Acta Ichthyologica et Piscatoria 52(2), 2022, 125–133 | DOI 10.3897/aiep.52.80093

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ACTA ICHTHYOLOGICA ET PISCATORIA

Estimating somatic growth of fishes from maximum age or maturity

Rainer FROESE[1]

1 *Helmholtz Centre for Ocean Research, GEOMAR, Kiel, Germany*

http://zoobank.org/791C8A32-9251-48E4-97DE-CB160F5C7728

Corresponding author: Rainer Froese (rfroese@geomar.de)

Academic editor: Wojciech Piasecki ♦ **Received** 4 January 2022 ♦ **Accepted** 26 April 2022 ♦ **Published** 16 May 2022

Citation: Froese R (2022) Estimating somatic growth of fishes from maximum age or maturity. Acta Ichthyologica et Piscatoria 52(2): 125–133. https://doi.org/10.3897/aiep.52.80093

Abstract

Growth in body size is a key life-history trait that has coevolved and is interlinked with maturation, maximum age, mortality, generation time, and the intrinsic rate of population growth. Growth parameters are therefore required inputs in the majority of assessment models used in conservation or fisheries management. However, because of the difficulties involved in the proper aging of individuals, growth parameters are unknown for the vast majority of species. Here, two new data-limited methods are presented to estimate somatic growth from maximum length combined with either length or age at maturation or with maximum age. A comparison with existing growth parameters of fishes (Actinopterygii and Elasmobranchii) shows that the estimates of the new methods fall within the range of established methods. The new methods apply to species with indeterminate growth, such as fishes or invertebrates, and were used here to produce the first growth parameter estimates for 110 species of fishes.

Keywords

age at first maturity, asymptotic length, maximum age, maximum length recruitment, von Bertalanffy growth equation

Introduction

The speed by which organisms increase in body size determines how fast they reach maturity and maximum size, i.e., the adult size and age range. The mean age of parents when their offspring are born defines generation time, which itself is linked to the intrinsic rate of population growth (Pianka 2000). The somatic growth rate is thus a central life-history parameter, especially in species like fishes or invertebrates which grow throughout their lives. Growth parameters are of key importance in population dynamic analyses for conservation or fisheries management (Ricker 1975). For example, the ratio (M:K) between natural mortality M and growth parameter K plays a central role in determining sustainable catch levels (Beverton and Holt 1957) or the optimum body size for capture (Froese et al. 2016).

The first-principle equation that is most widely used to estimate growth is the one proposed by von Bertalanffy (1938, 1951) building on the work of Pütter (1920). It describes the growth in body length (L) as a function of asymptotic length L_∞, a parameter K indicating how fast L_∞ is approached, and a parameter t_0 indicating the hypothetical age t at zero length, given that larvae or pups have a length larger than zero at hatching or birth, where L_t is the predicted length L at age t

$$L_t = L_\infty \left(1 - e^{-K(t - t_0)}\right) \qquad \text{[Eq 1]}$$

The hypothetical age at zero length t_0 typically has a negative value which is small compared to the maximum age. Different values of t_0 shift the growth curve along the age-axis without changing the values of L_∞ or K. For the sake of simplicity in data-limited methods, t_0 is assumed here to be zero and is omitted from the subsequent equations. Also, for easy comparison among species, length in fish is measured in centimeters and age in years, which implies that K has the unit year^{-1}. Note that the type of length, such as total length (TL), fork length (FL), standard length (SL), pre-anal length, or body width (WD) does not affect the estimate of K as long as the species grows roughly isometrically and thus changes its proportions during growth only in a minor way.

While measuring lengths in one of the above length types is straightforward in most species of fish, determining age e.g. from counting rings in hard structures such as scales, otoliths, vertebrae or spines is more demanding and prone to error. As a result, sufficiently large and reliable data sets for fitting Equation 1 [Eq 1] are missing for the majority of species (Froese and Binohlan 2003, Froese and Pauly 2021). The purpose of this study was to explore two less data-demanding methods, which use Equation 1 in a deterministic fashion, estimating growth parameters from maximum length combined with a maximum age, with length and age at maturation, or with any known length-at-age, such as the mean length of an outstanding year class.

Material and methods

Data on asymptotic length (L_∞), maximum length (L_{max}), maximum age (t_{max}), and length (L_m) and age (t_m) at first maturity were extracted from FishBase 08/2021 (Froese and Pauly 2021). Values for t_m were direct observations and not estimated from L_m and known growth parameters. Similarly, t_{max} values were based on direct observations and not derived from growth parameters. Values that had been marked as doubtful by FishBase staff were excluded from the analysis.

Solving Equation 1 for K and omitting t_0 gives Equation 2

$$K = -\frac{\ln\left(1 - \frac{L_t}{L_\infty}\right)}{t} \quad \text{[Eq 2]}$$

To estimate growth from the maximum length and maximum age, Equation 3 replaces age t with reported maximum age for a population and assumes that t_{max} is reached and reported at about 95% of L_∞ (Taylor 1958, Froese and Binohlan 2000). Following this reasoning, a proxy for asymptotic length is obtained as $L_\infty = 1.05L_{max}$ (Pauly 1984)

$$K = -\frac{\ln(1-0.95)}{t_{max}} = \frac{3.0}{t_{max}} \quad \text{[Eq 3]}$$

If several estimates of t_{max} are available for a population, e.g., as the oldest fish observed during periods of one or 5 years over the last 20–40 years, then these numbers can be used to derive a mean estimate of t_{max} with 95% confidence limits. Since the main source of uncertainty in Equation 3 is the estimate of t_{max}, its lower and upper confidence limits can be inserted in the equation to derive approximate confidence limits for K. Alternatively, plausible ranges of uncertainty can be derived by assuming that maximum age will be observed and reported in individuals with a body length between 90% and 99% of L_∞. Replacing 0.95 in Equation 3 with 0.90 and 0.99, respectively, then yields plausible ranges of K between $2.3/t_{max}$ and $4.6/t_{max}$. For example, for an observed t_{max} = 15 years, Equation 3 would predict K = 0.20. Applying the alternative rules for uncertainty gives plausible ranges of K as 0.15–0.31.

