PAPER

Insights into the Underwater Diving, Feeding, and Calling Behavior of Blue Whales from a Suction-Cup-Attached Video-Imaging Tag (CRITTERCAM)

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ABSTRACT

We examined the underwater behavior of blue whales using a suction-cup-attached video-imaging instrument (CRITTERCAM). We made 13 successful deployments (defined as tag duration of >15 min and successful recovery of the tag and data) totaling 19 hours of CRITTERCAMS on blue whales off California and in the Sea of Cortez from spring through fall (26 February to 30 September) between 1999 and 2003 . Whale diving depth and behavior varied widely by region and period, although deployments on different individuals in the same area and period often showed very similar feeding behavior. One deployment extending into night showed a diurnal shift in diving behavior with progressively shallower feeding dives as it became dark, with shift to shallow, apparently non-feeding dives during the night. Data and video from tags demonstrated that the characteristic series of vertical movements blue whales make at depth are lunges into dense aggregations of krill. These krill were visible streaming by the camera immediately before these lunges and more clearly when the whales' forward motion stopped as a result of the lunge. The progression of events leading up to and during the lunge could be documented from the head movement of whales and occasional views of the expanding throat pleats or lower jaw, and by changes in flow noise past the tag, indicating a rapid deceleration. One set of deployments in the Southern California Bight revealed consistent feeding at depths of 250-300 m, deeper than has been previously reported for blue whales. A loud blue whale vocalization was heard on only one deployment on a male blue whale in an interacting trio of animals.

Introduction

Blue whales are the largest animals that have ever lived. Their large size made them prime targets during the modern era of commercial whaling when fast catcher boats and explosive harpoons allowed whalers to hunt them. Consequently their populations were depleted from around 300,000 to around 10,000 animals (Gambell, 1979). Despite their protection from whaling in 1966 by the International Whaling Commission, their numbers remain very low and the lack of a significant recovery has prompted concern. While recent revelations of the continued illegal hunting of blue whales past 1966 have provided one explanation about their slow recovery (Mikhalev, 1997), other factors such as the availability of adequate prey as a result of changes in krill abundance driven by climate change or competition with other species cannot be ruled out.

New techniques and studies have provided a better understanding of some aspects of blue whale biology. This has included: 1) photographic identification studies that have provided estimates of abundance and movements (Sears et al., 1987; Calambokidis et al., 1990; Sears and Larsen, 2002; Calambokidis and Barlow, 2004), 2) ship surveys to examine distribution and abundance (Barlow, 1994; Forney and Barlow, 1998; Gerrodette and Forcada, 2003; Calambokidis and Barlow, 2004), 3) satellite tagging to examine movements (Mate et al., 1999), 4) acoustic studies using detections of vocalizations to examine the distribution, seasonality, and singing behavior of blue whales (Stafford et al., 1998, 1999; McDonald et al., 2001; Burtenshaw et al., 2004; Oleson et al. 2007c).

The underwater behavior of all whale species is extremely difficult to study. Suction-cup-attached archival tags have begun to provide more details about underwater behaviors, including feeding and social behaviors (Goldbogen et al., 2006; Oleson et al., 2007a; Johnson and Tyack, 2003; Baird et al., 2005, 2006). Blue whales, like other rorquals, are known to lunge feed, which is to use their expandable throats to engulf large volumes of prey and water before filtering this mixture through their baleens (Goldbogen et al., 2007). Dive data from blue and fin whales have revealed a series of rapid vertical movements underwater presumed to be feeding lunges (Croll et al., 1998, 2001a, 2001b; Acevedo et al., 2002; Goldbogen et al., 2006, 2007; Schorr et al., 2005; Calambokidis et al., 2003, Dolphin, 1987).

Here we examine some of the specific insights into feeding and calling behavior of blue whales provided by the images revealed from the deployment of CRITTERCAMS on blue whales.

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Methods

There were seven deployment efforts from 1999 to 2003, primarily in California (Table 1). Deployments occurred from July through September in various locations ranging from the Southern California Bight to off Bodega Bay in northern California. A single deployment was conducted in early March in the Sea of Cortez, Mexico.

National Geographic's CRITTERCAM provided underwater video (Hi-8), sound, depth and temperature (Marshall, 1998). The modified, Hi-8 recording camera with datalogger was housed in a 31-cm-long x 10-cm-diameter cylinder outfitted with a ring of high output red LEDs (turned on after the first three deployments) and hydrophone.

Tag deployments were conducted by approaching whales from behind in a 5.3-m rigid-hulled inflatable boat (RHIB) to a range of ~1–5m. The CRITTERCAM was deployed with a 3-5m pole and attached to the whale with a low-profile silicon suction cup (22 cm diameter) with the aid of a remote vacuum pump that generated active suction between the whale's skin and the suction cup. Approach methods were refined over the tagging period with success of attaching tags improving from less than 10% of approaches in initial efforts to close to 50% in later efforts. Whales were tracked and tags were retrieved by direction finding on the VHF transmitter incorporated with the tag.

Ancillary data including photographs, skin samples for genetics, positional, and behavioral data were collected from tagged animals before, during, and after deployment. Photographic identification of individual animals was conducted based on natural markings on the dorsal fin and side of the whale for comparison to catalogs of approximately 2,000 known individuals maintained by Cascadia Research (Calambokidis et al., 1990; Calambokidis and Barlow, 2004). Skin was collected from the tagged animals and associated animals where possible either from the inner surface of the suction cup or tagging apparatus, or by biopsy. DNA was extracted from each skin sample and compared to controls of known sex through simultaneous amplification of the ZFX/ZFY and SRY genes (Fain and LeMay, 1995). Samples were identified to sex through visualization of the fragmented DNA in an agarose gel. Male samples and controls required the presence of the SRY fragment at 200 base pairs, in addition to the ZFX/ZFY band between 400 and 500bp. Female samples and controls included only the ZFX/ZFY fragment.

