Using Digital Tags With Integrated Video and Inertial Sensors to Study Moving Morphology and Associated Function in Large Aquatic Vertebrates

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ABSTRACT

The anatomy of large cetaceans has been well documented, mostly through dissection of dead specimens. However, the difficulty of studying the world's largest animals in their natural environment means the functions of anatomical structures must be inferred. Recently, non-invasive tracking devices have been developed that measure body position and orientation, thereby enabling the detailed reconstruction of underwater trajectories. The addition of cameras to the whale-borne tags allows the sensor data to be matched with real-time observations of how whales use their morphological structures, such as flukes, flippers, feeding apparatuses, and blowholes for the physiological functions of locomotion, feeding, and breathing. Here, we describe a new tag design with integrated video and inertial sensors and how it can be used to provide insights to the function of whale anatomy. This technology has the potential to facilitate a wide range of discoveries and comparative studies, but many challenges remain to increase the resolution and applicability of the data. Anat Rec, 300:1935–1941, 2017. © 2017 Wiley Periodicals, Inc.

Key words: whale; functional morphology; feeding

This article includes AR WOW Videos. Video 1 can be viewed at https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532112940001, Video 2 can be viewed at https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532107199001, Video 3 can be viewed at https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532124921001, Video 4 can be viewed at https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532111959001.

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The functional morphology and physiology of large whales is notoriously difficult to study. Although intricate morphological detail can be obtained from dissections and medical bio-imaging techniques (Pivorunas, 1977; Cranford et al., 2008; Pyenson et al., 2012; Ford et al., 2013), little is known about how whales use anatomical structures to carry out specific functions and behaviors. As the largest animals on earth, their extreme size precludes laboratory or captive studies. Photogrammetry or videography from boats or aircraft can yield important information, but it is largely limited to views near the sea surface (Edel and Winn, 1978; Durban et al., in press). Therefore, researchers must rely on tracking devices to study these animals at depth. The recent development of whale-borne biologging tags containing a suite of sensors that measure body position and orientation has allowed the detailed reconstruction of underwater trajectories (Laplanche et al., 2015). This tag technology has enabled detailed study of physiology, ecology, and behavior in a wide range of taxa (Kooyman, 2004; Block, 2005; Rutz and Hays, 2009). Moreover, at greater temporal and spatial scales, biologging has interfaced with the physical sciences, notably physical oceanography (Roquet et al., 2013). At very fine scales, the development of biologging tags with integrated cameras enable researchers to examine the function of anatomical structures and how they are used during specific behaviors. In this article, we provide a description of the new camera-tag technology and a series of examples of how these tags can be used to further our understanding of the functional morphology of cetaceans.

CAMERA TAG TECHNOLOGY

Our experience with cetacean biologging devices led us to develop a new tag in collaboration with Customized Animal Tracking Solutions (www.cats.is) that integrates video with three-dimensional movement sensors (Cade et al., 2016). The video provides a time-series of observations of how body parts (i.e., appendages) move relative to the main body. The kinematics of the main body can be quantified using an inertial measurement unit within the tag and well-established digital signal processing techniques (Johnson and Tyack, 2003). This combined sensor capability was inspired by the earliest experiments with animal-borne video tags (Davis et al., 1999), such as National Geographic's Crittercam (Marshall, 1998; Marshall et al., 2007), which included early deployments on large whales (Calambokidis et al., 2007). In some tags we integrated dual cameras in two different tag designs: (1) cameras positioned laterally at ~45 degrees from the midline of the tag to provide a field of view greater than 180 degrees, and (2) forward and backward facing cameras (Fig. 1) to offer a concurrent view in front of and behind the animal. The movement sensors consist of tri-axial accelerometers, magnetometers, and gyroscopes sampling at 40–400 Hz. Light and temperature sensors within the tag record information about the physical environment and enable the duty cycling of the cameras to save battery power at very low light levels and a GPS sensor provides a geo-referenced position when the tag breaks the sea surface. Lastly, a time-depth recorder (TDR) within the tag measures the vertical position of the animal in the water column as a function of time.

