Diving and foraging behavior of toothed whales:
Do toothed whales compete for prey in the deep sea?

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Abstract

Recent studies on diving and foraging behavior of three species of toothed whales: the sperm whale, Cuvier's beaked whale and Blainville's beaked whale, are introduced. Their characteristic diving behaviors are summarized, compared and discussed. Despite a smaller physiological capacity of diving, Cuvier's beaked whales and Blainville's beaked whales forage smaller prey items at higher frequencies (28.9/dive and 27.8/dive) in deeper waters, whereas sperm whales forage larger prey, mostly squids, at lower frequency in shallower waters than the two beaked whales. The two species of beaked whales regularly exceeded their calculated ADL in their deep foraging dives, but sperm whales dived within their calculated ADL. The obvious differences in foraging depth and prey size of these three species indicate possible changes in mesopelagic prey fauna with depth.

Introduction

It is widely confirmed that many marine endotherms dive deep and long (Table 1). Since some birds can dive surprisingly deep and long despite a small body mass, the remarkable diving capacities of these animals raised two major questions about, (1) how they can dive so deep for so long and (2), how body mass affects diving capacity.

Regarding question (1), physiological studies have already provided answers. The diving animals generally extend their dives by increasing their capacity to store oxygen and by decreasing metabolic rate during dives (Butler, 2001). In other words, capacity to store oxygen and level of metabolic rate determine

Table 1. Known maximum dive depth and maximum dive duration recorded by animal-borne instruments and acoustic tools. These extraordinary ability raised questions: how are they able to tolerate to anoxia and how do they take preys?

Species	Maximum depth (Reference)
	Maximum duration (Reference)
King penguin	343m (Putz & Cherel 2005)
	9.2min (Charrassin et al. 1998)
Emperor penguin	564m (Kirkwood & Robertson 1997)
	27.6mim, (Sato K. unpublished data)
Weddell seal	741m (Testa 1994)
	67.0min, (Plotz et al. 2001)
Northern elephant sea	1525m (Delong and Stewart 1991)
	77min (Delong and Stewart 1991)
Southern elephant seal	1926m (Australian Antarctic Magazine 3, 2002)
	120.0min, (Slip et al. 1994)
Sperm whale	2085m (Watkins et al. 1993)
	112.0min (Clark 1976)
Northern bottlenose whale	1453m (Hooker & Baird 1999)
	70.5 (Hooker & Baird 1999)
Cuvier's beaked whale	1888m (Barlow et al. 1997)
	88.0min (Tyack et al. 2006)
Brainville beaked whale	1408m (Barid 2006)
	57.4min (Tyack et al. 2006)
Beruga	647m (Ridgway et al. 1984)
	22.9min (Martin & Smith 1992)
Narwhal	2370m (Laidre et al. 2003)
	26.2min, (Laidre et al. 2003)

diving ability unless animals rely on anaerobic metabolism, which is less efficient and produces lactic acid that needs further oxygen for it to proceed. To express the diving abilities of animals, Kooyman (1980) proposed the Aerobic Dive Limit (ADL), which indicates duration of aerobic metabolism and start of anaerobic metabolism (accumulation of lactic acid). Showing the calculated ADL in a formula: ADL=Stored O_2 /Metabolic rate, Kooyman et al. (1981) first measured ADL for adult Weddell seals (*Leptonychotes weddellii*) to be 21 minutes and suggested that 90% of their dives did not exceed ADL and seals extended surface time after ADL dives to release accumulated lactic acid.

Regarding question (2), allometric studies on air-breathing diving animals provided the answer. Comparing the diving performance of many endotherms, Schreer and Kovacs (1997) found strong allometric relationship for maximum dive duration and depth in relation to body mass among air-breathing diving animals. However, they noted mysticete whales and flying diving birds, which do not show significant relationships between diving capacity and body mass, as exceptions to this relationship. On the other hand, penguins, odontocete whales and phocid seals showed higher relationship than did other groups.

