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Biologist’s Toolbox

Opportunities for Improving Aquatic Restoration Science and Monitoring through the Use of Animal Electronic-Tagging Technology

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The ecological effectiveness of widespread and costly aquatic restoration efforts is often unknown. We reviewed studies incorporating electronic-tagging techniques (including radio, acoustic, satellite, biologging, and passive integrated transponder tags) into restoration-monitoring programs and discuss novel uses of these technologies and experimental design considerations. We found 25 studies, mostly published after 2005. Most were focused on salmonids or monitored the residency of species at artificial reefs. Few studies used site-level replication or data collected prior to restoration or at control sites, which limits the usefulness of their results for evaluating restoration effectiveness. The use of electronic tags and related sensors (e.g., temperature, depth) can reveal how habitats are used and their associated bioenergetic costs or benefits. These technologies are focused on individual- and population-level responses and complement traditional methods of assessing abundance, richness, and community composition but must be deployed in conjunction with well-designed experiments to truly better inform evaluations of restoration effectiveness.

Keywords: aquatic restoration, biotelemetry, biologging, fish habitat, monitoring

Billions of dollars have been spent on the restoration of aquatic habitats to protect biodiversity and enhance ecosystem services (Bernhardt et al. 2005); however, the success of these efforts is often uncertain. To verify that restoration results in such benefits, a monitoring program should be used to assess its effectiveness; however, such evaluations frequently do not occur or do not provide strong evidence of success or failure (Palmer et al. 2005). Traditional approaches to monitoring ecological responses to restoration activities are focused on populations or communities through the measurement of endpoints such as changes in abundance, richness, or community composition (Ford 1989). In recent years, more-detailed monitoring of the effectiveness of restoration activities has been called for, including measures of ecological processes (e.g., productivity) and animal physiology and behavior (Herrick et al. 2006, Cooke and Suski 2008, Lindell 2008). Advances in electronic-tagging technology provide novel options for assessing the responses of aquatic animals, including a variety of vertebrates (e.g., fishes, mammals, turtles) and large invertebrates (e.g., crabs), but this suite of research tools remains underused in aquatic restoration science.

A wide range of electronic-tagging tools are now available for use in aquatic systems. We define electronic tags to include all biotelemetry and biologging devices that are attached to or implanted in animals. The characteristics of biotelemetry and biologging are similar; both involve remote monitoring of behavioral, physiological, or environmental information. For biotelemetry, a signal emanating from a device (a transmitter) carried by the animal sends information to a receiver. The power for transmission can be derived from an external energy source (e.g., passive integrated transponders, or PIT tags; Gibbons and Andrews 2004), but transmissions are typically powered by an internal battery (e.g., radio and acoustic transmitters; Winter 1996). For biologging, information is recorded and stored in an animalborne device (an archival logger) and downloaded after the logger is later retrieved. The technologies can be coupled, first logging information then transmitting data, usually by satellite, when possible (e.g., pop-up satellite tags). In regard to biotelemetry devices or hybrid technologies, electronic tagging also requires receiver technology to track animals, which can be done manually (e.g., by boat, truck, foot) or by using automated receiver stations (e.g., underwater arrays of acoustic hydrophone receivers, satellites). We refer the
reader to Winter (1996) for details regarding the technological aspects of common electronic-tagging tools.

Traditional electronic-tagging studies have provided a wealth of information on habitat needs and the movement patterns of aquatic animals (especially fishes; for a review, see Lucas and Baras [2000]), which informs restoration design. Recent developments in electronic-tagging technology provide opportunities, suitable for a wide range of budgets, for novel approaches to monitoring the effectiveness of restoration activities. These advancements expand the potential uses of this technology for studying smaller animals (through technology miniaturization) and allow the incorporation of sensors into tags that measure a wide range of environmental (e.g., water temperature, salinity, dissolved oxygen) and physiological (e.g., tail beats, acceleration, heart rate) variables. Furthermore, animal movements and environmental variables can be measured over a variety of spatial and temporal scales, from microscale two- or three-dimensional positioning with submeter accuracy to the scale of oceanic basins (Aksesson 2002) and from seconds to years. Despite these options, few research or monitoring programs focused on biotic responses to aquatic restoration have included the use of electronic-tagging tools. In this article, we review published studies of aquatic restoration in which electronic tags were used on aquatic animals.