Three-dimensional movement tags with integrated video are a useful tool for making observations and measurements on how anatomy is used in different functional and behavioral contexts. Moreover, this technology provides insight into the environmental context for these behaviors, such as prey type and interactions with other species, as well as the presence and behavioral state of conspecifics. We have deployed these tags on several large whale species to date and our data have uncovered unique aspects of the functional anatomy of swimming, breathing, and feeding.

HOW ARE CONTROL SURFACES USED TO PERFORM MANEUVERS?

By placing the cameras on the whales so that the flukes or flippers are in view, we can gain insight into how cetacean control surfaces are used for locomotion and maneuvering. In general, cetacean flukes are oscillated dorsoventrally to produce thrust whereas the anteriorly placed flippers are used as paddles or hydrofoils to effect maneuvers (Fish et al., 2008; Weber et al., 2014; Segre et al., 2016). Many cetaceans also have a dorsal fin that may act as a rudder and provide stability to an otherwise highly maneuverable body (Fish, 2002). Although the video footage does not allow us to quantify the exact orientation of control surfaces explicitly (e.g., precise angle of attack of flippers), we can qualitatively determine how the flippers are used and when maneuvers are powered or unpowered by the flukes (Fig. 2, see Video 1: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532112940001).

WHAT ARE THE KINEMATICS OF THE SKULL RELATIVE TO THE BODY KINEMATICS DURING FEEDING?

We frequently observed dynamic feeding events that are executed by a series of coordinated maneuvers, particularly in rorqual whale species (Balaenopteridae). Feeding in rorquals consists of a rapid acceleration to high speed and the engulfment of a large volume of prey-filled water (Cade et al., 2016; Goldbogen et al., 2017), but until recently we lacked complete knowledge of how the engulfment phase overlaps temporally with the acceleration phase (Goldbogen et al., 2007; Simon et al., 2012). New tag observations provide video evidence of mouth opening and closure in relation to the kinematics of the body (Fig. 3, see Video 2: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532107199001) and inform how this feeding mechanism is modulated when foraging on different prey (Cade et al., 2016). These data are important because they help to inform biomechanical and hydrodynamic models of rorqual engulfment, which in turn provide improved estimates of the forces at play during feeding as well as the overall energy budgets of foraging (Potvin et al., 2009; Goldbogen et al., 2012). Moreover, some deployments also document the expansion of the ventral groove blubber, a defining anatomical feature of this clade that underlies the extraordinary engulfment capacity of these gigantic filter feeders (Orton and Brodie, 1987; Shadwick et al., 2013; Goldbogen et al., 2017).

HOW DOES THE BLOWHOLE FUNCTION DURING BREATHING SEQUENCES?

Whales are air-breathing divers that incur significant oxygen debt while searching for, pursuing, and capturing

