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REVIEWS

Age determination in common carp *Cyprinus carpio*: history, relative utility of ageing structures, precision and accuracy

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Abstract The common carp *Cyprinus carpio* is one of the most widely-distributed freshwater fishes in the world. Due to its value for conservation and fisheries in several native/translocated areas of distribution and its detrimental effects on the aquatic ecosystem in most invasive areas, robust age-based population dynamics models are required for successful management of this species. The present study provides a global review of age determination in carp, including a historical account of ageing methods, an assessment of the relative utility of ageing structures, and an evaluation of precision and accuracy (i.e. validation) of age estimates. Historically, scales were by far the most widely-employed structure, followed by the operculum, otolith, dorsal spine, vertebra and fin ray. However, in countries where carp is categorised as 'high risk' of impact, use of alternative structures to the scale was predominant. Causal criteria analysis showed scales and opercula to provide inconsistent evidence for successful annulus identification/counting, whereas consistent evidence was found for otoliths, dorsal spines, vertebrae and (pectoral) fin rays. Precision was always above reference thresholds for scales, whereas for otoliths, dorsal spines and fin rays was in several cases below. Accuracy was addressed sporadically and mostly in high-risk countries. It is suggested that dorsal spines or pectoral fin rays should be used in lieu of scales as non-lethal ageing structures, and otoliths (or vertebrae, pending more research) otherwise, and that validation should always be attempted as part of the set-up of more appropriate ageing protocols and use of correct terminology.

Keywords Causal criteria analysis · Dorsal spine · Fin ray · Operculum · Otolith · Scale · Vertebra

Introduction

Age determination in fish is fundamental for the management of fisheries (e.g. Hilborn and Walters 2013) and for understanding species' life histories and their population dynamics (Beddington and Kirkwood 2005). Various calcified structures (or 'hard parts'), including scales, opercula, vertebrae, spines, fin rays and otoliths (Casselman 1983), are available for ageing fish, and these structures are sometimes used in conjunction for comparative purposes (e.g. Vilizzi and Walker 1999; Khan and Khan 2009). Age

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determination typically involves the counting of annual (or daily) increments under the assumption that these were formed on an equivalent temporal interval. This assumption is verified through validation, which is equivalent to determining the accuracy of an age estimate (Campana 2001).

Not surprisingly, failure to accomplish the aforementioned accuracy–precision requirements is likely to result in erroneous age estimates. This ultimately leads to biased understanding of fish population dynamics, with consequences for the management and conservation of species (e.g. Campana 2001; Crook et al. 2013). Hence, the importance of age validation (cf. Beamish and McFarlane 1983) for fish and fisheries biologists (sensu Balon 1999), including the set-up of so-called 'production ageing' programmes (i.e. reference collections of ageing structures and quality control monitoring), which have become an intrinsic component of modern fisheries laboratories in many parts of the world (Campana 2001).

Highly valued in most of its native areas of distribution (Vilizzi 2012), the common carp *Cyprinus carpio* L. (hereafter, 'carp') is one of the most widely-distributed freshwater fishes in the world (Welcomme 1988; Casal 2006) due to introductions for farming and aquaculture that began in Roman times (Balon 1995; Copp et al. 2005). However, in many of its non-native areas the carp is regarded as an invasive (pest) species, with documented and often severe adverse impacts on freshwater ecosystems (Vilizzi and Tarkan 2015; Vilizzi et al. 2015). As one of the most studied freshwater fish species, both by historical and geographical extent, it is therefore not surprising that a vast amount of information has been generated on (amongst other ecological aspects) its age and growth (Vilizzi and Copp 2017). At the same time, population dynamics models have recently been developed for the management of carp in heavily-invaded regions of North America and Australasia (Brown and Walker 2004; Lechelt and Bajer 2016; Weber et al. 2011, 2016; Koehn et al. 2017). Since parameterisation of these models requires estimated ages and/or age-based growth parameters (e.g. von Bertalanffy growth function: VBGF), the availability of precise and accurate age estimates from reliable ageing structures is of paramount importance.

The present study provides a historical account of age determination in carp and evaluates the relative utility, precision and accuracy of the various ageing structures used. The specific objectives are to: (1) provide a historical evaluation (cf. 'narrative' review: sensu Webb et al. 2013) of the use and effectiveness of a range of ageing structures for carp; (2) assess the relative utility of these ageing structures through a 'systematic' review (sensu Webb et al. 2013) by means of an evidence-based, causal criteria analytical approach; and (3) evaluate the precision and accuracy (validation) of age estimates in carp. In light of the existing information, recommendations are made as to which ageing structure(s) should be routinely employed for ageing carp and how quality control programmes could be implemented. The ultimate aim is to assist fish biologists and fisheries managers to refine age and growth based population dynamics models for improved management of this important species.

Methodology

History

The literature material surveyed consisted of published sources, including peer-reviewed papers, theses, dissertations and, occasionally, reports. The criteria for inclusion of a study into the review were that it should: (1) have been carried out on carp living under natural conditions (i.e. in the wild); (2) provide mean length-at-age values and/or corresponding VBGF parameter estimates for the carp population(s) under investigation; and (3) 'explicitly' mention the structure(s) used for ageing (e.g. reference to 'standard ageing protocols', albeit most likely scale-based, was not accepted as sufficient evidence). These literature sources were then complemented with those studies investigating the morphology, physiology and processing techniques of the various structures used/attempted for ageing carp, with special emphasis on the otolith.

For each age-growth study selected as per above, the country of origin of the study and the distributional range of carp were noted. The species' areas of distribution were distinguished into native, native/translocated and introduced. As such, non-native carp populations were those either introduced or translocated into water bodies located outside the wild form's distributional range. This was based on the distributional map of the Eurasian landmass for wild carp provided by Kirpichnikov (1999; see also Chistiakov and Voronova (2009), noting that several countries span the carp's native, translocated and introduced ranges. Within the introduced range, countries were categorised as either 'medium risk' or 'high risk' relative to the presence of carp following Vilizzi et al. (2015), and those countries not originally included in that study were assessed based on additional evidence (i.e. Colombia: Zambrano et al. 2006; Greece: Perdikaris et al. 2016; Portugal: Almeida et al. 2013; South Africa: Marr et al. 2017).

Relative utility

The Eco Evidence approach (Norris et al. 2012; Webb et al. 2013), which is a form of causal criteria analysis adapted to the environmental sciences, was used for weighting and combining evidence from those studies investigating the relative utility of the ageing structures. The studies included were those dealing with age and growth that relied on a 'suite' of ageing structures as well as those specifically focused on the comparative aspects of such structures (notably, studies only qualitatively assessing the utility of a certain structure, i.e. without enumerating annuli, were not included). The Eco Evidence framework consists of eight steps (Table 1): in step 1, the utility of the six most widely-used ageing structures plus the eye lens (because of one comparative study including it) to age carp successfully was assessed; in step 2, the 'context' was defined as the ageing of carp at the global (worldwide) level; in step 3, the conceptual model assumed that each structure would allow to age carp successfully by the correct identification of annuli; in step 4, the conceptual model was exemplified by seven corresponding hypotheses (i.e. one for each ageing structure evaluated) of successful annulus identification/counting on the structure used; in step 5, the evidence provided in support consisted of the reviewed comparative studies; and in step 7 (note that step 6 was not necessary), given that the framework was originally designed for the evaluation of 'natural experiments' for the monitoring of ecological impacts, a 'best-match' approach was employed. To this end, following the weigthing system of Norris et al. (2012), for those studies that assessed the utility of a specific structure relative to other reference structure(s), a 'reference/control versus impact (no before)' design was matched that provides a weight of 2, with one control structure contributing an additional weight of 2, more than one control structure a weight of 3, and with the reference structure (only one in all cases) providing a weight of 0. Whereas, for those studies that evaluated a suite of structures simultaneously, a 'gradient response model' design was matched that

Table 1 Steps in the Eco Evidence causal criteria analysis framework (after Norris et al. 2012 and Webb et al. 2013) to investigate the relative utility of ageing structures for common carp *Cyprinus carpio*

Step	Framework definition	Study definition
1	Document the nature of the problem and draft the overall question (hypothesis) under investigation	Ageing common carp *Cyprinus carpio*. Is an ageing structure successful or unsuccessful for the purpose?
2	Identify the context in which the question will be asked	Ageing of carp at the global (worldwide) level
3	Develop a conceptual model and clarify the question	It is assumed that each structure as part of a comparative 'suite' would successfully age carp by the correct identification of annuli
4	Decide on the relevant hypothesis	Successful annulus identification/counting on the structure (seven in total) being used
5	Search and review literature, and extract evidence	Review of those studies relying on a 'suite' of ageing structures, including those specifically focused on comparative aspects
6	Revise conceptual model and previous steps if necessary	(Not necessary)
7	Catalogue and weight the evidence	After Norris et al. (2012) (see text for details)
8	Assess the level of support for the overall question (hypothesis) and make a judgement	After Webb et al. (2013) (see text for details)

provides a weight of 0, with up to three structures contributing also a weight of 0, four structures a weight of 2, and five structures a weight of 4.

