Reviews in Fisheries Science & Aquaculture, 23:329–345, 2015

ISSN: 2330-8249 print / 2330-8257 online
DOI: 10.1080/23308249.2015.1068737

The Global Status of Freshwater Fish Age Validation Studies and a Prioritization Framework for Further Research

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Age information derived from calcified structures is commonly used to estimate recruitment, growth, and mortality for fish populations. Validation of daily or annual marks on age structures is often assumed, presumably due to a lack of general knowledge concerning the status of age validation studies. Therefore, the current status of freshwater fish age validation studies was summarized to show where additional effort is needed, and increase the accessibility of validation studies to researchers. In total, 1351 original peer-reviewed articles were reviewed from freshwater systems that studied age in fish. Periodicity and age validation studies were found for 88 freshwater species comprising 21 fish families. The number of age validation studies has increased over the last 30 years following previous calls for more research; however, few species have validated structures spanning all life stages. In addition, few fishes of conservation concern have validated ageing structures. A prioritization framework, using a combination of eight characteristics, is offered to direct future age validation studies and close the validation information gap. Additional study, using the offered prioritization framework, and increased availability of published studies that incorporate uncertainty when presenting research results dealing with age information are needed.

Keywords age and growth, age, periodicity, validation, freshwater fish

INTRODUCTION

Age information is a cornerstone of fisheries science, used to estimate recruitment, growth, and mortality, that guides management decisions regarding harvest strategies and conservation programs (Maceina et al., 2007; Quist et al., 2012). Individual ages provide a means to examine the age-structure of a population and assess strong and weak year classes (Maceina, 1997; Quist, 2007). The ability to track daily ages of young-of-year fishes provides information on spawning and hatching dates and the ability to track cohorts through time to evaluate environmental influences (e.g., temperature and flow) on biological responses such as survival, growth, and condition (Tonkin et al., 2011; Humphries et al., 2013). Mean length-at-age data provide fisheries scientists with a measure of growth that can be compared with other populations across a species' native and non-native ranges (Beamish et al., 2005; Rypel, 2009). In addition, back-calculated length can be used to evaluate fish growth over an entire life span and determine changes in growth due to life-history events and environmental stochasticity (Campana and Thorrold, 2000). Finally, age frequency in a representative sample is often used to convey mortality rate information using catch curve analysis (Taylor et al., 2015).

Accuracy and precision of age data are needed to predict population responses through time resulting from climatic or habitat shifts, and facilitate conservation and management actions, including harvest strategies (Beamish and Mcfarlane, 1983; Campana, 2001). If age information is unreliable, population models used for prediction of population dynamics may result in the implementation of liberal catch limits and the potential for overharvest. For instance, Yule et al. (2008)

The authors are not aware of any perceived conflicts of interest. Any use of trade, firm, or product names is for descriptive purposes only and imply endorsement by the US Government.

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suggested non-reliable ageing structures resulted in faulty age information and inaccurate harvest models with the subsequent over-harvest and depletion of cicso (*Coregonus artedi*, Salmonidae) population abundances and a collapse of the fishery in Lake Superior, USA. As such, fisheries professionals need reliable information on the true ages of organisms of interest.

Age data can be acquired through various means, including direct use of known-age individuals, through analysis of length–frequency histograms, and interpretation of fish hard parts (e.g., calcified or bony structures; Quist et al., 2012). Direct measures of fish age reared in captivity is of limited value as age and growth information of these fishes may not adequately reflect wild fish (Campana, 2001); however, direct measures from wild fish tagged at an early age where age can be presumed is an exception. Annual cohorts can be tracked through time to assess growth; however, length–frequency analysis is limited to fishes that spawn over a relatively short period and young or short-lived fishes with relatively rapid growth as age groups will become bunched and indistinguishable when somatic growth declines (Isley and Grabowski, 2007).

The most common method of estimating age is examination of hard parts (i.e., calcified structures) using a process similar to dendrochronological research where individual rings are counted and correspond to periods of fast and slow growth over a period of interest (Campana, 2001; Quist et al., 2012). Ageing structures come in a variety of forms, including otoliths, vertebrate, opercula, cleithra, scales, and fin rays and spines, each of which has advantages and disadvantages in their use (Quist et al., 2012). External structures such as scales and spines can be removed non-lethally, and may be the preferred method when working with species of conservation concern. Internal structures, such as otoliths, require the fish to be euthanized, and structure removal may be more labor-intensive. Otoliths are often considered the most reliable ageing structures, but ages are often needed for species of concern of which few individuals remain, so other approaches such as scales and spines may be more desirable. The paradox is that alternative structures may result in bias of age estimates, particularly in older fish (Hamel et al., 2014) and may provide different interpretations compared with otoliths (Kowalewski et al., 2012).

Several assumptions must be met to effectively use hard parts for age and growth analysis. For example, growth mark deposition on ageing structures must be deposited at a predictable time (e.g., daily or annually) and these marks must be readily identifiable. However, these assumptions are difficult to assess because consistency and clarity of growth mark deposition may change both within an individual (e.g., as fish become reproductively mature) and among populations due to environmental conditions (Winker et al., 2010a; Quist et al., 2012). The formation of opaque growth zones has been attributed to changes in energy expenditures due to reproductive timing and reduced water temperatures (Hecht, 1980; Weyl and Booth, 1999). The resulting ambiguity in growth mark deposition manifests as either process error or interpretation error (Campana 2001). Process error is the absence of true annual marks, thereby the age of the organism is not certain (i.e., poor accuracy). Interpretation error, however, is the inability to replicate age estimates from hard part structures (i.e., poor precision; Maceina et al., 2007). Both process and interpretation errors may occur for a variety of reasons. Depending on environmental conditions, multiple marks may form (Weyl and Booth, 1999) and be misinterpreted as annuli. Slower growth rates as fish age often result in crowding marks making individual growth marks indiscernible (Whiteman et al., 2004). Therefore, validating these assumptions is considered critical to use hard part structures for attaining information for age and growth.

Age validation is the process of affirming the temporal scale that opaque and translucent bands (i.e., growth marks) are deposited in fish hard parts to accurately determine age (Beamish and McFarlane, 1983). There are multiple techniques that exist for age validation and can be divided into those determining the absolute (i.e., true) age of an individual or examining the periodicity of growth marks. The most accurate and precise method for determining the absolute age of an individual is using known-ages through mark–recapture, where a unique mark is applied and subsequent marks are counted upon recapture (Campana, 2001; Hamel et al., 2014). In addition, mark–recaptures of chemically tagged fishes (e.g., oxytetracycline) can be used to determine periodicity of natural marks after initial tagging (Duffy et al., 2012). Bomb radiocarbon (e.g., C^{14}) is yet another technique used to validate ages of some long lived fishes, but has limited application to short lived fishes (Campana, 2001; Davis-Foust et al., 2009). In addition, natural marks on ageing structures occurring at known dates can be used (Beamish and McFarlane, 1983). However, these techniques are not as robust as known-age mark–recapture techniques and often can only be used to assess periodicity of growth marks (Campana, 2001).

