=139$, 199a $n=120$, 199b $n=185$ and 199c $n=230$), grey circles, plotted against depth for the four whales.

whale, 72% of the dives were shallower than 400 m (Table 2, Figs. 2 and 3). From the inspection of bottom reflections generated by the echolocation clicks emitted by the whales, these shallow dives do not seem to be constrained by the bathymetry of the canyon, but signify that the whales target epipelagic prey. To the contrary some deep dives do include some benthopelagic foraging (Fig. 3).

Tagged male sperm whales spent 91% of the dive emitting usual clicks, with clicks being produced during the descent, bottom and ascent phase of dives (Table 2). Given the strong potential of usual clicks for long-range echolocation of prey (Madsen et al., 2002b; Møhl et al., 2003), it seems that the whales actively search for prey over a wide range of depths and in any stage of the dive. Echolocation throughout the ascent phase indicates that whales anticipate the presence of shallow water prey, as also indicated by the frequent shallow foraging dives. In contrast, sperm whales studied in lower latitudes usually start clicking at depths between 50 and 250 m depth on the descent and stop clicking early in the ascent phase (Madsen et al., 2002a; Douglas et al., 2005; Watwood et al., 2006), showing that they do not echolocate for food on the way back up to the surface.

The depth of the first click in dives performed by three of the four male sperm whales was correlated with

the maximum dive depth, with whales commencing to click later in deep dives. This suggests that these whales anticipated which depth to explore in each dive. The estimated detection range for aggregations of squid and fish by sperm whales is about 500 m (Møhl et al., 2003) and so a whale diving to 1000 or more meters is unlikely to detect the target prey layer until well into the descent, explaining the delayed start in clicking. The end of the search phase in relation to the maximum dive depth followed a less deterministic pattern compared to the first click of the dive, suggesting that on the way up to the surface different factors may determine the depth of the last click.

Male sperm whales off northern Norway emitted echolocation buzzes at depths as disparate as 17 m and nearly 1900 m (Fig. 2), suggesting that they were encountering prey items throughout a large part of the water column. While buzzes are normally reported to occur in the bottom phase of the dive (Jaquet et al., 2001; Drouot et al., 2004; Watwood et al., 2006), the male sperm whales off northern Norway emitted buzzes at shallow depths both during the descent and the ascent phase indicating that sperm whales encountered prey items in those portions of the dive as well (Fig. 2).

The depth of dives, and the number and duration of buzzes (Figs. 4 and 5), suggest two distinct foraging

modes. In shallow dives of less than about 500 m, usual clicks start within the first 15 m of the dive, and buzzes are infrequent, but of long duration (Table 3, Figs. 4 and 5). Conversely, in deep dives which are deeper than 500 m and may extend to more than 1600 m depth, usual clicks start at about 150 m and the buzzes are short, but frequent (Table 3, Figs. 4 and 5). This bimodal foraging pattern is especially evident for whale 199b. The average buzz interval was 65 s in deep dives ($n=129$) and 190 s in shallow dives ($n=24$). If this whale moved at a constant speed of 1 ms^{-1} (e.g. Whitehead et al., 1992; Watwood et al., 2006) while searching for prey, it would have encountered a prey item approximately every 65 m during deep dives and every 190 m during shallow dives. Although the pattern is not as clear for whale 196a and 199b, which seem to stay with one mode, the variation in the number of buzzes and the time interval between buzzes, with depth (Fig. 4), support the hypothesis that the whales feed on more sparsely distributed prey items during shallow dives and more densely distributed prey items during deep dives.

Wahlberg (2002) reported that the number of clicks produced by sperm whales between consecutive pauses, when the whales are assumed to recycle air, decreases with increasing dive depth and suggested that this may

relate to the restricted air volume available for sound production at depth (Madsen et al., 2002a). The short buzzes observed in deep dives follow the same trend, but a restricted air volume cannot fully explain our observations. Sequences of closely spaced buzzes, lasting for several minutes and including buzzes as long as 40 s, were emitted at 400 m depth (Fig. 4) where the quantity of air is already down to 2% of the total amount of air at the surface. In tag data collected in the Gulf of Mexico, a 12.4 m whale produced buzzes longer than 60 s in duration at depth >850 m (P.J.O.M, unpublished data). This shows that sperm whales are capable of emitting long buzzes at depth, and the bimodal distribution of buzz duration (Fig. 4) likely reflects differences in biosonar-based foraging rather than just hydrostatic limitations in sound production.

