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Seeking the Fountain of Youth

Fish Passage in China

Indexing Reservoir Aging

FUNCTIONAL AGE AS AN INDICATOR OF RESERVOIR SENESCENCE

It has been conjectured that reservoirs differ in the rate at which they manifest senescence, but no attempt has been made to find an indicator of senescence that performs better than chronological age. We assembled an indicator of functional age by creating a multimetric scale consisting of 10 metrics descriptive of reservoir environments that were expected to change directionally with reservoir senescence. In a sample of 1,022 U.S. reservoirs, chronological age was not correlated with functional age. Functional age was directly related to percentage of cultivated land in the catchment and inversely related to reservoir depth. Moreover, aspects of reservoir fishing quality and fish population characteristics were related to functional age. A multimetric scale to indicate reservoir functional age presents the possibility for management intervention from multiple angles. If a reservoir is functionally aging at an accelerated rate, action may be taken to remedy the conditions contributing most to functional age. Intervention to reduce scores of selected metrics in the scale can potentially reduce the rate of senescence and increase the life expectancy of the reservoir. This leads to the intriguing implication that steps can be taken to reduce functional age and actually make the reservoir grow younger.

La edad funcional como indicador de senescencia en reservorios

Se ha discutido que los reservorios se diferencian entre sí por la tasa a la cual manifiestan senescencia, sin embargo no ha habido esfuerzos para encontrar un indicador de senescencia que funcione mejor que la edad cronológica. Se construyó un indicador de edad funcional mediante una escala multimétrica que consiste en diez métricas descriptivas del ambiente de los reservorios que se previó que cambiaran de dirección a medida que aumenta la senescencia de los reservorios. En una muestra de 1,022 reservorios en los EE.UU., no se encontró correlación entre la edad cronológica y la edad funcional. La edad funcional estuvo directamente relacionada con el porcentaje de tierra cultivada y la capacidad de captación del reservorio, e inversamente relacionada con la profundidad de este. Más aún, algunos aspectos de la calidad para la pesca en el reservorio y características de las poblaciones de peces explotadas, también se relacionaron con la edad funcional. Una escala multimétrica como indicativo de la edad funcional de un reservorio presenta la posibilidad para intervenir en el manejo en varios frentes. Si un reservorio está envejeciendo en términos funcionales a una tasa acelerada, se pueden tomar acciones para remediar aquellas condiciones que más contribuyen con el envejecimiento funcional. La intervención dirigida a reducir las calificaciones sólo de métricas selectas puede potencialmente reducir la tasa de senescencia e incrementar la expectativa de vida del reservorio. Esto da pie a la curiosa implicación que es posible reducir la edad funcional de los reservorios y, de hecho, hacerlos más jóvenes.

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INTRODUCTION

Gerontologists have long recognized that definitions of age that focus exclusively on chronological age (years since birth) are incomplete because they are independent of human physiological and psychological factors (Baars and Visser 2007). Similarly, the rate at which reservoirs age may not be described best by chronological age. The rate of aging may depend on a diversity of attributes driven by climate and geography, catchment magnitude and composition, and reservoir hydrology and morphology. The crux of the problem with chronological age is that there are marked differences among humans and among reservoirs in the rate at which entities change over time. The implication of these differences is that chronological age and functional age (position along life span) may be only weakly related, and for many applications functional age may be more relevant.