To estimate growth from length and age at maturation, Equation 4 replaces age t in Equation 2 with the age where individuals have reached sexual maturity (t_m), L_t with the corresponding length L_m, and L_∞ with $L_{max}/0.95$

$$K = -\frac{\ln\left(1 - 0.95\frac{L_m}{L_{max}}\right)}{t_m} \quad \text{[Eq 4]}$$

Similar to Equation 3, approximate 95% confidence limits of K can be obtained from observed confidence limits of t_m or L_m. Alternatively, plausible ranges of K can be obtained from the observation that in species that mature e.g., on average at 3 years of age, some mature already at two and some at four years of age. Based on this common observation, a typical uncertainty range in the estimate of t_m can be construed as $0.67t_m$–$1.33t_m$. For example, for observed values of t_m = 3 years, L_m = 40 cm and L_{max} = 110 cm, Equation 4 would predict K = 0.14. Setting t_m to 0.67*3 and 1.33*3, respectively, gives a plausible range for K of 0.11–0.21.

Equation 4 can be used more generally for any case where a combination of length and age is known, such as an unusually large year class with a strong visible peak in length-frequency plots, see the example below.

Estimates of K resulting from the new methods are shown with only two significant decimals to avoid the impression of unrealistic high precision, given that these are data-limited methods with wide ranges of uncertainty.

All data and code used in this study are available from https://oceanrep.geomar.de/id/eprint/55916.

Results

Growth estimates derived from maximum length and length and age at maturation. The MATURITY table in FishBase 08/2021 (Froese and Pauly 2021) contained 170 records with reported age and length at first maturity as well as an estimate of the corresponding maximum length in the population, for altogether 120 species of fishes (Froese and Pauly 2021). Of these, 15 species had no previous growth estimates in FishBase (Table 1). For the remainder, a comparison with the 880 existing growth estimates showed that the new estimates of K fell within the previously observed range, without obvious bias (Fig. 1).

Table 1. List of fifteen species with first estimates of growth parameters (L_∞, K), as derived from age (t_m) and length (L_m) at first maturity and maximum length (L_{max}), with indication of family, locality of the population, and type of length measurements. TL stands for total length, SL for standard length, and WD for body width. Plausible ranges of K were calculated from an assumed uncertainty range of t_m of +/– 33%. See the supplement data (https://oceanrep.geomar.de/id/eprint/55916) and the MATURITY table in FishBase (Froese and Pauly 2021) for additional information and references.

Family	Species	Locality	Sex	t_m	L_m	L_{max}	Type	L_∞	K	95% CL
Acipenseridae	*Acipenser dabryanus*	Yangtze River	F	9	106	250	TL	263	0.06	0.04–0.09
Ariidae	*Sciades herzbergii*	Ceará	F	2.5	50.8	94.2	TL	98.9	0.29	0.22–0.43
Bothidae	*Bothus constellatus*	Gulf of Tehuantepec	F	5.5	10.1	15.7	TL	16.5	0.17	0.13–0.26
Characidae	*Gymnocharacinus bergii*	Valcheta	M	1	3.7	7.5	TL	7.88	0.63	0.48–0.95
		Valcheta	F	1	3.8	7.5	TL	7.88	0.66	0.49–0.98
Cichlidae	*Chaetobranchus flavescens*	Rupununi River	F	1	17	26	TL	27.3	0.97	0.73–1.46
Clupeidae	*Nematalosa erebi*	Murray River	U	2.5	19.9	39	TL	41	0.27	0.20–0.40
Gaidropsaridae	*Ciliata septentrionalis*	Severn estuary and Bristol Channel	M	1	7.18	12.2	SL	12.8	0.82	0.62–1.23
Gobiidae	*Knipowitschia longecaudata*	Caspian, Azov, and Black Sea basins	U	0.75	2	5	TL	5.25	0.64	0.48–0.96
Mobulidae	*Mobula birostris*	Indo–Pacific	F	6	445	680	WD	714	0.16	0.12–0.24
Muraenolepididae	*Muraenolepis microps*	South Georgia	M	4	24	35	TL	36.8	0.26	0.20–0.40
Notopteridae	*Chitala chitala*	Ganga River	F	3	75.5	122	TL	128	0.30	0.22–0.44
Pentacerotidae	*Pentaceros wheeleri*	Emperor Seamount	M	6	27	44	TL	46.2	0.15	0.11–0.22
		Emperor Seamount	F	7	28	44	TL	46.2	0.13	0.10–0.20
Salmonidae	*Stenodus nelma*	Arctic Ocean	Mx	12	75	150	SL	158	0.05	0.04–0.08
Triakidae	*Mustelus griseus*	Taiwan	F	5.65	72	101	TL	106	0.20	0.15–0.30
Triakidae	*Mustelus punctulatus*	Mediterranean	F	1.95	95	190	TL	200	0.33	0.25–0.50

F = female, M = male, Mx = mixed, U = unsexed.