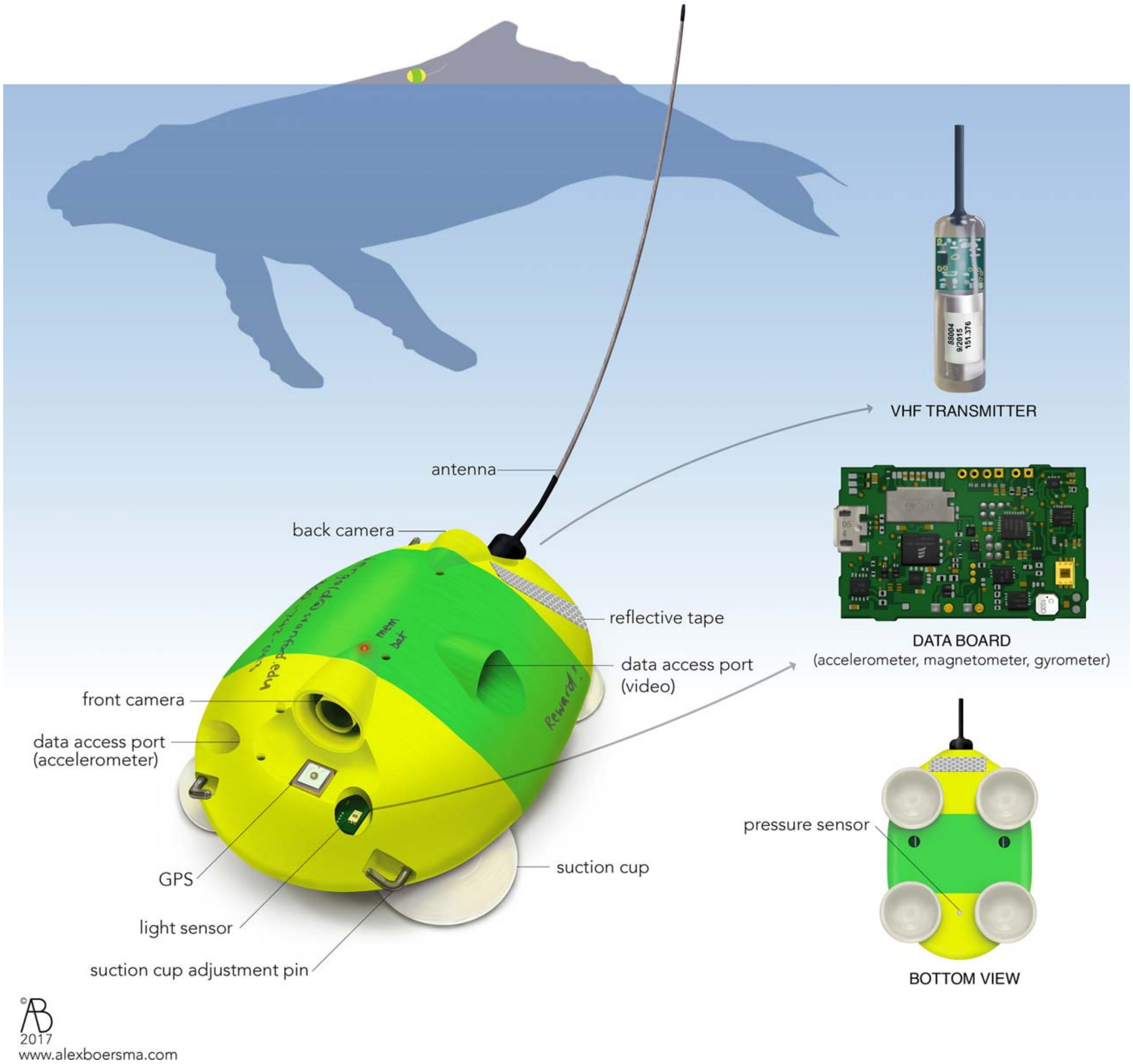

Fig. 1. A multi-sensor camera tag used for studying the biomechanics of free-swimming whales. The self-contained tag is archival, meaning that the data is recorded within the tag's memory and must be recovered for data download. The movement sensors within the tag are encapsulated to be waterproof and surrounded by floatation so that the tag floats to the sea surface after detachment from the animal. The weight distribution is designed so that the center of buoyancy of the tag forces the VHF transmitter's antenna to extend out of the water, thereby facilitating tag retrieval with traditional radio tracking equipment. Illustration by Alex Boersma.

prey at depth. After a dive, whales repay that oxygen debt through a series of breaths often referred to as a surface series (Roos et al., 2016). Typically, these breaths are taken as the whale is in motion, where the body arches and pitches to orient the dorsally positioned blowholes out of the water (Goldbogen et al., 2008). However, we note that some species may exhibit logging behavior and perform a series of breaths while remaining relatively stationary with a large portion of the body out of the water. During each breath, a large volume of air is expired and inspired in a very short amount of time (Brodie, 2001), thereby resulting in extremely high flow rates through the blowhole(s) (Kooyman et al., 1975). Although it is clear that the cetacean respiratory apparatus has undergone a suite of modifications for a fully aquatic life (Kooyman, 1973; Piscitelli et al., 2013), respiratory events in free-ranging whales have only been inferred from animal-borne sensor data (Goldbogen et al., 2008; Miller et al., 2010; Roos et al., 2016). By placing our movement-video tags directly behind the blowhole, we can document the precise opening and closing of the blowholes after a range of different dives and behaviors (Fig. 4, see Video 3: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532124921001). In future studies, this approach may enable

