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Short-lived fishes: Annual and multivoltine strategies

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Abstract

The diversity of life histories across the animal kingdom is enormous, with direct consequences for the evolution of lifespans. Very short lifespans (maximum shorter than 1 year in their natural environment) have evolved in several vertebrate lineages. We review short-lived fish species which complete either single (annual/univoltine) or multiple (multivoltine) generations within a year. We summarize the commonalities and particulars of their biology. Apart from annual killifishes (with >350 species), we detected 60 species with validated lifespan shorter than 1 year in their natural environment. Considering the low number of reports on fish lifespan (<5% of 30,000+ fish species; 1,543 species), the total number of short-lived fish species may be relatively high (>1,200 species). Short-lived fish species are scattered across 12 orders, indicating that short lifespan is not a phylogenetically conserved trait but rather evolves under specific ecological conditions. In general, short-lived fish species are small (typically 55 ± 35 mm), experience high predation (making them important part of ecosystem trophodynamics) and live in shallow warm waters with high productivity and stable abiotic conditions (e.g. Gobiidae, Clupeidae). Others utilize temporally constrained environments, where they survive unfavourable conditions as dormant stages (annual killifishes). They also utilize less productive environments; in this case, they migrate between productive and un-productive environments (e.g. Myctophidae, Salangidae). These species include the putatively shortest-lived (*Schindleria pietschmanni*: Schindleriidae) and earliest maturing (*Nothobranchius furzeri*: Nothobranchiidae) vertebrates and represent the lower limit of vertebrate longevity. Their examination may provide important insights into the evolutionary and mechanistic understanding of ageing.

KEYWORDS

ephemeral lifespan, extreme longevity, generation time, life history, otolith

1 | INTRODUCTION

Lifespan has a formative role on most other life-history traits as it defines the timeframe for completion of all life-determining processes (Stearns, 1992). Longevity in wild populations is the most relevant lifespan estimate from an evolutionary perspective, because it integrates all longevity-shaping forces of natural selection (Monaghan et al., 2008; Nussey et al., 2008). In particular, lifespan in natural populations is moulded by the mode and rate of extrinsic mortality (Maklakov et al., 2015; Medawar, 1952; Williams, 1957), dominated by predation, diseases, competition, natural disasters and accidental deaths (Reichard, 2017). Species with high extrinsic mortality are expected to evolve short lifespans (Medawar, 1952; Williams, 1957) and those species may provide critical insights into how natural selection limits lifespan.

Among vertebrates, several species are reported to have extremely short lifespans of several months in their natural environment (Depczynski & Bellwood, 2005; Karsten et al., 2008). One of the first references to a short-lived vertebrate dates from the 19th century when R. Collet used the term "annual vertebrate" for a transparent goby—*Aphia minuta* (Gobiidae) (Collet, 1878). Since then, vertebrates with a maximum lifespan equal to or shorter than a year have been reported from wild populations of a whole range of vertebrate taxa including fish (Depczynski & Bellwood, 2005), reptiles (Eckhardt et al., 2017) and mammals (Dickman & Braithwaite, 1992). All these species experience strong adult mortality induced by high predation rate (Depczynski & Bellwood, 2006), environmental constraints (Berois et al., 2016; Eckhardt et al., 2017) or exhibit high postreproductive mortality (Dickman & Braithwaite, 1992). Understanding the causes and consequences of extremely short lifespans is important for conservation management (Lessa et al., 2008), didactic purposes (Flindt, 2006) and for the development of evolutionary theories of life histories (Stearns, 1992).

Production of more than a single generation per year or development of dormant stages (or both strategies) is necessary for the persistence of short-lived species. Species with multiple generations within a year are termed multivoltine species (Crawford, 1981; Southgate, 1981) and are common among invertebrate taxa (Corbet et al., 2006; Crawford, 1981; Southgate, 1981), but relatively rare in vertebrates (Lambin & Yoccoz, 2001). Using dragonflies (Odonata), Corbet et al. (2006) demonstrated that multivoltinism is positively related to low latitude, in accordance with the prediction that multivoltine species are associated with high ecosystem productivity. To our knowledge, the term "multivoltine" is applied rarely (if ever) to ray-finned fishes (Actinopterygii). We believe that the term "multivoltine species" is appropriate for fish species fulfilling the criterion of multiple generations per year.

Ray-finned fishes are the most diversified vertebrate group with the occurrence of short lifespans. Among them, killifishes (family Nothobranchiidae in Africa and Rivulidae in the Neotropics, Cyprinodontiformes) are apparently the most diverse group of short-lived fishes, containing more than 270 and 420 described species respectively (Froese & Pauly, 2019) of which 350 species (i.e. approximately 50%) are so-called annual species (Huber, 2020). In annual killifishes, posthatching lifespan is supposedly shorter than a year, because they occur almost exclusively in regions where seasonal rainfall gives rise to temporary pools which desiccate within several months (Berois et al., 2016; Furness, 2016; Reichard & Polačik, 2019). Indeed, the duration of pool inundation is the main evolutionary force determining the evolution of annual killifish lifespan—species and populations from drier regions retain shorter lifespans in captivity (Blažek et al., 2017; Terzibasi et al., 2008). When their pool desiccates, all adults die and populations persist only as desiccation-resistant embryos buried in dry mud (Furness, 2016). The short lifespan and suitability for captive breeding have made annual killifishes a promising model for ageing research (Cellerino et al., 2016; Walford, 1969). Their high diversity and general awareness of their short lifespan contribute to the almost exclusive use of the term "annual fish" for annual killifish (Berois et al., 2016; Myers, 1952; Wourms, 1967), despite the fact that annual lifespan is not exclusive to annual killifish.

Paedomorphic species are another abundant group among exceptionally short-lived fishes (Kon & Yoshino, 2002; La Mesa, 1999, this study). Progenetic paedomorphosis represents a condition when maturation of the gonads is completed while somatic characters remain in a nonadult state (La Messa, 2011). In ray-finned fishes, this phenomenon is associated with body miniaturization (Johnson & Brothers, 1993; Rüber et al., 2007). For example, *Schindleria* spp. are very small (< 22 mm) scaleless gobies, with reduced pigmentation and ossification (Johnson & Brothers, 1993). Paedomorphic fish species with known lifespan are exceptionally short-lived. This is in striking contrast to the extended lifespan of paedomorphic amphibians (Voituron et al., 2011), providing interesting potential to study the environmental conditions and evolutionary mechanisms of this difference.