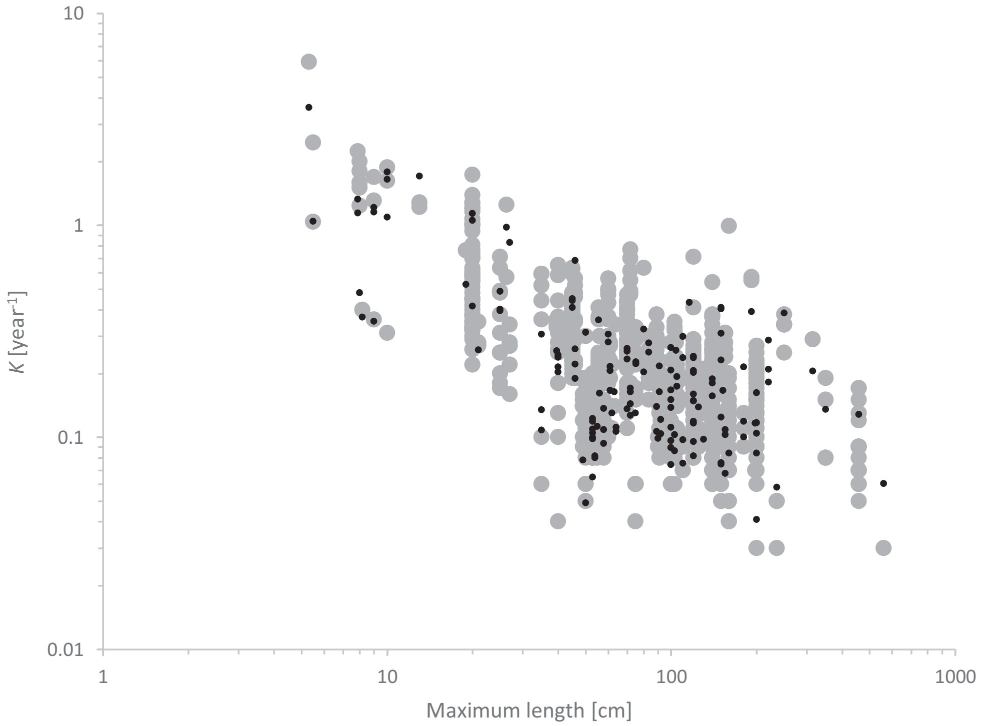

Figure 1. Comparison of 880 existing estimates of growth parameter K (grey dots) with 153 newly derived estimates from length and age at first maturity (black dots), plotted over the maximum length for 105 analyzed species, in log-log space.

The variability in Fig. 1 is wide because different species may be plotted over the same maximum length. In order to compare predictions of Equation 4 with growth estimates from accepted other methods at the species level, the six species with the highest number of independent growth estimates were selected (Fig. 2). This method of selecting species for the comparison was chosen for objectivity and in order to demonstrate the typical wide spread of growth parameter estimates. The estimates of parameter K derived from maximum age overlapped with the independent estimates in all six species.

Growth estimates derived from maximum length and maximum age. The POPCHAR table in FishBase 08/2021 contained 744 records with reported maximum age and the corresponding maximum length in the

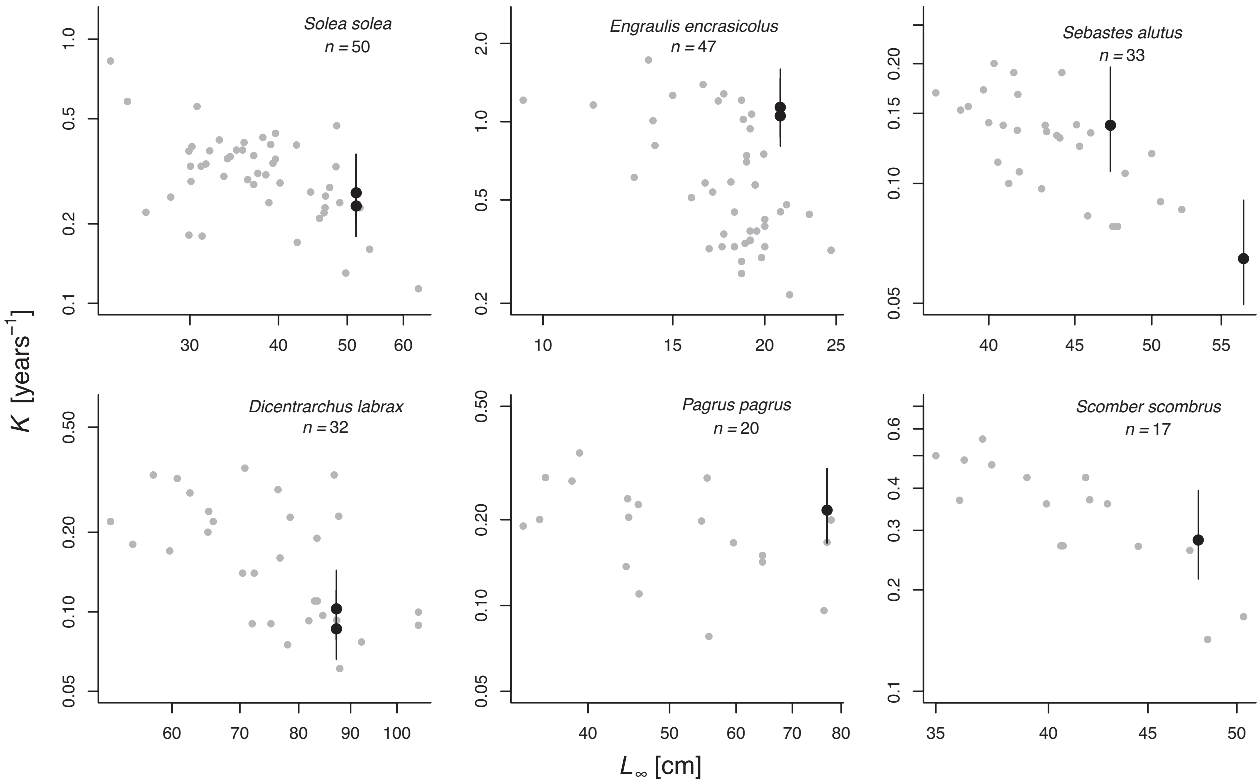

Figure 2. Comparison of growth parameters L_∞ and K derived with various data-rich methods (gray dots) and from maximum length and length and age at maturation (black dots with indication of plausible ranges), in log-log space. The double-dots in some of the species are caused by records with different length or age at maturation for the same population and the same maximum length.

population, for, altogether, 573 species (Froese and Pauly 2021). Of these, 105 species had no previous growth estimates in FishBase (Table 2). For the remainder, a comparison with the 2814 existing growth estimates in FishBase showed that the new estimates of K derived from maximum age fell within the previously observed range (Fig. 3), albeit with a slight tendency towards lower K values (see Table 3 and Discussion below).

