Use of CDMA Acoustic Telemetry to Document 3-D Positions of Fish: Relevance to the Design and Monitoring of Aquatic Protected Areas

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ABSTRACT

Knowledge of animal spatial ecology is essential for the design and siting of proposed aquatic protected areas (APAs), as well as the assessment and monitoring of existing ones. Acoustic telemetry is one of the primary tools for the assessment of animal movements in aquatic systems through either manual tracking or the establishment of fixed receiving stations. Recent technological developments in code division multiple access (CDMA) acoustic telemetry now enable the simultaneous real-time monitoring of numerous individual fish at fine time scales providing APA researchers with a robust new tool. Fish can be positioned in three-dimensions with sub-meter accuracy in both deep and shallow waters. Here, we describe a whole-lake environmental observatory that includes a 13-hydrophone acoustic telemetry array that has been used to monitor the position of 22 tagged fish at 15 sec intervals. Although we use a freshwater fish and environment as a case study, this telemetry system is equally useful for marine environments including under-ice. We evaluate the applicability of CDMA MAP technology to address pressing questions in applied APA research. The CDMA MAP system provides the flexibility to collect information at multiple spatial-temporal scales, responding to the varied levels of detail and precision required for different applications in APA research. When combined with the suite of other telemetry and monitoring approaches available, CDMA MAP technology will enable researchers to document the spatial ecology essential for improving APA science. Furthermore, because numerous animals from different trophic levels can be tracked in real time, CDMA MAP technology will also aid in our understanding of complex community-level dynamics consistent with the shift towards ecosystem-based APA management.

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INTRODUCTION

Efforts to conserve and restore both marine and freshwater environments are increasingly focusing on the use of aquatic protected areas (APAs) (Murray et al., 1999; Houde and Roberts, 2004). These protected areas are intended to achieve a diverse array of objectives such as protection of critical habitat, reduction of fishing effort and harvest (i.e., exploitation), and provision of spawning and recruitment refugia (Polunin, 2002; Shipley, 2004). Despite some disparate results, a growing accumulation of research supports the notion that aquatic protected areas are effective strategies for managing and conserving both freshwater (Saunders et al., 2002; Crivelli, 2002) and marine (Mosquera et

al., 2000; Cote et al., 2001; Halpern and Warner, 2002; Halpern, 2003) ecosystems based on endpoints such as increases in fish species richness, biomass and diversity. To further refine our understanding of aquatic protected area performance, scientists require detailed information on the spatial ecology and movement of aquatic organisms at relevant scales (Nowlis and Roberts, 1999; Pittman and McAlpine, 2003; Gaines et al., 2003). For example, selection and design of protected areas requires basic information of animal movement and habitat use to determine precisely where protected areas should be sited and how they should be managed (Kramer and Chapman, 1999; Roberts et al., 2003). Similarly, monitoring and assessment of existing protected areas requires knowledge of individual fish behaviour relative to protected area boundaries (Zeller and Russ, 1998). Although APAs are often viewed as an ecosystem-level approach (Shipley, 2004), there is still the need to understand the spatial ecology of individual organisms. Here, we describe a novel approach for examining the spatial ecology of animals and in particular fish relative to APAs focusing on a case study from a freshwater system.

Concept

Studies of fish spatial ecology are challenging for a variety of reasons leading researchers to utilize technological solutions such as telemetry (Lucas and Baras, 2000; Cooke et al., 2004). Telemetry has indeed become the standard tool for research and monitoring of fish behaviour in APAs (See O'Dor et al., 2001; Davis, 2004). However, we contend that at present, few studies have continuously monitored fish movement in real time or at a scale that enables sufficiently precise positioning to determine how much time an animal spends inside/outside specific habitats and potential or existing protected area boundaries. The most common approaches involve manual tracking of individuals at intervals ranging from hours to weeks and providing gross

estimates of position (e.g., Meyer et al., 2000; Holland et al., 1996; Russ and Alcala, 1996; Zeller and Russ, 1998). Acknowledging the need to obtain more detailed and continuous information for multiple individuals across broader areas, researchers have turned to acoustic fixed telemetry monitoring stations that continuously scan for tagged individuals and logging data when transmitters are detected (Lindholm and Auster, 2003). Strategic positioning of multiple stations coupled with the use of coded depth sensing transmitters yields even more detailed information on animal position (e.g., Cote et al., 1997; O'Dor et al., 2001; Parsons et al., 2003) but collisions received from overlapping transmissions reduces sampling efficiency (O'Dor et al., 2001) and can bias data (Gaines et al., 2003). In fact, until the recent development of acoustic code division multiple access (CDMA) MAP technology (See Niezgoda et al., 2002), it has been impossible to simultaneously monitor numerous individuals in real time with acoustic telemetry. CDMA enables multiple sensor transmitters to be detected simultaneously such that researchers can use more rapid pulse bursts and thus obtain more valid and precise positions for individual fish in relation to ambient parameters (i.e., temperature). Here, we describe the application of an acoustic CDMA MAP system as part of a broader ecological observatory to provide information on animal position at spatial and temporal scales that are needed to effectively assess APA performance.

The Ecological Observatory and Site Description

In 2003, a freshwater lake (Warner Lake, Queen's University Biological Station [QUBS]) was instrumented with a CDMA acoustic telemetry system as the backbone of an aquatic "ecological observatory". The observatory extends the traditional telemetry study involving manual triangulation of a few representative animals to a fully-automated all-season community and species-interactive multi-dimensional view.

