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Contribution to the Theme Section 'Biologging technologies: new tools for conservation'

Inter-animal telemetry: results from first deployment of acoustic 'business card' tags

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ABSTRACT: Prototype acoustic 'business card' (BC) tags were deployed on 4 free-swimming Galapagos sharks *Carcharhinus galapagensis* associated with a shark ecotourism operation near Haleiwa, Hawaii, USA. These transmitter/receiver tags employed mobile peer-to-peer (MP2P) technology that allowed the tagged sharks to exchange codes among each other and to detect other sharks implanted with standard one-way coded acoustic transmitters. Two tags were recovered (after 20 and 132 d); both tags had multiple detections of all other BC tags, and a comparison of detections made by these tags to those made by a fixed array of standard VR2 receivers indicated that the BC tags accurately captured the 'presence-absence' patterns of the other tagged sharks. Importantly, the BC tags detected sharks that were beyond the range of the fixed receiver array. The results indicate that the BC tag/MP2P approach can elucidate important inter-and intra-specific interactions among individuals in areas remote from traditional fixed receiver arrays.

KEY WORDS: Business card tags · MP2P · Shark movements · Inter-animal telemetry

INTRODUCTION

Significant new insights into the biology of many marine species could be achieved by being able to observe the timing, frequency, and duration of interactions between individual animals when they are moving freely in their natural environments. These insights are particularly pertinent to the improved management and conservation of heavily exploited or endangered species. Interactions of interest include intraspecific behaviors such as schooling (e.g. school cohesion, longevity), the timing and duration of spawning aggregations, and the timing and duration of mating pair formation. Inter-specific phenomena of interest include the timing and frequency of predator–prey interactions (e.g. how often tiger sharks and green turtles are in close proximity) and the dynamics of mixed species aggregations such as the co-occurrence of tunas with spotted dolphins.

For decades, biologists have used acoustic telemetry to study the movement patterns and physiology of free-ranging fishes (e.g. Yuen 1970, Carey & Lawson 1973, Carey & Robison 1981, Holland et al. 1992, 1996, Meyer et al. 2000, Meyer & Holland 2005). In addition to the basic acoustic and radio pingers of the early days of tracking, transmitters ('tags') are now available that store environmental and positional data before transmitting the archived record via underwater acoustic modem to underwater listening stations or, in the case of pop-up tags, to satellites (e.g. Holland et al. 2001, Voegeli et al. 2001, Bruce et al. 2006). Despite these technological advances, major gaps remain in our understanding of basic inter-individual interactions within and among species. The recent development of fast acquisition GPS technology (Rutz & Hays 2009) holds the promise of facilitating observations of close inter-individual interactions among air-breathing species that must come to the ocean surface, but for fishes, acoustic technologies offer the only realistic option for detecting inter-individual encounters.

Data on inter-individual interactions could be obtained by equipping individuals with tags that both transmit their own code and receive and store signals (i.e. tag number) from other tagged animals. In other

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words, when 2 or more tagged individuals come within transmission range, they exchange their individual identification codes and record the time at which the interaction occurred. This has been called the 'business card' tag (BC tag) concept. Importantly, the use of animal-borne mobile receivers takes the receiver (i.e. the tag) to the locations that are important to the animals rather than being situated in fixed locations that are chosen either as a best guess to be an important location by the researcher or because the receiver site is easily accessible. Thus, mobile peer-to-peer (MP2P) technologies offer new opportunities for characterizing interactions among animals in locations important to them rather than to the observer. The key attribute distinguishing the MP2P approach from traditional biotelemetry is that the exchange of information is between individuals (peers) rather than a transmission of data exclusively and directly from individuals to a base station such as a tracking receiver or listening station (e.g. Kortuem et al. 2001). The BC tag concept is not designed to detect 'ships passing in the night' interactions when animals are only very briefly and rarely in proximity to each other. Rather, the BC tag is intended to detect interactions that occur for periods of several minutes or more or, alternatively, brief individual events that are repeated frequently over prolonged periods.