Reservoirs vary in their geographical distribution, physical characteristics, and operational scheme, potentially creating large variability in functional age. Reservoirs tend to have large catchments and tributaries because they were engineered to capture as much water as possible to serve flood control, water supply, hydropower, or other purposes (Kennedy 1999). This unique hydrology can produce large input and retention of sediments and nutrients, although quantity may vary depending on climate, geology, and land cover. Thus, effects of inputs may differ depending on reservoir morphology. Depositional filling reduces depth and surface area and has been estimated to cause backwater isolation and habitat fragmentation (Patton and Lyday 2008). Wave action coupled with unnatural water level fluctuations dictated by operational goals alters shorelines that were once uplands and are maladapted to continuous flooding. Over time this promotes erosion and homogenization of once diverse littoral habitats (Allen and Tingle 1993). Well-established riparian zones and wetlands that provide key ecological services to natural lakes and the original river are generally limited to upper reaches near the entrance of tributaries but often degrade due to unnatural water level fluctuations (Miranda et al. 2014). Lack of woody debris deposition in the littoral zone, limited access to backwaters and wetlands, and lack of seed banks and stable water levels to promote native aquatic plants characterize barren littoral habitats in many reservoirs (Miranda 2008). Woody materials flooded during impoundment disintegrate within a few decades (Agostinho et al. 1999). Inequalities in the manifestation of these and other key variables can reduce the correlation between chronological and functional age.

A limited number of published studies have included chronological age as a covariate in models designed to describe or predict reservoir biological characteristics, but chronological age has seldom been a reliable covariate. Jenkins and Morais (1971) examined various metrics descriptive of sportfishing effort and harvest and concluded that although as expected chronological age was inversely related to harvest, it accounted for less than 5% of the variability in harvest. Miranda and Durocher (1986) reported that growth of fish in reservoirs declined rapidly soon after impoundment but subsequent reductions were minor, and Hendricks et al. (1995) reported that size of fish increased with reservoir age. In both of these studies, correlations with chronological age were unexpectedly low. Dolman (1990) reported that age did not help separate among distinct reservoir fish assemblages. Carol et al. (2006) noted that chronological age was surprisingly not a primary factor governing nutrient levels or fish assemblages in reservoirs. These studies suggest that chrono-

logical age is not a good predictor of reservoir senescence (i.e., the process of growing old in a detrimental sense). Our objective was to evaluate functional age as an indicator of reservoir senescence. To this end, we construct a multimetric indicator of functional age using in-reservoir descriptors expected to change over the life span of a reservoir. To evaluate the resulting indicator of functional age, we assess its correlation with external abiotic variables documented to change directionally with senescence.

METHODS

An indicator of functional age was constructed with a database assembled to document reservoir fish habitat status (Krogman and Miranda 2015). This database consisted of responses to an online survey completed by state natural resource agency personnel responsible for managing fish in reservoirs. The questionnaire included more than 50 questions that asked about environmental degradation issues within U.S. reservoirs 100 ha or more and within the catchments surrounding these reservoirs. Degradation status was scored by respondents on a six-point ordinal scale.

Twelve survey questions (metrics) characterizing within-reservoir degradation were selected to construct a multimetric indicator (Table 1). These metrics were chosen because they were expected to change directionally over the life span of a reservoir, thus potentially indicating senescence. The metrics rated reservoirs relative to extent of sediment, nutrients, and contaminants accumulation; water quality; loss of littoral habitat and structural habitat; and changes associated with shoreline erosion. All of these properties have been previously linked to reservoir senescence (Allen and Tingle 1993; Patton and Lyday 2008; Hargrove et al. 2010).

Factor analysis was applied to determine whether the 12 metrics tended to separate into more than one influential factor that may indicate different aspects of reservoir senescence. The factor analysis was applied to a similarity matrix reflecting the polychoric correlations of the 12 metrics, as suggested for ordinal data (Flora and Curran 2004). For each factor retained, a multimetric total score (a scale) was calculated as the sum of the ordinal ratings for each of the metrics loading high on the factor (correlation with axis $\geq |0.5|$). The total score for the scale was adjusted to 0–100, with a 0 indicating early functional age (all metrics scored as zero) and 100 indicating late functional age (all metrics scored as 5). Reliability of a scale was estimated with Cronbach's α , a measure of internal consistency. As a rule of thumb, a Cronbach's α of 0.7 or better suggests a reliable scale (Nunnally 1978).

