SUB-SURFACE AND NIGHT-TIME BEHAVIOR OF HUMPBACK WHALES OFF MAUI, HAWAII: A PRELIMINARY REPORT

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SUMMARY

Using suction-cup attached time-depth recorder/VHF radio tags, we documented the diving behavior of humpback whales off the west side of Maui, Hawaii. Between February and April 2000, tags were deployed on 15 individuals, and dive data were obtained from 13 of the 14 tags recovered. Reactions to tagging were observed less often than has been documented for biopsy darting, and were generally short-term. A total of 62 hours of dive data were obtained. All tagged whales were known or thought to be adult or sub-adult males, and most were involved in competitive groups for all or part of the time tags were attached. In many cases, dive depths were potentially limited by bottom depth, that is, many tagged whales were found in relatively shallow (<100 m bottom depth) water for all (n=5) or part (n=5) of the time tags were attached. Maximum dive depth was 176 m, and dives greater than 100 m in depth occurred an average of 1.37 times per hour (SD=2.35). Some of these deep dives were to the bottom. Excluding periods when tagged whales were known to be in less than 100 m of water, dives to over 100 m occurred an average of 1.73 times per hour (SD=2.52). Where the whales spent their time in the water column varied considerably between individuals. Whales that had modal depth distributions between 10 and 30 m spent some of their time apparently motionless at depth, a behavior similar to that documented for singing humpbacks. Most whales in competitive groups and one escort to a mother/calf pair spent the majority of their time in the top 10 m of the water column, while two individuals in competitive groups spent a substantial proportion of their time (10% and 29%) at depths greater than 100 m. We discuss a variety of factors that potentially influence diving behavior, including the presence of a calf within the group, time of day, and behavioral role. Management implications of dive data, including aerial survey calibration factors and exposure to depth-specific threats, are also discussed.

INTRODUCTION

In general, baleen whales are thought to be shallow divers. Both relative to body size and in absolutes, toothed whales, seals, sea lions, and even penguins dive to greater depths than have been documented for baleen whales (Schreer and Kovacs 1997). However, breath-holding capabilities (ie., dive durations) for baleen whales are more similar to what would be expected based on body size (Schreer and Kovacs 1997). As such, humpback whales (*Megaptera novaeangliae*), like other cetaceans, can spend the majority of their time beneath the water's surface.

Studies of sub-surface behavior of humpbacks have been limited. Humpback whales typically exhibit migratory behavior, with most individuals spending all or part of the winter in low-latitude "breeding" areas, and the summer months in high-latitude "feeding" areas. Because waters in the low-latitude breeding areas are relatively unproductive and thus fairly clear, some sub-surface observations of humpback whales have been made in these areas by divers, snorkelers, or through clear-walled chambers mounted on boats. Such underwater visual or video observation can provide valuable information on under-water behavior (e.g., Baker and Herman 1984), size (Spitz et al. 2000), and gender of individual whales (Glockner 1983), but is likely biased towards slow-moving individuals near the surface. Sonar-based studies to examine sub-surface behavior have been undertaken on one humpback whale feeding ground, and have produced valuable information on foraging dives of humpbacks (Dolphin 1987a, 1987b, 1988).

Such systems can be used to track whales underwater, though there are a variety of limitations of using sonar that constrain the quantity and quality of data that can be collected (Hooker and Baird 2000). Lastly, sub-surface behavior has been studied through the use of tags that measure dive depth, and either record the information in a data-logger which must be recovered, or transmit the information via an acoustic, VHF or satellite signal. For humpback whales, this technique has been limited to only a few short-term deployments of tags that transmit depth information, two in a foraging area (J. Goodyear, pers. comm.), one in a migratory area (Hamilton et al. 1997), and one in a wintering area (off Socorro Island, Mexico; J. Goodyear, pers. comm.). Applying such tags, particularly those that utilize data-loggers, provides a method of obtaining continuous and high-resolution information on dive depth which is not limited by water visibility or the depth of the whales themselves (Hooker and Baird 2000).

The primary goal of our research was to obtain a better understanding of the sub-surface behavior of humpback whales in the Hawaiian Islands, using data collected from remotely-deployed suction-cup attached time-depth recorder (TDR)/VHF radio tags (see Baird 1998a). In addition to providing a way to examine sub-surface behavior, such tags also allow for quantitative monitoring of behavior at night. Knowledge of where humpback whales spend their time in the water column may have a variety of management implications, both in terms of exposure to depth-specific threats (e.g., ship strikes, commercial fishing gear, and high intensity underwater sounds), and for determination of aerial survey calibration factors. This report discusses preliminary results from deployments of TDRs on humpback whales in Hawaii during February-April 2000. Humpback whales visit Hawaiian waters primarily during winter months (Herman and Antinoja 1977), and their presence there is thought to relate to breeding activities, rather than feeding. Thus contrary to most other diving mammals their sub-surface behavior is unlikely to be driven by the search for food. In our case, tags were deployed primarily upon male humpback whales, whose activities were directed mainly towards females or competitive interactions with other males. The data we obtained therefore apply primarily to humpback whales engaged in such social interactions.

METHODS

From February 26 through April 12, 2000, we used suction-cup attached TDR/VHF tags to examine the diving behavior of humpback whales off the west side of Maui, Hawaii, between the islands of Maui, Lana'i, and Kaho'olawe (between 20^{o} 35' and 21^{o} N, and 156^{o} 30' and 156^{o} 50'W). This area is thought to have one of the highest density of humpback whales within the Hawaiian Islands (Mobley et al. 1999), and the period that most of the data were collected (late February through early March) represents the typical period of peak abundance of humpback whales in the area (Mobley et al. 1999; Au et al. 2000).

