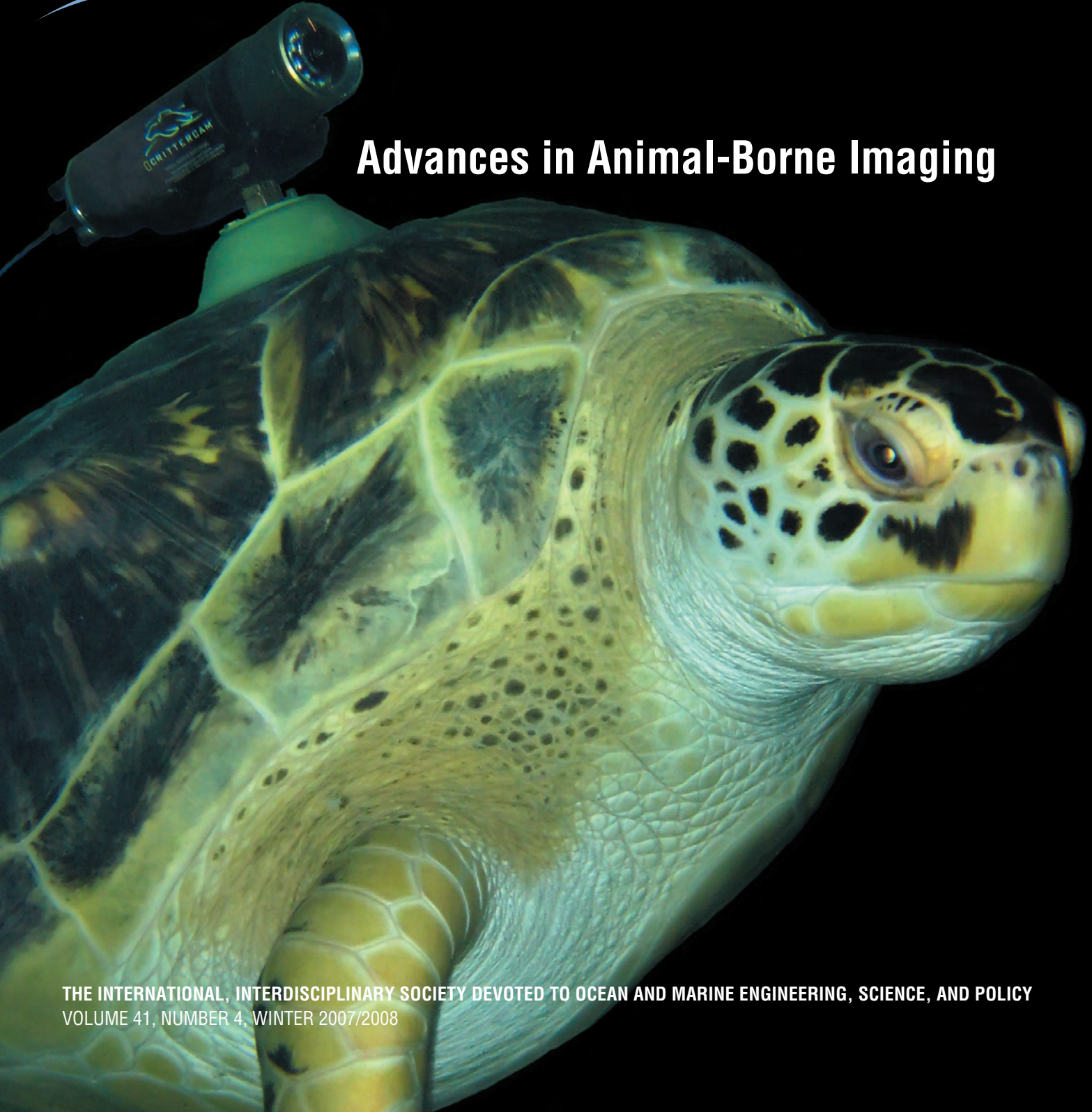


**Marine
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JOURNAL

Advances in Animal-Borne Imaging



THE INTERNATIONAL, INTERDISCIPLINARY SOCIETY DEVOTED TO OCEAN AND MARINE ENGINEERING, SCIENCE, AND POLICY
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Front Cover: National Geographic partnered with the National Aquarium in Baltimore to test the latest miniaturized version of the CRITTERCAM (Generation 5.7). A suction cup was used to attach the new Crittercam to Calypso, the Green Sea turtle, for a series of functionality and natural behavior testing. The new CRITTERCAM, at 2.25" in diameter and 10" long, was dwarfed by the 235-pound turtle. Photo by Corey Jaskolski.



Back Cover: National Geographic Society Remote Imaging Department researchers (guest editor Corey Jaskolski is in the front of the boat) use a deployment pole to attach a CRITTERCAM to a humpback whale calf. (They did not get a camera on the calf, but did attach a CRITTERCAM to her mother.) Photo by Kathi Koontz.

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Guest Editors: Greg Marshall, Birgit Buhleier,
Kyler Abernathy, and Corey Jaskolski

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ABSTRACTS

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Contributors can obtain an information and style sheet by contacting the managing editor. Submissions that are relevant to the concerns of the Society are welcome. All papers are subjected to a stringent review procedure directed by the editor and the editorial board. The *Journal* focuses on technical material that may not otherwise be available, and thus technical papers and notes that have not been published previously are given priority. General commentaries are also accepted, and are subject to review and approval by the editorial board.

CROSSTALK

Discussion about "Offshore Wind Electricity: A Viable Energy Option for the Coastal United States" by Walt Musial and "Economic and Social Benefits from Wave Energy Conversion Marine Technology" by Roger Bedard in the Fall 2007 special issue *Societal Benefits of Marine Technology and the Challenges of Tomorrow* (Vol. 41, No. 3)

Engineering and Environmental Challenges of Offshore Power Generation

I read with interest the two papers concerning the state of wind and wave energy conversion technology in the Fall 2007 *MTS Journal*. I believe their impact would be greatly strengthened if their authors had not glossed over certain important topics without providing supporting information and references. In Mr. Bedard's discussion of barriers to the development and use of wave energy in the U.S., it is difficult for me to accept his unsupported statement that "...no technology barriers are evident." I would argue that several seriously challenging technology hurdles remain to be overcome before this technology can be used in earnest in the ocean's harsh environment, among those being failsafe solutions to mooring, connecting safely to the power grid, and long-term reliability. Remembering Katrina, we need to recognize that this technology must be able to survive Category 4 and 5 hurricanes and 100-year storms, with winds exceeding 200 km/h and 30 m waves, for adequate protection of our oceans.

In Mr. Musial's paper on offshore wind electricity, environmental issues are brushed off practically without comment with his generalization, "Some of the costs associated with offshore wind can be attributed to the uncertainties with environmental and siting consequences that lead to unfounded negative perceptions (e.g., RADAR, avian impacts, tourism)...." Even if true, this is definitely a hot button in the public eye, and to assume the reader already agrees without further justification imparts a tone of presumption. The studies I have been able to find on the subject concern land-based installations and fauna, and their conclusions should not be assumed to apply equally in ocean environments.

These two papers left me with the disconcerting impression that their authors, rather than acknowledging that important engineering and environmental risks remain, are eager to push ahead with deregulation and funding of their projects.

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Author's Response

Although many of the issues raised by opponents to offshore wind are indeed unfounded, the author did not intend to imply that any environmental issue should be categorically neglected. In fact, offshore wind energy projects are in general being held to the highest standards applied to energy projects of any kind in the United States through the NEPA process. Even though no significant impacts have been discovered yet from eight years of studying installations in Europe, there remain many challenges and uncertainties with regard to siting offshore wind turbines in the United States, where no installations have reached the construction phase. None of the projects that may go forward in U.S. waters can take for granted that the impacts are fully understood or that European practices will deliver the same result here in the United States. A comparative risk approach should be taken to move ahead with caution, thoroughly monitor first projects, and adapt procedures to new information as it is obtained.

Walt Musial
National Wind Technology Center, National Renewable Energy Laboratory

Roger Bedard chose not to offer a written response to this Crosstalk discussion.

Advances in Animal-Borne Imaging

Greg Marshall

National Geographic Society Remote Imaging Department

The world still holds many secrets. Despite the extraordinary advances of science in the last two centuries, there are places on this blue planet humans have never been, and things we've never seen or even imagined. Many of the marine creatures we think we know by observing them in 'our world' spend the vast majority of their lives in hidden realms we have little or no access to. These animals routinely venture to places that are well beyond human physiological capacity. Inspired by the unreachable and the unknown, we've exercised technological prowess in an effort to penetrate this other world shrouded beneath the oceans' veil. We've sent man, woman, and machine into the depths to probe and process, and have gained new understanding and appreciation for the challenges these animals face in their world. Increasingly, streams of digital data reveal patterns of behavior and excursions to habitats that tantalize us with virtual glimpses of how these creatures function. Yet, we have not been able to see—to directly observe—these phenomena. Until recently we've been constrained to infer animal behavior and ecology from secondary or tertiary data sources. This issue of the *Marine Technology Society Journal* explores the current cutting-edge era of exploration and investigation of the hidden lives of some of the planet's most charismatic creatures using new animal-borne imaging and data-logging tools for discovery and science.

Twenty one years ago the first animal-borne imaging system designed for scientific research was deployed on a sea turtle to study its *in situ* behavior—from its perspective. Since then, practitioners have worked to inspire the evolution of this concept and attendant technologies. In early years, effecting such inspiration was something of a challenge, and one often heard a sobering assessment of the potential value of animal-borne imaging in research—perhaps something along the lines of “Are you nuts? The animals will go ballistic!” Surprisingly perhaps, this has not been the case; most animals seem to care little about the unusual electronic remora appended to their backs. This unexpected finding has increasingly emboldened researchers to consider use of animal-borne imaging tools to study difficult-to-observe animal behavior and ecology.

Time and technology have marched on and what was once considered impossible or uninteresting is now edging toward conventional. Ever miniaturizing video and digital technologies have enabled smaller, more streamlined, more robust, and data-rich systems to be developed. This progression led to more deployments on more species, gathering richer information, resulting in an expanding body of statistically supported assertions of novel behaviors and ecological relationships. And today, with the ongoing revolution in solid-state imaging systems that integrate video, audio, environmental, geospatial, and perhaps even physiological data streams, we can expect a quantum leap in application of these instruments. Deployments will deliver on the promise of coherent data sets to define new baselines of basic biology that will support meaningful conservation and management considerations. We have truly just scratched the surface of the potential of this concept.

In October 2007 the National Geographic Society hosted the first “Animal-Borne Imaging Symposium” at its headquarters in Washington, DC. More than fifty researchers from around the world participated in this inaugural conference to share their experiences using imaging systems to study wild, free-ranging animal behavior and ecology. Over three days, delegates presented some 50 papers on their work and hosted two dozen additional panels, films, and student/teacher activities exploring this concept. This publication stems, in part, from that gathering. Funding from NGS, NOAA, NSF, and ONR made the meeting possible, reflecting increasing interest and engagement in this still-emerging field of research. We are coming to realize that it is ever more critical to understand the fundamental relationships species have with their habitats and how those relationships may be impacted by human activities or changing environmental conditions. We protect what we care about, and care about what we understand.

The discoveries we make using novel technologies like those described in this special issue of the *Marine Technology Society Journal* enable us to achieve that understanding. With that we can help others learn to respect and care for the extraordinary species and systems on which we ultimately all depend. With caring can come conservation, and with conservation, hope—for a future at least as rich in biological diversity, complexity, and splendor as is our world today.

Papers in this Issue

Jerry Kooyman introduces this special issue with an insightful retrospective look at “Animal-Borne Instrumentation Systems and the Animals that Bear Them: Then (1939) and Now (2007).” He provides important context for how a desire to study wild, free-ranging animals precipitated a technological revolution that ultimately led to animal-borne imaging. Animals themselves can now serve as remote ocean observation platforms carrying instruments to characterize habitat over temporal and spatial scales relevant to their basic biology and life histories. Arthur et al. provide compelling evidence that even pilot projects exploring the utility of such imaging systems can prove insightful in “Using the CRITTERCAM to Assess Green Turtle (*Chelonia mydas*) Foraging Ecology in Moreton Bay, Australia.” Adimey et al. illustrate that despite amazing ongoing technical evolution of the instruments themselves, appropriate and effective attachment mechanisms can pose major challenges to successful field research, in “The Manatee Challenge: The Feasibility of Using CRITTERCAM on Wild Manatees.” The value of animal-borne imaging data depends on documenting natural animal behavior, so it is imperative that appropriate methods be employed in handling animals and deploying instruments. This can be a non-trivial proposition.

In their paper on the “Insights into the Underwater Diving, Feeding, and Calling Behavior of Blue Whales from a Suction-Cup-Attached Video-Imaging Tag (CRITTERCAM),” Calambokidis et al. illustrate one of the compelling values of animal-borne imaging research, namely discovering new and unexpected phenomena—in this case, deep foraging behavior. To paraphrase Adimey, “the great thing about (these systems) is that they show you things you don’t know you don’t know.” Parrish and Littnan’s paper on “Changing Perspectives in Hawaiian Monk Seal Research Using Animal-Borne Imaging” describes how animal-borne imaging deployments can also provide a ‘compass’ to help focus other targeted sampling efforts relevant to habitat characterization and, ultimately, management.

Herman et al. delve more deeply into the question of whether behavior observable from the surface is consistent with behavior at depth in “When Whales Collide: CRITTERCAM Offers Insight into the Competitive Behavior of Humpback Whales on Their Hawaiian Wintering Grounds” and how these new insights can impact conservation strategies for endangered species. Less endangered species may also be subjected to human-induced stresses that require attention, a subject explored by Skomal et al. in “The Use of Animal-Borne Imaging to Assess Post-Release Behavior as it Relates to Capture Stress in Grey Reef Sharks, *Carcharhinus amblyrhynchos*.” General interest papers by Auster et al. and Moore et al., while not specifically dealing with animal-borne imaging research, round out the issue with other interesting new technologies for remote marine exploration.

Our humanity rests in our humaneness, respect, and sensitivity for beings still wilder than ourselves. This special issue of the *MTS Journal* explores how one simple idea brought to fruition can help unveil the hidden lives of these magnificent creatures and, in turn, inspire us to care for the very things that sustain us all.

Animal-Borne Instrumentation Systems and the Animals that Bear Them: Then (1939) and Now (2007)

AUTHOR

Gerald Kooyman

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Introduction

There is an old proverb that says “a picture is worth 1000 words.” At the October 2007 Animal-Borne Imaging Symposium we learned that words are cheap compared to the effort to obtain images. It requires a considerable amount of time, creativity, risk, dedication, and persistence. There is almost no limit to the extreme distances to which image explorers will go—to the ends of the earth from the Arctic to the Antarctic, and everywhere else in between. In terms of risk—from free diving to place CRITTERCAMs on the dorsal fins of tiger sharks to the backs of sperm whales à la Captain Ahab with a close encounter and a short application stick. Financially, most efforts are piggybacked onto other projects, usually long-term ecological studies that make the field endeavors more economical, but still expensive. Considerable resources are committed to research and development, and National Geographic's CRITTERCAM program headed by Greg Marshall must be one of the largest and most successful.

Because of my longevity in the field of animal-borne instrumentation, I would like to review where it all began, from the simplicity of the first beginnings to the complexity of present day instruments. Much of this has been described previously in the more general context of Biologging devices (Kooyman, 2004). Here in particular I comment on the ultimate task to visualize directly what these animals are doing, or rather, letting them record what they are doing. I believe it all began about 1939 when the famous comparative physiologist P.F. Scholander, at that time young and

ABSTRACT

The history of animal-borne instrumentation is reviewed from the first basic depth gauge invented in the late 1800s, to the complex animal-borne imagery and archival systems of the present day. A major breakthrough occurred in 1964 when the first time-depth recorder was deployed on a Weddell Seal in McMurdo Sound, Antarctica. The next phase in the study of animals at sea was the use of microprocessors as archival recorders in the mid-1980s. These also were first attached to Weddell seals in McMurdo Sound. Microprocessor technology made possible the next major step of attaching a video camera housed in a submersible case (CRITTERCAM) to a loggerhead turtle. Since the 1990s the field of “Biologging” has flourished, with new additions of satellite and GPS tracking, and resulted in three major international symposiums in the past four years (2003-2007).

not so famous, was asking questions about breath-holding capacities in diving animals and conducting respiratory experiments on different kinds of aquatic birds and mammals. One of his basic questions was how deep do whales dive, and to obtain some idea he attached manometric tubes to the harpoon line used to spear fin whales. These straight, 60 cm-long, capillary copper tubes were dusted with a water-soluble dye. Under hydrostatic pressure water was forced into the tube that left a visible ring at the maximum pressure that represented the maximum diving depth of the whale. Using Boyle's gas law he calculated this maximum depth to be 350 m. This device was not new with Scholander. Similar recorders were first designed by Lord Kelvin (William Thomson) about 100 years earlier to overcome the problems of oceanographic research which relied on stopping the sailing vessel and dropping a weighted metric line. With the invention of the manometric depth recorder (i.e., capillary tube) the ship could remain under sail and save much time by allowing the weight to touch bottom, and then retrieving the line to determine the maximum compression within the capillary tube. Scholander's record for marine mammal dives remained in place for about 25 years, until Art Devries and Donald “Curly” Wohlschlag

matched that record using a Tsurumi-Seiki-Kosakusho depth gauge attached to a Weddell seal, which dived to 350 m (DeVries and Wohlschlag, 1964). Another Weddell seal broke the record the next year with the same TSK depth recorder when it dived to 600 m (Kooyman, 1966). All of these recording devices measured only the maximum depth the recorders reached. During that same year I also recorded the longest dive profile of a Weddell seal using a custom-made Time Depth Recorder (TDR). From that time forward a new perspective of how long and deep marine mammals might be able to dive and the characteristics of the dive in regard to the relationship of time and depth was established. These TDRs were bulky, heavy, and only recorded for the limit of the internal clock, which was a one-hour kitchen timer. Because of these limitations I also used manometric recorders to obtain numerous dive depths of Weddell seals and constructed the first frequency distribution of diving depths of a diving animal. These tubes were similar to those used by Scholander, whose method I discovered after much searching of the literature. I discovered the report in my own reprint collection of Scholander's classic work “Experimental investigations on the respiratory function in diving mammals and birds, 1940.” I modified

the design to use 64 cm, glass capillary tubing, with three bends to shorten the outside length of the recorder, and then wrapped it in neoprene rubber to protect it from breakage (Kooyman, 1965). Another modification was made using a coiled plastic capillary tube that was much smaller than the glass tubing, and this allowed me to attach the recorders to emperor penguins. Subsequently, a team of us attached these devices during one eventful day at Cape Crozier, Antarctica, where the birds were foraging near the ice edge. The emperor penguins set a new record for birds of 265 m (Kooyman et al., 1971), which remained in place until TDRs small enough to be attached to birds finally became available. This was not to happen for another 25 years.

The Early Years

There was still little work accomplished with marine divers from the mid-1960s to the mid-1970s. To resume studies of foraging behavior of marine mammals was a dream of mine, but there were no funds to redesign a TDR with more capability. The opportunity came in an unexpected way when Roger Gentry, then working on northern fur seals for the National Marine Fisheries Service, asked if I would join him in a Minerals Management-sponsored project to determine the effects of oil contamination on the thermal regulatory abilities of immersed fur seals. We were interested, but only if it included the foraging behavior of fur seals breeding on the Pribilof Islands. This all had to do with offshore oil exploitation of the Pribilof Shelf. The grant was approved and provided the funds to design and build, with the aid of an exceptional engineer/machinist, a TDR that would record for at least two weeks. This duration would cover the foraging cycle of a female fur seal nursing a pup. The TDR worked extremely well (Kooyman et al, 1976), and soon I had other applications that ranged from free-ranging studies of Weddell seals in the Antarctic (Castellini et al., 1992) to leatherback sea turtles in the tropics (Eckert et al., 1985). Both were the first studies of their kind. The studies helped to define the critical habitat of the species in question, and in the case of the leatherback sea turtle it was espe-

cially pertinent because of its endangered species status. Critical habitat has become an ever more important wildlife conservation issue. In addition to these, several other projects on fur seals were conducted with other collaborators. These results were eventually incorporated in a book on fur seal breeding and foraging behavior that was edited by Gentry and myself (1986).

Also in the early 1980s a joint project on the first diving studies of elephant seals was completed with a group at the University of California, Santa Cruz (LeBoeuf et al., 1986). Concurrently, Y. Naito at the National Institute of Polar Research (NIPR) was completing a new design of a very small TDR that was mechanical with the record stored on paper. Soon after, micro-processing technology was applied to the field of diving behavior, and TDRs evolved into archival recorders that logged several more variables in addition to time and depth. Roger Hill was the first to go commercial with these new and much smaller recorders, but since then several companies have produced those and other types of recorders for tracking behavior, distribution, ocean conditions, and physiological variables of all types while attached to large marine animals. For me the reduction in size of TDRs enabled me to fulfill a career-long goal of pursuing the foraging ecology and natural history of king and emperor penguins.

Attachment Technology

As animal-borne instrumentation was evolving so were methods of attachment. Harnesses were not and are not the ideal, and the epoxy and cyan acrylic glues and some specialized tapes have saved the day for long-term attachment of recorders to birds, seals and all sea turtles except the leatherback sea turtle, which until recently required a harness (Fossette et al., 2007). Whales are a special problem with their hairless, smooth and continuously sloughing skin. For the smaller dolphins that can be captured, a collar around the dorsal fin, which is often anchored with a pin through the dorsal fin, is used. For those whales too large or elusive for capture, the devices are connected to a tether anchored to the skin with a dart shot from a crossbow.

For short-term deployment on whales the preferred method is by suction cup. This procedure has been used by a variety of investigators. Never in my dreams of deploying recorders would I have thought this would be a viable method. First, because adhesion of the suction cup would not be strong enough; and second, a close approach would not be possible because of the shyness of the animal, or the timidity of the stalker. I was wrong on both counts. Some whales, such as sperm and beaked whales, are so exhausted after their dives that an extended recovery period is required as they rest at the surface. Others, such as the humpback whale, are so distracted by feeding that a small boat can approach a group shortly after the “lunge” and apply the recorder. I participated in some of these deployments this past summer (2007) and was amazed at the skill of the boat and CRITTERCAM handlers, and their success in deployment with special suction disks, the timed release, and the recovery.

CRITTERCAM

In the mid-1980s a young, athletic guy stopped by my lab to discuss his dream to deploy a camera on a large aquatic animal. This would enable him to get a better idea of the underwater life of aquatic animals from the animal's point of view. This was an attractive idea, but the supportive camera technology did not seem to be there. I don't recall my response to Greg Marshall, but no matter, CRITTERCAM and other similar camera systems are a proven success. For large animals that cannot be captured, the up-close attachment with suction disks is essential. This technology is applied to a wide variety of animals, but there are still limits. On-board video systems' size limits applicability to large animals. In addition, diving birds are too small to be a possible subject of study, unless under the exceptional conditions when they are emperor penguins diving under the isolated hole protocol in McMurdo Sound, Antarctica (Ponganis et al, 2001). Also, the shortness of the recordings and type of attachments limit their usefulness for a variety of questions that might be asked of the animals. New engineering concepts will continue in this fast devel-

oping field that will expand the application not only to marine animals, but to those on land and in the air.

Conservation

Of all technologies applied to acquiring knowledge about the environment and the animals that exist in them, imagery is the most captivating. Humans are visual animals and seeing is our most highly developed sensor of the external environment. It is not surprising that it holds the greatest interest for the public as well as for scientists. It is the major tool for developing public awareness, and it is employed in many ways not only as CRITTERCAM devices, but with hidden cameras at feeding hotspots, as well as along trails, to ROVs (Remotely Operated Vehicles) for the deep marine environment, to satellite imagery for habitat assessment, and even for the distribution of some megafauna.

Some examples are the discovery of new species, or the presence of species never seen alive before, with the use of hidden cameras in the forests of Vietnam and Burma. Even more striking is the recent book *The Deep* (Nouvain, 2007) that brilliantly illustrates many of the animals of the largest and least known ecological environment on the planet, the deep ocean. Yet, interestingly, in this environment so far from sunlight, many of the animals are highly dependent on vision to utilize the widespread presence of bioluminescence.