The present pilot study was designed to evaluate the performance of BC tags and to demonstrate the types of insight into animal behavior that these types of tags could provide. Under typical field conditions, we tested a prototype MP2P technology that uses acoustic transmissions to exchange unique identification codes between tagged animals during at-sea encounters. The time of these encounters was also stored by each tag. Experiments consisted of 2 types: (1) transmitter range and detection efficacy evaluations in controlled settings and (2) deployment of BC tags on free-ranging sharks. The host animals were Galapagos sharks *Carcharhinus galapagensis* associated with a shark cage-diving ecotourism operation in Hawaii. Specific questions addressed included: (1) Does transceiver duty cycle influence detection rates? (2) How frequently do BC tag-equipped sharks detect one another and other sharks carrying conventional one-way transmitters? (3) Can mobile and fixed receivers be combined to provide spatial context for shark encounter data?

MATERIALS AND METHODS

Overview. Detection range and detection efficacy experiments were conducted at the same location (21° 37′ 48″ N, 158° 08′ 25″ W) where the tags were subsequently deployed on free-ranging sharks. Following these tests, we deployed prototype Vemco BC tags on 4 Galapagos sharks captured at a cage-diving ecotourism site off Haleiwa, Oahu, Hawaiian Islands (Fig. 1). At the time of the experiment, the island of Oahu was surrounded by an array of 24 stationary receivers (Vemco VR2) capable of detecting both BC tags and conventional coded transmitters (Fig. 1). Before the BC tags were deployed, 32 sharks (21 Galapagos, 10 sandbar *Carcharhinus plumbeus*, and 1 tiger shark *Galeocerdo cuvier*) had previously been captured at the ecotourism site and equipped with conventional coded acoustic transmitters (Vemco V16, each with unique identification codes transmitted at randomized intervals ranging from 150 to 300 s). Thus, the experimental design allowed BC tag-equipped sharks to (1) detect one another, (2) detect other sharks equipped with conventional V16 transmitters, and (3) be detected by fixed receivers stationed at various locations around the island of Oahu.