The tags we used are the same as those used to study the diving behavior of several other species of cetaceans (Baird 1998a; Baird et al. 1999; Hooker and Baird 1999; Baird and Ligon in prep.). Each tag weighed about 400 grams and contained a VHF radio transmitter (Telonics, Mesa, AZ) with a 30 cm semi-rigid wire antenna, and a TDR (Wildlife Computers Mk6, Redmond, WA), which was set to sample depth and velocity once per second, and water temperature and light levels every 5 seconds. TDRs used for all but one deployment recorded depth at 1 m increments (accuracy +/- 1 m), while the remaining unit (deployed March 5) recorded depth at 2 m increments (accuracy +/- 2 m). The maximum depth range of the instruments was 250 or 500 m, respectively. Velocity was measured by rotation of a paddlewheel. Since precise velocity calibration varies with position of the tag on the body (Baird 1998b), and likely also with body size, velocity readings are presented as relative velocity. Water temperature sensors in these tags had an upper temperature limit of 22.7°C; surface water temperatures in Hawaii exceed this, thus temperature readings were only useful at depths greater than approximately 80 m (temperature ranged from approximately 22.5°C at 80 m to 20.5°C at 170 m). Light was measured with a photodiode (BPX 63, Siemens Microelectronics Inc, Cupertino, USA), which had a spectral sensitivity of 350-1100 nm, with peak sensitivity at 800 nm. Light values were recorded in uncalibrated units; calibration of the values followed McCafferty et al. (1999), with units converted to illuminance (lux) using the formula:

$$\ln(\text{lux}) = 0.13 \text{ TDR output} - 12$$

Tag bodies were constructed from syntactic foam (to allow tags to float after they fell off), and were attached with an 8 cm diameter suction cup (Canadian Tire). The inner surface of the suction cup was coated with silicone grease to increase adhesion, and small quantities of skin were sometimes collected from the inner surface of the cup, and preserved in a DMSO/salt solution for sexing (through the Southwest Fisheries Science Center, La Jolla, CA). Tags were deployed from a 7 m rigid-hull inflatable, using a crossbow, at distances of 5-15 m. We attempted to document reactions to tagging on video and also noted observed reactions immediately after tagging attempts. Once a tag was deployed, the tagged animal was followed for as long as possible, typically at a distance of 20-200 m. Observations of tagged whales were terminated when the whale was lost, or when we had to return to port due to sea conditions, or light or fuel considerations. Photographs of the dorsal fin region (obtained for all but two of the tagged whales) were used to confirm that a different whale was tagged each day, through a comparison of dorsal fin shapes and scar patterns.

We recorded continuous information on group size and composition, distance between individuals (and relative orientation within group), directionality of travel, approximate location (determined using the boat's GPS when within 200 m of tagged whales), interactions with other species, and the occurrence of specific behavioral events (e.g., breaches, tail-lobs). Video recordings were also made to augment behavioral notes, and subsurface video and visual observations of tagged whales were occasionally made by a snorkeler (M. Deakos, Kewalo Basin Marine Mammal Laboratory). Bottom depths in the vicinity of tagged whales were obtained using GPS locations and interpolating depths from values off a nautical chart (NOAA Chart 19347, Dec. 1997).

When tags were recovered, data were downloaded to a computer in a hexadecimal format. Data were processed in several ways using software provided by the TDR manufacturer (Wildlife Computers). The hexadecimal files were run through the program *Minimum-Maximum-Mean* (Version 1.22) to produce raw ASCII files with all data values (e.g., for plotting and calculation of the percentage of time at depth). As well, hexadecimal files were processed with *Zero-Offset-Correction* (Version 1.30) to correct for temperature-related drift in the surface values. The resulting files were processed with *Dive Analysis* (Version 4.08) to calculate statistics for each dive (dive durations, maximum depths, rates of descent and ascent). The resulting outputs of this program were ASCII files, which were then imported into *Excel* (Version 2000) and/or *Minitab* (Version 10.2) for statistical analyses and graphing. Rates of ascent and descent were calculated only for dives deeper than 15 m, and the start and end points for rate calculations were chosen using the *Dive Analysis* program, selecting periods of relatively constant descent or ascent covering at least half the total depth of the dive.

RESULTS AND DISCUSSION

Feasibility of Tagging

Fifteen tags were deployed in 31 tagging attempts (29 of the attempts involved the tag hitting a whale), and 14 of the 15 tags deployed were recovered (Table 1). Reactions to tagging attempts were classified into one of four categories (none, low, moderate, strong), based on the intensity and duration of the reaction (after Weinrich et al. 1991; Clapham and Mattila 1993). A "low-level" reaction was of low-intensity and short duration (e.g., a tail arch or fast dive), a "moderate" reaction was of medium intensity (e.g., a tail flick), and a "strong" reaction was of high intensity (e.g., a breach) and longer duration. Reactions were observed in 5 of 31 tagging attempts (17%), all five of which were tag hits (ie., no reactions were observed for the two missed attempts). Two of the five reactions were low-level (ie., tail arch and fast dive), and the remaining three reactions were moderate-level (ie., tail flick). No "strong" reactions were observed. All reactions were short-term, that is, all whales continued their pre-attempt behavior (including one whale which was singing prior to an attempt, reacted with a tail flick when the tag hit, and immediately resumed singing; M. Deakos, pers. comm.). No reactions of non-target individuals were observed in response to tagging attempts. Reactions to tagging were observed less often than reactions have been observed to biopsy darting of humpback whales, for which approximately 55-72% of individuals showed some sort of reaction (Weinrich et al. 1991; Clapham and Mattila 1993). It is interesting to note that only two tagging attempts were made on lone individuals, and both reacted with tail flicks; Clapham and Mattila (1993) also observed stronger and more frequent reactions by singletons than by groups. In general, whales involved in competitive groups (see Clapham et al. 1993) were far easier to approach (for tagging) than lone whales or whales in small groups (2-3 individuals), as was also observed by Bauer (1986).