To our knowledge, the occurrence of short-lived ray-finned fish species with a natural lifespan shorter than one year has not been systematically summarized. In this review, we aim (a) to provide an overview of short-lived ray-finned fish species with maximum lifespans equal to or shorter than one year in the wild. In general, we exclude reports of short lifespans of annual killifish from this review (since they have been reviewed elsewhere (e.g. Berois et al., 2016)), with exceptions where it was necessary to include them for appropriate interpretation of findings. (b) We use our unpublished results from wild populations of African annual killifish, *Nothobranchius furzeri*, to compare natural lifespans between this species and lifespan reports of other short-lived fish species. (c) We characterize the biology of short-lived fish species to determine common trends in their ecology and life history. (d) Finally, we define and characterize the terms "annual fish" and "multivoltine fish."

2 | MATERIAL AND METHODS

2.1 | Databases searched

We were principally interested in fish species that exhibit a maximum lifespan shorter than one year in their natural environment. First, we reviewed databases developed to record animal lifespans—AnAge database (Tacutu et al., 2013) accessed 30 May 2020 (https://genomics.senescence.info/species/), Longevity Records (McDonough et al., 2000) accessed 25 May 2020 (https://www.demogr.mpg.de/longevityrecords/0503.htm) and *rfishbase* package v. 3.0.4 (Boettiger et al., 2012) implemented in R environment (R Core Team, 2019) accessed 27 May 2020. Second, we evaluated the comprehensiveness of available fish species lifespan information using *rfishbase* to estimate the proportion of ray-finned fish species with reported maximum lifespan overall. Given that references in the databases often cited sources prone to imprecise data, such as "grey literature" or books, we used Google Scholar (https://scholar.google.com/) to search for the primary source of database information.

TABLE 1 Overview of shortcomings of age estimation from otolith readings based on criteria outlined by Campana (2001), and extended to include other potential biases relevant for our study

Index	Caveat
X	A different method than otolith reading was used for lifespan determination
a	Formation of daily growth increments in otolith was not validated for the studied species
b	The age at first otolith increment formation was not validated
c	The increments in outer edge of otolith show reduced readability—potential underestimate of maximum age
d	Sampling did not cover the potential for seasonal fluctuation in population age structure (i.e. sampling was performed less than three times within a year)
e	Species age estimate was based on sampling of a single population
f	Sample size was not provided, or was smaller than 100 when the whole body size spectrum per species was age determined or when less than 10 largest individuals were age determined

Note: Reported indices serve to determine possible shortcomings in data presented in Tables 2–4 and suggest where lifespan estimates may change in future when more studies have been conducted. The reported data on species lifespan in Tables 2–4 should be taken as an evidence of lifespan shorter than one year rather than as a precise estimate of maximum natural lifespan.

We used species Latin name in quotation marks and then added one of the following five search terms: *longevity*, *lifespan*, *life span*, *age*, *otolith*. Each term was used for a separate search. For each run, we checked the first 260 short text snippets/abstracts provided by Google Scholar. For relevant entries, we screened the source article to validate original information. We also searched those articles for any link to other records of short-lived fish species.

Third, we searched keyword "annual fishes" in Google Scholar (excluding patents and citations, accessed 8 June 2020) and checked the first 800 results out of a total of 1,360. Of the first 800 results 24 were irrelevant and were omitted. From the rest, 97.7% referenced annual killifish only. The term "annual fishes" was used instead of "annual fish" because the latter term provided only 2% of results related to short-lived fish species other than annual killifish (7 out of 300 checked results, 11,800 results in total). 57% of results (172 out of 300) related to annual killifish and 40% (121 of 300) yielded irrelevant results such as "statistics of annual fish harvest" etc. A search for the term "ephemeral fish" (65 results) returned almost exclusively nonrelevant results and, in a few cases, it returned the species already yielded by the previous searches.

2.2 | Criteria for suitable longevity report

The retrieved records were screened using the following criteria. The major criterion was that it had been externally peer-reviewed or published as a report of a relevant international authority (e.g. Food and Agriculture Organization of the United Nations, Australian Centre for International Agricultural Research or South Pacific Commission). In addition to peer-reviewed articles and reports, three theses/dissertations were also included as relevant resources.

The second criterion for selection was the method for age estimate. The following means of maximum lifespan estimates were considered reliable, reading of daily growth increments in otoliths (Pannella, 1971), following survival of individuals in the wild (Stearns, 1983) and duration of habitat existence in species from ephemeral habitats (Pen et al., 1993; Vrtílek et al., 2018). Given the variation in the quality of reported results, we ascribe notes to each reported maximum age estimate (Table 1) to pinpoint potential methodological issues (Campana, 2001).

Several studies used age estimating methods that did not fulfil our criteria and were thus omitted. Studies that estimated age using body size distributions were omitted, because age may be decoupled from body size when fish reach asymptotic body size (Choat & Robertson, 2002; O'Farrell et al., 2015). Reports that simply mentioned species maximum lifespan, but did not provide relevant information how the estimate was reached, were excluded from the main body of the paper and are summarized in Table S1. Some species have principally annual populations while other natural populations live longer than one year, such as *Gasterosteus aculeatus* (Gasterosteidae) (Giles, 1987) or *Rhodeus amarus* (Cyprinidae) (Konečná & Reichard, 2011). These species are not part of this review because they often live longer than one year in the wild. Similarly, species with sexual dimorphism in lifespan and only one of the sexes having a maximum lifespan of less than one year in the wild, such as *Gambusia* spp. (Poeciliidae) (Cabral & Marques, 1999) or *Ceratoscopelus warmingii* (Myctophidae) (Linkowski et al., 1993), were not included.

3 | RESULTS AND DISCUSSION

3.1 | Overview of short-lived fish species and their phylogenetic position

We found 60 species (Tables 2–4) other than annual killifish with reported maximum lifespan of one year or less in their natural environment. These species are distributed over 12 orders (Figure 1) suggesting that short lifespan has evolved independently several

TABLE 2 Overview of short-lived fish species from order Gobiiformes with natural lifespan shorter than one year

