

1 Temperature affects fish body sizes. Which sizes?

2 Running title: temperature and fish sizes

3

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31

32 **Abstract**

33 An extensive literature exists on how environmental conditions, especially temperature, impact
 34 animal body sizes. However, there remains considerable discrepancies, and misunderstanding,
 35 in the key definitions and concepts of body size used to describe observed impacts across studies.
 36 Size can be measured using continuous growth metrics, including von Bertalanffy growth
 37 coefficients, or static 'size' metrics, such as population-averaged length or mass, average size-at-
 38 (arbitrary)-age, size-at-maturity, adult size, asymptotic size, or the maximum observed size.
 39 Critically, these concepts of size are not equivalent, and temperature is likely to affect each in
 40 different ways. The use of these disparate size and growth metrics as response variables
 41 estimated across different biological scales (individual, population, or community) and empirical
 42 contexts (laboratory, field) has led to unnecessary confusion and apparent contradictions among
 43 practitioners. Here, we review nine common confusions associated with the measurement of
 44 'size' in fish and other water-breathing ectotherms. We then highlight outstanding knowledge
 45 gaps on how temperature and global warming might affect different size metrics. Clarifying
 46 concepts, definitions, and applications of body size measures is important as it can help reconcile
 47 divergent findings, target future research, and improve our predictions about the warming
 48 impacts on wild populations.

49

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67

68 **Introduction**

69

70 An animal's body size is considered a 'master trait' in theoretical and applied research (Litchman
 71 and Klausmeier, 2008; Shin et al., 2005; Woodward et al., 2005). Body size determines an
 72 individual's physiology, mortality risk and reproductive output, which in turn influence
 73 population demography, species resilience to exploitation and socio-economic value (Blackburn
 74 and Gaston, 1994; Jennings et al., 2001; Peters, 1986; Schmidt-Nielsen, 1984; White et al., 2007).
 75 The average body size of individuals in biological assemblages, particularly fish, has declined over
 76 time due to shifts in species composition and truncation of population size structure via changes
 77 in growth and mortality (Martins et al., 2023). In addition to direct human harvesting, climate
 78 change has also been implicated as a key driver of this trend, with shifts to smaller body sizes
 79 referred to as a third universal response to warming (Daufresne et al., 2009; Gardner et al., 2011;
 80 Sheridan and Bickford, 2011).

81

82 The anticipated 'shrinkage' of body sizes in fish communities may be due to fish growing to
 83 smaller adult or maximum sizes within populations or species, an increase in the abundance of
 84 smaller-bodied species, or trophic groups, with climate-driven redistribution, or a combination
 85 of both (see Cheung et al., 2013; Coghlan et al., 2024). Yet, the relative contribution of these
 86 individual physiological or environmental processes to realised fish communities remain to be
 87 properly quantified. Experimental evidence under controlled conditions shows that in many
 88 ectotherms, increased temperature leads to a faster growth rate of young juveniles and a
 89 decrease in size at maturity (the Temperature-Size Rule "TSR"; Atkinson, 1994; Horne et al., 2015;
 90 Ray, 1960). The degree of size reduction per °C warming is generally greater in aquatic than in

91 terrestrial species (Forster et al., 2012; Horne et al., 2015). However, studies conducted under
92 field conditions show mixed results, sometimes failing to support a negative relationship
93 between temperature and size of adult fish (e.g., Lindmark et al., 2023). Moreover, studies often
94 use different growth measures or body size metrics, which makes a general test of TSR
95 particularly challenging (Audzijonyte et al., 2020; Cappo et al., 2013; van Denderen et al., 2020).
96 As a result, despite decades of research, the temperature impacts on water-breathing
97 ectotherms and, more specifically, on fish size, continue to be a hotly debated topic.

98

99 Some of the contradictory findings of how temperature affects body size in the wild may arise
100 from researchers not considering causality under appropriate environmental conditions and at
101 appropriate ecological scales. For instance, the response of age-dependent growth, and other
102 biological rates, to warming can be highly non-linear depending on whether, and the extent to
103 which, the warming exceeds the thermal optimum for the variable in question (Kingsolver and
104 Buckley, 2017; Lindmark et al., 2022; Ørsted et al., 2022). Moreover, body size responses are not
105 only determined by changes in rates of growth and development at the individual level, but also
106 by the size- and density-dependent growth and changing mortality through predation and fishing
107 (Audzijonyte et al., 2013; Ohlberger, 2013). Although mechanistic explanations of how
108 temperature might affect fish growth and size are at the core of recent debate (Audzijonyte et
109 al., 2022, 2019; Pauly, 2021; Rubalcaba et al., 2020; Verberk et al., 2021), we argue that we
110 cannot make progress on understanding these mechanisms unless we clearly define the
111 terminology around size and growth when investigating temperature impacts. Critiquing or
112 exploring possible mechanistic explanations of temperature-size trends is *not* the focus of our
113 review. Rather, the goal of this paper is to highlight and clarify some of the common
114 misconceptions about the definitions of fish growth and size to facilitate a more informed
115 investigation of mechanisms and observed patterns.

116

117 The need for a clear definition of 'size' and its intrinsic relationship with growth rate was clearly
118 made by Kinne (1960), whose experimental results "indicate that the differences in growth rate
119 established in young fish do not persist throughout life. Initially slow-growing fishes may surpass
120 initially fast-growing fishes, and finally reach a greater length-at-age." Kinne (1960) clarified that
121 growth differs from size in that the latter has one dimension (length or weight), while the former
122 has two (length per time, or weight per time). Thus, as illustrated in Fig. 1A, to determine which

123 of two fish grows 'faster' or reaches a 'bigger' size, requires that the size or age at which the
124 variable of interest is measured be standardised.

125

126 The failure to standardise size or age measurements is the cause of much confusion when
127 interpreting empirical data. For instance, elevated temperatures often accelerate the growth of
128 young (= small) individuals, while reducing the final or maximum size that old (= large) individuals
129 can reach (Fig. 1A). The standardisation issue becomes even more complex when the 'growth' or
130 'size' of individuals are taken from an ensemble of fish of unknown age, *e.g.*, when a study
131 focuses on a population's size structure as measured by mean or maximum individual size (Fig.
132 1B). Moreover, it is important to restate the obvious fact that body size can be described by
133 either length or weight. Length can only increase throughout an individual's lifetime, whereas
134 weight reflects a combination of length and condition and may either increase or contract. Many
135 physiological modelling studies use weight, whereas fisheries analyses are often based on length,
136 which is easier to measure. The 'generic fish' conversion from length to weight uses weight (g) =
137 $0.01 \times \text{length (cm)}^3$, but there is a lot of inter-specific variation (Froese, 2006; Froese et al., 2014),
138 and where available, species-specific coefficients (*e.g.*, provided on FishBase) should be used
139 (Froese and Pauly, 2000). Importantly, length and weight frequencies and distributions in a
140 population will not be identical, since weight grows exponentially compared to length.