Indirect methods to validate the periodicity of annual growth zone formation include marginal increment analysis and the closely related edge analysis (Campana, 2001). Although labeled as the least desirable age validation methods in terms of accuracy and precision, marginal increment analysis and edge analysis are commonly employed techniques used among fisheries professionals (Campana, 2001; Beamish et al., 2005; Simmons and Beckman, 2012). The main premise of these two indirect validation methods is that as fish age over an annual time-step, measurements of the outermost margin of the ageing structure (i.e., marginal increment analysis) or the proportion of opaque to translucent zones (i.e., edge analysis) will resemble a sinusoidal shape when plotted across months (Campana, 2001). Other marginal increment type techniques, such as cross-dating procedures commonly employed in dendrochronology research, have been applied to a limited extent in validating ages of marine and freshwater fishes (Guyette and Rabeni, 1995; Black et al., 2005).

The need for validated age information of freshwater fish species has been repeatedly evoked within the fisheries science community. Early work by Van Oosten (1923, 1929) cautioned fisheries managers against assuming marks on hard parts as annuli, and suggested that validation of structures for all fish species was needed. Beamish and McFarlane (1983) called upon fisheries scientists to systematically validate ageing structures to better understand the reliability of the age information provided and how misuse may influence management actions. These authors stressed that inaccurate age information can negatively influence decisions regarding the management of commercial, recreational, and imperiled fishes (Beamish and McFarlane, 1983) and estimated that less than 3% (out of 500) of studies validated the range of ages used. Campana (2001) provided a review of various age validation methods and a summary of steps needed to conduct true age validation experiments. Campana (2001) also suggested that major strides had been taken with respect to the validation of ageing structures since the earlier call by Beamish and McFarlane (1983), but also warned that misuse of some techniques warranted additional concern; particularly, marginal increment analysis was often not appropriately applied. More recently, Maceina et al. (2007) provided a summary of age validation studies for common sport fishes in North America, highlighting that additional age validation studies are needed, and suggested that a comprehensive database of known-age validation studies would be valuable. The review by Maceina et al. (2007) highlighted the need to keep age validation a top priority as age validation studies are extremely critical for proper management and conservation of fishes and expand the compilation of validation studies worldwide.

Age validation studies are time-consuming, and a need exists to summarize existing information to prevent redundancy of effort as well as highlight areas where additional research is necessary. Undoubtedly, a great deal of work has been done on validating age structures across a wide range of taxa and ages. References to previous work suggesting ageing structures have been validated often do not explicitly state the range of ages that have been validated, or the range in ages in their study. Subsequently the current status of age validation for different species is needed. Therefore, the objectives of the current study were to gain an understanding of how the scientific community has responded to repeated calls for age validation over the last several decades and provide fisheries professionals a source for determining which ages have been validated, what techniques were used, and where additional efforts are needed from available literature. In addition, a prioritization framework is presented to guide future age validation studies and call for the continued inclusion of alternative approaches in the age validation toolbox.

METHODS

Response to Call for Age Validation

Temporal trends were examined in the prevalence of age validation studies following previous calls for age validation studies by Beamish and Macfarlane (1983) and Campana (2001). Papers containing "Age Validation" in the title or body of a manuscript were summarized from years 1983–2014 using Google Scholar. Regression analysis was performed to quantify the direction and rate at which changes in age validation research have occurred (R Core Team, 2014).

Sources of Information for Age Validation

Freshwater fish age validation studies were summarized by conducting a literature search using combinations of key words in both Web of Science and Google Scholar (*all words*: fish, inland, and freshwater; *exact phrase*: age validation; at least with one of the following words: vertebrate, spine, otolith, cleithrum, scale; without the word: marine) for every year from 1983–2014. The literature search was initiated to correspond with the original call by Beamish and MacFarlane (1983) for an increase in age validation studies. Initially, keywords, titles, and abstracts were examined to determine if a presumed validation experiment was performed. Then the methods and result sections of each paper were reviewed to determine validation technique, ages validated, and structures used in the analysis. Whether a study examined true age validation or frequency of periodicity was determined for each research paper. Definitions for validation and periodicity followed Campana (2001), and the term validation was treated to mean true age, which can only be determined from known age fishes or through mark and recapture studies (Beamish and MacFarlane, 1983; Campana, 2001). References to other methods were considered to mean the authors successfully or unsuccessfully found periodicity of annulus formation. In addition, the list of species where periodicity and validation work has been done was compared with both the United States Endangered Species Act (ESA) and the International Union for the Conservation of Nature (IUCN) lists of threatened and endangered freshwater fishes. Previous validation studies and calls for additional validation studies were done before Beamish and MacFarlane (1983), and if a paper in the initial search referenced additional research validating different ages or ageing structures, these studies were included where appropriate to be as comprehensive as possible in summarizing age validation work. However, the literature search only included peer-reviewed articles in English language journals, and therefore excluded some possible sources of ageing studies (i.e., theses, dissertations, management reports, and papers in other languages).

RESULTS

Response to Call for Age Validation

The number of studies with "age validation" in either the title or the body of the manuscript has risen through time, and

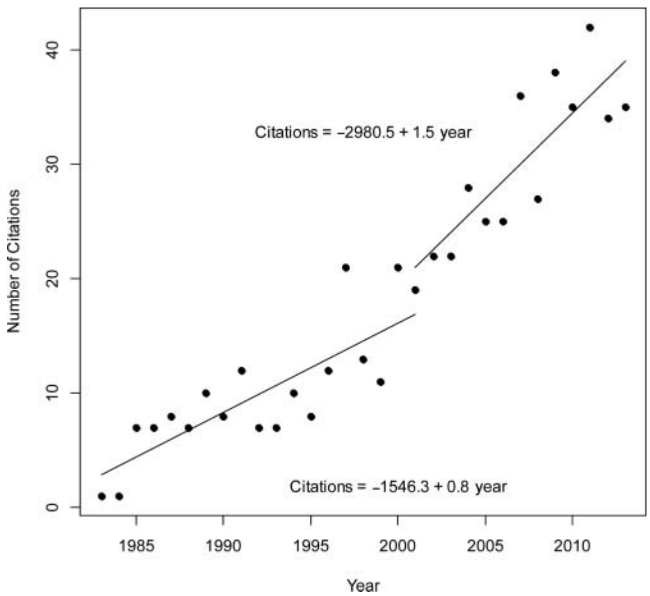

Figure 1 Number of citations containing "Age Validation" in the title or the body of the manuscript since 1983. An increase in the number of citations followed both calls for validation by Beamish and Mcfarland (1983) and Campana (2001).

appears to increase following calls for additional research (Figure 1). For instance, age validation studies increased following the initial call by Beamish and McFarlane (1983) and the rate of age validation studies further increased following an additional call by Campana (2001; Figure 1).