Functional age cannot be adequately evaluated in terms of its correlation with chronological age because a key premise is that chronological age does not reflect functional age—if there is a strong correlation, there would not be a need for functional age (Salthouse 1986). Instead, the ability of functional age to indicate senescence was evaluated relative to abiotic and biotic variables. Functional age is expected to increase with increased levels of landscape disturbances in the catchment (Jones and Knowlton 2005) and by reduced reservoir depth (Hargrove et al. 2010). Percentage cultivated land (including row crops, small grains, and fallow land) and mean reservoir depth were available from a database compiled by Rodgers and Green (2011). Conversely, functional age is expected to influence the structure and function of fish assemblages and fisheries. Fish descriptors available encompassed 17 metrics illustrative of fish abundance, population characteristics, and the recreational fishery. These

Table 1. Variables included in the online survey and selected to index functional age. Data were collected with a six-point ordinal scale with 0 = no impairment, 1= low, 2 = low to moderate, 3 = moderate, 4 = moderate to high, and 5 = high impairment. The description for each metric was available to respondents to the survey.

Metrics	Description	Percentage scored as	
		0 and 1	4 and 5
Mudflats	Seasonally flooded and exposed expansive soft sediments; unvegetated unless exposed for many months	59	15
Low connectivity to tributaries due to sediment	Sedimentation has decreased connectivity to tributaries during low flows, acting as a barrier to fish movement	65	8
Insufficient structural habitat	Lacking or deficient structure such as large woody debris, gravel substrates, or diverse bottom relief	34	22
Excessive nutrients	Excessive nutrients, primarily N or P, which may result in excessive primary productivity and reduced water quality	46	20
Harmful algae blooms	Frequent occurrence of algal blooms that may be toxic to aquatic ecosystems or inhibit public enjoyment	71	9
Excessive organic turbidity	Particulate organic matter, other than algae blooms, suspended in the water column	63	9
Extreme diel variation in dissolved oxygen	Potentially harmful daily changes in dissolved oxygen	86	4
Sedimentation	Settling of suspended sediments, which over time may reduce depth and homogenize substrates	35	28
Shore erosion	Removal of soil and terrestrial vegetation from the land-water interface due to weathering of banks or adjacent land slopes by water, ice, wind, or other factors	40	17
Loss of cove habitat due to depositional filling	Sedimentation has changed cove habitat including area reduction, isolation, fragmentation, and establishment of terrestrial vegetation in newly deposited land	47	17
Shore homogenization	A reduction of the shore's original habitat diversity by erosion or other processes	43	17
Homogenization of littoral substrates	A reduction of the substrate's original diversity by erosion and sedimentation	42	17

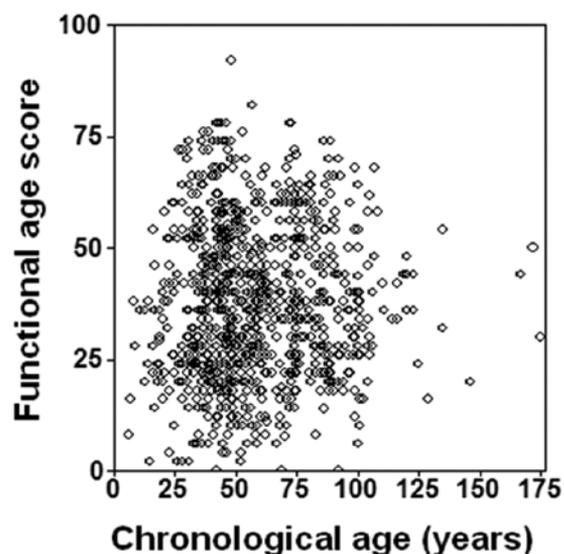


Figure 1. Functional age in relation to chronological age in 1,022 reservoirs ≥ 100 ha distributed throughout the continental United States.

fish metrics were available from the database compiled by Krogman and Miranda (2015) scored on a five-point ordinal scale. To reduce dimensionality of the fish database, the 17 metrics were submitted to the factor analysis procedure described earlier, and the factors that accounted for the most variability in the data set were evaluated relative to functional age.