Table 2. List of 105 species with first estimates of growth parameters (L_∞, K), as derived from maximum age (t_{max}) and maximum length (L_{max}), with indication of family, locality of the population, sex, and type of length measurements, where TL stands for total length, SL for standard length, FL for fork length, and WD for body width. The plausible ranges of K (CL) were derived from assuming that t_{max} was observed between 0.9 and 0.99 L_∞. See the supplement data (https://oceanrep.geomar.de/id/eprint/55916) and the POPCHAR table in FishBase (Froese and Pauly 2021) for additional information and references.

Family	Species	Locality	Sex	t_{max}	L_{max}	L_∞	Type	K	CL
Acipenseridae	*Acipenser sinensis*	Yangtze River (below Gezhouba Dam)	F	33	346	363.3	TL	0.09	0.07–0.14
Adrianichthyidae	*Oryzias sinensis*	East Asia	U	1	3	3.15	SL	3.00	2.30–4.60
Agonidae	*Hemitripterus bolini*	Bering Sea and Aleutian Islands	U	23	83	87.2	TL	0.13	0.10–0.20
Alepocephalidae	*Alepocephalus bairdii*	Southern Brittany	Mx	38	93	97.7	SL	0.08	0.06–0.12
Aphaniidae	*Aphanius baeticus*	Spain	U	2	3	3.15	SL	1.50	1.15–2.30
Bagridae	*Coreobagrus ichikawai*	Tagiri River	M	3	10.8	11.3	SL	1.00	0.77–1.53
Bagridae	*Coreobagrus ichikawai*	Tagiri River	F	4	9.35	9.8	SL	0.75	0.58–1.15
Bathymasteridae	*Bathymaster derjugini*	Sea of Okhotsk	U	8	18.1	19.0	TL	0.37	0.29–0.58
Bathymasteridae	*Bathymaster signatus*	N Kurils and SE Kamchatka	F	9	36	37.8	TL	0.33	0.26–0.51
Berycidae	*Centroberyx gerrardi*	Southern Australia	U	71	66	69.3	TL	0.04	0.03–0.06
Blenniidae	*Salaria fluviatilis*	Mediterranean (Europe)	U	5	13	13.7	SL	0.60	0.46–0.92
Carcharhinidae	*Carcharhinus galapagensis*	Circumtropical	F	24	370	388	TL	0.12	0.10–0.19
Carcharhinidae	*Negaprion brevirostris*	Eastern Pacific to Eastern central Atlantic	F	25	320	336	TL	0.12	0.09–0.18
Catostomidae	*Ictiobus cyprinellus*	Ontario	U	26	157	165	TL	0.12	0.09–0.18
Cebidichthyidae	*Cebidichthys violaceus*	Oregon–California	U	18	76	79.8	TL	0.17	0.13–0.26
Centrarchidae	*Ambloplites rupestris*	Ontario	U	13	43	45.2	TL	0.23	0.18–0.35
Characidae	*Astyanax mexicanus*	Tinaja cave	U	8	9	9.5	TL	0.37	0.29–0.58
Clupeidae	*Alosa killarnensis*	Lake Lough Lene	U	5	20	21	SL	0.60	0.46–0.92
Clupeidae	*Clupeonella abrau*	Lake Abrau	U	2	8	8.4	SL	1.50	1.15–2.30
Clupeidae	*Nematalosa erebi*	Lower Murray River	U	10	48	50.4	SL	0.30	0.23–0.46
Cobitidae	*Cobitis elongatoides*	Danube River	F	5	13	13.7	SL	0.60	0.46–0.92

Table continues on next page

Table 2. (Continuation)