Another possible explanation for the long buzzes in shallow dives is that these may reflect capture attempts on several prey items during the same buzz. The duration of a buzz relates to the time and likely the energy that the whale invests in capture attempts and so it is reasonable that a longer buzz be rewarded by a greater return. In echolocating bats, emission of a buzz signifies an attempt to capture a single prey item and prolonged buzzing occurs when bats target evading prey (e.g.

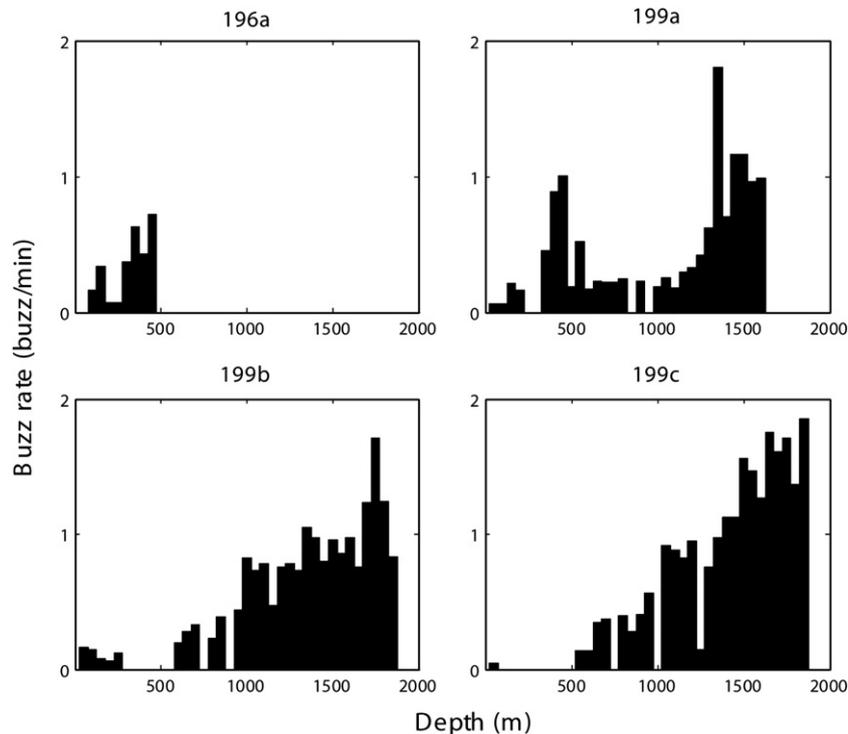


Fig. 5. Number of buzzes per minute spent in each depth bin for the four whales (196a $n=167$, 199a $n=142$, 199b $n=200$ and 199c $n=239$). Bin width is 50 m.

Griffin et al., 1960; Kalko, 1995). However, the anatomy of bats prevents these aerial mammals from echolocating and ingesting prey at the same time, a constraint that is not faced by the sperm whale with a sound generator that works independently of the buccal cavity (Wahlberg et al., 2005). Buzzing is seen as an echolocation phase where the predator locks its biosonar onto a single target (Griffin et al., 1960; Madsen et al., 2005), and it is problematic in that light to envision how the whale can shift between locking on to two different prey items in the same fast ICI buzz phase. Therefore, while we cannot rule out capture of several prey items per buzz for the sperm whale, we view the notion that each buzz, irrespective of duration, reflects an attempt to capture a single prey item the most parsimonious.

Not knowing the types of prey consumed by the tagged whales, we cannot directly link the whale behavior to a prey type (e.g. Barrett-Lennard et al., 1996; Bowen et al., 2002). However, the bimodal pattern in the number and duration of buzzes as a function of depth, suggests that sperm whales in this habitat adapt their foraging behavior according to the type and mobility of the prey they target. Mobile prey are likely to require more time to catch compared to slow or small prey, and this difference is likely reflected in the duration and distribution of buzzes. During deep water foraging, buzzes are generally much shorter than in shallow water, with whales spending less than half of the time on the average prey pursuit. Buzzes in shallow dives are not only longer, suggesting that the whale is targeting a moving prey, but also more widely spaced in time, resulting in longer search times between prey encounters. The occurrence of echolocation buzzes during shallow dives is lower compared to other areas of the world (Drouot et al., 2004; Miller et al., 2004a; Watwood et al., 2006), and may be explained by the consumption of sparsely distributed, but more energetically or possibly nutritionally rewarding prey items like larger fish (Martin and Clarke, 1986). The specific factors that determine the shifts between shallow and deep water foraging modes remain unclear, but are likely governed by the whale's perception of which mode would yield the highest net energy returns per unit of time: cheap shallow dives with few prey items or deep dives with more prey that require a bigger energetic and temporal investment to access. Either way, the depth of the first echolocation click indicates that the whales make a deliberate decision of whether to forage shallow or deep prior to the dive.