The one tag that was lost was deployed near the end of the season on a lone whale that was clearly traveling, and the whale was tracked for several hours before passing beyond the limits of our study area. Data were obtained from 13 of the 14 tags recovered (a TDR battery failure resulted in a loss of data from one tag), and these tags remained attached for an average duration of 4.8 hours (range from 0.12 – 17.11 hours; Table 1). Suction-cup attached VHF radio tags (not including time-depth recorders) have been previously used with humpback whales off Newfoundland and Massachusetts (Goodyear 1989) with an average attachment duration of about 15 hours (n=12). The shorter attachment duration from our study may be due to differences in tag size (our tags were larger due to the inclusion of a TDR), differences in whale behavior (whales in our study were often extremely active), or possibly differences in humpback whale skin shedding rates between Hawaii and Newfoundland/Massachusetts (which might be expected given differences in water temperature between these areas). The velocity meter on one of the tags was damaged during an apparently competitive interaction between the tagged whale (a primary escort in a competitive group) and another whale, thus velocity data were only obtained from 12 of the 13 tags.

Table 1. Details on tag deployments

Profile	**Date**	**Time**	**Duration (h)**	**Whale[1]**	**Group[2]**	**Sex**
A	Feb 26	13:24 – 19:21	5.94	1° escort	CG (calf)	
B	Feb 27	16:01 – 01:27	9.43	Escort	MCE	
C	Mar 4	11:32 – 15:20	3.81	2° escort	CG/lone?	
D	Mar 5	14:38 – 07:44	17.11		Dyad	
E	Mar 8	11:49 – 17:36	5.78	Challenger/1°	CG	Male[3]
F	Mar 9	09:37 – 14:00	4.37	1° escort	CG (calf)	
G	Mar 10	09:05 – 09:29	0.39	1° escort	CG (calf)	
H	Mar 10	15:21 – 23:22	8.02	1° escort	CG (calf)/MCE	Male[4]
I	Mar 12	13:25 – 17:38	4.21	2° escort	CG/lone	
J	Mar 26	10:21 - 11:39	1.30	Challenger/1°	CG	Male[4]
K	Mar 26	14:39 – 15:19	0.66	2° escort?	CG	
L	Mar 27	10:25 – 10:32	0.12	2° escort	CG	
M	Mar 27	12:38 – 13:49	1.18	1° escort	CG (calf)	
	Apr 8	10:49 – 18:10[5]		2° escort	CG	
	Apr 12	13:38 – 16:38[6]		Lone	Lone	
	Total		62.30			

[1]1°=Primary, 2°=Secondary, Challenger/1°=whale that challenged 1° escort and became 1°. [2]CG = Competitive Group, MCE = mother, calf, escort. [3]Confirmed as a male by a snorkeler - M. Deakos, pers. comm. [4]Confirmed as males through genetic sexing, A. Dizon, Southwest Fisheries Science Center, La Jolla, pers. comm. [5]TDR battery failure, thus no data collected and exact attachment duration unknown. [6]Tag lost, attachment duration unknown.

Sex of Tagged Whales

We believe that all of the whales tagged (at least those from which data were recovered) were probably adult or subadult males, based on their behavior and degree of scarring (see Chu and Nieukirk 1988; Clapham et al. 1993). One of the tagged whales was an escort to a mother/calf pair, a behavioral role typically held by males (Glockner 1983). One was a member of a dyad, had extensive scarring on the dorsal fin (see Chu and Nieukirk 1988), and was observed close (ie., approximately 2 m) behind and beside another adult-sized whale and surfacing shortly (ie., 4-6 seconds) after its companion, a behavioral role also typically held by males (M. Deakos, pers. comm.). The gender of three of the remaining 11 whales was confirmed (all as males), two through genetic analysis of skin samples (A. Dizon, pers. comm.), and one through underwater observations (M. Deakos, pers. comm.). All the remaining animals were associated with competitive groups, either as a principal escort (n=4) or secondary escort (n=4), and thus were all thought to be adult or subadult males (Clapham et al. 1993). It is possible, however, that some of the individuals may have been females, as a small proportion (up to 7%; Clapham et al. 1993) of individuals in these various roles have been confirmed as females. However, based on the proportion of females in these roles documented by Clapham et al. (1993), it is likely that at most only one of these individuals was a female.

Diving Patterns/Behavior

In total, just over 62 hours of dive data were obtained. Classifying or defining "dives" can be problematic (Hooker and Baird 2000), and a variety of different definitions and techniques can be used to discriminate between "surfacing" dives (the short and shallow dives that occur during respiration bouts) and the longer, usually deeper dives that serve other functions. We use several definitions for different parts of the following discussion: 1) a dive being any period of at least six seconds in which a whale went to at least three meters before returning to the surface; 2) dives of depth greater than one adult whale body length, ie., greater than 11 m (see Spitz et al. 2000); and 3) dives greater than 100 m depth. Each definition is somewhat arbitrary, but can be used to address specific questions and for comparisons between individuals. In total there were over 1300 dives greater than six seconds, in which the whale went to at least 3 m depth. A total of approximately 650 dives were deeper than one body length. Long (maximum 25.7 minutes) and deep (maximum 176 m) dives were regularly documented, with a total of 49 dives greater than 100 m. Calculated only for individuals for which we have greater than one hour of dive data (see below), the average rate of diving greater than 100 m was 1.37 dives/hour (n = 10 individuals, SD = 2.35, with a range from 0 to 6.2/hour), with 7.7% of all dives deeper than 11 m being > 100 m.

