

Article



The Relationship between Mean Length at Maturity and Maximum Length in Coral Reef Fish

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Abstract: This article proposes a mechanism that triggers first maturation and spawning in coral reef (bony) fish, which allows for predicting their length at first maturity. Thus, mean lengths at first maturity (L_m) and the corresponding maximum lengths (L_{max}) in 207 populations of 131 species of coral reef fish were assembled and used to test the hypotheses that (a) there is, in coral reef fish, a single value of a size-related parameter acting as a trigger for their maturation and eventual spawning, and (b) that this single value is statistically the same as that published previously for other bony fish. The results, based on the assembled L_m and L_{max} data and on estimates of the parameter D, which link the length of fish with the relative surface of their gills, covered 44 families and L_{max} values ranging from 1.8 to 181.6 cm and confirmed that the threshold in (a) exists. Also, we assessed (in b) that this threshold value, i.e., $L_{max}^D/L_m^D = 1.35 (\pm 0.02)$, is not statistically different from similar estimates for other groups of teleosts, notably semelparous salmonids, cichlids, sturgeons and Chinese and Turkish freshwater and marine fish. One implication is that given ocean warming and deoxygenation, coral reef fish will not only be smaller than they currently are, but also mature and spawn at smaller sizes, and thus produce fewer, smaller eggs.

Keywords: coral reef fish; GOLT; length at maturity; maximum length

Key Contribution: The main finding of this study is that in coral reef fish, the ratio of their metabolic rate at their maximum length (L_{max}) over their metabolic rate at first maturity (L_m) has a threshold value that triggers their maturation and spawning. This value is the same as in other groups of teleosts. This suggests that with ocean warming and deoxygenation, coral reef fish will mature and spawn at smaller sizes, leading to fewer and smaller eggs being produced.

1. Introduction

The age and, particularly, the size when fish mature are important parameters of their life history and are important for fisheries management [1,2]. Compared to mammals and birds, fish mature at much smaller lengths (L_m) than the maximum lengths reached in the population to which they belong (L_{max}), a feature even more pronounced when one deals with weight (W), where $W_m \ll W_{max}$ [3,4].

This "early maturation" of fish may have been the reason why ichthyologists and fisheries biologists have believed that the "energy" that was previously used in growth is, once maturity is reached, transferred to gonad development, slowing down their growth all the way until it ceases [5–7]. However, this belief, which has undoubtedly been reinforced by the perception of a transition in length growth curves, from fast to slow growth following first maturity (Figure 1a), cannot be upheld when growth curves in weight are considered (Figure 1b).

The notion that it is reproduction that slows down the growth of fish, which may be referred to as the "reproductive load hypothesis", is also refuted (i) by every lone goldfish in a bowl, whose growth ceases at some point although they have never reproduced, (ii) by



Citation: Chu, E.; Pauly, D. The Relationship between Mean Length at Maturity and Maximum Length in Coral Reef Fish. *Fishes* **2024**, *9*, 130. https://doi.org/10.3390/ fishes9040130

Academic Editor: Steven Saul

Received: 15 March 2024 Revised: 6 April 2024 Accepted: 7 April 2024 Published: 9 April 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). the fact that in 80% of fish species, it is the female who grow to larger sizes, although they have a bigger reproductive effort, and (iii) by the fact that sterile triploid fish do not exhibit higher growth rates than their fertile and diploid conspecifics [8]. There are other reasons why the "reproductive load hypothesis" is untenable [3,4], and the time has come to consider an alternative.



Figure 1. Two versions of the effect of reproduction on fish growth. (a) Representation of the "Reproductive Drain Hypothesis" (RDH), i.e., the notion that reaching the size at first maturity causes previously "linear" growth (line 1) to decline due to "energy" previously used for somatic growth being transferred to the elaboration of gonads, with the dotted line 2 implying a small, and line 3 a strong, transfer of "energy" (modified from Figure 2 in Lester et al. [9]). (b) When growth in weight is considered, the weight at first maturity (W_m) in most species of fish is reached at a size where growth is accelerating, i.e., well below the weight at which the maximum growth rate is attained (at W_i), as illustrated for yellowbelly threadfin bream (*Nemipterus bathybius*), based on data in Li et al. [10]. This is incompatible with the RDH.