Land use and reservoir depth are undoubtedly not the only variables influencing functional age and senescence. However, these two variables may well limit the minimum or maximum functional age attainable within a given reservoir. Similarly, functional age is not the only factor affecting fish assemblage and fisheries characteristics, but functional age may limit minimum or maximum levels of fish-related variables. These scenarios were examined with quantile regression (Cade et al. 1999), which tested whether the 5th or 95th percentiles of a dependent variable changed along the gradient of the independent variable. See Sidebar at the end of this article.

RESULTS

Complete data on chronological age and the 12 metrics were available for 1,022 reservoirs distributed throughout the continental United States, representing roughly 24% of all reservoirs 100 ha or more according to the National Inventory on Dams database (NID 2013). Chronological ages of the study reservoirs ranged from 7 to 176 years, with a median 54 years. Most study reservoirs were multipurpose (77%), with two or more primary uses. Primary uses listed included flood control (41%), municipal/industrial water supply (41%), fish/wildlife habitat or conservation (28%), hydropower generation (20%), irrigation (16%), navigation (8%), cooling (7%), water quality improvement downstream (3%), and assimilation of waste effluents (1%). In addition, 75% of the reservoirs listed recreation as a primary use either as the only primary use (7%) or along with other primary uses (68%).

The 12 metrics were attributed an array of scores by respondents (Table 1). The highest rated metric was sedimentation, with 28% of the reservoirs scored as 4–5 (i.e., above average to high). Next in decreasing order were insufficient structural habitat (22% scored 4–5), excessive nutrients (20%), shore homogenization (17%), and shore erosion (17%). The factor analysis suggested that the 12 metrics reflected mainly a single latent variable represented by factor 1. This factor accounted for 67% of the variability, axis 2 for 11%, and axis 3 for 10%. All 12 metrics were adequately correlated with the factor 1 loadings ($r = 0.52$ to 0.85 , all positive). The Cronbach's α analysis suggested that internal consistency among the metrics was maximized when organic turbidity and high diel oxygen variability were excluded. With the remaining 10 metrics, Cronbach's α was maximized at 0.89.

Functional age scores ranged from 0 to 94, with a median of 36. The distribution was skewed to the right, with 5th and 95th percentiles of 8 and 66, respectively. Reservoirs with the highest functional age scores generally occurred in the central United States from North Dakota to Texas and in agricultural regions

of the Midwestern United States. Thirteen reservoirs shared the lowest possible functional age scores (i.e., 0); these reservoirs were mostly at high elevations in the Rocky and Appalachian mountains. According to primary use, median functional age of reservoirs listed as hydropower generation was 34, flood control 40, irrigation 36, municipal/industrial water supply 36, recreation 36, fish/wildlife habitat or conservation 38, cooling 40, water quality improvement downstream 40, navigation 48, and assimilation of waste effluents 52. No statistical test was applied to verify if these means were different because 77% of the reservoirs were multipurpose; therefore, the uses listed are not mutually exclusive. A scatterplot of functional age against chronological age showed no discernible pattern (Figure 1), and functional age scores were not correlated with chronological age ($r = 0.04$; $P = 0.21$).

Functional age was highly variable relative to reservoir depth and catchment agriculture (Figure 2). Nevertheless, functional age showed a decreasing trend in its 95th percentile relative to mean depth (Wald's chi-square = 36.9; $P < 0.01$) but no trend in its 5th percentile (Wald's chi-square = 3.3; $P < 0.18$). This pattern suggests that depth limited the maximum functional age scores, and although higher scores could be attained in shallow lakes, often other mitigating variables prevented reaching high functional age. Conversely, functional age scores showed no trend in its 95th percentile relative to extent of cultivated land in the catchment (Wald's chi-square = 2.3; $P < 0.21$) but an increasing trend in its 5th percentile (Wald's chi-square = 598.1; $P < 0.01$). This pattern suggests that catchments with high levels of cultivated land almost always tend to have a high functional age and that catchments with low levels of cultivated land tend to have lower functional ages, although sometimes they may have high functional age due to something other than the effects of a cultivated catchment.