The observed changes in dive depth are unlikely to be driven by vertical migration of prey, as changes in dive depth were not gradual. Blachowiak-Samolyk et al. (2006) have shown that the dominant zooplankton taxa

in the Arctic region do not perform vertical migrations during periods of midnight sun, which corresponds to the latitudes and season our data were collected. Also, we would expect to observe broadly similar foraging behavior at different depths if the same prey is targeted. Future studies may include investigations on the presence and behavior of possible prey in the same area (e.g. Davis et al., 2007), allowing to identify target species during shallow and deep dives.

The diving and acoustic behavior observed from the four male sperm whales tagged off northern Norway is different from known foraging behavior in female and immature sperm whales at lower latitudes (Watwood et al., 2006). These apparent sex differences in foraging patterns are consistent with findings from stomach contents, which have shown differences in the composition of the diet of males and females (e.g. Evans and Hindell, 2004). Differences between sexes in habitat utilization and foraging behavior have been shown for different species of sexually dimorphic seals (Stewart, 1997; Le Boeuf et al., 2000; Beck et al., 2003; Page et al., 2005; Breed et al., 2006). In particular, sexual segregation in the northern elephant seal (*Mirounga angustirostris*) appears to develop during puberty, suggesting that sexual segregation in this species is more related to the demands of accelerated growth during this period of sexual maturation, rather than to differences in gross energy requirements of adults (Stewart, 1997). Male sperm whales also start to segregate from females during puberty and move to higher latitudes (Rice, 1989) while females with calves and juveniles remain in tropical and temperate waters within highly social matriarchal units (e.g. Whitehead and Weilgart, 2000), perhaps choosing areas with less food resources but with a lower density of predators (e.g. Corkeron and Connor, 1999). Male sperm whales need high energetic returns from foraging to obtain and maintain their great size, which may ultimately determine their access to females on the breeding grounds (Whitehead, 1994). The high primary productivity that supports the size, abundance, and caloric value of prey in high latitude habitats, like the Andøya canyon, may be a key factor that makes male sperm whales migrate to distant, but more profitable foraging grounds. However, given the small temporal and spatial resolution of the current dataset, the collection of additional data over longer periods and covering a larger portion of the population is needed in order to draw broader conclusions on behavioral differences between sexes and population. Nevertheless, the newfound plasticity in the foraging behavior of male sperm whales indicates that they can adapt to food resources, which in turn may explain the increasingly

incidence of depredation from longline fisheries that has been reported in several areas of the world (e.g. Kock et al., 2006).