It might be simply inferred from the above answers that larger toothed whales can dive deeper and longer than the smaller toothed whales within ADL dives, and that sperm whales would be the deepest and the longest divers since they have largest body mass among Odontocetes (known maximum: 24 metric tons for 11m female and 57 metric tons for 18m male, Rice, 1989). However, as seen in table 2, Cuvier's beaked whales and Blainville's beaked whales dive deeper depths and longer durations to sperm whales despite small body sizes (known maximum either body mass or body length: 2950kg for Cuvier's beaked whale and 4.3m for Blainville's beaked whale, Mead, 1989). This reversed diving capacity has already been studied and discussed from the point of view of physiological adaptation to extreme diving (Tyack et al., 2006). To understand the diving behavior of beaked whales we also need to study various aspects,
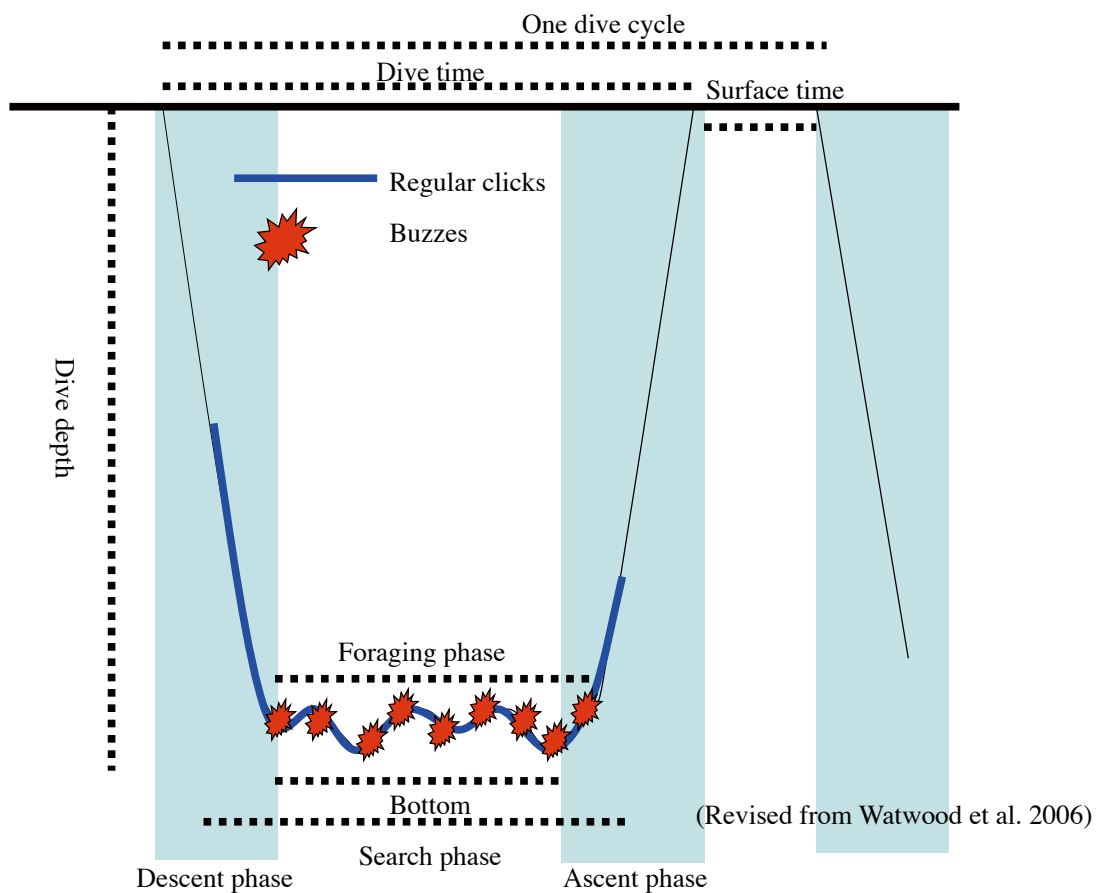

Fig. 1. Schematic dive profile of toothed whales and general dive parameters. The toothed whales start to produce regular clicks from a certain depth and cease them when they start to ascend (search phase). They also produce number of buzzes near bottom time (from first ascent to last descent) during their dives (foraging phase).

particularly foraging behavior, which may be affected by factors such as prey type and prey distribution. Beaked whales, just the opposite of sperm whales, are still mysterious species. However, recently Tyack et al. (2006), using advanced techniques, revealed the unique diving behavior of two beaked whales, Cuvier's beaked whale (*Ziphius cavirostris*) and Blainville's beaked whale (*Mesoplodon densirostris*), which provided us an opportunity to consider their foraging behavior also. Here we discuss the diving behavior

and foraging behavior of these two species of beaked whales, comparing them with sperm whales, the best-known species among the odontocete whales.