Species	Order (Family)	Voltinism	Largest specimen	Max. lifespan	Major source of mortality	Reference
Aphia minuta	Gobiiformes (Gobiidae)	Annual	55 mm TL	275 days[b]	Reproduction	Iglesias et al. (1997), La Mesa (1999)
Crystalogobius linearis	Gobiiformes (Gobiidae)	Annual	41 mm TL	225 days[a,b,e]	Reproduction	La Mesa (2001)
Eviota sigillata	Gobiiformes (Gobiidae)	Multivoltine	18 mm TL	59 days[b,d]	Predation	Depczynski and Bellwood (2005)
Eviota melasma	Gobiiformes (Gobiidae)	Multivoltine	27 mm TL	97 days[b,d]	Predation	Depczynski and Bellwood (2006)
Eviota queenslandica	Gobiiformes (Gobiidae)	Multivoltine	26 mm TL	99 days[b,d]	Predation	Depczynski and Bellwood (2006)
Eviota epiphanes	Gobiiformes (Gobiidae)	Multivoltine	19 mm TL	61 days[b,d,e,f]	Predation	Grant (2013); Longenecker and Langston (2005)
Trimma nasa	Gobiiformes (Gobiidae)	Multivoltine	17 mm SL	87 days[a,b,d,e]	Predation	Winterbottom and Southcott (2008)
Trimma benjamini	Gobiiformes (Gobiidae)	Multivoltine	23 mm SL	140 days[a,b,d,e,f]	Predation	Winterbottom et al. (2011)
Paedogobius kimurai	Gobiiformes (Gobiidae)	Multivoltine	16 mm SL	67 days[a,b,e,f]	Reproduction, predation	Kon and Yoshino (2002)
Mugilogobius chulae	Gobiiformes (Gobiidae)	Multivoltine	21 mm SL	137 days[c,e,f]	Predation	Kunishima and Tachihara (2019)
Mugilogobius sp.	Gobiiformes (Gobiidae)	Multivoltine	36 mm SL	150 days[c,e,f]	Predation	Kunishima and Tachihara (2019)
Istigobius decoratus	Gobiiformes (Gobiidae)	Annual	84 mm TL	266 days[c]	Predation	Kritzer, (2002)
Valenciennea muralis	Gobiiformes (Gobiidae)	Annual	111 mm TL	363 days[b,e]	Predation	Hernaman and Munday (2005)
Pseudogobius masago	Gobiiformes (Gobiidae)	Multivoltine	18 mm SL	124 days[b]	NA	Saimaru et al. (2018)
Brachygobius mekongensis	Gobiiformes (Gobiidae)	Multivoltine	14 mm SL	78 days[a,b]	NA	Morioka and Sano (2009)
Coryphoterus kuna	Gobiiformes (Gobiidae)	Multivoltine	15 mm SL	148 days[a,b,f]	Predation	Victor et al. (2010)
Coryphopterus personatus/hyalinus	Gobiiformes (Gobiidae)	NA	58 mm TL	195 days[a,b,d,e,f]	Predation	Beeken (2019)
Bathygobius coalitus	Gobiiformes (Gobiidae)	Annual	68 mm TL	307 days[b,c,e]	NA	Shafer (2000)
Schindleria sp.	Gobiiformes (Schindleridae)	Multivoltine	30 mm SL	60 days[a,b,e]	Reproduction, predation	Kon and Yoshino (2002)
Schindleria praematura	Gobiiformes (Schindleridae)	Multivoltine	24 mm TL	42 days[a,b,f]	Reproduction, predation	Landaeta (2002(; Whittle (2003)
Schindleria pietschmanni	Gobiiformes (Schindleridae)	Multivoltine	17 mm TL	29 days[a,b]	Reproduction, predation	Whittle (2003)

Note: Taxonomic group is assigned in accordance with Rabosky et al., 2018. Voltinism is considered as: "annual"—species with lifespan one year or shorter, which probably complete a single generation within a year , "multivoltine"—species complete two or more generations within a year (Corbet et al., 2006). The largest specimen refers to the size of the largest age determined individual, TL = total length, SL = standard length. Superscript letters for lifespan records are defined in Table 1. Age reports with more indices have higher likelihood of longevity estimate changing in the future. Common names of all listed species are given in Table S2.

times. Data on maximum fish age are generally scarce, because only 4.7% (1,543 of a total of 32,872 species) of extant ray-finned fish species have registered lifespans in *rfishbase*. In general, short-lived species are small with body size 55 ± 35 mm (median ± median absolute deviation, both rounded to 5 mm). Below, we provide definitions of annual and multivoltine fish and synthesize the evolutionary ecology and basic biological characteristics of the most commonly reported species.

3.2 | Biology of the most frequently reported groups of short-lived fish

3.2.1 | Short-lived gobies

The second largest group of fish species (after annual killifishes) with reported lifespan shorter than a year in our literature review were short-lived gobies (Gobiiformes) (Table 2). Short-lived gobies

TABLE 3 Overview of short-lived fish species from orders Clupeiformes and Myctophiformes with natural lifespan shorter than one year

Species	Order (Family)	Voltinism	Largest specimen	Max. lifespan	Major source of mortality	Reference
Spratelloides robustus	Clupeiformes (Clupeidae)	Annual	82 mm FL	241 days^{b}	Predation	Rogers et al. (2003)
Spratelloides delicatulus	Clupeiformes (Clupeidae)	Multivoltine	66 mm SL	159 days^{b}	Predation	Dalzell et al. (1987), Milton and Blaber (1993), Milton et al. (1991), Milton et al. (1993), Milton et al. (1989)
Spratelloides lewisi	Clupeiformes (Clupeidae)	Multivoltine	63 mm SL	179 days^{a,b}	Predation	Milton et al. (1991)
Spratelloides gracilis	Clupeiformes (Clupeidae)	Multivoltine	58 mm SL	149 days^{b}	Predation	Milton and Blaber (1993), Milton et al. (1991), Milton et al. (1989)
Clupeichthys aesarnensis	Clupeiformes (Clupeidae)	Annual	60 mm SL	243 days^{a,b}	Predation	Morioka et al. (2019)
Stolephorus carpentariae	Clupeiformes (Eugraulidae)	Multivoltine	71 mm TL	158 days^{b,e,f}	Predation	Hoedt (2002)
Stolephorus nelsoni	Clupeiformes (Eugraulidae)	Annual	103 mm TL	285 days^{b}	Predation	Hoedt (1989, 2002)
Stolephorus commersonnii	Clupeiformes (Eugraulidae)	Annual	158 mm TL	240 days^{b,c,e,f}	Predation	Hoedt (2002)
Stolephorus insularis	Clupeiformes (Eugraulidae)	Multivoltine	64 mm TL	126 days^{b,e,f}	Predation	Hoedt (2002)
Encrasicholina heteroloba	Clupeiformes (Eugraulidae)	Annual	90 mm TL	240 days^{b,c}	Predation	Milton and Blaber (1993), Milton et al. (1989), Wright et al. (1989)
Encrasicholina devisi	Clupeiformes (Eugraulidae)	Multivoltine	62 mm SL	122 days^{b}	Predation	Hoedt (2002), Milton and Blaber (1993)
Encrasicholina purpurea	Clupeiformes (Eugraulidae)	Multivoltine	63 mm SL	189 days^{b}	Predation	Struhsaker and Uchiyama (1976)
Encrasicholina punctifer	Clupeiformes (Eugraulidae)	Multivoltine	80 mm SL	114 days^{b,f}	Predation	Milton and Blaber (1993)
Engraulis japonicus	Clupeiformes (Eugraulidae)	Annual	137 mm SL	329 days^{b}	Predation	Yukami et al. (2008)
Benthosema suborbitale	Myctophiformes (Myctophidae)	Annual	33 mm SL	325 days^{b}	Predation, reproduction	Gartner (1991)
Benthosema pterotum	Myctophiformes (Myctophidae)	Annual	53 mm SL	300 days^{a,b}	Predation, reproduction	Gjøsæter (1981, 1984)
Benthosema fibulatum	Myctophiformes (Myctophidae)	Annual	83 mm SL	300 days^{a,b,d,f}	Predation, reproduction	Gjøsæter (1978, 1981)
Diaphus dumerilii	Myctophiformes (Myctophidae)	Annual	63 mm SL	360 days^{b,}	Predation, reproduction	Gartner (1991)
Symbolophorus evermanni	Myctophiformes (Myctophidae)	Annual	86 mm SL	249 days^{a,b,d,e,f}	Predation, reproduction	Gjøsæter (1987)
Myctophum spinosum	Myctophiformes (Myctophidae)	Annual	81 mm SL	302 days^{a,b,d,e,f}	Predation, reproduction	Gjøsæter (1987)

