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Diel variation in beaked whale diving behavior

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ABSTRACT

We investigate diel variation in beaked whale diving behavior using data from time–depth recorders deployed on six Blainville's (*Mesoplodon densirostris*) (255 h) and two Cuvier's (*Ziphius cavirostris*) (34 h) beaked whales. Deep foraging dives (>800 m) occurred at similar rates during the day and night for Blainville's beaked whales, and there were no significant diel differences in ascent rates, descent rates, or mean or maximum depths or durations for deep dives. Dive to mid-water depths (100–600 m) occurred significantly more often during the day (mean = 1.59 h⁻¹) than at night (mean = 0.26 h⁻¹). Series of progressively shallower “bounce” dives were only documented to follow the deep, long dives made during the day; at night whales spent more time in shallow (<100 m) depths. Significantly slower ascent rates than descent rates were found following deep foraging dives both during the day and night. Similar patterns were found for the Cuvier's beaked whales. Our results suggest that so-called “bounce” dives do not serve a physiological function, although the slow ascents may. This diel variation in behavior suggests that beaked whales may spend less time in surface waters during the day to avoid

near-surface, visually oriented predators such as large sharks or killer whales (*Orcinus orca*).

Key words: shark, killer whale, predator avoidance, vertical migration, Blainville's beaked whale, *Mesoplodon densirostris*, Cuvier's beaked whale, *Ziphius cavirostris*, Hawai'i.

Diel differences of behavior are pervasive for terrestrial animals, with species typically active either during the day or at night depending on whether their sensory systems are adapted for best performance in light or dark regimes. Even for species able to function equally well in both light and dark conditions, diel variation in behavior may occur in response to changes in predation pressure, availability of food, or potentially as a response to anthropogenic activities that exhibit a diel pattern (Lima and Bednekoff 1999, Railsback *et al.* 2005). Many species of odontocete cetaceans feed deep in the water column, relying primarily on echolocation, rather than vision, to detect prey. Yet diel vertical movements have been documented for several species of odontocetes, in most cases likely reflecting vertical movements of their prey associated with changing time of day. Many species of zooplankton are thought to exhibit diel vertical migrations in response to predation pressure; most occurring at depths during the day where low light levels reduce the risk from visual predators (Bollens *et al.* 1992). Predators of zooplankton may either follow their prey's diel migration, or may remain at shallower depths in the water column and feed at night when zooplankton rise toward the surface. Higher trophic level predators may similarly follow their prey's vertical movements, resulting in similar vertical movements of some marine top predators (*e.g.*, Croxall *et al.* 1985, Eckert *et al.* 1989, Watanabe *et al.* 2006). At least some of the diel patterns documented for cetaceans can be related to such corresponding vertical movements of zooplankton and associated organisms. Pantropical spotted dolphins (*Stenella attenuata*) in Hawai'i dive the deepest at sunset, apparently to meet the rising layer of diel migrators, and forage more at night than during the day, when prey are closer to the surface and easier to obtain (Baird *et al.* 2001). Spinner dolphins (*Stenella longirostris*) in Hawai'i spend the day resting in shallow waters and forage at night on prey that exhibit both vertical and horizontal migrations (Norris *et al.* 1994, Benoit-Bird and Au 2003). Long-finned pilot whales (*Globicephala melas*) in the Mediterranean Sea made their deepest dives around sunset, and swim speeds on deeper dives were greater than during shallower dives, suggesting increased foraging (Baird *et al.* 2002). Short-finned pilot whales (*Globicephala macrorhynchus*) off the Canary Islands spent more time foraging at night near the surface, based on acoustic tags recording echolocation clicks and dive depths (Aguilar de Soto 2006). Fish-eating killer whales (*Orcinus orca*) in the nearshore waters of the temperate eastern North Pacific also show diel changes in diving behavior, with shallower dives at night (Baird *et al.* 2005). Swim speed is also lower at night however, possibly because of the importance of vision in prey capture for this species (Baird *et al.* 2005).