When possible, the position of the whale was noted by collecting GPS data at each surfacing while the tag was attached. Prey fields near the whale positions were examined using a 50/200 kHz depth echosounder on the RHIB. The 200 kHz return signal was used to estimate the depth of the scattering layer (aggregations of prey), which was detected as the boat tracked the tagged whale. Starting in 2003, a more sophisticated hydro-acoustic system was used to map the prey fields, but this only occurred with the final CRITTERCAM deployment and is not considered further here (Newton et al. 2005).

TABLE 1

Summary of effort deploying CRITTERCAMS on blue whales.

Location	Start date	End date	Total deplmts.	>15 min & recov.	Hours
Bodega Bay, CA	19-Sep-99	21-Sep-99	1	1	1.5
Monterey Bay, CA	12-Sep-00	19-Sep-00	1	1	6.0
Sea of Cortez, MX	26-Feb-01	6-Mar-01	5	1	6.6
S Cal. Bight, CA	14-Jul-01	26-Jul-01	12	5	2.5
Monterey Bay, CA	16-Sep-02	20-Sep-02	7	2	1.3
S Cal. Bight, CA	21-Sep-02	24-Sep-02	6	2	0.7
Monterey Bay, CA	24-Sep-03	30-Sep-03	3	1	0.3
Totals			35	13	18.8

Results and Discussion

Summary of Deployments and Information on Individuals Tagged

Out of 35 deployments of CRITTERCAMS on blue whales for 1999 to 2003, 13 were successfully recovered with at least 15 minutes of dive or video data (Table 2) although technical or data loss problems resulted in no video from two and no dive data from three of these deployments. These represented samples from both sexes and a range of estimated sizes (age classes). Of the 13 deployments used in our analysis, 9 were determined to be males and 2 females based on skin samples collected primarily from the suction cups after deployment (sex on the remaining two could not be determined). Males were either alone or the trailing animal in a pair or trio. The two females were always the lead animals in a pair. In one case where both animals in the pair were sexed (including the non-tagged animal), it followed the same pattern of female in the lead and the male as a trailing member of the pair. These observations are consistent with observations in other areas of pairs of blue whales generally consisting of a lead female and a trailing male (Sears et al., 1999; Cascadia, unpublished data).

Sighting histories of nine of the tagged animals based on photo-ID (four did not have a suitable photo-ID) revealed at least three of the tagged whales were over 10 years old (Table 3). In cases where tags were deployed on one animal in a pair we usually had success identifying both members of the pair. For example, on the deployment on 14 September 2000 on two traveling animals, the tagged whale in

TABLE 2

Summary of deployments of Crittercams used in this article.

Date/time depl.	Location	Lat	Long	OffTime	H	Prim beh.	Group	ID#	Sex
9/20/99 14:13	Cordell Bank, CA	38 04.77	123 22.02	15:40	1.45	Traveling	Lead of pair	6	F
9/14/00 9:47	Monterey Bay, CA	36 48.02	121 57.40	>20:00	6.00	Milling	Lead of pair	111	F
3/1/01 15:31	Sea of Cortez, MX	25 02.55	110 46.11	22:05	6.57	Milling	Single		M
7/19/01 12:40	N San Nic. Is., CA	34 23.13	119 32.11	13:15	0.50	Milling	Single	2056	M
7/20/01 12:58	N San Nic. Is., CA	33 23.19	119 31.07	13:20	0.37	Milling	Single	1976	
7/21/01 13:34	N San Nic. Is., CA	33 23.15	119 29.37	13:50	0.27	Milling	Single		M
7/25/01 12:12	W San Miquel, CA	34 05.29	120 35.79	12:45	0.55	Milling	Trail of pair	1133	M
7/25/01 13:37	W San Miquel, CA	34 05.06	120 35.80	14:24	0.78	Milling	Trail of pair	1721	M
9/16/02 12:14	Monterey Bay, CA	36 46.59	121 57.02	13:20	1.10	Mill-travel	Trail of pair	620	M
9/19/02 9:50	Monterey Bay, CA	36 46.58	121 55.58	10:01	0.18	Milling	Single		M
9/21/02 11:00	Santa Barbara Channel, CA	34 08.27	119 51.50	11:25	0.42	Interaction/active	Trail of trio		M
9/24/02 12:01	Santa Barbara Channel, CA	34 07.81	119 46.37	12:18	0.28	Milling	Single	1849	
9/30/03 15:45	Monterey Bay, CA	36 33.54	121 58.65	16:00	0.25	Milling	Trail of pair	903	M

TABLE 3

Summary of resightings based on photo-ID of whales in this study. A bold T indicates tagging year.

	Years Seen																					Regions Seen
ID	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**00**	**01**	**02**	**03**	**04**	**05**	**06**	
6	X		X	X	X	X	X				X			**T**								Farallones, Monterey, S Ca., also 1991 Sea of Cortez
111		X			X		X								**T**		X					Farallones, Monterey, Pt. Arena, Ft. Bragg
620						X	X	X	X	X	X	X	X	X	X		**T**	X		X		Farallones, Monterey, Ft. Bragg, S Ca.
903									X			X						**T**				Monterey, S Ca.
1133										X						**T**						S CA, Pt. Vincente to Pt. Conception
1721																**T**						S Ca.
1849																	**T**				X	S Ca, W Baja (2006)
1976																**T**		X				S Ca., S of Pt. Vicente, Catalina Island
2056																**T**						S of Pt. Vicente, Catalina Island