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References

- Barrett-Lennard, L.G., Ford, J.K.B., Heise, K.A., 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Anim. Behav.* 51, 553–565.
- Beck, C.A., Bowen, W.D., McMillan, J.I., Iverson, S.J., 2003. Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Anim. Behav.* 66, 777–789.
- Berzin, A.A., 1972. The Sperm Whale. Israel Program for Scientific Translations, Jerusalem.
- Best, P.B., 1979. Social organization in sperm whales, *Physeter macrocephalus*. In: Winn, Olla (Ed.), *Behavior of Marine Animals*, vol. 3. Plenum, New York, pp. 227–289.
- Best, P.B., 1981. The task of the narwhal (*Monodon monoceros* L.): interpretation of its function (Mammalia: Cetacea). *Can. J. Zool.* 59, 2386–2393.
- Best, P.B., 1999. Food and feeding of sperm whales *Physeter macrocephalus* off the west coast of South Africa. *S. Afr. J. Mar. Sci.* 21, 393–413.
- Blachowiak-Samolyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., Falk-Petersen, S., Mouritsen, L.T., 2006. Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Mar. Ecol. Prog. Ser.* 308, 101–116.
- Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., Marshall, G.J., 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar. Ecol. Prog. Ser.* 244, 235–245.
- Breed, G.A., Bowen, W.D., McMillan, J.I., Leonard, M.L., 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proc. R. Soc., Sect. B* 273, 2319–2326.
- Caldwell, D.K., Caldwell, M.C., Rice, D.W., 1966. Behavior of the sperm whale *Physeter catodon* L. In: Norris (Ed.), *Whales, Dolphins and Porpoises*. University of California Press, Berkeley, pp. 677–717.
- Ciano, J.N., Huele, R., 2001. Photo-identification of sperm whales at Bleik Canyon, Norway. *Mar. Mamm. Sci.* 17, 175–180.
- Clark, S.T., Odell, D.K., 1999. Allometric relationships and sexual dimorphism in captive killer whales (*Orcinus orca*). *J. Mamm.* 80, 777–785.
- Clarke, M.R., 1980. Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. *Discov. Rep.* 37, 1–324.
- Clarke, M.R., Macleod, N., 1976. Cephalopod remains from sperm whales caught off Iceland. *J. Mar. Biol. Assoc. UK* 56, 733–750.
- Clarke, M.R., Paliza, O., Aguayo, A., 1988. Sperm whales of the southeast Pacific. Part IV. Fatness, food and feeding. *Invest. Cetacea* 21, 53–195.
- Clarke, M.R., Martins, H.R., Pascoe, P., 1993. The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philos. Trans. R. Soc. Lond., B* 339, 67–82.
- Corkeron, P.J., Connor, R.C., 1999. Why do baleen whales migrate? *Mar. Mamm. Sci.* 15, 1228–1245.
- Cranford, T.W., 1999. The sperm whale nose: sexual selection on a grand scale? *Mar. Mamm. Sci.* 15, 1133–1157.
- Davis, R.W., Jaquet, N., Gendron, D., Markaida, U., Bazzino, G., Gilly, W., 2007. Diving behavior of sperm whales in relation to behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico. *Mar. Ecol. Prog. Ser.* 333, 291–302.
- Dingle, H., 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, Oxford, UK.
- Douglas, L.A., Dawson, S.M., Jaquet, N., 2005. Click rates and silences of sperm whales at Kaikoura, New Zealand. *J. Acoust. Soc. Am.* 118, 523–529.
- Drouot, V., Gannier, A., Goold, J.C., 2004. Diving and feeding behaviour of sperm whales (*Physeter macrocephalus*) in the Northwestern Mediterranean Sea. *Aquat. Mamm.* 30, 419–426.
- Evans, K., Hindell, M.A., 2004. The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters. *ICES J. Mar. Sci.* 61, 1313–1329.
- Gordon, J.C.D., 1987. Behavior and ecology of sperm whales off Sri Lanka. Ph.D. dissertation, University of Cambridge, Cambridge, UK.
- Gosho, M.E., Rice, D.W., Breiwick, J.M., 1984. The sperm whale, *Physeter macrocephalus*. *Mar. Fish. Rev.* 46, 54–64.
- Griffin, D.R., Webster, F.A., Michael, C.R., 1960. The echolocation of flying insects by bats. *Anim. Behav.* 8, 141–154.
- Harvey, P.H., Bradbury, J.W., 1991. Sexual selection. In: Krebs, Davies (Ed.), *Behavioral Ecology: an Evolutionary Approach*, 3rd edition. Blackwell Scientific, Oxford, pp. 203–233.
- Jaquet, N., Whitehead, H., 1999. Movements, distribution, and feeding success of sperm whales in the Pacific Ocean, over scales of days and tens of kilometers. *Aquat. Mamm.* 25, 1–13.
- Jaquet, N., Dawson, S., Slooten, E., 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. *Can. J. Zool.* 78, 407–419.
- Jaquet, N., Dawson, S., Douglas, L., 2001. Vocal behavior of male sperm whales: why do they click? *J. Acoust. Soc. Am.* 109, 2254–2259.
- Jefferson, T.A., 1990. Sexual dimorphism and development of external features in Dall's porpoise *Phocoenoides dalli*. *Fish. Bull.* 88, 119–132.
- Johnson, M.P., Tyack, P.L., 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Oceanic Eng.* 28, 3–12.