The desktop Eco Evidence v1.1.1 analyser software (Nichols et al. 2011) was used for implementation of causal criteria analysis. Each 'evidence item' (=assessment of a certain structure) was assigned an overall (i.e. summation) evidence weight based on the weighting system defined above. For each of the seven structure-related hypotheses, the resulting weights were then summed for all evidence in favour of the hypothesis and for all evidence against the hypothesis. Following Norris et al. (2012), the sums were then compared to a threshold value of 20 points, which has proven satisfactory in previous applications of the methodology (Webb et al. 2013; Vilizzi et al. 2015). This resulted in one of four conclusions for each hypothesis (i.e. 'support for hypothesis': ≥ 20 in favour, < 20 against; 'inconsistent evidence': ≥ 20 in favour, ≥ 20 against; 'insufficient evidence': < 20 in favour, < 20 against; 'support for alternative hypothesis': < 20 in favour, ≥ 20 against). Importantly, to assess the level of support for the seven hypotheses, and therefore pass judgement (step 8 of the framework), the 'quantifiable effect' equated in all cases to successful (or unsuccessful) identification of annuli by using a certain ageing structure.

Precision and accuracy

The age-growth literature on carp was screened for studies that assessed the precision of ageing structures. Precision was evaluated both within interpreter and between interpreters, as well as between ageing structures. The two most widely-employed indices for measuring precision, i.e. the average percentage error (APE) and the coefficient of variation (CV), were used in the comparisons (see Campana 2001). Since both indices are considered to be superior to the percentage agreement (Campana 2001), albeit reported in some studies, this was not included in the review. As (empirical) target levels of desirable precision, the values of 5.5% for the APE and of 7.6 or 5% for the CV (Campana 2001) were used as thresholds for all comparisons.

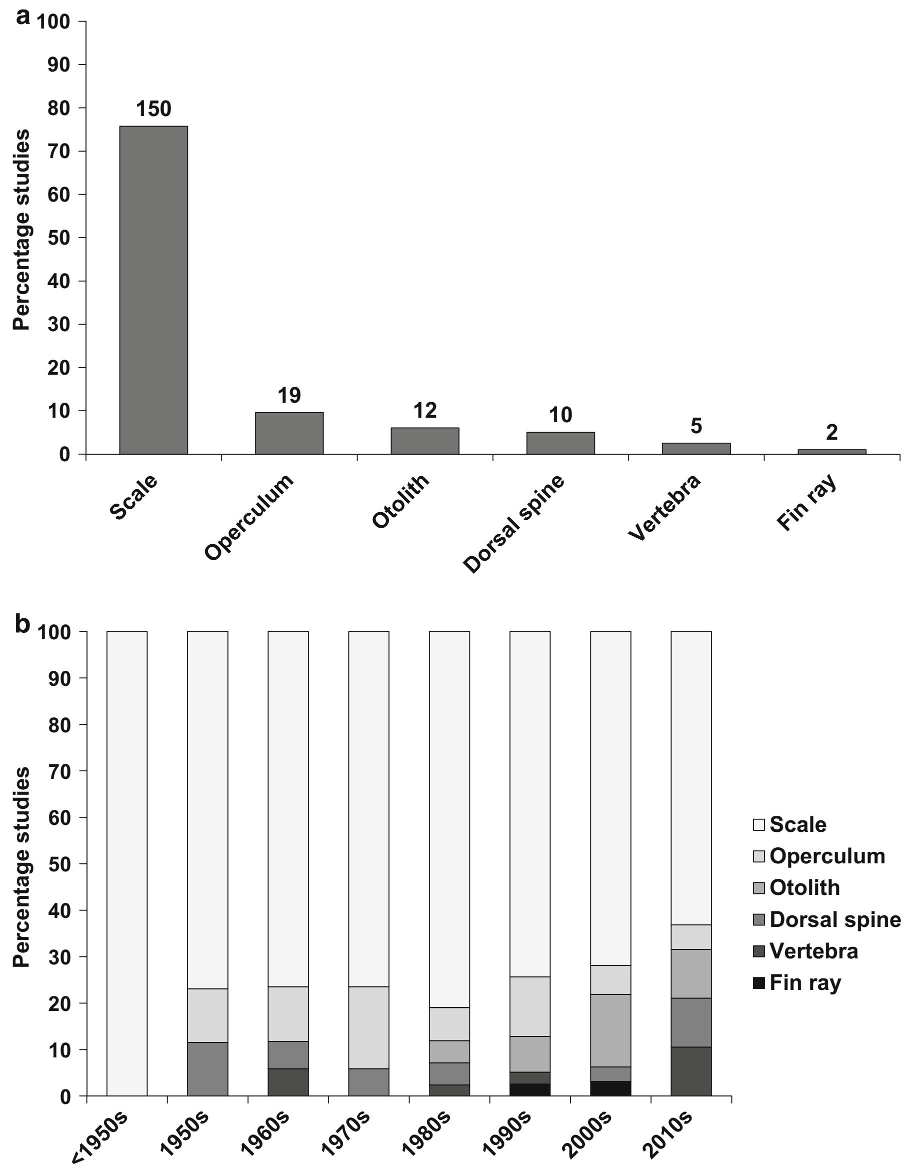
Similar to precision, the literature was screened for evidence of an evaluation of accuracy (validation). In some cases, this was the topic of a dedicated study, which was employed by the authors in support to one (or more) other related studies in which age and growth in carp were assessed. Validation methods were categorised as: (1) release of known age and marked fish; (2) mark-recapture of chemically-tagged fish; (3) discrete length modes sampled for age structures; and (4) marginal increment analysis (MIA) (terminology after Campana 2001). Finally, for each study both the structure(s) for which validation was accomplished and the location (country) where the study was conducted were noted.

Results

History

In total, 167 age-growth studies on carp spanning nearly 90 years provided information on the type of ageing structure(s) used (Table S1 in Supporting Information). Scales were by far the most commonly employed, followed (in decreasing order) by the operculum, otolith, dorsal spine, vertebra and fin ray (pectoral or anal) (Fig. 1a). However, unlike scales, which represented nearly 76% of the total proportion of studies, use of the other structures was always $< 10\%$. Scales were the only structure employed before the 1950s, and accounted for the largest proportion of studies in all decades from the 1950s onwards, and in the 2010s still represented 63% of the total studies (Fig. 1b). Use of opercula and dorsal spines started in the 1950s, of vertebrae in the 1960s, of otoliths in the 1980s, and of fin rays in the 1990s. Scales were the only structure employed for ageing carp in its native range, and were by far the predominant structure used in its native/translocated range, with only China and Turkey relying also on fin rays, opercula and vertebrae, respectively as alternative structures (Fig. 2). Whereas, the spectrum of structures, other than scales, used to age carp in its introduced range was broad and consisted of opercula, otoliths, dorsal spines, vertebrae, fin rays. This was especially in countries where carp was categorised as 'high-risk', e.g. South Africa and Australia, where scales were used in only 20 and 25% of the reviewed studies, respectively. An in-depth, ageing structure-wise historical description is provided below (see also Fig. 3).

Fig. 1 **a** Proportion of studies using one of the six most common structures for ageing common carp *Cyprinus carpio* (number of studies also indicated, noting that more than one structure was employed in some studies); **b** Same, over the study period



Scale

The age of cyprinid fishes has traditionally been estimated from scales (e.g. Jearld 1983; Mann 1991), with the identification of increment (annulus) patterns in carp dating back as far as the late 1700s (van Leeuwenhoek 1798; see also Jackson et al. 2007). However, it was at the turn of the nineteenth century that lepidological studies (i.e. investigating the morphology and characteristics of fish scales) contributed to the establishment of more rigorous protocols for annulus identification on this ageing structure (Hoffbauer 1898, 1905; see also Van Oosten 1928). Several age-growth studies have provided descriptions of the morphology of carp scales, with emphasis on the arrangement, pattern and (time of) formation of both annuli and circuli (i.e. thinner growth lines, including their ‘crossing-over’ or ‘anastomosis’), as well as related criteria for identification (Oliva 1955; Balon 1957; Vostradovský 1962; Das and Fotedar 1965; Effendie 1968; Jones 1974; Deng et al. 1981; Wang 1983; Johal et al. 1984). Also available are ‘dedicated’ lepidological studies that investigated: time of annulus formation (Frey 1942); morphology and arrangement