Education

Perhaps one of the most successful programs to reach the public in a specific way regarding the marine environment is the "CRITTERCAM Chronicles," aired as a series on PBS. Many of the Animal-Borne Imaging Symposium contributors to this volume know from the emails they have received after their segment was aired that such programs are viewed with interest by people concerned about the environment and its conservation. Whether it is through the images of CRITTERCAM, deep submersibles, or satellite images of large changes in habitat from rainforests to the Arctic Ocean, these have powerful effects on the awareness of the pub-

lic to our changing planet. It is our charge to make them effective tools to promote attitude changes and enthusiasm for the natural world.

Conclusions

1. Humans are primarily visual animals and imagery is one of the most effective tools for capturing an audience's interest and enthusiasm for a subject.
2. We value imagery greatly and will go to great lengths and expense to obtain the most informative images.
3. Images range from nano imagery to help understand the adhesive power of gecko feet (Autumn, 2007), to space imagery for a better appreciation of planet earth and wildlife populations (Barber-Meyer et al., 2007), to the marine world where marine animals are the cinematographers (Ponganis et al., 2000; Davis et al., 1999).

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Using Animal-Borne Imaging to Assess Green Turtle (*Chelonia mydas*) Foraging Ecology in Moreton Bay, Australia

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Introduction

Green turtles (*Chelonia mydas*) are endangered marine reptiles that live in the tropical and sub-tropical oceans of the world. They are primarily herbivorous, feeding on macroalgae, seagrass and mangrove fruit, depending on the foraging area (Bjorndal, 1997; Limpus and Limpus, 2000). However, two recent animal-borne imaging studies at separate sites have indicated green turtles may include a wider diversity of organisms in their diet (Heithaus et al., 2002; Seminoff et al., 2006). They are thought to forage selectively, consuming plants or parts of plants of highest nutritional value (Bjorndal, 1980; Forbes, 1994; Read and Limpus, 2002). Such inferences were derived from comparisons of available food sources and digesta in mouth contents, stomach lavage, deceased animal stomach contents and/or faecal analysis. Direct observations of foraging behaviour are rare in most marine turtle populations as human contact generally disrupts their normal behaviour.

Moreton Bay in southeast Queensland, Australia, provides an extensive foraging ground for a large population of green sea turtles. Dur-

ABSTRACT

Traditional techniques for studying green turtle foraging ecology, such as the analysis of food availability and ingested dietary material, have concluded that green turtles are primarily herbivorous but selective foragers. However, green turtles that forage during *Lyngbya majuscula* blooms are exposed to toxins produced by the cyanobacterium overgrowing the seagrass. We used the CRITTERCAM, an animal-borne imaging device, to observe green turtle foraging behavior in Moreton Bay, Australia, and to evaluate the system for assessing the impacts of *Lyngbya* blooms on green turtles. Eight large green turtles were captured while foraging on seagrass flats and each was fitted with a CRITTERCAM. The deployments yielded over 28 hours of video and associated time-depth records. Turtles swam almost continuously and rarely stopped to feed on seagrass. Six turtles were observed feeding and all six consumed gelatinous animals from the water column. This prey source was previously undocumented in the Moreton Bay green turtle population but described in other green turtle populations using the CRITTERCAM. Only one turtle was observed foraging on seagrass. The results of this study indicate that CRITTERCAM technology can provide insight into turtle diet selection and that it will be a useful tool in identifying the impacts of *Lyngbya* blooms on green turtle feeding ecology. This study has also demonstrated that turtles in Moreton Bay may have a more flexible diet than previously described, indicating they could potentially supplement their diet with alternate prey items when seagrass quality or quantity is compromised. Longer deployment times, with an initial acclimation phase, are required to more fully understand questions pertaining to feeding ecology.

ing the past decade, the intertidal seagrass flats of Moreton Bay have been subject to extensive summer blooms of a toxic cyanobacterium *Lyngbya majuscula* (Dennison et al., 1999; O'Neil and Dennison, 2005). The cyanobacterium is known to produce many biologically active compounds including Lyngbyatoxin A, a tumor-promoting and dermatitis-producing compound (Fujiki et al., 1981) that may potentially act in the aetiology of fibropapilloma tumours (Landsberg et al., 1999; Arthur et al., 2008). The incidence of fibropapilloma in immature turtles in Moreton Bay is the highest recorded at foraging sites in Australia (Limpus and Miller, 1994; Arthur et al., 2008). Green turtles appear to avoid *Lyngbya* when it is overgrowing seagrass in their foraging habitat, but may incidentally consume small amounts of the cyanobacterium that exposes them to Lyngbyatoxin A (Arthur et al., 2006; Arthur et al., 2008).

Prey selection by green turtles is poorly understood and, in general, there is a paucity of information regarding marine turtle sensory capabilities, particularly with regard to the chemical senses in foraging behavior (Bartol and Musick, 2003). Assessing behavioural ecology of wild animals is challenging when human presence may alter the natural behaviours of the study animals. Remote observational tools such as the CRITTERCAM have proved useful in studying free-ranging animals in their natural environment without human presence (Marshall, 1998).

The objectives of this pilot study were threefold: 1) to evaluate CRITTERCAM technology for recording green turtle foraging ecology in Moreton Bay, Australia, 2) to describe the impacts of *Lyngbya* blooms on foraging behaviour, and 3) to determine the sensory modalities of prey selection in green turtles.

TABLE 1

CRITTERCAM deployments on green turtles in Moreton Bay, Queensland, Australia, February 2007. Curved carapace length (CCL). Water temperature, depth and breaths per minute provided as the average (\pm SD). N/A – data not available. (*) turtle #8 was observed eating seagrass on one occasion.

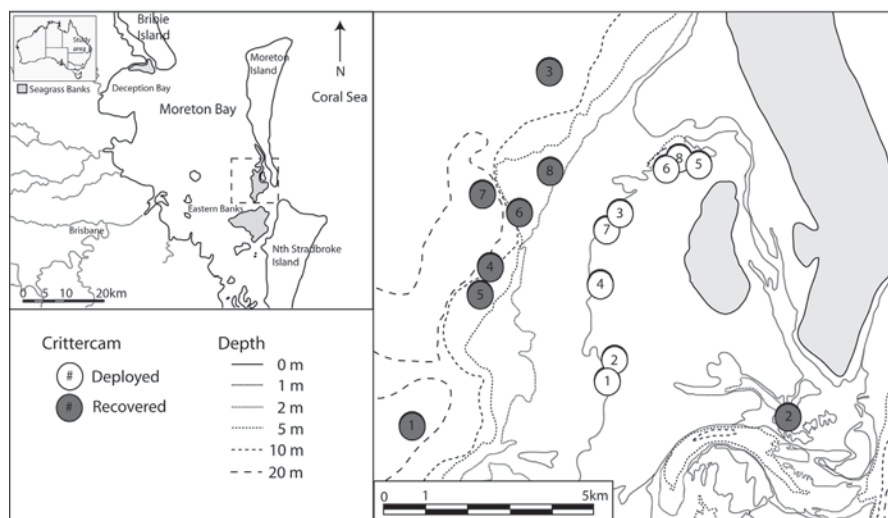
Deployment	Sex	CCL (cm)	Video	Water Temp ($^{\circ}$ C)	Av depth (m)	Max Depth (m)	Av. breaths per min	Gelatinous
								items consumed
								Av. # per hr
#1	M	96.0	3 hr 55 min	27.9 (0.3)	1.26 (1.12)	5.60	1.1	0.0
#2	M	100.0	1 hr 24 min	24.8 (0.5)	1.18 (0.65)	4.62	0.8	0.0
#3	F	104.8	3 hr 56 min	25.2 (0.5)	3.12 (1.38)	11.24	0.6	6.1
#4	M	88.0	3 hr 52 min	25.8 (0.3)	2.91 (1.59)	9.49	0.5	1.0
#5	M	99.4	3 hr 53 min	25.2 (0.5)	2.50 (1.50)	13.24	0.7	0.5
#6	F	106.1	3 hr 54 min	N/A	N/A	N/A	0.4	1.3
#7	M	94.2	3 hr 52 min	24.8 (0.4)	4.53 (2.88)	11.80	0.3	1.3
#8	M	102.0	3 hr 53 min	25.5 (0.4)	4.21 (2.09)	10.51	0.5	3.6*

Methods

Green sea turtles (*Chelonia mydas*) were captured by hand using the turtle rodeo technique from a 5 m aluminium hulled custom-built vessel (Limpus, 1978) in Moreton Bay, Queensland Australia (27 $^{\circ}$ 20'S, 153 $^{\circ}$ 22'E) between 4 and 10 February 2007. All turtles were tagged, or previous tags recorded, and measured (Limpus et al., 1994). Eight turtles were fitted with animal-borne imaging devices (CRITTERCAM; National Geographic Society, USA). The system used in this study was the Gen V CRITTERCAM, weighing 1.2 kg (in air, slight positive buoyancy underwater), measuring 7.6 cm diameter by 35 cm long. These underwater video recording systems have integrated sensors to measure and record pressure (depth), water resistivity (~salinity), velocity and 3-axis accelerometry (Marshall et al., 2007). CRITTERCAMs were mounted on the second vertebral scute of the turtle using a suction cup device and orientated to overlook one side of the turtle's head and neck (Reina et al., 2005). The carapace was cleaned to remove any material that may compromise the integrity of the seal, then the suction cup was pushed down on the carapace to remove air and checked for strength of attachment. The system was programmed to start recording immediately upon deployment and record continuously for four hours or until the microprocessor memory was full. The units then detached and floated to the surface to enable recovery by VHF radio tracking and visual scanning by a boat-based recovery team. Programmed time-based detachment and a magnesium burn-wire were employed as secondary and tertiary

FIGURE 1

Study site on the eastern banks of Moreton Bay, Australia, showing CRITTERCAM deployments and recovery locations in relation to seagrass beds and bottom bathymetry.



detachment mechanisms to ensure successful detachment. Cameras were recovered and data from the deployment were downloaded (Marshall, 1998; Reina et al., 2005).

Results

A total of 28 hr, 39 mins of video footage was obtained for eight turtles (six males and two females) with curved carapace length (CCL) ranging from 88.0 to 106.1 cm. Seven of the eight cameras recorded the full capacity of video, but Crittercam #2 detached prematurely at 71 mins (Table 1).

Upon release all turtles immediately swam toward deeper water west of the intertidal seagrass beds (Figure 1) and all but one of the

turtles swam virtually continuously for the duration of the deployment (Table 2). Surface durations were short and generally < 1 sec. Regardless of the water depth, turtles remained at a relatively shallow depth of 3 to 4 m while the deepest record was only 13.24 m. Turtle #8 was the only turtle to spend a significant amount of time stationary on the bottom and appeared to be resting for most of these events (Table 2).

No *Lyngbya* was observed by researchers on the intertidal seagrass flats during this study. However, turtle #1 was stationary on the bottom on two occasions and in both instances was surrounded by large aggregations of *Lyngbya* that had drifted off the intertidal flats. The *Lyngbya* was visible and identifiable even

TABLE 2

Time budget for green turtles in terms of swimming, resting, eating, and time spent at the surface (within top 1 m of water column) in mid-water and on the bottom (bottom clearly visible 1-2 m).

Deployment	Proportion of time (%)			Proportion of time (%)		
	Swimming	Resting	Eating	Bottom	Mid-water	Surface
#1	97.1	2.9	0.0	70.8	27.3	1.9
#2	100.0	0.0	0.0	83.1	16.9	0.0
#3	98.8	0.0	2.0	15.4	84.6	0.0
#4	97.4	1.7	0.4	18.1	81.9	0.0
#5	97.4	1.7	0.4	20.8	78.4	0.9
#6	98.9	0.9	0.2	12.8	87.2	0.0
#7	99.8	0.0	0.2	43.5	56.5	0.0
#8	69.7	29.4	0.9	79.5	20.5	0.0

though the camera had swivelled away from the head, and thus it was not possible to determine any feeding behaviour.

Six of the eight turtles were recorded foraging during the deployments. Turtle #8 foraged on the bottom amongst the seagrass *Halophila spinulosa* for ~20 sec. and this was the only segment of video footage to record seagrass foraging behaviour. The remainder of feeding observations occurred in mid-water and were on gelatinous material including jellyfish and ctenophores. Out of 86 gelatinous items encountered, 54 (63%) were consumed at rates between 0.0-6.1 items per hour (Table 1). In most instances this involved a single quick ingestion as the gelatinous animal moved past in the water column; however, in one case a turtle consumed a large nudibranch, *Melibe* sp. and took several minutes biting and swallowing the nudibranch in small parts. In all instances where turtles consumed gelatinous material, they visually tracked the item through the water column before catching and swallowing the prey.

Discussion

The CRITTERCAM proved to be a useful tool for observing wild animal behaviour without human presence. In this study, turtles were observed foraging regularly on gelatinous prey not previously recognised as important in this population's feeding ecology (Brand-Gardner et al., 1999; Read and Limpus, 2002). This does, however, mirror observations of green turtles in both northern and southern Great Barrier Reef, Australia; Shark Bay, Western

Australia; and the Gulf of California, Mexico, and suggests that green turtle diets are more flexible than previously recognised (Forbes, 1994; Tucker and Read, 2001; Heithaus et al., 2002; Seminoff et al., 2006). In addition, it documents that green turtles may have a more diverse diet than previously recognised and therefore are able to feed on other dietary items when seagrass availability is limited or compromised.

The unexpected occurrence of gelatinous material in green turtle diets also helps to explain the ingestion of plastic bags in the guts of some deceased green turtles from Moreton Bay (Haines and Limpus, 2000). Plastic bags in the water column look remarkably similar to gelatinous animals and when turtles mistakenly consume them, the indigestible plastic blocks the gut, often killing the turtle (Duguy et al., 1998; Bugoni et al., 2001). Erroneously consuming plastic also suggests that turtles are making mid-water foraging selections based on visual rather than chemosensory cues. Turtles have chemoreceptor organs within the nasopharyngeal duct connecting the external nares and internal nares located on the palate (Scott, 1979). Turtles are thought to 'smell' underwater by gular pumping of water over the chemoreceptor organs (Manton, 1979; Walker, 1959). Although turtles may select food based on both visual and chemical cues (Bartol and Musick, 2003), captive leatherback hatchlings, which feed principally on jellyfish, relied primarily on visual cues when selecting food. Either visual or chemical cues presented independently can elicit increased biting behavior and orientation toward the

cue (rheotaxis), but when both cues were presented simultaneously, turtles disregarded chemical cues in the current and oriented toward the food visually (Constantino and Salmon, 2003).

Large green turtles in Moreton Bay were thought to typically feed on seagrasses, based on past examination of mouth and crop contents (Limpus and Arthur, unpublished data). During this study turtles immediately swam away from the seagrass beds where they had been presumably feeding (Figure 1) and instead fed on gelatinous prey in the water column as they swam. If video footage were obtained from longer deployments, we anticipate that turtles would re-acclimate after capture stress and return to the intertidal seagrass habitats to forage on seagrass. Turtles in Moreton Bay that have been fitted with satellite tags have demonstrated a similar 'flee' behaviour, but returned to the seagrass flats a few days later (Limpus, unpublished data). A longer deployment of the CRITTERCAM would, hopefully, quantify the relative time budgets spent foraging amongst seagrass and macroalgae in comparison to invertebrate ingestion. In addition, additional deployments would record whether foraging turtles are effected when an active bloom of *Lyngbya* is present.

This baseline work established that the CRITTERCAM will be a useful tool for addressing the impacts of *Lyngbya* blooms. The video clearly identified *Lyngbya* presence suggesting that future studies will record the proximal impacts of these cyanobacterial blooms on green turtles. However, we foresee that future deployments will require longer deployment duration (3-4 days) with delayed video start for up to 48 hours to allow the turtles to return to normal foraging behaviour on the intertidal seagrass flats. Accordingly, a secure attachment method for the required deployment duration may be epoxy or glues as used for other CRITTERCAM deployments (Marshall et al., 2007).

In summary, this pilot study demonstrated that the CRITTERCAM presents a useful solution to remotely observing foraging behaviour of green turtles in the wild without the impacts of human presence. In addition, the use of CRITTERCAMs during *Lyngbya* blooms could better assess how harmful algal blooms may

impact green turtles and identify the mechanisms by which these turtles select for or against the toxic cyanobacterium when it is abundant in their foraging habitat.

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Meeting the Manatee Challenge: The Feasibility of Using CRITTERCAM on Wild Manatees

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Introduction

The West Indian manatee, *Trichechus manatus*, includes two subspecies: the Florida manatee (*Trichechus manatus latirostris*) and the Antillean manatee (*Trichechus manatus manatus*). Both are currently listed as endangered species throughout their range. Recovery goals for this species include establishing a stable and growing population resulting in eventual downlisting or delisting the manatee (U.S. Fish and Wildlife Service, 2007).

Manatees are one of the most extensively studied marine mammals; however, human activities continue to pose threats to the recovery of this species. In April 2007, the U.S. Fish and Wildlife Service conducted a status review on the West Indian manatee. This review indicated several major threats to the manatee population in Florida, including collisions with watercraft, the potential loss of warm water, and the presence of harmful algal blooms. Additional threats include entanglement in fishery gear, habitat degradation and loss, freshwater diversions and withdrawals, and crushing or isolation by water control structures. Understanding these threats and how they impact manatees are critical for effective management practices, future decisions, and the eventual recovery of the species. Animal-borne imaging can provide very detailed and specific information on animal behavior, habitat use, and population threats.

ABSTRACT

The West Indian manatee, *Trichechus manatus*, is currently listed as an endangered species throughout its range. Threats to the subspecies in Florida include watercraft collisions, the potential loss of warm water refuges, exposure to harmful algal blooms, entanglement in fishery gear, habitat degradation, freshwater diversions and withdrawals, and the crushing or isolation caused by water control structures. A study was initiated in 2001 to investigate several of these threats and develop methods to aid in endangered species recovery needs by exploring the feasibility of using CRITTERCAM, an animal-borne imaging and data-collection device, on Florida manatees. While the actual CRITTERCAM technology was appropriate for the goals of this study, the unique morphology of the species and its variable habitat made finding a method of attachment extremely challenging. An appropriate and reliable method of attachment to the manatee is necessary for the successful application of animal-borne imaging data collection. Methods previously used successfully on other species were explored, including various combinations of suction cups and adhesives, a nylon harness and a peduncle belt with a trailing tether. Over a span of several years, captive trials and field testing determined that the peduncle belt with connecting tether was the most appropriate method of attachment. Several iterations of this design were made in order to provide the necessary functionality for ensuring productive research with the CRITTERCAM on wild manatees.

Using CRITTERCAM with Manatees

A study was initiated in 2001 to address threats and recovery actions for Florida manatees investigating the feasibility of using CRITTERCAM, an animal-borne imaging and data collection device (Marshall, 1998; Marshall et al., 2007). This technology was chosen based on its successful use with other protected marine mammal species (Baird et al., 2003; Boness et al., 2006; Bowen et al., 2002; Calambokidis et al., 2002; Littnan et al., 2004; Parrish et al., 2000; Parrish et al., 2002; Parrish et al., 2005). The purpose of this study was to address recovery needs by further investigating habitat use and wild animal behavior, specifically in response to boat traffic, entanglement events, and interactions with water control structures. The capabilities of the CRITTERCAM itself were suitable to the goals of the research; however, an appropriate method of attachment needed to be developed. The unique morphology of the manatee—sparse hairs over the entire body, no fur, rough skin that continually sloughs, and a

body that could create concave to convex posture in multiple axes by bending, posed a significant challenge for using CRITTERCAM. Criteria for attachment design were similar to those for deployment of CRITTERCAM on most other species. The attachment method should: 1) not affect natural behavior, 2) release the assembly reliably using both active and passive mechanisms, 3) maintain a reasonable angle of view, 4) float in the proper orientation after release so that the integrated VHF recovery beacon is clear of the water, and 5) be relatively simple and inexpensive. One consideration unique to manatees was the high potential for entanglement of the assembly in their aquatic environment. This required the attachment system to include a “weak-link” element that would allow the manatee to break free of the apparatus if it became entangled.

Attachment Method Development

Initial testing of all attachment methods was conducted with two captive manatees at

Mote Marine Laboratory & Aquarium (IACUC approved). The CRITTERCAM itself is cylindrical with a domed glass front and tapering tail. Different generations of CRITTERCAM were used during the course of this work, starting with a 10.2-cm-diameter-by-41-cm-long system. The first attachment attempts mounted CRITTERCAM using suction cups on the dorsum side of the manatee. Cups of a variety of shapes, sizes and materials were directly applied to the skin with the aid of either suction, hard and soft tissue bio-adhesives, marine epoxies or denture cream. Although denture cream with a large suction cup (Figure 1) held the best, this design was not reliable for attachments expected to last more than a couple of hours, therefore, application in the field was not practical.

The second design included a two-part mounting plate and a harness constructed of soft, nylon webbing wrapped around the manatees' body approximately at the mid-body position near the umbilicus (Figure 2). Plastic buckles that secured the nylon straps provided a 'weak-link' with a breaking point between 250 and 300 pounds of force, which is within the range of breaking strengths incorporated in existing manatee tag attachment devices (Rathbun et al., 1987), allowing the animals to shed the harness if it became entangled. Using a flow meter, respiratory volume was analyzed as a measure of disturbance to determine if there were significant differences in harnessed and non-harnessed

manatees; no significant difference ($p > 0.05$, $n=2$) in respiratory volume was detected.

The harness was tested in a series of field experiments ($n=9$) during the spring of 2003 in Southern Lagoon, Belize, in collaboration with another long-standing capture and instrumentation study. These efforts resulted in 11 hours of recorded video. Counter to the captive manatee trials, atypical behaviors (e.g., body slapping, high surfacing, and swimming inverted in mud for what appeared to be an attempt to dislodge the camera) for wild manatees were observed immediately after release that appeared to be attempts to remove the harness. In some cases, the animal's activity caused the harness to detach within minutes of release. For those animals that did not break the harness free within a few minutes of release, the observed atypical behaviors tapered off and typically ceased in less than ten minutes as the manatee settled down. To quantitatively assess disturbance levels beyond immediate time of release, video data was used to calculate respiration rates over five minute periods following release and 30 minutes after release. Additional comparisons were not made beyond 30 minutes due to the small sample size of deployments that lasted longer than one hour ($n=2$). Although not significant, the trends in the data indicated a reduction in breathing rates after 30 minutes when wearing the belt ($p=0.085$, $n=4$, one-tailed T-test). Despite the behavioral and respiration evidence that implied some acclimation to the harness

(beyond the recovery from capture stress), the attachment method was abandoned due to the type and prevalence of these atypical behaviors observed from the wild manatees.

In 2004 a new attachment apparatus was designed, using a peduncle belt with the CRITTERCAM mounted on a trailing tether. This design was a modification of tag attachment methods used for more than 15 years with satellite and VHF telemetry studies on manatees. This form of radio tagging has a high record of success and safety with minimal impact on natural behavior (Deutsch et al., 1998; Weigle et al., 2001; Lander et al., 2001; Deutsch et al., 2003). This approach initially had been considered; however, it was abandoned due to foreseeable complications in its ability to deploy a directed, visual data collection tool, rather than the omni-directional antenna beacon and/or receiver typically deployed with this apparatus. As other attachment methods failed to perform as needed, the tethered system was reconsidered, and testing was performed.

The primary modification to the traditional manatee tagging design was to replace the 360-degree swivel joints at either end of the tether with hinge-type joints that limited movement to the vertical plane at the point of attachment to both the belt buckle and the CRITTERCAM (Figure 3). The traditional tether also was replaced with a stiffer nylon rod tether (Figure 4). The critical function of these modifications was to limit the range of motion of the trailing and buoyant camera to ensure that

FIGURE 1

Photograph of suction cup with denture cream adhesive and dummy camera on the dorsum of a captive manatee.