Warner Lake is a private research reserve located in eastern Ontario (44°31'N, 76°20'W) wholly enclosed on QUBS property enabling the deployment and field testing of equipment in an undisturbed setting. Furthermore, because fishing and boating activity is restricted to research personnel, it is possible to experimentally induce different exploitation and disturbance regimes. The small lake (18.2 hectare surface area) is comprised of two basins; a smaller shallow basin (max depth = 2m) and a slightly larger deeper basin (max depth = 7m). The entire shallow basin and the near shore regions of the deeper basin have extensive littoral zone characterized by emergent and submergent vegetation and fallen timber. The deeper areas have dense weed beds and the majority of the deeper bottom is covered by *Chara spp* algae. Warner Lake is a closed system for fish and has been the focus of a long-term study on the population ecology of largemouth bass (e.g., Suski, 2000). Beginning in 1992, researchers have conducted underwater nesting surveys of largemouth bass and implanted nesting males with passive integrated transponders (PITs) to monitor individual fish over time providing baseline data for the current research activity.

A pilot study, involving 22 largemouth bass instrumented with acoustic CDMA pressure-temperature transmitters was launched in October 2003 to trial the observatory. Largemouth bass are the largest and most abundant piscivore in the lake, and across North America are the most popular recreational sportfish (Pullis and Laughland, 1999) making them of great interest to fisheries managers. The current single species focus will be abandoned for community level monitoring at the termination of the trial period. The integration of CDMA technology into acoustic telemetry brings the capability of simultaneously monitoring large numbers of instrumented animals. Moreover, fine scale spatial-temporal sampling of large sample populations enables a methodological shift from monitoring a few individuals to an "ecological microscope" that can observe community-environmental interconnections.

CDMA MAP Telemetry System

The Warner Lake Ecological Observatory places requirements on acoustic telemetry monitoring that challenge or exceed the performance envelope of conventional (pulse-position signal coded) technologies. First, to allow for adequate statistical sampling across a cross-section of the biota, acoustic telemetry must have the ability to unambiguously and simultaneously monitor large numbers of tagged animals on a fine spatial-temporal scale. The inherent properties of CDMA that enable large numbers of transmitters to simultaneously communicate over the same frequency band (e.g. cellular telephony; Niezgoda et al., 2002) and provide sub-meter localization (e.g. GPS) lend themselves well to the observatory application. Second, water depth at the site precludes reliable vertical localization of instrumented fish by three-dimensional triangulation. To facilitate precise fish depth estimates an alternative approach is required, namely the use of high-resolution pressure sensing tags (resolution better than ±1m) in concert with two-dimensional triangulation. Third, the shallow littoral regions of the lake, representing key potential habitat for a number of species, requires reliable monitoring. Given that the observatory must provide uninterrupted data collection year round, including the winter months when ice covers the lake, the location of hydrophones must be constrained to the deeper parts of the lake. Such a constraint leaves the littoral zones outside the immediate footprint of the hydrophone array and raises the issue of position solution reliability within near-shore areas. By using hydrophone arrays larger than the theoretical minimum for two-dimensional triangulation (3 hydrophones) reliable tag positioning can take place outside the immediate footprint of the hydrophone array. Fourth, the observatory requires animal behavior to be monitored in relation to ambient water temperature particularly during season transitions. The most efficient and precise means of relating animal location to water temperature is through the use of temperature sensing tags.

To meet the acoustic telemetry requirements of the observatory a CDMA based telemetry system (Lotek MAP_600 P8 configuration) was installed at the observatory. The telemetry equipment consists of two multi-port MAP_600 receivers monitoring a total of 13 hydrophones distributed in such geometry as to provide coverage of the lake, including the littoral zones. Equipment was configured to monitor 8 hydrophones (large basin) with one receiver and the remaining 5 hydrophones (small basin) on the other receiver. A CDMA temperature-pressure sensing transmitter (repetition rate 15 seconds) was also placed at each moored hydrophone location. Although not required for reliable system operation, these transmitters provided static points to monitor ambient water temperature and acted as fixed-point checks for detection performance. Cabling, electrically connecting hydrophones to shore-based receiving equipment, was routed along the bottom of the lake to one point on the shoreline and brought out of the water through an insulated ABS pipe. Hydrophones were moored from fixed posts (steel piping driven into the lake bottom) at approximate depth of 1.5 meters from the water surface to ensure that lake ice conditions would not damage or move the hydrophones. To facilitate sub-meter positioning of instrumented fish all hydrophones were surveyed using differential GPS (± 0.2 meters).

In October 2003, 22 largemouth bass were tagged with CDMA temperature-pressure sensing acoustic transmitters (Lotek CTPM11-25, 11mm x 60mm, repetition rate 15 seconds, life expectancy of 1 year) using the surgical approaches outlined in Cooke et al. (2003). The repetition rate of the tags was selected to ensure transmitter longevity through the fall-winter and winter-spring transitions. Depth and temperature resolution for the fish tags was ± 0.3m (accuracy 0.3m) and ± 0.8°C (accuracy 0.8°C), respectively. In combination with moored tags a total of 35 acoustic transmitters were operational during the study period (October 2003 to April 2004). Over one 24-hour period the transmitter population accounted for 126,720 possible transmission events (unique individual identification every 15 seconds, and ambient sensor data alternating every 15 seconds between temperature and pressure).

System Performance

System analysis and qualification experiments were conducted to assess measured performance in relation to acoustic telemetry requirements of the observatory. Analysis of detection and position solutions generated between October 2003 and April 2004 indicated that on average 75% of tag transmission events were translated into position solutions. Strong littoral utilization of tagged fish, particularly in areas consisting of underwater obstacles to acoustic propagations (logs, rocks and submergent vegetation) account for much of the localization outage (transmission events detected on fewer than three hydrophones).