141

142 In the following sections, we discuss issues that arise when studying growth, measuring size and
143 exploring size distributions. Sometimes the source of a common confusion is conceptual, in which
144 cases we point to the deeper mechanisms; in other instances, it is semantic. Our aim is to identify
145 some of these common misconceptions and provide recommendations for which specific
146 measures of size or growth are appropriate in a given situation and which terminology is correct.

147

148 The first four of the nine misconceptions that we aim to clarify relate to five different concepts
149 of body size (either length or weight): size-at-maturation, adult size, mean size in a population,
150 asymptotic size and maximum size (Fig. 1).

151

Box 1: Glossary

Body size: an attribute of an individual that is measured as a single dimension, either weight or length, at a single point in time. Body size can be averaged across individuals but must be measured at the individual level. While a fish's weight can increase or decrease over time, length can only increase. Length for fish can be measured as standard, fork or total length (SL, FL, TL, respectively).

Growth: a rate measured using two dimensions, (1) body size and (2) time, *i.e.*, change in length or weight per unit time. It can be measured as an absolute change in size per time (e.g. grams per day) or as a rate (per unit time) at which asymptotic size is approached (e.g., von Bertalanffy, see Box 2). Sometimes growth is defined as 'mass-standardised growth rate' or *specific growth rate* = g per gram per day (Perry et al., 2015)

Size-at-maturity (L_{mat} or W_{mat}): the size at which an individual first becomes reproductively mature. While size-at-maturity is measured at an individual level, it is also often reported as the average of a population or a species (e.g., size at 50% maturity, L_{50} , is the size at which 50% of the population is mature).

Size-at-age: the size of an individual at a given point in time. Note that while size-at-age defines size at a fixed age, size-at-maturity does not, because fish in a population or species may mature at different ages.

Adult or mature or final size: in *determinate* growers, growth stops around maturation time and individuals remain at the same 'adult' size. In contrast, some organisms, such as fish or reptiles, keep growing throughout their lifetimes and are often called *indeterminate* growers. Organisms that keep growing throughout their lives do not have a single 'adult', 'mature', or 'final' size, although a population or species can have a maximum size (below).

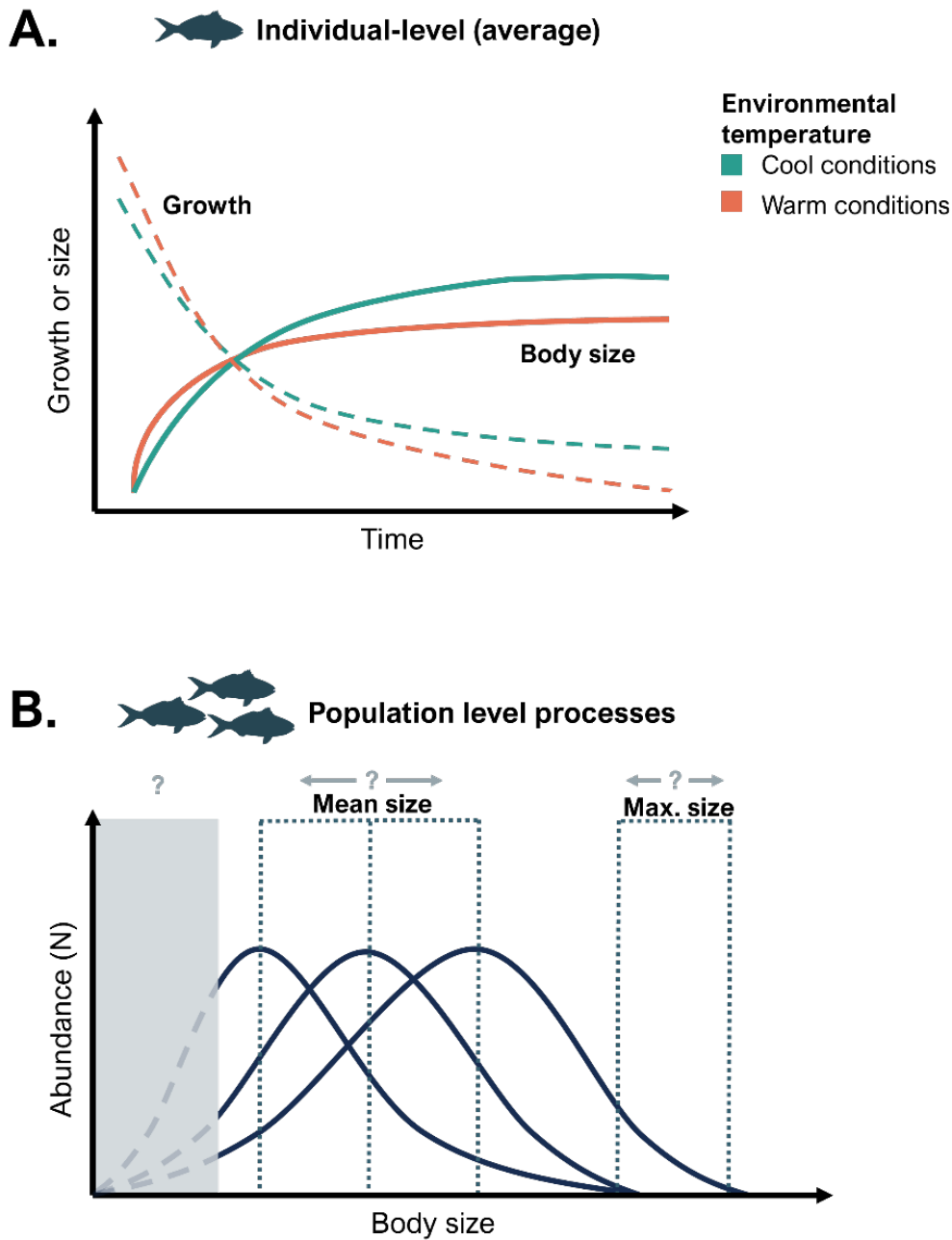
Maximum size (L_{max} or W_{max}): sometimes measured as the largest known size recorded for an individual within a population or species, or alternatively defined as a 95th or 99th quantile of a size frequency distribution.

Asymptotic size ($L_{\infty} = L_{inf}$; $W_{\infty} = W_{inf}$): estimated in length or weight at an individual, population, or species level after fitting a growth curve (e.g. a von Bertalanffy curve, see Box 2) to observations of many individuals. Asymptotic size indicates the size an individual (or average individual, if measured at a population or species level) approaches through growth.