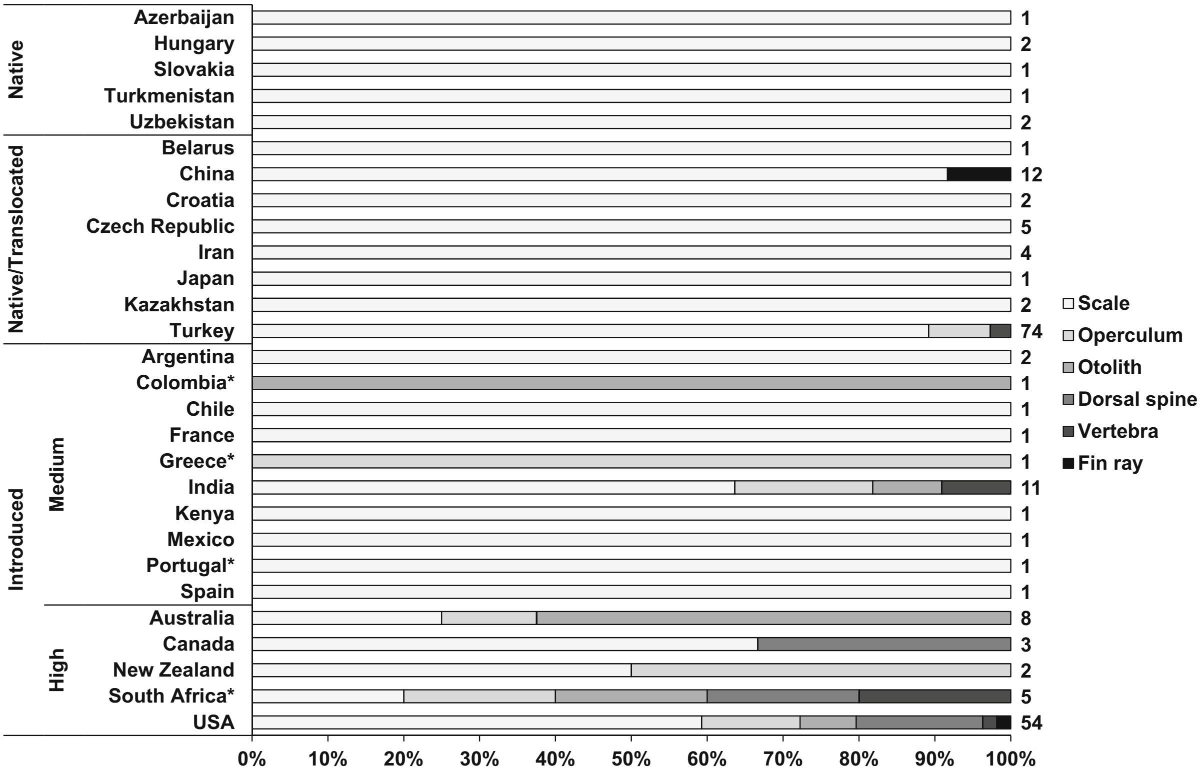


Fig. 2 Proportion of studies using one of the six most common structures for ageing carp according to country (including total number of populations aged). Countries are grouped based on carp's origin (see text for explanation), with 'High' and 'Medium' indicating the risk level of introduced-origin countries based on Vilizzi et al.'s (2015) categorisation (risk level of countries marked by an asterisk evaluated in the present study)

of so-called 'radii' (Matsui 1949); criteria for identification of 'true' and 'false' annuli (Talaat and Oláh 1986); early developmental stages of scale formation (El-Fiky 1993); genetics of scale pattern formation (Casas et al. 2013); arrangement of scales (in mirror carp: see below) as a natural marker for individual fish identification (Huntingford et al. 2013); and the ultrastructure of the focal region of regenerated scales as an alternative to the use of molecular markers for identification of (invasive) carp populations (Johal et al. 2014).

The scales of mirror carp (the scalation variant genetically referred to as 'scattered' (Balon 1995; Kirpichnikov 1999) have also received attention in age determination studies. Das and Fotedar (1965) were the first to estimate the age of mirror carp successfully—they also contributed a detailed description of annulus patterns and criteria for their identification. Similarly, in all other age-growth studies of mirror carp (mainly carried out in Anatolia, Turkey: Sarıhan 1980; Akyurt 1987; Karakoç and Sarıhan 1987; Okumuş and Tekelioğlu 1987; Çetinkaya et al. 1995a, b; Kırankaya and Ekmekçi 2004; Kırankaya 2007; but see Prochelle and Campos 1985), no difficulties in annulus identification have seemingly been reported (but see Gümüş 1998). This is contrary to other studies, which have pointed to a total lack of interpretability of scales in this carp scalation variant (Linfield 1982; Vilizzi 1997).

Despite the predominant use of scales for ageing carp, several drawbacks with the interpretation of these structures have been encountered, including: (1) crowding of annuli towards the edge in older fish, (2) supernumerary rings (cf. 'spawning checks' and 'pseudo-annuli'), (3) re-sorption, (4) lack of deposition of the first annulus, and (5) difficulties in locating the first annulus (Krumholz 1956; Christenson and Smith 1965; Starrett and Fritz 1965; Marlborough 1967; Linfield 1982; Lubinski et al. 1984; Fernández-Delgado 1990). On the other hand, the advantages

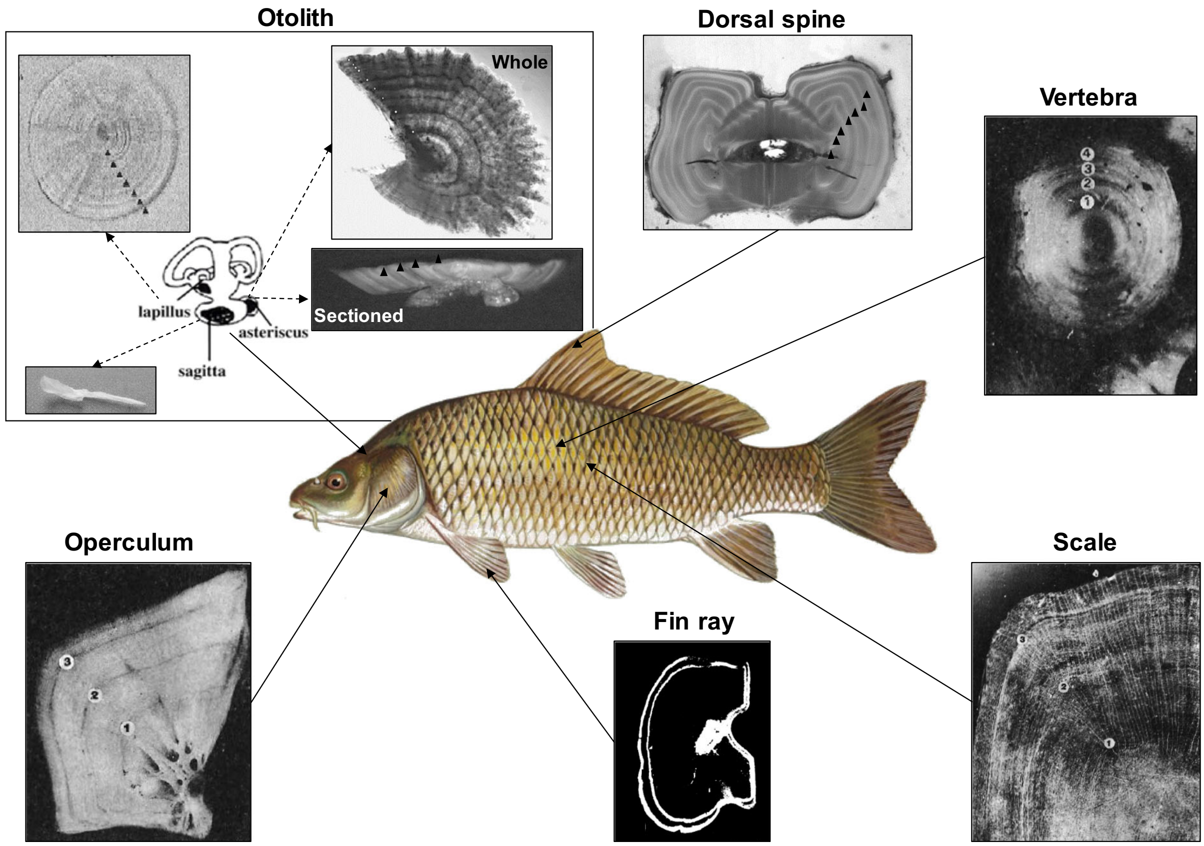


Fig. 3 Pictorial representation of the structures used for ageing carp

with using scales include: (1) their ease of collection and preparation, and (2) the possibility for mark-recapture studies (i.e. scale removal need not harm the fish).