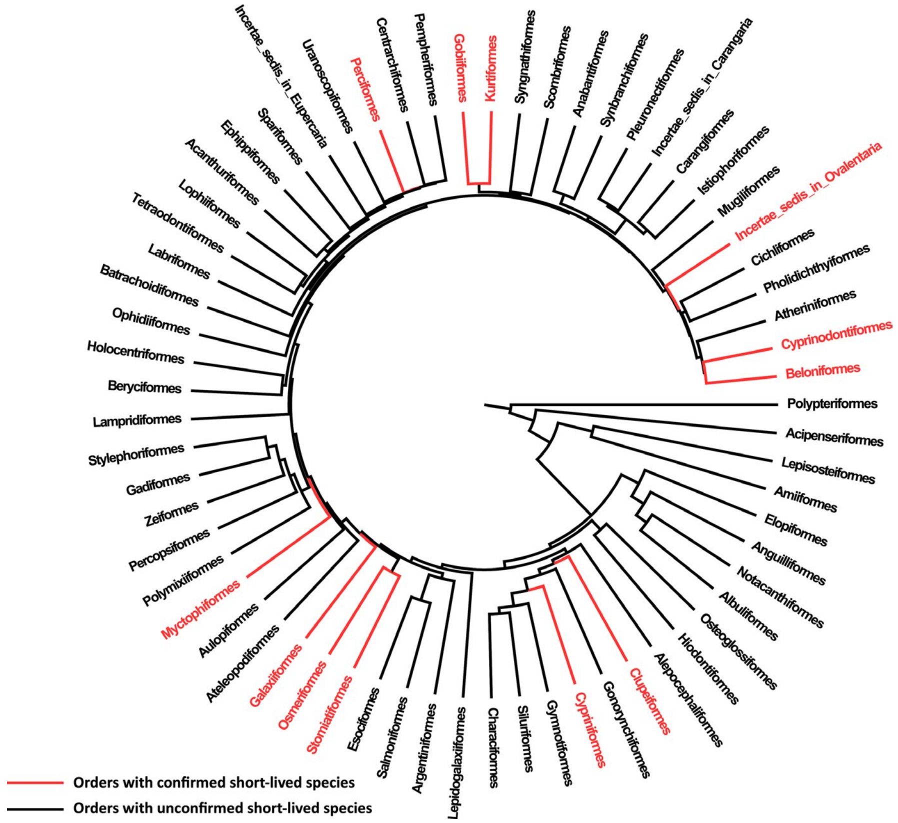
Note: Taxonomic group is assigned in accordance with Rabosky et al., 2018. Voltinism is considered as "annual"—species with lifespan one year or shorter, which probably complete a single generation within a year, "multivoltine"—species complete two or more generations within a year (Corbet et al., 2006). The largest specimen refers to the size of the largest age determined individual, TL = total length, SL = standard length, FL = fork length. Superscript letters for lifespan records are defined in Table 1. Age reports with more indices have higher likelihood of longevity estimate changing in the future. Common names of all listed species are given in Table S3.

TABLE 4 Overview of a short-lived fish species from less frequently reported orders

Species	Order (Family)	Voltinism	The largest specimen	Max. lifespan	Major source of mortality	Reference
Ostorhinchus rubrimacula	Kurtiformes (Apogonidae)	Annual	44 mm SL	274 days^{a,b,d,e}	Predation	Longenecker & Langston, 2006)
Rhabdamia gracilis	Kurtiformes (Apogonidae)	Annual	46 mm SL	322 days^{a,b,f}	Predation	Dalzell et al. (1987), Milton and Blaber (1993)
Rhabdamia cypselurus	Kurtiformes (Apogonidae)	NA	45 mm SL	105 days^{a,b,f}	Predation	Milton and Blaber (1993)
Apogon erythrinus	Kurtiformes (Apogonidae)	NA	NA	120 days^{a,b,d,e,f}	Predation	Longenecker and Langston (2005)
Plecoglossus altivelis	Osmeriformes (Plecoglossidae)	Annual	172 mm SL	355 days^{c}	Reproduction	Tsukamoto and Kaiihara, (1987)
Salanx ariakensis	Osmeriformes (Salangidae)	Annual	157 mm SL	354 days^{b,d,e,f}	Reproduction	Yuhao et al. (2001)
Neosalanx taihuensis	Osmeriformes (Salangidae)	Annual	75 mm SL	<365^{a,b,c,e}	Reproduction	Wu et al. (2011)
Rasbora rubrodorsalis	Cypriniformes (Cyprinidae)	Multivoltine	31 mm SL	121 days^{a,b}	NA	Morioka et al. (2014)
Esomus metallicus	Cypriniformes (Cyprinidae)	Multivoltine	47 mm SL	118 days^{a,b}	NA	Morioka and Vongvitchith (2014)
Tanichthys albonubes	Cypriniformes (Cyprinidae)	Multivoltine	NA	130 days^{e,f}	NA	Shi et al. (2008)
Engraulicypris sardella	Cypriniformes (Cyprinidae)	Annual	112 mm TL	251 days^{c}	Predation, reproduction	Rufli and van Lissa (1982; Thompson and Bulirani (1993)
Galaxiella nigrirostrata	Galaxiiformes (Galaxiidae)	Annual	48 mm TL	<365 days^{X}	Reproduction, habitat duration	Pen et al. (1993)
Galaxiella pusilla	Galaxiiformes (Galaxiidae)	Annual	35 mm TL	<365 days^{X}	Reproduction, habitat duration	Humphries (1986)
Enneapterygius atriceps	Blenniformes (Trypterigiidae)	Multivoltine	26 mm SL	117 days^{a,b,f}	Predation	Longenecker and Langston (2005)
Salarias patzneri	Blenniformes (Blenniidae)	Annual	59 mm TL	340 days^{b,e}	Predation	Wilson (2004)
Parambassis siamensis	Ovalentaria (Ambassidae)	Multivoltine	41 mm SL	148 days^{b}	NA	Okutsu et al. (2011)
Vinciguerria nimbaria	Stomiiformes (Phosichtidae)	Annual	56 mm SL	240 days^{a,b}	Predation, reproduction	Stequert et al. (2003); Tomás and Panfili (2000)
Heterandria formosa	Cyprinodontiformes (Poeciliidae)	Multivoltine	NA	120 days^{a,b,e,f}	Predation	Soucy and Travis (2003)
Hypoptychus dybowskii	Perciformes (Hypoptychidae)	Annual	78 mm SL	365 days^{e}	Reproduction, predation	Narimatsu and Munehara (1997)