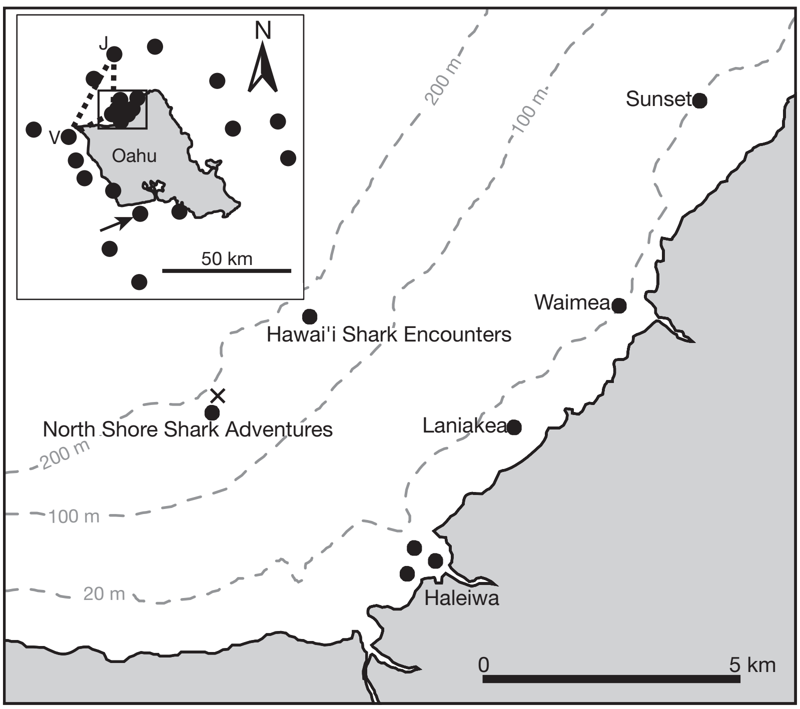

Fig. 1. North coast and island of Oahu (inset) showing locations of acoustic receivers (●) and capture site of Galapagos sharks equipped with business card (BC) tags (×). Inset: dashed lines indicate movements of BC-tagged (BCT) Shark BCT4 among 4 of the 24 fixed VR2 receiver stations around Oahu; detections occurred at the 2 inshore shark tourism moorings and fish-aggregating devices J and V. Arrow denotes tagging location of a sandbar shark tagged as part of a separate experiment but detected by BCT4

BC tag technical specifications. The prototype BC tag combined a 69 kHz ultrasonic transmitter and receiver in a single device (Table 1). The identification coding system used by this device is identical to the Vemco VR system of underwater receivers and coded-pulse ultrasonic transmitters. Each BC tag transmits a unique identification code and can be set to either high or low transmission power (Table 1). The BC tag receiver is constantly cycled on and off based on 3 user-programmable parameters: (1) receiver on time: the time, in seconds, that the receiver is actively listening; (2) duty cycle: the overall percentage of the time (on average) that the receiver is on; and (3) receiver off time randomization: the percentage of randomization applied to the off time. The off time is when the receiver is 'deaf' and the tag ID code is being transmitted. The off time is randomized to avoid synchronization that could lead to multiple BC tags always being in receiver mode at the same time, in which case they would never detect each other. In normal operation mode, the BC tag alternately transmits its ID and listens for other tags in the area. BC tags can also be set to transmit during the receive cycle, resulting in short deaf periods to avoid self-detection. The tag must be physically recovered to retrieve stored data. Stored data are retrieved from the BC tag via an infrared data link to a computer running the BC tag application software.

Prelilminary testing of BC tag parameters. Preliminary field testing was performed to determine detection ranges at the selected field site and to aid parameter selection for the subsequent deployment of BC tags on sharks. The goal was to find a duty cycle that would optimize the probability of BC tags detecting each other during a spatial encounter (i.e. a potentially brief period when 2 BC tag-equipped sharks swim within detection range of one another) while maximizing the lifetime of the tag (i.e. the battery). Tests consisted of fixing 2 BC tags to moorings at the ecotourism sites and deploying another 2 BC tags from a skiff that was initially positioned over the fixed tags and then allowed to slowly drift up to 1.6 km away. Both skiff and mooring deployments included 1 BC tag set to high transmission power and 1 set to low transmission power. A VR100 receiver aboard the skiff recorded BC tag transmissions and geographic position of the drifting skiff for each BC tag transmission received. The detection range of successful BC tag–BC tag communications was calculated by comparing 'time-stamped' BC tag detection records with the georeferenced VR100 'master' record of all BC tag transmissions recorded during drift tracks. BC tag detection range and performance tests were carried out in calm conditions with varying tidal currents. In total, 5 drift tests were performed (drift track lengths = 550 to 1473 m, durations = 0.6 to 1.4 h, speed over ground = 0.4 to 1.2 km h^{-1}, mooring BC tag to skiff BC tag distances = 35 to 1600 m). During the first 2 drift tests, BC tags were set to listen for 20 min, followed by a transmission phase of between 8.8 and 17.6 min. This setting proved to be highly ineffective, producing only 3 BC tag–BC tag detections within a total test time of 1.9 h. Consequently, a more rapid duty cycle was selected for the subsequent 3 drift tests: BC tag duty cycles were set so that each tag transmitted for between 2.2 and 4.4 min (during which time tags were 'deaf' to incoming codes) and then listened for 5 min, repeating this cycle throughout the deployment. This duty cycle yielded approximately 7 listening and 7 transmission phases h^{-1}. Three drift tracks were conducted over a total period of 3.3 h with this rapid BC tag duty cycle. Each drift track had a different start position and orientation, producing drifting-skiff BC tags to fixed-mooring BC tag ranges of between 35 and 1400 m. The total number of successful BC tag–BC tag detections during 3.3 h of the rapid duty cycle ranged from 6 to 20 for low power transmissions, and 9 to 25 for high power transmissions. Maximum BC tag–BC tag detection ranges for tags transmitting at high power ranged from 170 to 925 m (mean ± SE = 630 ± 180 m). Maximum BC tag–BC tag detection ranges for tags transmitting at low power ranged from 158 to 547 m (mean = 426 ± 90 m). Note that as with the current tests, acoustic tag detection ranges can be very variable both from site to site and at the same site over time. This variability depends on factors such as sea state, oceanographic conditions, tag orientation, anthropogenic noise, and the number of tags in the area that can cause transmission 'collisions.'