- Johnson, M.P., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N., Tyack, P.L., 2004. Beaked whales echolocate on prey. *Proc. R. Soc. Lond., B Biol. Sci.* 271, 383–386.
- Kalko, E.K.V., 1995. Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). *Anim. Behav.* 50, 861–880.
- Kawakami, T., 1980. A review of sperm whale food. *Sci. Rep. Whales Res. Inst.* 32, 199–218.
- Kleiber, M., 1975. *The Fire of Life: An Introduction to Animal Energetics*. R.E. Krieger Publishing, NY.
- Kock, K.H., Purves, M.G., Duhamel, G., 2006. Interactions between cetacean and fisheries in the Southern Ocean. *Polar Biol.* 29, 379–388.
- Laberg, J.S., Vorren, T.O., Dowdeswell, J.A., Kenyon, N.H., Taylor, J., 2000. The Andøya Slide and the Andøya Canyon, north-eastern Norwegian-Greenland Sea. *Mar. Geol.* 162, 259–275.
- Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., Houser, D.S., 2000. Foraging ecology of northern elephant seals. *Ecol. Monogr.* 70, 353–382.
- Lettevall, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., Christal, J., McCall Howard, P., 2002. Social structure and residency in aggregations of male sperm whales. *Can. J. Zool.* 80, 1189–1196.
- Lindfors, P., Tullberg, B.S., Biuw, M., 2002. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behav. Ecol. Sociobiol.* 52, 188–193.
- Lockyer, C., 1976. Body weights of some species of large whales. *J. Cons. Int. Explor. Mer.* 36, 259–273.
- Madsen, P.T., 2002. Sperm whale sound production. Ph.D. dissertation, University of Aarhus, Aarhus, Denmark.
- Madsen, P.T., Payne, R., Kristiansen, N.U., Wahlberg, M., Kerr, I., Møhl, B., 2002a. Sperm whale sound production studied with ultrasonic time/depth-recording tags. *J. Exp. Biol.* 205, 1899–1906.
- Madsen, P.T., Wahlberg, M., Møhl, B., 2002b. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behav. Ecol. Sociobiol.* 53, 31–41.
- Madsen, P.T., Johnson, M., Aguilar de Soto, N., Zimmer, W.M.X., Tyack, P.L., 2005. Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J. Exp. Biol.* 208, 181–194.
- Main, M.B., Weckerly, F.W., Bleich, V.C., 1996. Sexual segregation in ungulates: new directions for research. *J. Mamm.* 77, 449–461.
- Martin, A.R., Clarke, M.R., 1986. The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. *J. Mar. Biol. Ass. U.K.* 66, 779–790.
- Miller, P.J.O., Johnson, M.P., Tyack, P.L., 2004a. Sperm whale behaviour indicates the use of rapid echolocation click buzzes “creaks” in prey capture. *Proc. R. Soc. Lond., B Biol. Sci.* 271, 2239–2247.
- Miller, P.J.O., Johnson, M.P., Tyack, P.L., Terray, E.A., 2004b. Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J. Exp. Biol.* 207, 1953–1967.
- Møhl, B., Wahlberg, M., Madsen, P.T., Heerfordt, A., Lund, A., 2003. The monopulsed nature of sperm whale clicks. *J. Acoust. Soc. Am.* 114, 1143–1154.
- Mullins, J., Whitehead, H., Weilgart, L.S., 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Can. J. Fish. Aquat. Sci.* 45, 1736–1743.
- Okutani, T., Nemoto, T., 1964. Squids as the food of sperm whales in the Bering Sea and Alaska Gulf. Tokai Regional Fisheries Laboratory. *Sci. Rep. Whales Res. Inst.*, 18. Tokyo.
- Page, B., McKenzie, J., Goldsworthy, S.D., 2005. Inter-sexual differences in New Zealand fur seal diving behaviour. *Mar. Ecol. Prog. Ser.* 304, 249–264.
- Papastavrou, V., Smith, S.C., Whitehead, H., 1989. Diving behavior of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Can. J. Zool.* 67, 839–846.
- Rice, D.W., 1989. Sperm whale. *Physeter macrocephalus* Linnaeus, 1758. In: Ridgway, Harrison (Ed.), *Handbook of Marine Mammals*, vol. 4. Academic Press, London, pp. 177–233.