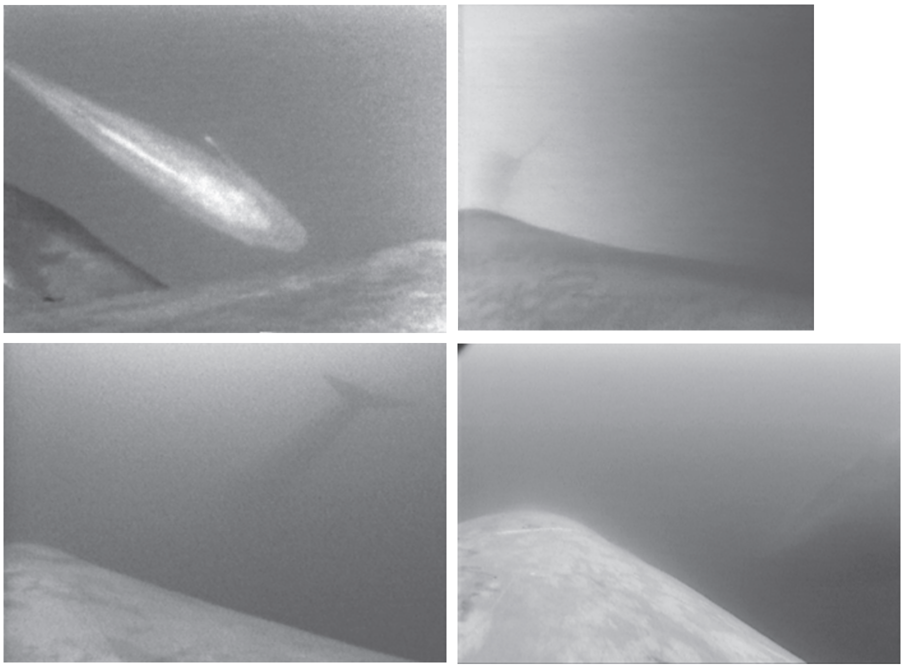
TABLE 4

Summary of key findings on deployments of CRITTERCAMS on blue whales.

DateTimeOn	Location	# Dives	Max Dep	Max Dur	Dive descriptions	Visual feeding/prey observation	Detection of other whales
9/20/99 14:13	Cordell Bank, CA	8	>90	0:16:06	Generally shallow dives, no lunge feeding. Sensor cut-off at 90 m	None despite very good visibility	None
9/14/00 9:47	Monterey Bay, CA	NA			Dive record lost both shallow lunges and deeper dives	Prey visible during near-surface lunges incl on back of whale	trail whale comes into view below lead whale
3/1/01 15:31	Sea of Cortez, MX	99	135	0:07:34	Lunge feeding dives transitioning shallower at dusk switching to short, shallow apparently non-feeding dives	Lunges apparent from head movement and sound, after last lunge in series animal stays oriented upward. Single krill visible in a few frames.	None
7/19/01 12:40	N San Nic. Is., CA	NA				Krill visible during deep lunges, distended pleats seen as tag comes off	None
7/20/01 12:58	N San Nic. Is., CA	3	255	0:07:55	Deep lunge-feeding dives 200-250 m	NA	NA
7/21/01 13:34	N San Nic. Is., CA	2	293	0:09:50	Deep lunge-feeding dives 240-290 m	NA	NA
7/25/01 12:12	W San Miquel, CA	3	265	0:09:26	Deep lunge feeding dives 210-260 m	Throat pleats visible distending, krill flying by and close up during lunges	2nd whale visible ahead during ascent
7/25/01 13:37	W San Miquel, CA	4	280	0:11:02	Deep lunge feeding dives 210-260 m	Krill going by and close up during lunges	None
9/16/02 12:14	Monterey Bay, CA	NA				Krill visible going by in dark, very faint illumination	Lead visible above water during surfacing and ahead of whale as they ascend
9/19/02 9:50	Monterey Bay, CA	1	165	NA	Shallow dive followed by deep dive where camera comes off on initial lunge	Krill visible immediately before camera detaches	None
9/21/02 11:00	Santa Barbara Channel, CA	1	183	NA	Shallow dive then after surfacing stay at 10-12 m before and during call, tag comes off on descent at 183m	None	2nd whale adjacent during call then passes ahead and tagged whale accelerates and follows
9/24/02 12:01	Santa Barbara Channel, CA	3	150	NA	After two shoreter dives, comes off during apparent lunge feeding dive at 150m	No kill seen, but camera fails prior to reaching max depth	None
9/30/03 15:45	Monterey Bay, CA	2	214	NA	Several shallow dives before deep dive to >200m where camera comes off	Krill visible near where tag detaches at 214m during what appears to be a lunge	Lead whale in view ahead and to right of tagged whale as they begin a descent

FIGURE 1

Glimpses of other whales captured by CRITTERCAM. Clockwise from top left: a) view of trail animal below tagged whale on 14 September 2000, b) lead animal seen ascending ahead of tagged animal on 25 July 2001, c) lead whale seen ahead of tagged whale during ascent on 16 July 2002, and d) the head of a second whale seen on the right side of tagged whale immediately before and during loud vocalization on 21 September 2002.