Size spectrum: the distribution of abundance or biomass in a population, species, or community as a function of size. It is often characterised by its slope and intercept from a linear model on log-transformed data.

Temperature-size rule (TSR): a widely observed phenotypically plastic reduction in size-at-maturity of an individual ectotherm growing under warming that increases its initial growth rate.

von Bertalanffy growth function (VBGF) and size corrected growth coefficient A – See Box 2.



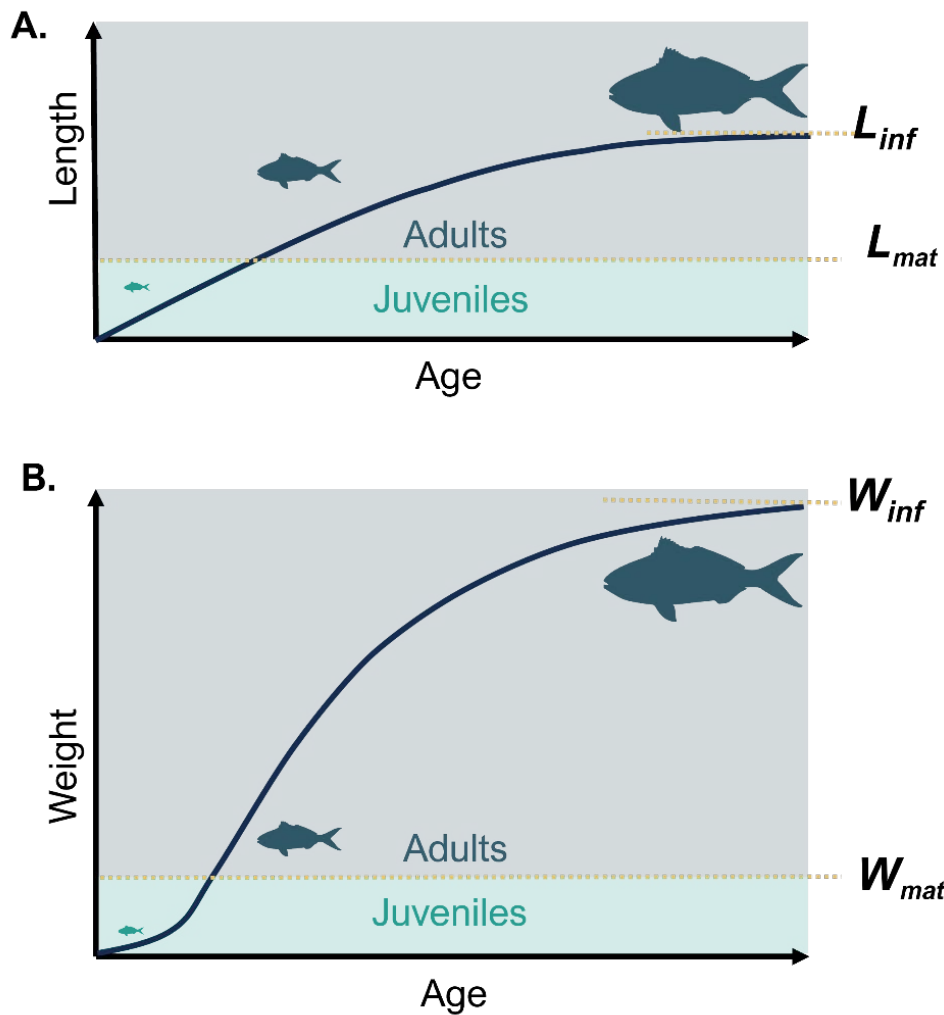
157 **Fig. 1.** Expectations of potential fish growth patterns in warmer conditions: **A:** Growth and body size (size-
 158 at-age) at two different temperatures. **B:** Potential size frequency distributions in a population, with
 159 different mean and maximum sizes determined by the relative numbers (abundance) of different size fish.
 160 Panel A reflects declining specific growth rate in individual length through their lifetime, whereas panel B
 161 relates to population processes shaped by growth rate, recruitment, and mortality. The abundances of
 162 the smallest fish in panel B are often unknown or hard to assess, which is why this part is shaded. Arrows
 163 and question marks above mean and maximum size suggest that the direction of their change with
 164 warming is not known.

165 **1. Distinctions between size-at-maturity, adult size and asymptotic size: theories on**
166 **temperature impacts on maturation size may not apply to asymptotic size**

167

168 Animals can generally be separated into two groups based on their growth trajectories: (1)
169 *determinate* growers, where growth ceases around the time of maturation, and (2)
170 *indeterminate* growers, where individuals keep growing throughout their adult life, beyond
171 maturation. While ‘mature’ size can be considered equivalent to ‘adult’ or ‘final’ size in
172 determinate growers such as most insects, confusion arises when these terms are used
173 equivocally for indeterminate growers such as fish. One example where this has occurred is in
174 the context of the Temperature Size Rule (TSR; Atkinson, 1994). This rule was derived through
175 observations of the effect temperature had on maturation size of ectotherms (animals and plants)
176 grown under controlled, ‘benign’ conditions in the laboratory. Whereas stressfully high
177 temperatures resulted in obvious reductions in growth rate (as did insufficient nutrition or
178 competition), it was not obvious why smaller size-at-maturity was observed under temperature
179 conditions that initially promoted increased growth rates (Berrigan and Charnov, 1994).
180 Importantly, because most of the available data were from species with determinate growth,
181 temperature impacts on ‘maturation’ size often became known as temperature impacts on ‘adult’
182 size. Yet, the TSR does not postulate anything about the temperature impacts on sizes beyond
183 those observed at maturation for indeterminate growers, such as the maximum or asymptotic
184 sizes. Nevertheless, the TSR has commonly been extended to make predictions about these
185 measures of size in warmer conditions (including by some authors of this study, Audzijonyte et
186 al., 2016; Lindmark et al., 2023; van Rijn et al., 2017). It is likely that smaller maturation sizes
187 under TSR will correlate with smaller asymptotic sizes in fishes, since there is a well-established
188 overall correlation between these two size measures in fish (Thorson et al., 2017). Yet, rigorously
189 extending the TSR predictions to asymptotic or maximum sizes of fish requires further study by,
190 for example, looking at intra-specific relationships between maturation and asymptotic sizes
191 across temperature gradients, which to our knowledge this has not been explicitly tested.

192



193

194

195 **Fig. 2.** In taxa that continue growing after maturation (i.e., indeterminate growers), such as fish, 'adult'
 196 size refers to a wide range of lengths (A) and even larger ranges of weights (B) between maturation and
 197 asymptotic size.