The 17 fish/fishery metrics submitted to the factor analysis to reduce dimensionality produced four interpretable factors that together accounted for 67% of the variability in the metrics (Table 2). Factor 1 accounted for 26% of the variability in the 17 metrics and reflected *fishing quality* as it was positively correlated (correlation with axis $\geq |0.5|$) with fishing pressure, catch rate, frequency of fishing tournaments, angler satisfaction, predator standing stock, overall standing stock, and population density. Factor 2 accounted for 17% of the variability and reflected *size and growth* as it was positively correlated with size structure, condition, and growth rate. Factor 3 accounted for 14% of the variability and reflected *recruitment* as it was positively correlated with recruitment to age 1, recruitment to adulthood, and population density. Factor 4 accounted for 10% of the variability and reflected *mortality* as it was positively correlated with natural mortality, fish kills, and standing stock of exotic species.

These four factors showed various patterns relative to functional age (Figure 3). For factor 1, the 5th (Wald's chi-square = 4.2; $P = 0.04$) and 95th (Wald's chi-square = 6.4; $P = 0.02$) percentile regressions decreased relative to functional age, suggesting higher *fishing quality* at low functional age but high variability. In contrast, for factor 4, the 5th (Wald's chi-square = 24.6; $P < 0.01$) and 95th (Wald's chi-square = 17.0; $P < 0.01$) percentile regressions increased relative to functional age, suggesting higher *mortality* at high functional age but also high variability. Factors 2 and 3 showed hump-shaped patterns in the 95th (Wald's chi-square = 4.3 and 14.3; $P = 0.03$ and < 0.01 , respectively) percentiles but no trend in the 5th percentiles (Wald's chi-square = 0.2 and 0.1; $P = 0.69$ and 0.74, respectively), sug-

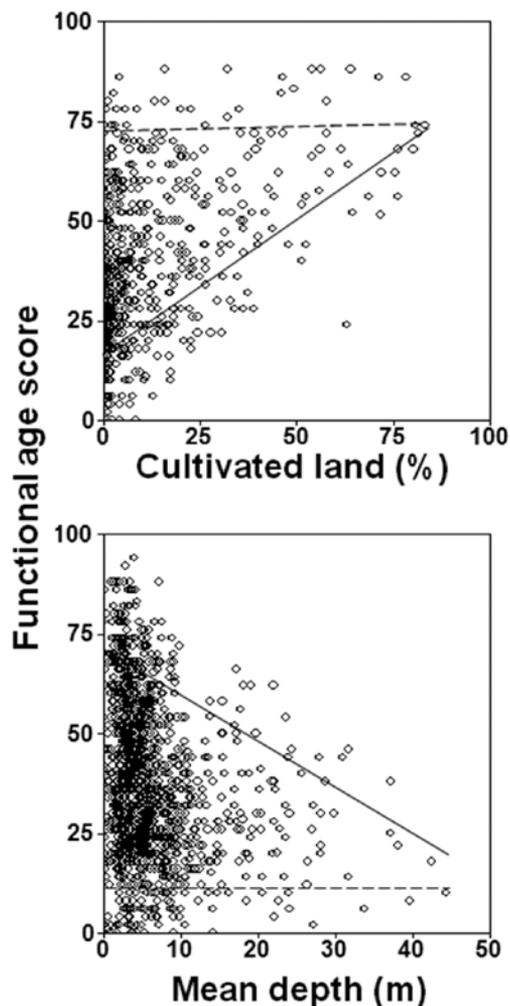


Figure 2. Functional age in relation to percentage of cultivated land in the reservoir catchment and to mean depth in the reservoir. The lines represent the 5th and 95th percentiles; the slopes of dashed lines were not statistically significant, $P > 0.05$. Catchments with high levels of cultivated land almost always had high functional age, whereas catchments with low levels of cultivated land had low functional ages, although sometimes had high functional age probably due to something other than cultivated land. Deep lakes limited the maximum attainable functional age scores, and although higher scores could be attained in shallow lakes, other variables may have prevented reaching high functional age.

gesting intermediate functional age scores optimized maximum *size and growth* and *recruitment*.