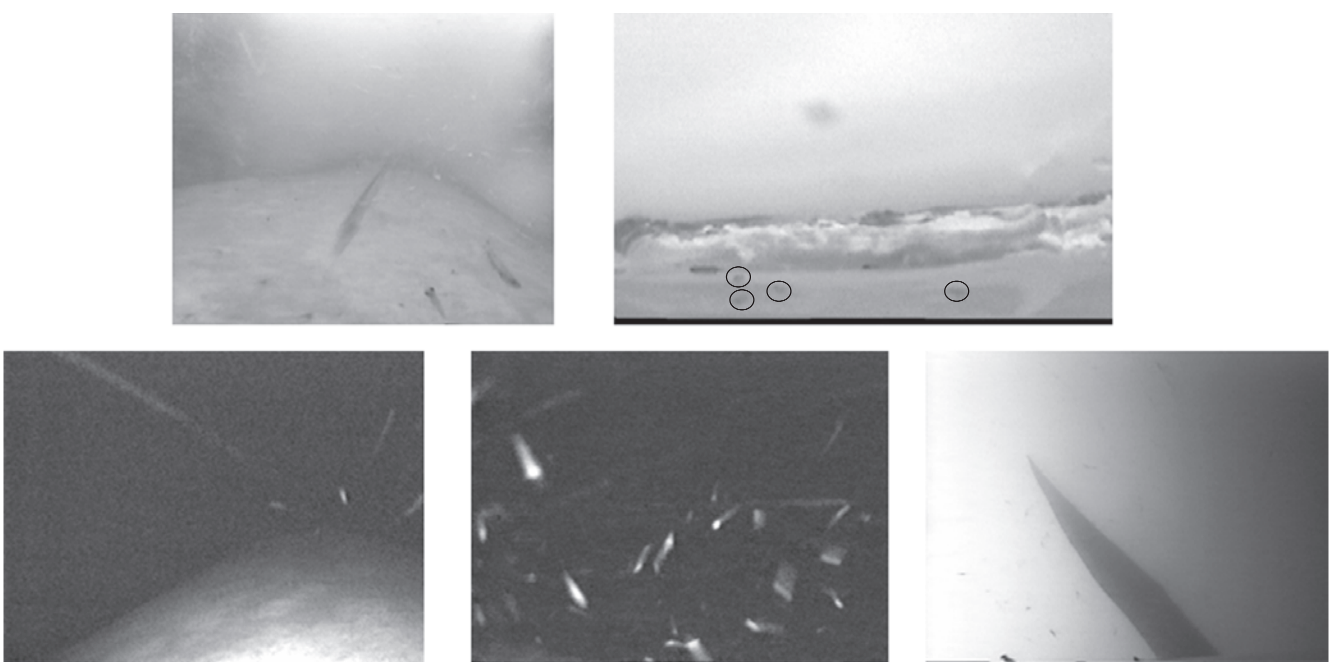


the lead was ID# 111 previously identified in 1987 and 1990 in the Gulf of the Farallones and in 1992 off both Fort Bragg and Point Arena. The trailing animal (ID# 283) was first identified in 1988 in the Gulf of the Farallones and seen in 1989 in Mexico and in 1992 in both Santa Barbara Channel and the Gulf of the Farallones.

While prior observations of blue whales have provided information on how they are associated while at the surface, it has not been known if these associations continue at depth. Deployments on whales in pairs or trios occasionally captured views of another whale (five of seven or 71%) but this occurred in none of the four deployments on single whales with video (Table 4). The sightings of other individuals were typically just brief glimpses (Figure 1). None of the images of other whales showed cooperative feeding at close ranges as is seen in some other species like humpback whales; however, one important caveat is that the ability to detect this was limited due to poor water clarity, limited light during deeper dives, and the field of view provided by CRITTERCAM.

FIGURE 2

Images of krill from CRITTERCAM showing: a) close up of krill after a feeding lunge near the surface, b) krill out of the water on the back of a surface lunge-feeding blue whale, c) appearance of krill illuminated by LEDs in whale rapidly swimming through krill layer, d) krill illuminated by LED after whale has slowed during a lunge at depth, and e) krill silhouetted against the surface of the water with pectoral fin of whale in view.



These findings indicate that inter-whale associations (or lack thereof) seen at the surface continue underwater. For example, the lead and follow orientations noted at the surface were consistent with the positioning seen underwater in the video. Sightings of a second whale from the deployment on the lead animal occurred on at least two occasions on the same deployment when the tagged lead animal (a female) was feeding near the surface and the other animal came into view swimming below it. The final deployment with another whale visible involved a case where loud vocalizations were heard and is described in more detail below.

Detection of Prey

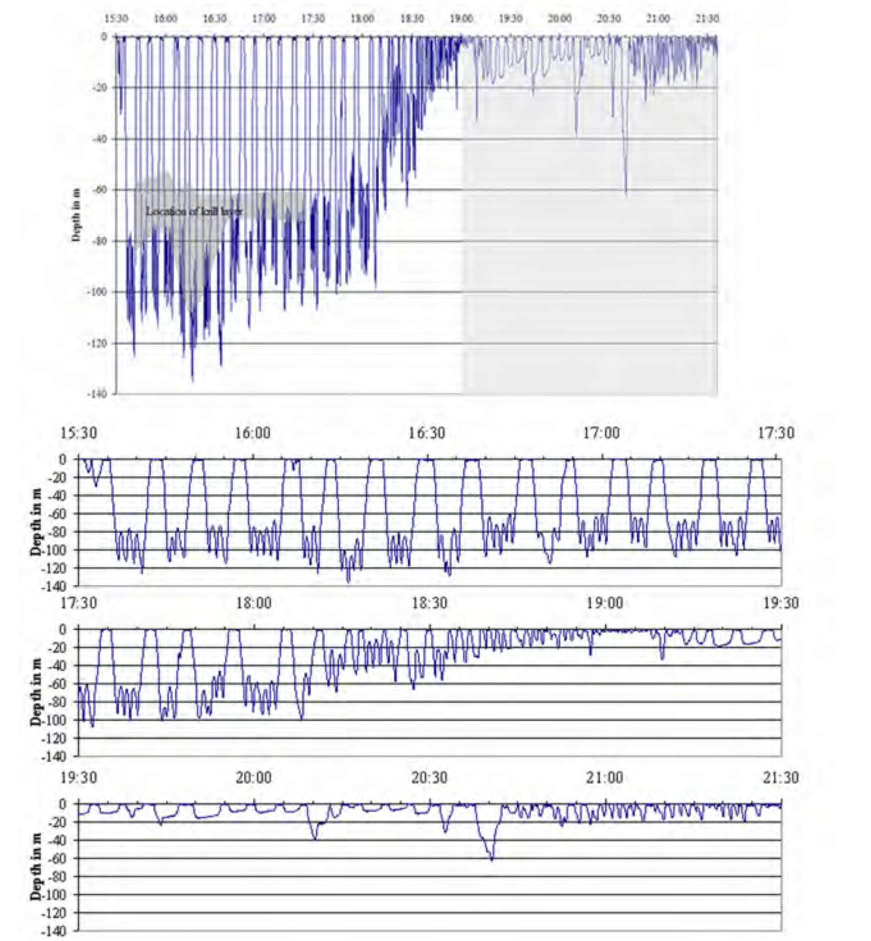
Krill, the exclusive prey of blue whales, was observed in 8 of the 11 deployments where footage was available (Table 4). Prey was primarily detectable on deployments of cameras that had the LED lights turned on (all except first three deployments) which illuminated the prey at deeper depths or when whales were feeding near the surface where ambient light was available (Figure 2). Surface feeding and visible prey in ambient light occurred in a single deployment on the lead whale of a pair of whales on 14 September 2000 in Monterey Bay. No dive data were available from this deployment because the tag was not recovered until 3 days later, resulting in memory loss. The six hours of video imaging on this one deployment clearly showed krill during repeated feeding lunges by the whale just below and at the surface.