Why would male humpback whales dive over 100 meters, something that has been rarely documented on feeding grounds (Dolphin 1987a)? Various factors may determine or constrain the dive behavior documented for different individuals. The duration of tag attachment itself may be important, as short duration attachments may be insufficient to produce a reasonable sample of the behavior of an individual. Assuming that our sample durations are reasonable, factors which may be important in determining or constraining dive behavior include bottom depth (in shallow water, whales are obviously not able to dive deep), the presence of an infant in the group (which might limit the dives of its mother, and thus influence the behavior of males), time of day, and the behavioral role of the tagged whale (e.g., escort to mother/calf pair versus primary or secondary escort in a competitive group). In terms of tag duration, the three shortest attachments were each less than an hour, and appear to be limited as representations of diving behavior (see Figure 1), thus most of our analyses were restricted to the 10 whales which were tagged for longer than an hour.

Dive Depth in Relation to Bottom Depth

In terms of comparing dive depths to bottom depths, not all whales were followed for the duration of tag attachments, so it was not always possible to determine bottom depth near tagged whales. As well, some inaccuracy occurs since the research vessel might be as much as 200 m from the tagged whale. It should also be noted that obtaining bottom depths from nautical charts requires some interpolation between depth values shown on the charts. Whales were tagged in

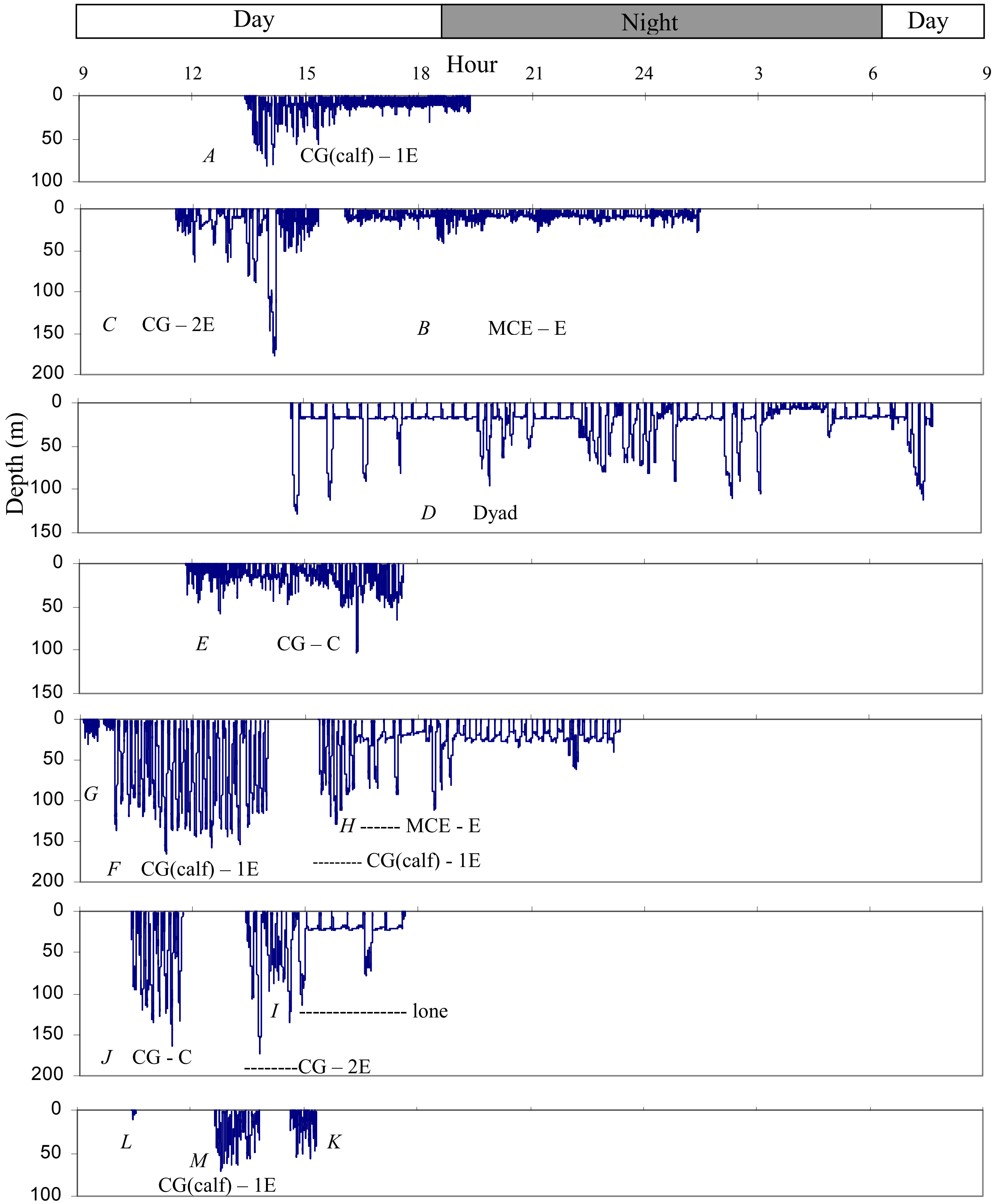

Figure 1. Depth data with time of day. Date indicated by letter: *A* - Feb 26; *B* - Feb 27; *C* - Mar 4; *D* - Mar 5; *E* - Mar 8; *F* - Mar 9; *G* and *H* - Mar 10; *I* - Mar 12; *J* and *K* - Mar 26; *L* and *M* - Mar 27. Group type (CG=competitive group, MCE=mother/calf/escort) and tagged whale (E=escort, 1E=primary, 2E=secondary, C=challenger). Periods of different group types indicated for *H* and *I*.

water ranging from approximately 55 meters to 233 m deep (mean depth at time of attachment = 103 m), and tags detached (or whales were left or lost) in depths ranging from 40 to 296 m deep (Table 2). Bottom depths for five deployments did not exceed 100 meters, and an additional five tagged whales were in less than 100 m of water at some point during the tag attachment. Thus bottom depth potentially constrained dive depths for many tagged whales, and even ignoring the small sample size, depths recorded should not be considered representative as maximums that male humpback whales dive to in the Hawaiian breeding grounds, but rather as depths attained in relatively shallow water. For the periods in which we have information on bottom depth simultaneous with dive depth, there is some variability in where whales dive to in the water column. Some dives were to the bottom (see Figure 2), while others were only to mid- or surface-waters.