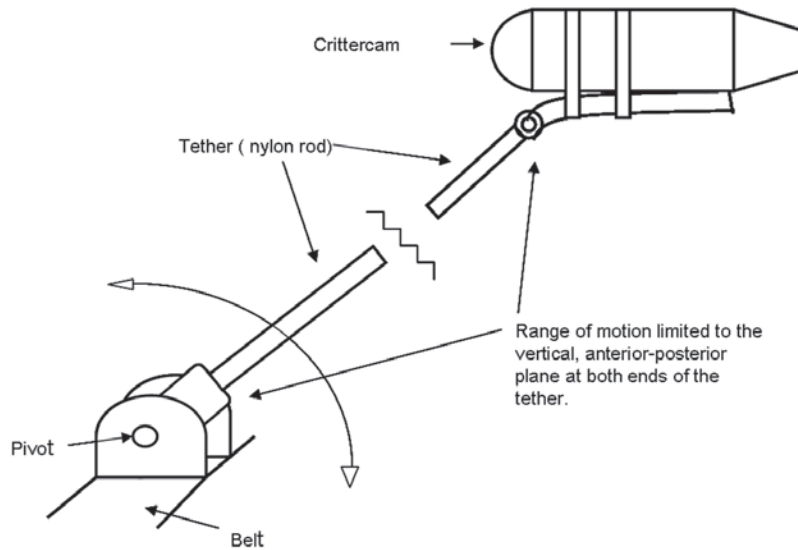
FIGURE 2

Photograph of nylon harness with dummy camera on the dorsum of a captive manatee.



FIGURE 3

The range of motion was restricted to the vertical plane at both ends of the tether to ensure stabilization with the horizontal plane of the water surface and proper orientation of the tethered CRITTERCAM towards the manatee.



the field of view of the camera remained pointing forward towards the manatee as much as possible. Having a hinged joint where the CRITTERCAM mounted to the end of the tether, rather than a fixed mount, was intended to allow the CRITTERCAM to slip free if fouling debris caught under its leading edge. The belt also contained a “weak-link” to serve as a safety release, similar to that designed for the harness.

The next modification involved the release mechanisms for the belt, tether and camera assembly. Standard procedure for CRITTERCAM attachment devices employ an active release mechanism, triggered electronically by the CRITTERCAM via an external port, and a passive mechanism of a naturally corrosive element that will function independently if the CRITTERCAM electronics fail. For economic and ecological reasons, it was preferable to recover the belt and tether, as well as the CRITTERCAM. A belt release was the most efficient way to retain the entire assembly; however, there were concerns regarding placing both release mechanisms on the belt. These included: (1) the presence of exterior wires down the outside length of the tether increased the chances of encountering snagging points in the environment, resulting in the potential for release failures, (2) ensuring proper float-

ing orientation of the assembly with the antenna recovery beacon fully emergent, and (3) entanglement hazards associated with the entire floating assembly.

Based on the above concerns and the initial belt design tested with wild manatees in 2003, the active and passive release mechanisms were located at opposite ends of the tether. The active release mechanism utilized electrically enhanced corrosive reaction in a “burn-wire” link (i.e., a thin, steel wire element of the attachment device that would corrode and break within minutes of an electrical current being passed through it in the presence of saltwater) that held the CRITTERCAM to the distal end of the tether. This release was triggered at a specified time programmed in the CRITTERCAM electronic system. The passive mechanism consisted of nuts made of a magnesium alloy, threaded onto steel bolts securing the ends of the belt around the manatees’ peduncle. The release timing of this mechanism was influenced primarily by the thickness of the nut(s) used and the salinity of the water, which was quite variable in the surrounding environment, making this method of detachment less precise than the active mechanism. Here, as is the common practice on other CRITTERCAM

FIGURE 4

Photograph of peduncle belt and tether with CRITTERCAM attached to a wild manatee.



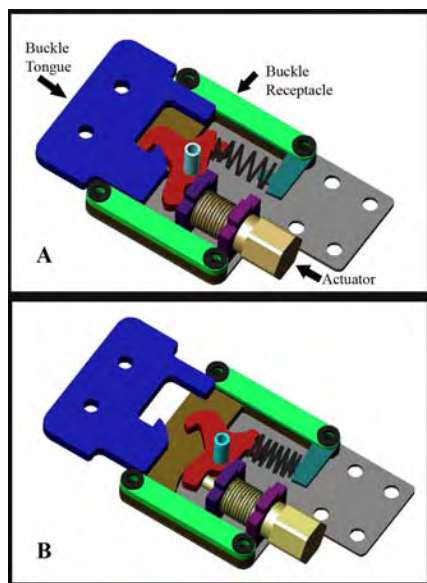
projects, the passive mechanism served as a backup release mechanism. The thickness of magnesium nut for a given deployment was selected such that it would be expected to hold longer than the release time set for the active mechanism.

Though the active release mechanism freed the CRITTERCAM from its fixed position on the end of the tether, a 2-meter length of monofilament was attached between the CRITTERCAM and the distal end of the tether, secured out of the way in a small coil during the deployment. This line was intended to simultaneously keep the belt and tether with the CRITTERCAM for recovery and to help ensure that the CRITTERCAM would float free with the VHF antenna exposed at the surface in case the rest of the apparatus became entangled in submerged debris.

In addition, the modified design included an angled polyethylene shield at the distal end of the tether to protect the lens of the CRITTERCAM from impact with foreign objects in the water. This design was tested in Belize in the spring of 2004 in 10 deployments and a total 37.5 hours of video. The primary goals of the project were

FIGURE 5

Peduncle belt buckle with electronically activated release. A) Buckle in closed and latched position, B) Protractor triggered, latching mechanism moves to allow tongue to slip free.



achieved in that manatees no longer displayed adverse behaviors associated with the use of the harness attachment method, and the camera remained in the proper orientation on the manatee, providing a useful perspective for passive observation.

Additional problems associated with the release mechanisms persisted due to the fact that both active and passive mechanisms relied on an electrolytic reaction with the surrounding water to function. Systems were deployed both in full salt water environments near offshore cays, as well as in brackish lagoons systems. This variation in salinity had a dramatic effect on the reaction time of the magnesium nuts as they deteriorated and made it difficult to accurately set the timing rate for the passive release. Both the burn-wire release and the passive release mechanism effectively cease to function in fresh water. If manatees move back into brackish or saline water, these mechanisms can resume, though in the case of the burn-wire, it will depend on whether enough charge is left in the battery. The passive release would eventually give way regardless of the water quality, but this uncertainty of recovery interfered with efficiency of the research.

To counter these challenges, it was determined that minimally the active release mechanism needed to be designed to function reliably independent of environmental conditions. Therefore, a buckle was developed, similar to a car or airplane seatbelt buckle, that would be opened by a protractor—an electrically initiated device that extends a pin upon activation—triggered at a specific time by the CRITTERCAM (Figures 5A and 5B). The buckle was integrated with the belt releasing the entire assembly simultaneously. The protractor was electronically triggered by the CRITTERCAM, necessitating running wire down the entire length of the tether. Concerns about vulnerability were addressed by using thick, waterproof wires and embedding them in a groove excavated along the length of the rod. Passive mechanisms remained the same, with the recognized susceptibility to variations in salinity, but it was believed that the reliability of the primary mechanisms (the protractor release buckle) would compensate for the less predictable passive mechanism.

The camera shield also was removed to reduce drag, as previous deployments revealed that manatees in this environment encountered less potentially damaging artifacts than originally thought. Additional streamlined foam elements were added alongside the body of the CRITTERCAM to ensure proper floatation of the entire apparatus in fresh water as well as salt water systems, particularly as CRITTERCAM would no longer be separately released from the tether.

In the fall of 2006 and the spring of 2007, additional field trials ($n=3$, $n=6$ respectively) were conducted in Belize. In a few cases, the buckle mechanism opened prematurely under the substantial and multi-directional stresses put on the apparatus by the strong movements of the manatees immediately upon release. Currently, the buckle system is being modified to reduce the internal play between the tab and buckle in order to ameliorate this problem. It is our belief a viable design has finally been developed for conducting significant animal-borne imaging research using CRITTERCAM on wild manatees.

Conclusions

Focus on the technical challenges of development and improvement of animal-borne imaging devices can sometimes overshadow the very real and critical challenges of attachment, deployment and recovery. The Remote Imaging team at National Geographic has devised and improved on a number of methods for attachment for a variety of species; some are easier than others. Manatees have posed one of the greatest challenges to date with respect to the attachment of CRITTERCAM. The distinctive morphology of the manatee created one set of obstacles; the manatee's habitat posed others, namely the high potential for entanglement in natural and artificial structures, foreign objects, debris, and the range of fresh, brackish and saline waters that they move through regularly.

A total of 28 deployments have been conducted since field trials were first initiated in Belize in 2003. Although much of this effort has been focused on testing attachment methods, images and information were obtained on foraging behavior, traveling, socializing, resting, respiration, and vocalization patterns. Perfecting the method of attachment has been a critical process that will enable this project to further research designed to address management recovery needs for not only the Florida manatee, but other discrete manatee populations throughout their range.

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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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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.

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.

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.

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).

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 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

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.

ID	Years Seen																Regions Seen						
	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	X			T	X	X				Farallones, Monterey, Ft. Bragg, S Ca.
903							X		X									T					Monterey, S Ca.
1133								X								T							S CA, Pt. Vicente to Pt. Conception
1721																T							S Ca.
1849																	T	X					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

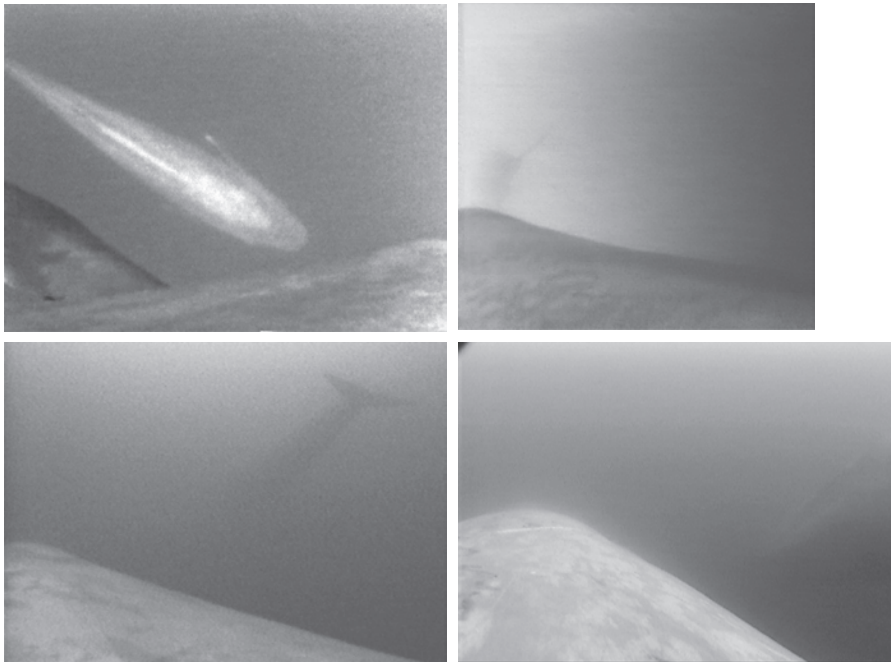
TABLE 4

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

Date/Time/On	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 shorter 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.

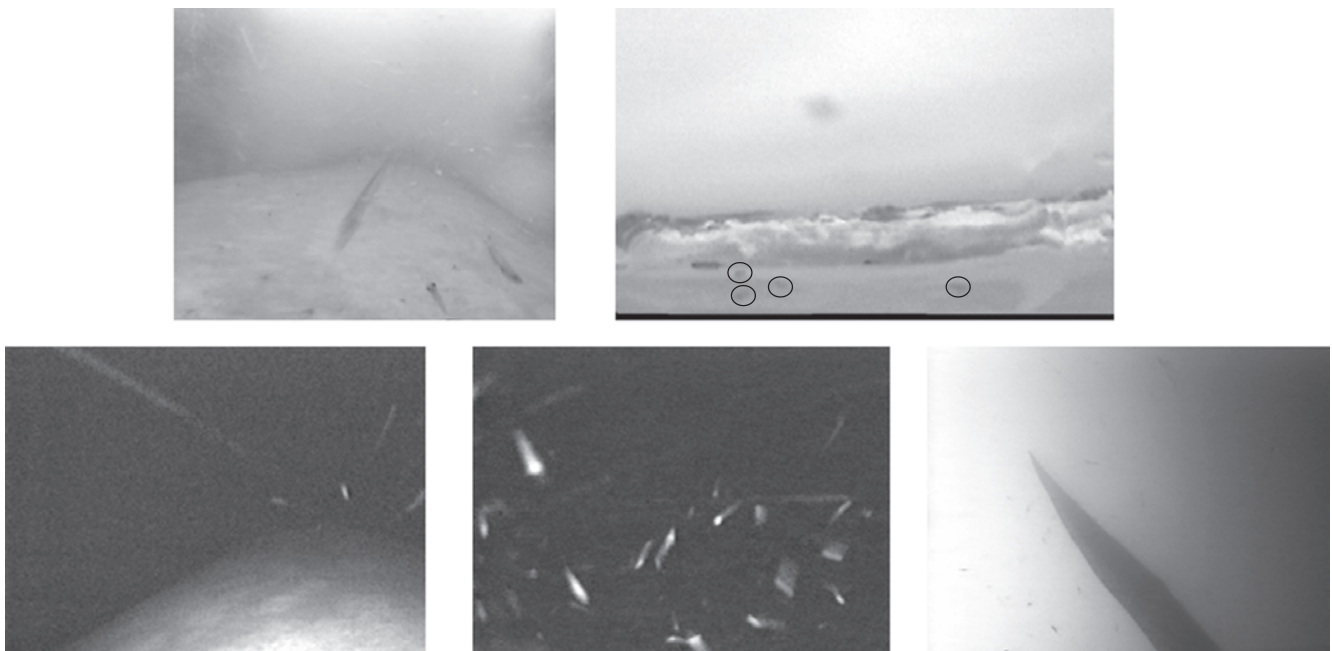


the lead was ID# 111 previously identified in 1987 and 1990 in the Gulf of the Farallones and in 1992 off both Fort Bragg and Point Arena. The trailing animal (ID# 283) was first identified in 1988 in the Gulf of the Farallones and seen in 1989 in Mexico and in 1992 in both Santa Barbara Channel and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

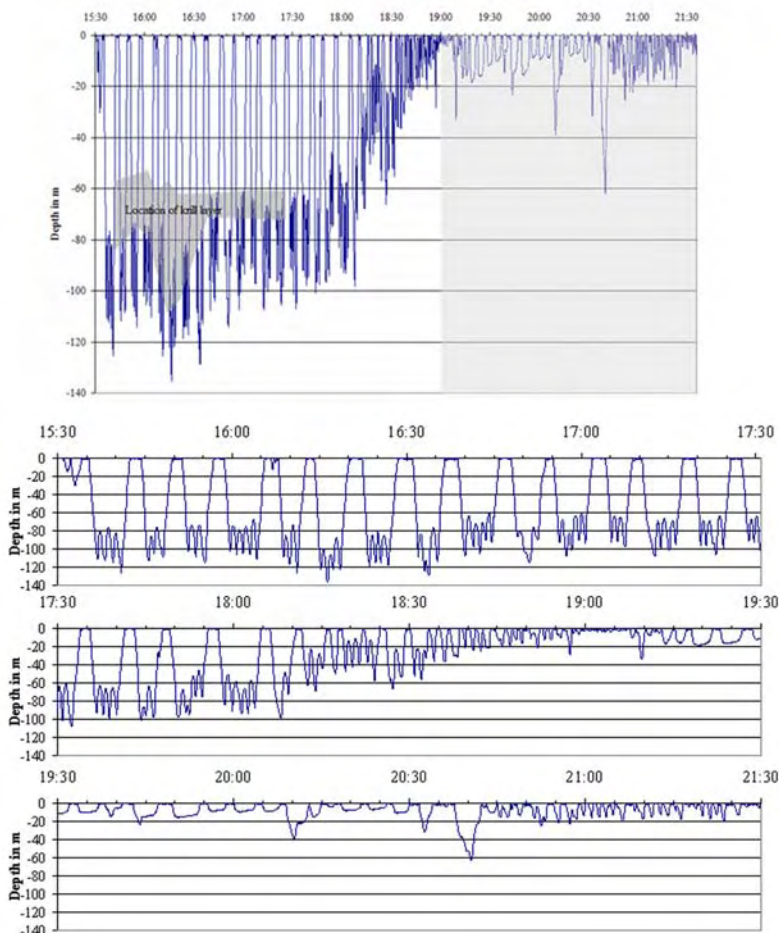
Krill, the exclusive prey of blue whales, was observed in 8 of the 11 deployments where footage was available (Table 4). Prey was primarily detectable on deployments of cameras that had the LED lights turned on (all except first three deployments) which illuminated the prey at deeper depths or when whales 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

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.



throat pleats when they became distended during a lunge feeding event.

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 just 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).

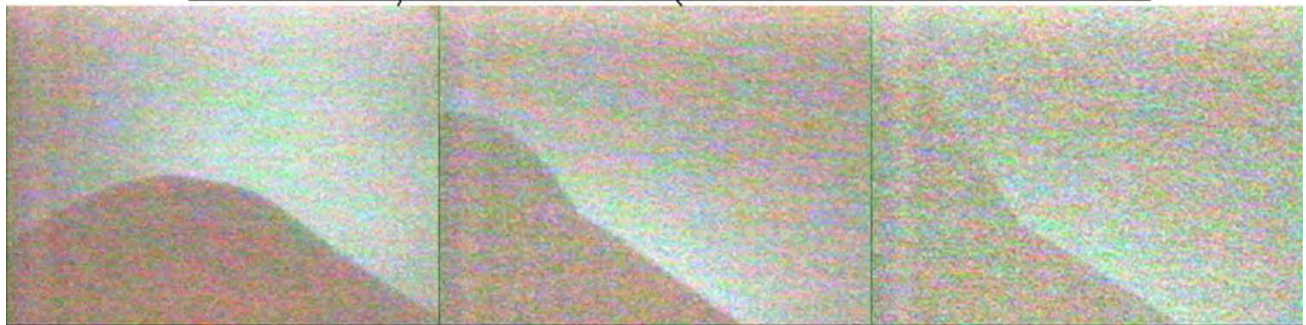
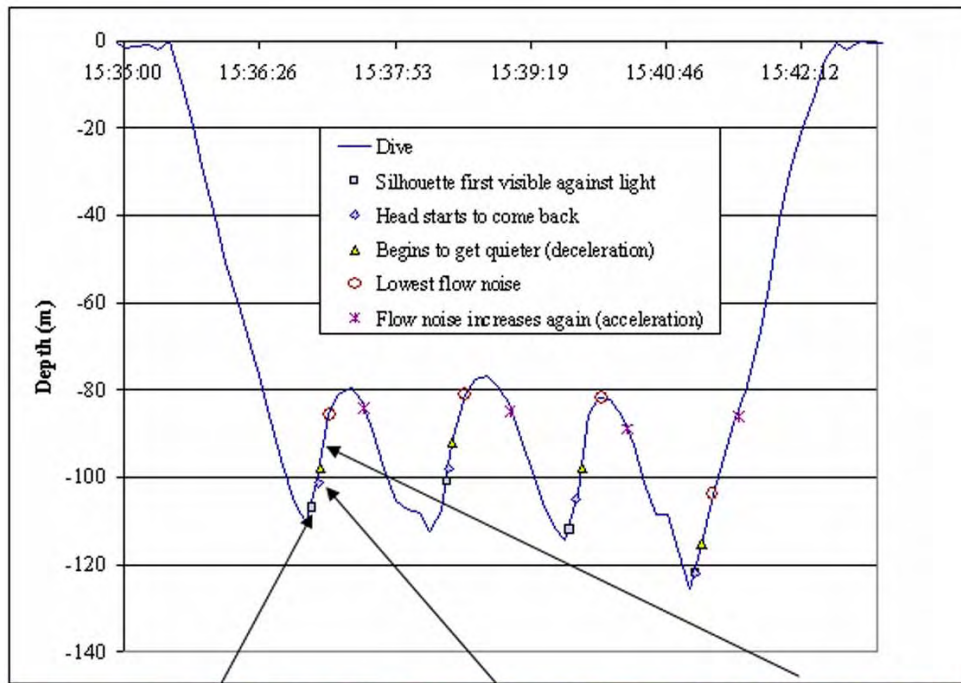
An unexpected finding of this analysis is the frequent occurrence of a lunge (head coming back followed by a rapid deceleration) on the final ascent. This final-ascent lunge is only barely discernable from the dive record itself and appears as only a slight slowing of the rate of ascent. The chronology 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.

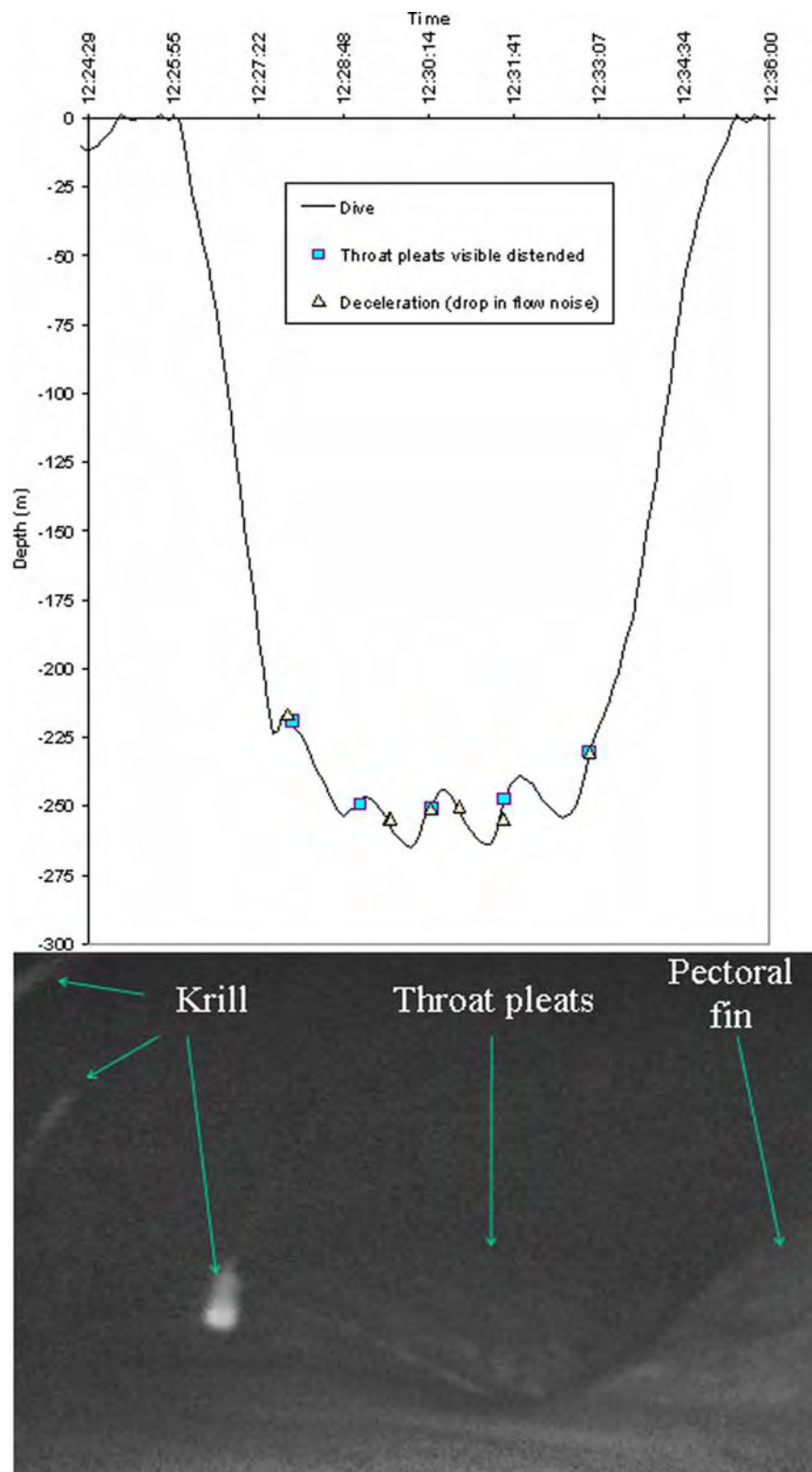
The detection of this final lunge is important when considering the energetic costs of lunge feeding. Croll et al. (2001a) demonstrate that the dive duration in blue and fin whales is shorter than expected from oxygen stores due to these lunges being energetically costly. Acevedo et al. (2002) calculate 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 propor-

tion 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.