Sources of Information for Age Validation

A total of 1351 articles were reviewed using both Web of Science and Google Scholar. Studies where phrases such as "age validation" or "validation" appeared in titles and abstracts, but were either a comparison of precision estimates among structures or did not conform to the above definitions of periodicity and validation were subsequently excluded. A subset of 168 (12%) of the 1351 original articles examined could be defined as either validation ($n = 76$, 6%) or periodicity ($n = 92$, 7%) studies. Periodicity and age validation studies were found for 21 freshwater fish families and 88 species (Tables 1 and 2). However, no species was validated over the entire expected range of longevity. A relatively small group of families ($n = 3$) accounted for 50% of validation studies, including Centrarchidae ($n = 26$; 17%), Cyprinidae ($n = 25$; 15%), and Salmonidae ($n = 26$; 17%). The use of known-age fish either through mark–recapture or through laboratory methods for true validation accounted for approximately 42% of the studies deemed either validation or periodicity studies (Table 2); whereas 58% of the studies validated the periodicity of annual marks (Table 1). The ESA list contained 153 fish species, or stocks of the same species (e.g., salmonids) of which 13 (9%) had validation studies. The IUCN red list for fishes comprised 489 different species, of which 9 (2%) had validation performed. Geographic distribution of age validation studies spanned the earth and included 19 countries from five continents, yet 80% of the studies were from North America (USA and Canada).

A prioritization framework was developed that can be used as a guide to direct future studies as the science of age validation progresses. Using the proposed prioritization framework, time and effort can be directed to achieving the greatest return in terms of validating ageing structures in a systematic fashion without redundancy. Research is directed to species where age validation is most likely to succeed, species where age validation has been started, and species with the greatest commercial, recreational, and conservation values. The proposed validation framework comprises eight categories and includes invasive potential, availability of alternative techniques, fish biology, previous age validation, feasibility of true validation, management status, conservation status, and the geographical location and habitat stability within a fish's range (Table 3). Characteristics specific to each category can be used to determine if a species should be given a low, medium, or high priority in terms of the need to perform an age validation study. A single species will likely not have characteristics identifiable to only one priority level, and thus fisheries professionals will have to decide what combination of characteristics best warrants further study.

DISCUSSION

The contribution of reviews of validation studies, particularly by Beamish and MacFarlane (1983) and Campana (2001), is apparent by the increase in literature with "age validation" in either the title or abstract in the decades following calls for validating ageing structures. The fisheries science community has attempted to respond to the challenge by conducting validation studies for at least a few sport fish and a limited number of threatened or endangered fishes. Although multiple age validation studies may exist for a single species, the range of ages is often limited, and few ageing structures have been validated across geographical scales for large-ranging species. Knowledge gaps exist throughout the life span of many fishes with information for the oldest individuals often being very limited (e.g., channel catfish only has age validation for 0 to 4 years, yet can live >20 years; Gerhardt and Hubert, 1991). Studies involving the first few years of life were common for both periodicity and validation and is likely due to a general inability to complete long-term validation studies and difficulty in discerning ages of older individuals (Hamel et al., 2014). Largemouth bass appear to be one exception with validation of otoliths throughout the majority of its life span (Buckmeier and Howell, 2003) and throughout multiple geographic ranges (Yodo and Kimura, 1996; Buckmeier and Howell, 2003; Beamish et al., 2005; Taylor and Weyl, 2013).

Table 1 Periodicity studies for freshwater fish by family and species

Family	Common name	Genus species	Country	Status	Scale	Method	Structure	Reference
Acipenseridae	Lake Sturgeon	*Acipenser fulvescens*	USA	NL	A	BRC, KA	FR, OT	Bruch et al. (2009)
	Lake Sturgeon	*Acipenser fulvescens*	USA	NL	A	MRCT	FR	Rossiter et al. (1995)
	White Sturgeon	*Acipenser transmontanus*	USA	ESA	A	MRCT	FR	Rien and Beamsderfer (1994)
	Shovelnose Sturgeon	*Scaphirhynchus platorynchus*	USA	ESA	A	MIA	FR	Whiteman et al. (2004)
	Shovelnose Sturgeon	*Scaphirhynchus platorynchus*	USA	ESA	A	MIA	FR	Rugg et al. (2014)
Anguillidae	American eel	*Anguilla rostrata*	Norway	NL	A	KA	OT	Vøllestad and Næsje (1988)
	American eel	*Anguilla rostrata*	USA	NL	A	MR	OT	Berg (1985)
	American eel	*Anguilla rostrata*	USA	NL	A	MRCT	OT	Oliveira (1996)
	Australian longfinned eel	*Anguilla reinhardtii*	Australia	NL	A	MRCT	OT	Pease et al. (2004)
	Japanese eel	*Anguilla japonica*	Taiwan	NL	A	KA, MIA	OT	Lin and Tzeng (2009)
Catastomidae	Lost River Sucker	*Deltistes luxatus*	USA	ESA, IUCN	D	CT	OT	Hoff et al. (1997)
	Shortnose Sucker	*Chasmistes brevirostris*	USA	ESA, IUCN	D	CT	OT	Hoff et al. (1997)
	White Sucker	*Catostomus commersonii*	Canada	NL	A	MR	FR	Beamish and Harvey (1969)
	White Sucker	*Catostomus commersonii*	USA	NL	A	MR	FR	Quinn and Ross (1982)
	White Sucker	*Catostomus commersonii*	USA	NL	A	EA	OT	Thompson and Beckman (1995)
	Brassy Jumprock	*Moxostoma sp.*	USA	NL	A	MIA	OT	Bettinger and Crane (2011)
	Notchclip Redhorse	*Moxostoma collapsum*	USA	NL	A	MIA	OT	Bettinger and Crane (2011)
	River Redhorse	*Moxostoma carinatum*	USA	NL	A	EA	OT, OP	Beckman and Hutson (2012)
	Cui-ui	*Chasmistes cujus*	USA	ESA	A	MIA	OP	Scoppettone (1988)
	Chinese Sucker	*Myxocyprinus asiaticus*	China	NL	D	KA	OT	Song et al. (2008)
Centrarchidae	Largemouth Bass	*Micropterus salmoides*	USA	NL	A	MIA	OT	Crawford et al. (1989)
	Largemouth Bass	*Micropterus salmoides*	Zimbabwe	NL	A	EA	OT	Beamish et al. (2005)
	Largemouth Bass	*Micropterus salmoides*	USA	NL	A	MR	SC	Maraldo and MacCrimon (1979)
	Largemouth Bass	*Micropterus salmoides*	Japan	NL	A	EA, BC	OT	Yodo and Kimura (1996)
	Largemouth Bass	*Micropterus salmoides*	S. Africa	NL	A	EA, MRCT	OT	Taylor and Weyl (2013)
	Black Crappie	*Pomoxis nigromaculatus*	USA	NL	A	MIA	OT, SC	Shramm and Doerzbacher (1982)
	White Crappie	*Pomoxis annularis*	USA	NL	A	MIA	OT	Maceina and Betsill (1987)
	Bluegill	*Lepomis microchirus*	USA	NL	A	MIA	OT	Hales and Belk (1992)
	Bluegill	*Lepomis microchirus*	USA	NL	A	CT	OT	Mantini et al. (1992)
	Redbreast Sunfish	*Lepomis auritus*	USA	NL	A	CT	OT	Mantini et al. (1992)
	Redear Sunfish	*Lepomis microlophus*	USA	NL	A	CT	OT	Mantini et al. (1992)