Differential GPS was used to qualify localization performance with respect to precision and accuracy. A series of experiments was conducted that towed 5 fish tags (additional transmitters to the 35 deployed on fish and moored from hydrophones) behind a boat throughout the lake (particularly the littoral zone). Tow tag depths where distributed in the first 1.5 meters of the water column. The antenna of the GPS unit (Trimble TSC1, ± 0.2 m) was placed directly above the tow tags. Position solutions generated by the receiving equipment were post-processed to identify and threshold filter "gross" outliers (Niezgoda et al., 2002). Figure 1 shows the position solutions of tow tags in relation to the DGPS track for filtered (Figure 1a) and unfiltered (Figure 1b) position solutions. Figure 2 shows the position estimates and DGPS tracks plotted in time and one geographic coordinate for both N-S (Figure 2a) and E-W (Figure 2b). Figure 3 illustrates time versus depth and temperature information from the tags. Figure 3 summarizes depth and temperature information collected from the tow experiment where depth was computed from pressure sensor data. Temperature data shown on Figure 3 appears to fluctuate between two values (approximately 10°C and 11°C). This apparent fluctuation is due to quantization of the sensor output signal on-board the transmitter and reflects the inherent resolution of temperature data (± 0.8°C) for this particular model of fish transmitter. Quantization at the pressure sensor also leads to a

similar effect whereby depth estimate resolution is ± 0.3m. Overall, Figures 1 through 3 illustrate some of the key benefits of CDMA telemetry in relation to observatory requirements. First, the tow experiment demonstrates the ability to achieve sub-meter precision and accuracy both inside and outside (littoral zones) of the hydrophone array footprint. Second, fine scale temporal sampling is achieved in a transmitter traffic environment consisting of 40 transmitters (average rate of position solution per transmission events was approximately 75% or better). Third, the pressure sensor on the fish tags enable realization of three-dimensional positioning in shallow water with sub-meter resolution. Fourth, temperature information from fish sensor tags can be directly correlated to animal location. Detailed information on system performance and outlier filtering processes is forthcoming (G. Niezgoda, unpublished data).

Closer examination of Figures 1 through 3 indicates that when the tow tags were outside the footprint of the hydrophone array, "fine-scale" outliers appear (less than 1% of all position solutions computed for the tow experiment). As discussed in Niezgoda et al. (2002), such outliers are a consequence of numerical instability that may arise when there is insufficient linear independence in the geometry between hydrophones and the transmitter location. All positioning systems based on hyperbolic triangulation (including the Global Position System, i.e., GPS) are susceptible to outlier occurrence given the "right" combination of receiver and transmitter geometry. Experience has shown that areas outside the immediate footprint of a hydrophone array are more prone to outliers than when a transmitter is inside the hydrophone footprint. Typical mitigation strategies include increasing the number of hydrophones that can take part in a position solution and careful design of the hydrophone geometry. Such system-induced outliers can be mitigated by the judicious selection of hydrophone array size (number of hydrophones) and geometry (Niezgoda et al., 2002). However, when numerically induced outliers do appear, an objective and automatic means of identification is re-