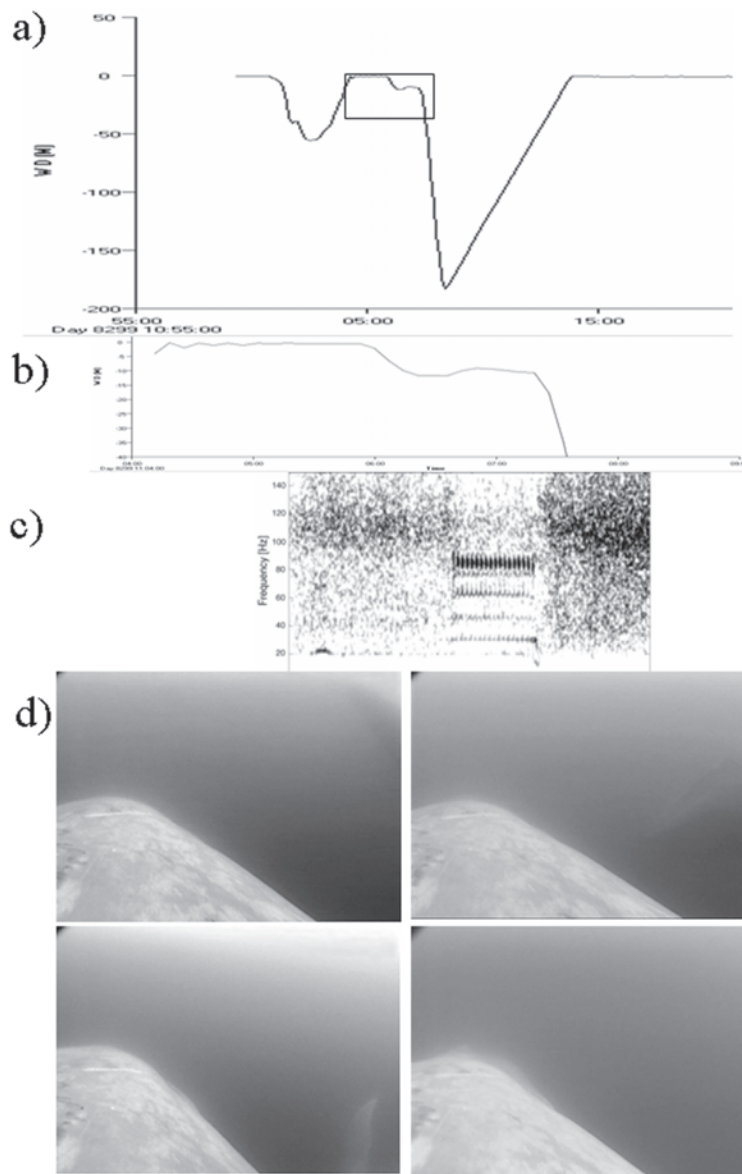
A wide range of sophisticated instruments can now be attached to whales to provide quantitative measurements of activities and behavior. Images from instruments like CRITTERCAM have proved essential for interpreting and providing a context for these measurements. Images were particularly important in 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

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Changing Perspectives in Hawaiian Monk Seal Research Using Animal-Borne Imaging

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ABSTRACT

The use of animal-borne imaging devices on the endangered Hawaiian monk seal has greatly helped understand where and how they forage. Those devices provide high-resolution data on the behavior, foraging habitat, and prey of seals, and the ecological community where they live. They have indicated that some monk seals regularly forage in mesophotic (100-300 m) and subphotic (>300 m) habitats rather than just in shallow reef habitats. The collected imagery is also helping to guide the development of further research, conservation, and management plans. Use of animal-borne imaging has resulted in substantial progress in understanding the foraging landscape of monk seals. Any refinements in this technology will certainly inform further population recovery efforts.

Introduction

Animal-borne imaging may be an effective supplemental tool in behavioral research. Indeed, it has greatly enhanced knowledge of the foraging behavior and marine habitat use of Hawaiian monk seals. Hawaiian monk seals are among the last tropical seals on Earth. Retaining similar anatomical features for 13 million years, they are now threatened with extinction. An estimated 1,200 seals live in the Hawaiian Archipelago, virtually all in the remote Northwestern Hawaiian Islands (NWHI) (Figure 1)

(Carretta et al., 2006). Since the late 1970s, a considerable amount of effort has been devoted to clarifying the demography and foraging ecology of Hawaiian monk seals using a variety of methods (Baker and Johanos, 2002; Parrish, 2000, 2002, 2005; Stewart et al., 2006). Animal-borne imaging is the latest advancement in research, resulting in important insight about the underwater activities of seals. Here, we review the historical context of monk seal research and then describe the important contributions that animal-borne imaging has made.

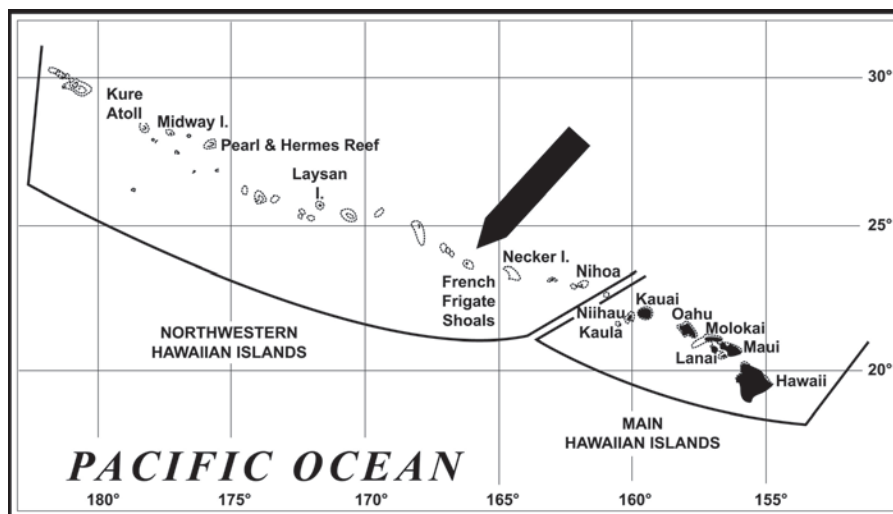
Historical Context Recovery of Monk Seals

The monk seal population in the NWHI declined substantially during the 20th century owing to direct hunting, disturbance associated with mining of guano, fishing and harvest of bird eggs, the introduction of dogs at seal colonies, and disruption from other human activities. More development and disturbance to the seals came with World War II when airfields, harbors and bases were built to support large-scale military operations. After the war the Hawaiian monk seal population was dangerously low and in need of protection. Consequently, the monk seal was designated as endangered by the U.S. government in 1976. The National Oceanic and Atmospheric Administration (NOAA) was assigned the lead responsibility for research and management of the species.

The earliest monk seal research involved direct and simple classic descriptions of the animals and their habitat by naturalists during expeditions to the remote NWHI (Kenyon and Rice, 1959; Kenyon, 1981). Though some seal species live along continental coastlines, Hawaiian monk seals live on the peaks (islands and atolls) of volcanic pinnacles that rise from the abyssal seafloor of the Pacific plate to form the Hawaiian Archipelago. Seals that populated the six primary colonies in the NWHI seemed isolated and largely restricted to their host atolls. The passing of endangered

FIGURE 1

Map of the Hawaiian Archipelago with major islands and atolls labeled. French Frigate Shoals is the primary breeding colony located in the central portion of the archipelago.



species and marine mammal protection legislation in the mid-1970s spurred an annual effort of remote field camps to monitor the seal population at each of those sites. Minimizing disturbance initially enhanced the growth of the seal population with the greatest increases at colonies where military or navigational bases closed. For example, French Frigate Shoals (FFS) Atoll, the former site of a Coast Guard station, became a Fish and Wildlife Service research station. FFS rapidly became the primary breeding colony for monk seals in the Northwestern Hawaiian Islands.

Need to Define Critical Habitat

Part of designating the Hawaiian monk seal as an endangered species was to define the critical habitat the seals needed for foraging. The area designated included reef waters (<20 m) adjacent to the sand beaches where the seals hauled out. The seals' diet was thought to be a combination of fish, cephalopods, and crustaceans based on fragments of prey found in seal scats and spews (DeLong et al., 1984). In the mid 1980s the population increase at FFS peaked (Figure 2) and in the years since has shown a continuous decline (Gilmartin et al., 1993). Understanding the reasons for that decline became the focus of research investigations in the early 1990s. Eight out of ten pups were dying before their third year (Baker

et al., 2006). There was a trap fishery for lobster and a hook and line fishery for deep-slope large bodied snappers and groupers. Both of those fisheries generally operated on the oceanic banks between the atolls that host seal colonies. There was concern that the fisheries might be competing with monk seals for fish.

Emerging telemetry and data logging technology spurred some of the first studies of movement patterns of monk seals. Prior to this, researchers had only been able to attach time depth recorders to seals to see what depths the seals visited most often (DeLong et al., 1984). With the availability of seal-mounted satellite transmitters it was determined that many of the seals were routinely making oceanic transits to neighboring banks (Abernathy, 1999; Stewart et al., 2006), movements that had previously been thought uncommon. Complementary studies with captive seals that examined the dynamics of digestion on various prey found that seals digest and pass a meal in less than eight hours, meaning that the scats found on the beach might represent prey only from the closest reefs (Goodman-Lowe, 1998; Goodman-Lowe et al., 1999). Collectively, those data suggested that seals could be feeding at distant locations on different prey types and excreting all the evidence of their meal before they got back to the beach.

Early reports that suggested reef habitats as the primary foraging habitat of endangered Hawaiian monk seals were inconsistent with data emerging from recent telemetry studies. But the spatial resolution of locations derived from satellite tracking of foraging seals was too coarse to document the use of the diverse habitats that occur over very small areas at and near atolls.

Animal-Borne Imaging

Between 1995 and 2003, deployment of CRITTERCAMS (Marshall, 1998) on Hawaiian monk seals was an annual element of studies of their foraging ecology at FFS (Figure 3). For the first time biologists were able to see the habitats the seals were visiting, the fish that lived there, and the tactics that seals used to catch them. Initial deployments focused on adult males, the most robust group of seals. The cameras were glued to the hair on the seals' backs so that the recorded images showed the area in front of the seal and its head visible in the lower central portion of the frame. The CRITTERCAM also recorded sound, and archived measurements of temperature and dive depth and duration. An on-board computer controlled camera operation based on pre-determined recording regimes. The computer could be programmed to record periodically by time interval, or only when wet, or by depth or temperature threshold. Because the foraging habitat of monk seals can range from a meter deep in fringing reefs to several hundred meters at subphotic depths, video recordings were made for 90 seconds every 15 minutes regardless of depth. In general, the CRITTERCAMS were removed from seals when they hauled out within about a week after attachment.

During the years that CRITTERCAMS were deployed on adults the cameras were reduced in size so they could be attached to juvenile seals. The juvenile segment of the seal population suffers the highest mortality and injury from shark predation and entanglement in active or derelict fishing gear (Bertilsson-Friedman, 2002; Henderson, 1984, 2001). Juvenile seals also appeared to be in poorer physical condition than adults, suggesting the limited prey availability might account for their poor condition and low survival at FFS. Emaciated seals are most commonly seen dur-

FIGURE 2

Declining trend in annual beach counts of seals and pups born at French Frigate Shoals. Photo inset is of a starving young monk seal.

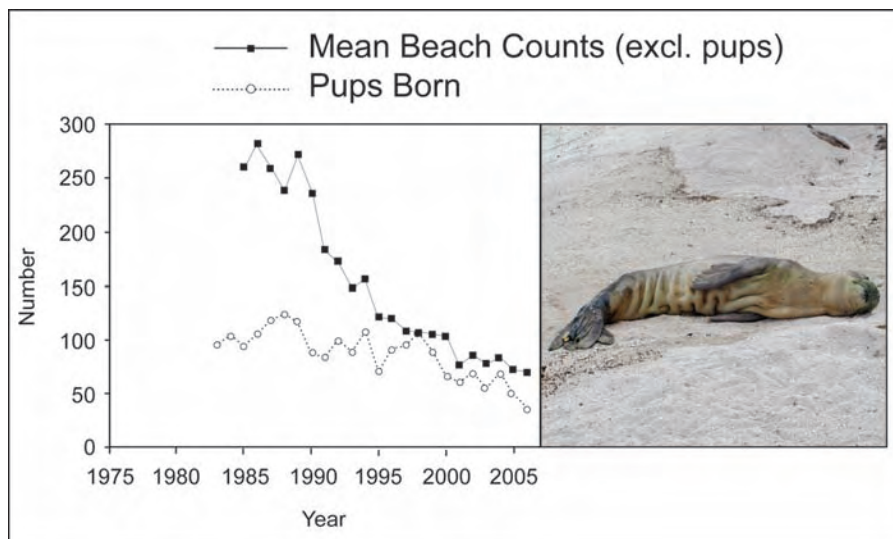
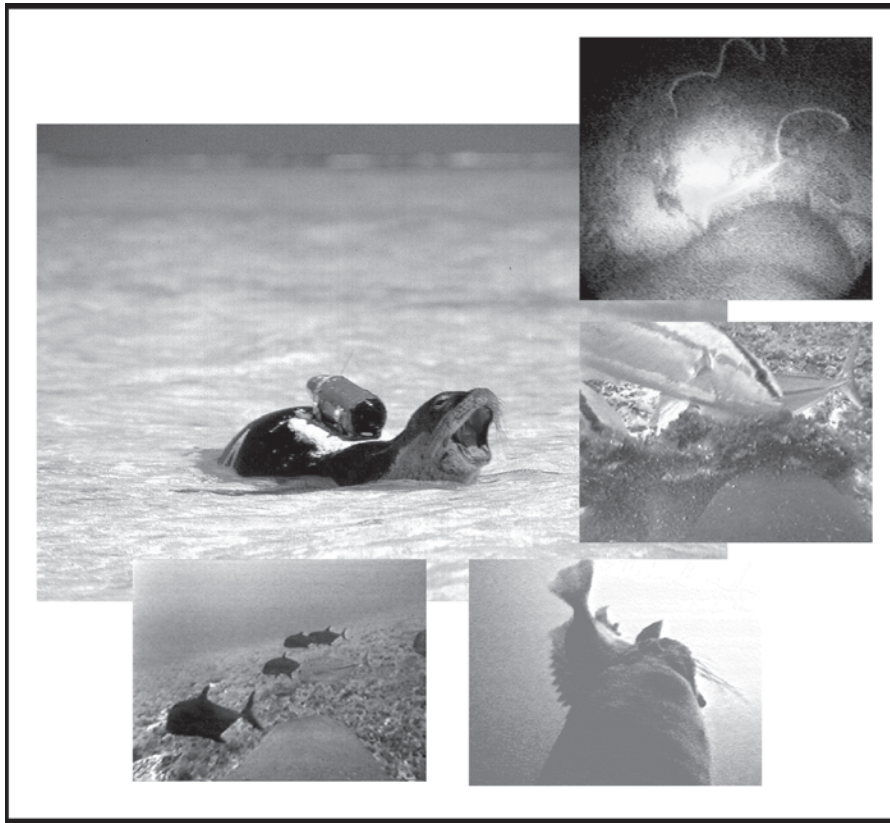


FIGURE 3

Photo of an adult monk seal fitted with the CRITTERCAM animal-borne imaging device. Insets are frame captures from the CRITTERCAM video.



ing their first year and less common by the time they are three for those that survive. The smaller CRITTERCAMs provided an opportunity to document the transition of pups from suckling to foraging independently once weaned when four to six weeks old.

Findings—Adult Males

Foraging time

Thirty five adult males were outfitted with CRITTERCAMs between 1995 and 2000. The resulting data provided new remarkable insight about the foraging behavior and foraging habitats of Hawaiian monk seals. The video images demonstrated that seals spent about half their time, when at sea, interacting with other seals, vocalizing into open water, or sleeping in underwater caves (Parrish et al., 2000). Most seals that were observed feeding traveled outside the atoll onto the deep slope rubble fields and sand terraces to find prey. Some transited through oceanic waters to neighboring banks where they foraged on summits and deep slopes that were

thought previously to be too distant to use. Seals often ate the same type of reef fish that they swam by and ignored when in shallow reef habitats. Prey items larger than 20 cm were rarely eaten (Parrish et al., 2002, 2005). Seals were seen to eat octopus, lizard fish, flatfish, sand wrasses, trigger fish, and eels.

Foraging habitat

Seals used different feeding tactics in different habitats. Some seals specialized by searching sand fields and were adept at digging out wrasses and eels by burrowing their heads deep (~45 cm) in the sand to capture the hiding fish. Other seals sequentially searched large loose rocks, sometimes a meter across and weighing more than 20 kg. They would slip their head and shoulders under to move the rock and eat prey hiding beneath. Five of the cameras deployed were equipped with night vision to document feeding activities at night. These cameras had a ring of red light emitting diodes around the lens that was enhanced for recording with

an image intensified lens. The five seals were fitted with these cameras and all that fed were seen to travel outside the atoll to find food on the deep slopes. Some feeding occurred in the shallows as the seals were en route to spending most of their time feeding on the slope. Three of the seals visited some patches of filamentous black corals on the slope that sheltered a large number of eels (Parrish et al., 2002). One seal was documented to commute between its favorite resting cave in the atoll lagoon during the day and out to the black coral patch at night and some seals that swam offshore and dove to subphotic depths of 300 m or more. Because those seals were not equipped with night vision cameras, feeding was confirmed by sounds of the seal interacting with the bottom recorded by the hydrophone. One exception was a video segment where a seal ascended into illuminated depths carrying a 30 cm fish in its mouth.

Findings—Juveniles

Nine juveniles (male and female) between the ages of 1 and 3 were instrumented with the smaller camera systems. Unexpectedly, the first year seals (FYS) did not feed in the shallows of the atoll; instead they traveled out on to the deep sand fields at 100 m where the adults feed (Parrish et al., 2005). The two- and three-year-old seals spent more time foraging in shallower habitats including searching under rocks to catch small fish hiding underneath. In one video segment a FYS was observed making an unsuccessful attempt to flip over a large rock.

Camera effects

All the CRITTERCAMs were deployed on healthy juvenile seals, so the data obtained is assumed to represent good foraging habitat and viable feeding strategies. Juveniles that were clearly emaciated couldn't be burdened with the CRITTERCAM and it is unknown what habitats and prey those seals were trying to exploit. Littnan et al. (2004) evaluated the effect of the camera attachment on the seals behavior by deploying 10 time-depth recorders (TDR) to compare dive records of the same seals during and after the CRITTERCAM deployments. A total of six TDR records were available to compare foraging behaviors with and without the camera systems. Dive variables, such as depth, du-

ration, and descent/ascent rates, did not significantly differ. Cumulative effects on foraging trip duration and percent time submerged were not detected. These results suggested the cameras were not a substantial impact to the seals for short deployments (Littnan et al., 2004). The condition and well-being of the seals was verified over successive years of follow-up surveys and all the seals were alive and in good condition (Baker and Johanos, 2002).

New Research Directions

Animal-borne imagery helped interpret data from dive recorders and satellite tags and provided a guide to invest our conventional research tools. CRITTERCAM served as a “compass” which directed how to apply or even develop new research tools. Some examples are listed below.

Sand Trawls and the Link to Changing Oceanography

The sand fields on the terraces of the deep slope were identified as an important forage grounds for the seals. Parrish et al (2005) estimated that FYS that foraged there ate around ~1.0 kg of fish each day when foraging. That quantity is consistent with the daily feed weight of juvenile seals held in captivity. Knowing this, researchers could now use small conventional bottom trawls to estimate the abundance of seal prey in the sand and develop an annual index of prey recruitment. Flounder account for most of the prey in those habitats and range between 5 and 12 cm in length. Larval flounders, which are an abundant component of the plankton, settle at 3 cm and grow quickly, attaining a size of 10 cm (the size seals feed on) in as little as 6 months. The rapid growth of flounders and other sand fish may be the best link yet identified between the abundance of monk seal prey and variable oceanography.

Re-evaluation of Satellite Telemetry

Data from the CRITTERCAMs supported findings from earlier telemetry studies and indicated a greater amount of foraging at deeper depths relative to shallow habitats (Abernathy, 1999; Stewart et al., 2006). This prompted a re-evaluation of the subphotic component of

previous satellite dive data (Abernathy, 1999). Even though deeper diving was a small percentage of the diving activity of the seals with satellite tags, the CRITTERCAM data suggested it was all foraging behavior. Review of prior satellite positions in the FFS region revealed that the subphotic dives occurred over the span of months and were made by some seals with a concentration of positions at two locations (Parrish et al., 2002). At shallower depths CRITTERCAM had shown some monk seals to target specific habitats and it was possible that the seals diving to subphotic depths had found some similar patch habitat. Surveys conducted using the Hawaii Undersea Research Laboratory's *Pisces* submersibles revealed beds of deepwater corals (Parrish et al., 2002). Similar surveys made in adjacent areas where seals didn't concentrate their subphotic foraging found no coral and were barren basalt and carbonate bottom. The seals' use of this habitat seemed analogous to the seals with the CRITTERCAM commuting to the patches of whip corals to feed on eels at shallower slope depths.

Prey Biomass Surveys

The seals' use of subphotic depths as feeding grounds prompted a survey of prey resources in the subphotic. Fish assemblages close and distant from the major seal colonies were compared and revealed regional differences in prey where low biomass corresponded with a location close to seal colonies and high biomass was distant from seal colonies (Parrish, in review). It is unknown whether this indicates prey resources are approaching carrying capacity for monk seals, or if these differences are the result of other ecological processes, or if it's some combination of both factors.

Competition with Other Apex Predators

The 42 CRITTERCAMs deployed on monk seals showed that seals were often followed by an entourage of large jacks and sharks. These predators follow the seals closely waiting for them to flush prey from hidden location, which they would then compete for (Parrish et al., in review). It is unknown how much prey seals lose to these uninvited escorts and whether this could partially explain why young seals appear to suffer the worst survivorship.

Conclusions and Future Applications

Our impressions of monk seals as provincial animals that stay close to the beaches on which they rest have clearly changed to that of an animal that travels inter-island and has an enviable knowledge of the archipelagos' submarine landscape. The change in this perspective is largely due to advances in seal-mounted instruments including dive recorders, satellite tags and, most notably, imaging devices such as CRITTERCAM. Several studies remain to better understand the ecology of the species and develop successful conservation strategies. One of the most intriguing observations has been the increase of monk seals in the main Hawaiian Islands—an area with extensive fishing. The seals exhibit better body condition than seals in the remote Northwestern Hawaiian Islands, and telemetry studies indicate that the seals don't have to travel far to obtain their daily ration of food (Littnan, Pers. comm.). Reasons for this difference are unknown. One hypothesis is that fishing in the main islands may have removed many of the jacks and sharks that compete directly or indirectly for the same prey seals eat. Continued development of seal-mounted imaging technology is essential to advance research efforts and assist the recovery efforts of the endangered Hawaiian monk.

The application of CRITTERCAMs to ecological studies of monk seals has proven extremely valuable. Despite the great success of these systems, they could be improved by increasing the functionality and capacity, shifting to solid-state technology, and decreasing the size and mass. Key additions would be: environmental and biological sensors (e.g., temperature, salinity, sophisticated acoustic recorder); high-resolution GPS system, and greater integration of movement data (i.e., dive depth, video, and location). The value of each deployment would be greatly increased by extending the battery life and amount of data that can be recorded. Shifting to solid-state technology will reduce instrument failure resulting from harsh treatment of the cameras when they are deployed (i.e., monk seals continually smashing cameras against rocks as they flip them). However, all of these additions must balance with the need for maintaining a small package that limits drag on study animals and will allow for longer deployments.