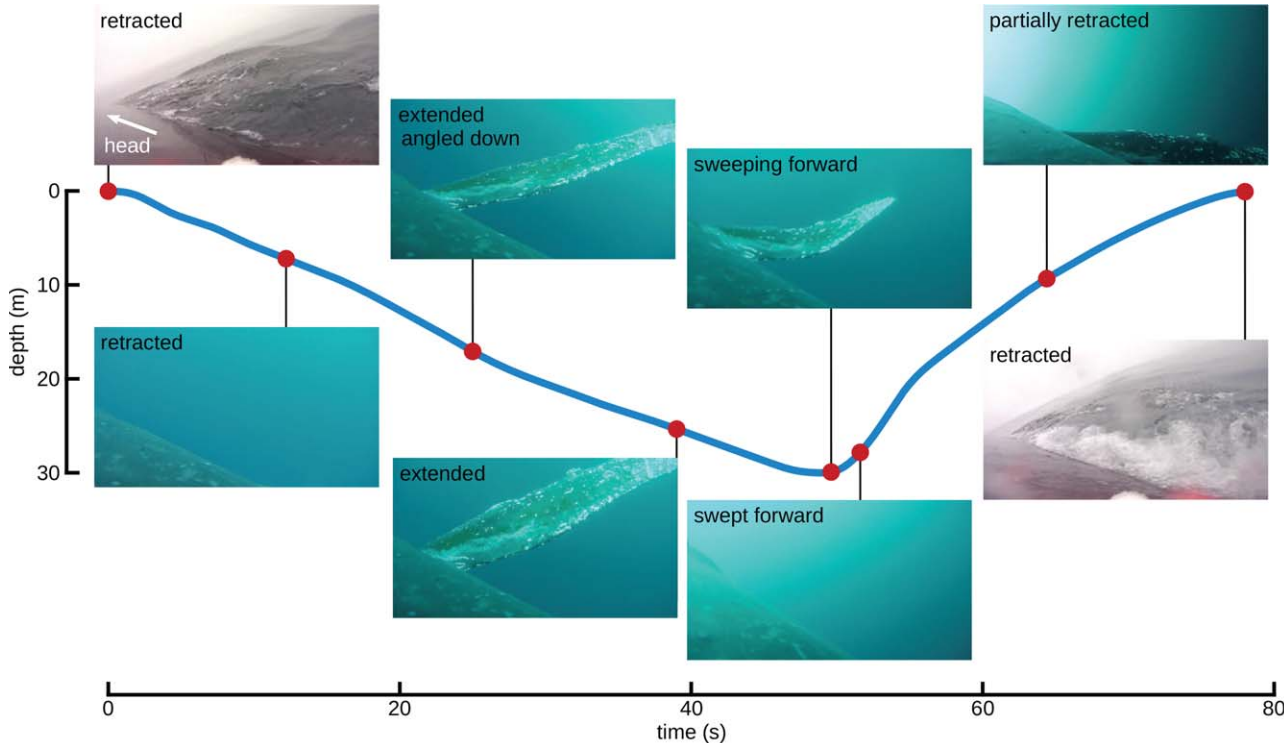

Fig. 2. A camera tag reveals the complex flipper movements used by a humpback whale to perform a feeding lunge during a shallow dive. The tag was placed on the right side of the body facing the flipper (see Video 1: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532112940001).