Diving physiology of sperm whales and beaked whales

Among the odontocete whales, sperm whales are the best-known species in terms of foraging ecology and behavior (Clark, 1976; Clark, 1980; Kawakami, 1980; Watkins, et al., 1993; Amano and Yoshioka, 2003) and beaked whales are the opposite. Recently, Watwood et al. (2006) studied diving behavior of sperm whales in Atlantic Ocean, the Gulf of Mexico and the Ligurian Sea, where sperm whales are abundant, and we summarized the data they obtained using acoustic recording tags (Dtag) (Table 2).

Table2. Diving behavior data of sperm whale, cuvier's beaked whale and Blainville beaked whale. (Numbers in parenthesis:mean)

	Max. depth	Dive duration	Descent rate	Pitch	Ascent rate	Pitch	Surface
Sperm whale	643.6~985.2	44.2~45.7	1.1~1.3	51.7~57.9	1.3~1.5	52.8~64.0	8.1~9.9
Cuvier's beaked whale	737~1322 (1070)	50.8~84.5 (58.0)	1.3~1.7 (1.5)	60~83 (72)	0.3~1.1 (0.7)	13~58 (35)	10~142 (63)
Blainville's beaked whale	640~1251 (835)	34.3~57.4 (46.5)	1.3~1.9 (1.6)	62~82 (74)	0.4~0.9 (0.7)	11~49 (28)	25~181 (92)

(From Watwood et al. 2006 & Tyack P. et al. 2006)

With regard to beaked-whale diving behavior, however, almost nothing is known. They are supposed to inhabit deep waters (Mead, 1989; Heyning, 1989) and thus be deep divers. There were no reports on their diving behavior except for one observation of a dive of 30 minutes duration for a Cuvier's beaked whale (Heyning, 1989) and one dive of 1453m depth and 80 minutes duration for a northern bottle-nosed whale, *Hyperodon ampullatus* recorded by a time-depth recorder (Hooker and Baird, 1999). Using Dtags, Tyack et al. (2006) studied two species of beaked whales from the Ligurian Sea and the Canary Islands. They also presented dive depth and duration data together with unique dive profiles. Dive data of sperm whales and beaked whales are summarized in Table 2, and dive profiles of three species of toothed whales are modified and shown in figures 1-3. It is very clear that both species of beaked whale dived deeper and longer than sperm whales (Table 2). Both species of beaked whale dived with higher slightly descent rates and steeper dive angles than did sperm whales, but they ascended slowly at lower angles than sperm whales, and they had longer surface times than sperm whales. These data suggest that generally the beaked whales dive to deep waters at high speeds and surface slowly and rest longer at the surface than sperm whales. Distinct differences between sperm whales and the beaked whales were found again in their dive profiles. Sperm whales dived a regular pattern without extending their surface time, but the beaked whales made several sequential shallow dives following deep dives (deep foraging dive (DFD) by Tyack et al., 2006). Hooker and Baird (1999) also presented a dive profile for the northern bottlenose-whale similar to the dives of the Cuvier's beaked whale and the Blainville's beaked whale in this study. Although it was the first report of
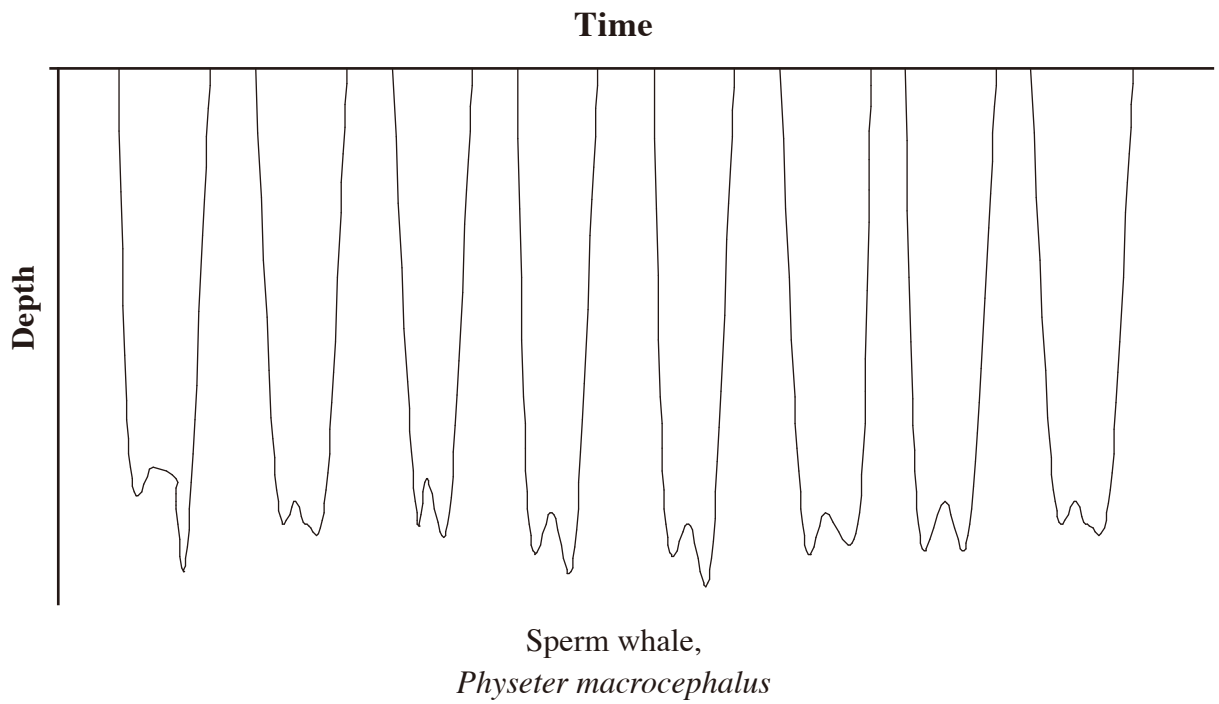
Time