Diel variation in cetacean behavior may have a variety of implications for management. Diel variation in migration rates or distance from shore could influence shore-based population estimates (Perryman *et al.* 1999). If individuals rest or feed at or near the surface only during certain times of the day, they may be more susceptible to vessel impact or disturbance from vessel traffic during those periods (*e.g.*, Danil

et al. 2005). Conversely, during such times of high surface activity, individuals may be more readily detected if visual detection is important for mitigating impacts due to seismic surveys, vessel traffic, or naval sonar use (*e.g.*, Anonymous 2006). The ability to detect vocalizing individuals using passive acoustics (*e.g.*, Moretti *et al.* 2006) could also vary by time of day if individuals only vocalize when foraging and diving deep (*e.g.*, Johnson *et al.* 2004), and foraging behavior follows a diel pattern. Species that are caught in deep-set nets or long-lines may also be more susceptible to fisheries interactions at certain times of the day if deep foraging dives follow a diel cycle.

Beaked whales (Family Ziiphiidae) make among the longest and deepest dives of any cetacean, with at least some species foraging at depths of 1,000 m or more during the day (Hooker and Baird 1999, Baird *et al.* 2006a, Tyack *et al.* 2006). Published studies have not addressed diel variation in beaked whale diving behavior in detail, as sample sizes of nighttime dive data have been limited. Deep dives have been documented both in the day and at night (Hooker and Baird 1999, Baird *et al.* 2006a); however, based on small sample sizes, Baird *et al.* (2006a) noted that both Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales spent more time in near-surface waters at night. With only a single day/night record for each species no analyses of diel patterns were undertaken.

Among the cetaceans, beaked whales are unusual in their apparent susceptibility to injury or death associated with high-intensity mid-frequency naval sonars (*e.g.*, Balcomb and Claridge 2001, Cox *et al.* 2006). The pathogenic mechanisms resulting in injury or death are unknown (Cox *et al.* 2006, Rommel *et al.* 2006), but several aspects of their diving behavior have been suggested as potentially related to such susceptibility. Deep foraging dives, often exceeding an hour in duration, have substantially slower ascents than descents, and have been reported to be followed by an extended period of progressively shallower "bounce" dives (Baird *et al.* 2006a, Tyack *et al.* 2006). It has been questioned whether these "bounce" dives may serve as recompression dives to reduce the likelihood of gas embolisms (Cox *et al.* 2006, although see Zimmer and Tyack 2007). The proportion of time individuals spend near the surface, in depths where nitrogen may build up within tissues, may affect their susceptibility to anthropogenic impacts (Zimmer and Tyack 2007).

Detecting beaked whales, either visually or acoustically, is becoming increasingly important in association with naval exercises or sonar use, to try to mitigate impacts (see *e.g.*, Anonymous 2006). Given the long dive times and low surfacing profiles, detecting beaked whales visually is problematic, to say the least (Barlow and Gisiner 2006). Passive acoustic detection is also challenging; Johnson *et al.* (2004) and Tyack *et al.* (2006) documented that Cuvier's and Blainville's beaked whales produce sounds primarily when foraging at depths (*e.g.*, below approximately 400 m), thus limiting detection with surface hydrophones. Active acoustic detection may also be possible (*e.g.*, Hooker and Baird 1999, Ellison and Stein 2001), although detection at great depths (*e.g.*, >400 m) has not been verified. For all of these detection issues, understanding diel patterns of vertical use of the water column is critical. Examining this variation in behavior may also shed light on aspects of the diving behavior of beaked whales that may put them more at risk of anthropogenic impacts. We examine diel patterns of diving behavior with a sample of day/night dive data from two species, Cuvier's and Blainville's beaked whales, tagged with time–depth recorders off the west coast of the island of Hawai'i.

METHODS

Fieldwork was undertaken off the west side of the island of Hawai'i in each year from 2002 through 2007. Methods have been described in detail in Baird *et al.* (2006a), and are summarized briefly here. Suction-cup attached tags containing a Mk9 time–depth recorder (Wildlife Computers, Redmond, WA) and a VHF radio transmitter (ATS, Isanti, MN) were attached to beaked whales using either a cross-bow (RX-150, Barnett International, Odessa, FL) or a 5.2-m carbon-fiber pole. All tagged individuals were photographed and individually photo-identified following the methods of McSweeney *et al.* (2007). Tags were recovered using signals from the VHF transmitter.