We focus our review on the creation, enhancement, rehabilitation, or alteration of physical habitats with the objective of conserving or restoring aquatic biota. We acknowledge that these activities do not all fit a strict definition of ecosystem restoration (i.e., returning ecosystem structure and function to a predisturbance condition; Shields et al. 2003), but we use the term restoration more broadly to encompass the range of activities described above. We included all aquatic restoration activities and taxa but excluded those that did not specifically involve the physical alteration of aquatic environments, in part because electronic tagging in these activities (e.g., dam removal) has been reviewed elsewhere. Specifically, we excluded studies of fish passage effectiveness (Roscoe and Hinch 2010, Bunt et al. 2012), flow regime alterations (Murchie et al. 2008), and fish-attracting devices for which the purpose was studying fish or facilitating their capture (Dempster and Taquet 2004). We acknowledge an inherent literature bias toward fish and large invertebrates, but we discuss the range of aquatic taxa that could be studied directly (by tagging) or indirectly (e.g., by studying tagged predators’ diets). Our objectives were to review and characterize the use of electronic-tagging technology in assessing biotic responses to the physical restoration of aquatic habitats and to identify options and experimental design considerations for the use of electronic-tagging methods in future research and monitoring programs for habitat restoration.

**Literature search**

Two academic search engines, Thomson Reuters’s Web of Knowledge and the Food and Agriculture Organization of the United Nations’s Aquatic Sciences and Fisheries Abstracts, were used to review the scientific literature in October 2011, along with supplemental searches using Google Scholar. A Boolean search term was used to encompass all studies in aquatic ecosystems, all types of electronic tags, and all forms of habitat restoration. The comprehensive search term was (aquatic or freshwater or marine or fish or fishes) and (telem* or ((radio or acoustic or electronic) and (transmitter* or tag*))) or (sonic or ultrasonic) and (transmitter* or tag*) and (archival and logger) or (PSAT or (pop-up and satellite and archival and tag*)) and (restor* or compensation or mitigat* or rehabilitat* or (habitat and (create* or enhance*))) or (habitat or reef) and artifi*), where the asterisk (*) is a search wildcard. The search returned a broad array of studies, many of which were unrelated to the telemetry and physical restoration of aquatic habitats. In addition to excluding studies focused on fish passage, flow regime alteration, and fish-attracting devices, studies that did not involve electronic tagging or aquatic environments were excluded, along with those in which stocking or the introduction of organisms was evaluated. For studies of artificial habitats, only those constructed to create animal habitat were included; structures intended for human use (e.g., farm ponds, oil platforms, urban structures) were excluded.

Each study was reviewed by summarizing the location, type of restoration activity, year of study, study species, ecosystem or habitat, and electronic-tagging method and sensors used. Other monitoring techniques used to complement electronic tagging (e.g., mark–recapture or abundance surveys) were described. The experimental design was described by listing the sampling method (manual or automated), study duration, and sample size. To evaluate the soundness of the experimental design (and thus the ability of the study to estimate effectiveness), we described whether control sites were used (including both natural and unrestored habitats), whether site replication was included (for either controls or treatments), and whether prerestoration data were collected. These measures helped distinguish between studies that quantitatively demonstrated changes resulting from restoration activities and those in which behavior was simply observed in restored habitats. In studies with controls, endpoints were generally compared between restored habitats and natural or unrestored habitats. In studies without controls or prerestoration data, endpoint data were generally provided as summary statistics (e.g., home range size or residency time). We summarized whether the studies provided evidence that restoration actions were effective and described that evidence and any conclusions of the study.