198

199 **2. Adult size is not a defined measure for indeterminate growers, and not a useful concept for** 200 **fish**

201

202 As shown in Fig. 2, 'adult' size incorporates a range of possible body sizes beyond the point of
 203 maturation in indeterminate growers. For example, Atlantic cod (*Gadus morhua*) can mature at
 204 a size (weight in this example) of 1-2 kg and grow to almost 100 kg, which means that adult
 205 weights can range over two orders of magnitude. This property of fishes causes challenges when
 206 trying to explore broad-scale theories and patterns surrounding body size and its relationship to
 207 abundance and distribution which rely on 'adult size' as the key metric (Brown, 1995; Gaston and
 208 Blackburn, 2000). Most macroecological studies have historically been applied to determinate

209 growing animals like birds and mammals, for which adult body size is essentially equivalent to
210 size at maturity and maximum size. Consequently, these studies do not explicitly state which
211 measure of size is used (Gillooly et al., 2016; Savage et al., 2004). However, for animals such as
212 fish, there is no single ‘adult’ size that describes a mature individual and the body size metric
213 being used must be clearly defined when macroecological theories are tested in fish.

214 **3. The distinction between asymptotic size and maximum size in a population or species**

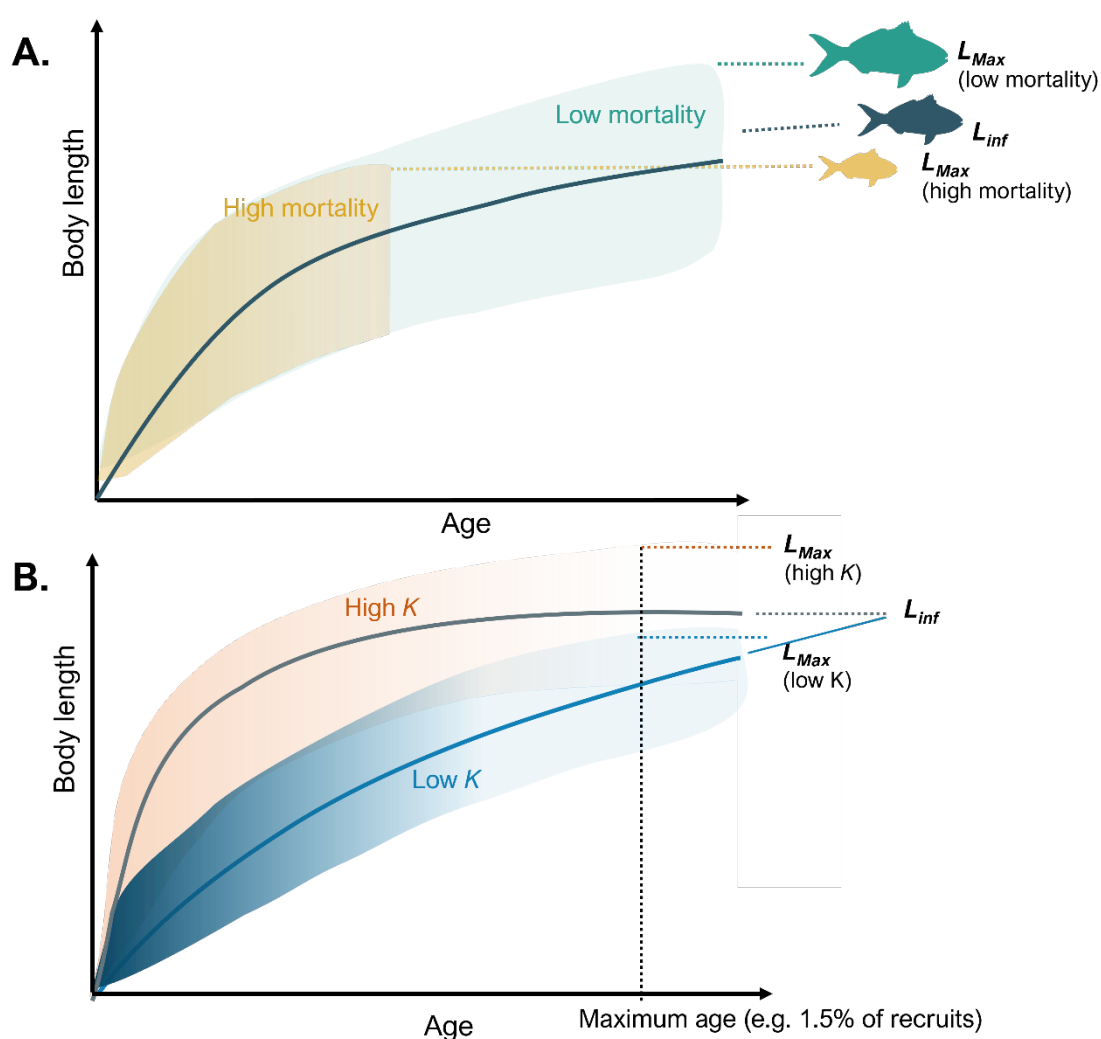
215
216 Maximum length L_{max} (or weight) is generally defined at the population or species level, where
217 the largest individual in the population represents the ‘maximum’ size for that sample (Fig. 3). It
218 is sometimes recommended that instead of a single observation, the upper 90–99th percentile be
219 used to estimate maximum size in a population, as these values may be less sensitive to fishing,
220 sampling bias or observer error (ICES, 2023; Östman et al., 2023). The asymptotic size, or in this
221 specific case asymptotic length (L_{inf}), is estimated (rather than measured) after fitting a growth
222 curve, usually a von Bertalanffy growth curve (Box 2). This model can be fitted to size-at-age data,
223 ideally with data at the individual-level, but often it is done with average size-at-age (across e.g.,
224 cohorts or populations). ‘Asymptotic length’ then refers to individual, population or species level
225 characteristics. Therefore, maximum size is a biological property that is observed, whereas
226 asymptotic size is a mathematical property that must be estimated. At an individual level, L_{inf} is
227 always larger than L_{max} because the former defines the size that an individual approaches through
228 growth. At a population or species level, L_{inf} is averaged across individuals, which means that
229 some individuals can reach sizes larger than L_{inf} .