Time of sunset and sunrise were used to delineate day- and nighttime data. For individuals whose tags stayed on for more than one day/night cycle, dive statistics were calculated separately for each day- and nighttime period, and mean values for each of the dive statistics (for “day” or “night”) were used in statistical comparisons among individuals. Dive rates (# dives h^{-1}) were calculated for dives with a maximum depth of 100–600 m and for dives >800 m. Dive statistics (durations, maximum depths, ascent, and descent rates) were calculated as per Baird *et al.* (2006a) for dives >800 m. We also compared the proportion of time spent between 22 and 72 m in depth, the depths at which Zimmer and Tyack (2007) predict to be most important for nitrogen uptake into tissues. Statistical analyses were conducted with Minitab 13 using paired *t*-tests, with each individual's day- and nighttime values treated as a pair, thus the sample size for all statistical tests were the number of individuals tagged. Percentage change from day to night was calculated as: $(\text{value night} - \text{value day})/\text{value night} \times 100$.

RESULTS

Dive data were obtained from two Cuvier's and nine Blainville's beaked whales. Tags deployed on both of the Cuvier's beaked whales (one in November 2004 and one in November 2006) and six of the Blainville's beaked whales (one in September 2004, three in April 2006 and two in November 2006) were applied in the day and remained on into the night. One of the six Blainville's beaked whales was tagged twice during the same encounter; the initial tag deployed remained on longer than the second tag, so only data from the initial tag deployed were used. Data from the two individuals tagged in 2004 were analyzed previously by Baird *et al.* (2006a). Tag attachments for Blainville's beaked whales that remained on into the night (two adult males, three adult females, and one adult female/large subadult) ranged from 18.63 to 78.32 h (sum = 253.7 h, day = 125.0 h, night = 128.7 h), and for Cuvier's beaked whales (one adult female, one adult male) were for 9.75 and 34.18 h (sum = 43.9 h, day = 23.8 h, night = 20.1 h). All data obtained were from different individuals (based on distinctive markings; see McSweeney *et al.* 2007).

For Blainville's beaked whales, there were no significant day/night differences in the rate of deep (>800 m) dives, or the mean duration, mean depth, maximum duration, maximum depth, ascent rate, or descent rate of deep dives (Table 1). For deep dives (>800 m), descent rates were significantly greater than ascent rates both during the day ($P < 0.001$) and at night ($P = 0.001$), with average ratios of descent to ascent rates of 2.22 during the day and 1.85 at night. Dives to mid-water depths (100–600 m) occurred approximately six times more frequently during the day than

Table 1. Comparison of diving parameters for Blainville's beaked whales with both day- and nighttime dive data ($n = 6$).

Variable	Day Grand mean (SD) range	Night Grand mean (SD) range	% change from day to night	Significance (paired <i>t</i> -test)
Longest time < 50 m (min)	45.06 (31.02) 14.9–98.8	91.73 (32.30) 60.5–153.7	50.9	0.036
% time < 50 m	38.16 (5.06) 33.7–3.4	56.95 (12.36) 41.1–72.7	33.0	0.004
% time > 500 m	21.86 (2.82) 18.3–24.0	28.2 (6.3) 20.5–37.4	22.5	0.098
% time between 22 and 72 m	13.53 (2.76) 9.19–17.25	21.21 (13.04) 9.01–39.37	36.2	0.142
Dive rate (# dives/h) 100–600 m	1.59 (0.54) 0.86–2.37	0.26 (0.20) 0.0–0.53	–511.5	0.001
Dive rate (# dives/h) > 800 m	0.38 (0.09) 0.30–0.52	0.46 (0.09) 0.33–0.56	17.4	0.253
Mean duration (min) > 800 m	54.36 (3.61) 51.0–60.2	51.31 (5.10) 43.3–57.5	–5.9	0.118
Mean depth (m) > 800 m	1,099 (183.8) 896–1,409	1,052 (114.6) 872–1,182	–4.5	0.493
Maximum duration (min)	61.06 (4.85) 53.07–68.2	61.47 (12.4) 48.87–83.38	0.7	0.867
Maximum depth (m)	1,254.5 (249.96) 985–1,599	1,237.7 (919.42) 903–1,443	–1.35	0.931
Ascent rate (m/s) > 800 m	0.68 (0.12) 0.50–0.83	0.78 (0.11) 0.63–0.92	12.8	0.248
Descent rate (m/s) > 800 m	1.51 (0.13) 1.36–1.67	1.44 (0.20) 1.13–1.67	–4.9	0.127

SDs calculated from a single value for each individual. Ranges shown using a single value for each individual.