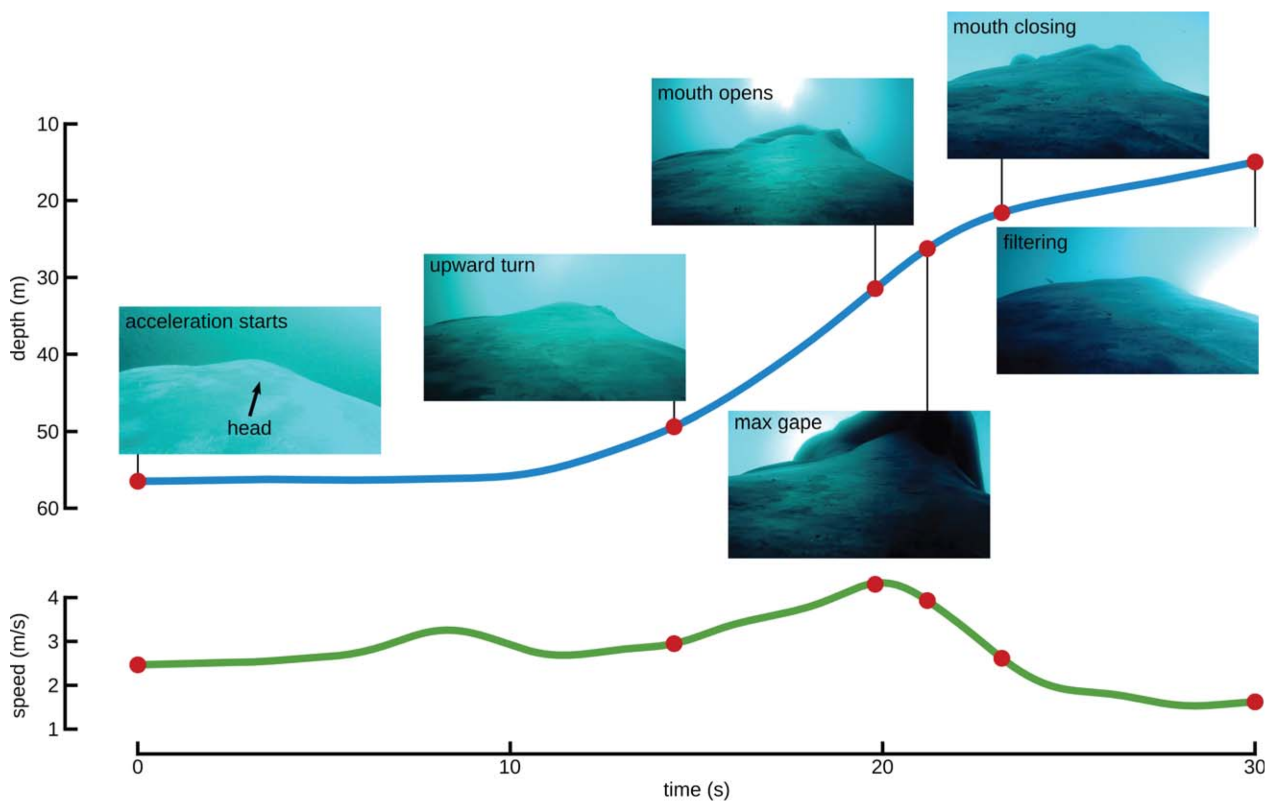

Fig. 3. A video of a lunge-feeding blue whale is synchronized with the depth (blue) and speed (green) profiles recorded by the tag sensors to determine the exact timing of biomechanical events such as the mouth opening, maximum gape, and mouth closure. The tag was located on the dorsal surface of the whale, slightly to the left of the mid-line and facing forward, where the movements of the head were visible during feeding (Cade et al. 2016) (see Video 2: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532107199001).