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Table 1 Periodicity studies for freshwater fish by family and species *(Continued)*

Family	Common name	Genus species	Country	Status	Scale	Method	Structure	Reference
Cichlidae	Three-spotted Tilapia	*Oreochromis andersoni*	Botswana	NL	A	MIA	OT, SC	Booth et al. (1995)
	Blunthead cichlid	*Tropheus moorii*	Zambia	NL	A	MRCT	OT	Egger et al. (2004)
Claridae	African Sharptooth Catfish	*Clarias gariepinus*	S. Africa	NL	A	MRCT	OT	Weyl and Booth (2008)
Clupeidae	Gizzard Shad	*Dorosoma cepedianum*	USA	NL	A	MIA	OT	Clayton and Maceina (1999)
	Alewife	*Alosa pseudoharengus*	USA	NL	A	LF	OT	LaBay and Lauer (2006)
Cottidae	Mosshead Sculpin	*Clinocottus Globiceps*	Canada	NL	A	MIA	OT	Mgaya (1995)
Cyprinidae	Common Carp	*Cyprinus carpio*	Australia	NL	A	MIA	SC, OP, OT	Vilizzi and Walker (1999)
	Common Carp	*Cyprinus carpio*	Australia	NL	A	MRCT	OT	Brown et al. (2004)
	Common Carp	*Cyprinus carpio*	S. Africa	NL	A	MRCT, EA, LF	OT	Winker et al. (2010a)
	Duskystripe Shiner	*Luxilus pilsbryi*	USA	NL	A	EA	OT	Simmons and Beckman (2012)
	Striped Shiner	*Luxilus chrysocephalus*	USA	NL	A	EA	OT	Simmons and Beckman (2012)
	Roundtail Chub	*Gila robusta*	USA	ESA	A	MIA	OT	Brouder (2005)
	Utah Chub	*Gila atraria*	USA	NL	A	MIA	OT	Johnson and Belk (2004)
	European barbel	*Barbus sclateri*	Spain	NL	A	MIA	OT	Escot and Grando-Lorencio (2001)
	Sharpnose shiner	*Notropis oxyrhyncus*	USA	IUCN	D	CT	OT	Durham and Wilde (2008)
	Smalleye shiner	*Notropis buccula*	USA	IUCN	D	CT	OT	Durham and Wilde (2008)
	Plains minnow	*Hybognathus placitus*	USA	NL	D	CT	OT	Durham and Wilde (2008)
	Redeye labeo	*Labeo cylindricus*	Mozambique	NL	A	MIA	SC	Weyl and Booth (1999)
	Redeye labeo	*Labeo cylindricus*	Kenya	NL	D	CT	OT	Nyamweya et al. (2012)
	Smallmouth yellowfish	*Labeo-barbus aeneus*	S. Africa	NL	A	EA, MRCT	OT	Winker et al. (2010b)
	Largemouth yellowfish	*Labeobarbus kimberleyensis*	S. Africa	IUCN	A	EA, MRCT	OT	Ellender et al. (2012b)
	Orange River mudfish	*Labeo capensis*	S. Africa	NL	A	EA, MRCT	OT	Winker et al. (2010b)
	Schizothorax o'connori	*Schizothorax o'connori*	Tibet	NL	A	MIA, EA	OT, VT, OP	Baoshan et al. (2011)
	Largemouth yellowfish	*Labeobarbus kimberleyensis*	S. Africa	IUCN	D	KA	OT	Paxton et al. (2013)
Esocidae	Northern Pike	*Esox lucius*	UK	NL	A	MR	SC, OP	Frost and Kipling (1959)
	Northern Pike	*Esox lucius*	Canada	NL	A	MRCT	SC, CL	Laine et al. (1991)
	Northern Pike	*Esox lucius*	UK	NL	A	MRCT	SC	Mann and Beaumon (1990)
	Northern Pike	*Esox lucius*	Canada	NL	A	CT	FR, CL	Babaluk and Craig (1990)
	Northern Pike	*Exox lucius*	Norway	NL	A	MR	MB	Sharma and Borgstrom (2007)

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Table 1 Periodicity studies for freshwater fish by family and species *(Continued)*