Table 1. Prototype business card (BC) tag technical specifications

Parameter	Specification
Physical	
Diameter	22 mm
Length	121 mm
Weight (in air)	66 g
Operating temperature	−5 to +40°C
Battery	AA lithium, non-replaceable
Receiver	
Frequency	69 kHz
Memory	8 MB (ca. 1 million detections)
Transmitter	
Frequency	69 kHz
Output power (low)	>147 dB re 1 µPa @ 1 m
Output power (high)	>153 dB re 1 µPa @ 1 m

BC tag experimental deployment settings. Based on these duty cycle results, BC tag receiver listening time was set to 5 min and transmission times to between 2.2 and 4.4 min during actual deployments on sharks (Table 2). Of the 4 BC tags deployed on Galapagos sharks, all were set to transmit at high power; 2 were

Table 2. Business card (BC) tag settings during actual field deployments on sharks. See text for definitions of settings

BC tag number	Receiver on time (s)	Receiver duty cycle (%)	Receiver off time randomization (±%)	Transmit during receive?	Tag output power	Min. time receiver off (s)	Max. time receiver off (s)
1	300	60	33	No	High	134	266
2	300	60	33	Yes	High	134	266
3	300	60	33	Yes	High	134	266
4	300	60	33	No	High	134	266

set to transmit during receive and 2 to listen only during receive (Table 2).

Shark capture, tagging, and BC tag recovery. Sharks were captured using handlines baited with mackerel and brought alongside a 6 m skiff, where they were tail-roped and inverted to initiate tonic immobility (Holland et al. 1999). Sharks were measured in this position and then rolled upright to provide access to the dorsal surface. BC tags were attached to sharks via a braided stainless steel wire leader connected to a titanium steel dart inserted through the shark's skin at the base of the dorsal fin and locked in place through the ceratotrichia. The hook was then removed and the shark released. The entire handling process took less than 15 min, and all sharks swam away vigorously on release. BC tag-equipped sharks re-sighted at the ecotourism sites were recaptured with baited handlines and the BC tags retrieved by cutting the wire leader.

RESULTS

Two of 4 BC tags were recovered from Galapagos sharks after 20 and 132 d at liberty (Table 3). The recovered BC tags had recorded 4506 and 4875 detections of 28 and 30 transmitter-equipped sharks, respectively. Each recovered BC tag had detected all 3 other BC-tagged Galapagos sharks on multiple occasions. Detections from the array of fixed VR2 receivers revealed that BC tag-equipped sharks spent periods of days or weeks more or less constantly associated with the ecotourism sites where they were initially captured and tagged. Both recovered BC tags had logged thousands of detections of other sharks around the ecotourism sites. One shark (BC-tagged, BCT4) was also detected by receivers attached to fish-aggregating devices (FADs) up to 30 km away from the release site (Fig. 1).