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When Whales Collide: CRITTERCAM Offers Insight into the Competitive Behavior of Humpback Whales on Their Hawaiian Wintering Grounds

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Introduction

Worldwide, humpback whales (*Megaptera novaeangliae*) migrate annually between high-latitude, summer feeding grounds and low-latitude, winter reproductive grounds (e.g., Nishiwaki, 1959; Chittleborough, 1965; Dawbin, 1966). Summers and much of the fall season are spent feeding on fish and zooplankton (e.g., *Euphasia* sp.). Winters and early spring are spent in reproductive activities, including calving, calf rearing, and a variety of behaviors that together comprise the mating system of the whales. In the North Pacific, summer feeding grounds extend from central California northward and westward along the entire rim of the North Pacific to eastern Asia. Winter reproductive grounds are limited to three principal regions: (1) the west coast of Baja California and the outlying Revillagigedo Islands in the eastern Pacific; (2) the main Hawaiian Islands in the central Pacific; and (3) the Ogasawara (Bonin) Islands and portions of the Ryukyu Islands south and southwest of Japan in the western Pacific (Nishiwaki, 1959; Baker et al., 1986; Calambokidis et al., 2001b). The Hawaiian Islands are currently the major wintering grounds for North Pacific humpback whales, with the Mexican grounds receiving

ABSTRACT

Despite years of study, the humpback whale mating system remains an enigma. Sustained observations of subsurface behavior may help reveal important components of the mating system. In 2005 and 2006, we deployed CRITTERCAM, an animal-borne imaging and data-logging tool, on humpback whales in their winter grounds. We focused our efforts on competitive groups, believed to be the epicenter of mate selection. Over 27 days of fieldwork in Maui waters we deployed 10 front- or rear-facing CRITTERCAMs on escorts (males) in competitive groups. This work revealed: (1) Five whales swimming to depths of over 150 m, with one animal diving down 298 m; (2) Instances of competitive behavior (inflated pleats, chasing) occurring along the seafloor; (3) The displacement of a primary escort (the whale closest to the female) by a challenger; (4) A detailed time budget of one principal escort maintaining his position over a 73-min observation window; (5) Threats and body strikes between secondary escorts; (6) Apparent affiliative behavior by females, including possible pectoral fin stroking of a principal escort and drafting in a principal escort's pressure wave; and (7) A secondary escort resting on the bottom while sculling its pectoral fins through the substrate, throwing up clouds of sand. In summary, CRITTERCAM allowed us to observe diving behavior and sustained micro-interactions between animals in competitive groups occurring far below the surface. Such observations can have significant bearing on interpretation of the mating system by assisting in uncovering behaviors that may be involved in mate guarding, dominance hierarchies, and female choice.

somewhat lesser numbers, and the Japanese grounds hosting relatively few whales (Calambokidis et al., 2001b). The major summer migratory link for whales visiting Hawaii is the waters of Southeast Alaska and adjoining regions (Baker et al., 1986; Calambokidis et al., 2001b). In this paper, we focus on the whales visiting the Hawaiian Islands in an attempt to gain a better understanding of their mating system, employing CRITTERCAM technology to help us visualize and record the underwater activities of the whales.

CRITTERCAM is an animal-borne, video, audio, and data-logging system (Marshall, 1998). It has been deployed previously on baleen whales in their summer feeding grounds, including blue whales (*Balaena musculus*) in Monterey Bay, California (Calambokidis et al., 2001a; Calambokidis et al., 2003) and humpback whales in southeast Alaska (Sharpe et al., 2003). Feeding ground

deployments have also been attempted on bowhead whales (*Balaena mysticetus*) in Greenland and on right whales (*Eubalaena glacialis*) in the Bay of Fundy with limited success (Kyler Abernathy, personal communication, 2007). Here, we report on the first deployments of CRITTERCAM in the winter reproductive grounds of a baleen whale—a series of successful deployments on humpback whales in waters off the island of Maui.

Despite over 30 years of observation of the whales in their winter grounds, actual mating has never been witnessed (Clapham, 2000; Pack et al., 2002). However, young calves are seen each winter season, principally between the months of January to April, and the 11-12 month gestation period of the whales suggests that mating must take place during the winter season or its shoulders (see Clapham, 2000 for a review). Our goal was to place cameras on individual humpbacks within

active social groups of adult whales that seem to be organized for mate selection, in hopes of gathering observations and data that might help reveal some key elements of the mating system, and, possibly, even mating.

The humpback whale mating system is complex and its various components have yet to be assembled into an integrated view of the system (cf. Herman & Tavolga, 1980; Clapham, 1996; Darling et al., 2006, for some attempts at integration). Some major components of the mating system have been identified and include exclusive parental investment by the female; a male-biased operational sex ratio in the winter grounds of about 2:1 (Herman & Tavolga, 1980; Craig & Herman, 1997); male song (Payne & McVay, 1971; Helweg et al., 1992; Darling & Berube, 2001; Darling et al., 2006); apparent male polygyny, but with paternity distributed among the males (Cerchio et al., 2005); a 2–3 year birthing interval with occasional post-partum estrus (Chittleborough, 1958); and males escorting females with or without calf, but preferring those without calf (Herman & Antinaja, 1977; Craig et al., 2002). When multiple escorts organize around a single female, the group typically travels rapidly while subsets of the males compete vigorously and aggressively through threats, chases, and direct body strikes to obtain and defend the position closest to the female (Darling et al., 1983; Tyack & Whitehead, 1983; Baker & Herman, 1984; Clapham et al., 1992).

Our efforts at CRITTERCAM placement were focused on these latter so-called *competitive* groups. Tyack and Whitehead (1983) termed the lone female in the competitive group the “nuclear animal” (NA), though we will simply refer to her here as the female. The male occupying and defending the position nearest the female and carrying out most of the displays, chases, and aggressive behaviors towards other males was called the “principal escort.” The males vying for the position occupied by the principal escort were termed “challengers.” The remaining males, those not directly competing for proximity to the female, were called “secondary escorts.” The female neither exhibits nor receives aggression.

The competitive group thus seems a likely social unit in which courtship, mate selection

by the female, and eventually mating may occur. It may also be possible that the principal escort is carrying out mate guarding, having previously mated with the female, and is now seeking to prevent others from doing so. Clapham (1996; 2000) discounts this possibility, however, suggesting that mate guarding is typically much briefer than the many hours often spent by the principal defending his role.

Unraveling the structure of the humpback mating system has been difficult in large part because of the observational challenges. The intricacies of a social group may be teased out to a degree by prolonged observations of surface or near-surface activities of the whales from vessels accompanying the groups as they travel (e.g., Mobley and Herman, 1985), but the deeper underwater activities are largely unobservable. Considering that humpbacks spend about 90% of their time in the wintering grounds underwater (Helweg & Herman, 1994), imaging their subsurface activities for relatively prolonged periods is critical to understanding their mating system. Swimmers snorkeling at the surface (e.g., Pack et al., 2002; Spitz et al., 2002) or wearing SCUBA or rebreather gear (e.g., Pack et al., 2004) can obtain relatively short-term underwater observations and video records of humpbacks. However, these types of observations are opportunistic, and any prolonged views require that the whales be slow moving or stationary.

CRITTERCAM offers a promising solution to these limitations in obtaining sustained, underwater observations. It can be used to gather continuous video records of behaviors, social interactions, vocalizations, and complementary data, including dive depths and swimming velocity. Additionally, depending on the light sensitivity of the particular cameras used, the ocean bottom may be visualized, especially in the clear waters of Hawaii and the relatively shallow seas preferred by the whales (ca. 183 m or less in waters between Maui and Lanai). Our main objective, then, was to place CRITTERCAMs (either front- or rear-facing) on the principal escort in a competitive group to enable us to view behaviors and interactions taking place involving the principal escort, the female, and the challengers. Before, during, and after CRITTERCAM placement, we sought to learn as much as possible

about the competitive group through observations from our deployment boat, including GPS location of the group, photo-identification of individuals, social roles of individuals, and, where possible and if necessary, underwater observations by a snorkeler to confirm the identity of the female.

Methods Research Effort

Fieldwork occurred in the Auau channel in the “four-island region” of the Hawaiian Islands in 2005 and 2006. This region consists principally of shallow (< 183 m) waters between the islands of Maui, Molokai, Lanai, and Kahoolawe. However, some areas, for example the center of the Pailolo channel between Maui and Molokai, drop below 183 m. During winter and spring months, the four-island region hosts one of the densest concentrations of humpback whales in the Hawaiian Islands (Herman et al., 1980; Mobley et al., 1999).

Our objective was to locate competitive groups of humpback whales and deploy CRITTERCAM on an escort (preferably the principal escort) in the group. Competitive groups were located by sight from small outboard powered boats (either a 6-m Boston Whaler or a 7-m Seaswirl Striper) and were identified by the presence of three or more adult-sized whales and the occurrence of competitive behaviors such as blocking, head lunging, linear bubble trails, and body strikes (e.g., Tyack & Whitehead, 1983; Baker & Herman, 1984). Prior to deployment of CRITTERCAM, the competitive group was closely observed to identify the various participants according to their behavioral role (e.g., female, principal escort, challengers and secondary escorts, as described earlier). We also obtained identification photographs of these individuals by using digital cameras (Canon D30 or D60) equipped with 100–300 mm zoom lenses to photograph the unique pattern on the ventral surface of a whale’s tail flukes when it dove (Katona et al., 1979). As necessary, a swimmer equipped with snorkeling gear and a video camera (Sony TRV-7) in a Jaymar customized housing was deployed to verify the sex of individuals either through the presence of a hemispheric lobe just caudal to the genital slit indicating female, or its absence

FIGURE 1

Left: Front-facing CRITTERCAM system attached to deployment pole. Center: Deployment of CRITTERCAM from 6-m Boston Whaler. Right: Successful deployment of CRITTERCAM system.



indicating male (True, 1904; Glockner, 1983). Once these tasks were accomplished, we attempted to deploy CRITTERCAM.

The CRITTERCAM System

In order to give ourselves maximum flexibility, we used both front- and rear-facing CRITTERCAM systems during our field seasons, February and March of 2005 and 2006. The CRITTERCAM systems were approximately 35 cm in length (including 15-cm-long polyurethane flotation tail foam) with an outer diameter of 7.6 cm. Each unit weighed approximately 1.2 kg in air and was slightly positively buoyant in water. Inside the waterproof housing was either a digital or analog video camera. In LP mode, maximum record-time was 124 min for a digital camera and 360 min for an analog camera. The housing was equipped with a single uncalibrated omnidirectional hydrophone connected to the microphone input of the camera (Figure 1, left).

We attached CRITTERCAM from the bow of our vessel with a suction cup device applied using a retractable pole that extended beyond the boat approximately 4 m (Figure 1, center). The suction cup was 22-cm diameter relaxed and 23-cm diameter flattened. No pressure was required to attach the cup as CRITTERCAM was applied by actively evacuating air from the suction cup shouldering the CRITTERCAM package. Compressed air from a SCUBA tank on board the vessel was directed through flexible tubing to a Venturi suction pump that pulls a vacuum in the line connected to a one-way valve in the suction cup, evacuating air from the cup and firmly emplacing the CRITTERCAM system. Once the suction cup was secured, a

release line attached to a PVC clamshell apparatus holding the CRITTERCAM was pulled. In response, the clamshell opened, the CRITTERCAM package was released from the attachment pole, and the whale swam freely away (Figure 1, right). The CRITTERCAM system was also outfitted with a VHF antenna to assist in retrieval.

Deployment and Recovery

Once the CRITTERCAM was attached, the boat remained with the targeted whale as long as possible to continue parallel observations of group activity and behavior. A VHF signal from the CRITTERCAM system occurred each time the targeted whale surfaced, enabling the boat to remain close, or to recover the system should the boat be unable to continue to follow the group (e.g., due to poor sea conditions). Once the CRITTERCAM was released from the whale

(either at a pre-programmed time of day, or when recording time completed, or because the whale's activities resulted in removing the CRITTERCAM), the device floated to the surface. The system was either retrieved visually or located and retrieved by homing on the VHF signal (32-km range) with a Yagi antenna.

CRITTERCAM field procedures were conducted under NMFS Permit Nos. 731-1504 to Robin Baird and 774-1714-01 to Southwest Fisheries Science Center in 2005, and under 707-1531-00 to The Dolphin Institute in 2006.

Results

Through 27 days of effort over two winter seasons (2005 and 2006), we achieved 10 successful CRITTERCAM deployments on principal escorts and secondary escorts (Table 1) for a

TABLE 1

Summary of successful CRITTERCAM deployments.

Deployment	Day	Year	Behavior Role*	Group Size	Deployment Duration (min)	Camera Direction
1	1-Feb	2005	PE	7	73	Front
2	8-Feb	2005	PE	8	45	Front
3	20-Feb	2005	PE	4	180	Rear
4	22-Feb	2005	SE	20	10	Rear
5	22-Feb	2005	PE or CH**	20	4	Rear
6	22-Mar	2006	PE	7	89	Front
7	24-Mar	2006	PE/SE***	7	125	Front
8	28-Mar	2006	SE	13	159	Front
9	29-Mar	2006	SE	6	49	Rear
10	29-Mar	2006	PE	6	69	Front

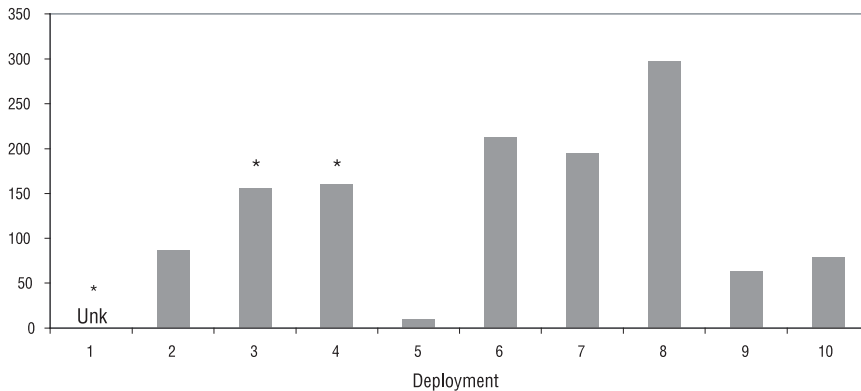
* PE = principal escort, CH = challenger, SE = secondary escort.

** The large group size and intense level of competition made it difficult to determine whether the tagged animal in Deployment 5 was the principal escort or one of many challengers.

*** The animal in Deployment 7 is denoted with two behavioral roles because it was initially the principal escort but during the deployment was displaced and became a secondary escort.

FIGURE 2

Greatest depth of dive by deployment number. Asterisk (*) indicates that the seafloor was visible on the video. For deployment 1, CRITTERCAM failed to collect depth data.



total deployment time of 13.6 hours. The duration of deployment varied greatly, often as a result of the level of competition in the group.

The CRITTERCAM systems recorded depth, as well as video data. The maximum dive depth varied greatly by animal, ranging from 10 to 298 m (Figure 2). In three instances the seafloor was visible (Deployments 1, 3, and 4). Because of the great depths recorded and the general bathymetry of the Auau Channel we suspect that the animals in deployments 6, 7, and 8 may have traveled to the seafloor as well, but we could not confirm this as the video screen was black due to the lack of light.

Video data from deployments 1 and 3 showed aggression between escorts traveling just above the seafloor. In Deployment 1, the principal escort (with CRITTERCAM attached)

charged the secondary escort. The female was also present at depth. In Deployment 3 (rear-facing camera attached to the principal escort), a secondary escort that was positioned to the side and behind the principal escort at approximately 156 meters depth (seafloor visible) inflated his pleats (Figure 3), presumably in an aggressive display similar to an inflated head lunge often seen by males at the surface (e.g., Baker & Herman, 1984).

CRITTERCAM also provided data on dive rates, as well as unexpected behavior along the seafloor. In Deployment 4, after CRITTERCAM was attached to a secondary escort, that whale immediately dove to approximately 150 m, returned to the surface, remained there for approximately 70 sec, and again traveled to the seafloor. This sequence of dives allowed us

to calculate individual descent and ascent rates (Table 2). The mean dive rate was 1.49 m/sec. A second ascent is not documented because the camera disjoined from the whale while the whale was at depth. When the whale returned to the seafloor following his second dive, he sculled his pectoral fins in the substrate for approximately 55 sec, stirring up vast plumes of sand. He then remained stationary, resting on the bottom, for approximately 35 sec. Finally, he slowly moved forward while turning slightly toward his left side, rubbing his body, and eventually the CRITTERCAM system, on the seafloor, at which point the camera detached. The camera remained buried in the sand for approximately 30 min until the bottom current freed it and it floated to the surface where we recovered it.

CRITTERCAM data also allowed for an in-depth analysis of how one principal escort maintained his role over a 73-min observation window (Figure 4). To determine this time budget we categorized the principal escort as either “with” or “away from” the female. We determined this by noting abrupt changes in direction or speed (generally from stationary to fast swim, though actual speeds could not be determined), as well as the presence of secondary escorts or the female in the video frame. These data showed that the principal escort divided his time between staying close to the female and moving away from her to engage secondary escorts and possible challengers. During each behavioral state (“with” or “away from”) we also documented the occurrence of chases/charges. Figure 5 shows that when the principal escort was away from the female he actively aggressed (engaged in a chase or charge strike) in 77% of episodes. An episode was defined as a change in state (e.g., from “with” female to “away from” female). Thus, the principal escort followed a general pattern in which he (1) maintained his position near the female, (2) left

FIGURE 3

Secondary escort inflating his pleats along the seafloor. Rear-facing CRITTERCAM is deployed on the principal escort, visible in the bottom left corner of the frame.



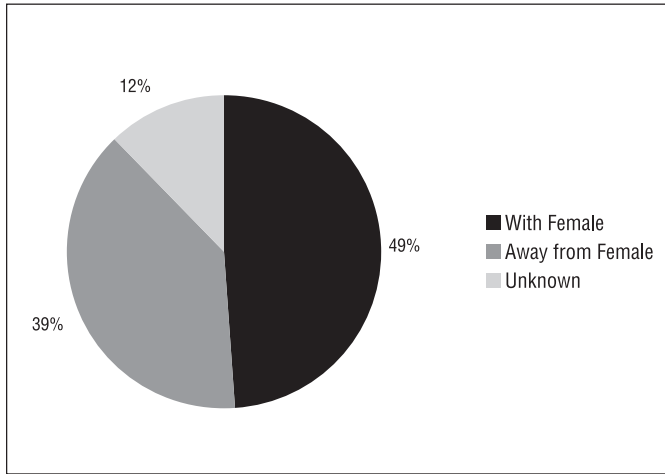
TABLE 2

Descent and ascent rates between the surface and the seafloor of the secondary escort in Deployment 4. A second ascent is not shown because the camera came off when the whale rubbed its back on the seafloor.

Time (sec)	Distance (m)	Direction of Travel	Rate of Travel (m/sec)
88	145	Descent	1.65
112	147	Ascent	1.31
100	151	Descent	1.51

FIGURE 4

Percent time one principal escort in a 7-animal competitive group spent “with” and “away from” the female over a 73-minute observation window.



the female to chase a secondary escort, and (3) returned to the female following the chase.

CRITTERCAM also allowed us to observe the continuous sequence of behaviors leading to the displacement of a principal escort by a challenger. We deployed CRITTERCAM on a principal escort that we named “Low” because of the shape of his dorsal fin (Deployment 7). This whale, 13 min earlier, had displaced a principal escort who had maintained his position close to the female for at least three hr (as determined from our boat-based surface observations). Approximately 45 min after Low’s successful displacement of the prior principal escort, we observed a new challenger, “Plateau,” displace Low (Table 3) and thus become the new principal escort. The direct aggression and ultimate resolution between the two escorts occurred over a period of 1 min and 11 sec. During this time two extended

TABLE 3

Sequence of events resulting in the displacement of the principal escort “Low” by the challenger “Plateau.”

Behavior	Start Time	End Time	Duration
Acceleration by Low	0:00:00	0:00:06	0:00:06
Strike back-to-back between Low and Plateau	0:00:06	0:00:21	0:00:15
LBT by Plateau*	0:00:33	0:00:37	0:00:04
Strike back-to-back between Low and Plateau	0:00:37	0:00:58	0:00:21
2 tail strikes by Plateau on Low’s head	0:00:58	0:01:01	0:00:03
LBT by Plateau	0:01:04	0:01:11	0:00:07
Displacement confirmed			

*LBT = linear bubble trail (after Baker & Herman, 1984)

body strikes between the animals were observed (15 and 21 sec in duration, respectively). The animals pressed against each other with such force as to tear skin. The interaction apparently concluded when Plateau delivered two tail strikes to Low’s head. After this point, based on subsequent CRITTERCAM video and boat-based observations, we determined that

Plateau had displaced Low and now maintained the position closest to the female.

CRITTERCAM, particularly rear-facing cameras, also provided data on interactions between secondary escorts. We observed direct aggression between secondary escorts (neither animal was directly defending the position closest to the female) (Figure 6, left and center)

FIGURE 5

Chases and charge strikes by one principal escort over a 73-minute observation window when he was either “with” or “away from” the female. Those instances when the affiliation was unknown have been omitted from these analyses.

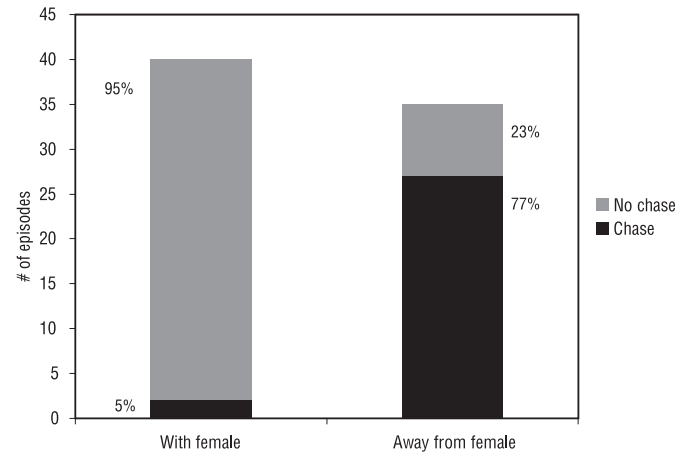


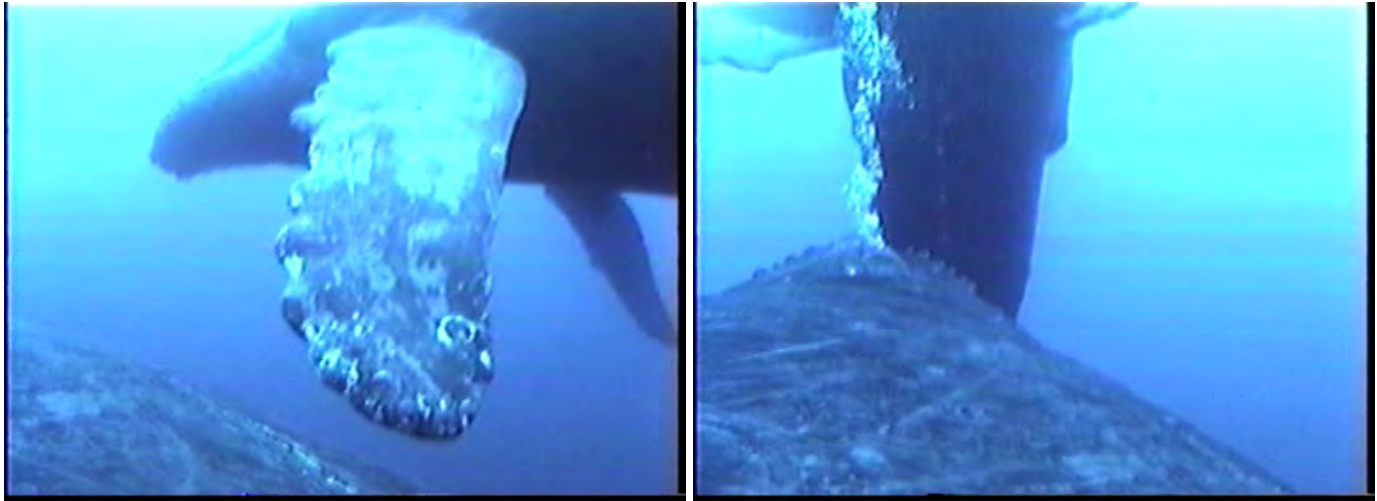
FIGURE 6

Competitive behavior between secondary escorts. Left: Two secondary escorts charge, striking each other. Center: Two secondary escorts charge, striking each other as the top animal performs a linear bubble trail. Right: Penis extrusion by a secondary escort.



FIGURE 7

Female in close proximity to principal escort. Left: The female extends her pectoral fin out towards the principal escort. Right: The female's ventral side faces the principal escort as he emits a bubble stream.



(cf. Tyack & Whitehead, 1983; Pack et al., 2002). In addition, we observed a penis extrusion (Figure 6, right), presumably a display, by one secondary escort in the presence of another when the female was not in the immediate vicinity (cf. Pack et al., 2002).