Operculum

The operculum has proven a valid complement or alternative to scales in carp age-growth studies. This structure has generally been used in conjunction with either scales only (English 1952; McConnell 1952; Rehder 1959; Jester 1974; Çetinkaya 1992; Çetinkaya et al. 1995a, b; Şen 2001; Tempero et al. 2006) or scales plus other hard parts (Effendie 1968; Lubinski et al. 1984; Cochrane 1985; Raina 1987; Bhandari et al. 1993; Vilizzi and Walker 1999), and seldom on its own (Tsimenide 1978; Çolakoğlu and Akyurt 2011) (Table S1 in Supporting Information).

Ridge-like projections radiating from the fulcrum (referred to as 'buttresses' or 'fingers of bone': English 1952 and McConnell 1952, respectively) may often obscure the first one to three annuli, challenging in such cases correct age estimation. The relative ease of collection of the operculum (albeit involving the sacrifice of the fish) is offset by the time required to prepare it for examination. In this respect, conventional processing methods (i.e. boiling to allow skin separation and/or scrubbing with a stiff brush) may prove time consuming compared to the removal and preparation of scales (e.g. Jones 1974).

Otolith

The unique chronological properties of otoliths relative to other calcified structures for ageing fish are widely known, and these typically relate to both annulus and micro-increment counting but also to micro-chemistry examination (Campana and Thorrold 2001). The anatomical differences in the vestibular apparatus of (typical) non-ostariophysan versus ostariophysan (cyprinoid) teleost fishes have been described (Secor et al. 1991), and specifically for carp

(Li et al. 2009). Briefly, in non-ostariophysan teleost fishes, the sagitta (saccular aragonitic otolith) is routinely used for annulus identification and the lapillus (utricular aragonitic otolith) for micro-increment identification, whereas the third pair of otoliths, namely the vateritic lagenar asterisci, is not generally employed. On the contrary, in ostariophysans (including carp), the asteriscus has proven useful for reliable annulus counts (see below), unlike the inconspicuous, needle-shaped sagitta. Whereas, similar to the other teleost fishes, the lapillus is useful for micro-increment enumeration (see below and Fig. 3).

In carp, the use of otoliths for their chronological properties (including ageing) has been fraught with difficulties and terminological inconsistencies (Table 2). The first attempts to use otoliths for ageing carp failed as a result of what was reported as 'small size' of the pair examined (Jones 1974; Wichers 1976; Hume et al. 1983)—a statement that most likely points to the examination of the lapilli (see also Bishai and Labib 1978). Only starting from the mid-1980s were otoliths successfully used to age carp (Lubinski et al. 1984; Raina 1987; Pinilla et al. 1992), and these were most likely the asterisci, which in one study were referred to as the 'largest' pair of otoliths but erroneously called 'sagittae' (Lubinski et al. 1984). However, it was not until the mid-1990s that the peculiarities of carp otoliths were finally clarified (Vilizzi and Walker 1995), indicating the usefulness of the asterisci for annulus identification (Vilizzi and Walker 1998, 1999; Vilizzi et al. 1998) and of the lapilli for microincrement counts (Vilizzi 1998). These studies have since paved the way for: (1) refinement of validation of annulus counts on asterisci (Brown et al. 2004; Winker et al. 2010) and of micro-increment counts on lapilli (Smith and Walker 2003); (2) implementation of related age-growth studies on both adult (Diggle et al. 2004; Brown et al. 2005; Coulter et al. 2008; Bajer et al. 2009; Winker et al. 2011; Colvin et al. 2012; Hutchison et al. 2012; Amouei et al. 2013) and 0 + carp (Gilligan and Schiller 2003; Diggle et al. 2004; Phelps 2006; Britton et al. 2007; Phelps et al. 2008; Hutchison et al. 2012); (3) ageing structure comparisons (Yılmaz and Polat 2008; Yates et al. 2016); and (4) biometrical studies of otolith to body length relationships (Bostanci 2009). However, some other studies have still used the incorrect terminology (Gümüş 1998; Diggle et al. 2004; Amouei et al. 2013), or omitted explicit mention of the pair used (Temizer and Şen 2008; Aydin et al. 2009; Omar and Amohamed 2016).

Unlike the lapilli, which require sectioning for micro-increment counts (except in larvae with < 10–30 micro-increments: Vilizzi 1998; Gilligan and Schiller 2003), annulus counts can be made either on whole or sectioned asterisci (Vilizzi and Walker 1999). However, the majority of age-growth studies has relied on the sectioning method (Diggle et al. 2004; Brown et al. 2005; Coulter et al. 2008; Bajer et al. 2009; Winker et al. 2011; Colvin et al. 2012; Hutchison et al. 2012; Amouei et al. 2013), and only two of them have examined whole asterisci (Winker et al. 2011). Whereas, the 'broken-and-burnt' method (www.afsc.noaa.gov/refm/age/procedures.htm; accessed 30/12/2017) has so far been attempted for ageing structure comparisons only (Aydin et al. 2009) (Table 2). Finally, in the majority of age-growth studies, otoliths have been used as the only ageing structure (Pinilla et al. 1992; Vilizzi and Walker 1998; Brown et al. 2003, 2005; Diggle et al. 2004; Coulter et al. 2008; Bajer et al. 2009; Winker et al. 2011), and less frequently in association with other hard parts (Colvin et al. 2012; Lubinski et al. 1984; Raina 1987; Vilizzi and Walker 1999) (Table S1 in Supporting Information).

Although not strictly related to ageing, the use of otoliths for micro-chemistry studies in carp emphasises the importance of the correct identification of the pair employed (cf. Vilizzi and Walker 1995). Thus, studies have used either the 'larger' asterisci (Crook and Gillanders 2006; Blair 2008; Li et al. 2011; Blair and Hicks 2012) or the lapilli (Macdonald et al. 2010; Crook et al. 2013; Macdonald and Crook 2014), even though remarkable differences in microchemistry have been observed between the two pairs, suggesting the need for their concomitant employment (Macdonald et al. 2012).

The process of otolith extraction (i.e. of asterisci and, especially, lapilli) in carp, apart from being 'destructive', can be fairly involved relative to non-ostariophysan fishes (Vilizzi and Walker 1999; Macdonald et al. 2012), and if the sectioning method is being used, then further processing time is required (Vilizzi and Walker 1999; Brown et al. 2005). In a comparative study of whole and sectioned asterisci (Vilizzi and Walker 1999), no substantial advantage was found in annulus identification using the sectioning method. This finding has been indirectly

Table 2 Historical summary of outcomes from studies evaluating the use of otoliths for ageing carp (including 0 + juveniles). (after Campana and Thorrold 2001)

Source	Purpose	Whole	Sectioned	Outcome
Jones (1974)	Annuli	–	–	Found 'too small to be of practical use' for age determination (presumably, lapilli)
Wichers (1976)	Annuli	–	–	Difficulty in 'finding and handling' due to small size (presumably, lapilli)
Bishai and Labib (1978)	Annuli	–	–	Unspecified otoliths examined but found unreliable (for carp under farming conditions)
Hume et al. (1983)	Annuli	–	–	Found to be 'too small and difficult to extract' (presumably lapilli)
Lubinski et al. (1984)	Annuli	√	–	'Largest' (unspecified, but likely asterisci) pair of otoliths used, but incorrectly referred to as 'sagittae'
Raina (1987)	Annuli	√	–	Otolith pair unspecified, but likely asterisci and examined as whole
Pinilla et al. (1992)	Annuli	√	–	Otolith pair unspecified, but likely asterisci and examined as whole
Vilizzi and Walker (1995)	Annuli	√	–	Identification of asterisci, lapilli (and sagittae) for use in carp ageing studies, with qualitative evaluation of annulus counts on asterisci
Gümüş (1998)	Annuli	√	–	Validation of annulus counts on asterisci (incorrectly referred to as 'sagittae')
Vilizzi (1998)	Microstructure	n/a	n/a	Validation of microincrement counts in 0 + individuals using lapilli
Vilizzi and Walker (1998)	Annuli	√	–	Validation of annulus counts on asterisci by marginal increment analysis (MIA) (see also Table 7)
Vilizzi et al. (1998)	Annuli	√	–	Evaluation of precision of annulus counts on asterisci
Vilizzi and Walker (1999)	Annuli	√	√	Analysis of both whole and sectioned asterisci and validation by MIA (see also Table 7)
Gilligan and Schiller (2003)	Microstructure	n/a	n/a	Microincrement counts on lapilli used for ageing 0 + individuals
Smith and Walker (2003)	Microstructure	–	√	Validation of microincrement formation in lapilli from 0 + individuals and detection of first increment formation
Brown et al. (2004)	Annuli	–	√	Validation of annulus counts on sectioned asterisci by mark-recapture (see also Table 7)
Diggle et al. (2004)	Annuli	–	√	Sectioned otoliths used, but asterisci incorrectly referred to as 'lapilli', and lapilli (for ageing 0 + carp) incorrectly referred to as 'sagittae'
Brown et al. (2005)	Annuli	–	√	Determination of age and growth as per Brown et al. (2004)
Crook and Gillanders (2006)	Chemistry	n/a	n/a	Asterisci used for chemical signatures to identify recruitment sources
Phelps (2006)	Microstructure	n/a	n/a	Microincrement counts on lapilli used for ageing 0 + individuals
Britton et al. (2007)	Microstructure	n/a	n/a	Microincrement counts on lapilli used for ageing 0 + individuals
Blair (2008)	Chemistry	n/a	n/a	Asterisci used for chemical signatures to identify recruitment sources
Coulter et al. (2008)	Annuli	–	√	Sectioned asterisci used for age estimation
Phelps et al. (2008)	Microstructure	n/a	n/a	Microincrement counts on lapilli used for ageing 0 + individuals
Temizer and Şen (2008)	Annuli	√	–	Unspecified otoliths used for ageing structure comparison
Yılmaz and Polat (2008)	Annuli	√	–	Asterisci and lapilli used for ageing structure comparison