Table 3. *Carcharhinus galapagensis.* Summary data for Galapagos sharks equipped with business card (BC) tags. Dates shown as mm/dd/yy

BC tag number	Total length (cm)	Sex	Date deployed	Date recovered	Days at liberty
1	185	M	05/19/08	–	–
2	235	M	05/19/08	06/08/08	20
3	230	M	05/19/08	–	–
4	235	M	05/28/08	10/07/08	132

The first BC tag-equipped shark recaptured (BCT2) was absent from the ecotourism site for 2 d immediately after release but was then detected daily at this location for the remaining period at liberty (Fig. 2). During the 2 d of absence from the VR2 array, this fish detected 11 other sharks (including 1 of the BC-tagged animals) that were not being detected at that time by the VR2 array. After the 2 d of absence, BCT2 returned to the ecotourism site where, after 18 d, it was recaptured. During this period of residency, it detected all other V16-tagged sharks that were also being detected during this period by the VR2 attached to the mooring buoys.

The second BC tag-equipped shark recaptured (BCT4) was detected regularly around the ecotourism site for 24 d after release. It then left the area; the dramatic change in the number of detections made by BCT4 after 21 June 2008 clearly delineates when this shark left the shark ecotourism site (Fig. 2c). On the day following its departure, BCT4 was detected at FAD 'J' located 21 km from the ecotourism site and, 2 d later, at FAD 'V'. The distance between FAD J and V is 37 km, and the timing of the detections by the VR2 receivers on these FADs shows that BCT4 moved between these 2 locations in 19.25 h – a straight line speed of 1.9 km h^{-1} (Fig. 1). This shark was not detected again by VR2 receivers on the FAD array or the VR2 units on the ecotourism buoys, but it was recaptured at the ecotourism site 104 d later, at which point the tag battery was dead. For the initial 24 d period of almost constant residency, a comparison of the detections of bottom lines in Fig. 2a and b shows that BCT4 was detecting BCT1 when the VR2 array was not (even though the VR2 array was detecting BCT4; top line, Fig. 2a). Closer inspection of the timing of these events reveals that the VR2 detections of BCT4 were occurring during the day, whereas BCT4 was detecting BCT1 at night. That is, BCT4 was leaving the ecotourism site at night and meeting BCT1 at some other location remote from the array.

After BCT4 left the shark tourism site on 22 June (indicated by absence of hits after this date, top line in