Variables used as measures of restoration effectiveness (i.e., endpoints) that were derived from electronic-tagging methods were described. Residency described the duration for which an animal remained present in a habitat and whether the animal returned on a daily, seasonal, or annual...
basis. This variable was synonymous with site fidelity and contrasted with homing, which described a return to a location after an animal was transported and released elsewhere. Studies in which habitat selection was evaluated on the basis of use relative to availability were separated from studies in which habitat associations were simply described; in the latter, either it was done qualitatively or habitat selection was evaluated without a measure of habitat availability (e.g., tests of differences among the proportion of detections in each habitat). The term activity was used to describe measures of distance moved over time or to determine whether animals were stationary or active. This was contrasted with studies of both swimming speed (based on physiological sensors) and movement paths, in which spatial movement patterns were described. Finally, in some studies, home ranges were calculated over a defined temporal period, using minimum convex polygons, kernel density estimates, or other approaches.

Results of the literature search

Electronic-tagging techniques have been applied in few studies to monitor aquatic restoration activities and their effectiveness. We found only 26 studies matching our criteria, with the earliest published in 1975 (see the supplemental material, available online at http://dx.doi.org/10.1525/bio.2013.63.5.12). Only five of the studies were published prior to 2000 (figure 1). The most commonly assessed restoration activity was the creation of artificial reefs, followed by reconfiguration of stream channels. Other aquatic restoration techniques were rarely listed. A few studies were focused on vegetation removal; the use of cattle exclosures; the addition of large woody debris; or the restoration of wetlands, coastal marshes, or estuaries.

Almost all studies involved fishes; only one study was focused on a different taxon (see the supplemental material): Collins and colleagues (1992) examined the behavior of the European lobster (Homarus gammarus) at artificial reefs. Salmonids were the most commonly studied taxa and were the subject of 42% of the studies in our review.

In most studies, acoustic (58%) or radio (42%) telemetry was used to collect data (see the supplemental material); PIT tags were used only once (Linnansaari et al. 2009). Prior to 2005, only active tracking was used. Since then, 65% of the studies included passive tracking techniques. The studies’ durations ranged from 50 hours to 5 years, with an average duration of just under 1 year. Eight studies lasted for a month or less, whereas nine studies lasted for a year or more. On average, 31 individuals were tagged per study; 65% of the studies had a sample size between 10 and 60. Most studies were focused on a single species, although in each of three studies, two species were tagged. Comparison of restoration treatments with controls occurred in 58% of the studies, but pre- and posttreatment monitoring was reported in only five studies. Site replication was reported in eight studies and generally involved monitoring the same treatment replicated across sites (e.g., Reynolds et al. 2010), although in one study (Topping and Szedlmayer 2011), no single treatment was replicated, despite the monitoring of multiple sites.

Sensors were used in six studies. Sammons and colleagues (2003) used radio tags equipped with mortality sensors to confirm the fate of individuals, and Prince and colleagues (1975) monitored short-term movements of an individual bass (Micropterus sp.) with a temperature-sensing acoustic tag. Radio tags equipped with electromyogram (EMG) sensors were used in three studies. EMG signals were calibrated with swimming speed data for field measurements of energy expenditure, either at only treatment sites (Enders et al. 2007) or at both treatment and control sites (e.g., Makiguchi et al. 2007). In three studies, double tagging with depth- and temperature-sensing data loggers was used to complement radio-tag information and enabled the researchers to determine the horizontal and vertical position of fish (e.g., Makiguchi et al. 2007). The semelparous strategy of the study species (Pacific salmon) also facilitated the retrieval of the data loggers.

A variety of behavioral responses and endpoints were quantified in the studies. Site fidelity, habitat use, and movement or activity patterns were the most frequently quantified, along with the number of residency days. In a minority of the studies, behavior was also compared in restored habitats with behavior in natural or unrestored habitats or under prerestoration conditions. Other responses that were measured included homing ability following displacement (Reynolds et al. 2010), environmental cues associated with dispersal events (Topping and Szedlmayer 2011), and the selection and bioenergetic consequences of migratory routes (Makiguchi et al. 2007).