- Remell, L.E., Whitehead, H., Escribano, R., 2004. Sperm whale habitat use and foraging success off northern Chile: evidence of ecological links between coastal and pelagic systems. *Mar. Ecol. Prog. Ser.* 275, 289–295.
- Ruckstuhl, K.E., Neuhaus, P., 2000. Sexual segregation in ungulates: a new approach. *Behaviour* 137, 361–377.
- Ruiz-Cooley, D., Gendron, D., Aguiñiga, S., Mesnick, S., Carriquiry, J.D., 2004. Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. *Mar. Ecol. Prog. Ser.* 277, 275–283.
- Santos, M.B., Pierce, G.J., Boyle, P.R., Reid, R.J., Ross, H.M., Patterson, I.A.P., Kinze, C.C., Tougaard, S., Lick, R., Piatkowski, U., Hernandez-Garcia, V., 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996. *Mar. Ecol. Prog. Ser.* 183, 281–294.
- Sarvas, T.H., 1999. The effects of the deep scattering layer on the diving behavior of sperm whales off Andøya, Norway. M. Sc. thesis, University of Helsinki, Helsinki, Finland.
- Skarøhamar, J., 2004. Variability in circulation and hydrography in North Norwegian coastal waters. M.Sc. thesis, University of Tromsø, Tromsø, Norway.
- Stewart, B.S., 1997. Ontogeny of differential migration and sexual segregation in northern elephant seals. *J. Mamm.* 78, 1101–1116.
- Sundby, S., 1984. Influence of bottom topography on the circulation at the continental shelf off Northern Norway. *Fiskeridir. Skr., Ser. Havunders.* 17, 501–519.
- Thode, A., Mellinger, D.K., Stienessen, S., Martinez, A., Mullin, K., 2002. Depth-dependent acoustic features of diving sperm whales (*Physeter macrocephalus*) in the Gulf of Mexico. *J. Acoust. Soc. Am.* 112, 308–321.
- Wahlberg, M., 2002. The acoustic behavior of diving sperm whales observed with a hydrophone array. *J. Exp. Mar. Biol. Ecol.* 281, 53–62.
- Wahlberg, M., Frantzis, A., Alexiadou, P., Madsen, P.T., Møhl, B., 2005. Click production during breathing in a sperm whale (*Physeter macrocephalus*). *J. Acoust. Soc. Am.* 118, 3404–3407.
- Watkins, W.A., Daher, M.A., Fristrup, K.M., Howald, T.J., Notarbartolo di Sciara, G., 1993. Sperm whales tagged with transponders and tracked underwater by sonar. *Mar. Mamm. Sci.* 9, 55–67.
- Watwood, S., Miller, P.O.J., Johnson, M.P., Madsen, P.T., Tyack, P.L., 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J. Anim. Ecol.* 75, 826–835.
- Weilgart, L., Whitehead, H., 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Can. J. Zool.* 66, 1931–1937.
- Whitehead, H., 1993. The behaviour of mature male sperm whales on the Galapagos breeding grounds. *Can. J. Zool.* 71, 689–699.
- Whitehead, H., 1994. Delayed competitive breeding in roving males. *J. Theor. Biol.* 166, 127–133.
- Whitehead, H., 1996. Variation in the feeding success of sperm whales: temporal scale, spatial scale and relation to migration. *J. Anim. Ecol.* 65, 429–438.
- Whitehead, H., Weilgart, L., 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* 118, 275–296.
- Whitehead, H., Weilgart, L., 2000. The sperm whale: social females and roving males. In: Mann, Connor, Tyack, Whitehead (Eds.),

- Cetacean Societies: Field Studies of Dolphins and Whales. University of Chicago Press, Chicago.
- Whitehead, H., Waters, S., Lyrholm, T., 1991. Social organization of female sperm whales and their offspring: constant companions and casual acquaintance. *Behav. Ecol. Sociobiol.* 9, 285–289.
- Whitehead, H., Brennan, S., Grover, D., 1992. Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. *Can. J. Zool.* 70, 912–918.
- Whitehead, H., McLeod, C.D., Rodhouse, P., 2003. Differences in niche breadth among some teuthivorous mesopelagic marine predators. *Mar. Mamm. Sci.* 19, 400–406.
- Zimmer, W.M.X., Tyack, P.L., Johnson, M.P., Madsen, P.T., 2005. Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. *J. Acoust. Soc. Am.* 118, 3337–3345.