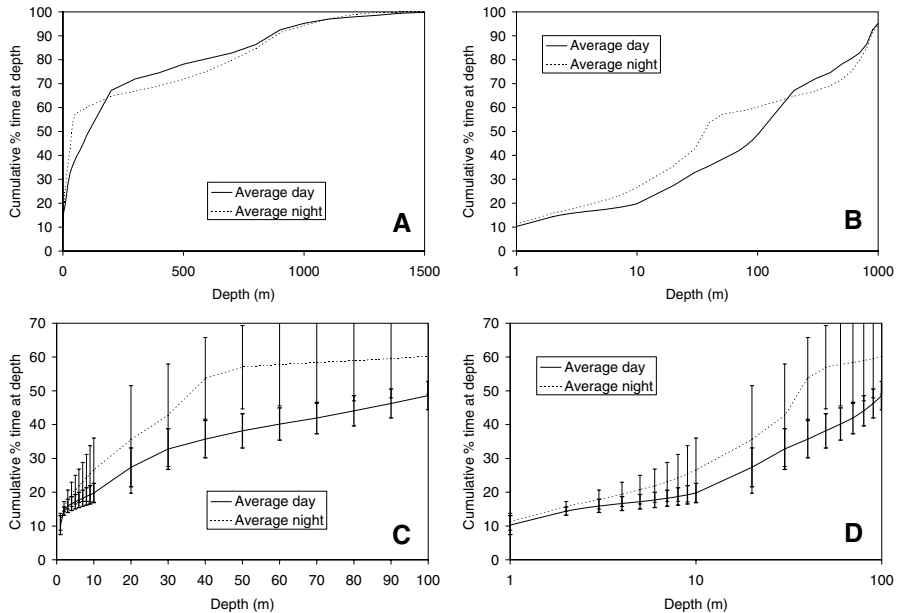


Figure 1. Cumulative percentage of time at or less than specified depths during the day (solid line) or at night (dashed line) for all six Blainville's beaked whales with both day- and nighttime data. (A) Entire water column. (B) Top 1,000 m on a log scale. (C) Top 100 m on a linear scale. (D) Top 100 m on a log scale. Bars represent ± 1 SD. SDs calculated from individual means.

at night ($P = 0.001$). The proportion of time spent at depths < 50 m, as well as the longest continuous period of time spent at depths < 50 m, were significantly greater during the night than during the day ($P = 0.004$ and 0.036 , respectively; Table 1, Fig. 1).

While sample size precluded statistical testing for Cuvier's beaked whales, the same trends in diving parameters between the day and night were found for that species (Table 2, Fig. 2), with similar effect sizes. The ratios of descent rates to ascent rates for deep (> 800 m) dives were similar to those of Blainville's beaked whales (2.36 during the day, 1.86 at night). Dives to mid-water depths (100–600 m) occurred 4.5 times more frequently during the day than at night for Cuvier's beaked whales. While more time was spent < 50 m during the night (42.9% vs. 12.7%), more was also spent below 500 m at night (43.0%) than during the day (35.4%).

DISCUSSION

Cuvier's and Blainville's beaked whales were documented diving to depths of 1,484 and 1,599 m, and remaining submerged for up to 94.58 and 83.38 min, respectively (Table 1). Both species are thought to forage primarily on deep (*e.g.*, > 800 m) dives (Baird *et al.* 2006a, Tyack *et al.* 2006). In general, at night individuals of both species spent a greater proportion of their time below 500 m in depth and

Table 2. Comparison of diving parameters for Cuvier's beaked whales with both day- and nighttime dive data ($n = 2$).