Observation of Whale Feeding Behavior

Two deployments provided insights into the lunge feeding dives. The first was the longest complete record and was deployed on 1 March 2001 in the Sea of Cortez; it recorded diving behavior from late afternoon into the night. Although the tag did not have lights, the depth of the lunges was such that, for several hours before sunset, the head of the whale was silhouetted against the daylight when the camera aimed toward the surface. The second deployment occurred on 25 July 2001 off southern California where the tag was placed on the side of the animal just above the pectoral fin and provided a view of the throat pleats when they became distended during a lunge feeding event.

FIGURE 3

Change in blue whale dive behavior during 6-hour tag deployment in the Sea of Cortez, Mexico, on 1 March 2001. Top panel shows full dive profile including location of krill layer based on depth sounder readings and time after sunset (shaded). Bottom three panels show detailed dive profiles in 2-hour periods representing feeding, transition and nighttime periods.



In addition to providing insight into how whales approach prey, the deployment on the whale feeding in the Sea of Cortez also showed a dramatic shift in feeding and diving behavior at night (Figure 3). Comparison of the dive profile of this animal with the presence of a krill layer detected from a boat following behind the whale showed it was diving to below the krill layer and then coming into the lower portion of the layer (Figure 3). Depth of feeding dives became progressively shallower into the evening in response to the vertical migration of prey, a pattern seen on deployment of other tags on blue whales (Croll et al., 1998; Oleson et al., 2007a). Dive intervals went from averaging over 5 min prior to 1830 h (n=25, mean=5 min 32 sec, SD=91 sec) to close to 2 min after 1830 (n=70, mean=2 min 4 sec, SD=65 sec). Similarly, maximum dive depth during each series decreased from an average of 100 m (SD=25 m) to jut 16 m (SD=9.6 m) in the same periods and the sawtooth feeding dives were no longer seen.

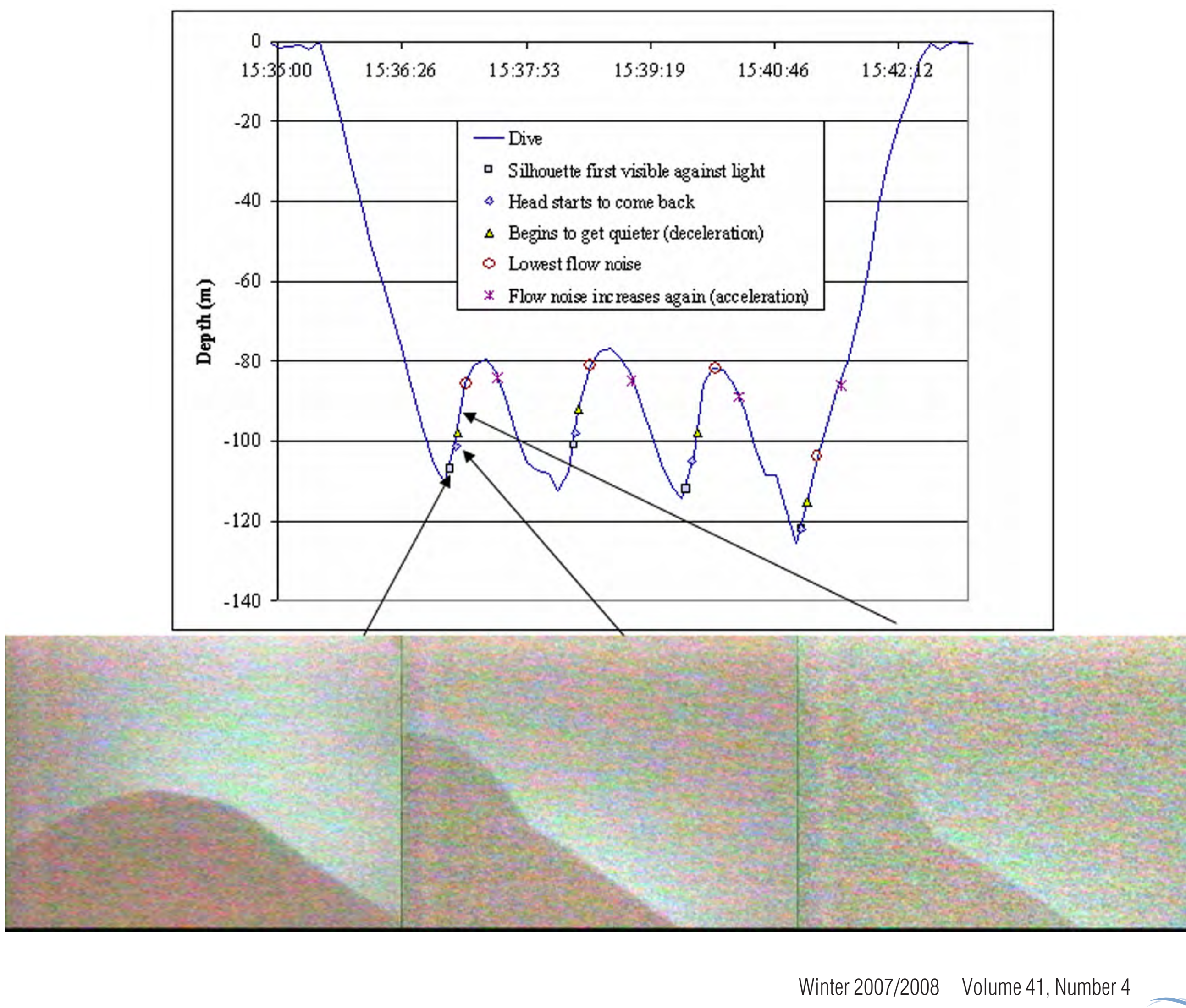
Even though the absence of lights on this deployment reduced visibility when the camera was turned away from the water surface, the silhouette of the animal against the surface (when aimed up) and sound levels provided insight into the mechanics of feeding (Figure 4). From 1530 to 1800, all but one of the 16 dives showed a similar pattern as detailed in Figure 4. This pattern was still observed as foraging dives became progressively shallower (Figure 4). The silhouette of the animal came into view against the light background of the surface when the dive record indicated the animal had begun the short vertical ascent toward the krill layer and a few seconds later the whale raised its head. We interpreted this head-raise as indicating the animal opened its mouth because immediately after the head came back (approximately halfway up the short vertical ascent), flow noise decreased dramatically, indicating a mouth-open event had slowed the animal's movement. Coincident with the head coming back the silhouette of the lead animal disappeared into darkness, indicating the camera was no longer pointed up. While this motion gave the appearance that the animal inverted into the krill layer, the lack of a pitch and roll sensor on this generation of instruments also makes it possible that a roll or some other motion turned the animal away from aiming towards the surface. The lowest flow noise level occurred just before the shallowest portion of the vertical movement. Flow noise did not begin to increase again until the animal was descending prior to another lunge. This pattern of events is consistent with that described for fin whales (Goldbogen et al., 2006).