Family	Common name	Genus species	Country	Status	Scale	Method	Structure	Reference
Hiodontidae	Goldeneye	*Hiodon alosoides*	Canada	NL	A	LF	OP	Donald et al. (1992)
Lepistostidae	Alligator Gar	*Atractosteus spatula*	USA	NL	A	CT	OT, FR, SC	Buckmeier et al. (2012)
Percidae	Walleye	*Sander vitreus*	Canada	NL	A	CT	OP	Babaluk and Campbell (1987)
	Rainbow Darter	*Etheostoma caeruleum*	USA	NL	A	EA	OT, SC	Beckman (2002)
Petromyzontidae	American Brook Lamprey	*Lethenteron appendix*	USA	NL	A	CT	ST	Beamish and Medland (1988)
	Mountain Brook Lamprey	*Ichthyomyzon greeleyi*	USA	NL	A	CT	ST	Medland and Beamish (1987)
	Sea Lamprey	*Pertrpmyzon marinus*	USA	NL	A	CT	ST	Beamish and Medland (1988)
	Southern Book Lamprey	*Ichthyomyzon gagei*	USA	NL	A	CT	ST	Medland and Beamish (1991)
Polyodontidae	Paddlefish	*Polyodon spathula*	USA	NL	A	MR	DB	Scarnecchia et al. (2006)
Retropinnidae	Australian Smelt	*Retropinna semoni*	Australia	NL	A	CT	OT	Tonkin et al. (2008)
Salmonidae	Arctic Grayling	*Thymallus arcticus*	USA	NL	A	MRCT	OT	DeCicco and Brown (2006)
	European Grayling	*thymallus thymallus*	UK	NL	A	MR	SC	Horká et al. (2010)
	Atlantic Salmon	*Salmo salar*	USA	ESA	A	MR	SC	Havey (1959)
	Redband Trout	*Oncorhychus mykiss sub sp.*	USA	NL	A	MRCT, MIA	OT, SC	Schill et al. (2010)
	Brook Trout	*Salvelinus fontinalis*	USA	NL	A	MR	SC	Cooper (1951)
	Brook Trout	*Salvelinus fontinalis*	USA	NL	A	CT	OT	Hall (1991)
	Brook Trout	*Salvelinus fontinalis*	USA	NL	A	MR	SC	Alvord (1954)
	Brown Trout	*Salmo trutto*	New Zealand	NL	A	MR	FR, SC, OT	Burnet (1969)
	Brown Trout	*Salmo trutto*	USA	NL	A	MR	SC	Alvord (1954)
	Bull Trout	*Salvelinus confluentus*	USA	ESA	A	MR	FR, SC	Zymonas and McMahon (2009)
	Chinook Salmon	*Oncorynchus tshawytscha*	USA	ESA	A	MR	SC	McNicol and MacLellan (2010)
	Lake Trout	*Salvelinus namaycush*	Canada	NL	A	BRC	OT	Campana et al. (2008)
	Rainbow Trout	*Oncorynchus mykiss*	USA	NL	A	MRCT	OT, SC	Hining et al. (2009)
	Rainbow Trout	*Oncorynchus mykiss*	USA	NL	A	MR	SC	Alvord (1954)
	Lake Whitefish	*Coregonus clupeafomis*	Canada	NL	A	MR	FR	Mills and Chalanchuk (2004)
	Lake Whitefish	*Coregonus clupeafomis*	Canada	NL	A	MR	FR	Mills and Beamish (1980)
	Lake Whitefish	*Coregonus clupeafomis*	USA	NL	A	KA	SC	Van Oosten (1923)
	Lake Whitefish	*Coregonus clupeafomis*	USA	NL	A	CT	SC	Hogman (1968)
	Bloater	*Coregonus hoyi*	USA	NL	A	CT	SC	Hogman (1968)
	Kiyi	*Coregonus kiyi*	USA	NL	A	CT	SC	Hogman (1968)

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Table 1 Periodicity studies for freshwater fish by family and species *(Continued)*

Family	Common name	Genus species	Country	Status	Scale	Method	Structure	Reference
Sciaenidae	Freshwater Drum	*Aplodinotus grunniens*	USA	NL	A	LF	OT	Goeman et al. (1984)
	Freshwater Drum	*Aplodinotus grunniens*	USA	NL	A	BRC	OT	Davis-Foust et al. (2009)
Siluridae	European Catfish	*Silurus glanis*	Turkey	NL	A	MIA	VT	Alp et al. (2011)

NOTE: Status refers to the conservation status of the species, and is either not listed (NL), or is listed under the Endangered Species Act of 1972 (ESA), or under the International Union for the Conservation of Nature (IUCN). Scale refers to whether the structure was validated for annual (A) or daily (D) marks. Methods included bomb radio-carbon dating (BRC), mark-recatpure (MR), use of known-age fish (KA), or mark–recapture with chemically tagged fish (MRCT; e.g., oxytetracychline), chemical tags (CT), length–frequency (LF), marginal increment analysis (MIA), edge analysis (EA), and back-calculation (BC). Structure refers to the ageing structure used, and includes fin rays (FR), otoliths (OT), opercula (OP), scales (SC), spines (SP), vertebrae (VT), cleithra (CL), or branchialstegal rays (BR). Age refers to the age range currently validated for the species.

Examining periodicity and validation of multiple structures for species occupying large ranges, even if the structures have been already validated in another location, may likely be needed. For instance, the rate of deposition of opaque zones on aesteriscus otoliths in common carp (*Cyprinus carpio* Cyprinidae) differed between populations in South Africa (Winker et al., 2010a) and Australia (Vilizzi and Walker, 1999). Kowalewski et al. (2012) found disagreement for ages estimated from otoliths and scales across a large portion of the geographic range of bluegill (*Lepomis machrochirus* Centrarchidae) in the USA and urged management agencies to not mix assessments with the two structures. The lack of consistency in ageing structure use and validation of ageing structures across large geographical ranges limit the ability of researchers to make large-scale predictions regarding climatic influences on population growth and structure and also monitor invasive species population trajectories during initial establishment and following management actions (e.g., removal). Therefore, using the proposed prioritization framework, species with broad geographical ranges and high invasive potential (i.e., have established outside of their native ranges) along with inconsistency in previous age validation attempts would be high-priority species moving forward.

Validation studies for at risk and endangered freshwater fishes were limited, and very little is known regarding the validity of ageing structures for many of the most critically imperiled fishes. The lack of knowledge regarding imperiled fishes and the validity of their internal ageing structures will persist because of both legal constraints and low abundance. Therefore, new approaches to validation may be necessary or alternative metrics of population structure beyond age may be needed (Dawson et al. 2009). For instance, Hamel et al. (2014) suggested less reliance on imprecise and inaccurate fin rays and increased use of mark–recapture methods when validating ages of Acipenseridae sturgeons. In some instances closely related species may provide a means to either validate the age structures of threatened species or prove the method unreliable (Simmons and Beckman, 2012; Rugg et al., 2014).