230
231 Assuming perfect sampling and in situations where mortality is high, the maximum observed size
232 will be considerably smaller than L_{inf} (Fig. 3A) since few fish survive to old ages. In contrast, the
233 same growth pattern in a population with very low average mortality means that a considerable
234 number of fish will be larger than L_{inf} , because about half of the individuals in a population are
235 expected to grow to a size larger than that the estimated L_{inf} value (Fig. 3A). However, the latter
236 statement will only be true for fish that during their lifetimes approach sizes close to L_{inf} (Fig. 3A).
237 This is because the rate at which individuals approach L_{inf} , or more specifically the mortality and
238 growth rate ratio (M/K), also determines the relationship between L_{inf} and L_{max} . If M/K ratio is
239 high (e.g. slow growth rate), fish may remain relatively far from L_{inf} even at maximum age and

240 therefore L_{max} will be considerably smaller than the estimated theoretical L_{inf} (Hordyk et al., 2015)
 241 (Fig. 3B). In a theoretical case where $M/K = 1.5$ and there is no variation in growth rate, the L_{max}
 242 = $0.95 * L_{inf}$ (Hordyk et al., 2015; Taylor, 1958). This prediction appears general enough because a
 243 similar relationship is observed empirically in many fished populations (Froese and Binohlan,
 244 2000; but see Pauly, 2021 for a further discussion on why these estimates may not apply for very
 245 large, fast-growing fish such as tuna). Potential sampling biases must also be considered, because
 246 the probability of observing a large fish will depend on sampling intensity and method, which
 247 becomes especially important when estimating maximum fish sizes from small samples.

248

249



250

251 **Fig. 3.** Maximum and asymptotic size (L_{inf} in this specific example) can differ depending on mortality in
 252 the population (A) or how fast individuals reach this asymptotic size (B). Shading in both panels
 253 illustrates the distribution of individual size-at-age. In A - under low mortality some individuals will be
 254 larger than L_{inf} (and this number depends on the variation around size at maximum age, panel B), but

255 under high mortality very few individuals will live to old ages, so the observed maximum size will be
256 considerably smaller. In B – if the von Bertalanffy growth coefficient K is small and initial growth is slow
257 (blue), fish may not approach their L_{inf} even at maximum age (here defined as age to which 1.5% of
258 recruiting fish survive; Dureuil and Froese, 2021), and maximum size will be smaller than L_{inf} . If K is high
259 and initial growth is fast (orange), maximum size can be larger than L_{inf} , depending on the mortality rate
260 (A).

261 Most studies on theoretical abundance-size relationships in fish use asymptotic size as a key
262 species characteristic (Andersen and Beyer, 2006). In contrast, studies relating body size to
263 empirical abundance observations or species vulnerability to fishing often use maximum size
264 (Dulvy et al., 2014; Walls and Dulvy, 2021). The distinction between the two measures is
265 important for biological interpretation of findings and should be explicitly acknowledged when
266 comparing results from such studies. However, it must be noted that using either of the two
267 measures as a species characteristic is challenging given that both maximum and asymptotic sizes
268 are likely to be affected by temperature (and other environmental conditions) and thus vary
269 extensively across populations of the same species (see FishBase at www.fishbase.org for
270 examples of observed maximum length and asymptotic length estimates across species' ranges).

271

272 **4. The distinction between mean size and maximum, asymptotic or maturation size**

273

274 In general, few individuals of indeterminate growers in natural populations reach sizes near their
275 potential maximum due to variation in growth, mortality and individual performance. Given that
276 much of macroecology is concerned with general patterns in ecosystem structure and
277 functioning, averages can be more informative than extremes. Unlike maximum size, average or
278 mean size is summarised over the whole range of sizes sampled in a population and is more
279 representative of the size and ecological role of an average individual, assuming that sampling
280 selectivity is accounted for. Although the distinction between asymptotic or maximum and mean
281 size seems obvious, these measures are often confused in studies exploring temperature effects
282 on fish sizes. For instance, studies that suggest that 'decreasing animal body sizes is a third
283 universal response to global warming" (Daufresne et al., 2009; Gardner et al., 2011) or that fish
284 are expected to 'shrink' by 14-25% by 2050 (Cheung et al., 2013) often refer to growth and
285 asymptotic sizes, although sometimes the size measure is not defined (e.g. Daufresne et al., 2009).
286 Note that the terms 'decreasing' or 'shrinking' in these cases refer to fish growing to smaller

287 asymptotic sizes and does not imply that fish literally ‘shrink’, as would result from a negative
288 growth rate (due to e.g. reduced weight or condition).

289

290 Temperature impacts on fish mean sizes might be different to those of asymptotic size. A study
291 of 335 coastal fish species using data from underwater visual surveys showed that higher
292 temperatures (through space or time) led to variable mean observed length responses across
293 species, with declines in some species and increases in others (Audzijonyte et al., 2020). These
294 two contrasting body size responses to temperature – variable response in mean sizes but
295 ‘shrinking’ asymptotic sizes - are not necessarily contradictory. If juveniles grow faster in warmer
296 conditions and populations consist mostly of young fish, average sizes might increase with
297 temperature, even if fish grow to a smaller L_{inf} (Fig. 1B). Of course, changes in growth and size-
298 at-age are likely to affect mean sizes in a population, but increasing size-at-age does not
299 necessarily lead to larger mean size and vice versa (Lindmark et al., 2022; Ohlberger et al., 2023;
300 Oke et al., 2020). More empirical studies are needed to understand the relative roles of growth
301 and mortality in shaping species size distributions and how temperature driven changes in size-
302 at-age might affect population size properties (mean and variance of body sizes) under natural
303 conditions.

304

305 The next two common misconceptions are related to definitions and measures of growth and
306 how these are linked to size. While the distinction may seem obvious, there is considerable
307 confusion about these concepts in the literature.

308

309 **5. The distinction between growth and size**

310

311 Naturally, an individual’s growth rate determines its body size at any given point in time, but
312 faster growth does not necessarily mean larger body size — it depends on the time or age at
313 which the body size is measured. This seems like an obvious fact, yet there are numerous
314 examples in the literature confusing the relationship between faster growth rates and larger body
315 sizes. This is especially true for otolith-based growth and biochronology studies that aim to relate
316 growth to temperature and other environmental factors (Morrongiello and Thresher, 2015).
317 While an increasing number of studies explicitly consider age- or life-stage dependent growth

318 (e.g., Barrow et al., 2021; Campana et al., 2023), many still talk about growth in general,
319 independently from the age at which the growth was measured (Ong et al., 2018). When such
320 studies find ‘faster’ growth in response to increased temperature (e.g., Thresher et al., 2007) they
321 might infer, implicitly or explicitly, that the individuals in question will also become larger in
322 warmer temperatures (but see Baudron et al., 2014, in which they suggest the opposite).