Sperm whale,
Physeter macrocephalus

Fig. 2. Typical dive profiles of sperm whale (revised from Amano and Yoshioka 2003and Watwood et al 2006).

Time

Cuvier's beakedwhale,
Ziphius cavirostris

Blainville's beaked whale,
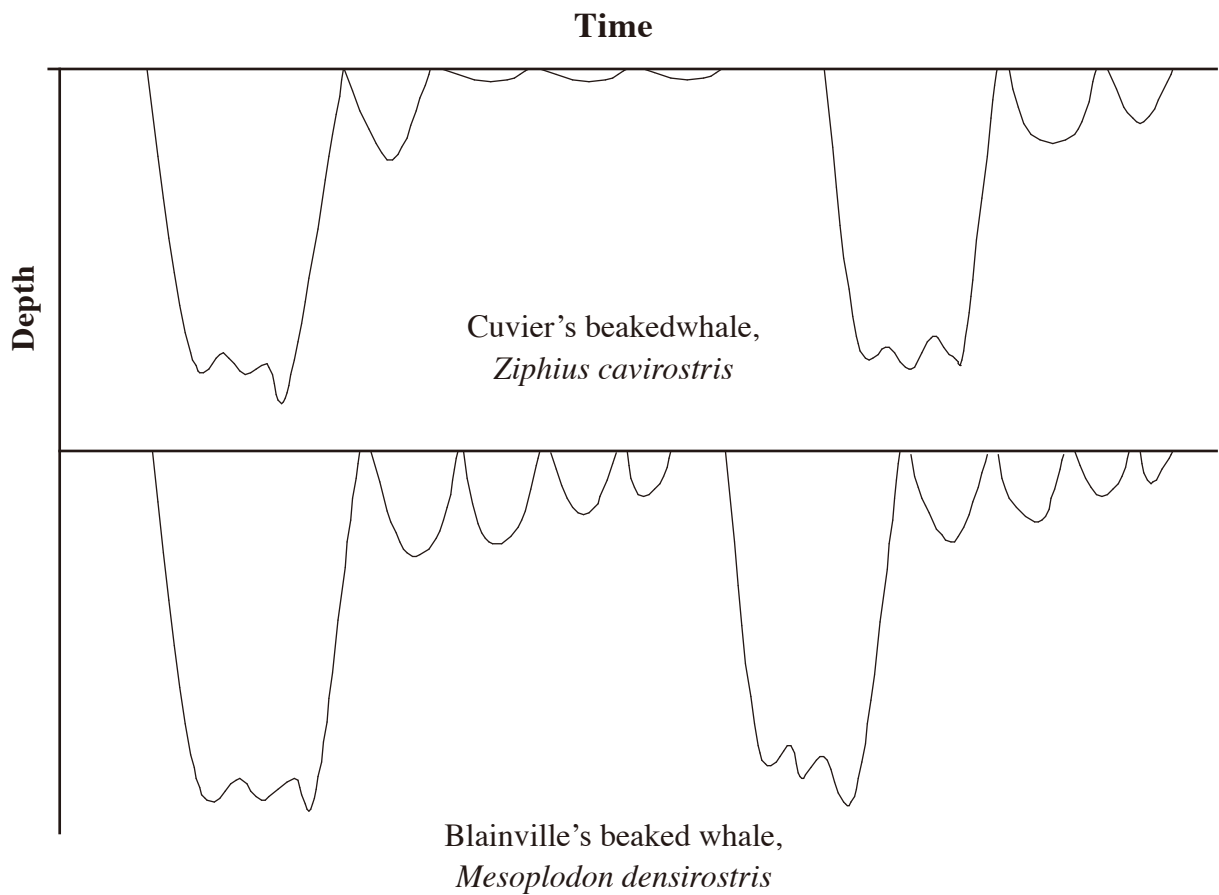*Mesoplodon densirostris*