FIGURE 1

Aerial overlay of differential GPS with CDMA position solutions in Warner Lake. (A) includes outlier filtering (See Niezgoda et al., (2002)). (B) includes all unfiltered position solutions. Color figures are available on the Marine Technology Society Web site in electronic form.
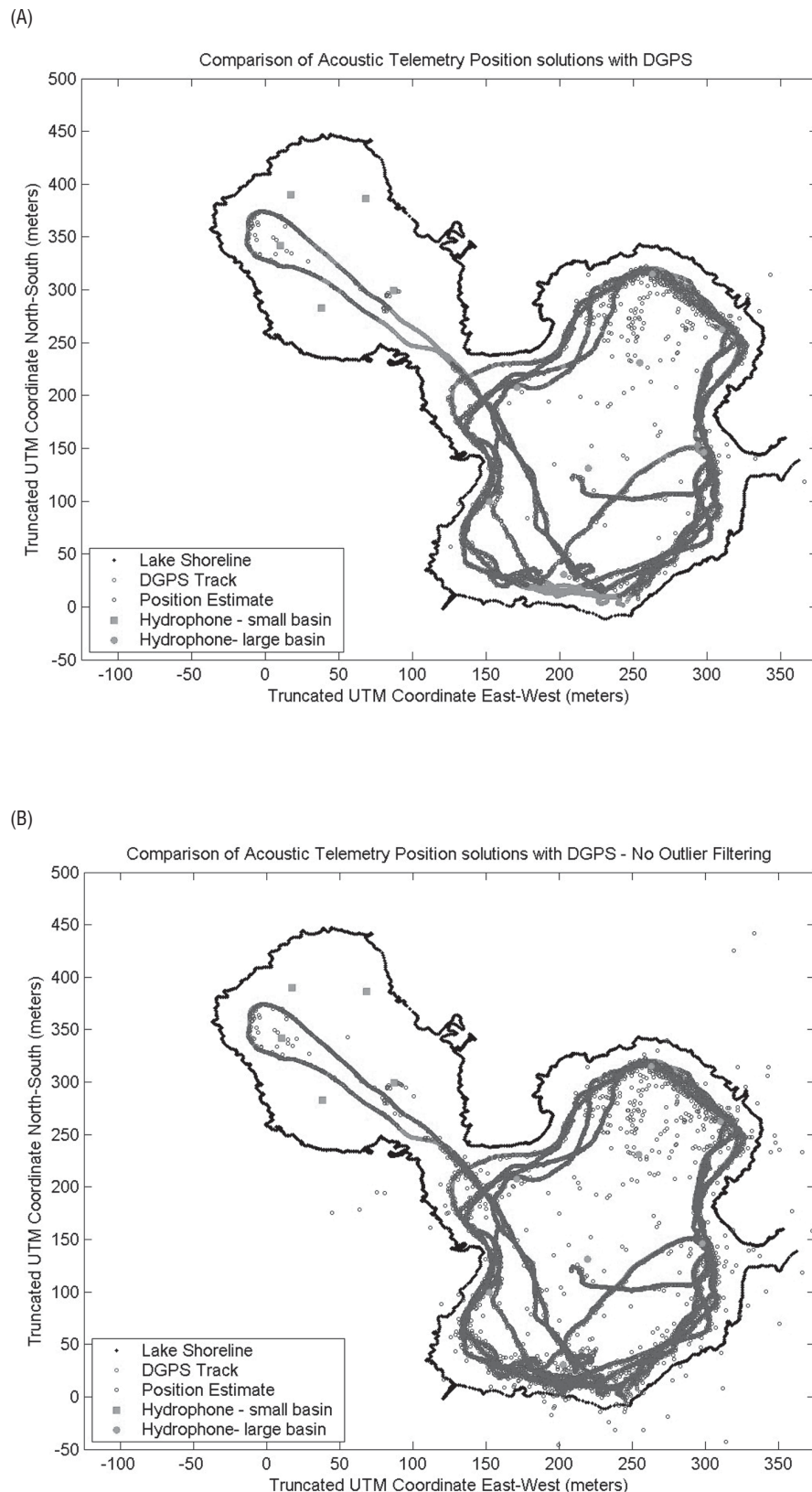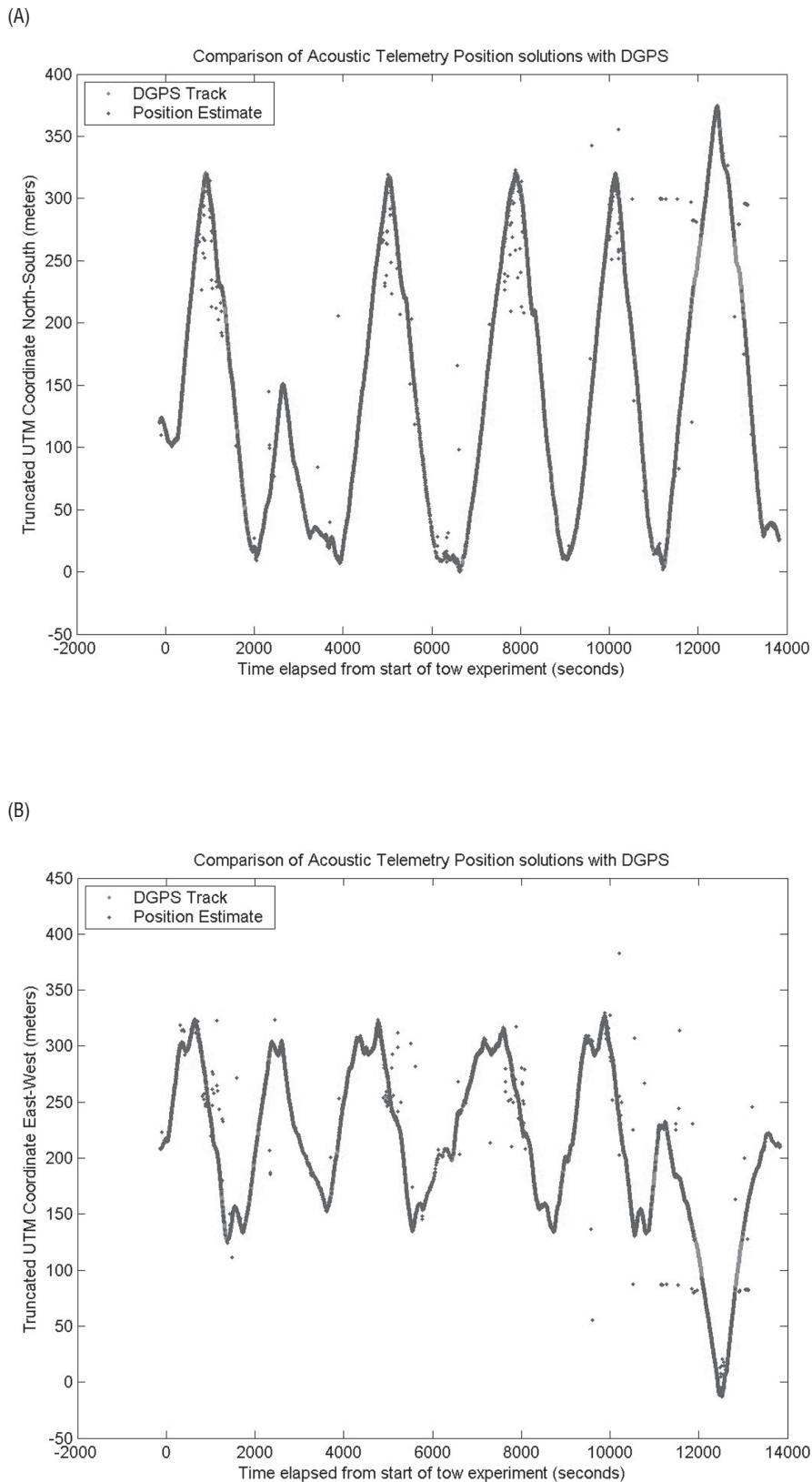
(A)

(B)

FIGURE 2

Temporal evaluation of tow experiment with respect to (A) North-South coordinates and (B) East-West coordinates in Warner Lake. Color figures are

(A)

Comparison of Acoustic Telemetry Position solutions with DGPS

(B)

Comparison of Acoustic Telemetry Position solutions with DGPS

quired. The outlier identification metric as used in this paper (Niezgoda et al., 2002) can be applied to filter the data at the discretion of the user. Typically, the application of outlier filtering is an optimization exercise trading data resolution for outlier removal as the filter threshold level is tightened. Such a trade-off becomes most apparent (and critical) in areas outside the footprint of the hydrophone array. A case in point is the 'channel' region connecting the large and small basins of the lake where position solution coverage is shown in Figure 1a to be intermittent. This channel area is well outside the footprint of both hydrophone arrays (and in some cases line-of-sight for some hydrophones) resulting in a region of reduced position solution reliability. The loss of tow tag position solutions is due to outlier filtering. In Figure 1b outlier filtering has been removed exposing the raw data and when compared to Figure 1a demonstrating the tradeoff between transmitter track resolution and outlier removal.