Note: Taxonomic group is assigned in accordance with Rabosky et al., 2018. Voltinism is considered as “annual”—species with lifespan one year or shorter, which complete a single generation within a year, “multivoltine”—species complete two or more generations within a year (Corbet et al., 2006). The largest specimen refers to the size of the largest age determined individual, TL = total length, SL = standard length. Superscript letters for lifespan records are defined in Table 1. Age reports with more indices have higher likelihood of longevity estimate changing in the future. Common names of all listed species are given in Table S4.

FIGURE 1 Distribution of short-lived (annual or multivoltine) fish species within Actinopterigian fish orders. Orders with confirmed presence of short-lived fish species are in red. Orders without confirmed presence of short-lived fish species are in black. Primary source of data is Rabosky et al., 2018https://fishtreeoflife.org/taxonomy/. Figure was produced by Fig tree software v 1.4.4. (Rambaut, 2018)



include both marine and freshwater species (Morioka & Sano, 2009; Winterbottom et al., 2011), and bottom dwelling and pelagic species (Depczynski & Bellwood, 2006; Iglesias et al., 1997). Paedomorphic species are common in this group, for example *Paedogobius kimurai* (Gobiidae), (Kon & Yoshino, 2002) or *Schindleria* sp. Those species are estimated to produce nine generations per year (Kon & Yoshino, 2002). This is the highest number of generations produced per year among fish species, and conceivably among all vertebrates. The vast majority of the known short-lived goby species inhabit tropical coral reefs, where they represent an important part of trophic network, feeding on detritus and zooplankton and being predated by piscivores (Brandl et al., 2019; Wilson, 2004; Winterbottom & Southcott, 2008). Given their small body size, the predation pressure can become a major constraint for their lifespan (Depczynski & Bellwood, 2006; Winterbottom & Southcott, 2008). Most of the short-lived goby species reproduce repeatedly and retain the male parental care typical for other gobies (Depczynski & Bellwood, 2006; Patzner et al., 2011).

3.2.2 | Short-lived clupeids and myctophids

Clupeids (Clupeiformes) with a maximum lifespan shorter than a year in the wild (Table 3) are mostly found in tropical and subtropical marine environments (Hoedt, 2002; Struhsaker & Uchiyama, 1976), but are also reported from freshwaters (Morioka et al., 2019). Short-lived clupeids are small pelagic species feeding mostly on zooplankton. The major source of adult mortality in short-lived clupeids is predation by larger pelagic fish (Blaber et al., 1990; Milton et al., 1991) and commercial fishery also significantly contributes to their mortality (Milton et al., 1991; Morioka et al., 2019). Lifespan data from the short-lived clupeids are available because of their economic importance for human consumption and as a tuna-baitfish (Milton et al., 1993). Similarly to short-lived gobies, short-lived clupeids rarely reach their asymptotic body size and their growth remains linear throughout their natural lifespan in the wild (Rogers et al., 2003; Struhsaker & Uchiyama, 1976). This may be a result of intensive predation, restricting them from reaching asymptotic body size. Alternatively, explosive growth may be a strategy to increase fecundity (Barneche et al., 2018; Williams, 1966; Winemiller & Rose, 1993) and escape increased mortality at small size (Meekan et al., 2006; Miller et al., 1988). Mature short-lived clupeids spawn repeatedly in open water at intervals of several days (Clarke, 1987; Rogers et al., 2003).

Lantern fishes (Myctophiformes) are small bioluminescent species inhabiting mesopelagic and benthopelagic habitats (Catul et al., 2011). They perform diurnal migration and occupy resource-rich epipelagic waters at night (Gartner, 1991). Despite spending a large amount of time in cold and resource-poor deep waters, their life-history traits are defined by epipelagic conditions, as their early development, feeding and reproduction take place in the epipelagic zone (Catul et al., 2011; Gartner, 1991). The lantern fishes with lifespans shorter than a year are from warm-water regions and their distribution only borders temperate zones (Table 3). Lantern fishes contribute to the transfer of energy from the epipelagic habitat to deeper ocean zones by their diurnal migrations (Catul et al., 2011).

They constitute an important food resource for marine predators (Cherel et al., 2010) and experience a similarly short lifespan to pelagic clupeids (Table 3).

3.2.3 | Rarely reported groups of short-lived fish species

Several ray-finned fish orders may contain many species with maximum lifespans shorter than a year in the wild, but there is a paucity of reports given their limited access, low economic value and lower attractivity for applied and fundamental research. One noteworthy group is Asian Osmeriformes (especially families Plecoglossidae and Salangidae) – small fish species with amphidromous and landlocked populations (Iguchi, 1996; Wu et al., 2011). These species are semelparous and adults die soon after spawning (Iguchi, 1996; Wu et al., 2011). Spawning is observed twice per year, because they comprise both autumn-spawning and spring-spawning populations (Iguchi, 1996; Wu et al., 2011). Most salangids appear to have maximum lifespans shorter than a year (Shouzeng & Dagang, 1994). Unfortunately, rigorous examinations are scarce or inaccessible to us, because they are published in national languages.