In several studies, other techniques were combined with telemetry to strengthen the evaluation of restoration. For example, Gent and colleagues (1995) incorporated creel-survey data (on angler effort and catch) into their study.
to further document the response of the largemouth bass (*Micropterus salmoides*) to manipulated water quality. Capture-based techniques were used by Douglas and Abery (2009) to assess brown trout (*Salmo trutta*) abundance following willow removal in stream reaches. Espinoza and colleagues (2011) used capture data of seasonal abundance to complement telemetry for habitat use of the gray smooth-hound shark (*Mustelus californicus*) in a restored estuary. Tupper and Able (2000) combined capture information and a stomach-content analysis with telemetry to examine the movements and feeding habitats of the striped bass (*Morone saxatilis*) in restored and reference salt marshes. Lintermans and colleagues (2010) used radio telemetry and underwater video to evaluate the use of alternative artificial habitats by the Macquarie perch (*Macquaria australasica*) in an Australian reservoir.

In many of the studies, conclusive evidence was not provided of restoration effectiveness, because they lacked controls, replication, or prerestoration monitoring and simply documented residency. Basic evidence of restoration effectiveness in most of the studies was cited when animals used restored habitats over extended periods. A subset of studies demonstrated preferential selection of restored over unrestored habitats. Linnansaari and colleagues (2009) found that Atlantic salmon (*Salmo salar*) parr used a restored reach in all seasons, whereas they avoided a control reach during spring and fall. Similarly, Stoessel and Douglas (2005) showed that brown trout residency was greater in areas where willows (*Salix spp.*) had been removed than in unaltered sites. No evidence was presented that the restoration projects had failed to meet their objectives.

### Summary of existing studies

Our review revealed that few studies have incorporated electronic tagging into monitoring the effectiveness of aquatic restoration activities, but the use of tagging has increased rapidly in the past decade. To date, few studies included strong experimental designs (e.g., the use of controls or before–after comparisons), which limits the usefulness of the results for evaluating effectiveness. In particular, prerestoration monitoring was lacking, as was site-level replication. Monitoring efforts involving electronic tagging most commonly employed measurements of residency at restored sites over a period of months to years. This information cannot be obtained through traditional sampling techniques unless they are intensive and employ mark–recapture procedures, but the results of residency studies provide only basic monitoring data and inform future detailed assessments. Without an experimental component, residency is insufficient to truly assess the effectiveness of a restoration action. For instance, no information is gained on whether the productivity of the system increased or whether the new habitat merely concentrated animals (i.e., whether the habitat improved conditions for survival, growth, and reproduction; Hindell 2007, Cooke and Suski 2008).

Despite the lack of proper experimental design in many of the studies reviewed, there are examples in which sound experimental design led to conclusive results that informed future restoration activities. For instance, Lintermans and colleagues (2010) used radio telemetry to assess the preference of the Macquarie perch, a threatened fish in an Australian reservoir, among three artificial habitats. Their study design included preconstruction monitoring, replicates for each of the constructed habitat types, the monitoring of unaltered control habitats, and a multiseason approach. The results on habitat selection and diel movement patterns demonstrated that the Macquarie perch actively selected artificial rock reefs. Concurrent telemetry-based evaluations of habitat selection in a different reservoir indicated that another threatened fish, the two-spined blackfish (*Gadopsis bispinosus*), would also use artificial rock reef habitats. These results informed the design of new habitats for mitigating habitat losses from reservoir enlargement (Lintermans 2012). Applying this type of experimental design to more aquatic species and ecosystems would undoubtedly advance the science of aquatic restoration.

It is possible that studies finding no effect of restoration activities were missed in our review because of biases against publishing nonsignificant results; however, we included technical reports from government agencies in our review, which reduces the possibility of such bias. Given the costs of and need for restoration of many aquatic ecosystems, it is vital to understand which restoration actions are ineffective or—worse—have deleterious effects on aquatic organisms. Studies that fail to detect a response to a given restoration action are important to publish, because they indicate that alternative approaches to aquatic restoration may be required.

Traditionally, electronic-tagging studies have informed restoration activities by identifying habitat selection at different spatial and temporal scales, but telemetry is rarely incorporated into postrestoration monitoring as validation. As an example of prerestoration sampling, Horton and Guy (2002) identified habitat selection by the spotted bass (*Micropterus punctulatus*) in a Kansas creek using radio telemetry. Habitat selection was evaluated at multiple scales, and the authors recommended that restoration efforts focus on increasing large woody debris and undercut banks in pools (Horton and Guy 2002). Habitat selection data can be explicitly collected prior to each planned restoration activity, although most electronic-tagging studies of habitat selection can also contribute knowledge germane to the design of restored habitats. The assumption is that results are transferable across sites, at least within the same ecoregion.