Fig. 3. Typical dive profiles of Cuvier's beaked whale and Blainville's beaked whale.

beaked whales, shallow dives were not noted. Tyack et al. (2006) explained the dive patterns of the beaked whales as a physiological adaptation to the extremely deep and long dives. Assuming the super-saturation condition of PN2 that causes decompression sickness, they hypothesized that the subsequent shallow dives following deep dives serve for recompression, much like the process adopted to prevent decompression sickness by human divers, and also serve to extend the time needed to metabolize lactic acid accumulated by ADL-exceeding dives. Indeed, Watwood et al. (2006) and Tyack et al. (2006) estimated ADL for sperm whales and beaked whales using scaling by a power of -0.25 and the measured ADL of Weddell seals. Those were 43~54 minutes, 25 minutes and 33 minutes for lean mass 8000~20000 kg of sperm whales, and lean mass 2000 kg of Cuvier's beaked whale and lean mass 630 kg of Blainville's beaked whale respectively (Table 3). These data suggest that sperm whales stay within their ADL but that beaked whales

Table 3. Depth and duration of seach phase and foraging phase and number of buzzes during foraging phase.

	Search phase			Foraging phase		
	start~end	duration	% of dive	start~end	duration	% of dive
Sperm whale (No. busses:18)	96.7~611.5	36.0~37.4	80.7~81.4	514.7~679.8	28.2~28.7	61.3~63.5
Cuvier's beaked whale (No. buzzes: 29.8)	457~856	32.8	56.6	863 (Buzz depth: m)		
Blainville's beaked whale (N0. Buzzes: 28.6)	426~738	26.4	56.8	724(Buzz depth: m)		

(From Watwood et al.2006 & Tyack P. et al. 2006)

Prey size estimated from buzz account

Sperm whale (Body mass: 8000~20000kg, Feeding rate: 3% of BM)
25.2 DFD/day→453.6buzzes/day→529.1g~1322.8g/buzz
(320~360buzz/day, 800g~2300g/buzz for Mediterranean and Gulf of Mexico-Miller P.(2004))

Cuvier's beaked whale (Body mass: 2500kg, Feeding rate: 3% of BM)
11.2DFD/day→333.8buzzes/day→224.7g/buzz