Variable	Day		Night		% change from day to night
	Grand mean (SD)	range	Grand mean (SD)	range	
Longest time < 50 m (min)	5.9 (1.4)	5.0–6.9	113.6 (67.1)	66.2–161.1	94.8
% time < 50 m	12.7 (0.54)	12.4–13.1	42.9 (11.6)	34.7–51.1	70.4
% time > 500 m	35.6 (0.19)	35.3–35.6	43.0 (12.9)	33.9–52.1	17.6
% time between 22 and 72 m	5.68 (0.67)	5.2–6.2	9.12 (9.8)	2.2–16.0	33.8
Dive rate (# dives/h) 100–600 m	0.85 (0.32)	0.63–1.08	0.20 (0.0)	0.20–0.20	–325.0
Dive rate (# dives/h) > 800 m	0.37 (0.08)	0.31–0.43	0.43 (0.23)	0.27–0.59	13.9
Mean duration (min) > 800 m	70.3 (9.7)	63.4–77.2	65.7 (8.5)	59.7–71.7	–7.0
Mean depth (m) > 800 m	1,334.0 (87.4)	1272–1,396	1,230.6 (139.5)	1,132–1,329	–8.4
Maximum duration (min)	81.37 (18.69)	68.15–94.58	69.47 (9.99)	62.4–76.53	–17.1
Maximum depth (m)	1,467 (24.04)	1,450–1,484	1,317.5 (160.51)	1,204–1,431	–11.35
Ascent rate (m/s) > 800 m	0.64 (0.01)	0.63–0.65	0.72 (0.04)	0.69–0.75	11.1
Descent rate (m/s) > 800 m	1.45 (0.0)	1.45–1.45	1.34 (0.41)	1.05–1.63	–8.2

SDs calculated with a single value for each individual. Ranges shown using a single value for each individual.

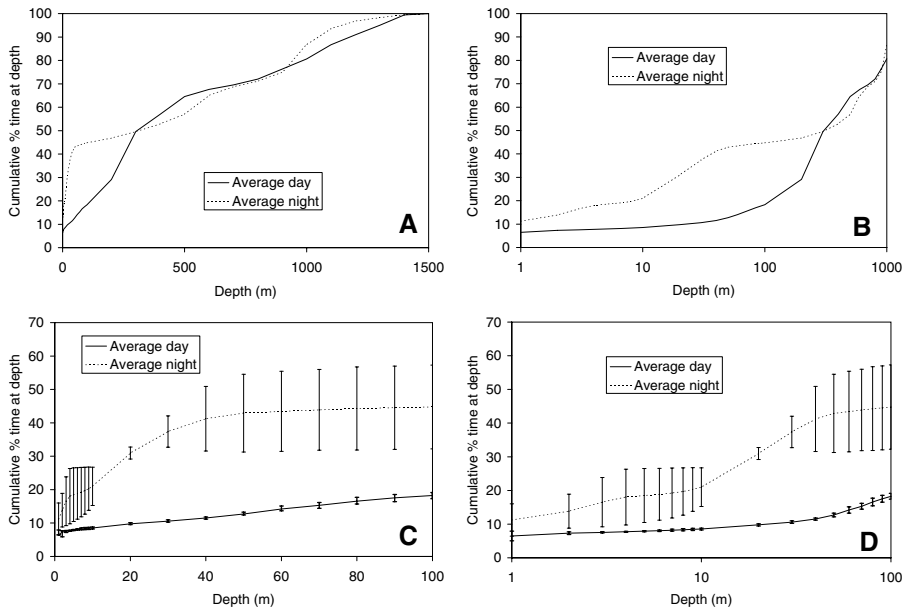


Figure 2. Cumulative percentage of time at or less than specified depths during the day (solid line) or at night (dashed line) for all two Cuvier's beaked whales with both day- and nighttime data. (A) Entire water column. (B) Top 1,000 m on a log scale. (C) Top 100 m on a linear scale. (D) Top 100 m on a log scale. Bars represent ± 1 SD. SDs calculated from individual means.