Table 2 continued

Source	Purpose	Whole	Sectioned	Outcome
Aydin et al. (2009)	Annuli	√	(√)	Unspecified otoliths used for ageing comparison between whole and 'broken-and-burnt' methods
Bajer et al. (2009)	Annuli	–	√	Sectioned asterisci used for age estimation
Bostanci (2009)	–	n/a	n/a	Investigation of otolith biometry to body length relationship using asterisci
Li et al. (2009)	Chemistry	n/a	n/a	Analysis of the hierarchical microstructure of the three pairs of otoliths
McDonald et al. (2010)	Chemistry	n/a	n/a	Lapilli used for chemical signatures to identify recruitment sources
Winker et al. (2010)	Annuli	√	–	Whole asterisci used and validation through mark-recapture showing biannual growth zone formation (see also Table 7)
Li et al. (2011)	Chemistry	n/a	n/a	Asterisci used to investigate their thermoluminescence properties for lake pollution identification
Winker et al. (2011)	Annuli	√	–	Determination of age and growth as per Winker et al. (2010)
Blair and Hicks (2012)	Chemistry	n/a	n/a	Asterisci used for chemical signatures to identify recruitment sources
Colvin et al. (2012)	Annuli	–	√	Sectioned asterisci used for age estimation
Hutchison et al. (2012)	Annuli	√	–	Whole asterisci from 0 + and 1 + fish used for attempted age determination
Macdonald et al. (2012)	Chemistry	n/a	n/a	Both asterisci and lapilli used for chemical signatures to delineate riverine populations
Amouei et al. (2013)	Annuli	–	√	Sectioned otoliths (incorrectly referred to as 'sagittae', but presumably lapilli or asterisci: their Figs. 3 and 4, respectively) used for age estimation
Crook et al. (2013)	Chemistry	n/a	n/a	Lapilli used for chemical signatures to identify recruitment sources
Macdonald and Crook (2014)	Chemistry	n/a	n/a	Lapilli used for chemical signatures to identify recruitment sources
Omar and Amohamed (2016)	–	n/a	n/a	Comparative morphological study on asteriscus (though not specified in study)
Yates et al. (2016)	Annuli	–	√	Sectioned asterisci used for ageing structure comparison

'Purpose' refers to the three main uses of otoliths in fish chronological studies

corroborated by the ability to identify clearly biannual increment deposition on whole asterisci, with sections discarded because of poor interpretability (Winker et al. 2010).

Dorsal spine

In carp, the dorsal spine consists of a large bone with a strongly-serrated posterior edge (Bănărescu 1964). Although its first documented use for ageing carp dates back to the mid-1960s (Carlton and Jackson 1964; Starrett and Fritz 1965), previous studies had already referred to 'standard methods' of scale and spine analysis (Schoonover and Thompson 1954; Jackson 1955; Sandoz 1960). A more recent experimental study using fluorescent markers demonstrated the formation of so-called *lignes d'arrêt de croissance* (Meunier and Pascal 1981/1982), which provided a physiological basis for their use in a follow-up assessment of the growth of an individual cohort of carp (Jestin et al. 1985). The dorsal spine has been used either as the sole ageing structure (Wichers 1976; Katzenmeyer 2010; Weber et al. 2015) or, more often, in conjunction with others (Schoonover and Thompson 1954; Jackson 1955; Sandoz 1960; Starrett and Fritz 1965; Lubinski et al. 1984; Colvin et al. 2012) (Table S1 in Supporting Information).

Different sectioning planes along the length of the dorsal spine have been shown to result in deviations in back-calculated growth from annuli (Wichers 1976).

This issue was recently addressed in a study showing that sections taken at $\leq 25\%$ of the length of the dorsal spine would provide the most precise age estimates. As a non-lethal method, the use of this structure to estimate age in carp has proved a valid alternative to scales, even though more time is required for preparation and sectioning compared to the latter (Jearld 1983).

Vertebra

Vertebrae have been used traditionally to age elasmobranchs (Jearld 1983), but also carp, with the first documented report being from the late 1960s (Effendie 1968). Vertebrae have since been used in conjunction with other structures (Cochrane 1985; Bhandari et al. 1993). The most detailed description of the vertebra-based ageing method in carp is from a study on this species under farming conditions, which showed successful age determination in a sub-tropical climate (Bishai and Labib 1978). More recently, the only two age-growth studies relying exclusively on vertebrae (Yılmaz et al. 2012; Yüce et al. 2016) seem to have drawn from comparative studies pointing to the higher reliability of vertebrae (Temizer and Şen 2008; Yılmaz and Polat 2008) (Table S1 in Supporting Information). Vertebrae from the anterior part of the dorsal spine have been used, with the third (Bishai and Labib 1978) or 7th and 8th (Bhandari et al. 1993) having proved more reliable in some cases.

Fin ray

The use of fin rays as a reliable method for age determination for fishes including carp was demonstrated long ago (Boyko 1950). However, use of these structures in carp age-growth studies remains limited, and is found either in conjunction with scales (Liang et al. 1993) or, more recently, alone (Weber et al. 2010)—in the latter case based upon findings on their reliability and precision (Phelps et al. 2007, 2008) (Table S1 in Supporting Information). Similar to the dorsal spine, the use of fin rays does not require sacrificing the fish and, in general, appears to be a good alternative to scales (cf. Beamish 1981).

Other ageing methods

Although not a calcified structure, the weight of the eye lens has been proposed as an alternative method for ageing carp (Carlton and Jackson 1968). However, overlap in eye lens weight ranges between older age classes may represent a limitation on the use of this method (Crivelli 1980). No age-growth studies on carp populations have so far employed the eye lens.

Finally, the use of telomere length has recently been investigated as an alternative (non-lethal) method to increment-based age estimations on hard parts (Izzo et al. 2014). Telomeres are nucleotide and protein complexes located at the ends of vertebrate chromosomes. Findings from the only study so far investigating this method reported a significant increase in telomere length with increasing fork length, but also reported limitations due to poor distinction of individual age classes.

Relative utility

In total, 26 studies were found in which a comparative assessment of two or more ageing structures was provided (Table 3). Not surprisingly, the majority of assessments involved scales, followed by opercula, otoliths and dorsal spines, and vertebrae and fin rays (plus one assessment on the eye lens). Causal criteria analysis indicated inconsistent evidence for the usefulness of the scale and operculum, but supported the hypothesis of successsful annulus identification/counting for otoliths, dorsal spines, vertebrae and fin rays—but insufficient evidence for the eyes lens, due to only one comparative study being available (Table 4). Notably, two studies (i.e. Jones 1974; Hume et al. 1983) pointing to the limitations of some hard parts other than scales were not included into the systematic review because their findings were of qualitative value only (i.e. no evaluation or counting of annuli).