Brainville beaked whale (Body mass: 800kg. Feeding rate:3% BM)
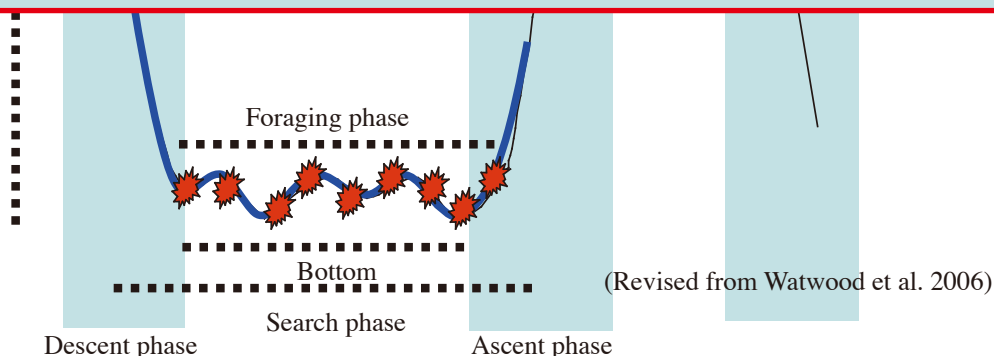10.46DFD/day→299.2buzzes/day→80.2g/buzz

(Revised from Watwood et al. 2006)

Fig.4. prey size was estimated using average buzz numbers of three species of the toothed whales and feeding rate of body mass (BM) per day. Sperm whale feed large prey by low emission rate of buzzes compared with the beaked whales.

far exceed their ADL.

Foraging behavior

Watwood et al. (2006) and Tyack et al. (2006) studied foraging behavior of sperm whales and Cuvier's beaked whales and Blainville's beaked whales using Dtags, which can record two types of echo-location acoustic sounds produced by the toothed whales during dives: regular clicks and buzzes (also called creaks). According to them, regular clicks were made most of time during descent and bottom phases of their dives and rarely during ascent, whereas buzzes were emitted mostly during bottom phases (Fig.3). They implicated clicks as being long-range echolocation for mesopelagic prey and buzzes as being prey-locating and prey-capture echolocation. Assuming that buzzes are equivalent to prey capture and success in capturing prey located by buzzes, it can be supposed that the number of buzzes represents the number of prey successfully captured by the whales during dives. Click and buzz data by Watwood et al. (2006) and Tyack et al. (2006) are summarized in Fig 4, suggesting that Cuvier's beaked whales and Blainville's beaked whales capture prey in deeper waters than sperm whales. From proposed buzz data and diving data and applying 3% of body mass as feeding rate, we can estimate prey size for the three species of toothed whales. Sperm whales forage prey sized between 529.1g and 1322.8 g, whereas Cuvier's beaked whales and Blainville's beaked whales forage prey averaging 224.7 g s and 80.2 g respectively. Miller et al. (2004) reported the prey size of sperm whales varied between 800 g in the Gulf of Mexico and 2300 g in the Mediterranean Sea. These data shows that there is some variation according to region. Despite the variation, the distinct difference in prey size of the toothed whales may indicate three possible scenarios: (1) sperm whales prefer large prey and select large prey exclusively, (2) beaked whales cannot forage large prey that can flee quickly and are obliged to depend on small prey that are predominant in deeper waters than the shallow depths where sperm whales forage, and/or (3) severe competition between sperm whales and the beaked whales has led small beaked whales to forage in deeper waters where there is less prey, and where there is no choice of prey size because the small beaked whales have less diving capacity at such depths. We also compared feeding efficiency as shown in Table 4. Feeding efficiency was shown by ratio of DFD time to dive cycle. When we include sequential shallow dives following DFD into surface time, efficiencies of both beaked whales were very low. Indeed it is obvious that the beaked whales do not forage

Case (1): shallow dives were not included into surface time
•Sperm whale : 0.53 (from table 3, Watwood, 2006)
•Cuvier's beaked whale : 0.50 (from vocal duration in table 2, Tyack, 2006)
•Brainville beaked whale: 0.53(from vocal duration in table 2, Tyack, 2006)
Case (2): shallow dives were included into surface time
•Sperm whale : 053(from table 3, Watwood, 2006)
•Cuvier's beaked whale : 0.27(from vocal duration in table 2, Tyack, 2006)
•Brainville beaked whale: 0.19(from vocal duration in table 2, Tyack, 2006)

Table 4. Dive Efficiency (dive time/ dive cycle) of three toothed whales. Efficiency of Cuvier's beaked whale and Blainville's beaked whale differs remarkably by inclusion of shallow dives into surface time.