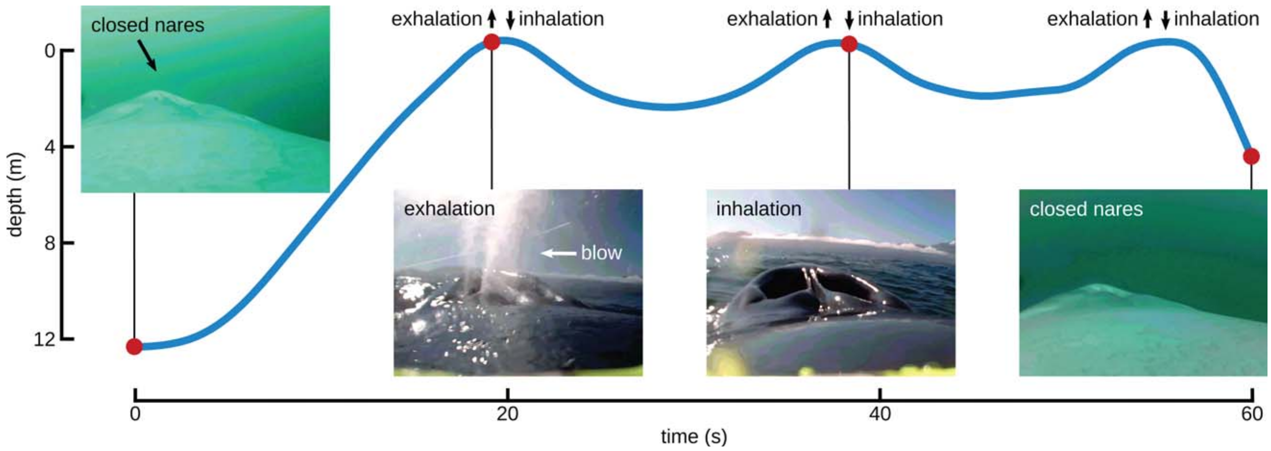

Fig. 4. A video of the blowhole of a breathing blue whale is used to determine the timing of the inhalation and exhalation and can be used to estimate the relative energetic consequences of different behaviors (see Video 3: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532124921001).