Precision and accuracy

Precision was evaluated by eleven studies in total, which analysed the scale, operculum, otolith, dorsal spine, (pectoral) fin ray and vertebra (Table 5). Within interpreters, the mean APE was lowest for the otolith, followed by the scale, operculum and dorsal spine; between interpreters, this index was again lowest for the otolith, followed by the operculum and scale (no data were available for the dorsal spine). Within interpreters, the mean CV was lowest for the otolith, followed by the operculum, scale and dorsal spine (one

Table 3 Studies assessing the relative utility of ageing structures for carp (arranged in order of their proportion across studies: see Fig. 1a)

Source	Design	Sampling units	Ageing structure						
			Scale	Operculum	Otolith	Dorsal spine	Vertebra	Fin ray	Eye lens
Bhandari et al. (1993)	Type II	2 (independent)	**S**	**S**	–	–	**S**	–	–
Bishai and Labib (1978)[a]	Type II	4 (independent)	U	U	U	–	**S**	–	–
Boyko (1950)	Type I	1 (control: Sc); 1 (impact: Fr)	U	–	–	–	–	**S**	–
Carlton and Jackson (1964)	Type I	1 (control: Sc); 1 (impact: Fr)	U	–	–	**S**	–	–	–
Carlton and Jackson (1968)	Type I	2 (control: Sc, Ds); 1 (impact: El)	**S**	–	–	**S**	–	–	**S**
Cochrane (1985)	Type II	4 (independent)	U	U	–	–	**S**	–	–
Colvin et al. (2012)	Type II	2 (independent)	–	–	**S**	U	–	–	–
Effendie (1968)	Type II	3 (independent)	U	**S**	–	–	**S**	–	–
English (1952)	Type II	3 (independent)	U	**S**	–	U	–	–	–
Gümüş (1998)[b]	Type II	5 (independent)	U	**S**	**S**	–	**S**	U	–
Jackson et al. (2007)	Type II	2 (independent)	U	–	–	**S**	–	–	–
Jester (1974)	Type II	2 (independent)	**S**	**S**	–	–	–	–	–
Liang et al. (1993)	Type II	2 (independent)	U	–	–	–	–	**S**	–
Lubinski et al. (1984)	Type II	4 (independent)	**S**	**S**	U	**S**	–	–	–
McConnell (1952)	Type I	1 (control: Sc); 1 (impact: Op)	U	**S**	–	–	–	–	–
Phelps et al. (2007)	Type II	5 (independent)	U	U	**S**	–	U	**S**	–
Raina (1987)	Type II	3 (independent)	**S**	**S**	**S**	–	–	–	–
Rehder (1959)	Type II	2 (independent)	**S**	**S**	–	–	–	–	–
Sanchez (1970)	Type II	2 (independent)	**S**	U	–	–	–	–	–
Starrett and Fritz (1965)	Type II	3 (independent)	U	U	–	**S**	–	–	–
Temizer and Şen (2008)[c]	Type II	4 (independent)	**S**	U	–	–	**S**	U	–
Tempero et al. (2006)	Type II	2 (independent)	**S**	**S**	–	–	–	–	–
Vilizzi and Walker (1999)	Type II	3 (independent)	U	**S**	**S**	–	–	–	–
Weber and Brown (2011)	Type II	2 (independent)	–	–	–	**S**	–	**S**	–
Yates et al. (2016)	Type II	4 (independent)	U	–	U	**S**	–	**S**	–
Yılmaz and Polat (2008)	Type II	5 (independent)	**S**	**S**	**S**	–	**S**	U	–

The 'best-match' study design used for carrying out causal criteria analysis (see Table 1) is indicated as Type I [Reference/control vs. impact (no before)] and Type II (Gradient response model). In the former, one 'impact' structure (i.e. the one of main interest) is comparatively evaluated against one or more 'control' structures; in the latter, two or more 'independent' structures are being compared (*Ds* dorsal spine, *El* eye lens, *Fr* fin ray, *Sc* scale). For each comparison: S = successful identification/counting of annuli (bold type); U = unsuccessful identification/counting of annuli

[a]Carp studied under farming conditions

[b]Sub-operculum also evaluated

[c]Urohyal, sub-operculum, inter-operculum, pre-operculum, cleithrum, lacrimal and branchiostegal bones also evaluated

study only); whereas between interpreters, this index was lowest for the dorsal spine, followed by the fin ray, otolith, operculum and scale. Values below the 5.5% threshold for the APE were achieved for the operculum (one study out of three) and the otolith (three studies out of seven; but also for the only available assessment on the vertebra); below 5% for the CV were achieved for the dorsal spine (two studies

Table 4 Results of causal criteria analysis for the seven ageing structures evaluated for carp (see Table 3)

Structure	Conclusion	Number of evidence items			Summed weights		
		Total	In favour	Against	Total	In favour	Against
Scale	Inconsistent evidence	24	10	14	99	40	59
Operculum	Inconsistent evidence	18	12	6	75	47	28
Otolith	Support for hypothesis	9	6	3	45	30	15
Dorsal spine	Support for hypothesis	9	7	2	34	28	6
Vertebra	Support for hypothesis	8	7	1	42	35	7
Fin ray	Support for hypothesis	8	5	3	41	22	19
Eye lens	Insufficient evidence	1	1	0	5	5	0

The hypothesis is that of successful annulus identification on the structure being used (see Table 1)

out of four) and the fin ray (one study out of two); and below 7.6% for the CV (but higher than 5%) were achieved for the operculum (one study out of four), the otolith (three studies out of five), and the dorsal spine (two studies out of four)—noting that in the latter case all four studies assessing between-interpreter precision by the CV fell below the desirable levels of precision. Across studies, the mean APE was always above threshold, whereas the (between-interpreter) CV was below the higher threshold for the dorsal spine and fin ray. There were in total eight between-structure comparisons for precision, which was assessed by the APE and/or CV (Table 6). The range in index values was quite broad and only in one case did the APE fall well below the desirable threshold (unlike the CV, which was always well above).

In total, 14 studies validated annulus counts in carp, thereby assessing their accuracy (Table 7). The scale, operculum, otolith and vertebra were the structures for which validation was achieved. This involved the follow-up of fish of known age, mark-recapture, marginal increment analysis, and the examination of length modes. The overall range of age classes for which validation was achieved was 1–7 for the scale (2–7 based on mark-recapture), 1–15 for the operculum (marginal increment analysis and length modes only), 1–15 for the otolith (1–12 and 14 as a combination of mark-recapture and fish of known age), and 1–7 for the vertebra (1–6 fish of known age). Except for the Czech Republic and Turkey, where carp is native and native/translocated, respectively, all other countries where validation studies were conducted fell into the species' introduced range, where carp poses a medium or high risk level of impact on the aquatic ecosystem.

Discussion

According to the present review, scales have been both historically and traditionally the most widely-employed structure for ageing carp, even though in countries where the species carries a high risk of impact, use of alternative structures (i.e. operculum, and especially otolith, dorsal spine, vertebra and fin ray) has become increasingly common. The inconsistent evidence revealed by causal criteria analysis about the utility of scales and opercula to age carp successfully as opposed to otoliths, dorsal spines, vertebrae and (pectoral) fin rays emphasises the requirement for re-considering the routine use of 'traditional/old-style' ageing methods but also for ensuring validation of age estimates. This contention is further supported by the better precision achieved by otoliths, dorsal spines and fin rays compared to scales. For further studies on carp age and growth, it is therefore suggested that dorsal spines or pectoral fin rays should be selected as non-lethal ageing structures, and otoliths (and, possibly, vertebrae) when sacrificing the fish does not pose a logistic problem.

History

Given the century-long history of scientific studies on carp, it is not surprising that the entire range of available methods for ageing fish (i.e. scale, otolith, fin ray or spine, centrum or vertebral, and flat bone: Casselman 1983) has been used on this species. Yet, at the global level, the present findings indicate that the scale method has been predominant in age-growth studies on carp, regardless of the more recent advances in fish age determination with special emphasis on the

Table 5 Studies evaluating the precision of five ageing structures for carp

Source	Scale				Operculum				Otolith				Dorsal spine				Fin ray (pectoral)			
	APE		CV		APE		CV		APE		CV		APE		CV		APE		CV	
	W	B	W	B	W	B	W	B	W	B	W	B	W	B	W	B	W	B	W	B
Brown et al. (2004)	–	–	–	–	–	–	–	–	**4.30**[a]	**4.98**	*5.98*[a]	*6.90*	–	–	–	–	–	–	–	–
Diggle et al. (2004)	–	–	–	–	–	–	–	–	**4.82**	–	–	–	–	–	–	–	–	–	–	–
Hutchison et al. (2012)	–	–	–	–	–	–	–	–	**4.97**	–	–	–	–	–	–	–	–	–	–	–
Jackson et al. (2007)	–	–	–	28.1	–	–	–	–	–	–	–	–	–	–	–	**4.9**	–	–	–	–
Vilizzi and Walker (1999)	5.61	9.15	7.94	12.94	**5.32**	6.99	*7.52*	9.89	5.64	6.23	7.97	8.80	–	–	–	–	–	–	–	–
Vilizzi et al. (1998)	9.12	9.97	12.90	12.99	11.28	10.73	15.95	15.04	12.33	12.71	17.43	17.97	–	–	–	–	–	–	–	–
Watkins et al. (2015)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*6.2*[b]	–	–	–	–
Weber and Brown (2011)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*6.6*	–	–	–	9.9
Winker et al. (2010)	–	–	–	–	–	–	–	–	5.54	–	*7.03*	–	–	–	–	–	–	–	–	–
Yates et al. (2016)	–	–	–	15.4	–	–	–	17.6	–	–	–	–	–	–	–	**3.0**	–	–	–	**4.9**
Yılmaz and Polat (2008)[c,d]	8.86	–	18.02	–	11.01	–	21.80	–	9.06	–	17.08	–	13.56	–	27.07	–	–	–	–	–
Mean	7.86	9.56	12.95	17.36	8.30	8.86	11.74	14.18	6.67	7.97	11.10	11.22	13.56	–	27.07	*5.18*	–	–	–	*7.40*
SE	1.13	0.41	2.91	3.63	2.98	1.87	4.22	2.27	1.11	2.40	2.53	3.42	–	–	–	0.81	–	–	–	2.50