Family	Species	Locality	Sex	t_{max}	L_{max}	L_{∞}	Type	*K*	CL
Cobitidae	*Cobitis ohridana*	Moraca River basin	F	3.5	8.3	8.7	TL	0.86	0.66–1.31
Cottidae	*Gymnocanthus herzensteini*	Primorye	F	17	42	44.1	TL	0.18	0.14–0.27
Cottidae	*Hemilepidotus jordani*	Bering Sea and Aleutian Islands	U	30	65	68.3	TL	0.10	0.08–0.15
Cyprinidae	*Barbus caninus*	Europe	U	5	25	26.3	SL	0.60	0.46–0.92
Cyprinidae	*Gymnocypris firmispinatus*	Anning River	M	9	16.3	17.1	TL	0.33	0.26–0.51
Cyprinidae	*Gymnocypris firmispinatus*	Anning River	F	13	24.2	25.4	TL	0.23	0.18–0.35
Cyprinidae	*Luciobarbus graellsii*	Spain	U	16	65	68.3	SL	0.19	0.14–0.29
Cyprinidae	*Onychostoma barbatulum*	Taiwan	U	7	26	27.3	TL	0.43	0.33–0.66
Fundulidae	*Fundulus heteroclitus*	East coast of North America	U	4	10	10.5	SL	0.75	0.58–1.15
Galaxiidae	*Galaxias olidus*	Australia: Goulburn, Torbreck, Howqua, and Taggerty rivers	U	4	13	13.7	SL	0.75	0.58–1.15
Gobiidae	*Acentrogobius pflaumii*	Swan–Canning estuary	Mx	3.9	9.6	10.1	TL	0.77	0.59–1.18
Gobiidae	*Amblygobius phalaena*	Pioneer Bay, Orpheus I.	M	1.17	10.2	10.7	TL	2.56	1.97–3.93
Gobiidae	*Amblygobius phalaena*	Pioneer Bay, Orpheus I.	F	1.17	10.5	11.0	TL	2.56	1.97–3.93
Gobiidae	*Babka gymnotrachelus*	Black, Azov, and Caspian Sea basins	U	5	16	16.8	SL	0.60	0.46–0.92
Gobiidae	*Economidichthys trichonis*	Lake Trichonis, Lysimachia	U	1.8	2.5	2.6	SL	1.66	1.28–2.56
Gobiidae	*Knipowitschia caucasica*	Eurasia	U	2	5	5.3	SL	1.50	1.15–2.30
Gobiidae	*Knipowitschia croatica*	Bosnia–Herzegovina, Croatia	U	2	4.7	4.9	SL	1.50	1.15–2.30
Gobiidae	*Knipowitschia longecaudata*	Caspian, Azov, and Black Sea basin	U	2	4	4.2	SL	1.50	1.15–2.30
Gobiidae	*Knipowitschia milleri*	Acheron River (lower stretch)	U	2	2.6	2.7	SL	1.50	1.15–2.30
Gobiidae	*Stiphodon percnopterygionus*	Okinawa Island	F	2	3.5	3.7	SL	1.50	1.15–2.30
Gobiidae	*Stiphodon percnopterygionus*	Okinawa Island	M	2	3	3.15	SL	1.50	1.15–2.30
Gobiidae	*Trimma benjamini*	Helen Reef (Hotsarihie Reef), Hatohobei State	U	0.39	2.29	2.4	SL	7.68	5.90–11.8
Gobiidae	*Valenciennea muralis*	Pioneer Bay, Orpheus I.	M	1	11.6	12.2	TL	3.00	2.30–4.60
Gobionidae	*Romanogobio albipinnatus*	Northern Caspian basin (Volga, Ural)	U	5	11.5	12.1	SL	0.60	0.46–0.92
Gobionidae	*Romanogobio belingi*	Eastern Europe	U	5	11.5	12.1	SL	0.60	0.46–0.92
Gobionidae	*Romanogobio benacensis*	Italy, Slovenia	U	4	10	10.5	SL	0.75	0.58–1.15
Gobionidae	*Romanogobio ciscaucasicus*	Caspian Sea	U	6	11	11.6	SL	0.50	0.38–0.77
Gobionidae	*Romanogobio kesslerii*	Europe	U	5	11	11.6	SL	0.60	0.46–0.92
Gobionidae	*Romanogobio tanaiticus*	Don River drainage	U	5	10	10.5	SL	0.60	0.46–0.92
Gonostomatidae	*Cyclothone braueri*	Rockall Trough, NE Atlantic (near 55°N, 12°W)	F	1.25	3.8	3.99	SL	2.40	1.84–3.68
Heptapteridae	*Pimelodella kronei*	Southeastern region of Brazil	U	15	15	15.8	TL	0.20	0.15–0.31
Hexagrammidae	*Pleurogrammus azonus*	Northern Sea of Japan	U	12	50	52.5	TL	0.25	0.19–0.38
Latridae	*Latris lineata*	Tasmania	M	29	81.5	85.6	FL	0.10	0.08–0.16
Latridae	*Latris lineata*	Tasmania	F	43	95	99.8	FL	0.07	0.05–0.11
Lestidiidae	*Lestrolepis japonica*	Kagoshima Bay	U	4	19	19.9	SL	0.75	0.58–1.15
Leuciscidae	*Anaecypris hispanica*	Guadiana drainage (Spain, Portugal)	U	3	6	6.3	SL	1.00	0.77–1.53
Leuciscidae	*Pelasgus minutus*	Europe	U	6	5	5.25	SL	0.50	0.38–0.77
Leuciscidae	*Tropidophoxinellus hellenicus*	Peloponnese	U	4	9.3	9.8	SL	0.75	0.58–1.15
Liparidae	*Liparis fabricii*	Barents Sea	U	6	21	22.1	TL	0.50	0.38–0.77
Liparidae	*Palmoliparis beckeri*	Pacific off the North Kuril Islands	U	8	42	44.1	TL	0.37	0.29–0.58
Lutjanidae	*Etelis radiosus*	Lihir Island group (seamount)	U	14	70	73.5	SL	0.21	0.16–0.33
Lutjanidae	*Paracaesio stonei*	Lihir Island group (seamount)	U	15	37	38.9	SL	0.20	0.15–0.31
Mobulidae	*Mobula birostris*	India	U	20	680	714	WD	0.15	0.12–0.23
Mobulidae	*Mobula japanica*	Punta Arenas de la Ventana (24°03′N, 109°49′W), SE Baja California	Mx	14	240	252	WD	0.21	0.16–0.33
Muraenidae	*Muraena augusti*	Northeastern Central Atlantic	Mx	17.9	90	94.5	TL	0.17	0.13–0.26
Myctophidae	*Diaphus suborbitalis*	Suruga Bay	U	2.5	6.7	7.0	SL	1.20	0.92–1.84
Myctophidae	*Diaphus theta*	South Kurile region	U	6	11.7	12.3	SL	0.50	0.38–0.77
Myctophidae	*Lampanyctus macdonaldi*	Rockall Trough, NE Atlantic (near 55°N, 12°W)	U	6	13.5	14.2	SL	0.50	0.38–0.77
Oreosomatidae	*Allocyttus niger*	Tasmanian waters	U	100	47	49.4	TL	0.03	0.023–0.046
Oreosomatidae	*Allocyttus niger*	Chatham Rise and Puysegur-Snares	U	153	45.5	47.8	TL	0.02	0.015–0.030
Oreosomatidae	*Allocyttus verrucosus*	Western coasts of Australia	U	100	42	44.1	TL	0.03	0.023–0.046
Oreosomatidae	*Neocyttus rhomboidalis*	Australia (all states)	U	100	47	49.4	TL	0.03	0.023–0.046
Pentacerotidae	*Pentaceropsis recurvirostris*	Esperance (33°45′S, 121°55′E), Western Australia	M	43	55.3	58.1	TL	0.07	0.05–0.11
Pentacerotidae	*Pentaceropsis recurvirostris*	Esperance (33°45′S, 121°55′E), Western Australia	F	55	64.5	67.7	TL	0.05	0.04–0.08
Pentanchidae	*Galeus melastomus*	Rockall Trough	M	7	64	67.2	TL	0.43	0.33–0.66
Percichthyidae	*Nannoperca australis*	Australia	U	5	8.5	8.9	TL	0.60	0.46–0.92
Percichthyidae	*Nannoperca variegata*	Australia	U	4	6.2	6.5	TL	0.75	0.58–1.15
Percichthyidae	*Percilia irwini*	Andalién and Biobío rivers basins	Mx	4	9.6	10.1	TL	0.75	0.58–1.15
Percidae	*Gymnocephalus schraetser*	Danube River drainage	U	15	25	26.3	SL	0.20	0.15–0.31
Polynemidae	*Polydactylus macrochir*	Northwestern Australia	U	20	170	178	FL	0.15	0.12–0.23
Polyprionidae	*Stereolepis gigas*	California (off Santa Cruz Island)	U	62	220	231	TL	0.05	0.04–0.07
Pomacentridae	*Stegastes rectifraenum*	Lower Baja Peninsula, Gulf of California	U	11	12	12.6	SL	0.27	0.21–0.42
Salmonidae	*Coregonus danneri*	Lake Traunsee	U	6	22	23.1	SL	0.50	0.38–0.77
Salmonidae	*Coregonus lucinensis*	Lake Breiter Luzin	U	6	16	16.8	SL	0.50	0.38–0.77
Salmonidae	*Coregonus renke*	Germany	U	7	29	30.5	SL	0.43	0.33–0.66