The ability to successfully validate ageing structures may in part depend on differing life-history strategies and fish biology. For instance, members of the Centrarchidae family are ideal candidates for age structure validation studies because they typically are not long-lived, have short generation times, spawn annually, and have higher rates of juvenile survival due to nest building and guarding (i.e., equilibrium and opportunistic strategist; Winemiller and Rose, 1992). However, some equilibrium or opportunistic species (i.e., silver carp, *Hypophthalmichthys molitrix* Cyprinidae) undergo multiple spawning events per year (Carlson and Vondracek, 2014), which may induce multiple growth marks and hinder validation. In addition, age validation has proven difficult for many long-lived fishes with late maturation, delayed spawning cycles, and low juvenile survival (i.e., periodic strategist; Winemiller and Rose, 1992). Periodic strategist are often some of the most endangered species as their life history characteristics (i.e., delayed maturation and low juvenile survival) are not commensurate with extensive alteration to ecosystem processes such as changes to river flow regime and habitat (Olden et al. 2006). Estimation of ages of sturgeon species (e.g., Acipenseridae) has been difficult and often results in highly variable age estimates among readers and potentially great misrepresentation of true age (Kock et al. 2011; Stewart et al. 2015). In instances where there is a low feasibility in obtaining accurate and precise age estimates, large-scale studies using mark–recapture methods of known-age fishes may provide a promising alternative to traditional hard-part measurements.

Earlier calls have been made to have all structures across all ages validated for a given species (Beamish and McFarlane 1983). Validation of daily and annular marks should be performed when hard parts are used to determine age; however, validation studies may not be possible or necessary in all instances (e.g., endangered species) and is likely question- and context-dependent. Back-calculation of lengths for channel catfish using otoliths and spines have provided comparable estimates to known growth rates over a broader range of ages than those currently validated (Michaletz et al., 2009). Therefore, in some instances, the assumption that validation of ages for younger individuals spans to older individuals may be a valid assumption. However, this assumption is likely to only

Table 2 Validation studies for freshwater fish by family and species

Family	Common name	Genus species	Country	Status	Scale	Method	Structure	Age	Reference
Acipenseridae	Pallid Sturgeon	*Scaphirhynchus albus*	USA	ESA; IUCN	A	MR, KA	FR	1–7	Koch et al. (2011)
	Pallid Sturgeon	*Scaphirhynchus albus*	USA	ESA; IUCN	A	KA	FR	1–6	Hurley et al. (2004)
	Pallid Sturgeon	*Scaphirhynchus albus*	USA	ESA; IUCN	A	MR, KA	FR	ND	Hamel et al. (2014)
Catastomidae	Razorback Sucker	*Xyrauchen texanus*	USA	ESA; IUCN	A	KA	OT	1–6	McCarthy and Minckley (1987)
	Razorback Sucker	*Xyrauchen texanus*	USA	ESA; IUCN	D	KA	OT	1–49	Bundy and Bestgen (2001)
Centrarchidae	Largemouth Bass	*Micropterus salmoides*	USA	NL	A	KA	SC	1–2	Prather (1966)
	Largemouth Bass	*Micropterus salmoides*	USA	NL	A	KA	SC	1–4	Prentice and Whiteside (1975)
	Largemouth Bass	*Micropterus salmoides*	USA	NL	A	KA	OT	2–5	Taubert and Tranquilli (1982)
	Largemouth Bass	*Micropterus salmoides*	USA	NL	A	KA	OT	1–5	Hoyer et al. (1985)
	Largemouth Bass	*Micropterus salmoides*	USA	NL	A	KA	OT	1–16	Buckmeier and Howell (2003)
	Largemouth Bass	*Micropterus salmoides*	USA	NL	D	KA	OT	1–151	Miller and Storck (1982)
	Smallmouth Bass	*Micropterus dolomieu*	USA	NL	A	KA	OT, SC	1–4	Heidinger and Clodfeller (1987)
	Smallmouth Bass	*Micropterus dolomieu*	USA	NL	D	KA	OT	1–14	Graham and Orth (1987)
	Spotted Bass	*Micropterus punctulatus*	USA	NL	D	KA	OT	1–94	DiCenzo and Bettoli (1995)
	Black Crappie	*Pomoxis nigromaculatus*	USA	NL	A	KA	OT, SC	1–5	Ross et al. (2005)
	White Crappie	*Pomoxis annularis*	USA	NL	A	KA	OT, SC	1–3	Hammers and Miranda (1991)
	White Crappie	*Pomoxis annularis*	USA	NL	D	KA	OT	1–100	Sweatman and Kohler (1991)
	White Crappie	*Pomoxis annularis*	USA	NL	A	KA	OT, SC	1–5	Ross et al. (2005)
	Bluegill	*Lepomis microchirus*	USA	NL	A	KA	SC	1–3	Prather (1966)
	Bluegill	*Lepomis microchirus*	USA	NL	A	KA	OT	1	Schramm (1989)
	Bluegill	*Lepomis microchirus*	USA	NL	D	KA	OT	1–125	Taubert and Coble (1977)
	Green Sunfish	*Lepomis cyanellus*	USA	NL	D	KA	OT	1–170	Taubert and Coble (1977)
	Redspotted Sunfish	*Lepomis miniatus*	USA	NL	D	KA	OT	1–119	Roberts et al. (2004)
	Pumpkinseed Sunfish	*Lepomis gibbosus*	USA	NL	D	KA	OT	1–176	Taubert and Coble (1977)
Cichlidae	Baringo Tilapia	*Oreochromis niloticus baringoensis*	Kenya	NL	D	KA	OT	1–30	Nyamweya et al. (2010)
Clupeidae	American Shad	*Alosa sapidissima*	USA	NL	A	MR, KA	SC	1–6	Judy (1961)
	American Shad	*Alosa sapidissima*	USA	NL	D	KA	OT	1–25	Savoy and Crecco (1987)
	American Shad	*Alosa sapidissima*	USA	NL	A	MRCT, KA	OT	3–9	Duffy et al. (2012)
	Gizzard Shad	*Dorosoma cepedianum*	USA	NL	D	KA	OT	1–71	Davis et al. (1985)
Cyprinidae	Colorado Pikeminnow	*Ptychocheilus lucius*	USA	ESA; IUCN*	D	KA	OT	1–165	Bestgen and Bundy (1998)
	Common Carp	*Cyprinus carpio*	Australia	NL	D	KA	OT	1–35	Vilizzi (1998)
	Common Carp	*Cyprinus carpio*	Australia	NL	D	KA	OT	1–20	Smith and Walker (2003)
	Bighead Carp	*Hypophthalmichthys nobilis*	USA	NL	A	KA	FR, SC	1–2	Nuevo et al. (2004)
	Fallfish	*Semotilus corporalis*	USA	NL	D	KA	OT	1–14	Victor and Brothers (1982)
	Northern Pikeminnow	*Ptychocheilus oregonesis*	USA	NL	D	KA	OT	1–29	Wertheimer and Barfoot (1988)
	Roundtail Chub	*Gila robusta*	USA	ESA	A	KA	OT	1–3	Brouder (2005)
	Roundtail Chub	*Gila robusta*	USA	ESA	D	KA	OT	ND	Brouder (2005)
	Barbel	*Barbus barbus*	UK	NL	D	KA	OT	1–17	Vilizzi and Copp (2013)
	Smallmouth yellowfish	*Labeobarbus aeneus*	S. Africa		D	KA	OT	1–100	Paxton et al. (2013)
	Kabyabya	*Opsaridum tweddleorum*	Malawi	NL	D	KA	OT	0–33	Morioka and Matsumoto (2007)