had higher rates of deep (>800 m) dives than they did during the day (Table 1, 2), although these differences were not statistically significant. The depths and durations of these deep dives were also similar between the day and night, suggesting that both species forage as much during the night as they do during the day. This also indicates that the prey of both species of beaked whales in Hawaiian waters either do not exhibit diel vertical migrations, or that the whales switch prey species at night to deeper-water species. Little is known of the diet of either species in Hawaiian waters, although elsewhere they are thought to feed primarily on deep-water squid (for Cuvier's) and deep-water squid and fish (for Blainville's) (MacLeod *et al.* 2003, Santos *et al.* 2007). In our efforts only a single prey item, a squid (*Histioteuthis boylei*), has been recovered from foraging Cuvier's beaked whales (Baird, unpublished data). Diel vertical migrations of *H. boylei* have not been reported, and other species of *Histioteuthis* are known to remain at depth both during the day and at night (Watanabe *et al.* 2006). Our finding of deep foraging dives occurring roughly equally during the day and night suggests that passive acoustic detection of vocalizing Cuvier's and Blainville's beaked whales (*e.g.*, Moretti *et al.* 2006), should be similarly effective both during the day and night. While our results are only from a single study area and our sample size is small, diving patterns of these two species appear very stereotypic; dive patterns from our study are very similar to the dive patterns that Tyack *et al.* (2006) report for the same species from studies in the Mediterranean and Canary Islands. Regardless, more long-duration deployments on Cuvier's beaked whales are required, given our results for that species are based on only two individuals.

Despite the similar rates of deep dives both during the day and at night, there were diel differences in diving behavior (Fig. 1, 2). During the night both species spent more time in near-surface (<50 m) waters; although our sample size is small, in the case of Cuvier's beaked whale this difference was striking (12.7% during the day *vs.* 42.9% at night), despite the increased time spent below 500 m in depth (Table 2). The tendency for both species to spend more time either near the surface or at depths below 500 m reflects the almost complete absence of what has been termed "bounce" dives (Cox *et al.* 2006) following the long, deep dives during the night. Given this, it seems unlikely that such dives serve a physiological function. Zimmer and Tyack (2007) noted that, in theory, all air spaces of beaked whales should have collapsed at depths closer to 70–100 m, and thus these so-called bounce dives were unlikely to serve a recompression function as they do for human divers. Ascent rates of dives greater than 800 m were significantly slower than descent rates both during the day and at night, suggesting that the slow ascents serve some physiological purpose. However, most of the reduction in ascent rates occurs at depths below the theoretical depth of lung collapse (Baird *et al.* 2006a, Tyack *et al.* 2006), thus the lower ascent rates may not function in reducing the nitrogen saturation in their bodies. The increased presence of Blainville's and Cuvier's beaked whales at shallower depths of the water column during the night should increase the likelihood of their detection using active acoustic methods, such as those employed in association with the U.S. Navy's low-frequency active sonar (Ellison and Stein 2001). The reduction in size of air-filled cavities during deep dives may reduce the target strength for active acoustics, thus detection may be greater in near-surface waters. However, both species also spent a greater proportion of their time below 500 m in depth at night, and active acoustic detection of beaked whales below such depths has not been tested.

If beaked whales are feeding at depth at similar rates during the night as during the day, why would they spend less time in mid-water depths (100–600 m) and more time at shallow (<50 m) depths during the night? Based on studies using acoustic tags that detect echolocation clicks (Johnson *et al.* 2004, Tyack *et al.* 2006), and the shape of dives <600 m (*i.e.*, typically flat-bottomed U-shape, or parabolic dives; Baird, unpublished data), it appears that foraging is unlikely to occur during either shallow (<50 m) or mid-water (100–600 m) dives. One possibility is that predation pressure is higher in near-surface waters during the day than at night, and that beaked whales modify their diving behavior in relation to predation risk (Heithaus and Frid 2003). Predators of beaked whales may include both large sharks (Long and Jones 1996) and killer whales (Notarbartolo-di-Sciara 1987, Mead 1989), and beaked whales in Hawaiian waters are also regularly bitten by parasitic cookie-cutter sharks of the genus *Isistius* (McSweeney *et al.* 2007). Cookie-cutter sharks are thought to exhibit diel vertical migrations, spending time near the surface at night (*e.g.*, Nakano and Tabuchi 1990), so the beaked whale dive patterns we have documented may bring them into more regular contact with cookie-cutter sharks than if they remained at mid-water depths as they do during the day. At least three species of large predatory sharks are found in Hawaiian waters that might fatally attack beaked whales, tiger (*Galeocerdo cuvier*), Galapagos (*Carcharhinus galapagensis*), and white (*Carcharodon carcharias*) sharks (Wetherbee *et al.* 1996, Boustany *et al.* 2002, Weng *et al.* 2007). Whether any of these species attack adult beaked whales is unknown, but Long and Jones (1996) provide evidence of approximately 5-m-long white sharks attacking a juvenile (~3 m long) Cuvier's beaked whale and Stejneger's beaked whale (*M. stejnegeri*) off California. Shark attacks do occur on beaked whales in Hawai'i; McSweeney *et al.* (2007) noted scars on both a Cuvier's