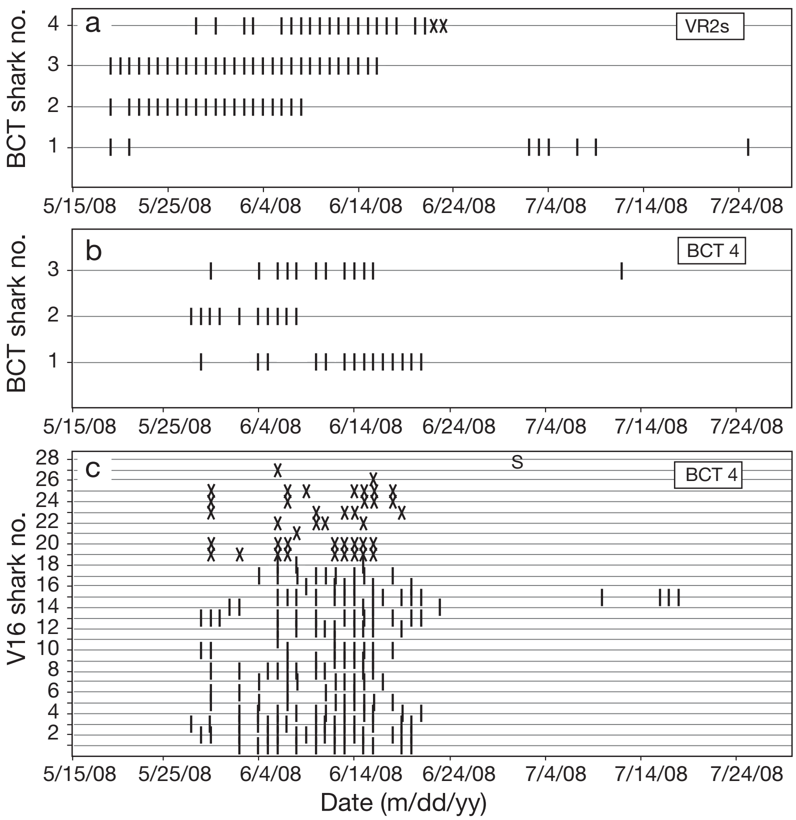

Fig. 2. *Carcharhinus galapagensis.* Abacus plots showing (a) detection dates of 4 business card tag (BCT)-equipped sharks by VR2 receivers stationed at ecotourism sites (vertical lines) and offshore fish-aggregating devices (×); (b) detection dates (vertical lines) of BCT 1, 2, and 3 by BCT4; (c) detection dates of V16-equipped sandbar (crosses) and Galapagos (vertical lines) sharks by BCT4. Detection of a sandbar shark tagged on the south shore of Oahu (see Fig. 1) marked by 's'

Fig. 2a), it detected 3 other tagged sharks that were beyond the range of any fixed receivers in the array. While out of range of any VR2, BCT4 detected a V16-equipped Galapagos shark on multiple occasions between 10 and 20 July 2008 (Fig. 2c, line 13), and on 12 July, it also detected BCT3. On 2 July, it detected a female sandbar shark ('s' in Fig. 2c, line 28) that was tagged on the south shore of Oahu as part of a separate experiment (Fig. 1). Female sharks tagged on the south shore seem to avoid the north shore of Oahu, but both males and females have been detected on the west shore (C. G. Meyer unpubl. data), suggesting that this encounter may have occurred when BCT4 moved to the west shore of Oahu.

DISCUSSION

This study represents the first use of MP2P technology in tags deployed on marine animals. At the ecotourism sites where multiple sharks made repeated visits, BC tags programmed with fairly rapid on/off duty cycles (e.g. 7 listening-transmission cycles h^{-1}) were able to detect tagged sharks with an efficacy close to that of the VR2 receivers that were in permanent 'on' (listening) mode. Certainly, the BC tags were able to accurately capture the basic presence-absence characteristics of the other tagged sharks. Perhaps more exciting, the 2 recovered BC tags detected other tagged sharks when they were out of range of the receivers in the fixed array. That is, the BC-tagged sharks were traveling beyond the range of the fixed receivers to sites that were populated by other tagged sharks. These types of result are a validation of the potential utility of the BC tag concept wherein the tagged animals carry the monitoring system to places that are biologically significant.

Our experimental design included both moving peers (V16- and BC tag-equipped sharks) and fixed peers (VR2 receivers). This combination provided greater insight into shark behavior than would have been derived independently from either fixed receivers or BC tags. The BC tags yielded temporal data on encounters with other transmitter-equipped sharks, and the VR2 receivers provided a spatial context for some of this information. By comparing the VR2 and BC tag records, we were able to determine that dense clusters of detections logged by BC tags occurred in shark aggregations associated with cage-diving sites. Similarly, based on the delay (typically, about 30 min) between BCT4 being detected at the ecotourism mooring during the day and BCT1 at night and on the swim speeds exhibited by BCT4 moving between FADs J and V (1.9 km h^{-1}), these nightly interactions were probably occurring about 1000 m from the ecotourism mooring site. Less frequent detections of other tagged sharks occurred at unknown locations.