Table 2. Bottom depths associated with tagged humpbacks (note only start and "end" bottom depths are given, while location (and thus bottom depth) were recorded at five minute intervals).

Profile	**Date**	**Depth at tag attachment (m)**	**Maximum depth between attachment and detachment/whale left (m)**	**Depth at departure[1]/ detachment[2] (m)**	**Maximum dive depth recorded (m)**
A	Feb 26	232	296	296[1]	82
B	Feb 27	75	74	46[1]	42
C	Mar 4	82	82	53[1]	176[3]
D	Mar 5	155	238	92[2]	128
E	Mar 8	91	128	84[2]	103
F	Mar 9	86	287	287[2]	165
G	Mar 10	55	73	73[2]	30
H	Mar 10	102	152	90[1]	128
I	Mar 12	141	180	91[2]	173
J	Mar 26	110	170	157[2]	163
K	Mar 26	77	77	46[2]	57
L	Mar 27	80	80	64[2]	10
M	Mar 27	53	77	40[2]	69
	Mean	103			

[1]Depth where research vessel discontinued follow. [2] Depth where tag detached from whale.
[3]Tagged whale left before deep dive recorded, thus the whale moved into deeper water.

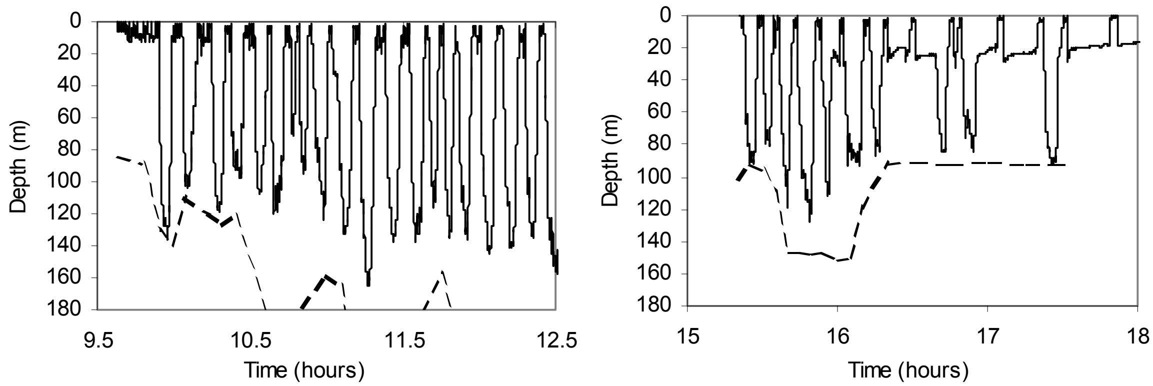

Figure 2. Examples of humpback whale dive depths (solid lines) in relation to bottom depth (dashed lines) when some dives were near bottom. March 9 (left). March 10 (right). In both cases the tagged whales were primary escorts in competitive groups that contained calves, although on March 10, group structure changed at approximately 1620 hours, leaving the tagged whale as the escort to a mother/calf pair. Bottom depth was determined by recording GPS location of the research vessel (attempting to remain within 200 m of the tagged whale) every 5 minutes and interpolating depths off a nautical chart (plotted on the graphs every 5 or 10 minutes, depending on bathymetric gradients).

The Influence of Calves on Diving Behavior

Although we did not try to tag calves or mothers of calves, the presence of a calf in a group might influence the behavior of a male through the actions of its mother (e.g., if the mother is diving deeply the male will likely follow, given the high levels of competition that occur between males, see e.g., Baker and Herman 1984). It is unclear, however, whether dives by a female with a calf would be shallower than a female without a calf (if the calves' diving abilities are insufficiently developed to allow it to dive deep), or deeper (if the female is diving deeply to try to minimize disturbance or harassment of calves in competitive groups). Several authors (e.g., Baker and Herman 1984; Mattila et al. 1989; Smultea 1994) have suggested that females with calves may not always be willing participants in competitive groups, as the aggressive interactions between males may result in some risk to the calf. Cartwright (1999) noted that calf behavior did change when single or multiple adult males were present in a group. In our study, there were three occasions where we had small groups (3 or less) of whales where a female was definitely (the Feb 27 mother/calf/escort group and the March 10 group after the secondary escorts left) or possibly (the March 5 dyad) present. On average, deeper dives were recorded when no calf was present (Figure 1B, 1D, 1H). Obviously a larger sample size of such groups is required to confirm whether such dive patterns are typical for groups with only a single adult male present. When multiple males are in a group, any possible influence of the presence of a calf is less clear; the greatest frequency of deep dives (> 100 m) was recorded for a male in a competitive group when a calf was present (6.2/hour; March 9, Figure 1F), but such deep dives were also recorded in these groups when no calf was present (e.g., 5.4/hour; March 26, Figure 1J). Tagging nuclear animals (ie., presumed females) in groups when calves are present and absent would be required to confirm whether it is the female which males are following to these depths, and whether the females' diving behavior differs depending on the presence of a calf.