Table continues on next page

Table 2. (Continuation)

Family	Species	Locality	Sex	t_{max}	L_{max}	L_∞	Type	K	CL
Salmonidae	*Coregonus vandesius*	UK	U	10	20	21	SL	0.30	0.23–0.46
Salmonidae	*Salmo ferox*	British Isles	U	23	80	84	SL	0.13	0.10–0.20
Salmonidae	*Salvelinus alpinus*	Circumpolar	U	32	110	115	SL	0.09	0.07–0.14
Salmonidae	*Salvelinus gracillimus*	Lake Leynavatn, on Streymoy Island	U	8	35	36.8	SL	0.37	0.29–0.58
Salmonidae	*Salvelinus murta*	Lake Thingvalla	U	18	48	50.4	SL	0.17	0.13–0.26
Salmonidae	*Salvelinus struanensis*	Loch Rannoch and Loch Ericht	U	8	36	37.8	SL	0.37	0.29–0.58
Salmonidae	*Salvelinus thingvallensis*	Lake Thingvalla	U	17	24	25.2	SL	0.18	0.14–0.27
Salmonidae	*Salvelinus youngeri*	UK Scotland	U	9	25	26.3	SL	0.33	0.26–0.51
Schindleriidae	*Schindleria praematura*	nearshore (27°10′S, 109°20′W)	U	0.25	2.09	2.19	SL	11.98	9.20–18.4
Sciaenidae	*Cynoscion othonopterus*	Colorado River delta, Gulf of California, Sonora	Mx	8	101	106	TL	0.37	0.29–0.58
Scorpaenidae	*Scorpaena loppei*	Balearic Islands	M	5	12.8	13.4	TL	0.60	0.46–0.92
Serranidae	*Cephalopholis miniata*	Kuwait	U	26	34	35.7	TL	0.12	0.09–0.18
Serranidae	*Cephalopholis miniata*	Great Barrier Reef	U	30	47.5	49.9	TL	0.10	0.08–0.15
Serranidae	*Epinephelus bleekeri*	Kuwait	U	24	65	68.3	TL	0.12	0.10–0.19
Serranidae	*Epinephelus polylepis*	Kuwait	U	41	74	77.7	TL	0.07	0.06–0.11
Serranidae	*Plectropomus pessuliferus*	Red Sea	U	19	96	100.8	TL	0.16	0.12–0.24
Somniosidae	*Somniosus microcephalus*	Greenland	F	392	502	527	TL	0.01	0.006–0.012
Sparidae	*Calamus brachysomus*	North Peru	F	15	44	46.2	TL	0.20	0.15–0.31
Sparidae	*Calamus brachysomus*	North Peru	M	15	51	53.6	TL	0.20	0.15–0.31
Sparidae	*Sparodon durbanensis*	Tsitsikamma and Bird Is.	M	26	95	99.8	FL	0.12	0.09–0.18
Squalidae	*Squalus megalops*	Canary Islands	F	32	88	92.4	TL	0.09	0.07–0.14
Syngnathidae	*Phyllopteryx taeniolatus*	Aquarium of the Pacific, Long Beach, CA	U	3.5	38.6	40.5	SL	0.86	0.66–1.31
Syngnathidae	*Syngnathus abaster*	Eastern Atlantic	U	4	19	19.9	SL	0.75	0.58–1.15
Tincidae	*Tinca tinca*	Eurasia	U	20	60	63	SL	0.15	0.12–0.23
Triakidae	*Mustelus californicus*	Eastern Pacific	F	12	163	171	TL	0.25	0.19–0.38
Trichomycteridae	*Trichomycterus itacarambiensis*	Olhos d'Água Cave, Itacarambi, Mina Gerais	U	7	8.3	8.7	SL	0.43	0.33–0.66
Valenciidae	*Valencia hispanica*	Catalonia	M	3	6.7	7.0	TL	1.00	0.77–1.53
Valenciidae	*Valencia hispanica*	Catalonia	F	4	7.1	7.5	TL	0.75	0.58–1.15
Valenciidae	*Valencia letourneuxi*	Albania/western Greece	U	3	7	7.4	SL	1.00	0.77–1.53

F = female, M = male, Mx = mixed, U = unsexed.

The variability in Fig. 3 is wide because different species may be plotted over the same maximum length. In order to compare predictions of Equation 3 with growth estimates from accepted other methods at the species level, the six species with the highest number of independent growth estimates were selected (Fig. 4). The estimates of parameter K derived from maximum age overlapped with the independent estimates in all six species. In three species t_{max}-based estimates are also the ones with the highest estimate of L_∞, which is not a bias of the method but of data reporting, with lower estimates of maximum age being less likely to be published (see Discussion below).

Discussion

The growth parameter estimates derived with the new methods proposed in this study were applicable to a wide range of species, sizes, and habitats (Tables 1 and 2). The estimates of K derived from length and age at maturation fell within the ranges from previous studies (Figs. 1 and 2), with a median K which included the median K of previous studies for these species within its 95% confidence limits (Table 3). The estimates of K derived from maximum age also fell within the ranges from previous studies (Figs. 3 and 4) albeit with a median K which was lower (0.2 vs. 0.24) and which did not include the median K of previous studies within its 95% confidence limits (Table 3). This may be caused by a bias in (or lack of) publishing (and compilation in FishBase) of maximum ages that are less than an already published highest reported maximum age for a given species. Such underreporting (and under-compilation) of lower maximum ages may explain that the presented growth estimates derived from t_{max} apply mostly to long-lived populations with lower values of K compared to K values derived from short-lived populations. This may serve as a reminder that the quality of the results of the new methods (Equations 3 and 4) fully depends on the quality and applicability of the few input data, which should be therefore carefully researched and discussed.