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in their shallow dives. Low efficiency may also suggest that the beaked whales have no choice of prey size and were obliged to forage on any size prey found during chance encounters. There have been no studies to explain the differences in foraging behavior between them. However, using swim-speed/depth-data loggers, Amano and Yoshioka (2003) found burst swimming in sperm whales, which occurred several times per dive during bottom phases. They suggested that sperm whales might be chasing squid, their preferred prey. Burst-swimming during deep dives increases metabolic rate exponentially resulting in a reduction of dive time or exceeding ADL. However sperm whales kept regular interval dives and no extended surface time
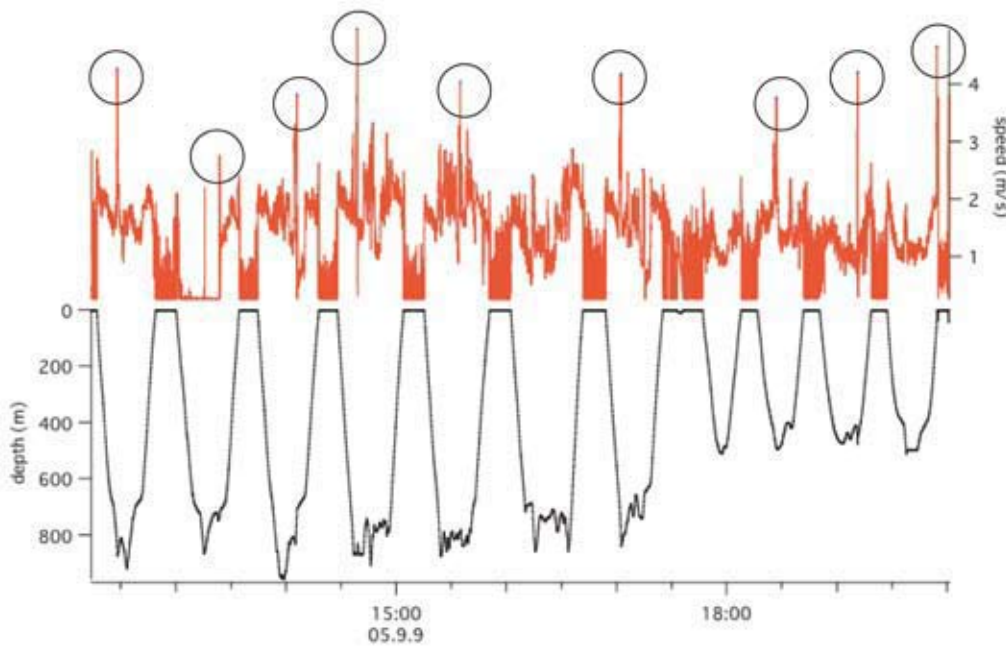
Unpublished data from K. Aoki

Fig. 5. Amano and Yoshioka (2003) found burst swimming of during bottom phase of dive and suggested ad prey chasing behavior (Figure prepared by K. Aoki).

for recovery from anaerobic dive was found. This suggests that sperm whales can make burst swims within ADL. Given that burst swimming is prey capturing behavior, this also suggests that prey obtained by burst swimming might be qualitatively or quantitatively beneficial, because cost of burst swims needs to be compensated by prey income. Thus only sperm whales can afford to forage large size prey selectively and the beaked whales do not. However we cannot explain the reason why the beaked whales forage in such depths and why sperm whales do not and We hypothesize that competition for squids between toothed whals and vertical prey distribution patterns affect the diving and foraging pattern of the toothed whale species. Although we are not sure about the differences between burst-swimming cost and additional diving cost for sperm whales and the foraging depths of beaked whales, sperm whales will not be rewarded if only small prey is distributed in deep water, since judging from the number of buzzes by the beaked whales feeding rate does not increase exponentially with depth. This suggests that burst swimming is much more beneficial than deep diving for sperm whales.

To ensure understanding of deep foraging behavior of the toothed whales, prey information is essential. Although toothed whales prefer to forage for squid, unfortunately our information on squids is still very poor. We need to study both toothed whale and squid behaviors simultaneously.

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