DISCUSSION

It has long been conjectured that reservoirs differ in the chronological rate at which they manifest senescence (Pegg et al. 2015), but so far no attempt has been made to find an indicator that performs better than years since impoundment. In gerontology and related fields, the term “functional age” has been used as a descriptive label for research efforts that have suggested that functional capabilities are likely to be more meaningful than mere chronological age for characterizing the senescing status of an individual. Although the goal of monitoring a person's or a reservoir's capacity for functioning has practical implications, the concept of functional age has generated controversy in the gerontology literature (Costa and McCrae 1980) and is likely to do so in the reservoir ecology literature.

Table 2. Results of factor analysis applied to 17 fish and fishery metrics submitted to factor analysis. Factors 1-4 reflected *fishing quality*, *size and growth*, *recruitment*, and *mortality*, respectively. Values in bold identify correlations with axis $\geq |0.5|$ and were used to name the factors.

Metrics	Description	Factor			
		1	2	3	4
Standing stock	Biomass of the fish community in the reservoir	0.67	0.33	0.22	-0.01
Prey standing stock	Biomass of prey fish species in the reservoir	0.44	0.47	0.05	0.05
Predator standing stock	Biomass of predator fish species in the reservoir	0.71	0.23	0.26	-0.13
Prey-predator ratio	Biomass of prey in relation to biomass of predators	0.37	0.24	0.05	-0.08
Exotic species standing stock	Biomass of unwanted introduced species	-0.05	0.01	0.11	0.54
Fish kills	Localized die-offs associated with unsuitable water chemistry	-0.07	-0.02	0.01	0.73
Catch rate	Pace at which anglers hook fish, regardless of size	0.77	0.22	0.27	-0.03
Fishing pressure	The relative amount of fishing effort received by the reservoir	0.79	0.13	0.01	0.05
Angler satisfaction	Overall contentment of anglers with catch rates and fish size	0.68	0.34	0.23	-0.16
Frequency of tournaments	Regularity with which the reservoir is chosen for organized tournaments, whether small or large tournaments	0.64	-0.07	0.03	0.09
Population density	Relative abundance of principal target species	0.58	0.23	0.52	-0.10
Size structure	Quality of the length distribution of the target population	0.26	0.79	0.16	-0.11
Condition	Average observed weight of individual fish in the population relative to expected weight for the species	0.11	0.88	0.07	-0.02
Growth rate	Rate of increase in length	0.15	0.83	0.10	0.05
Natural mortality	Mortality attributed to factors such as environmental conditions or interactions with other species; does not include mortality due to fishing	-0.02	-0.04	-0.14	0.66
Recruitment to age 1	Juveniles that survive their first year of life	0.20	0.02	0.87	-0.04
Recruitment to adulthood	Juveniles that reach reproductive maturity	0.27	0.21	0.83	-0.12