Values for APE and CV below the 5.5 and 5% thresholds, repectively, in bold, and of CV below the 7.6% threshold in italics. Decimal places as reported in the original study

APE average percent error, *CV* coefficient of variation, *W* within interpreter, *B* between interpreters

[a]Average of two interpreters

[b]Between section planes 1 and 2

[c]Vertebra also evaluated (APE = **4.70**[3]; CV = 9.86[3])

[d]Values averaged over three water bodies

use of the otolith (Campana and Thorrold 2001). There are several possible reasons for this somewhat 'conservative' status in the ageing of carp:

Anatomical features

The otolith method was originally developed and implemented for marine fishes and referred to also as the 'sagitta' method (Casselman 1983), because of the use of the sagittal pair of otoliths (Secor et al. 1991). In the case of carp, as previously discussed, it is the asteriscus pair of otoliths that is the most prominent and useful for annulus counting, but it is also more difficult to locate and extract relative to the sagittae of non-ostariophysans. This is evinced by the difficulties that have been encountered by early researchers (Table 2), leading in some cases to somewhat hasty conclusions as to the lack of usefulness of otoliths for ageing carp in general (Jones 1974; Hume et al. 1983). The unique structure of the ostariophysan vestibular apparatus in carp appears therefore to have been one of the factors contributing to the observed delay in the use of the otolith method in this species, both for annulus (asteriscus) and microincrement (lapillus) counting.

Limited longevity

As a result of using otoliths, mainly through their sectioning but often coupled with bomb radiocarbon dating (Campana 2001), several marine species (in many cases of high commercial fisheries value) have been shown to be much longer lived than previously thought (Campana 2001), with validated ages often in the range of 50–100 years (e.g. Black et al. 2005; Tracey et al. 2016). With regard to longevity, estimated ages of 35 (Bajer and Sorensen 2010) and 23 years (Brown et al. 2003) have been reported for carp based on otolith sections, although the oldest (mark-recapture validated) age using this method has been up to 14 years (Brown et al. 2004). On the other hand, published otolith-based age-growth data on carp have so far been limited to the 1–19 years old range (Vilizzi and Copp 2017), indicating the need for further research (especially regarding validation) into this ageing method. At the same time, references to exceptionally old carp, albeit occasionally encountered in the literature, have been so far mostly anecdotal and based on individuals reared in captivity (e.g. Flower 1935; Einsele 1956), hence in habitat conditions that are likely to differ profoundly from those of populations in the wild. Also, findings about carp longevity in some cold-climate water bodies of North America (Köppen-Geiger climate class D: Peel et al. 2007), albeit most likely not as pronounced as that of some marine species, are relatively recent (Bajer and Sorensen 2010) and may have therefore been responsible for the lack of adoption (as originally suggested by Vilizzi 1997) of the more advanced

Table 6 Studies evaluating between-structure precision for ageing carp

Comparison	APE	CV	Source
Scale versus Operculum	8.38	11.85	Vilizzi and Walker (1999)
Scale versus Otolith[a]	8.70	12.30	Vilizzi and Walker (1999)
Scale versus Dorsal spine[b]	–	37.65	Jackson et al. (2007)
Scale versus Pectoral fin ray	15.4	–	Phelps et al. (2007)
Operculum versus Otolith[c]	9.94	14.05	Vilizzi and Walker (1999)
Otolith versus Fin ray	**1.2**	**–**	Phelps et al. (2007)
Dorsal spine versus Pectoral fin ray[b]	–	9.10	Weber and Brown (2011)
Vertebra versus Pectoral fin ray	6.8	–	Phelps et al. (2007)

Values for APE below the 5.5% threshold (Campana 2001) in bold. Decimal places as reported in the original study

APE average percent error, *CV* coefficient of variation

[a]Average of Scale versus Whole otolith and Scale versus Sectioned otolith

[b]Average of two interpreters

[c]Average of Operculum versus Whole otolith and Operculum versus Sectioned otolith

Table 7 Studies validating annulus formation in carp

Source	Structure	Method	Age classes	Country	Origin	Risk level
Bajer et al. (2009)	Otolith	Known age	1–3, 5, 6	USA	Introduced	High
Bishai and Labib (1978)[a]	Vertebra	Known age	1–6	Egypt	Introduced	–
Brown et al. (2004)	Otolith	Mark-recapture	3–12, 14	Australia	Introduced	High
Cazorla and Pizarro (2000)	Scale	Modes	1–7	Argentina	Introduced	Medium
Cochrane (1985)	Vertebra	Modes	1–7	South Africa	Introduced	High*
Colautti and Freyre (2001)	Scale	MIA	1–6	Argentina	Introduced	Medium
Gümüş (1998)[a]	Otolith	Known age	1–3	Turkey	Native/translocated	Low
McConnell (1952)	Operculum	Modes	1–8	USA	Introduced	High
Oliva (1955)	Scale	Mark-recapture	2–4	Czech Republic	Native/translocated	Low
Oyugi et al. (2011)	Scale	MIA	1–5	Kenya	Introduced	Medium
Tempero et al. (2006)	Scale	Mark-recapture	3–7	New Zealand	Introduced	High
Vilizzi and Walker (1998)	Otolith	MIA	1–5	Australia	Introduced	High
Vilizzi and Walker (1999)	Scale, Operculum, Otolith	MIA	1–15	Australia	Introduced	High
Winker et al. (2011)	Otolith	Mark-recapture, MIA, Modes	1–7	South Africa	Introduced	High*

Method Known age = release of known age and marked fish; Mark-recapture = mark-recapture of chemically-tagged fish; Modes = discrete length modes sampled for age structures; MIA = marginal increment analysis (terminology after Campana 2001). Risk level of introduced-origin countries based on Vilizzi et al.'s (2015) categorisation (marked by an asterisk evaluated in the present study)

[a]Carp studied under farming conditions or captivity (for Egypt, risk level does not apply)

methods of otolith sectioning (possibly coupled with bomb radiocarbon dating) in this species so far.

Carp status

The status of carp as native, native/translocated or introduced has clearly affected the interest (or lack thereof) revolving around the use of ageing structures other than scales. Thus, in countries where carp is native, the scale method has been highly predominant, and this may have been an outcome of the more limited interest in carp as an invasive species. On the other hand, the stark predominance of studies relying upon alternative ageing structures to the scale (and operculum) in countries where carp is introduced is a reflection of the level of risk posed by this species on the aquatic ecosystem (Vilizzi et al. 2015).

Relative utility

In the present study, causal criteria analysis has provided for an objective, evidence-based comparative evaluation of the relative utility of ageing structures in carp. The inconsistent evidence reached for the scale and the operculum reflects the difficulties often encountered in annulus identification in these structures. This suggests that alternative structures to the scale should be used whenever carp is to be released after capture, and to the operculum when sacrificing the fish does not represent a problem. Regardless, the scale alone (Cazorla and Pizarro 2000; Colautti and Freyre 2001; Oyugi et al. 2011) and the scale and operculum together (Tempero et al. 2006) were recently used successfully in validated studies (Table 7). However, the populations of carp were in the former case 'short-lived' (1–7 years) and in the latter 'medium-lived' (1–12 years), and always in temperate climates (types Cfa and Cfb, Köppen-Geiger system) (note that the 'relative longevity' of these populations is gauged after Vilizzi and Copp 2017).

Support for the hypothesis of successful annulus identification/counting was provided for the (non-lethal) dorsal spine and fin ray methods and for the (lethal) otolith and vertebra methods. In a recent comparative study, pectoral fin rays and the dorsal spine were found to provide clear and easy-to-enumerate annuli, with the latter structure being preferred because of its more regular shape (Yates et al. 2016). These results corroborate previous findings on the reliability of both these non-lethal ageing structures (Phelps et al. 2007; Weber and Brown 2011), even though underestimation of age from the dorsal spine relative to the otolith has been reported (Colvin et al. 2012). With regard to the otolith and vertebra, the former was found to be more useful in a comparative study (Phelps et al. 2007), whereas in another study both structures were considered of similar utility (Yılmaz and Polat 2008). On the other hand, the majority of (recent) studies focusing on the use of otoliths alone have been able to age successfully carp with estimated (albeit not validated) ages over 20 years (Brown et al. 2003; Bajer and Sorensen 2010), even though there have been disagreements as to the value of using either whole or sectioned asterisci. In this respect, Brown et al. (2004) confidently and successfully aged carp using otolith sections, hence without facing the problems relating to the crowding of annuli at the edge (in older fish) as emphasised in other studies (Vilizzi and Walker 1999; Winker et al. 2010). Nor did Brown et al. (2004) report on the presence of 'discontinuities' (Vilizzi and Walker 1999; Winker et al. 2010), especially near the otolith core, which led Vilizzi and Walker (1999) to distinguish three morphological classes of asterisci. Recent findings of biannual growth zone formation based on the examination of the whole asteriscus (Winker et al. 2010), as opposed to complete unreadability reported for this structure (Yates et al. 2016), further obscure the picture and suggest that the use of whole and/or sectioned asterisci (or their lack of usefulness for ageing carp altogether) could be driven by population- or waterbody-specific factors.