Relevance to APA Design and Monitoring

At present, the Warner Lake Ecological Observatory is still involved in the trial stage and there has yet to be an opportunity to manipulate exploitation patterns. Data collected during the trial stage will serve as whole-lake baseline information prior to any experimentation. Nonetheless, there are already several findings relevant to the study, design, and management of APAs. Furthermore, our experience with this system enables us to discuss the potential broader application of CDMA technology to address protected area issues in other freshwater or marine systems.

There are several findings relevant to APA design and management that have been derived from the acoustic array. First, a single fish can utilize virtually the entire lake in short periods of time ranging from hours to days. In fact, very little of the entire system is not utilized or traversed by one of the tagged fish on at least some occasion during a 24 hour period (Figure 4a and 5a). Although clearly evident from these figures,

Temperature and depth information collected during tow experiment from sensor tags in Warner Lake. Color figures are available on the Marine Technology Society Web site in electronic form. Experiments were conducted with 5 pressure/temperature tags (additional transmitters to the 35 deployed on fish or moored from hydrophones) towed behind a boat. The tow experiment focused on the littoral areas of the lake (zones used heavy by the fish) to assist in qualifying performance outside the footprint of the array. The 5 test tags transmitted every 5 seconds, alternating data transmission between pressure and temperature sensor data.

Pressure and Temperature readings from towed sensor tags
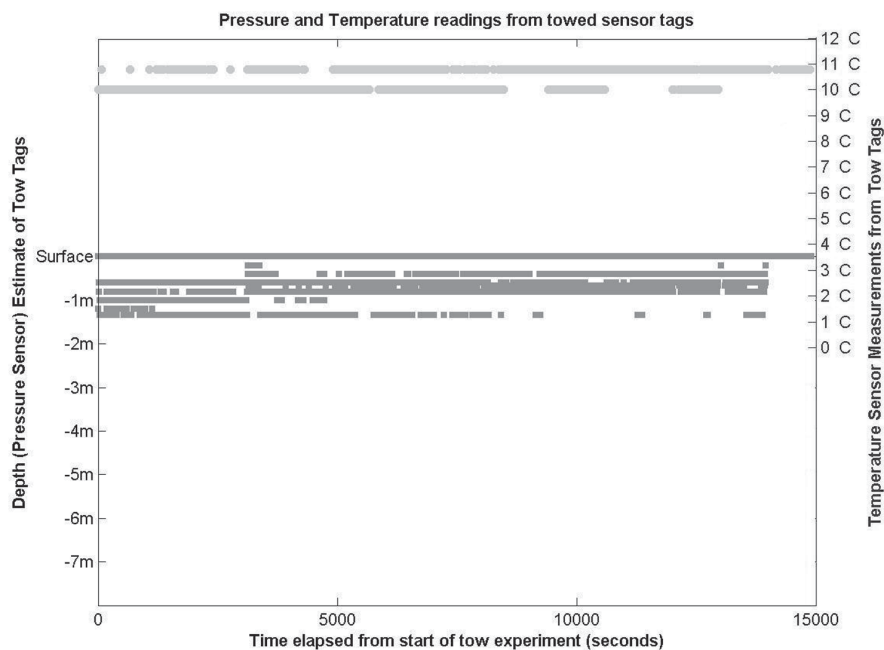
this point is even more apparent when data are visualized as an online animation highlighting movement patterns (See http://www.lotek.com/queensvideo.htm). This pattern of whole lake use is also evident when positions for all fish in the lake are plotted on a single map over one-day periods and evaluated with respect to density (See Figures 4b and 5b). Seasonal influences are evident in these figures and must also be considered when designing APAs. For example, in early November (Figure 4a) fish are distributed throughout the lake with little overlap among individuals (i.e., density plots). However, in late March, fish are congregated in several locations evidenced by the large patches of high density with 5 or more fish present leaving the southern end of the deep basin devoid of tagged fish (Figure 5b).

The level of detail provided in this study is particularly relevant to the assessment of fish activity near the boundaries of proposed or existing reserves. Conventional mobile tracking underestimates fish movement and activity (Demers et al., 1996; Cooke et al., 2001) and does not provide the temporal or spatial resolution necessary to evaluate fine-scale boundary issues. Even fixed stations that are capable of listening for transmitters continuously are unable to provide this level of detail because collisions between transmitters reduce the number of valid signals that are logged (Løkkeborg et al., 2002) even when the acoustic transmitters are coded. The default approach to minimizing collisions in acoustic systems is to randomize transmission intervals of the signal on each tag over periods, typically between 30 sec and 120 seconds (See O'dor et al., 2001). Collisions still occur, and when coupled with large numbers of fish and the infrequent signal transmissions, the temporal resolution is further diminished resulting in underestimates of fish movement (Løkkeborg et al., 2002). Inclusion of CDMA principles in a wireless data logger would eliminate the aforementioned collision problem.