and a Blainville's beaked whale from attacks by large sharks. While little is known of the vertical movements of any of these species in Hawaiian waters, they are thought to be predominantly near-surface (*e.g.*, top few hundred meters) predators (*e.g.*, Holland *et al.* 1999, Papastamatiou *et al.* 2006, Weng *et al.* 2007). There is uncertainty regarding whether large sharks are more or less likely to attack large marine mammals during the day or at night, based in part on methods used to study shark foraging and the inherent difficulties of studying predation of intermittent feeders such as sharks. Much of what is known about diel feeding in sharks comes from catch rates using baited hooks, a scenario quite dissimilar to detection and capture of a large free-swimming cetacean. In addition, the sharks in question exhibit a shift in diet with size, with only larger individuals feeding on marine mammals (Tricas and McCosker 1984, Lowe *et al.* 1996). Tiger sharks do forage both during the day and at night, but catch rates have been reported to be significantly lower at night off Australia (Heithaus 2001). Based on examination of the visual system and departure times from baits, white sharks are thought to be primarily a diurnal predator (Gruber and Cohen 1985, Strong 1996). Given the abilities of cetaceans to detect potential predators using both vision and echolocation, and the importance of vision in prey capture for sharks (Strong 1996), white sharks are thought to use stealth in attacking cetacean prey (Long and Jones 1996). Clearly however, more information is needed on diel foraging behavior of large sharks in Hawaiian waters to better understand the relationship between shark behavior and beaked whale diving patterns.

Killer whales are rare in Hawaiian waters, but are thought to feed at least in part on marine mammals there (Baird *et al.* 2006*b*). Both fish-eating and mammal-eating killer whales primarily spend their time in the top 100–200 m of the water column, and both appear to exhibit reduced activity at night, possibly reflecting the importance of vision in prey capture for this species (Baird *et al.* 2005; Baird, unpublished data). It has been suggested that predation avoidance may also be the reason why Cuvier's and Blainville's beaked whales vocalize only at depths below approximately 400 m (Tyack *et al.* 2006), and we suggest that beaked whales spend more time in near-surface waters at night due to reduced predation pressure.

In assessing factors that influence the susceptibility of beaked whales to impacts from mid-frequency sonar, Zimmer and Tyack (2007) discuss how beaked whales might react to sounds of predators such as killer whales. If killer whales are detected acoustically at a distance, beaked whales might modify their diving patterns to increase horizontal displacement away from the potential threat, thus potentially increasing the proportion of time spent at shallow depths (*e.g.*, 22–72 m) where uptake of nitrogen into the body is more likely to occur. If beaked whales do not discriminate between killer whale calls and high-intensity mid-frequency sonars, and act in a similar way to both, such a reaction to mid-frequency sonar could put beaked whales at more risk of decompression-like symptoms as found in several strandings (*e.g.*, Jepson *et al.* 2003, Fernandez *et al.* 2005). Mid-frequency sonar associated with naval exercises may continue for an extended period and propagate for a greater distance than the higher frequency (and lower intensity) calls of killer whales, thus potentially eliciting a response for an extended period (Zimmer and Tyack 2007). If predation pressure by killer whales is lower at night than during the day, it is possible that beaked whales may react less to killer whale sounds at night, and potentially to mid-frequency sonar use at night. Sound playback experiments currently being undertaken with beaked whales (Southall *et al.* 2007) could be used to test this supposition.

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