(Continued on next page)

Table 2 Validation studies for freshwater fish by family and species *(Continued)*

Family	Common name	Genus species	Country	Status	Scale	Method	Structure	Age	Reference
Ictaluridae	Channel Catfish	*Ictalurus punctatus*	USA	NL	A	KA	SP	1–2	Sneed (1951)
	Channel Catfish	*Ictalurus punctatus*	USA	NL	A	KA	VT	1–3	Appelget and Smith (1950)
	Channel Catfish	*Ictalurus punctatus*	USA	NL	A	KA	OT	1–4	Buckmeier et al. (2002)
	Channel Catfish	*Ictalurus punctatus*	USA	NL	A	KA	SP	1–4	Prentice and Whiteside (1975)
	Channel Catfish	*Ictalurus punctatus*	USA	NL	D	KA	OT	1–18	Holland-Bartels and Duvall (1988)
	Channel Catfish	*Ictalurus punctatus*	USA	NL	D	KA	OT	1–60	Sakaris and Irwin (2008)
	Flathead Catfish	*Pylodictis olivaris*	USA	NL	A	KA	SP	4–5	Turner (1980)
	Flathead Catfish	*Pylodictis olivaris*	USA	NL	D	KA	OT	1–72	Sakaris et al. (2010)
	Blue Catfish	*Ictalurus furcatus*	USA	NL	D	KA	OT	1–60	Sakaris et al. (2010)
Lepistomidae	Alligator Gar	*Atractosteus spatula*	USA	NL	A	KA	OT	1–1	Buckmeier et al. (2012)
Moronidae	Striped Bass	*Morone saxatilis*	USA	NL	A	KA	OT, SC	1–4	Heidinger and Clodfelter (1987)
	Striped Bass	*Morone saxatilis*	USA	NL	A	MR, KA	OT	3–7	Secor et al. (1995)
	Striped Bass	*Morone saxatilis*	USA	NL	D	KA	OT	1–69	Jones and Brothers (1987)
	Hybrid Striped Bass	*Morone saxatilisxchrysops*	USA	NL	A	KA	OT	1–2,5	Snyder et al. (1983)
Mugilidae	Freshwater Mullet	*Myxus capensis*	S. Africa	NL	A	KA	OT	10	Ellender et al. (2012a)
Nothobranchiidae	Turquoise killifish	*Nothobranchius furzeri*	Mozambique	NL	D	KA	OT	7–66	Polacik et al. (2011)
Percidae	Walleye	*Sander vitreus*	Canada	NL	A	KA	OT	3	Erickson (1983)
	Walleye	*Sander vitreus*	USA	NL	A	KA	OT, SC	1–4	Heidinger and Clodfelter (1987)
	Walleye	*Sander vitreus*	USA	NL	D	KA	OT	1–19	Miller and Tetzlaff (1985)
	Walleye	*Sander vitreus*	USA	NL	D	KA	OT	14–42	Parrish et al. (1994)
	European Perch	*Perca fluviatilis*	New Zealand	NL	D	KA	OT	1–82	Kristensen et al. (2008)
Percicthyidae	Golden Perch	*Macquaria ambigua*	Australia	NL	D	KA	OT	1–15	Brown and Wooden (2007)
	Golden Perch	*Macquaria ambigua*	Australia	NL	A	KA	OT	1–9	Mallen-Cooper and Stuart (2003)
	Golden Perch	*Macquaria ambigua*	Australia	NL	A	KA	OT	1–23	Stuart (2006)
	Murray Cod	*Maccullochella peelii*	Australia	IUCN	A	KA	OT	1–4	Gooley (1992)
Salmonidae	Brown Trout	*Salmo trutto*	Spain	NL	D	KA	OT	1–7	Dodson et al. (2013)
	Chinook Salmon	*Oncorynchus tshawytscha*	Canada	ESA	A	MR, KA	SC	1–4	Godfrey et al. (1968)
	Chinook Salmon	*Oncorynchus tshawytscha*	Canada	ESA	A	KA	SC, FR		Chilton and Bilton (1986)
	Chinook Salmon	*Oncorynchus tshawytscha*	Canada	ESA	A	KA	OT		Murray (1994)
	Chinook Salmon	*Oncorynchus tshawytscha*	Canada	ESA	D	KA	OT	90–155	Neilson and Green (1982)
	Chinook Salmon	*Oncorynchus tshawytscha*	USA	ESA	A	KA	SC, FR	1–3	Copeland et al. (2007)
	Sockeye Salmon	*Oncorhynchus nerka*	Canada	ESA	D	KA	OT	1–26	Wilson and Larkin (1980)
	Lake Trout	*Salvelinus namaycush*	USA	NL	A	MR, KA	SC		Cable (1956)
	Lake Trout	*Salvelinus namaycush*	USA	NL	A	KA	BR		Bulkley (1960)
	Rainbow Trout	*Oncorynchus mykiss*	Australia	NL	A	MR	OT	1–4	Faragher (1992)

NOTE: Status refers to the conservation status of the species, and is either not listed (NL), or is listed under the Endangered Species Act of 1972 (ESA) or under the International Union for the Conservation of Nature (IUCN). Scale refers to whether the structure was validated for annual (A) or daily (D) marks. Methods included mark-recatpure (MR), use of known-age fish (KA), or mark–recapture with chemically tagged fish (MRCT; e.g., oxytetracychline). Structure refers to the ageing structure used and includes fin rays (FR), otoliths (OT), scales (SC), spines (SP), vertebrate (VT), or branchialstegal rays (BR). Age refers to the age range currently validated for the species.