Key to a discussion of acoustic telemetry for assessment of APAs is an understanding of the types of data and questions possible from using different technologies as well as their limitations (See Table 1). In fact, we advocate a multi-level approach consistent with the ecological observatory approach whereby a variety of sensors and technologies are applied to adjust the "microscope" to different levels of detail. For example, if there is a question dealing with fidelity of a group of animals to a large system, an omni-directional coded acoustic logger would provide the information needed to answer the specific query. However, if that research revealed that fish were occupying a specific habitat feature that was near a proposed or existing boundary, then the "microscope" would need to be adjusted and refocused at a finer scale. This would point to a 3-dimensional positioning system. Again, if the researchers were tagging few animals, then a pulse-coded system may suffice. However, if the researchers require the deployment of many tags in a small area or high resolution sensor tags, then CDMA technology is required (e.g., 40 sensor ID tags deployed at the observatory). Issues such as the rate of movement for the animal in question also affect decisions regarding technology. In another example, recent research efforts have focused on how APAs may increase the number of large predators (such as sharks; Micheli et al., 2004), thus increasing predation on lower trophic levels. To our knowledge, there have been no successful attempts to quantify the predatory-prey interactions of individual fish with respect to APA performance. CDMA technology would enable the monitoring of numerous tagged predators and potential prey. With an appropriate repetition rate and the continuous simultaneous monitoring of an aquatic community using CDMA technology, for the first time we would be able to evaluate large and fine scale predator-prey dynamics contributing to our understanding of APA function. Forthcoming developments in nano-tag technology could enable the tracking of smaller animals and life stages to look at key recruitment and source sink issues (Crowder et al., 2000) in APA science. Likewise, wireless variants of a CDMA system would permit a broader scope of applications.

Spatial distribution of 22 telemetered largemouth bass in Warner Lake on Nov 6, 2003 for a 24 hour period. (A) provides individual position solutions whereas (B) provides density histograms at a 1m² scale. This period corresponds to the Winter transition when fish begin to reduce activity associated with a drop in water temperature. Color figures are available on the Marine Technology Society Web site in electronic form.

(A)
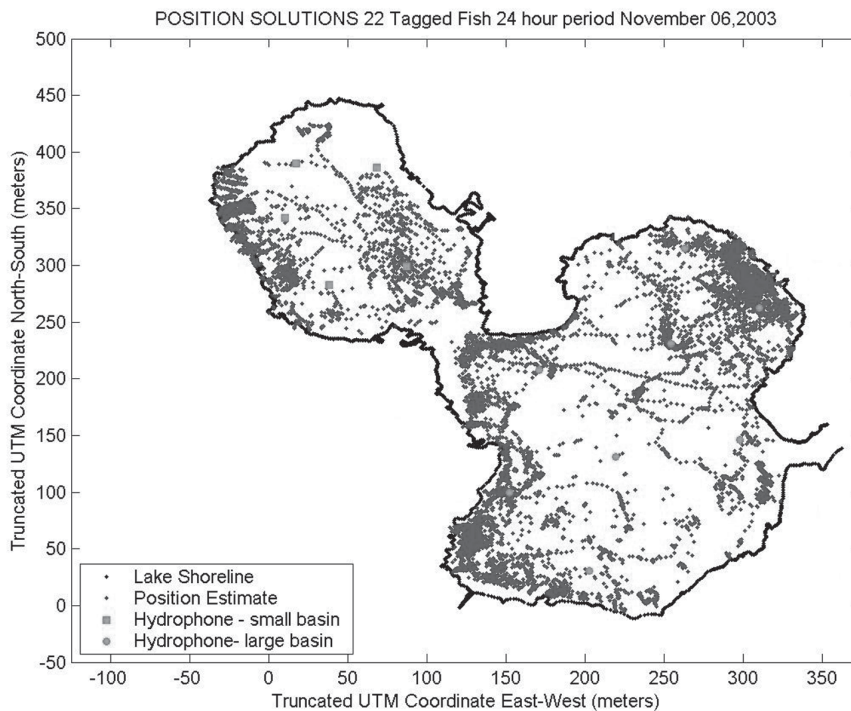
(B)
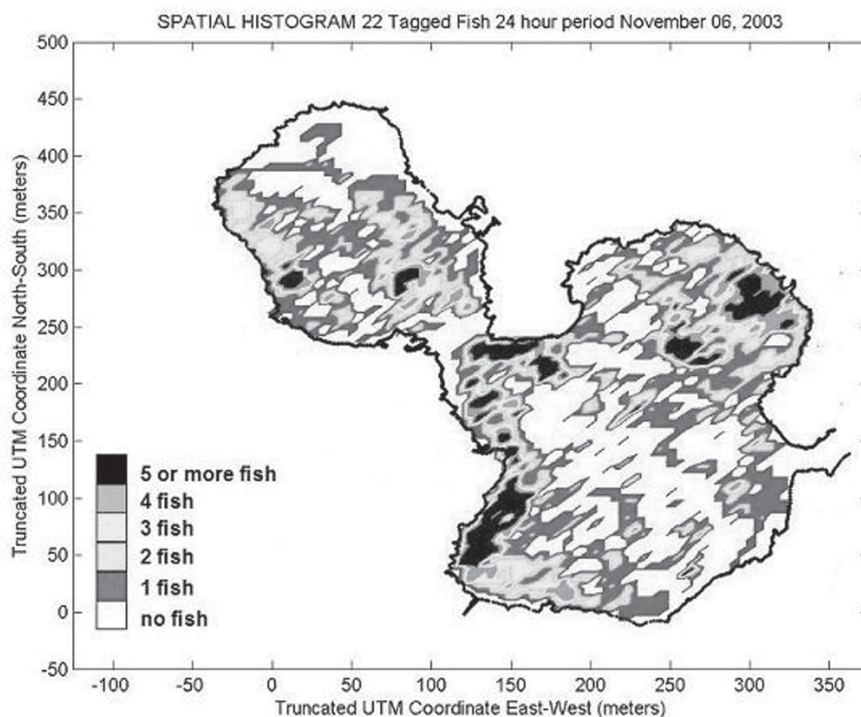
In APA research, sometimes the spatial extent of the area that needs to be monitored is much larger than that of Warner Lake necessitating a larger array footprint. The horizontal footprint of a hydrophone array used for positioning is primarily restricted by two factors; the maximum cable run between a receiver and hydrophones (600 meters for the telemetry system used at the Observatory) and the reception range of the system. To a large extent the logistics and economics of receiver location and routing paths for hydrophone cable dictates the maximum attainable footprint of the array. In larger systems such as the open ocean, this factor may be important, but for Warner Lake, overall lake size and cable lengths were not limiting. The second factor, reception range, is determined by the source level of the transmitter (158dB re 1μPa for the fish tags used at the Observatory) and the characteristics of the environment (i.e., ambient noise, salinity level, the presence of haloclines and thermoclines). In the case of the Observatory reception range was not a limiting factor. Thus, although this specific suite of tools was appropriate for Warner Lake, it may not be applicable to all situations and would require site-specific assessments prior to deployment.