323

324 However, as explained earlier, ‘faster’ growth is not necessarily incompatible with expecting
325 smaller body sizes due to warming, and faster growth is not incompatible with ‘shrinking’ of fish
326 in warmer waters (Wootton et al., 2022). This clearly illustrates the importance of standardising
327 age in comparisons. The distinction between early growth and body size at later life stages also
328 must be considered when making extrapolations from laboratory studies, where temperature
329 effects on growth and sizes are typically explored for early stages of life (Laurel et al., 2008) and
330 which are insufficient to understand the often opposite effect of elevated temperature in adult
331 fish (Morrongiello et al., 2014; but see Wootton et al., 2022 for lab study).

332 **6. The distinction between growth rate and von Bertalanffy K**

333

334 Growth is the process of increasing in size (Pütter, 1920). It can be described as the change in
335 length or weight over time (days, weeks, months, years) and can be applied at an individual
336 level (i.e., repeated measures of the same individual, such as by back calculation of length-at-
337 age from biochronologies, e.g. Huss et al., 2019), but also at the population or species level,
338 when change in length or weight is calculated from size-at-age of individuals of different ages.
339 Sometimes in fisheries or aquaculture studies growth is measured in young fish over short time
340 periods, and in such cases, it is assumed to be exponential, such that the instantaneous growth
341 can be described as the difference in log weight over a period t (Ricker, 1975). This additive
342 change in log weight is not very intuitive and therefore it is often re-expressed as ‘specific
343 growth’, which has the unit of percent increase in weight per unit time (Crane et al., 2020). Yet,
344 a more common metric to describe growth is the K parameter estimated from fitting the von
345 Bertalanffy growth function (VBGF) to size-at-age data (Box 2), because it is easily compared
346 across populations or species, and has direct use in fisheries models (Beverton and Holt, 1957;
347 Ricker, 1975). As defined above, K , originally termed the ‘growth constant’ (von Bertalanffy,
348 1938) and often referred to as the von Bertalanffy coefficient, is the rate at which L_{inf} or W_{inf} is

349 approached. It has the dimension of 'per time' (t^{-1}) only, not the dimension of growth (i.e. size t^{-1}) (Beverton and Holt, 1957; von Bertalanffy, 1957).

351

Box 2. Describing growth

The growth of fish is frequently described by the **von Bertalanffy growth function** (VBGF; von Bertalanffy, 1938), largely based on the Pütter growth model (Pütter, 1920), which for length is:

$$L_t = L_{inf} (1 - e^{-K(t-t_0)}) \quad (\text{Eq. 1})$$

where L_t is the length at age t , L_{inf} is the asymptotic length, K describes the speed at which L_{inf} is approached (dimension is time^{-1} , usually year^{-1}), while t_0 is the hypothetical age at zero length. The VBGF is often fitted to a sample of age-length (or age-weight) data from a population or a species, but it can also be used to describe individual growth (Lindmark et al., 2023).

K is often used in comparative studies (Bigman et al., 2023a, 2023b; Gislason et al., 2010; Pauly, 1980; Thorson 2017) that explore life-history and physiological trait relationships across different species. However, despite its popularity and simplicity, K can be hard to estimate accurately, and care is needed in its interpretation (Charnov, 2010). First, K in the VBGF is highly sensitive to the sufficient representation of both young and old fish, especially in species whose growth is bi-phasic (with different K values between early and late phases of ontogeny; e.g. Lester et al., 2004; Trip et al., 2014). Consequently, estimated values of K can vary wildly if sample sizes are small (see Prince et al., 2023 for further discussion). Second, accurately estimating early growth in a VBGF is statistically challenging, since the left side of the curve depends on the assumptions about size at zero age. This parameter is estimated from the data or derived from growth curve extrapolation that estimates theoretical (negative) age at zero length (t_0 in the VBGF) (Pardo et al., 2013). Third, K is correlated to the asymptotic size: a small species reaches its (small) asymptotic size faster than a large species and therefore has higher K than larger species. However, a higher K does not mean that smaller species grow faster, in terms of change in size per time.

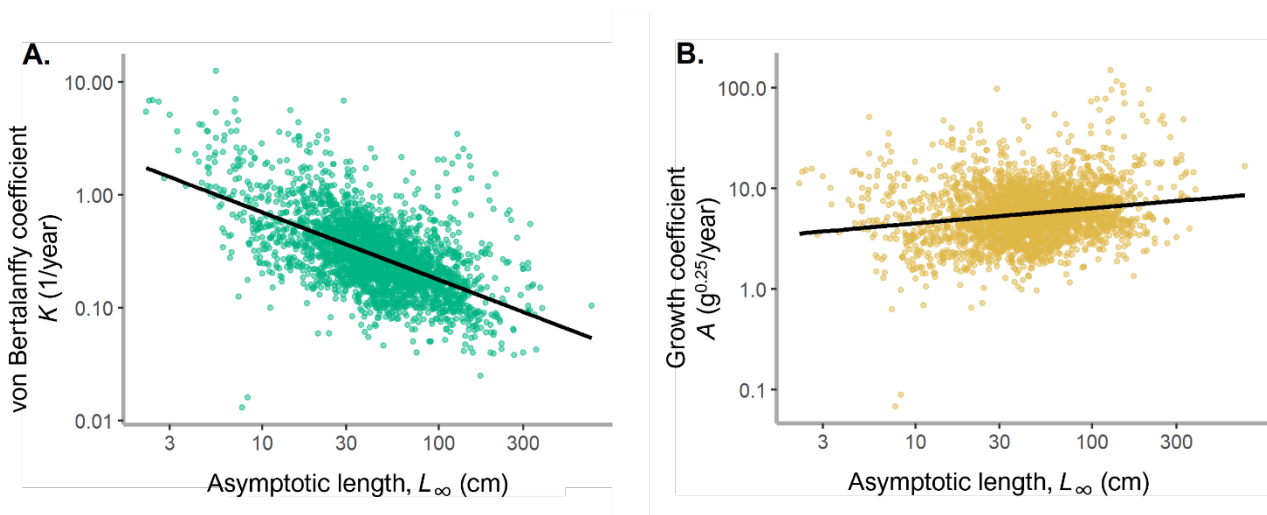
One can get around the correlation between K and L_{inf} by using the physiological formulation of the von Bertalanffy growth model

$$\underbrace{\frac{dm}{dt}}_{\text{Growth rate}} = \underbrace{A m^{2/3}}_{\text{Acquisition of weight}} - \underbrace{B m}_{\text{Loss of weight}} \quad (\text{Eq. 2})$$

The equation can be interpreted as stating that the growth rate (weight per time) is the difference between the net acquisition of weight ('anabolism') and losses to respiration, activity, and reproduction ('catabolism'). The growth coefficient A can be interpreted as the size-corrected growth rate and analysis of growth data shows that the size-corrected growth coefficient does not depend on asymptotic size (Andersen, 2020; Kearney, 2021): smaller species have (on average) similar growth rates as larger species (Fig. 4). The solution of Eq. 2 is exactly the von Bertalanffy growth function in Eq. 1 (see Andersen, 2019). The size-corrected growth coefficient A is related to K and the asymptotic weight W_∞ as: $K = AW_\infty^{-1/3}/3$ (Gallucci and Quinn, 1979). Alternatively, one can also apply a re-parametrised version of the VBGF where the correlation between K and L_{inf} is reduced (e.g., see the Gallucci and Quinn, 1979 and ; Mooij et al., 1999 parameterisations, where a new parameter ω is defined as $K \times L_{inf}$ and describes early life growth rate).