Alternatively, in several studies excluded from our review, fish responses to potential restoration actions were experimentally evaluated in mesocosm ponds or streams (e.g., Goldsmith et al. 2008, Orpwood et al. 2010). In these studies, PIT tags were used and behavioral responses were evaluated in a controlled experiment that lasted from days to weeks. For example, Orpwood and colleagues (2010) examined
selection by the common roach (*Rutilus rutilus*) of artificial brushwood shelters over open waters and reed beds across a range of densities. In such studies, multiple restoration techniques can be rapidly assessed and compared, and they hold great promise for increasing our understanding of biotic responses to habitat restoration. We excluded them from our review because the effectiveness of an actual restoration activity was not specifically monitored in a natural system, but they do inform an understanding of what might be most effective. Even so, repetition of the approach across species would be necessary for community-level restoration, in contrast to species-specific targeted restoration.

**Recommendations for future studies**

Electronic tagging provides opportunities for assessing more than the presence or relative abundance of animals at restored sites. Electronic-tagging studies can differentiate between species that remain resident in restored habitats and transients and can quantify the duration and timing (diel, seasonal) of habitat use. Furthermore, electronic tagging can be used in environments and conditions in which traditional survey methods would be difficult or impossible, such as in turbid, deep, or flowing water; during floods; or in winter, under ice. Electronic-tagging studies of residency at restored habitats are easier to interpret when restored habitats represent discrete areas in a matrix of unsuitable habitat (e.g., artificial reefs in a large, flat basin). In such cases, only coarse-resolution passive tracking is needed to confirm habitat use.

Advances in electronic-tagging technologies provide novel options for evaluating more than habitat selection and residency. New technologies facilitate the evaluation of restored habitat quality, but such evaluations have been performed in only a few studies (see Enders et al. 2007, Makiguchi et al. 2007). For example, sensors in electronic tags can measure the energetics of habitat use that inform growth estimates, as well as the limnological environment in relation to habitat associations. In terms of energy use, devices that measure fine-scale locomotor activity, such as the frequency of tail beats, EMG activity of axial swimming muscles (Cooke et al. 2004), and jet pressure in cephalopods (e.g., using pressure transducers; Webber and O’Dor 1986) or that measure direct metabolic indicators, such as heart rate or opercular rates (reviewed in Cooke et al. 2004), can identify the costs of occupying different habitats (e.g., contrasting energy use at restored versus degraded habitats, comparing energy use through different reaches of fluvial systems to evaluate whether there are flow refugia in restored habitats; see Makiguchi et al. 2011). In some cases, two- or three-dimensional telemetry arrays can monitor swimming speed at a high resolution to estimate energy use (Hanson et al. 2007).

Electronic tags equipped with environmental sensors that measure temperature, salinity, acidity, or dissolved oxygen can provide detailed data on conditions encountered by animals. Given that physicochemical properties can influence energy use, monitoring environment concomitantly with energy use is a powerful approach for quantifying habitat quality. Increasingly, electronic tags are equipped with cameras that can record (and some even transmit) photographs or video for documenting intra- and interspecific interactions and for indirectly monitoring species that are or life stages of a species at which individuals are too small to study with electronic tags themselves. Some electronic tags can help quantify feeding rates (e.g., camera footage, tilt sensors for benthic fishes, hall sensors to measure mandibular chewing in crabs) or document spawning events. PIT tags enable the identification and measurement of individual animals for life, because there is low tag loss, and recaptured animals can be reevaluated (e.g., for growth, condition). Collectively, this suite of sensor and tagging technologies gives researchers the capacity to assess individual relationships with different habitats, including those that are newly created or restored, and whether they meet the physiological requirements for growth, reproduction, and survival.