Conclusion

CDMA acoustic telemetry is a robust new tool for the assessment of APA design as well as monitoring. As emphasized earlier, the Warner Lake Ecological Observatory can be viewed as in the context of an "ecological microscope" where the CDMA acoustic telemetry array (with pressure/temperature sensing transmitters) is integral but supplemented with other forms of data collection equipment such as water quality, hydro-acoustics (for habitat, shoreline, lower tropic level monitoring), geolocation data storage tags and video etc. The scientific success of such a monitoring and research program is intrinsically linked to the data management and treatment. Without the appropriate data handling and integration tools, data mining and hypothesis testing become intractable assuming

FIGURE 5

Spatial distribution of 22 telemetered largemouth bass in Warner Lake on March 29, 2003 for a 24 hour period. (A) provides individual position solutions whereas (B) provides density histograms at a 1m² scale. This period corresponds to the Spring transition when fish begin to increase activity associated with an increase in water temperature and ice-out on the lake. Color figures are available on the Marine Technology Society Web site in electronic form.

(A)
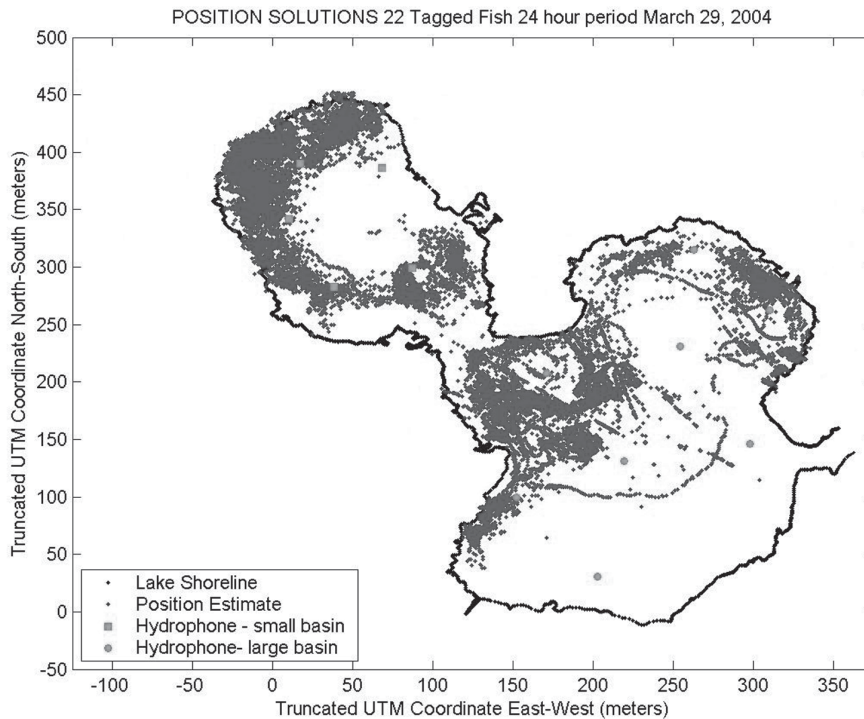
(B)
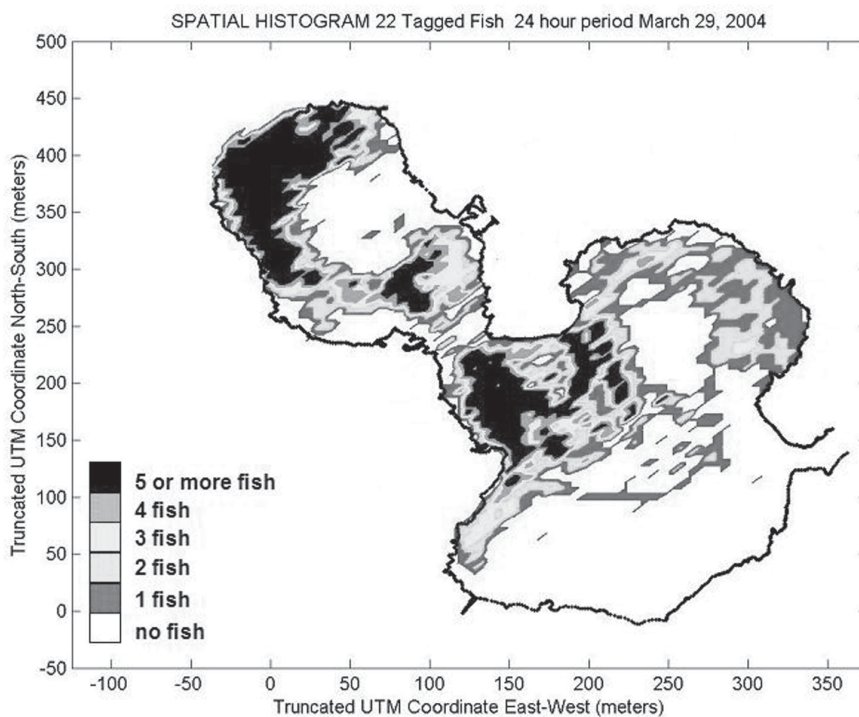
that there is interest in the interaction between multiple variables in a complex environment. We advocate a broad multi-species and system level approach to the assessment of APA function that incorporates the telemetry technique that is appropriate for the specific questions, spatial-temporal scale and system.