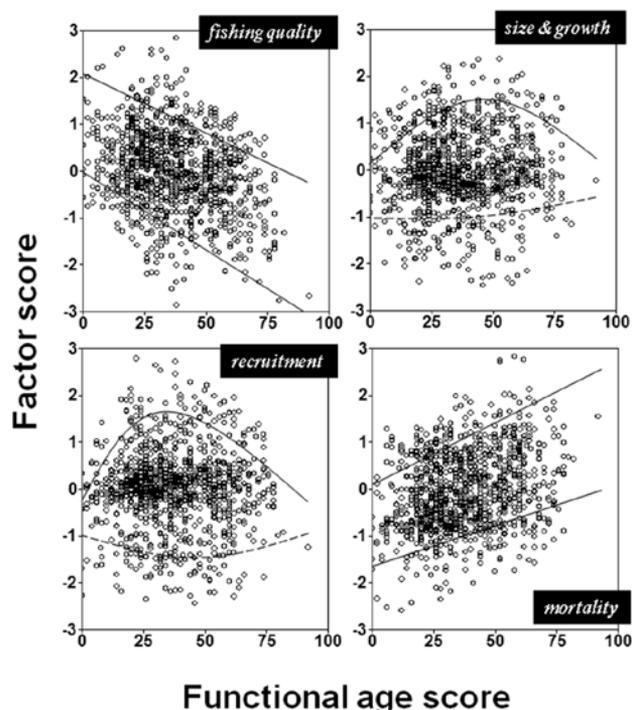


Figure 3. Plots of factors 1-4 relative to functional age. The lines represent the 5th and 95th percentiles; the slopes of dashed lines were not statistically significant, $P > 0.05$. For the *fishing quality* factor, the 5th and 95th percentile regressions (solid lines) decreased, suggesting higher fishing quality at low functional age but high variability. For the *mortality* factor, the 5th and 95th percentile regressions increased relative to functional age, suggesting higher fish losses at high functional age but also high variability. The *size and growth* and *recruitment* factors showed hump-shaped patterns in the 95th percentiles, suggesting intermediate functional age scores optimized their scores.

In reservoirs 100 ha or larger, chronological age was not correlated with functional age. This result suggests that reservoirs differ widely in terms of how quickly they senesce. This finding is not entirely surprising considering how diverse reservoirs are relative to in-reservoir and off-reservoir characteristics and to hydraulic variables. Given that functional age was assembled with metrics expected to worsen as reservoirs senesce, we suggest that functional age does track senescence. Moreover, functional age was directly related to percentage of cultivated land in the catchment and inversely related to reservoir depth, both as expected. Also as expected, the *fishing quality* factor was inversely related to functional age and the *mortality* factor was directly related to functional age. The *size and growth* and *recruitment* factors were optimized at intermediate levels of functional age, suggesting that fish population characteristics key to maintaining desirable recreational fisheries will eventually decline if a reservoir is allowed to senesce. Thus, functional age may be a useful indicator of reservoir senescence.

However, this indicator has limitations that reduce its accuracy. Scoring of the metrics that make up functional age depends on the perception and professional judgment of respondents, and these may vary depending on experiences. There are several reported limitations associated with relying on professional judgment (Jenkins and Hine 2003). Survey respondents likely differed in familiarity with reservoir habitats and perception of impairment (i.e., subjective calibration of the six-point scale), potentially producing unequal scoring for reservoirs with essentially equal status. To promote equivalence of responses among

Quantile Regression

Ordinary least-squares regression estimates the rate of change in the mean of the response variable as a function of a predictor variable. Quantile regression extends the ordinary regression model by estimating the rate of change in the median (50th percentile) or any other percentile in the response-predictor relationship. The *n*th percentile of a set of numbers is the number below which *n*% of the values fall. Quantile regression may be particularly useful when (1) extremes are important, such as when there are relationships along the edges of a distribution (e.g., 5th or 95th percentiles), or when (2) the rate of change in the response, expressed by the regression coefficient, depends on the quantile (Cade and Noon 2003). Quantile regression through the upper or lower extremes of a distribution may be the best estimate of the effects expected from the predictor variable because values toward the middle of the distribution may be more heavily influenced by other variables.