Diving Behavior at Night

Diving patterns at night could clearly differ from those during the day, if light levels in the water column affect behavior. Helweg and Herman (1994) found no change in the occurrence of singing behavior at night, using a bottom-mounted hydrophone in deep water offshore of the island of Kauai. They did however find that the occurrence of competitive groups did change with time of day, with competitive groups being observed most often in late afternoon (these latter observations were restricted to daylight hours). More recently, Au et al. (2000), using a hydrophone in shallow water off Maui, did find a change in the occurrence of singing behavior with time of day, with a peak at night. Four of the tagged whales in our study had tags remain attached after dark, and one tag stayed on throughout the night, falling off the next morning. Unfortunately we were not able to follow tagged whales after dark, and thus cannot comment on the behavior and group composition for tagged whales (ie., whether they remained in the same type of group after dark). It should be noted however that group membership changes normally on the scale of hours, rather than days (Mobley and Herman 1985), suggesting that group composition may have changed for the tagged whales. A visual comparison of overall dive depths in relation to time of day (Figure 1) shows no clear pattern. A comparison of day and night dive parameters (mean depth and duration using all dives, and for dives greater than one body length) for these four individuals also showed no significant differences (t-tests, p's > 0.05), however given the small sample size the power of these tests is low. Goodyear (1989) documented slight differences in day/night behavior of humpback whales on a feeding ground, with a higher frequency of feeding at night than during the day, in response to changes in the behavior of prey at night. Given that humpbacks are not thought to feed in Hawaiian waters (see Salden 1989 for a possible exception), and that virtually all of the data collected was from whales engaged in social interactions of one sort or another, the diving behavior of these whales is presumably driven by social factors. The primary mechanism that might drive changes in behavior at night would be light levels, if vision plays an important role in the social interactions that occur (Au et al. 2000). Measuring light in the water column, particularly using light sensors attached to living animals that likely do not remain in a constant orientation, is problematic. Regardless, on a broad scale, light values from the photometers on our tags show what one would expect in terms of light transmission in the relatively clear waters around Hawaii. Light level obviously decreased with depth during the day, but even at 120 meters light levels during the day are still very high relative to levels at the surface at night (Figure 3).

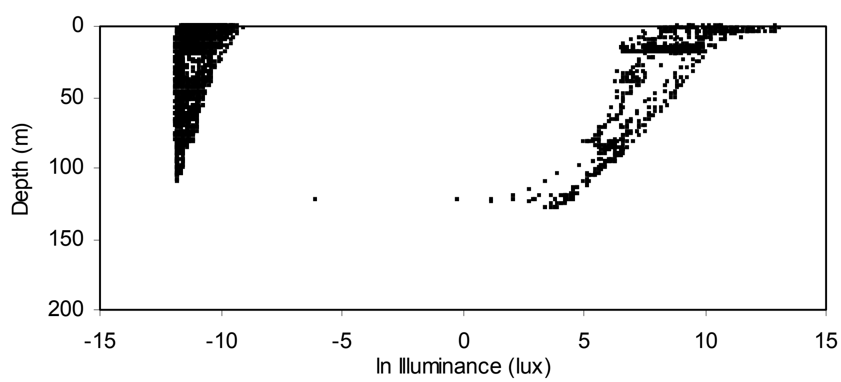

Figure 3. Change in light level with depth for two time periods; 1430-1815 hours (right hand values) and 2000-0500 hours (left hand values), taken from tag deployed from March 5, 2000.

Table 3. Percentage of time spent in different depth categories averaged for the 10 longest-tagged humpback whales.

Depth category (m)	Mean% time in depth category	SD	Cumulative % time
0 -10	39.55	20.57	39.55
11 - 20	26.51	13.29	66.06
21 - 30	11.65	11.84	77.71
31 - 40	4.25	2.77	81.96
41 - 50	3.04	2.28	85.00
51 - 60	2.47	2.28	87.47
61 - 70	2.14	1.73	89.61
71 - 80	1.66	1.54	91.27
81 -90	1.97	1.91	93.24
91 - 100	1.55	2.36	94.79
101 - 110	1.39	2.17	96.18
111 - 120	1.31	2.33	97.49
121 - 130	0.92	1.75	98.41
131 - 140	0.72	1.73	99.13
141 - 150	0.30	0.56	99.43
151 - 160	0.23	0.40	99.66
161 - 170	0.15	0.26	99.81
171 - 180	0.09	0.22	99.90

Behavioral Role in Group

On average about 40% of a whale's time was spent in the top 10 meters of the water column, and about 95% of the time was spent in the top 100 meters (Table 3). Where the whales spent their time in the water column varied dramatically between individuals, however (Figure 4, Table 3), depending primarily on behavior. Whales which had modal depths between 10 and 30 m (individuals D, H and I in Figure 4) all spent some time motionless at depth (see e.g., Figure 5) at times when they were known or thought to be either alone (March 12, Figure 1I), in a dyad (March 12, Figure 1D), or as an escort in a mother-calf-escort group (March 10, Figure 1H, after the secondary escorts from the competitive group had left). This motionless behavior appears similar to what has been described for singing humpback whales (Tyack 1982). These individuals spent only between 15 and 23% of their time in the top 10 meters of the water column, whereas individuals which did not exhibit such "motionless" behavior could spend up to 70% of their time in the top 10 meters. Two whales in competitive groups exhibited bimodal patterns of time at depth, one a primary escort (Figure 4F) and one a challenger (Figure 4J), with both whales frequently diving over 100 m. In general among diving mammals, dive depth tends to be strongly correlated with dive duration (and this has previously been reported for foraging humpback whales in Alaska; Dolphin 1987b). However in this study, the strength of the relationship between dive depth and dive duration varied dramatically between individuals, that is, for some individuals all long dives were also deep dives, while other individuals dove for long periods but remained relatively shallow (e.g., the approx. 20 m "motionless" dives, Figure 5).