Precision

A most notable outcome of the overall assessment of precision in carp ageing estimates was the failure of scales in all cases to provide levels of either APE or CV below desirable thresholds. Whereas in the case of the operculum, the target was reached but only in one study. These findings mirror the outcomes of causal criteria analysis (also considering that this included five of the eleven studies assessing precision: Tables 3 and 5), and the between-structure comparisons of the scale versus dorsal spine, scale versus fin ray, and operculum versus otolith further support the use of the dorsal spine or fin ray in lieu of the scale as non-lethal structures, and of the otolith versus the operculum as a lethal structure, as indicated above (note that no operculum versus vertebra comparison was available).

In the present study, selection of two threshold values for the CV and evaluation of precision in general reflects the adoption of a more flexible approach than one merely dictated by 'cast-in-stone' reference values. Thus, the recommended (higher) CV threshold of 7.6% was retained given its meta-analytical foundation, although slight preference was given to the (lower and more conservative) APE threshold of 5%, which has been suggested as a "reference point for many fishes of moderate longevity and reading complexity" (Campana 2001, p. 224). In this respect, carp can effectively be categorised as a fish of moderate longevity (Vilizzi and Copp 2017), especially when compared to marine species, and the reading complexity of its ageing structures also match the above definition. Further, it is argued that the very strict 5% threshold value for the APE expected in some ageing laboratories (Morison et al. 1998), whilst a solid indicator of the reproducibility of annulus counts, may by itself be biased by laboratory-specific protocols for annulus interpretation (hence, training of interpreters), which may differ from other laboratories (cf. Yates et al. 2016).

Except for two studies (Vilizzi et al. 1998; Yılmaz and Polat 2008), precision was overall satisfactory for the otolith and in several cases below reference thresholds. With the exception of one study (Yılmaz and Polat 2008), the target and close-to-target precision values achieved with the dorsal spine are a strong indicator of the reliability of this ageing structure. However, as the only available comparison between the dorsal spine and pectoral fin ray did not achieve target precision (Weber and Brown 2011), a final evaluation of the ‘best’ structure (if any) to choose between the two should be based on additional considerations related to morphology and preparation (see below: *Directions for future research*). Finally, the target value for precision reached in the only study dealing with the vertebra points to the potential value of this structure as an alternative to the otolith, although the lack of an evaluation of precision between these two structures again involves additional consideration as to which one would likely prove the most valuable.

Accuracy

Given the very large number of published studies on the age and growth of carp (Vilizzi and Copp 2017), it is remarkable that only a minor proportion of them has provided an evaluation of accuracy. Also, of the studies addressing accuracy, about three-quarters validated absolute age (i.e. through the follow-up of fish of known age, mark-recapture and, to some extent, assessment of discrete length modes), with the rest validating growth increment formation only (i.e. by means of MIA). Whilst validation of absolute ages may often represent a demanding and costly task (as in mark-recapture studies) or prove unfeasible (as with fish of known age), the use of MIA can be easily achieved under almost any circumstances (e.g. limited funding, lack of access to fisheries enterprises). It is therefore argued that MIA should represent the ‘minimal requirement’ for future age-growth studies on carp.

Excluding the two studies on carp reared in captivity and including only those achieving validation of absolute ages, the scale and the otolith were the structures for which the most rigorous assessment of accuracy has been achieved so far. On the other hand, lack of validation of absolute ages based on the dorsal spine, fin ray or vertebra methods prevents drawing any further conclusions as to the ultimate reliability of these structures, and points to the necessity of future structure-specific validation studies (see Yates et al. 2016).

Directions for future research

The outcomes of the present study corroborate the conclusions of a recent evaluation of ageing structures for carp that scales are overall unreliable and that the dorsal spine and, secondarily, the pectoral fin ray represent more valid alternatives (Yates et al. 2016). On the other hand, the conclusions reached in that study about the otolith differ from the majority of the other studies relying on this structure and also with the present review.

Below, some suggestions and guidelines are provided that are meant to assist researchers in future ageing studies on carp:

- Unless validated, the use of the scale is discouraged in favour of the dorsal spine or (pectoral) fin ray whenever a non-lethal structure is required. Inexpensive and fast preparation techniques for the dorsal spine and fin ray are available (Koch and Quist 2007). However, due to its more regular shape, use of the dorsal spine may be preferred to that of fin rays (Yates et al. 2016). Sections taken at $\leq 25\%$ of the total length of the dorsal spine have been shown to provide the most precise age estimates, with the section plane located at the 25% threshold being regarded as quite satisfactory (Watkins et al. 2015). This finding indicates that dorsal spine disarticulation (or total amputation) can be avoided, resulting in less stress (and long-term handicap) to the fish. Also, partial regeneration of the dorsal spine following amputation has been shown to occur, albeit slowly and at a higher sectioning plane that the 25% distance from the base (Kalish-Achrai et al. 2017). Similar to the scale, age estimation based on the operculum is discouraged in favour of the otolith whenever sacrificing the fish does not pose a problem. Finally, the vertebra could be also used in lieu of the operculum, but more research is needed as to the reliability of this structure for ageing carp, including a more precise definition of which vertebra(e) are most suitable for annulus counting.
- As a corollary to the above conclusions, it is argued that use of the dorsal spine (or fin ray) should not yet be considered a replacement for the otolith. This is contrary to the argument put forward by Watkins et al. (2015, p. 694) that “[s]upport for otoliths as the premier age estimation structure has waned as more efficient, non-lethal structures are verified”. In this respect, whilst estimated ages of up to 27 and 24 years have been provided by use of the dorsal spine and

pectoral fin ray, respectively (Weber and Brown 2011; see also Jackson et al. 2007), estimated ages up to 35 years have been found with the otolith section method (Bajer and Sorensen 2010). Clearly, the current paucity of studies on potentially long-lived populations (especially those of the colder regions of North America) prevents drawing any further conclusions in regard. It is also suggested that the more advanced method of bomb radiocarbon dating should be trialled on carp otoliths (Campana 2001), even though it is unlikely that even longer-lived carp populations would achieve longevities similar to those of some marine fishes. Use of both the dorsal spine (or pectoral fin ray) and otolith (preferably sectioned, in case of long-lived populations) should therefore be attempted whenever populations of carp are investigated for the first time (e.g. Yates et al. 2016). In case of similarity in age estimates, use of the dorsal spine or pectoral fin ray may be preferable for practical reasons (Koch and Quist 2007), even when release of carp back into the waters is discouraged (e.g. http://www.dpi.nsw.gov.au/fishing/pests-diseases/freshwater-pests/species/carp/groups/recreational-fishers; accessed 30/12/2017). Finally, the potential relationship between the microstructure of the vateritic asterisci (Li et al. 2009) and the difficulties oftentimes encountered in successful annulus identification (as opposed to the annuli of the aragonitic sagittae in non-ostaryophysans) deserves investigation.

- As highlighted in a recent review of carp growth at the global scale (Vilizzi and Copp 2017), the disparate ageing methods employed with over-reliance on the use of scales and 'near-chronic' lack of an evaluation of precision and accuracy may well represent a confounding effect for the refinement of population dynamics models based on age distributions and dynamic rate functions (Ricker 1975). This limitation could only be resolved through consistently-designed (albeit resource-demanding), global studies on carp age and growth and through the set-up of inter-laboratory programmes involving the creation of reference collections and quality control monitoring (Campana 2001). As recommended above, minimal validation of estimated ages (cf. MIA) should always be ensured, so as to avoid the shortcomings associated with 'word-of-mouth' scientific practice. In this respect, the adoption of appropriate ageing protocols for carp should be extended to all of its areas of distribution worldwide (hence, outside North America, Australia and South Africa, where 'modern' ageing methods have become routine). These include not only regions with warm and/or arid climates (e.g. Central and South America, Africa), where carp is predicted to expand further its invasive range of distribution (Zambrano et al. 2006; Crichigno et al. 2016; Maiztegui et al. 2016), but also those areas where the species plays an important commercial role for fisheries, as in Anatolia, Turkey (Gaygusuz et al. 2015) and in the Caspian Sea region (Abdullaev 2011; Amouei et al. 2013; Sedaghat et al. 2013).

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