As an example, consider the percentage composition of Orangespotted Sunfish *Lepomis humilis* in floodplain lakes of the Lower Mississippi River (Miranda 2011) illustrated in Figure 4. A decreasing trend was apparent in the upper edge of the distribution (95th percentile) of Orangespotted Sunfish percentage composition in the fish assemblage but no trend in the lower edge (5th percentile). This pattern suggested that lake depth limited the maximum attainable relative abundance of Orangespotted Sunfish, and although greater relative abundances could be attained in shallower lakes, often other variables prevented reaching high relative abundances in every lake. The upper edge of the distribution may most closely approximate the limiting effect of depth in the absence of other variables that may influence Orangespotted Sunfish relative abundance.

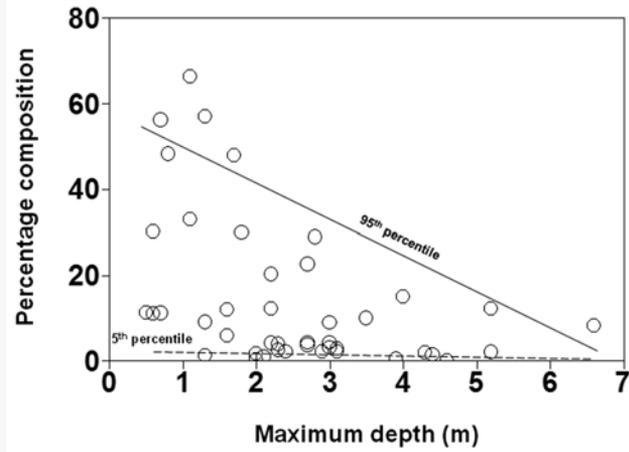


Figure 4. Orangespotted Sunfish percentage composition in the fish assemblage of 42 floodplain lakes relative to lake maximum depth. The 5th and 95th percentiles of the percentage composition were estimated with quantile regression.

respondents and reduce error, each question was coupled with an expanded narrative to help focus respondents. Nevertheless, error in scoring probably remained. Various other methods exist for reducing the occurrence or magnitude of these inaccuracies, although often at various costs (Bernard et al. 1984; Huber and Power 1985). Further improvement in accuracy of scoring may be obtained by upgrading to objective onsite quantitative habitat surveys but at a substantial rise in cost and likely without matching increases in evaluation accuracy.

The concept of functional age has advantages. Combining multiple metric scores to assemble an indicator of senescence presents the possibility for management intervention from multiple angles. If it is determined that a reservoir is functionally aging at an accelerated rate, action may be taken to remedy the conditions contributing most to functional age. Intervention to reduce scores of selected metrics can potentially reduce the rate of senescence and increase the life expectancy of the reservoir. This leads to the intriguing implication that steps can be taken to reduce functional age and actually make the reservoir grow younger.

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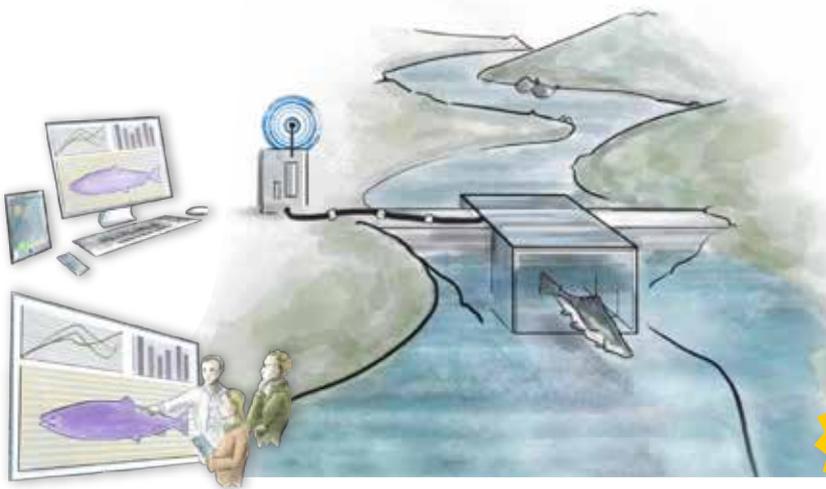
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