In some cases, CRITTERCAM deployed on an escort provided data on female behavior. In Deployment 1, the female and principal escort (with CRITTERCAM attached) were observed stationary and in close proximity on at least four occasions for durations ranging from 48 sec to over three min. In one instance, the female sculled her pectoral fins, moving them very close to the principal escort (Figure 7, left). In another episode, the female and principal escort were stationary, positioned rostrum-to-rostrum with the female's ventral side facing the principal escort as the principal escort emitted bubbles from his blowhole (Figure 7, right).

In Deployment 5, we observed the female maintain her position next to the principal escort in a fast-moving competitive group, though he moved his flukes more rapidly than she. The principal escort executed 24 beats over 63 seconds ($0.38 \text{ beats sec}^{-1}$), while the female executed 14 ± 3 beats in that same time period ($0.22 \pm .05 \text{ beats sec}^{-1}$). This difference in beat rate suggests that the female may have been drafting in the principal escort's pressure wave, an activity that would in theory require her to remain close to the principal escort.

Discussion

Behavioral Observations

These first deployments of CRITTERCAM on humpback whales in their winter reproductive grounds have provided new details on the underwater activities, organization, and interactions of humpback whales in competitive groups, the target social unit we chose for deployments. We have verified some classical observations and inferences made from boat observations or from brief opportunistic "looks" while snorkeling in the presence of these groups. In particular, we observed details that built upon knowledge of the general structure of the group as originally described by Tyack and Whitehead (1983). We observed strongly agonistic behaviors between secondary escorts that did not appear to be associated with challenges to the principal escort or direct efforts to gain proximity to the female. Previous descriptions of secondary escort aggression were in the context of one secondary escort challenging the principal escort (Tyack & Whitehead, 1983; Pack et al., 2002). The significance of secondary escorts positioned considerably rearward of the principal escort and the female but striking each other is not clear. We suggest it may be a way for escorts to establish hierarchies at multiple levels. Some papers have indicated that there might be collaboration between males in competitive groups, based on observations of two or three escorts joining and disaffiliating from a com-

petitive group together and not aggressing towards each other (e.g., Clapham et al., 1992; Darling et al., 2006). These arguments must be conditioned by our own findings that there can also be agonistic exchanges among secondary escorts, in addition to the well-documented agonistic behavior between the principal escort and challengers. These interactions between secondary escorts, both agonistic and possibly collaborative, need further study.

Another new finding for humpback whales on their wintering grounds was their extensive use of the complete water column, from surface to bottom. In those cases when our cameras had low-light capabilities, we clearly viewed the CRITTERCAM wearer and some of the associated whales (including the female) diving to the bottom and traveling along it. Baird et al. (2000) used time-depth recorder/VHF radio tags (without video capability) to document humpback whales off Maui diving to depths as great as 176 m. In some cases, they inferred that a tagged whale dove to the bottom by comparing whale dive depth with bottom depth as determined from the GPS location of the dive and subsequent inspection of nautical charts. In contrast to our CRITTERCAM deployments, Baird et al. (2000) had no accompanying behavioral observations at depth. The maximum dive depth we recorded using CRITTERCAM was 298 m, almost twice as deep as the maximum reported by Baird et al. The maximum dive depth on

two other deployments, 195 and 212 m, also exceeded the depths reported by Baird et al.

We also documented, for the first time, detailed behavioral records at depth. Some of the agonistic behaviors we observed at the surface often continued along the seafloor, such as chases and charge strikes and the inflation of the throat pleats. Inasmuch as CRITTERCAM provided the unique opportunity to observe bottom behavior, it raises the question of whether the absence of observations of mating may be because mating takes place at depth (cf. Pack et al., 2002).

In addition to these competitive behaviors, we also observed a secondary escort wearing CRITTERCAM traveling close to the sandy substrate and sculling its pectoral fins back and forth through the sand at approximately 150 m depth, and eventually knocking the CRITTERCAM off. We cannot determine whether the removal of CRITTERCAM was the artifact of natural behavior such as rubbing and exfoliation, or whether this was a deliberate act. The deployment on this animal also provided preliminary data on dive rates. We recorded a maximum descent rate of 1.65 m sec⁻¹ and an ascent rate of 1.31 m sec⁻¹. CRITTERCAM deployments should be further analyzed to establish more accurate dive rates, as well as dive characteristics such as those reported in Williams et al. (2000).

CRITTERCAM observations also revealed the microstructure of the behavior of the principal escort relative to challengers and to the female. A 73-min observation window of one principal escort established a pattern alternating between remaining close to the female and leaving her to chase or strike other whales that apparently offered challenges or strayed too close. Almost always (77% of the time), if the principal escort left the vicinity of the female it was to chase away other escorts. On two occasions, the principal escort initiated chases in the vicinity of the female, presumably if a challenger approached close to the female. These data suggest that the principal escort establishes a “no-swim zone” for challengers that if penetrated leads to a chase.

In another deployment, we observed a clear displacement of a principal escort by a challenger, characterized by a rapid exchange of body strikes culminating in two tail strikes

by the challenger on the head of the principal escort. All this transpired in slightly more than one minute, revealing the rapidity with which displacements can occur. Timing, level of aggression, and duration of aggression may all be key elements of male success in acquiring and maintaining the role of principal escort (cf. Baker & Herman, 1984). To establish whether rapidity is the norm requires many more observations.

The prevalence of aggressive interactions among the escorts within a competitive group understandably suggests that these males are sorting out and establishing their positions within that group. The principal escort, by maintaining and defending a position close to the female, might also be seen as demonstrating his fitness to the female as a reproductive partner. Under this scenario the female role might be viewed as passive, waiting for this sorting process to reach some resolution. However, our observations suggest that the female may exhibit choice for preferred mates. We did not observe, for example, the female actively attempting to leave or dissociate from the principal escort. Rather, some of our observations suggested that the female was choosing to remain with the principal escort. In one deployment we observed the principal escort and female stationary and close to each other while the female repeatedly extended her pectoral fin out towards the male and possibly contacted his body. During this same deployment, we also observed the principal escort and the female poised perpendicular to each other, rostrum to rostrum, the female head down, ventrum toward the male, while he remained horizontal. In another deployment, this time within a fast swimming competitive group, the female was seen apparently drafting in the pressure wave of the male, either not beating her flukes or beating them relatively slowly as the principal escort beat his flukes rapidly. These observations suggest that the female may actively solicit a male as part of the sorting process. Deakos (2002) also considered the role of females, suggesting that an adult female may slap her pectoral fins on the surface to incite competitive behavior between surrounding males, presumably to assist her in selecting the most fit mate. Given the enormous investment of the female in pregnancy,

birth, and prolonged lactation, a choice of a fitter male would seemingly increase the probability of her birthing a fitter calf.

Suggested Improvements in CRITTERCAM Technology

Our efforts have demonstrated the value of CRITTERCAM in the study of humpback whales on their wintering grounds. Most importantly, CRITTERCAM provided new views of humpback whale subsurface behavior and social interactions at depths that were largely unobservable previously. The data obtained with CRITTERCAM provided information useful for an improved understanding of the humpback whale mating system; however, mating was not observed. Improvements to the CRITTERCAM system should help reveal even more about the mating system of this species, and possibly provide opportunities for documenting mating behavior. The following improvements should be considered:

1) *Enhanced low-light capabilities.*

CRITTERCAM recorded humpback whales in the winter grounds diving to depths undocumented previously. Little light is available at those depths. On some deployments we could see the bottom clearly, but on other deployments we could not. Enhancing CRITTERCAM with low-light video recording capabilities would increase the ability to document the behavior and social interactions of humpbacks at deep depths, as well as to image their environment.

2) *Calibrated acoustics.*

Male humpback whales are well known for their production of “song” on the wintering grounds (see Helweg et al., 1992 for a review). However, the function of song remains an enigma, and little is known about their other vocalizations on the wintering grounds. Our CRITTERCAM recordings revealed so-called “social sounds” (after Silber, 1986) during some behaviors within the competitive group, especially during highly aggressive activities. Currently, CRITTERCAM is outfitted with an uncalibrated hydrophone and auto-gain recording equipment. By upgrading to calibrated hydrophones and a recording instrument with manual gain adjustments, precise acoustic measurements could be made of vocalizations in the behavioral contexts in which they occur.

3) *GPS recording and tracking abilities.* Currently, there is no way to record the track of the CRITTERCAM whale as it travels from one location to another, other than by either visually observing the whale from a nearby boat and recording a GPS of the boat's location, or by recording the GPS location of the CRITTERCAM when deployed and retrieved by the boat. Having CRITTERCAM outfitted with the ability to record a GPS/time stamp when the CRITTERCAM whale surfaces would allow for the re-creation of the whale's track, a factor important in the analysis of group dynamics and habitat use.

4) *Smaller systems.* The size of the current CRITTERCAM system is quite small in relation to the large (12-m, 40-ton) humpback whale. However, smaller, lighter cameras would allow for longer poles and thus deployments from greater distances, possibly enabling us to deploy on females or on whales in other group types (e.g., singers or whale pairs).

5) *Longer recording capabilities.* The longest deployment we obtained was 180 min. However, competitive groups may last for longer periods, even into evening hours before resolving. Thus, having longer deployment and recording capabilities for CRITTERCAM could be invaluable in obtaining sustained focal observations of the activities in individual groups.

6) *Multi-directional viewing.* When deploying CRITTERCAM, we had to choose whether we wanted a front- or a rear-view in relation to the deployment animal. Whales live in a multi-dimensional environment in which conspecifics, particularly in competitive groups, are all around them. Access to more concurrent views (at a minimum, in front and behind them simultaneously) would greatly enhance our ability to analyze the complex and enigmatic interactions of the whales.

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The Use of Animal-Borne Imaging to Assess Post-Release Behavior as it Relates to Capture Stress in Grey Reef Sharks, *Carcharhinus amblyrhynchos*

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Introduction

Sharks, like many species of fish, are exploited by extensive recreational and commercial fisheries throughout the world. In an effort to control fishing mortality and restore stocks to sustainable levels, fisheries management agencies have implemented measures that result in the release of sharks by recreational and commercial fisheries (NMFS, 2007). Such measures range from minimum sizes and bag limits to the complete prohibition on retention of various species (NMFS, 2007). To date, little is known of the post-release behavior and potential mortality associated with the catch and release of sharks (Skomal, 2006).

Regardless of fishing gear, captured fish are exposed to varying degrees of stress, which includes the cumulative impacts of physical trauma and physiological stress (Skomal, 2007). The magnitude of either stressor is dependent on capture method and handling. Physical trauma, which is characterized by external and internal tissue damage associated with the capture method, can be quantified through physical and histopathological examination of fishes after capture (Skomal, 2007). Physiological stress refers to homeostatic disruptions of the internal milieu of fish associated with high anaerobic activity, muscular fatigue, and time out of water (Skomal, 2006). Typically, changes in blood biochemistry, par-

ABSTRACT

Sharks are subjected to extensive commercial and recreational fisheries worldwide. Current management, which imposes bag limits, minimum sizes, and quotas, mandates the release of large numbers of sharks each year, but little is known of post-release behavior and survivorship. Using animal-borne imaging technology, we examined the effects of handline capture on post-release behavior of six grey reef sharks, *Carcharhinus amblyrhynchos*, at Johnston Atoll (Central Pacific) as it relates to physical trauma and physiological stress induced by capture. To quantify the extent of physical trauma, 25 grey reef sharks (including these six), ranging from 56–135 cm fork length, were examined for evidence of external tissue damage after 2.0–12.8 minutes of handline capture. In addition, these fish were blood sampled to quantify relative changes in acid-base biochemistry. Although blood lactate increased and blood bicarbonate decreased significantly relative to the duration of the capture event, blood pH did not drop significantly and there was no evidence of respiratory or metabolic acidoses. Post-release behavior, as evidenced by animal-borne imaging, included group (n=3) and solitary (n=2) activities that had been previously described in this species. A single shark exhibited aberrant behavior, which included a two-minute period of disorientation, lack of movement, and loss of equilibrium; this behavior was attributed to extensive physical trauma associated with hook damage. When coupled with quantified information relative to the capture event, we found that animal-borne imaging is a useful tool for collecting direct observations of post-release behavior in sharks so that fishery managers and researchers can better assess the impacts of various capture techniques.

ticularly acid-base status, relative to the capture event are used to provide quantitative information about the magnitude of physiological stress (Wells et al., 1986; Skomal, 2006). However, to develop meaningful measures to reduce the lethal and sub-lethal effects of catch and release, indicators of physiological stress and physical trauma must be directly linked to observations of post-release behavior and survivorship.

Standard methods for assessing post-release behavior in fishes, which typically include natural or artificial confinement (Muoneke and Childress, 1994), are simply not applicable to large fishes like sharks. To date, methods for assessing survivorship and behavior in sharks have included conventional tagging, acoustic telemetry, and high technology satellite tagging (reviewed by Skomal, 2007). While these methods provide indirect

observations that can be used to characterize behavior (e.g., depth, rate of movement), direct observations of shark interactions with the environment, conspecifics, and other animals are lacking.

Animal-borne imaging systems have been used on numerous animals, including sharks, to provide direct observations of behavior and how it relates to ecology and life history (e.g., Heithaus et al., 2001). However, no study to date has deployed an animal-borne imaging system to assess post-release behavior as it relates to capture stress. This application not only provides direct observations to fishery managers, but also allows researchers to determine if behavioral data are related to the natural ecology of the species or induced by stress. The objective of this study was to deploy an animal-borne imaging system, CRITTERCAM (National Geographic Society, Washington, DC),

to observe the post-release behavior of grey reef sharks, *Carcharhinus amblyrhynchos*, captured on handlines at Johnston Atoll in the Central Pacific. These observations were compared to levels of physical trauma and physiological stress quantified through direct observation and blood sampling, respectively.

Methods

This work was conducted at Johnston Atoll (Central Pacific, 16.735°N, 169.528°W) in 2001-2003 as part of a larger comprehensive study on the ecology of grey reef sharks in this area (P. Lobel, pers. comm). In April 2001 and 2002 and June 2003, 25 (15 males and 10 females) grey reef sharks ranging from 56-135cm fork length were caught on handline and brought immediately to the vessel for blood sampling and, in some cases, tagging before release. The handline comprised a single barbless shark hook crimped to stainless steel wire (1 m) attached to braided nylon line (8 m). To quantify the capture event, the time from first hook-up to physical handling of the shark was defined as fight time, handling time was defined as the duration of time initiated when the shark is first secured to time of release, and total fight time was the cumulative period of fight time and handling time. All sharks were quickly inspected for signs of physical injury, hook placement, and tissue damage. All hooks were cut with bolt cutters and removed from the shark prior to release.

To observe post-release behavior, six of the blood sampled grey reef sharks were randomly chosen and fitted with the CRITTERCAM animal-borne imaging system (Gen 4, National Geographic Society; see Marshall, 1998 for system details). This particular model of the CRITTERCAM differed from that described by Marshall (1998) in that it was smaller (7.6 cm diameter, 32 cm length) and contained a mini DV tape-based image recording system with 2 hr 5 min video capacity. The system was placed over the dorsal fin of each shark using a V-style clamp secured together with a programmable electronic burn-wire system and a back-up galvanic magnesium link. For maximum duration deployments, the burn-wire was programmed to release after two hours.

Blood Analysis

Once close to the vessel, each shark was secured by the tail and inverted to induce tonic immobility. Blood was drawn as quickly as possible by caudal venipuncture in volumes of 2–3 ml and processed immediately for blood gases (pO_2 and pCO_2) and pH with a portable blood gas analysis system (IRMA, International Technidyne Corporation, Edison, NJ, USA); blood bicarbonate (HCO_3^-) was derived using standard equations (Tietz, 1987). All blood gas and pH measurements were standardized to 25°C. After blood gas analysis, 5 μ l of the remaining blood was used to measure whole blood lactate with a portable blood lactate analyzer (Lactate Pro, Fact Canada Consulting Performance Ltd., North Quesnel, BC, Canada); blood lactate levels were not determined in the three sharks sampled in 2002 due to the lack of an analyzer. Changes in blood biochemistry relative to total fight time were modeled using regression analysis (Statgraphics Plus 4.0, Manugistics, Inc., Rockville, MD).

Results

Using a handline, grey reef sharks were quickly brought to the vessel and secured for blood sampling and CRITTERCAM deployment; average fight, handling, and total fight times were 4.3 min (1.0-10.0), 1.9 min (0.3-7.3), and 6.0 min (2.0-12.8), respectively (Table 1). All 25 sharks were hooked in the jaw and, with two exceptions, showed no signs of extensive tissue damage and only minor bleeding from the hook wound. In two sharks, GR0203 and GR0303, the hook point pierced the upper palette and exited the orbit of the eye causing tissue damage and bleeding from this region.

Based on regression analysis, we found that blood pH and gases (pO_2 and pCO_2) were not significantly influenced by total fight time (Figure 1A, B). However, blood lactate and bicarbonate increased and decreased significantly with total fight time, respectively, although the relationships based upon the values of the correlation coefficient ' r ' were weak (Figure 1C, D).

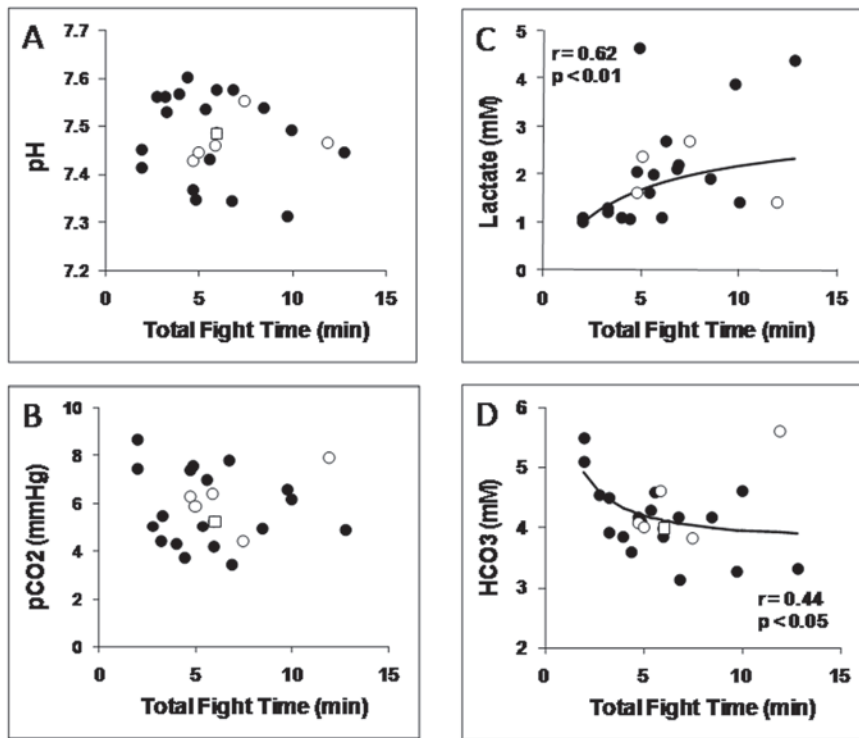
TABLE 1

Grey reef sharks blood sampled and observed with CRITTERCAM (indicated by track and behavior).

Sample	Date	FL (cm)	Sex	Time (min)			Track	Behavior
				Fight	Handle	Total Fight		
GR0101	4/3/2001	91	F	4.7	0.7	5.4		
GR0201	4/19/2002	107	F	3.1	2.8	5.9	42	Group
GR0202	4/21/2002	114	F	2.5	0.3	2.8		
GR0203	4/21/2002	124	M	5.0	1.0	6.0	20	Aberrant
GR0301	6/21/2003	91	M	2.0	3.0	5.0	58	Group
GR0302	6/22/2003	112	F	5.0	1.0	6.0		
GR0303	6/25/2003	102	M	4.0	0.4	4.4		
GR0304	6/25/2003	76	M	5.4	1.5	6.9		
GR0305	6/26/2003	71	M	1.0	1.0	2.0		
GR0306	6/26/2003	56	M	2.5	0.8	3.3		
GR0307	6/26/2003	91	F	5.2	1.6	6.8		
GR0308	6/27/2003	107	F	3.4	1.5	4.9		
GR0309	6/27/2003	117	M	4.6	7.3	11.9	71	Group/Solitary
GR0310	6/28/2003	66	F	4.0	0.8	4.8		
GR0311	6/28/2003	135	M	4.1	3.4	7.5	126	Solitary
GR0312	6/28/2003	72	F	3.0	0.3	3.3		
GR0313	6/30/2003	135	M	5.5	4.3	9.8		
GR0314	6/30/2003	124	M	2.9	2.7	5.6		
GR0315	6/30/2003	112	F	3.0	1.0	4.0		
GR0316	6/30/2003	124	M	5.0	1.3	6.3		
GR0317	6/30/2003	132	M	7.0	1.5	8.5		
GR0318	6/30/2003	122	F	10.0	2.8	12.8		
GR0319	6/30/2003	109	M	9.0	1.0	10.0		
GR0320	6/30/2003	102	M	1.0	1.0	2.0		
GR0321	7/1/2003	124	M	4.0	0.8	4.8	121	Solitary
Mean				4.3	1.9	6.0		

FIGURE 1

Linear relationships of total fight time to blood (A) pH, (B) $p\text{CO}_2$, (C) lactate, and (D) HCO_3^- in grey reef sharks; CRITTERCAM-monitored sharks are indicated with open circles and square (GR0203).



CRITTERCAM deployments ranged from 20-126 minutes (Table 1); tracks shorter than the maximum of two hours were associated with the V-clamp slipping off the relatively

small dorsal fin of this species. Grey reef sharks exhibited three behaviors (Table 1). Upon release, three sharks (GR0201, GR0301, GR0309) immediately joined a school of six

or more sharks and moved synchronously as a group through multiple depths with little horizontal movement. These sharks frequently displayed “nose to tail” following behavior during these tracks (Figure 2). One of these sharks (GR0309) remained with the group for only nine minutes and exhibited solitary behavior thereafter. Two sharks (GR0311, GR0321) remained solitary for the entire deployment, moving frequently from the surface to the bottom while covering large horizontal distances. Although these sharks encountered solitary conspecifics, neither shark initiated group behavior. A single shark, GR0203, exhibited what appeared to be aberrant behavior. Upon release, the shark moved along a nearby bulkhead, abruptly collided with the bottom rubble, and stopped, thereafter settling on the bottom and rolling on its left side as it lost equilibrium (Figure 3). The shark remained on the bottom for two minutes before resuming solitary swimming behavior. Unfortunately, the CRITTERCAM remained on this shark for only nine additional minutes before slipping off. Although this fish did not exhibit blood biochemistry that would be indicative of severe physiological stress (Figure 1), it was one of the sharks that suffered internal tissue damage associated with its right eye, which was pierced by the point of the hook (Figure 4).

FIGURE 2

Still image captured from CRITTERCAM video footage showing “nose to tail” group swimming behavior of grey reef shark GR0201.



FIGURE 3

Still image captured from CRITTERCAM video footage showing grey reef shark GR0203 settled on bottom with equilibrium loss, rostrum of shark is resting against coral rubble; note orientation of nearby fish in upper-right corner.



FIGURE 4

Still image captured from video footage of grey reef shark GR0203 prior to release; note hook point (box) piercing orbit of shark's right eye.



Discussion

Animal-borne imaging technology, like CRITTERCAM, provides a useful tool for directly observing the behavioral response of grey reef sharks to capture stress. When compared to the physical and physiological effects of the capture event, these observations indicate that the former may influence the post-release behavior of grey reef sharks more than the latter. Using imagery collected by CRITTERCAM, we conclude that grey reef sharks subjected to short fight and handling times during handline capture are likely to exhibit natural behavior upon release unless exposed to extensive physical trauma. Moreover, this capture technique did not cause significant physiological perturbation that impacted post-release behavior.

Although studies on sharks are limited, it has been demonstrated that fish subjected to exhaustive exercise associated with capture exhibit physiological disturbances that are manifested in blood biochemistry. In general, exhaustive exercise associated with capture typically causes: an increase in blood lactate levels; the marked decrease in blood pH resulting from metabolic (H^+) and respiratory (pCO_2) acidoses; and the disturbance of ionic, osmotic, and fluid volume homeostasis with hemoconcentration and increased plasma electrolytes (reviewed by Pickering, 1981; Adams, 1990; Wood, 1991; Milligan, 1996; Wendelaar Bonga, 1997; Kieffer, 2000; Skomal, 2007).