An unexpected finding of this analysis is the frequent occurrence of a lunge (head coming back followed by a rapid deceleration) on the final ascent. This final-ascent lunge is only barely discernable from the dive record itself and appears as only a slight slowing of the rate of ascent. The chronology of events is similar to the other lunges except the animal never changed from an upward angle and remained silhouetted throughout the lunge and then it continued its ascent to the surface.

The deployment that occurred on the side of the whale (25 July 2001) west of San Miguel Island off southern California lasted a little more than half an hour and recorded two completed dive sequences. The whale rolled on its left side at the time of deployment, resulting in the unusual placement of the tag low on the right side of the body. This whale was feeding in an area with one of the densest concentrations of blue whales we had encountered in 20 years of research off California. We estimated about 200 blue whales feed-

FIGURE 4

Detail of a single foraging dive (first lunge feeding dive) from 1 March 2001 deployment in the Sea of Cortez showing timing of visual and acoustic cues related to lunge feeding. Images are single frames from the video record by Crittercam which was positioned just behind the head. Arrows indicate the approximate location that each image was taken during the first lunge. Images show head silhouetted against the lighter water surface and then the head would come back. Within 1 sec of right frame the view went completely black again except for the final-ascent lunge.



ing along a 7 nm stretch of the shelf edge (a zone about 1 nm wide). The four deployments made in this area and just to SW off San Nicolas Island during the same period consistently showed the deepest diving and feeding of any of our deployments. Whales were diving to nearly 300 m and lunge feeding at depths ranging from 200 to 290 m (Table 4). We suspect the feeding behavior of this one whale probably was representative of others in the area.

On each of the ascent stages of the dives, the throat pleats could be seen distending outward. This occurred a little more than halfway up the vertical ascent stage of that section of the dive (Figure 5). The appearance of the distended throat pleats generally coincided with the sharp drop in flow noise. The speed at which the high density of krill was streaming by the camera also slowed such that individual krill could be seen (see Figure 2). This is similar to the position within the lunges identified by the rapid drop in flow noise on the deployment on 1 March 2001 discussed in detail above. Also similar to that deployment, the throat pleats were seen distending on the final ascent on the 25 July deployment, indicating a feeding lunge had occurred even though this was again barely detectable from the dive profile only.