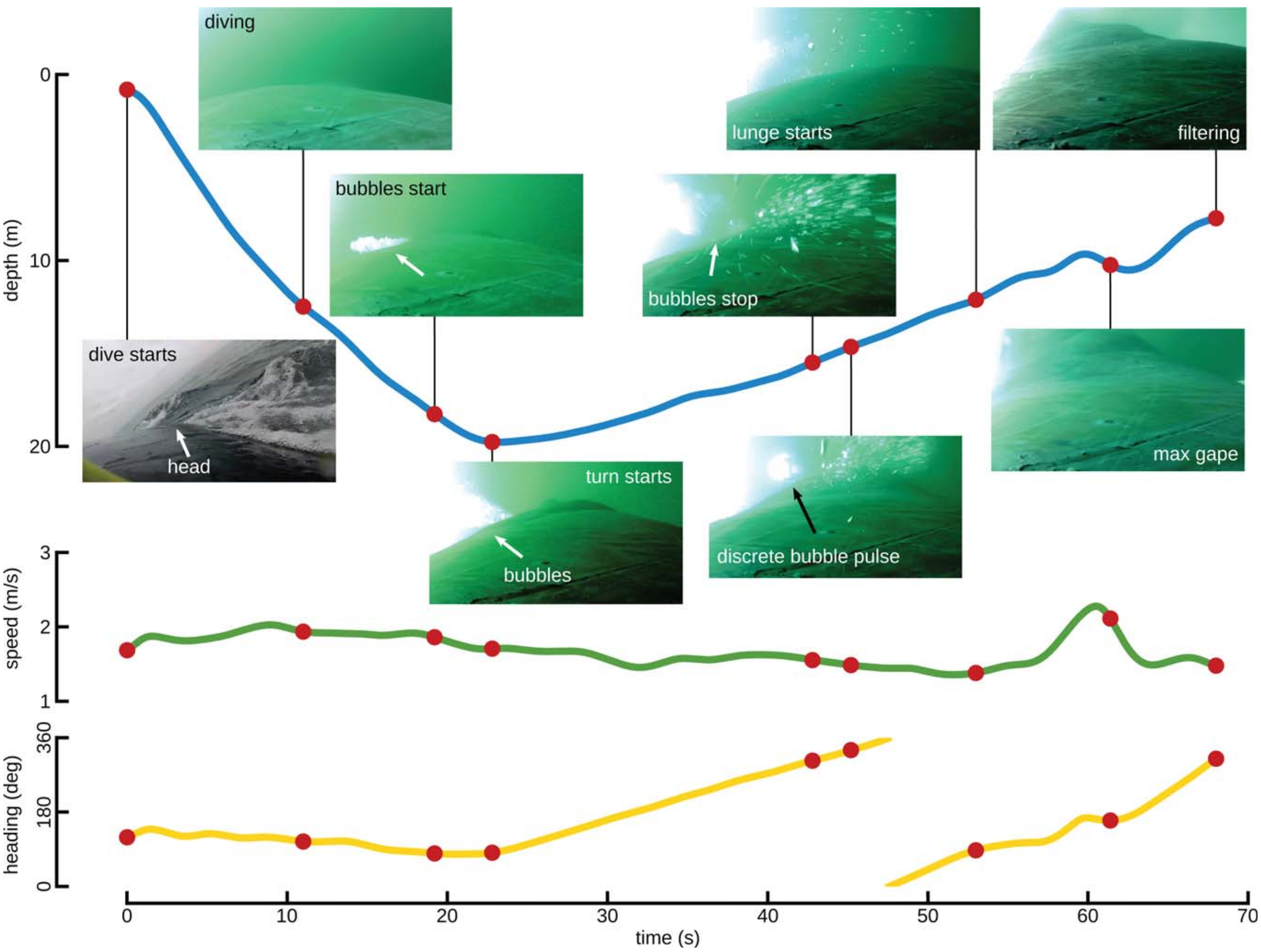

Fig. 5. A camera tag reveals the timing of bubble production used during bubble-net foraging behaviors in humpback whales. The whale performs a shallow dive (0 s, blue depth profile), begins releasing a stream of bubbles (19 s) before initiating a turn (23 s, yellow heading profile) around the prey, and then performing a feeding lunge (53 s, green speed profile). The tag, containing two cameras, was located just anterior to the dorsal fin and slightly on the animal's right side. The images in the figure were recorded with the right camera, which was oriented toward the head. (see Video 4: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532111959001).

researchers to explore the relationship between specific respiratory patterns and diving performance.

Not only are cetacean blowholes used for gas exchange at the sea surface, but they are also used to produce bubbles in association with specific functions (Tyack, 2000; Reidenberg and Laitman, 2007). Our preliminary studies have provided direct observations of many of these phenomena in the context of feeding. A tag deployment on a humpback whale (*Megaptera novaenagliae*) foraging in the western North Atlantic Ocean shows bubble production used to create a spiral-shaped net to corral agile prey (Fig. 5, see Video 4: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532111959001). Bubble-net feeding is a complex foraging strategy that is used by individual whales or teams that cooperatively feed through task specialization (Wiley et al., 2011). Although the use of bubble-nets as part of this strategy has been well documented (Leighton et al., 2007; Friedlaender et al., 2009; Hazen et al., 2009), these video tags provide complementary data on the coordination of bubble production and the fine-scale body movements of this complex feeding strategy (Fig. 5, see Video 4: https://players.brightcove.net/656326989001/default_default/index.html?videoId=5532111959001).

CONCLUSIONS

The advent of multi-sensor tags has revolutionized the study of animals that cannot be studied in the laboratory. As a result, these tools have also transformed our ability to study animals behaving naturally. In one respect, the data from these tags represent digital natural history: a time-series of observations from an animal's perspective. These observations reveal previously unrecognized phenomena of animal physiology, behavior, and ecology. In addition, movement data from these tags provides insight into how animals move and feed in their natural environment. Although pure experimental science—where all factors are under the researcher's control—is not possible with this approach, we can quantify processes that occur during natural experiments as animals modulate their movement and behavior in response to changes in their environment. The perpetual redesign and evolution of these biologging devices will yield sensors with entirely new capabilities, enhanced resolution, and greater power efficiency. As a result, researchers will have a wide range of tags available to study an equally diverse set of species, improving our understanding of how animals work in nature.

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