These examples show that spatial context is needed to better interpret BC tag data. Currently, we can determine when animals have encountered each other, but unless these events occur near a fixed receiver, we cannot know precisely where the interactions are occurring. Deploying acoustic locator transmitters ('beacons') at multiple known locations throughout areas of interest could help to identify the locations of events recorded by the current generation of BC tags. This approach would be relatively inexpensive and suitable for use even in deep-water settings (i.e. long-life transmitters on simple weighted moorings could be dropped from the surface into deep water with no requirement for recovery). In the future, more sophisticated BC tags could receive positional information from surface peers transmitting GPS positions via ultrasonic encoding. Such peers could include ships, ocean buoys, air-breathing marine animals, or even the host animal equipped with multiple instruments (e.g. a shark equipped with a surgically implanted BC tag and an external towed GPS tag that is capable of communicating with the implanted acoustic transmitting tag). Archival (non-transmitting) tags are already available that can detect and record GPS coordinates encoded in the echosounder emissions of surface vessels (Star-Oddi). Hybrid tags combining MP2P technologies with light-based geolocation capabilities are also theoretically possible, but the size and power requirements of such devices have not yet been investigated.

Even without improved geolocation capabilities, the success of the current small-scale testing of BC tags hints at the insights that could be derived from the deployment of these types of devices. The potential applications include conservation-related questions such as the degree of cohesion of groups of marine mammals while they are at sea, and school fidelity dynamics in heavily exploited species such as tunas. Population assessments are frequently based on tag-recapture data that presuppose uniform mixing of tags within the larger population. These assumptions would benefit from understanding the longevity of school cohesion and whether there are long-term bonds between individuals that violate the assumption of uniform mixing of tags. These questions could be addressed by placing BC tags on multiple animals from a single school. Several species of sharks (including heavily exploited blue sharks) show sex-dependent geographic separation, and understanding the timing and duration of mating-related mixing would inform estimates of when these species are particularly vulnerable to exploitation. The same considerations apply to reef fishes that aggregate at spawning sites. Also, exposure of endangered species to predation risk could be assessed by tagging both predators and prey — such as tiger sharks and green turtles — at sites where these interactions are known to occur.

One major limitation of the prototype BC tag is that it lacks the ability to autonomously transfer archived data; the tags must be physically recovered to download information. Despite this limitation, our results show that the prototype BC tag can still provide valuable data in situations where there is a high probability of physically recovering the tags. For instance, based on previous tagging studies, high recovery rates can be anticipated from certain commercial fisheries (e.g. 20 to 40 % in some FAD-associated tuna fisheries; Dagorn et al. 2007) and from predator-prey systems where either predator or prey occasionally come ashore or are predictable in their movements (e.g. seals, turtles, penguins) such that BC tags could be recovered at haul-out or resting sites. Remote download capability (either sonically underwater or via VHF in air) would be an important enhancement for future BC tags and would considerably increase their utility for studying biological systems and decrease the cost per datum for recovered information.

Numerous engineering challenges are associated with making future, more sophisticated generations of the BC tag and allied MP2P networks for use in marine settings. For example, energy consumption may ultimately limit BC tag capabilities. Sonic transceiving technologies are energy intensive, and the prototype BC tag batteries were dead after <4 mo of deployment. The duty cycle of current BC tags could be adjusted to conserve energy, but this may compromise BC tag ability to detect peers. Our results suggest that BC tags programmed with rapid duty cycles can document a spectrum of behaviors ranging from schooling (or aggregative behavior) to occasional encounters between instrumented marine animals. However, short duty cycles are the most energy expensive. Duty cycles designed around key times of interest such as crepuscular or nocturnal periods or lunar or seasonal rhythms could significantly extend the lifetime of BC tags.

Information exchanged between peers can range from simple unique identification codes to complex data sets encapsulating an animal's historical activities and environments. Peers can be anything from conspecific individuals to inanimate objects such as ships, ocean buoys, or autonomous gliders. MP2P architecture allows the histories of multiple individuals to be collected and passed to a base station by a single peer. Because data retrieval is challenging in marine settings, peer-to-peer data transfer offers major advantages over conventional 'direct path' methods of data recovery where each individual must either be recovered or remotely communicate data to a base station. Results from the present study support starting with simple architecture and allowing empirical data from real-world deployments to guide iterative development of future generations of marine animal MP2P systems.

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