Further advances in electronic tagging can expand study design beyond the sensors described above. For example, miniaturization in tag or transmitter designs now allows very small animals to be studied. This facilitates the study of multiple life stages and smaller species or taxa than was previously possible. To date, few studies have incorporated electronic tagging of taxa other than fishes in restoration research. Information on multiple taxa and trophic levels is required to fully understand the response of the biotic community to habitat restoration, although this may still be more feasible in marine rather than freshwater environments because of taxon size. With the development of inexpensive stationary receivers that require little maintenance (especially acoustic receivers), continual long-term monitoring at fine temporal scales, even under harsh conditions, is possible. Fine-scale arrays and new business-card-size tags and cameras can be used to study ecological interactions (e.g., predator–prey interactions, schooling) across individuals and species, extending beyond one taxonomic group (Holland et al. 2010).

Frequent manual tracking or the use of fixed telemetry arrays can determine how soon after construction or restoration habitats are used by animals. Electronic tags are ideal for monitoring how quickly animals colonize constructed or reconnected habitats and how aquatic animals move between various elements of the wider habitat mosaic; however, the rate of colonization into new habitats (e.g., artificial reefs or various structures in reservoirs) has been tracked using animals tagged from surrounding environments in few studies. Such studies could reveal the distances from which colonizers travel to newly created sites and their site fidelity once the new habitats have been found. Moreover, it is also possible to quantify migration among metapopulations and thus improve population estimates in and around restored and degraded habitats (Bacheler et al. 2009).

The selection of electronic-tagging methods depends on the study question, environment, and budget. Options are
often constrained by environmental conditions, because certain tags do not work in all environments. For example, the transmission of acoustic signals can be blocked by dense macrophytes or turbulent waters, and radio telemetry is of limited value in saltwater or when depths are greater than 5 meters (depending on conductivity; Winter 1996). Similarly, PIT tags have limited use in marine environments (but see Jørgensen et al. 2005). Biologging tags are not appropriate when fine-scale spatial information is required but can be useful in closed systems in which systemwide restoration has occurred and physiological endpoints are of interest. For example, biologgers could be used to compare the conditions experienced by organisms in artificial and natural lakes.

Given the cost of most electronic-tagging methods, careful consideration must be given to experimental design to ensure that the results are informative and scientifically sound. Many of the studies reviewed here were largely observational, without an experimental component. Habitat creation activities are essentially ecological experiments, and the relative effectiveness of alternate designs could be assessed with the help of electronic tagging. When it is possible to do so, monitoring should begin prior to restoration and at multiple control sites (Underwood 1994). When multiple control sites are unavailable or the costs of electronic tagging and monitoring at multiple sites are prohibitive, a single control site could be acceptable, provided that the study is carefully designed, analyzed, and interpreted (Stewart-Oaten and Bence 2001). Alternatively, a reference-condition approach may be applicable when before-treatment data are unavailable or cannot be obtained (e.g., the habitat is terrestrial prior to restoration; see Bowman and Somers 2005).

The number of animals to tag depends on whether multiple size classes and sexes will be monitored, the size of the population, the response variable to be measured, and statistical analyses; therefore, sample size and power calculations should be conducted at the experimental design stage (Winter 1996, Rogers and White 2007). In general, estimates of population-level parameters such as residency and survival will require large sample sizes (e.g., more than 30–50 animals), whereas detailed behavioral or physiological studies may be reasonably conducted on fewer than 10 animals in homogeneous conditions. When sample sizes are small, electronic-tagging data may be combined with other observational data to inform models of population-level processes.

To date, the use of electronic tagging has been limited in aquatic restoration science. Only a subset of the existing studies employed a strong experimental approach, and there was little repetition of study design across systems, taxa, or restoration activities. Given the high costs and efforts often required and the limitations of tagging small-bodied species and animals in early life stages, electronic-tagging methods are not appropriate for addressing all questions germane to the effectiveness of aquatic habitat restoration actions. However, traditional community-level monitoring approaches are often insufficient for assessing all questions on the long-term success of these activities (Herrick et al. 2006). Electronic tagging can provide direct information on animal behavior, bioenergetic and physiological responses, and interspecific interactions, and data collection can occur under conditions that would otherwise prohibit field measurements.

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References cited