In contrast, blood acid-base status, as indicated by pH and gases, were not influenced in grey reef sharks subjected to short bouts of handline capture (Figure 1A, B). Although blood lactate, a significant end-product of anaerobic metabolism and exhaustive exercise, did increase with capture duration, blood bicarbonate levels were sufficient to buffer the potential impacts of the concomitant proton load, thereby preventing metabolic acidosis. These results differ markedly from other studies conducted on sharks and can likely be attributed to capture method as well as inherent interspecific differences in physiology. Püper et al. (1972) and Holeyton and Heisler (1978) stimulated spotted dogfish (*Scyliorhinus stellaris*) with electric shocks until fatigued and observed a significant drop in pH coupled with a rise in blood carbon dioxide and blood lactate. Cliff and Thurman (1984) examined changes in blood biochemistry in dusky sharks, *Carcharhinus obscurus*, caught on rod and reel and found that blood pH and bicarbonate declined, while carbon dioxide, metabolites (glucose, lactate), and electrolytes increased. Hoffmayer and Parsons (2001) found significant increases in blood lactate, while pH declined in serially sampled Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, after rod and reel capture. Spargo (2001) subjected sandbar sharks, *Carcharhinus plumbeus*, to 10 minutes of rod and reel angling and found significant changes in blood acid-base status. Similarly,

Skomal (2006) found significant disturbances in acid-base status in blue (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and spinner (*Carcharhinus brevipinna*) sharks subjected to rod and reel capture.

It is important to note that our ability to quantify physiological change in response to stress is hampered by our lack of baseline data. This is an inherent problem with this study and many of the aforementioned field studies during which the very act of handling and blood sampling the animal induces physiological stress. Given this methodological constraint, which is not likely to be rectified, we must acknowledge this potential limitation to the study.

Based on CRITTERCAM footage, we conclude that group and solitary swimming behaviors exhibited by five of the six grey reef sharks in this study were natural swimming patterns. Visual observations of free-swimming animals in Enewetak Atoll, Marshall Islands, allowed McKibben and Nelson (1986) to characterize three activity patterns in grey reef sharks: solitary individuals, loose aggregations, and polarized schools. By their definition, a polarized school consisted of more than two dozen closely-spaced sharks swimming just above the bottom, occasionally forming circular milling groups. Three of the sharks in the current study joined a school after release. While it was difficult to ascertain the number of sharks in each group, it appeared to be numerous individuals. McKibben and Nelson (1986) characterized lone individuals as solitary sharks usually found over shallow reefs and near lagoon pinnacles, much like the solitary behavior exhibited in this study.

We conclude that the post-release behavior of a single grey reef shark (Figure 3) that settled on the bottom for two minutes was not natural and likely associated with tissue damage from the hook (Figure 4). In general, sharks are obligate ram ventilators and there are no data to suggest that grey reef sharks differ from this physiological constraint. Images of GR0203 collected by the CRITTERCAM system clearly show that this shark collided with coral rubble, stopped swimming, settled on the bottom, and lost equilibrium. Based on the behavioral patterns reported by McKibben and Nelson (1986) and those observed in the other five sharks in this study, it is likely that this particular shark

was impacted by the capture event. The physiological biochemistry of this individual was not indicative of excessive stress, yet this particular shark was the only tracked shark that was severely wounded by the capture event. Hence, there is strong evidence to suggest that physical trauma likely caused this behavioral response.

Although acoustic telemetry and satellite-based tagging have been used to assess the impacts of physical trauma on post-release survivorship in sharks and billfishes (Domeier et al., 2003; Gurshin and Szedlmayer, 2004; Horodysky and Graves, 2005), neither method provided direct observations like those obtained in this study using animal-borne imaging. However, it should be emphasized that the relatively short duration of these tracks allows us to draw conclusions as they relate only to the acute effects of capture stress on post-release behavior. As such, the ultimate fate of GR0203 could not be determined due to the short duration of the track. However, improved methods for attachment coupled with newer models of CRITTERCAM, and other animal-borne systems, now allow for longer tracks (eight hours), which increase the utility of this approach.

Assessing the impacts of capture and handling methods on shark behavior is difficult. When coupled with direct observations of post-release behavior, qualitative and quantitative information about physiological stress and physical trauma allows researchers to examine causative factors associated with that behavior. The use of CRITTERCAM, and other animal-borne systems, provides a useful tool for collecting direct observations of post-release behavior so that fishery managers and researchers can better assess the impacts of various capture techniques.

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Camera Configuration and Use of AUVs to Census Mobile Fauna

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ABSTRACT

There is a diversity of shapes and sensor configurations used in the design of autonomous underwater vehicles (AUVs). Cameras and lighting (for both still and video imaging) are common sensor systems and have traditionally been configured to produce orthogonal images of the seafloor. Such imagery provides invaluable small-scale, high-resolution data for studies of seafloor geology and sessile invertebrate communities. However, using orthogonal imagery to census the diversity of mobile fauna has limitations caused by avoidance. A simple analysis using species-individual curves demonstrated that species richness was generally lower in surveys using orthogonal images when compared to forward-looking oblique images despite encountering the same number of individual fishes. This pattern was consistent when contrasting data from separate AUV and ROV surveys at boulder reefs in the Gulf of Maine as well as from down-looking and forward-looking cameras simultaneously collecting video imagery from a camera sled in a variety of habitats. These results indicate a need to evaluate the effects of camera configuration on the performance of abundance and diversity indicators developed from image data acquired using AUVs and other vehicles. Further, we recommend that AUV designers endeavor to accommodate oblique angles for cameras and associated lighting within vehicle design parameters in order to support missions that improve detection of mobile fauna.

The evolution of autonomous underwater vehicles (AUVs) has resulted in a range of vehicle shapes and configurations that support a diversity of sensors and control systems (Bellingham, 1997; Fornari, 2004). Increasingly, digital still or video technology is a common part of sensor packages. Cameras and lighting (for both still and video imaging) on AUVs have traditionally been configured orthogonal (i.e., downlooking or vertical) to the seafloor. This configuration has a range of benefits, in terms of image quality, post-dive analysis, and the trade-offs between vehicle design and the ability to carry camera system components.

Consistent image quality can be achieved when the variation in the distance between the camera and electronic flash (or other light source) with the seafloor are minimized, as such configurations can result in relatively even exposure across the entire image area. Most AUVs operate at higher velocities than occupied submersibles or remotely operated vehicles (ROVs) and vehicle designs attempt to maximize hydrodynamic qualities by mounting cam-

eras and other sensors within external vehicle fairings. Even for vehicles that operate at low velocities, hydrodynamic shapes maximize vehicle endurance by minimizing energy requirements needed for propulsion per unit distance.

The record of scholarly publications resulting from the use of such camera arrangements demonstrates the utility of AUVs for surveys of seafloor geology and sessile fauna (e.g., Shank et al., 2003; Singh et al. 2004; Yoerger et al., 2007). For example, the SeaBed AUV was used to conduct long linear photographic surveys of deep coral reefs off Puerto Rico where images were used to produce unique data on species composition and abundance of corals as well as associated sessile fauna in a topographically complex environment (Singh et al., 2004; Armstrong et al., 2006). In contrast, occupied submersibles and remotely operated vehicles are commonly used to census fishes and other mobile fauna in areas of complex topography (e.g., Auster et al., 2003; Trenkel et al., 2004). Obliquely mounted imaging systems maximize the probability of

encounters with species and individuals by reducing avoidance reactions due to close (or overhead) approaches (e.g., Koslow, 1995) and survey more area per unit of track line distance (Auster et al., 1989; Barry and Baxter, 1993). Little work has been done to compare the utility of different camera configurations for conducting transects to census mobile fauna. Here we provide a preliminary evaluation of the utility of using image systems on AUVs to assess the species composition of fishes in particular habitats. Species richness was used as the metric, a relatively coarse measure in relation to other metrics of interest such as abundance and size composition. Based on the results of our analysis we also discuss approaches to improve the utility of such vehicles for this task.

First, we compared the diversity of fish species that were observed at deep boulder reefs (DBRs) in Stellwagen Bank National Marine Sanctuary in the western Gulf of Maine (NW Atlantic) using both the SeaBed AUV (Figure 1 a and b) and the Kraken ROV

(a highly modified MaxRov Mk I; Deep Sea Systems International, Falmouth, Massachusetts). DBRs are discrete features composed of piled, boulder size (i.e., minimum diameter of 256 mm) rocks and are bounded by smaller diameter gravel, sand or mud sediments (sensu Auster and Lindholm, 2005). We used video transect data from ROV dives during June 2002 and non-overlapping still photographic transects from an AUV dive at the same DBR in March 2003 to produce representative species-individual curves (i.e., accumulated species richness as the number of individual fishes encountered along transects increased) from both survey systems. This approach allowed us to ignore differences in area of coverage and transect length of the different imaging systems as only fishes encountered along transects were plotted against number of species (i.e., the comparisons are independent of density). Transects with maximum and minimum species richness for both vehicles are included to

illustrate the range of variability associated with faunal distributions. Further, three AUV transects are included to illustrate the range of variation, as some transects had only a single species (i.e., Acadian redfish *Sebastes fasciatus*). Transects in both years and for both survey systems were conducted over an area primarily composed of piled boulders and boulders distributed over coarse sand such that crevices provided shelter along the boulder-sediment margin (Figure 1 c).

Figure 2 illustrates the relationship between the cumulative number of individual fish encountered along transects and the cumulative number of species. Logarithmic regression functions provided a best fit. Note that ROV dives consistently encountered a greater diversity of fishes per fish encountered along transects. While this pattern can be attributed to differences in the distribution and abundance of fishes between years, we have not seen differences of such magnitude from ROV census transects

alone. Here the disparate ranges of species-individual relationships are consistent with an effect related to vehicle-camera configuration and altitude above the bottom.

In order to better evaluate the potential role of camera configuration on census performance, we compared fish diversity and abundance data from DBR, gravel, and mud habitats using both down-looking and forward-looking video cameras mounted to a towed camera system (cameras were both 12.7 mm CCD; 3.5 mm lens; 470 horizontal lines resolution; down- and forward-looking cameras covered approximately 3.24 m² and 6.5 m² respectively at 0.75 m above the seafloor). Imagery was acquired simultaneously from both cameras and covered the same track lines during deployments (i.e., in August 2001). Here too, results demonstrate consistent underestimates of diversity by the camera in the down-looking configuration. We do note that the camera system was deployed closer to the

FIGURE 1

(a) The Seabed AUV comprises two hydro-dynamically shaped cylinders attached by vertical struts. The system can operate to 2000 m depth and conduct photographic, side-scan sonar and bathymetric surveys. A 1024 x 1280 pixel resolution camera with 12 bits of dynamic range was used for photographic imaging. Illumination was provided by a 150-W electronic flash. The flash is mounted 1.4 m aft of the camera to reduce the effects of common volume backscatter. (b) The layout of sensors on the AUV. Note that the camera is mounted at the bow of the bottom hull. (c) A typical image obtained from the SeaBed camera of boulder reef habitat and fauna. Dominant fishes are Acadian redfish (*Sebastes fasciatus*) with a single cunner (*Tautoglabrus adspersus*) at center left (from color original).

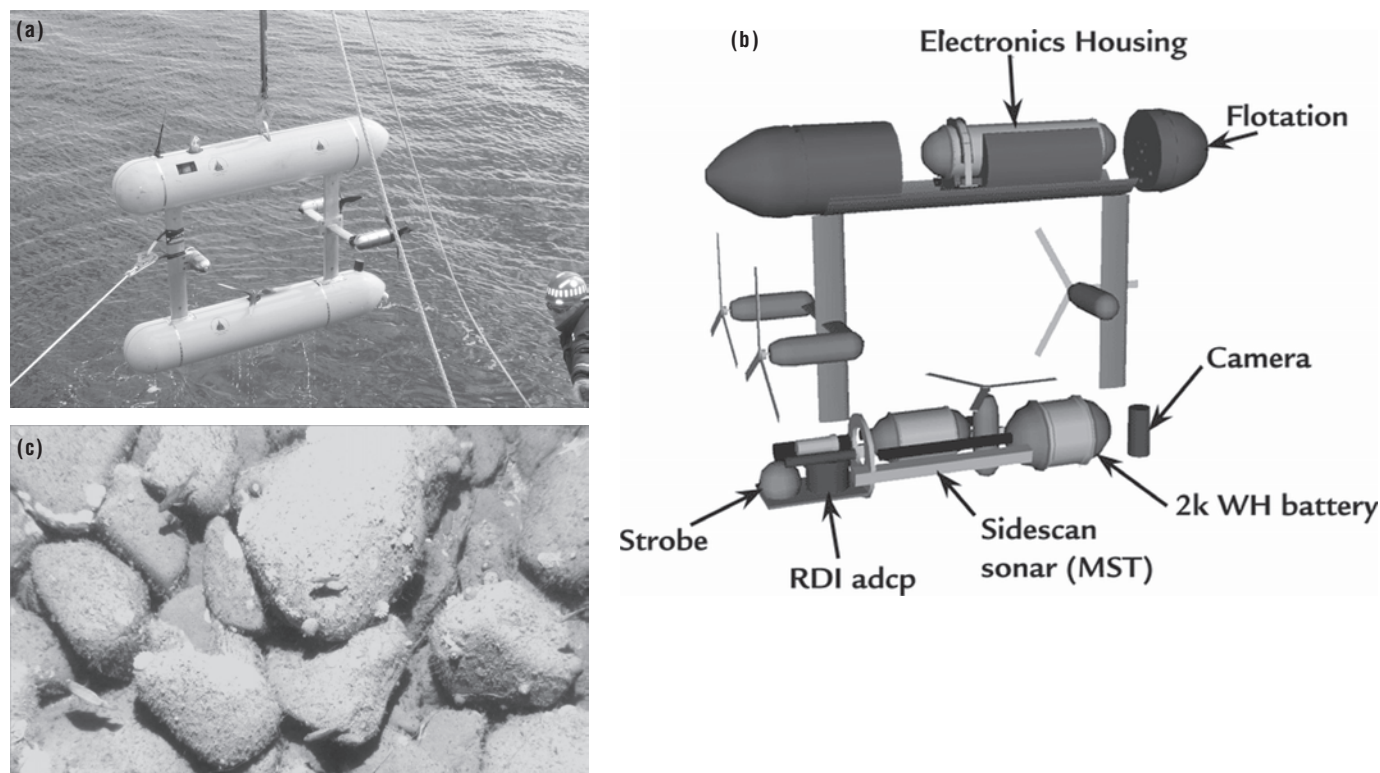
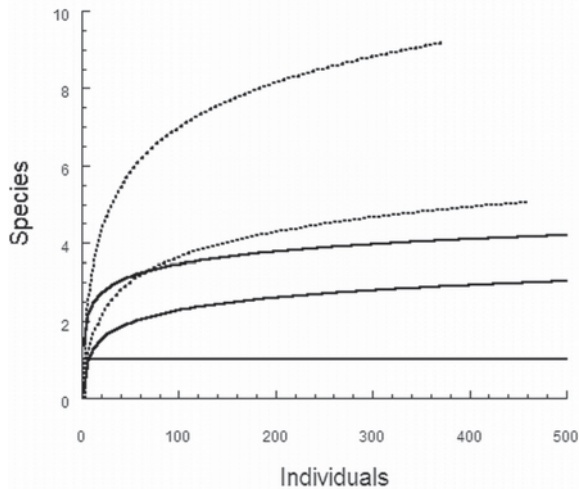


FIGURE 2

Species-individual curves from AUV (solid line) and ROV dives (dotted line) based on the regression model (i.e., $Y = m_0 + m_1 \cdot \log_{10} X$). Note that one AUV transect resulted in detection of a single species while all AUV dives detected fewer species than ROV dives. Curves from ROV dives represent the minimum and maximum species accumulation regressions from the dive series.



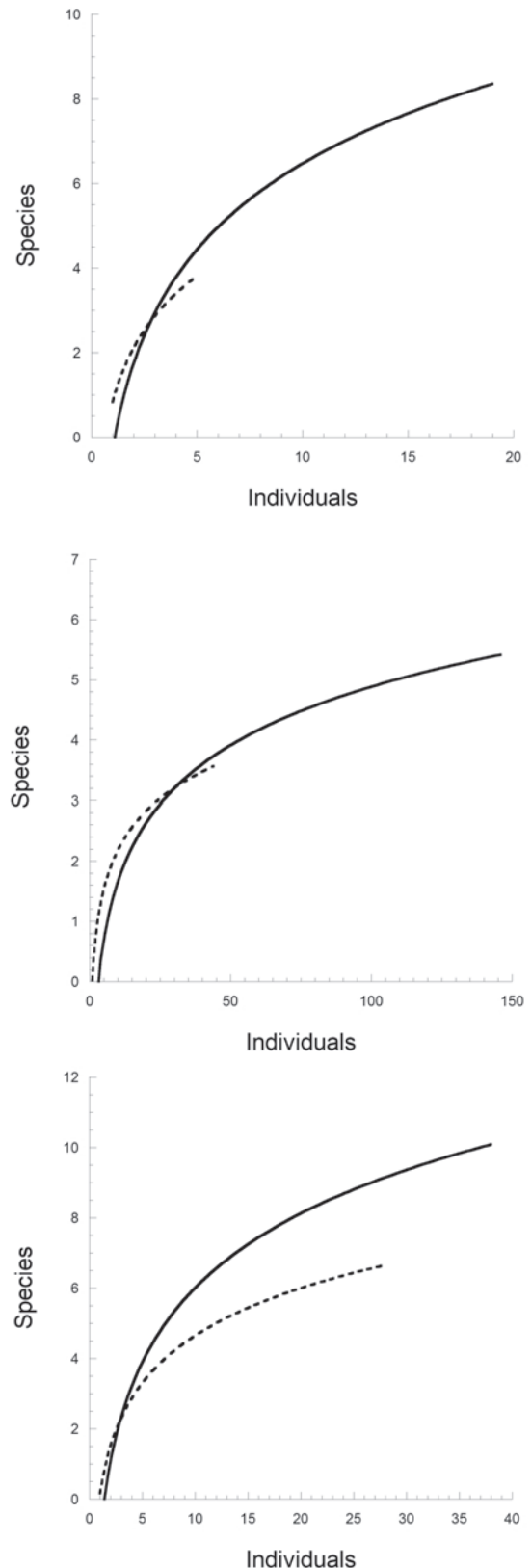
seafloor (ca. 0.75 m) rather than the nominal altitude of the SeaBed AUV (ca. 2-3 m). While altitude (distance) from individual fishes clearly is a factor resulting in avoidance reactions, these data sets exhibit the same pattern as the previous analysis.

Here we do not suggest that the relationships we describe are absolute in terms of relative differences based on camera configuration. Nor do we discount the utility of using orthogonally mounted camera configurations in a systematic fashion to produce useful data sets that are internally consistent. For example, avoidance reactions can produce the same type of response within a species and abundance indices collected by the same vehicle over space or time can produce good estimates of variation in relative abundance (Stoner et al., in press). Finally, we cannot fully discount that some differences in performance between the AUV and ROV could be attributed to variations in vehicle size, speed of approach, and noise produced by various subsystems (e.g., electronic flash and capacitors, electric thrusters, hydraulic power unit). One important difference is the use of continuous light sources on ROVs while AUVs use electronic flash pulsed at various intervals.

We do suggest that our simple analyses indicate a need to better evaluate the effects of camera configuration and altitude on the performance of abundance and diversity indicators developed from image data acquired using down-looking cameras from AUVs and other vehicles. Experiments focused on comparing survey results based on variation in camera configuration and altitude (and perhaps speed) are clearly needed. We recommend that AUV designers endeavor to accommodate oblique angles for cameras (forward or side-looking) and associated lighting within vehicle design parameters in order to support missions that improve detection of mobile fauna in the image sensor range of the vehicle and reduce the effects of avoidance.

FIGURE 3

Species-individual curves for boulder reef (top), gravel (center), and mud habitats (bottom). Regressions (as in Figure 2) are from data based on the forward-looking (solid line) and down-looking (dotted line) video cameras.



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Including Whale Call Detection in Standard Ocean Measurements: Application of Acoustic Seagliders

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Introduction

Over the past decade, detection of calls on fixed recorders deployed in remote regions of the world ocean has provided startling new perspectives on the seasonal occurrence of large whales (e.g., Moore et al., 2006; Mellinger et al., 2007). Multi-year records of blue whale (*Balaenoptera musculus*) calls are now documented from ten ocean regions including the Gulf of Alaska (Stafford, 2003), North Pacific (Watkins et al., 2000; Stafford et al., 2001), Eastern Tropical Pacific (Stafford et al., 1999), Northern mid-Atlantic (Nieukirk et al., 2004), Northeast Atlantic (Mellinger and Clark, 2003), Antarctic Peninsula (Širović et al., 2004), Scotia Sea (Širović et al., 2006), Indian Ocean (Stafford et al., 2004), eastern Antarctic coast, and southern Australian waters (Gedamke et al., 2007). Blue whale calls are arguably the 'best' signal for long-range detection, due to their low frequency (16-100 Hz), long duration (20-100s) and loudness (50 W or 188 dB re 1 μ Pa at 1 m), but calls of other species including fin, humpback, right and sperm whales were also recorded at many of these locations. Unfortunately, concomitant oceanographic measurements are often lacking in these studies, although such measures are essential to investigations of cetacean habitat selection and their role in marine ecosystems. Without a suite of standard oceanographic measurements (e.g., temperature, conductivity, optical backscatter, dis-

ABSTRACT

Over the past decade, fixed recorders have come into increasing use for long-term sampling of whale calls in remote ocean regions. Concurrently, the development of several types of autonomous underwater vehicles has demonstrated measurement capabilities that promise to revolutionize ocean science. These two lines of technical development were merged with the addition of broadband (5 Hz to 30 kHz) omni-directional hydrophones to seagliders. In August 2006, the capability of three Acoustic Seagliders (ASGs) to detect whale calls was tested in an experiment offshore Monterey, California. In total, 401 dives were completed and over 107 hours of acoustic data recorded. Blue whale calls were detected on all but two of the 76 dives where acoustic data were analyzed in detail, while humpback and sperm whale calls were detected on roughly 20% of those dives. Various whistles, clicks and burst calls, similar to those produced by dolphins and small whales, were also detected, suggesting that the capability of ASGs can be expanded to sample a broad range of marine mammal species. The potential to include whale call detection in the suite of standard oceanographic measures is unprecedented and provides a foundation for mobile sampling strategies at scales that better match the vertical and horizontal movements of the whales themselves. This capability opens new doors for investigation of cetacean habitats and their role in marine ecosystems, as envisioned in future ocean observing systems.

solved oxygen, chlorophyll) to complement the whale call detections, researchers are left to search for environmental records from nearby moorings or satellite images that best match the recorder deployments. This method often results in comparatively crude depictions of whale habitat features (e.g., Moore et al., 2002), and hampers efforts to include whales in predictive models of marine ecosystems.

The development of several types of autonomous underwater vehicles over the past decade promises to revolutionize ocean science (Howe and Miller, 2004; Bellingham and Rajan, 2007). One such platform, the Seaglider (Figure 1a), engineered at the University of Washington (UW) with support from the Office of Naval Research (ONR) and the National Science Foundation (NSF), is a small (2.8 m) autonomous underwater vehicle designed to dive from the ocean surface to a programmed depth while measuring a standard suite of oceanographic parameters (Eriksen et al., 2001; Rudnick et al., 2004). Seagliders are low power, comparatively quiet and capable of multiple dives to 1,000 m over distances of tens to thousands of kilometers.

The glider is propelled by buoyancy force (a pump moves oil between internal and external rubber bladders, changing the volume and thus the density), while vehicle direction is controlled by shifting the battery pack fore and aft and side to side. Wings provide hydrodynamic lift to propel the vehicle forward as it sinks or rises, at speeds up to 0.7 knots (Eriksen, 2001). Global Positioning System (GPS) and Iridium units provide navigation and communication capability whenever the units surface.

In 2005, Seagliders deployed in the North Pacific and the Labrador Sea set duration (191 days), distance (over 3,000 km), and dive records (over 600 dives; Mercer et al., 2007). This endurance spurred plans for broader application of these platforms to oceanographic investigations. The capacity to produce, detect, and record underwater sounds seemed a logical next step in Seaglider development and one that could link whale call detection capabilities developed for fixed recorders to mobile platforms. So, in 2006, two acoustic subsystems were added to three Seagliders, which subsequently went to sea in trials near

FIGURE 1

Acoustic Seaglider (ASG) deployment during the PLUSNet MB06 experiment (a) and internal assembly display (b).