Table 3. Comparison of new and previous median estimates of K, where n is the number of estimates for the same species.

Parameter	K	
	from L_m and t_m	from t_{max}
***n* new**	153	628
Median new	0.174	0.200
95% confidence limits	0.149–0.231	0.187–0.230
***n* previous**	880	2814
Median previous	0.19	0.243
95% confidence limits	0.18–0.19	0.235–0.250

If data for maturation and maximum age are available for a given population and are deemed equally reliable, then Equations 3 and 4 can be combined

$$K = \frac{\left(\frac{3.0}{t_{\max}} - \frac{\ln\left(1 - 0.95\frac{L_m}{L_{\max}}\right)}{t_m}\right)}{2} \qquad \text{[Eq 5]}$$

For example, maximum age (t_{max} = 20 years) and maturation (t_m = 6 years, L_m = 445 cm WD, L_{max} = 680 cm WD) data are available for the Giant manta *Mobula birostris* from the Indo–Pacific (Tables 1 and 2). Solving Equation 5 for these values gives K = 0.16. Deriving uncertainty from $2.3/t_{max}$ and $4.6/t_{max}$ gives a plausible range of K = 0.14–0.20, assuming that uncertainty is higher in the estimation of maximum age compared to length and age at maturation.

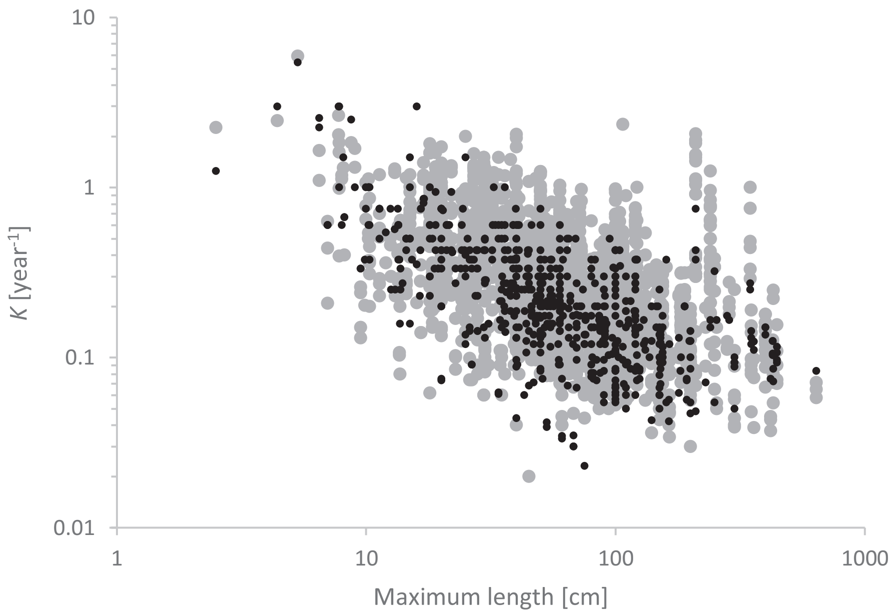

Figure 3. Comparison of 2814 existing estimates of growth parameter K (grey dots) with 628 newly derived estimates from maximum age (black dots), plotted over the known maximum length for 467 species.