Some Galaxiiformes from Australia are confirmed to have maximum lifespans shorter than a year (Humphries, 1986; Pen et al., 1993). Specifically, two small species *Galaxiella nigristriata* (Galaxiidae) and *Galaxiella pusilla* (Galaxiidae) (Humphries, 1986; Pen et al., 1993) live in rivers, creeks and seasonally desiccating pools in river alluvia (Coleman et al., 2015; Humphries, 1986). These species are able to survive habitat desiccation for an extended period of time in a wet mud or under logs and rocks (Coleman et al., 2015). They reproduce repeatedly at several-day intervals and die soon after maturity (Pen et al., 1993). This suggests that spawning effort combined with habitat duration contribute significantly to their mortality (Humphries, 1986; Pen et al., 1993).

We found very few records of short lifespan from other fish orders (Table 4). For example, small species of seahorses (Syngnathiformes) are expected to have a maximum lifespan shorter than a year but, to our knowledge, no data from the wild are available. To our knowledge, there is only one frequently cited work which suggests *Hippocampus zosterae* (Syngnathidae) as having an annual lifespan (Strawn, 1958), but this study was not designed to specifically estimate longevity or maximum lifespan of this remarkable fish. Seahorse otoliths are a poor marker of age which complicates rigorous records of their natural lifespan (Do et al., 2006). It is surprising that we could not find any verified record of a short-lived characid (Characiformes). The ecology of many characids is similar to that of the short-lived fish species described above – they are small and live in resource-rich shallow waters with high predation pressure (Weitzman & Vari, 1988), which are apparently ideal conditions for the origin and maintenance of an annual (or shorter) lifespan. We believe that our failure to document quantification of their apparently short lifespan is related to the paucity of data from the core of their distribution. Alternatively, we may have missed some reports, especially those published in local languages. There is also a relatively high number of species from other taxa where maximum lifespan shorter than a year is generally assumed but rigorous evidence is missing (Table S1). We believe that there are potentially many other species within the genera mentioned in Tables 2–4 which can also have a maximum lifespan of less than a year.

3.3 | Delimitation of annual and multivoltine fish species

It is customary to refer to short-lived fish species with a lifespan shorter than one year as "annual fish" (Berois et al., 2016; Liu et al., 2000; Myers, 1952; Wourms, 1967). In accordance with Etymonline.com ("Etymonline.com," 2020) and the Cambridge Dictionary ("Cambridge Dictionary," 2020), "annual" means something "happening once a year." This is undoubtedly the case for fish species with maximum lifespans longer than half a year (Table 2–4) and most appropriate for fish species with a life cycle that follows seasonal dynamics with one-year periodicity. We prefer to call these species "annual" rather than "univoltine" (having a single generation per year, Corbet et al., 2006) but these terms could be used interchangeably depending on the context (lifespan—annual, reproduction—univoltine).

Several fish species complete multiple generations within a year and it is therefore difficult to term them annual species. This has been argued by Wilson J. E. M. Costa earlier and has led to his redefinition of *Nematolebias* (Rivulidae) Costa, 2002 from "annual killifish" to "seasonal killifish" (Costa, 2002). "Seasonal fish" is another term coined for killifish from seasonal pools (Pienaar, 1968), albeit with rare use in the literature. "Seasonality" in the term "seasonal fish/killifish" correctly reflects the exclusively temporary occurrence of these species during the rainy season.

Many short-lived fish species complete their generations irrespective of any seasonality (Tables 2–4). For example *Schindleria* sp. occurs in tropical waters and it has been estimated that they complete up to nine generations within a year (Kon & Yoshino, 2002). *Eviota* spp. (Gobiidae) or *Paedogobius kimurai* can complete up to seven generations (Depczynski & Bellwood, 2006; Kon & Yoshino, 2002) and *Encrasicholina dewisi* (Engraulidae) can complete three generations per year (Hoedt, 2002; Milton & Blaber, 1993). More species with similar life histories are listed in Tables 2–4. For these fish species, we suggest using the term "multivoltine fish." Voltinism refers to the number of generations (from birth to sexual maturity) produced by an organism per year. This term enables us to separate short-lived species into univoltine (limited to a single generation per year) and multivoltine (capable of completing more than one generation per year) (Corbet et al., 2006). Voltinism is a common concept in entomology (Corbet et al., 2006; Southgate, 1981) and has also been used for short-lived mammals (Lambin & Yoccoz, 2001). We note that generations of a multivoltine species may be distinct (nonoverlapping) or overlapping (Bjørnstad et al., 2016). We encourage the use of terms "annual" (or "univoltine" when appropriate due to focus on the generation turnover) for short-lived fish species which complete their life cycle and produce a single generation within a year. We propose the use of term "multivoltine" in relation to short-lived fish species with multiple generations (from hatching to maturity) within one year.

3.4 | Evolutionary ecology of short-lived fish species

3.4.1 | Environment

Typical environments inhabited by short-lived fish species are tropical or subtropical shallow warm waters with high productivity and high predation rates. For example, short-lived clupeids live and reproduce in warm resource-rich pelagic waters (Milton et al., 1995) and short-lived gobies are mostly found on coral reefs (Depczynski & Bellwood, 2006). Year-round high productivity and warm water support stable food resources for early developmental stages of short-lived species occurring throughout the year (Kon & Yoshino, 2002; Morioka et al., 2014). Such conditions also support rapid developmental rates and early maturity (Munch & Salinas, 2009). Highly productive environments possess high biodiversity, often maintained by high predation pressure on early life stages (Caley, 1993; Connell, 1978). Short-lived fish species are small-bodied and are predated throughout their lives, truncating their lifespan (Caley, 1993; Depczynski & Bellwood, 2006).

Short-lived species from seasonal or resource-poor environments have developed coping mechanisms to deal with periods of unfavourable conditions. For example, annual killifish survive harsh periods as dormant embryos in dry mud (Furness, 2016). An alternative strategy for short-lived fish species is migration between productive and less productive environments (Gross et al., 1988). For example, myctophids undertake diurnal migration between deep and resource-poor mesopelagic and resource-rich epipelagic zones (Gartner, 1991). Adults of Asian amphidromous species spawn in rivers but juveniles feed in resource-rich marine and brackish waters (Gross et al., 1988; Shouzeng & Dagang, 1994). The absence of fish species with maximum lifespans of less than a year in cold climates and deep-water environments is likely a real phenomenon rather than simply due to a lack of verified records, because cold environments do not appear to support life histories with a short lifespan (Munch & Salinas, 2009).

3.4.2 | Reproduction

A short lifespan produces strong selective pressure for early maturity (Stearns, 1992; Williams, 1957). *Nothobranchius furzeri* matures at the age of 14 days posthatching in the wild (Vrtílek et al., 2018). In the paedomorphic *Schindleria pietschmanni*, adults have been confirmed at the age of 18 days (Whittle, 2003). Dwarf gobies from coral reefs are reported to mature within 1–2 months (Depczynski & Bellwood, 2006). In contrast, the maturity of semelparous species is postponed and mostly coincide with the maximum lifespan (Iguchi, 1996; Shouzeng & Dagang, 1994).