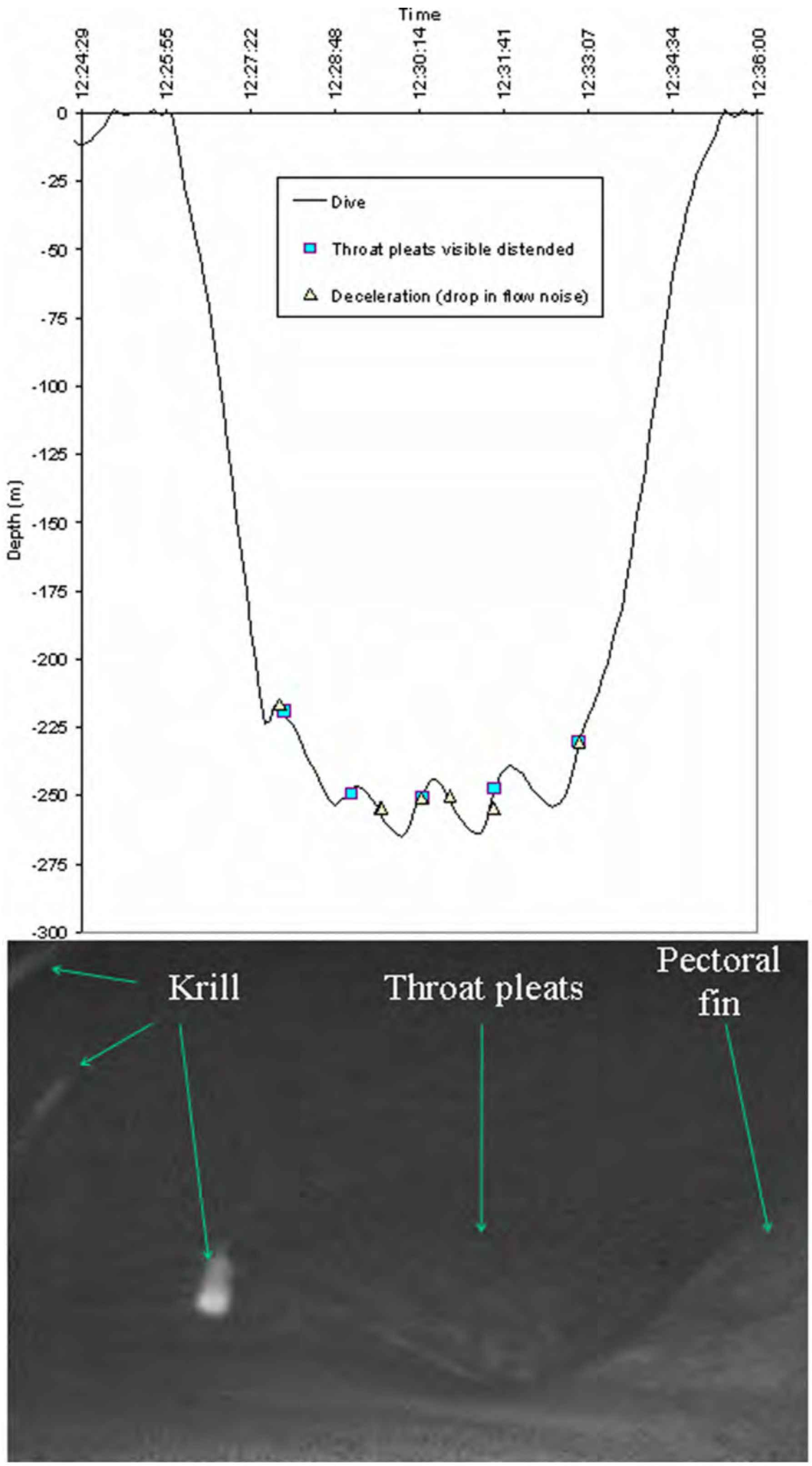
The detection of this final lunge is important when considering the energetic costs of lunge feeding. Croll et al. (2001a) demonstrate that the dive duration in blue and fin whales is shorter than expected from oxygen stores due to these lunges being energetically costly. Acevedo et al. (2002) calculate the relationship between number of lunges (based solely on the dive profile) and surface recovery time to support this assertion. Dive profiles alone may not provide an accurate estimate of the number of lunges. Visual and acoustic data from the CRITTERCAM helped identify lunge feeding occurring in one portion of the dive cycle that was not apparent from the dive profile alone.

Fluke Beat Rate

Slow oscillations of the body of whales representing apparent fluke beats could be discerned from the video footage (Williams et al., 2000). An analysis of the fluke beat rates from the first 1999 deployment of a CRITTERCAM on blue whales was used to describe their use of

FIGURE 5

Detail of feeding dive on 25 July 2001 near San Miguel Island, southern California, showing locations in dive sequence when throat pleats became visible (photo) and also when flow-noise decreased dramatically indicating deceleration. Photo is single frame from CRITTERCAM video showing the right pectoral fin on right, throat pleats distended (center) and several krill (left).



stroking and gliding especially on descent into deeper waters when animals become more negatively buoyant due to compression of air spaces (Williams et al., 2000). Fluking rates among the diving species were compared for the blue whale, the largest animal, and were 6–10 strokes per minute (0.1 to 0.2 Hz) during periods of stroking. This fluking frequency is also consistent with recent allometric studies (Sato et al., 2007), which showed that bigger animals flap their appendages at a slower rate than do smaller ones. The deployment that served as the basis for that study was our first deployment and represented a traveling animal that remained in relatively shallow (<100 m) clear water that afforded a good view of the entire body and the rates of fluke beats.

We found variability in how clearly fluking rates could be quantified from the CRITTERCAM footage. This was in part dependent on the position of the tag on the whales (tags located further aft showing this more clearly than those near the head of whales). In deeper dives even the lights on the CRITTERCAM could only illuminate a small area of the body, making it more difficult to assess fluke beats. Since the CRITTERCAM deployments, use of accelerometers on tags that provide pitch of the whale have proved a more effective way to examine fluking rates and other aspects of swimming kinematics (Goldbogen et al., 2006). Despite these limitations, the general pattern described by Williams et al. (2000) for the initial CRITTERCAM deployment is consistent with what was seen on other deployments; fluking occurred at the beginning of a descent and strongly during ascents (including feeding lunges), but largely ceased during the main portion of the descents to depth.

Vocalizations

Loud calls were detected on only one tag deployment suggesting that vocalizations are infrequent for feeding whales. The CRITTERCAM deployments were not ideal for examining occurrence of vocalizations due to some problems with electronic or mechanical interference and the low-frequency flow-noise present when whales were moving at higher speeds through the water. However, studies using dedicated acoustic tags have reached a similar conclusion that only a relatively small proportion of blue whales are calling, especially when feeding (Oleson et al., 2007a, 2007b).

The single detection of loud calls occurred on 21 September 2002 on a relatively brief deployment on the trailing animal in a trio (determined to be a male). This was our only deployment on a member of a trio. After tag deployment the whale made a shallow dive to 55 m, surfaced 7 times then dove to a depth of 10-12 m for approximately one minute. The 13 sec call occurred at the end of this period with the whale nearly motionless (no body movement or flow noise) at 10m depth. One of the other animals in the trio (likely the other trailing whale based on surface observation), came into view next to the tagged whale and then passed and continued ahead, descending at a steep body angle (Figure 6). The call consisted of low-frequency pulses matching what has been termed the "A" call of eastern North Pacific blue whales (see Oleson et al., 2007a for a description of calls including this one). At the end of the call, the tagged whale rapidly accelerated and dove deeper in the direction of the other animal. The tag came off a few minutes after the call while the animal was swimming rapidly.