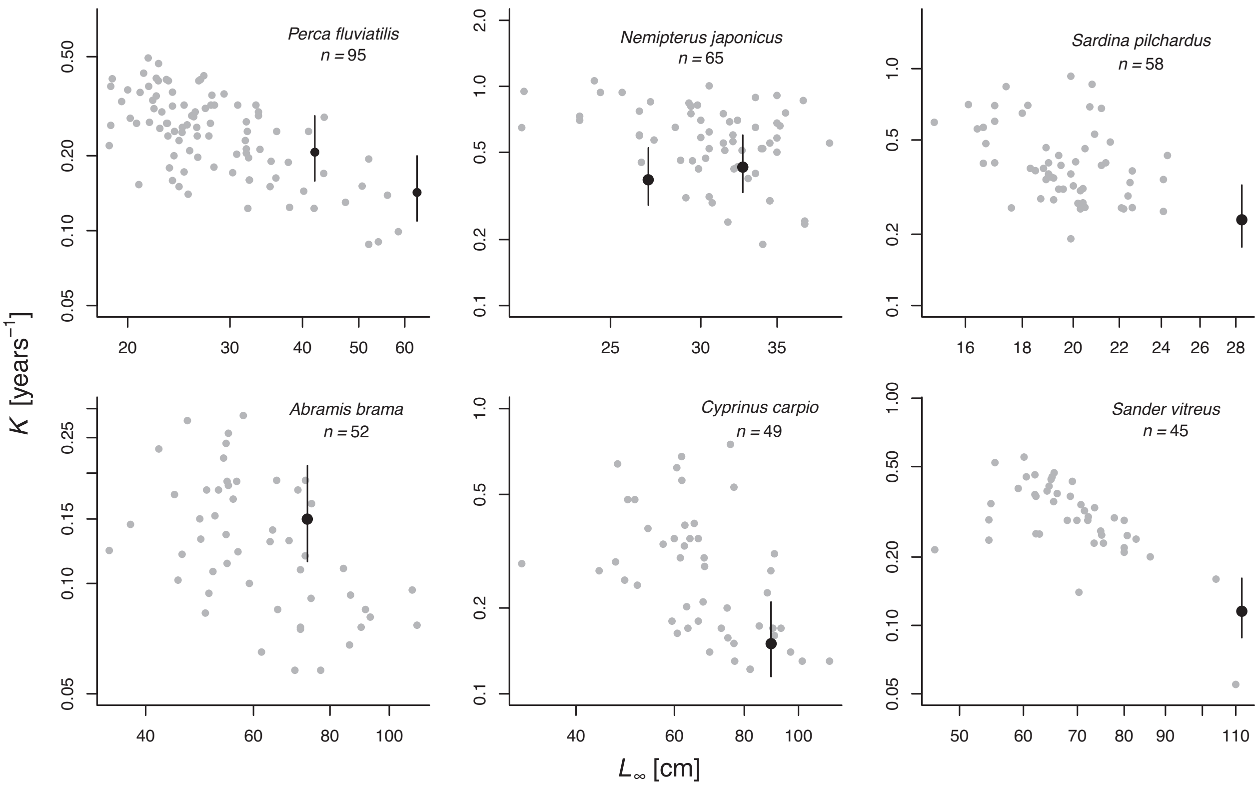

Figure 4. Comparison of growth parameters L_∞ and K derived with various data-rich methods (gray dots) and from maximum length and maximum age (black dots with indication of plausible range), in log-log space.

The method of estimating growth from the maximum length and a smaller length for which the corresponding age is known is not limited to length and age at maturation (Equation 4) but can be applied to all cases where age is known for a certain length. This also means that Equation 4 is applicable to early maturing species, such as many gadoids, as well as late maturing species, such as sharks. For example, cod (*Gadus morhua*) in the western Baltic Sea had a string of years (2014–2020) with very bad reproductive success, however, with one intermediate year (2016) where reproductive success was close to the mean value of previous years (Froese et al. 2020; ICES 2021). A plot of length frequencies from a commercial trawl fisher in Kiel Bight in spring 2021 (Froese et al. 2022) shows a clear peak of 5-year-old individuals of the 2016 year class, with a mean length of 76.6 cm length (CL = 75.6–77.6 cm, SD = 6.7, n = 186) and a maximum length of 106 cm (Fig. 5). Inserting these numbers into Equation 4 gives $K = 0.23$. Since there is little doubt about the age of the fish, the spread of lengths in the 5-year-old fish was used to derive approximate 95% confidence limits by inserting mean length plus-minus 2 SDs in Equation 4, resulting in a plausible range of K = 0.17–0.33. A proxy for L_∞ was obtained as 1.05 L_{max} = 114 cm. An independent study based on survey data from 2000–2012 gives growth parameters of the western Baltic cod as L_∞ = 119 cm and K = 0.15 (Froese and Sampang 2013, p. 31), i.e., with a similar asymptotic length but with a lower rate of increase. Given the absence of other year classes, the faster growth of the 2016 year class could result from the reduced intraspecific competition (Froese et al. 2022).

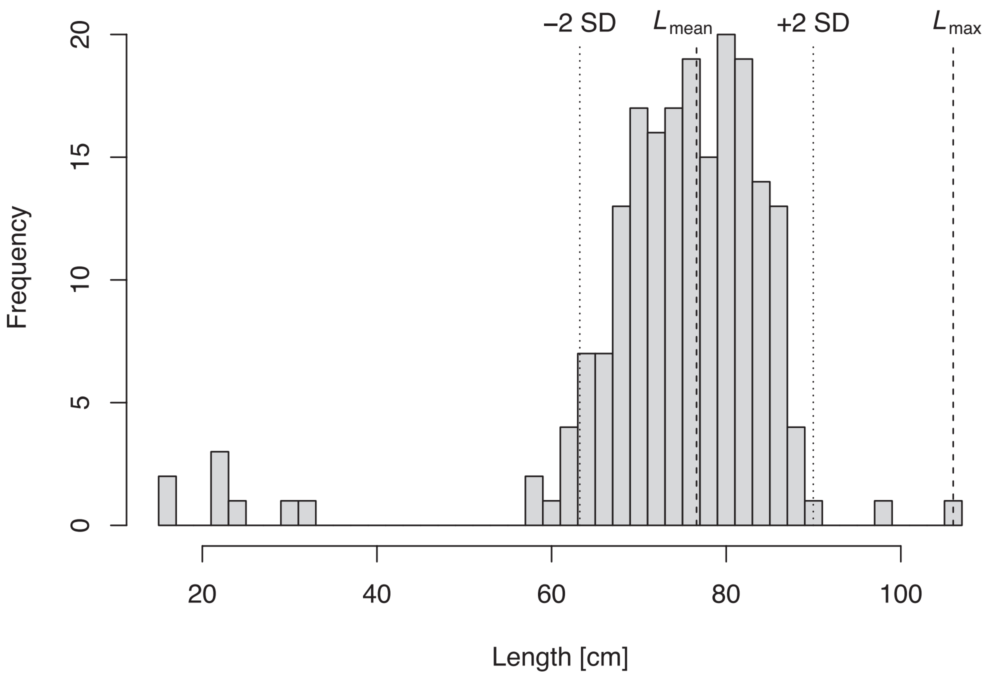

Figure 5. Length-frequencies of trawl catches of cod in Kiel Bight in spring 2021, with indication of maximum length L_{max}, mean length L_{mean} of the cohort of 2016, and two standard deviations SD around the mean.

Overall, the growth estimates derived with the new methods presented in this study appear suitable for consideration and preliminary guidance in applications for conservation or management (Figs. 1–4, Table 3). The results are flagged as preliminary because of the few data behind the equations. Thus, users are advised to collect additional size-at-age data and perform standard fits of Equation 1, where the results of the methods presented in this study can be used as the required start values for non-linear regressions or as priors in Bayesian analyses.

Journals should accept growth estimates performed with the new methods as new knowledge if they are the first for a given species. In order to facilitate the conservation and management of natural resources, FishBase (Froese and Pauly 2021) will continue to compile growth parameters, including results obtained with the new methods presented in this study.

Acknowledgment

Thanks are due to the FishBase team for compiling the data behind the Tables and Figures in this study. Thanks are also due to Daniel Pauly and Henning Winker for useful comments on the manuscript. This study was supported by the German Federal Nature Conservation Agency (BfN) with funds from the Federal Ministry of the Environment, Nature Conservation and Nuclear Safety (BMU), under grant agreement FKZ 3521532201.

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