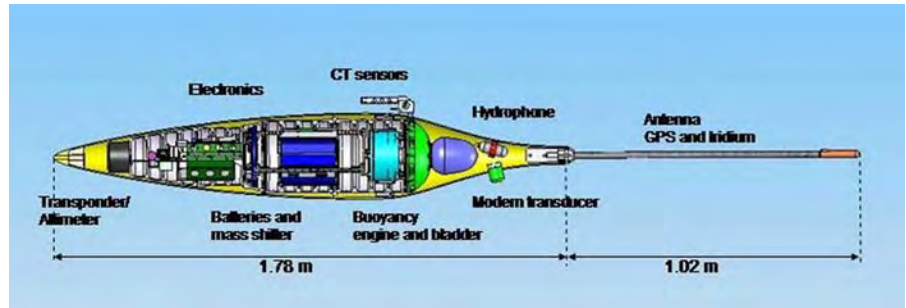


Monterey Bay, California. The ability of these platforms to simultaneously record oceanographic data and whale calls while completing a series of operational dives was demonstrated and is provisionally reported here.

Methods

Seaglider Modifications

Three Seagliders became 'Acoustic Seagliders' (ASGs) with the addition of broadband (5 Hz to 30 kHz) omni-directional hydrophones in the tail cone (Figure 1b). One of the gliders was also fitted with a modem subsystem to provide two-way underwater communications capability, as described in Howe (2006). The modem frequency band was 23-27 kHz and, as this glider transmitted very infrequently, specifics as to this aspect of performance are not discussed further here. Each broadband hydrophone was connected to a low-power processor (CF2) and coupled to a flash memory (4 Gbyte) and a low-temperature hard disk (60 Gbyte) for long-term data storage. This onboard processing and storage allowed the acoustic data to be digitized with 120 dB of dynamic range (over two gain channels) with a system noise level floor of 34 dB re $1\mu\text{Pa}/(\text{Hz})^{1/2}$.



Experimental Procedures

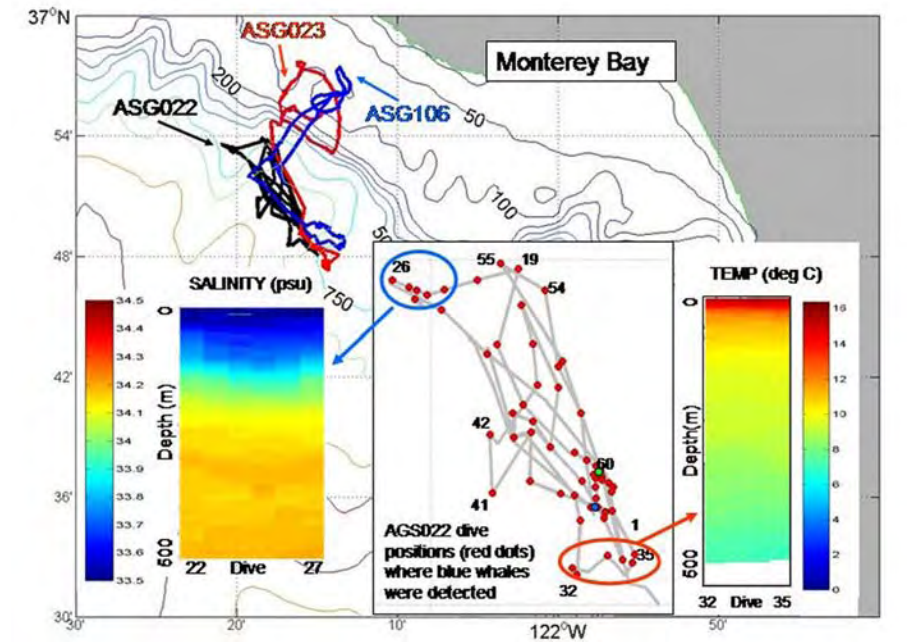
The three ASGs were deployed just north-west of Monterey Bay, California, from 12-23 August 2006, as part of the ONR PLUSNet MB06 experiment. Two gliders (ASG 022 and 023) sampled at 5 kHz, while the modem-instrumented glider (ASG 106) sampled at a rate up to 64 kHz with low pass filtering at 30 kHz. Power spectra were calculated *in situ* for a small subset of the data and telemetered back to shore with the other oceanographic data when the glider surfaced; in the future the results of more sophisticated *in situ* processing can be available in near-real time to support other contemporaneous activities.

Results

In total, 401 dives were completed and over 107 hours of data recorded, with deployments in both shallow continental shelf (50-200m) and deep slope-basin (200-900m) habitats offshore central California (Figure 2). Continuous acoustic recording typically lasted 10-20 minutes, followed by a short pause (3-5 minutes) while the glider was on the surface, then another recording period. Other mission requirements prevented more continuous data collection. Significant glider self noise was limited to the brief periods when the buoyancy pump was running, typically at dive apogee, or the even shorter

FIGURE 2

Track of three ASG deployments northwest of Monterey Bay. Inset details track of ASG 022, with dots depicting locations where loud blue whale calls were received. Example salinity and temperature panels given for two dot-cluster locations at track boundary.



periods when the roll or pitch motors were running. Overall, on a dive lasting an hour, < 5 minutes of acoustic data were contaminated with self noise. Over 80% of the acoustic sample (86h) was recorded on ASG 022 during the first nine days of the experiment. An additional 10h of acoustic data were recorded on ASG 023, with 11.5h of recording on ASG 106 divided between sampling at 5 kHz (2.5h) and 64 kHz (8.9h).

Acoustic data from 76 dives completed by ASG 022 (60 dives) and ASG 023 (16 dives) were downloaded and analyzed with the aid of species-specific call detectors, developed using ISHMAEL (Mellinger, 2001) and by visual and

TABLE 1

Number of dives when calls of four whale species were identified on two ASGs during the experiment offshore Monterey Bay, California, August 2006.
E = occurrence of echolocation click series

Platform	No. Dives	Blue Whale (# calls)	Humpback Whale	Sperm Whale	Killer Whale*	Unknown Odontocete (E)
ASG 022	60	58 (904)	12	16	2	16 (9)
ASG 023	16	16 (49)	3	1	0	0

* provisional ID, due to very low signal/noise

aural examination of spectrograms. Both gliders recorded calls from blue, humpback, and sperm whales, as evidenced by species' diagnostic calls (Table 1; Figure 3). Blue whale calls were de-

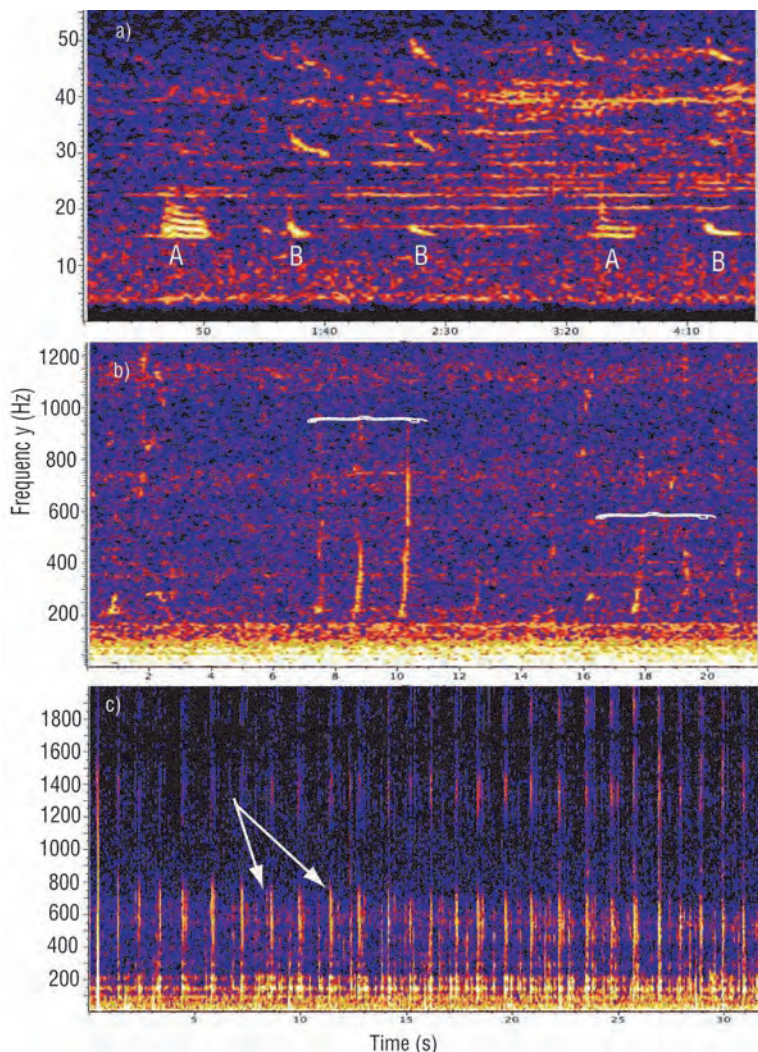
tected on all but two of the 76 dives, with a total of 953 individual calls counted. Humpback whale calls were detected on roughly 20% of dives conducted by each ASG, while sperm whale calls were far more prevalent on the ASG 022 dives (27%) than on ASG 023 dives (6%). This difference is likely attributable to the greater number of ASG 022 dives conducted seaward of the shelf break where deep-diving sperm whales are more common.

Some calls could not be positively attributed to species (Table 1). Signals that appeared to be killer whale calls were detected twice on one of the ASG 022 dives, but these were very faint. On sixteen ASG 022 dives, various whistle, clicks, and burst calls, similar to those produced by dolphins or small whales, were detected, with echolocation clicks noted on 9 of the 16 dives. Finally, sea lion barks and seabird calls were recorded on 15 and 9 occasions, respectively, on ASG 022; and on one occasion each on ASG 023. These detections occurred at the beginning and ends of dives, when the gliders were close to the surface.

To demonstrate the capability of ASGs to integrate whale call detections with conventional oceanographic measures, loud blue whale calls (i.e., from nearby whales) were matched to ASG dive locations (Figure 2: inset track) and composite temperature and salinity panels derived to show the associated real-time hydrography. Not surprisingly, there was a clear temperature and salinity cline at roughly 130-200 m in the area where the blue whales were detected (Figure 2: inset hydrography). These results complement data from a long-term study of blue whales within Monterey Bay, wherein whales have been shown to forage on dense euphausiid aggregations that occur between 150-200 m along the edge of Monterey Bay Submarine Canyon (Croll et al., 2005).

FIGURE 3

Example of (a) blue, (b) humpback and (c) sperm whale calls recorded on ASGs. Diagnostic features include the A-B-B sequences produced by blue whales in the eastern North Pacific, distinctive triplet upglides of humpback whales (bracket) and the broadband clicks of sperm whales (arrows). Note: frequency/time axes vary by species.



Discussion

We are very encouraged by the results of this initial ASG experiment, in that blue, humpback, and sperm whale calls were prevalent in the data record. The detection of higher-frequency calls and echolocation clicks associated with smaller whales and dolphins suggests that with additional engineering, ASGs will be able to routinely detect signals from a broad suite of marine mammal species. Moreover, we were surprised to note that sea lions and seabird calls were heard when the ASGs were near the surface. Overall, this experiment demonstrates that, with refinement of marine mammal call classification tools anticipated via ongoing efforts such as the PAMGUARD program (<http://www.pamguard.org>) and others, the routine inclusion of marine mammal calls as a standard ocean metric is within our technical grasp.

The capability of the ASGs to include whale calls as an oceanographic metric compiled with standard temperature and conductivity measures provides unprecedented opportunities to develop mobile sampling strategies for these top-predators over varied temporal and spatial scales. Until now, passive acoustic sampling for marine mammals has been conducted via static deployments of fixed recorders, or by towing a cabled array behind ships conducting transect surveys (e.g., Barlow and Taylor, 2005). In both cases sampling is confined in space and time, often at scales that are mismatched to the natural history of the target species. Conversely, Seagliders are capable of sampling at vertical and horizontal scales similar to the diving and foraging movements of the whales themselves. For example, given reports of intensive blue whale feeding in Monterey Bay (Croll et al., 2005), foraging hotspots north and south of the bay (e.g., Oleson et al., 2007) and the results of our experiment, one can imagine that much more could be learned about the dynamics of blue whale movements and behavior from an array of ASGs sampling all along the California shelf break. Indeed, a suite of mobile and fixed sensors sampling across a range of ecological scales is exactly what is envisioned in most ocean observatory plans (e.g., Howe and Miller, 2004).

Future Applications and Partnerships

For many oceanographers, the question may be: why do this? Why sacrifice precious battery power for acoustic data acquisition, storage and processing for the identification of marine mammal calls? There are many possible answers to such a question, and we list three we think important here.

1) Understanding marine mammal ecology, the when, where and why in the life history of these ocean-going predators provides a framework for investigating ocean dynamics. Patterns of marine mammal distribution and movements reflect oceanographic variability, from local to basin scales—thus, these highly adapted animals can inform oceanographers of potentially overlooked ocean structure and lead to enhanced sampling protocols over the long term.

2) Development of acoustical oceanography requires underwater noise budgets that account for sound contribution from marine mammals calls, which can be seasonally significant (e.g., Curtis et al., 1999), as well as sounds from sonorous fishes (Rountree et al., 2006), earthquakes (Smith et al., 2004), wind and rain (Nystuen, 2001) and anthropogenic sources such as ships, sonars and geophysical surveys (Dahl et al., 2007). Quantification and integration of these sources to standard databases are fundamental to the type of acoustic sensing anticipated in future ocean observatories (Howe and Miller, 2004).

3) Future ocean resource assessment and management requires the type of fine-scale measurement and data availability that only autonomous mobile ocean sensors can provide. Seaglider trials in other ocean areas provide further evidence of their utility as a tool for investigation of baleen whale feeding ecology (e.g., Baumgartner et al., 2006) and for mitigation of naval training activities (e.g., Sanderson, 2007). Perhaps the most useful contribution of future ASG deployments is the potential, with development of species-specific signal detectors, to transmit the identity and location of animals in near real-time to users on shore or at sea. The need for timely and regional information about marine mammal distribution, abundance, and movements is bound to increase with expanded military, commercial, and recreational activities in the oceans.

Partnerships among academia, agencies, and advocacy organizations can foster development of ocean observing systems wherein ASGs can contribute. For example, we were fortunate to conduct the PLUSNet experiment in the vicinity of the long-term study site that scientists at the University of California, Santa Cruz (UCSC) maintain for blue whales in the upwelling system of Monterey Bay Canyon (Croll et al., 2005). Currently, the UCSC Center for Integrated Marine Technologies supports a nascent ocean observing system, including data fields from HF radar, moorings, ship surveys, remote sensing, bioacoustics, and apex predator tagging (<http://cimt.ucsc.edu/bioacoustics.htm>). Our results demonstrate the capability of ASGs to add to this suite of data, which anticipates the type of data streams planned for the NSF ocean observatories program ORION and the Integrated Ocean Observing System. Integration of passive acoustic sensors in Seagliders augment sampling in both space and time, providing the backbone of information required as we enter a new era of ocean exploration.

Acknowledgments

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The Hydrogen Age

By Geoffrey Holland and James Provenzano

Gibbs Smith, 2007

370 pp., \$24.95

Reviewed by John F. Bash

The world is on the cusp of a revolution, a revolution that will usher in a new age—"The Hydrogen Age". Geoffrey Holland and James Provenzano have written a most comprehensive and superbly researched treatise on hydrogen. The authors maintain a balanced argument for the virtues of hydrogen and explain the political realities associated with this paradigm shift. This is not pie in the sky but an unfolding energy revolution. Holland and Provenzano methodically build a solid case for hydrogen as the ultimate grand enabler.

The authors walk the reader through the history of hydrogen. They provide a hydrogen 101 chemistry lesson in terms that allow the layman to appreciate the concepts and a refresher course for those with a chemistry background.

Hydrogen is often labeled as dangerous. Holland and Provenzano clearly lay out the properties of hydrogen, its relative dangers, and safe handling procedures, debunking the unfounded fear label with solid facts.

This book explains in detail how hydrogen is used in fuel cells to provide electrical energy with heat and pure water as a by-product. This energy carrier can be locally produced, providing environmentally clean energy free from foreign entanglements, and provides the answers to fight global warming. Hydrogen is a win/win for energy and the economy.

Seven of the twenty chapters are devoted to the current and future uses of hydrogen. Hydrogen is cost effective today in many applications. These include forklift operations, remote backup power, and power sources for cameras. With mass production, many more applications will join the cost-effective ranks.

The book explains in detail the real cost of oil and other fossil fuels. When these real costs are explained, hydrogen looks cheap.

A chapter on the "Energy Internet" was particularly interesting to this reader. Automotive fuel cells act as mobile power plants that can be linked together much like the computer-driven Internet. When not on the highway but in the home driveway or at the office, the fuel cell-powered automobile could plug into a collection point and generate electricity for the grid. In the middle of the day the power demands are greatest for the grid system. This is precisely when these cars can provide their much needed supplemental power. With proper coding the automobile owner can receive credit for the power generated. If produced on a large scale this would eliminate the need for new power plants and replace many older ones. Now that's economy!

The 367 pages of *The Hydrogen Age* flow by quickly with a clear and smooth writing style. References are conveniently located at the end of each chapter. The book provides suggested reading, recommended web sites, an extensive bibliography, and an easy-to-use full index. This book provides a powerful source document and will be the kind of book that will be repeatedly used as a reference for energy-related facts.

The Hydrogen Age is a must read for all believers in hydrogen as the next energy carrier. It should also be read by the skeptics and nay-sayers to enlighten their thinking. It is a complete teaching tool that ends with optimism for the future and a roadmap to make the journey.

Benedict Arnold's Navy

By James L. Nelson

McGraw Hill, 2007

386 pp., \$14.95 (Paperback)

Reviewed by John F. Bash

Benedict Arnold's *Navy: The Ragtag Fleet that Lost the Battle for Lake Champlain but Won the American Revolution* is a fascinating account of an American hero turned traitor and his exploits in the Revolutionary War. Author James Nelson illuminates a little known segment of American history and suggests to the reader that the much maligned Benedict Arnold was in fact a significant player in winning the Revolution.

Before the war Arnold was an accomplished man of the sea. He was successful, wealthy, ambitious and aggressive, all attributes he used with vigor to support the revolutionary forces. His travels were detailed from Ticonderoga to Quebec, back to Ticonderoga then to Saratoga, playing a key role in leading troops with valor. Arnold's efforts were a major factor in keeping the British from cutting the Colonies in half, an act that could have ended the American effort. His prowess as a seaman helped construct a fleet of ships on Lake Champlain, then fight these ships to challenge a country with the most powerful navy in the world. This bodacious effort turned out to be a factor in the ultimate British loss of the Colonies. Nelson's nautical descriptions are impressive about both ship construction and vessel maneuvering. His writing style provides a very readable account of early United States history. Examples of his writing are illustrated in the following quotes from the book:

At the very head of Arnold's division was an advance guard of thirty men called the "forlorn hope," that less-than-optimistic eighteenth-century term for the men destined to be first through the breach. This division was led by Arnold himself and included Eleazer Oswald. (pg. 147)

The thirty-two-gun fifth-rate Pearl and the frigate Carysfort sailed from Cork, Ireland, that week with forty-one ships in convoy, carrying seven battalions of British troops. The military bands struck up their martial tunes, but the drama of the moment, with music in the air and a great fleet of ships loosening sail and winning their anchors, could not make the troops crammed on board forget that they were leaving behind all they knew and were sailing to war in a strange wilderness country thousands of miles away. (pg. 205)

Realizing that a frontal assault was suicide, Arnold saw that the vulnerable spot in the British defense was the stockade in the open field between the two redoubts. Wheeling his horse, he charged off toward the head of the troops under Learned's direct command, riding through the gap between the American and British lines amidst a storm of musket fire. (pg. 355)

The author describes a passionate man who would have been touted as one of the nation's greatest heroes had his anger, pride, ego and envious contemporaries not caused a reverse of loyalty and an effort of spiteful revenge. History has not been kind to Benedict Arnold. This book does not excuse him but sets the record straight.

Benedict Arnold's Navy is a well documented book with a useful index. However, there is a dearth of maps and illustrations. With only two sketchy maps at the book's beginning and a handful of sketches from the Fort Ticonderoga museum, the author missed an opportunity to better walk the reader through the many travels and battles of Arnold and a the movements of both armies.

Nelson is an author of both fiction and non-fiction. His writing skills bring history to life and his exhaustive research provides a window into a little known part of American history. This book is recommended for all those interested in the American Revolution and early history of the United States Navy.

Wye Island: Insiders, Outsiders, and Change in a Chesapeake Community

(Special Reprint Edition)

By Boyd Gibbons

(with a new forward by Andrew Rome)

RFF Press, 2007

230 pp., \$22.95 (soft cover; cloth cover available for \$45.00)

Reviewed by Jason Goldberg

U.S. Fish and Wildlife Service

Change, it seems, is life's only constant. *Wye Island* is therefore ironic given that it has stood the test of time remarkably well since its original 1977 publication. In many ways, it could have been written this year instead of thirty years ago. It remains a thought-provoking, insightful, and entertaining book that will be of interest and value to anyone with even just a casual interest in sustainable development and community perceptions regarding change.

In Adam Rome's new foreword, he quotes James Rouse, who says, "I can think of no image in America to which we can point as an adequate demonstration of what ought to be...[yet] there are new forms of development for ecologically sensitive land that can respect the land, the water, the fauna and the flora and accommodate rational, sensitive, imaginative development. [T]here are decent alternatives to sprawl and clutter and the ravaging of rivers." The book proceeds to challenge our perceptions not by detailed analyses of environmental impact statements or economic data (which are valuable tools), but through story-telling in the manner of *A Civil Action*. Owners, developers, rich, poor, natives, and visitors are all given an opportunity to speak. The results are surprising, sometimes shocking, always enlightening, and add an important dimension to the debates on development happening today.

Wye Island is a small island located along Maryland's Eastern Shore, a stretch of land on

the eastern side of the Chesapeake Bay. It is a common half-joke that people in the Washington, D.C. area buy vacation or retirement properties there to enjoy its idyllic settings, then immediately complain about the people moving from D.C. who are impacting their new relaxed lifestyle. Meanwhile, the area's natives complain about the "chickenneckerers," so-called for the bait we bring on weekends to fish for crabs, also bringing crime, traffic, and a disrespectful attitude. The book centers around James Rouse, an Eastern Shore native and developer, who proposed a plan to develop Wye Island, and the controversy that immediately ensues. Rouse is not your stereotypical developer. He is painted as ahead of his time, going to great lengths to find a way to make Wye Island into an early "smart growth" community rather than just another series of "McMansions," each with its own pier. Still, the plan does involve bringing several thousand new residents to the area, and the people living nearby are suspicious and skeptical. Resistance to change, or what is appropriate, is the book's common refrain.

Gibbons has done a great service in showing, through the use of brilliant (if sometimes a little one-sided) biographical story-telling, the many perspectives that need to be explored to fully understand all dimensions of effective community planning. Some reasons resisting change seem at least partly justified. For example, some of the locals who grew up along the Eastern

Shore are afraid that they cannot afford to live there anymore because of skyrocketing real estate values caused by the influx of wealthy outsiders. I can only hope that others, such as the blatantly racist opinions for keeping outsiders away, have long since disappeared. Other perspectives, such as those of a wealthy couple who built a fortress in the area, border on the wacky and absurd, but form part of the tapestry that Gibbons has weaved together.

Wye Island challenges our perceptions. The developer is the "good guy." Others profiled, while often his antagonists, are not necessarily the "bad guys." They just fear change, for reasons that you may empathize with, laugh at, or get angry at. You may agree or disagree with Rouse's plan for the island; I found his plan's logic and process informative and compelling. The book is fascinating and will be of value to any MTS member interested in seeing environmental issues in a new light and wanting to understand the nature of "change" better. Members with an interest in education should consider this book, as it teaches valuable lessons without hitting you over the head, simply by letting different people tell their story in their own words. This book could serve as a great point for debate in the college classroom. *Wye Island* was one of the American Library Association's "Ten Most Notable Books in 1977." It continues to stand out as a compelling text, and deserves a high recommendation for any environmental library.

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