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Fig. 4. Negative correlation between L_{inf} and K across different species (A) is removed when growth rate is expressed as growth coefficient (B). Redrawn from Andersen (2019).

358 Studies exploring the impacts of temperature on fish growth range from examinations of

359 individually-resolved laboratory responses, to broad-scale macroecological comparisons across

360 space or time. Laboratory studies have often used absolute metrics, such as change in body

361 weight per time (in grams or percent, with or without body weight standardisation) (Kellogg and

362 Gift, 1983; Lindmark et al., 2022). Studies that have tested impacts of temperature on size in

363 natural populations often used VBGF coefficient K or asymptotic length estimated from spatially

364 separated populations or where warming occurred through time (Baudron et al., 2014; Lindmark

365 et al., 2023; Trip et al., 2014; van Denderen et al., 2020).

366 The two co-occurring life-history responses to warming that satisfy the definition of the TSR
367 (Atkinson, 1994) are: (i) faster initial growth and (ii) smaller size at maturity. Both responses can
368 happen when K has a high value, however, K alone can be unreliable for testing the TSR because
369 K is mathematically correlated with asymptotic size. Therefore, instead of using K alone to test
370 the TSR, we suggest that estimates of initial or early growth should be combined with
371 independent measures of size later in ontogeny (size at maturity, or asymptotic size in an
372 extension of the TSR, Wootton et al., 2022; see misconception 1, above). Likewise, measuring
373 response of maturation or asymptotic size alone is also insufficient.

374 The final three misconceptions we discuss below extend from direct measures of growth and size
375 and relate to how different temperature impacts on fish (and other ectotherm) body sizes have
376 been analysed.

377 **7. Temperature impacts on intraspecific size spectrum slopes are not necessarily the same** 378 **impacts on mean or asymptotic sizes**

379

380 When it comes to population or species-level measures of size structural demography, individual
381 size distributions provide the most information. At the community level these distributions are
382 characterised by the 'size spectrum'. The size spectrum describes the distribution of abundance
383 or biomass across the observed body sizes, and is often expressed as the log abundance of all
384 individuals within logarithmic body size classes (Trebilco et al., 2013). The size spectrum concept
385 is most commonly used at the community level, where the log-log scale abundance-size
386 relationship is often negative and linear, and shows remarkable consistency in the slope value
387 across broad aquatic realms (Heather et al., 2021; Sprules and Barth, 2016). However, size
388 spectrum slopes can also be used to describe intra-specific size distribution properties (e.g., the
389 juvenile part of the spectrum; Andersen and Beyer, 2006; Lindmark et al., 2023) and it is the intra-
390 specific application that we will refer to in this review.

391

392 According to size spectrum theory, the slope of the intraspecific size spectrum of a population is
393 generally less steep than the slope of the community size spectrum (Andersen and Beyer, 2006).
394 The slope is determined by a combination of growth rate and mortality: faster growth or lower
395 mortality leads to shallower slopes and vice versa. This means that changes in growth, even
396 extensive changes, may not necessarily change the size structure of a population if they are

397 associated with corresponding changes in mortality (e.g., Lindmark et al., 2023). For example,
398 size spectrum slopes of two perch populations that experienced an average temperature
399 difference of almost 8°C were similar, because faster growth in warmer conditions was
400 compensated for by higher mortality (Lindmark et al., 2023). It is not yet clear how temperature
401 and the TSR might affect intra-specific size spectrum slopes, because the TSR does not include
402 predictions about mortality changes. Similar to the average size or the maximum size, the
403 estimated size spectrum slope is an aggregated measure of a population's size demography that
404 is the result of a combination of physiology (growth) and ecology (predation mortality), and it is
405 also sensitive to the size ranges of individuals included in the calculations.

406

407 **8. The distinction between intra and inter-specific temperature responses**

408

409 Although this review focuses on intra-specific processes, a lot of confusion around the
410 temperature impacts on fish body sizes relates to the conflation of intra- and inter-specific
411 processes. Temperature-related body size responses at the population-level are driven by
412 changes in growth, mortality and recruitment. While community-level responses are also
413 affected by intra-specific processes, the main driver can often be changes in species abundances
414 and composition (Coghlan et al., 2024). Importantly, at the community-level, intra-specific
415 responses can reinforce or counteract each other (Martins et al., 2023). For example, a widely
416 cited modelling study by Cheung et al. (2013), which predicted a 14-24% 'shrinking' of fish from
417 2000 to 2050, states that about half of this change will be due to decreases in asymptotic sizes
418 of fish (change in growth) and another half from changes in community composition. Differences
419 between community-level and population-level responses also apply to mean (rather than
420 asymptotic or maximum) fish sizes in empirical data. Thus, mean fish length can either be larger
421 or smaller in warmer waters at the intra-specific level (Audzijonyte et al., 2020), whereas at a
422 community level mean fish length decreases by ~5% per 1 °C of warming through space (Coghlan
423 et al., 2024). Similarly, fish community size spectrum slopes have been shown to be slightly
424 steeper in warmer conditions (Arranz et al., 2019), but the extent of steepening due to warmer
425 temperature may be more nuanced compared to other drivers (e.g., fishing or pollution in macro-
426 invertebrate size spectra; Perkins, 2021; Pomeranz et al., 2022).