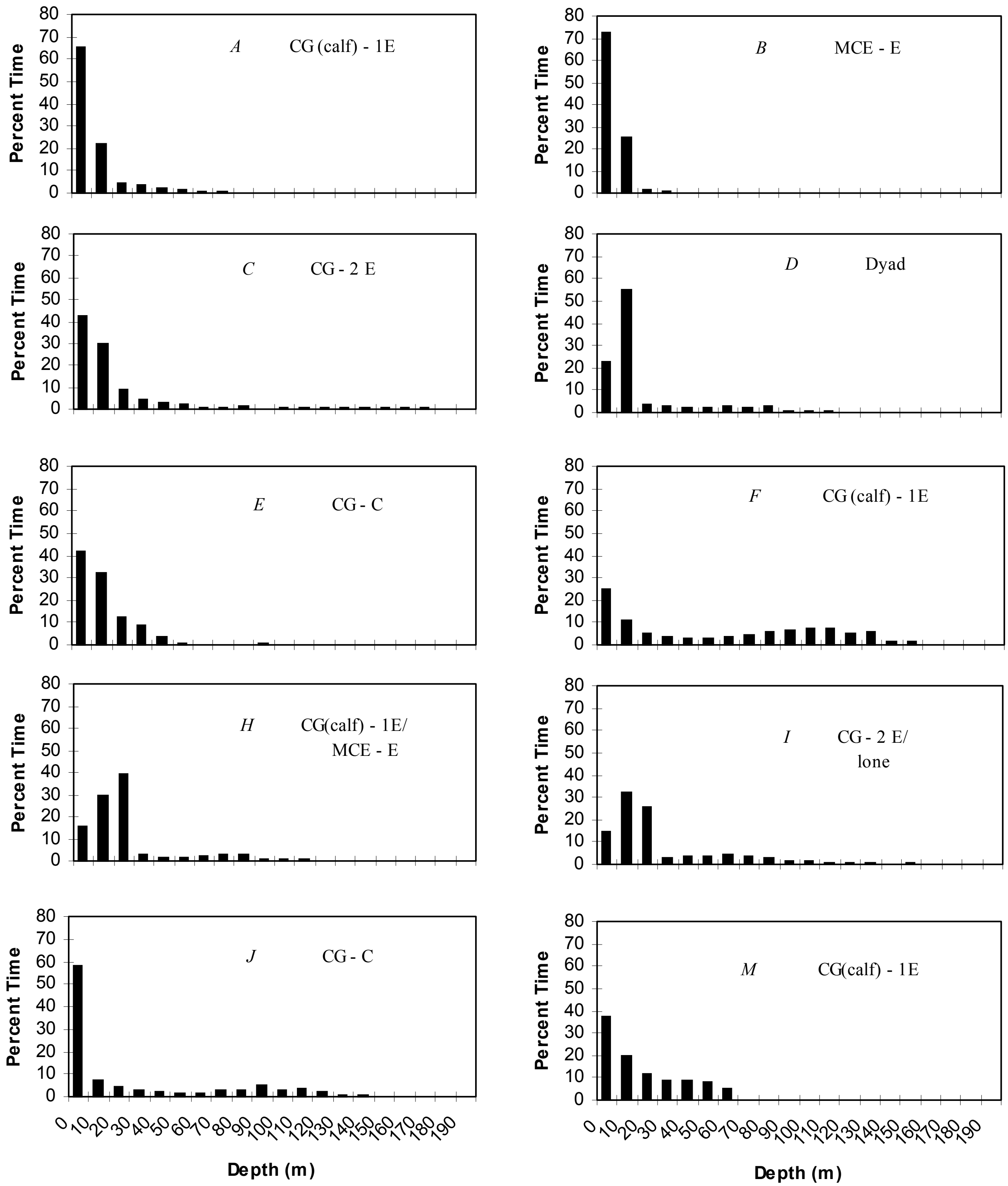

Figure 4. Time at depth for whales for which tags remained attached for greater than one hour. Start/end categories for each depth bin are shown. Date (*A* - Feb 26; *B* - Feb 27; *C* - Mar 4; *D* - Mar 5; *E* - Mar 8; *F* - Mar 9; *H* - Mar 10 #2; *I* - Mar 12; *J* - Mar 26 #1; *M* - Mar 27 #2), group type (CG=competitive group, MCE=mother/calf/escort) and tagged whale designations (1E=primary escort, E=escort, C=challenger, 2E=secondary escort) are the same as in Figure 1.

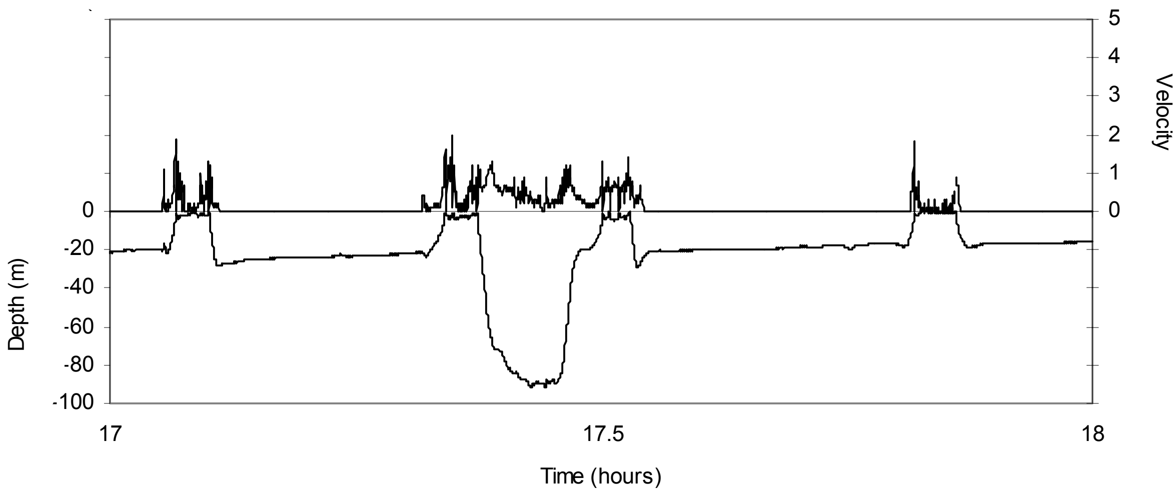

Figure 5. One hour of velocity (top) and depth (bottom) data from a humpback whale, March 10, 2000 (see Figure 1H). During this time the whale was thought to be an escort to a mother-calf pair. Two complete dives are shown (15 and 17 minute durations) where velocity drops to zero and depth remains relatively constant at approximately 20 meters. Based on these depth and velocity readings, during this period the whale appeared to remain motionless, similar to the behavior of "singing" humpback whales (see Tyack 1982).