The finding that the caller was probably a male in fairly shallow water is consistent with other observations of blue whales. Research on calling behavior of blue whales using a larger dataset of deployments of three types of tags as well as visual and acoustic tracking of blue whales has indicated that apparently only males produce the long repeated broadcast calls (singing) characteristic of this species (Oleson et al., 2007a; McDonald et al., 2001). Similar findings have been reported in the closely related fin whale (Croll et al., 2002). Singing whales (repeatedly calling) are generally solitary traveling males while intermittent callers are sometimes associated with other whales (Oleson et al., 2007a). While the social interactions of blue whales in these larger groups is not well understood, the existence of male-female pairs with the female in the lead and the high-speed behavior of trios suggests it may be analogous to the competitive surface active groups in humpback and right whales that typically consist of a lead female followed by competing males (Clapham et al., 1992; Kraus and Hatch, 2001). The visual data from the CRITTERCAM indicates this calling behavior of blue whales may also be a part of the interactions among these competitive groups.

Conclusions

Deployments described here provided insights into the underwater life of blue whales. Blue whales were generally feeding despite the wide range of dates and locations that were sampled by our tagging efforts. Depth of feeding varied widely from at the surface to nearly 300m, deeper than had been found in past studies. One deployment that extended into night showed a diurnal shift in diving behavior with the whale gradually shifting to shallower feeding with the onset of darkness and then into shallower dives that did not appear to be related to feeding at night. Data and video from tags demonstrated that the characteristic series of rapid ascents that blue whales make at depth are lunges into dense aggregations of krill. This was based on visible krill at the time of these movements, the observation of the head movement of whales or of expanding throat pleats, and changes in flow noise indicating a rapid deceleration.

A wide range of sophisticated instruments can now be attached to whales to provide quantitative measurements of activities and behavior. Images from instruments like CRITTERCAM have proved essential for interpreting and providing a context for these measurements. Images were particularly important in detecting prey and whale response to prey as well as the presence and interactions with conspecifics. These instruments also provided a unique viewpoint and perspective of life from the whale's point of view.

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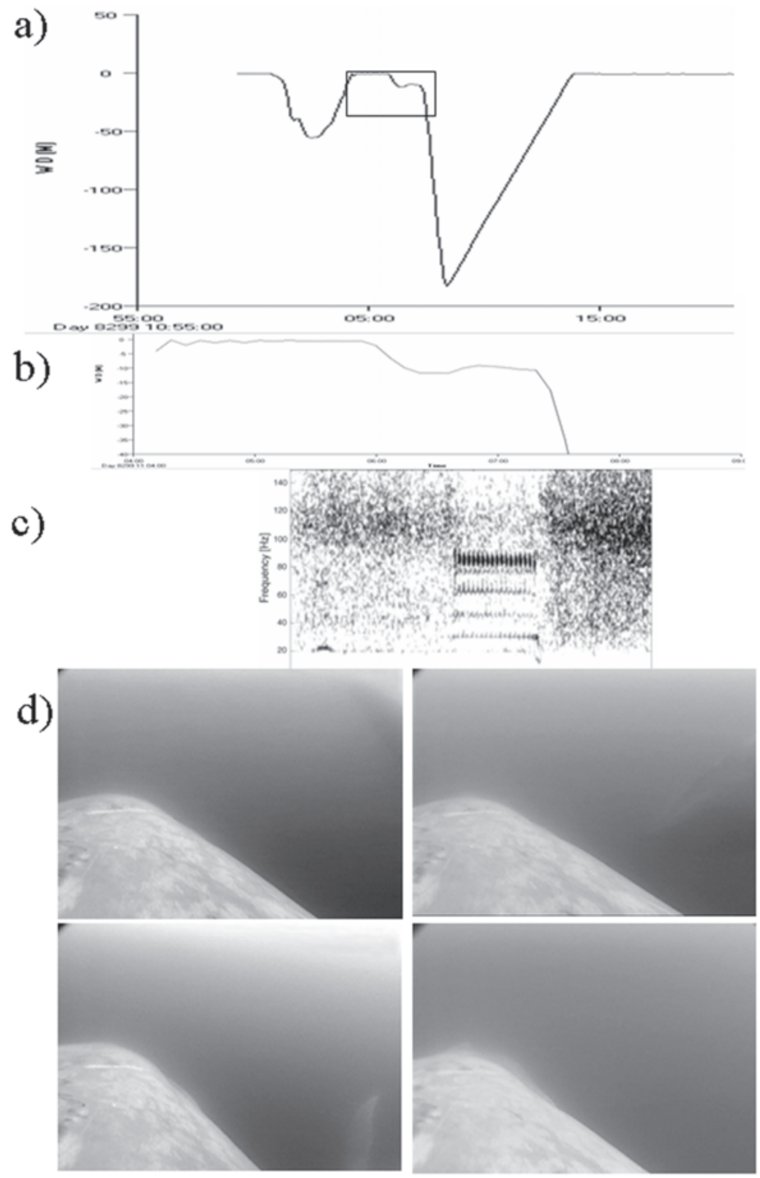
FIGURE 6

Detail of 21 September 2002 deployment on male blue whale where loud vocalization is heard. a) Overall dive profile, final ascent is where tag came off the whale, b) detail of boxed section where call occurred, c) spectrogram of call and also showing increase in flow noise immediately after call, d) sequence from video showing tagged whale and second whale on right passing.



CRITTERCAM deployment. Todd Chandler assisted with deployments and tracking of whales. Annie Douglas, Lisa Schlender, and Erin Falcone conducted data entry and management and photographic matching. Sex determinations for whales sampled off California were conducted at Southwest Fisheries Science Center; Barb Taylor, Susan Chivers, and Carrie LeDuc were helpful with this; Luis Enriquez Paredes from Universidad Autonoma de Baja California in Ensenada analyzed the samples from the Sea of Cortez. Ulrike Wolf examined the associations in blue whale pairs. Funding came in part from National Geographic, the Office of Naval Research Grant Number N00014-00-1-0942 (Bob Gisiner COTR), the Tagging of Pacific Pelagics program under Sub-award Agreement from UCSC # S0179709 (Dan Costa, COTR), and the generous support and help of Michiru Ogino. John Hildebrand, Joe Olson, Bill Burgess, and Jeremy Goldbogen provided important insight and discussions. The manuscript was improved by comments by Jeremy Goldbogen and several anonymous reviewers.

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