427

428 The same difference between community and population levels applies to the processes
429 describing growth, size-at-age, or other temperature and environmental influences. Within
430 species, populations living in warmer environments typically have lower scaling of growth
431 coefficient A (Box 2) to temperature ($Q_{10} = 1.1$, where Q_{10} is the factor by which the variable
432 increases for every 10 °C increase in temperature) compared to the scaling observed across
433 different species in warmer and cooler environments ($Q_{10} = 1.2-1.4$) (van Denderen et al., 2020).
434 Note that both of these Q_{10} values are lower than the broad scale metabolic theory predictions
435 (Brown et al., 2004). In all, cross-species comparisons of temperature impacts, and adaptations
436 to these impacts cannot be extrapolated to intra-specific levels because the mechanisms
437 operating at these scales are likely to be different (see discussion in Audzijonyte et al., 2019) and
438 they will have different implications for fisheries and ecosystem dynamics.
439

440 **9. Distinctions between spatial and temporal responses to temperature that apply to both** 441 **growth and size**

442
443 To date, many studies aiming to predict fish population or community responses to warming look
444 at growth or body size responses to temperature across spatially separated populations. Similarly,
445 the often-observed spatial patterns of decreasing adult (however defined) body sizes of
446 organisms at higher temperatures within and across species (e.g., Bergmann's Rule and James',
447 rule, respectively) (Bergmann, 1848; James, 1970; but see Riemer et al., 2018) are often cited as
448 support for predictions about climate change on fish size (Daufresne et al., 2009). This space-for-
449 time substitution may be informative, but it cannot be assumed *a priori* that the extrapolations
450 from space to time will hold, because the drivers of spatial and temporal patterns in growth and
451 body size may not be the same (Klesse et al., 2020; Perret et al., 2024). In some cases, spatial and
452 temporal comparisons of species' responses to temperature suggest a qualitative similarity, but
453 very different rates. For example, the underwater visual census data on 335 fish species around
454 the Australian continent found an overall positive and significant correlation between mean size
455 response to temperature across space and time (Audzijonyte et al., 2020). Yet, changes through
456 time were almost 10 times faster than changes across space; and, despite the overall positive
457 correlation, there were many cases where temporal changes were opposite from those observed
458 across space. Such varied responses could happen, for example, depending on how close the

459 different populations are to their thermal limits, which can determine whether warming
460 increases or decreases growth and size. Thus, while there is a positive correlation overall
461 between temperature and the growth coefficient (e.g., coefficient A in van Denderen et al., 2020),
462 warming above the thermal optimum may reduce early growth and other biological processes
463 (Brett, 1971; Englund et al., 2011). This was demonstrated in banded morwong, where positive
464 near-linear effects of temperature on growth (measured as mean otolith increment per year for
465 fish between 7 and 9 years) were found in populations from cooler regions, but negative effects
466 of warming were seen in warmer areas (Neuheimer et al., 2011). These findings show that the
467 use of spatial patterns to infer responses to warming should ideally be validated using temporal
468 data, because the effects of spatial and temporal climate variation on a trait can differ in many
469 ways: the form of the relationship (linear or concave), the sign of the relationship and the
470 magnitude. Yet, temporal data are often hard to obtain on a sufficiently long timescale and, given
471 that most growth data come from commercially important species, in many cases is also strongly
472 affected by the direct and indirect effects of fishing (Morrongiello et al., 2021, 2019).

473

474 Concluding remarks, recommendations and future directions

475

476 This review aimed to clarify some of the common confusions about growth and body size – in
477 fish, but also in other organisms with indeterminate growth. During the preparation of this
478 manuscript, it became clear that confusions and inaccuracies are extremely common, as the co-
479 authors continuously had to correct each other. We conclude with some recommendations that
480 could help to avoid further confusions and increase the impact of future studies.

481

482 1. When referring to temperature, environmental, or human impacts on fish growth or body
483 sizes, it is essential to be clear about the specific measure of size or growth used. This specific
484 measure should be clearly defined in the abstract.

485 2. It is important to make a distinction between body size measures that are largely
486 determined by growth (asymptotic or maturation size) versus the population-level processes that
487 are a result of growth and mortality (mean or maximum size, size spectrum slopes). However, we
488 note that even seemingly growth-related measures can be affected by mortality in cases where

489 mortality is size selective. This is often observed in heavily fished stocks where individuals with
490 fast growth are underrepresented in older age classes.

491 3. Asymptotic size is a good measure to characterise an outcome of an individual's,
492 population's or species' growth trajectory (ideally after accounting for size-selective mortality).
493 In contrast, maximum size in a population or species is a measure of growth and demography
494 (although not a very robust one, since it depends on sampling). Both asymptotic and maximum
495 size measures require adequate sampling to be estimated reliably, although maximum size likely
496 needs more samples. Importantly, maximum and asymptotic size should not be used
497 interchangeably.

498 4. It is important not to assume that predictions of temperature impacts observed for one
499 measure of growth or size (e.g. maturation size) will also hold for other measures (e.g. asymptotic
500 size). While there are studies showing strong correlations between some of these measures, the
501 temperature impacts on them have not necessarily been explicitly tested.

502 5. It is recommended that inter-specific or cross-species comparisons of temperature impacts
503 on growth use asymptotic size or size at a defined ontogenetic point (e.g. maturation). Estimates
504 of asymptotic size are made using adequate size-at-age data (Prince et al. 2023). Further research
505 is needed to understand how temperature and other environmental factors affect asymptotic
506 size across populations within a species. If the temperature co-variation with asymptotic size is
507 extensive and systematic, the use of asymptotic size as a species characteristic should be done
508 with caution.

509 6. When comparing growth rates across populations or species, efforts should be made to
510 account for the inter-dependence of von Bertalanffy K and L_{inf} . This can be done by using the
511 growth coefficient A (Andersen, 2019) or the growth performance index ϕ' of Pauly (2010).

512 7. When assessing temperature impacts on body sizes and growth it is essential to critically
513 assess the spatial and temporal scales at which these assessments are done and consider
514 appropriate body size or growth metrics for the questions at hand.

515 8. It is important to avoid misusing the TSR and quantitative models (e.g., Deutsch et al., 2022)
516 that predict size-at-maturity under benign conditions by applying them directly to field data
517 without taking mortality and other environmental factors encountered in field populations into
518 account. Instead, we suggest that the TSR and measured or predicted growth under no-stress
519 conditions may be useful as a reference of warming-induced growth and body size changes,
520 against which the impacts of environmental influences in natural populations can be compared.

521

522 Finally, we conclude that to more adequately assess temperature impacts on fish populations
523 and communities, understand the mechanisms underlying these impacts, and make predictions
524 about possible climate change effects, we urgently need more body size data from a large variety
525 of species and populations, especially from unfished populations, given that signals of
526 temperature and fishing are often interlinked (Audzijonyte et al., 2013; Morrongiello et al., 2019).
527 Such datasets are currently being assembled through a range of underwater surveys (diver or
528 camera based) and citizen science initiatives, and it is imperative that these datasets become
529 available and analysed in a rigorous manner with clear definitions of growth and body size
530 metrics studied.

531

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535

536 **Data availability statement**

537 This manuscript does not present any new data.

538

539 **Conflict of interest statement**

540 The authors declare not conflicts of interest.

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