Short-lived species are expected to invest heavily in reproduction to assure its success before death (Gunderson, 1997; Williams, 1966). Investment can be realized by offspring quantity or intensive parental investment into survival of a small number of offspring. These divergent strategies are both common in short-lived fish species. Parental investment includes livebearing as in *Heterandria formosa* (Poeciliidae) (Soucy & Travis, 2003), mouthbrooding as in *Rhabdamia gracilis* (Apogonidae) (Fowler & Bean, 1930), and egg fanning and paternal nest guarding in marine gobies (Sunobe, 1998). In contrast, pelagic short-lived clupeids (Milton & Blaber, 1993), small tropical freshwater cyprinids (Morioka et al., 2014; Morioka & Vongvitchith, 2014) and Australian galaxiiforms (Humphries, 1986; Pen et al., 1993) repeatedly lay batches of eggs and do not invest in parental care. Semelparous Asian salangids invest in a single reproductive bout (Shouzeng & Dagang, 1994). The diversity of these reproductive strategies in short-lived species likely arises from the diversity of environments they inhabit (Winemiller & Rose, 1993), from seasonal savanna pools to ocean mesopelagic zones (Gartner, 1991; Reichard & Polačik, 2019), and from phylogenetic signals.

3.4.3 | Body size

Small species are generally assumed to have a short lifespan (Goatley & Bellwood, 2016; Hatton et al., 2019). Body size of the confirmed short-lived fish species in the current review spans from 14 mm in *Brachygobius mekongensis* (Gobiidae) to 220 mm in the piscivorous *Austrolebias elongatus* (Rivulidae) (Alonso et al., 2020). On the other hand, higher mortality in small species is not universal because various factors such as the use of shelters (Munday & Jones, 1998) and experience with predators (Goatley & Bellwood, 2016) varies among species. The relationship between body size and longevity is complex, but we confirm that short-lived fish species are generally small.

Small size may have ecological and metabolic benefits which contribute to maintenance of small body size in some species. Small species can use a wider range of shelters (Hernaman & Munday, 2005; Munday & Jones, 1998), have lower probability of being detected by predators (Goatley & Bellwood, 2009), may utilize niches inaccessible to large fish species (Munday & Jones, 1998), can maintain denser populations per area than larger species (Ackerman et al., 2004). They also have relatively lower metabolic demands and their digestive tract can be more easily filled (Ackerman et al., 2004). The metabolic benefits of small body size may be the mechanism behind the apparent absence of a trade-off between instantaneous growth and reproduction seen in short-lived fish species (Depczynski & Bellwood, 2006; Milton & Blaber, 1993; Winterbottom & Southcott, 2008).

3.5 | The shortest-lived fish

An extremely short lifespan is a consequence of extreme conditions such as extreme predation pressure or ephemeral environments (García et al., 2019; Reichard & Polačik, 2019; Riesch et al., 2015).

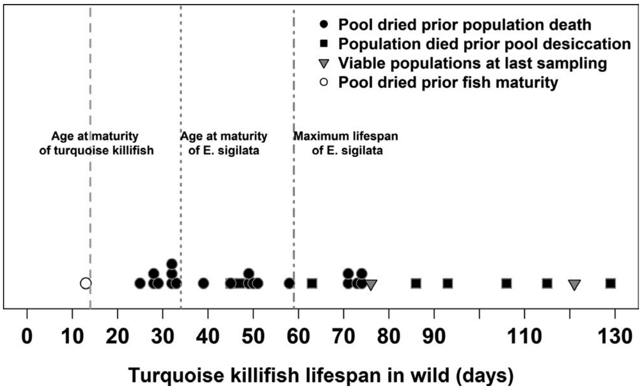


FIGURE 2 Lifespan of wild *Nothobranchius furzeri* populations in southern Mozambique. Median population lifespan is 50 days (95% confidence interval: 45–75 days). Populations inhabiting pools which dried prior to the death of all fish are depicted as black circles. Populations which disappeared prior to pool desiccation are present as black squares. Populations with inundated pools and viable populations at last sampling on 29 May 2016 (and unknown maximum lifespan) are marked as grey inverted triangles. Empty circle is a population with only juveniles. Grey vertical lines delimit common age at maturity of wild *N. furzeri*, age at maturity of *Eviota sigillata*, and maximum lifespan of *Eviota sigillata*

The relatively common occurrence of maximum lifespan shorter than one year in natural populations of ray-finned fish is unique within vertebrates.

Eviota sigillata (Gobiidae) is currently considered as the shortest-lived vertebrate with a maximum posthatching lifespan of 59 days in the wild. Our review identifies a number of other candidates for the shortest vertebrate lifespan. The most relevant is the group of small paedomorphic gobies such as *S. pietschmanni* from Hawaii (with a maximum age of 1 month assessed from 148 individuals over a 3 year sampling period (Whittle, 2003)) or a much smaller species *Schindleria brevipinguis* (<9 mm, but age not assessed (Watson & Walker, 2004)). The method of *Schindleria* spp. age estimate, however, still remains to be verified.

Among nonpaedomorphic species, the turquoise killifish *N. furzeri* from Africa is sexually mature in 2 weeks (Vrtílek, Žák, Pšenička, et al., 2018) and has a typical natural lifespan of weeks to months (Vrtílek, Žák, Polačik, et al., 2018). Prior to the report of a two-month lifespan in wild *E. sigillata* (Depczynski & Bellwood, 2005), *N. furzeri* was described as the shortest-lived vertebrate with its 3-month lifespan in captivity (Valdesalici & Cellerino, 2003). Here, we report our data from 30 wild populations of *N. furzeri* (see Supplementary methods) with a maximum lifespan from 25 to >129 days (Figure 2). Notably, 27% ($N = 8$) of wild *N. furzeri* populations with adult fish died before 34 days – the age when *E. sigillata* reaches sexual maturity (Depczynski & Bellwood, 2005). Short pool duration is not a constraint for population survival (Vrtílek, Žák, Pšenička, et al., 2018), which was supported by confirmation of viable populations in two repeatedly inundated pools which were previously inundated for less than 34 days. This is likely due to early maturity (14 days, Vrtílek, Žák, Pšenička, et al., 2018) and high daily fecundity (60 eggs per day, Vrtílek, Žák, Blažek, et al., 2018) of *N. furzeri*. These results suggest that *N. furzeri* can sustain viable populations even in more time-constrained environments and can be considered as the shortest-lived nonpaedomorphic vertebrate.