Regressions of dive depth (using all dives > 6 seconds) versus duration for different individuals were all positive, and produced r^2 values (that is, the proportion of the observations which are explained by the regression equation) ranging from 0.23 to 0.93. Those in the lower range of r^2 values were individuals which exhibited "motionless" behavior (March 5, $r^2 = 0.23$; March 10, $r^2 = 0.37$; March 12, $r^2 = 0.24$), and the one individual escorting a mother-calf pair (February 27, $r^2 = 0.28$). The r^2 values for the regressions between depth and duration for all other individuals ranged from 0.55 to 0.94 (mean = 0.68), indicating a consistent relationship between dive depth and duration.

If we limit our analyses to dives greater than one body length (>11 m), the relationship between dive depth and dive duration changes dramatically for some individuals. For the three individuals which spent some time in motionless dives, regressions of dive duration versus depth all resulted in negative relationships, r^2 values were extremely low (0.02 – 0.04), and none of the relationships were significant (p values from 0.09 to 0.99). For the one whale tagged as an escort to a mother-calf pair (Figure 1B), the relationship between dive depth and duration was also negative ($r^2 = 0.05$, $p = 0.03$). As with the regressions using all dives, no matter what depth, all other whales (that is, those whales thought or known to be in a competitive group for the period they were tagged) had positive and significant (all p's < 0.001) relationships between dive depth and duration (r^2 ranged from 0.25 to 0.92, mean = 0.60). This means that for these whales, it may be possible to roughly predict dive depths based on the duration of the dive.

Management Implications of Diving Data

There are a number of potential management implications of dive data (Payne et al. 1997). Knowledge of the proportion of time spent at different depths in the water column is relevant to aerial survey calibration. For surveys in Hawaiian waters, water clarity is often extremely good, and it is possible to spot whales well beneath the surface. The exact depth at which whales can be spotted is unknown, however. We present information on the proportion of time near the surface, broken down into three-meter depth categories, for such aerial survey calibration (Table 4). As reflected in the values for 10-m depth categories (Figure 4), the proportion of time spent in the top three meters of the water column varied dramatically between individuals, ranging from about 6% to 51% of an individuals time (mean = 14%, n = 10 individuals, tagged for longer than 1 hour). With such high levels of variability, a larger sample size is required before such information will be of great value for aerial survey calibration factors. In addition, the depths at which whales can be spotted from an aircraft in different sighting conditions will need to be determined. As the proportion of time spent at different depths in the water column seems to depend to a large degree on group composition (see above; Figure 4), such values will need to be calculated for whales in different types of groups (e.g., mother/calf/escorts, singletons, dyads).

Table 4. Percentage of time spent in different depth categories near the surface, averaged for the 10 longest-tagged humpback whales.

Depth category (m)	Mean % time in depth category	SD	Cumulative % time
0-3	14.47	13.35	14.47
3-6	9.20	4.40	23.68
6-9	11.72	12.16	35.41
9-12	9.07	8.34	44.48
12-15	6.15	3.32	50.62

The other primary management implication of the data obtained relates to where in the water column humpback whales spend their time. The most important potential depth-specific threat to humpback whales is probably that of high-intensity underwater sounds. For example, within the study area the U.S. Navy has plans to expand their shallow water submarine training range, involving the installation of a number of sound sources at depths as shallow as 110 m (Hogarth[1]). While the potential impact of such sounds sources is unknown, data obtained in this study demonstrate that humpback whales do regularly dive to depths greater than 100 m, including dives to, or near to, the bottom (see e.g., Figure 2), and thus may be exposed to relatively high sound levels. Of the 13 whales tagged, five did not spend any time in water with a bottom depth greater than 100 m. Of the eight that did spend time in water depths greater than 100 m, seven were documented to dive to depths of greater than 100 m, suggesting that such deep diving is not unusual for whales in deeper water. In fact, one of these whales spent more than a quarter of its time (28.7%) at depths greater than 100 m (Figure 4F), and another spent just over 10% of its

[1] Hogarth, W.T., Acting Regional Administrator, National Marine Fisheries Service, Southwest Region. February 3, 1998 letter to R.L. Wohlechlegel, Naval Undersea Warfare Center, Hawaii.

time at such depths (Figure 4J). If we examine dives only greater than one body length, and exclude whales which were only found in water where bottom depth was less than 100 m, 11% of the dives recorded were to greater than 100 m. Calculation of the rate of deep diving (>100 m) using only those whales which were found in water greater than 100 m deep gives a rate of 1.73 deep dives/hour (n = 8 individuals, SD = 2.52).

Mean sustained rates of ascent and descent documented for a total of 31 deep (>70 m) dives of one individual were 1.29 and 1.51 m/sec, respectively. Rates of ascent and descent for deep dives of foraging humpback whales are substantially greater than those we documented (Dolphin 1987a). The longest dive we documented for an "active" animal (ie., where the animal was actively swimming, based on velocity readings) was 15.6 minutes. Given this as a breath-holding limit, and assuming there are no other physiological or physical limits to diving, the maximum depth that could be reached with our rates of ascent and descent is 655 m (or 842 m using the ascent/descent rates documented by Dolphin 1987a). Whether humpback whales can or do dive to such depths is unknown, however given our small sample size, the observed frequency of deep dives, and the fact that many of these appeared to be bottom-limited, it is likely that humpback whales in Hawaiian waters do regularly dive to depths exceeding the 176 m maximum documented in this study.

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