hold for certain species with shorter life spans where crowding of annual marks is less of an issue compared with long-lived species. When estimates of growth are the principle question, alternatives to back-calculation using hard parts may be sufficient. For instance, Erhardt and Scernacchia (2013) found similarity in growth and age estimates derived from mark–recapture, fin ray, and scale methods for large migratory bull trout *Salvelinus confluentus*. Therefore, in cases where

Table 3 A priority framework for directing future age validation studies

Characteristic	Priority Level: Low	Priority Level: Medium	Priority Level: High
Invasive potential	Species has shown little potential to invade outside native range.		Species has shown considerable capability in its ability to invade and establish outside native range. Species has proven capable of altering ecosystem processes in invaded regions (i.e., Common Carp or Flathead Catfish).
Alternative techniques	Long-term mark–recapture in place	Some stocking of known-age individuals has occurred; chemical markings.	No other techniques available.
Fish biology	Fish with little or no bony structure useful for age validation (i.e., Polyodontidae). Inconsistent spawning.		Fish with multiple bony structures useable for age validation.Annual spawner.
Previous work	No previously published work has been performed. Consistency in studies examining accuracy or periodicity for some ages at multiple geographic locations.		Previously published studies on periodicity and accuracy for multiple ages with little to no consistency.
Feasibility	Short term studies not likely to produce true validation but may provide some verification of periodicity of marks, i.e., marginal increment analysis; chemical tags.		Long-term studies with sufficient resources to provide true validation of marks, i.e., known-age mark–recapture.
Management status	Not heavily managed. Limited recreational or commercial value.	Managed through stocking only.	Heavily managed through stocking and harvest regulation. High recreational or commercial value.
Conservation status	Not currently listed.	Listed locally. i.e., state or provincial.	Federally or internationally listed, i.e., US Endangered Species Act; International Union for the Conservation of Nature.
Geographical location/habitat stability	Little distinction among seasons. Extreme environments or environments with high variability.	Little temperature variability. Seasonal patterns exist, including flooding, i.e., tropical floodplain rivers.	Temperate environments with distinct seasons. Low prevalence of extreme stochastic events.

empirical growth data corroborates back-calculated growth information from ageing structures or where alternative methods can be used to predict growth (e.g., mark–recapture), age validation may be less of a priority. We as fisheries professionals need to prioritize where traditional validation of ageing structures can significantly aid management of fish populations and where alternative methods may be more appropriate, and then begin to apply those new methods.

Inconsistent definitions of periodicity and validation were prevalent and greatly hindered the categorization of study objectives (i.e., periodicity of annulus formation over a given period versus validating annual marks as the true age of an individual). Validation was often used to describe measures of precision among readers. This result was not surprising, as differences and confusion exist even among previous calls for validation. Validation has been defined as a means of proving a technique is accurate; accuracy has also been suggested to be less valuable than measures of precision or reproducibility (Beamish and McFarlane, 1983). As a result, many papers published since Beamish and McFarlane (1983) have used the term validation when periodicity of annulus formation was actually examined (Campana, 2001). The definitions used by Campana (2001) is recommended where validation refers to the assessment of the process error involved in hard structure formation due to the non-occurrence of formation of an interpretable mark on a hard structure on a daily or annual time step. Therefore, future researchers should bear in mind that validation applies only to instances where the true age can be determined. Consequently, the term periodicity should be used in all other studies.

Papers describing unsuccessful validations or aberrations in periodicity (e.g., >1 growth zone per year) are also needed to prioritize future research efforts. For example, Rugg et al. (2014) evaluated situations where the ageing structure was producing neither accurate nor precise estimates of pallid sturgeon (*Scaphirhynchus albus* Acipinceridae) and shovelnose sturgeon (*Scaphirhynchus platorhynchus* Acipinceridae) age and growth. Buckmeier et al. (2012) provided evidence that annulus formation was not validated for pectoral fin rays from the age of 6 years and older alligator gar, but could be useful for age of <6 years. These authors also suggest that otoliths would be the preferred method as pectoral fin rays and scales were much more variable. Paragamian and Beamesderfer (2003) found white sturgeon (*Acipenser transmontanus* Acipinceridae) fin ray estimates of age were 30–60% less than ages assigned from mark–recapture estimates, and observed growth estimates could not be achieved using age-specific estimates from fin rays. Publications that highlight discrepancies among ageing structures and failed validation attempts are needed (Paragamian and Beamesderfer, 2003; Winker et al., 2010a).

Consistency in growth depositional rates across large geographical scales (i.e., continents) is an important consideration, particularly for wide-ranging cosmopolitan species and highly invasive species, and can be used to further prioritize future validation research. Largemouth bass is a popular sport fish that is ubiquitous in the USA and has been established on multiple continents where the species can become invasive (Taylor and Weyl, 2013). Common carp is another potentially invasive species, and is responsible for reduced water quality and competition for food resources among other benthic fishes (Weber and Brown, 2009). Our review suggests similarity in growth zone deposition across the geographical range of largemouth bass, but conflicting outcomes for common carp (Winker et al., 2010a; Taylor and Weyl, 2013). Vilizzi and Walker (1998) and Brown et al. (2004) documented annual deposition of growth zones for common carp in Australia; however, Winker et al. (2010a) documented a biannual (i.e., two marks per year) deposition rate in South Africa. Due to the uncertainty presented by ambiguous or conflicting periodicity patterns in growth zone deposition, our prioritization framework would direct efforts at documenting similarities or differences in periodicity and validation of ageing structures for potentially widespread and invasive species.

Studies beyond those discussed here have undoubtedly been performed and were either inaccessible or found only in reports, theses, or dissertations. Studies were excluded that did not undergo the peer-review process and were not accessible to the larger scientific community. In addition, only journals printed in English were examined, and an unknown amount of literature may exist in non-English formats. Therefore, perhaps greater accessibility to age validation studies could reduce information gaps. Maceina et al. (2007) suggested that a centralized database be established to which true validation studies and studies evaluating periodicity could be easily added and searched. A centralized database could be a significant contribution to fisheries science as well as the understanding and interpretation of ageing structures. Further, prioritizing validation of ageing structures among species using the proposed framework, and incorporating alternative methods where traditional methods are inappropriate (i.e., long-term mark–recapture studies for species of concern) will push forward the science of fish age determination.

ACKNOWLEDGMENTS

We thank the University of Nebraska–Lincoln for funding and support and students from the Quantitative Fisheries Science course for discussion and initial work on the project.

FUNDING

The Nebraska Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement among the US Geological Survey, the Nebraska Game and Parks Commission, the University of Nebraska, the US Fish and Wildlife Service, and the Wildlife Management Institute.

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