Although the aquatic system we used as a case study was small, and our primary goal in developing the Warner Lake Ecological Observatory was not to assess APA function, we believe that this is a useful model for developing and testing techniques that need to be applied to APAs.

When examining ecological systems, the "ecological microscope" has different levels of magnification ranging from broad-scale manual tracking and hydroacoustic surveys down to finer-scale magnification such as sub-meter positioning, localized hydroacoustics, data storage tags and video. Thus, the CDMA acoustic technology does have the potential to contribute to understanding of much larger (than our insular system) APAs. Indeed, prior to deploying a fine-scale positioning system (with a relatively small coverage footprint such as we used here) broader-scale studies are required to identify specific habitats of interest. Collectively, when CDMA technology is applied to both mobile and fixed tracking, it provides the means of large-scale manual tracking down to fine-scale (localized) positioning. CDMA also enables researchers to overcome boundaries that are not just physical but temporal, following fish in real time throughout multiple seasons or at the level of seconds. Also, statistical and experimental design constraints in the context of temporal sampling rate (transmitter repetition rate) and the number of telemetered animals have been limited prior to the introduction of CDMA MAP technology. Collectively, we foresee a key role of CDMA MAP technology in the APA community as we strive to better understand the complex factors that underlie APA function. Furthermore, this technology also has a role in the design and siting of APAs and their boundaries, a contentious but important topic in APA science.

TABLE 1

Comparison and contrast of different acoustic telemetry techniques that can be applied to design and monitoring of aquatic protected areas[1]. Details in each box provide a brief overview of the capability and utility of the different approaches for achieving the desired APA performance parameter.

APA performance parameter	REQUIREMENTS / LIMITATIONS		
Spatial resolution **Temporal resolution** **Real time monitoring** **(e.g. allows for perturbation studies)** **Simultaneous monitoring of large numbers of animals** **Sensor instrumentation** **Identification of critical habitats** **Boundary definition and assessment** **Community Dynamics** **Broad-scale assessment of spatial ecology**	**Acoustic telemetry techniques that arise from an underlying technological base** **Increasing spatial / temporal resolution** →		
	Mobile tracking	**Fixed station data logging (absence / presence)**	**Localization using hyperbolic triangulation**
	Typically on the order of meters to kilometres. Provides low resolution that may underestimate movement	The use of range cells can provide sector localization of animals (meters to kilometres)	Sub-meter accuracy and precision.
	Available only when a fish is acquired and being tracked. Operator fatigue and economics limit tracking to hours or at most days.	Dependent on the rate of animal passage and the rate of tag transmission.	On the order of seconds.
	Available only when a fish is acquired and being tracking. Continuous but typically sporadic sampling.	Limited to animal passage within the reception range of the receiver. Continuous but sporadic.	Requires access (on-site or remote) to the receiver. Continuous and fine temporal/spatial resolution.
	Requires multiple receivers and operators making this use of manual tracking economically non-viable	Requirements depend on target species and the chance the multiple tagged animals pass the station at the same time. Typical approach at present.	Realized through appropriate signal coding and receiving equipment. Enables the ability to monitor animal interactions. Provides statistically valid sampling sizes.
	Integration of sensor tags into manual tracking enables broader scale integration of such information as temperature / depth utilization.	Key to such monitoring applications as estuarine environments (halocline/ thermoclines). Depth profiling of migrating animals.	Enables three-dimensional positioning in sites that make three-dimensional triangulation economically or logistically impossible. Correlation of ambient environment data from sensor tags correlated with position.
	Dependent on animal dynamics. For animals with limited movement or restricted range manual tracking may be sufficient. Otherwise, can provide general indication of critical habitat (a precursor to fixed station or localization telemetry). Combining mobile and fixed stations is also a robust approach.	Next level of magnification prior to localization study. Assisting in further narrowing down the location of habitats. May not be economically viable if area of observation is very large.	Lower levels of magnification have been used to identify general location of habitat. High resolution triangulation provides micro-scale monitoring (meters) of potential habitat.
	Given poor spatial / temporal resolution characteristics of manual tracking crude estimates can be made of boundaries.	Next level of magnification prior to localization study. Assisting in further narrowing down the location boundaries by the use of telemetry gates.	Ideally suited assuming that the geographic scale is appropriate to the reception range and transmission power of the tags.
	Tracking of multiple individuals not viable.	Lack of spatial/ temporal resolution makes measurements crude.	Ideally suited to correlate movement with animal interaction
	Ideally suited given the opportunity to track fish over long distances.	Allows large areas to be converted (or seeded with data loggers).	Limited to reception range of receivers and transmission power of tags.

[1]In some freshwater systems, particularly shallow lotic environments, radio telemetry may be most the appropriate technique. Similarly, in large open systems where animals may traverse entire oceans, archival or pop-up satellite transmitters may be the most appropriate technology.

Acknowledgements

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