The intrinsic limits of longevity in these remarkably short-lived species can be determined by comparison with captive survival. Unfortunately, the relevant data are available only for *N. furzeri* where the maximum lifespan in captivity ranges from 3 to 17 months depending on population and holding conditions (Cellerino et al., 2016). Depczynski and Bellwood, (2006) note that *Eviota* spp. attain a longer maximum lifespan in captivity than in the wild and a captive lifespan of 2 years was reported for a closely related species *Eviota nigriventris* (Randall & Delbeek, 2009). We would like to highlight that advances in our knowledge of species with extreme life histories will very likely lead to the discovery of other fish species with an even shorter lifespan.

3.6 | Decoupling maximum lifespan from ageing

It appears that the maximum lifespan of the majority of short-lived fish species is decoupled from ageing in their natural environment. This is because their lifespan is terminated by ecological constraints, precluding sufficient time for the development of senescent changes. Thus the growth asymptote is not reached in short-lived gobies and clupeids (Depczynski & Bellwood, 2006; Struhsaker & Uchiyama, 1976) and there is no detectable reproductive senescence in wild *N. furzeri* (Vrtílek, Žák, Blažek, et al., 2018) despite their clear reproductive senescence in captivity (Žák & Reichard, 2021).

When kept in the protective environment of captivity, some species live long enough to develop senescence. It is probable that the lifespan extension induced by protective conditions in captivity is stronger in short-lived than long-lived vertebrate species (Tidière et al., 2016). Unfortunately, information related to the captive lifespan of short-lived fish species is largely anecdotal. Among gobiids, Depczynski and Bellwood, (2006) mention that *Eviota* spp. live much longer in captivity than in the wild, and that they reach the senescent stage. *Coryphopterus personatus/hyalinus* (Gobiidae) has a maximum lifespan of 195 days in the wild but can reach 4 years in captivity (Beeken, 2019). More rigorous evidence comes from short-lived cyprinodontiforms such as annual killifish (discussed in detail above) and *H. formosa*, that lives only up to 4 months in the wild (Soucy & Travis, 2003) but commonly for 14 months in captivity (Ala-Honkola et al., 2011). However, lifespan extension in captivity is far from universal. For example, benefits for semelparous species from a captive environment are negligible, because they ultimately die after reproduction (Iguchi, 1996). In addition, some short-lived fish species have a shorter maximum lifespan in captivity than in the wild or do not survive in captivity at all (e.g. *Stolephorus* spp., *Thryssa* spp. *Encrasicholina* spp., all Engraulidae (Hoedt, 2002; Milton et al., 1989)). Those short-lived species which can be kept in captivity can provide important insights into the intrinsic constrains of organismal longevity, as seen in annual killifish (Genade et al., 2005; Hu & Brunet, 2018).

3.7 | Caveats

Our knowledge of fish age is limited to a few species. Maximum lifespan is known for less than 5% of almost 33,000 described fish species (based on data from *rfishbase* (Boettiger et al., 2012; Froese & Pauly, 2019)). It is plausible that slightly more fish species have known longevity estimates, as *rfishbase* is still being developed and data from the Fish Base website (Froese & Pauly, 2019) converted to this package (Boettiger et al., 2012). This may contribute to the relatively low absolute number of reported short-lived fish species. Another caveat is that our knowledge of short lifespan is certainly biased towards economically and scientifically important species. A relatively small number of rigorous studies with small coverage over the ray-finned fish phylogeny prevents us from using a relevant phylogenetically corrected meta-analytic approach. Nonetheless, we believe that our sample size of more than 50 species makes the abovementioned generalizations on short-lived fish biology valid.

Longevity determination in short-lived species is often performed by counting the daily increments in otoliths (Pannella, 1971) and this is subject to some difficulties (see (Campana, 2001; Stevenson & Campana, 1992) for review). Thus, we list potential caveats in our overview (Table 1) which should reflect the variance in the accuracy of reported ages in Tables 2–4. In otolith readings, a higher number of increments may cause age underestimation due to problematic recognition of separate increments (Hoedt, 2002). Determination of age of first otolith increment formation is often absent in the species studied, but has only a small impact on maximum lifespan estimates, because it creates a bias of only a few days. The maximum lifespan of annual killifish from seasonal pools can be estimated from pool duration, as performed previously (Terzibasi Tozzini et al., 2013). However, annual killifish populations may disappear before the pool desiccates ((Vrtílek, Žák, Polačik, et al., 2018), Figure 2) and in such cases, the natural killifish lifespan is overestimated. In general, we have included the longevity report from studies only in species where it was generally assumed that they usually have a maximum lifespan shorter than one year in their natural environment. We note that with an increase in the number of studies related to the natural lifespan of fish species some species can be detected as longer lived than currently assumed.

3.8 | Summary

The unpreceded species richness and ecological diversity of ray-finned fish species results in a multitude of life-history strategies, including extremely short lifespans. The maximum natural lifespan of *S. pietschmanni* from Hawai is 1 month, wild *N. furzeri* populations live for 25–120+ days and *E. sigillata* lives for a maximum of 2 months. These species represent the shortest maximum lifespans among vertebrates. An important outcome of this review is that short-lived fish species are not as rare as expected. We speculate that the relatively scarce evidence of extremely short lifespan in fishes arises from a lack of interest in age determination in small fish species rather than rarity of this life history. In light of this, the unverified evidence of short-lived fish species in characiform fishes and other small tropical species is especially surprising. This contrasts with the ecological significance of short-lived fish species, which are essential in the transfer of energy in ecosystems where they occur (Brandl et al., 2019; Catul et al., 2011; Milton et al., 1991). They have economic importance as a food resource for human consumption (clupeids), are used as a baitfish (Milton et al., 1989), harvested for fishmeal production (Catul et al., 2011) and used in the ornamental fish trade (Genade et al., 2005; Randall & Delbeek, 2009). Last but not least, short-lived species which are easily bred in captivity are valuable models for evolutionary and biomedical research (Cellerino et al., 2016). We believe that our review contributes to more extensive studies into the biology and diversity of short-lived fish species.

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CONFLICT OF INTEREST

Authors declare no conflict of interests.

AUTHOR CONTRIBUTION

JZ designed the study; JZ did the literature research; JZ, MV, MR wrote the draft of manuscript; MV, JZ, MP, MR, RB collected the field data for wild lifespan of *N. furzeri*; JZ, MV, MR, MP, RB approved the final version of submitted manuscript.

DATA AVAILABILITY STATEMENT

All referenced studies included in this review can be found in the Reference section. Raw data for *Nothobranchius furzeri* lifespan are available in Figure 2. No other unique data were generated as part of this work.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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