The hypothesis proposed by Pauly [11], based on 34 species and 56 populations of marine bony fish, to replace the 'reproductive load hypothesis' has since been shown to apply to a vast number of other species [12–16].

Here, two hypotheses based on Pauly [11] are tested for 131 species of coral reef fish: (a) that there is, in coral reef fish, a single value of a size-related parameter acting as a trigger for their maturation and eventual spawning, and (b) that this single value is statistically the same as that published previously for bony fish.

The underlying growth model considered here was proposed by Pütter [17], and has the form

$$dW/dt = HW^d - kW \tag{1}$$

where dW/dt is the rate of growth, HW^d is the rate of protein synthesis, which is dependent on the oxygen supplied by the gills, and kW is the spontaneous denaturation rate of protein, a process requiring no oxygen, but which removes "working" proteins from the bodies of fish, and which, therefore, requires these proteins to be resynthesized [18,19]. Important here is that the parameter d in HW^d is related to the gill surface area (S, and hence oxygen supply) through a relationship is of the form $S \propto W^d$ (or respiration $\propto W^d$), with d < 1.

The parameter d < 1 implies that, as weight increases, kW will increase faster than HW^d, and that, when the rate of protein synthesis equals the rate of protein denaturation, growth ceases (at W_{max}). The overwhelming majority of bony fish (i.e., excluding those breathing air) have d ranging between 0.6 and 0.9 [20,21], but always less than 1 [22,23].

It is commonly accepted that fish start maturing when environmental stimuli "trigger" the hormonal cascade that leads to maturation and spawning [24]. However, this does not explain the fact that long-lived fish, despite experiencing—as juveniles—multiple spawning seasons and, thus, being exposed to the same environmental stimuli, do not actually start spawning until later in life, when a critical size is reached [23].

Therefore, a size-related internal readiness event ought to occur before any external stimuli and their triggering effect are perceived. The hypothesis proposed by Pauly [11] is that this internal readiness is established, in an individual fish, when its metabolic rate (Q_m) relative to its (maintenance) metabolic rate (Q_{maint}) decreases below a critical level (Q_m/Q_{maint}) . It is this readiness that causes the fish to start responding to the external triggers [23].

Pauly [11] demonstrated that L_{max}^{D} vs. L_{m}^{D} , with D = 3(1 - d), is algebraically equivalent to Q_{m} vs. Q_{maint} and, based on a variety of marine fish species, that the critical level (Q_{m}/Q_{maint}) is 1.36 (95% C.I. 1.22–1.53). This estimate was confirmed by studies that produced estimates not significantly different from 1.36, pertaining to 3 species and 51 populations of semelparous freshwater salmonids [12]; 7 species and 41 populations of cichlids [13]; 96 species and 24 populations of marine and freshwater fish from Chinese waters [14]; 22 species of sturgeons [15]; and 57 species and 120 populations of marine and freshwater fish from Turkish waters [16].

The ubiquity of this ratio suggests that this is a trait that has been conserved through millions of years of evolution. Here, we test this ratio on 207 populations in 131 coral reef fish species.

2. Materials and Methods

The maximum length (L_{max} ; fork length; in cm) and mean length at first maturity (L_m ; fork length; in cm) of coral reef fish from various geographical locations were collected from the published literature on dioecious fish, i.e., hermaphroditic species—when known as such—were excluded. Care was taken to assemble data that (i) covered most families of coral reef fish (ii) originating from the Atlantic, Indian and Pacific Oceans, and the waters of both economically developed and developing countries, and (iii) which spanned a wide range of sizes. In total, 207 pairs were assembled and used for analysis. In cases where only the asymptotic length (L_{inf}) was available, L_{inf} was multiplied by 0.95 to obtain an approximate value of L_{max} [25].

The L_{max} values were then converted into W_{max} estimates using the parameters (a, b) of the length–weight relationship (LWR) obtained from FishBase (www.fishbase.org) in the form of $W = a \cdot L^b$. Length–weight relationships from the same locality were used when available. In cases where several LWRs were available (e.g., in *Acanthurus chirurgus*) or in cases where no LWRs were available for the species in question, the Bayesian estimates of a and b from FishBase were used, which account for seasonal variations and other sources of uncertainly in the LWR [26]. Also, note that the precision of the a and b estimates of the LWR had a minimal effect on the consideration that follows.

We used the empirical equation

$$d = 0.674 + 0.0357 \cdot \log(W_{\text{max}}) \tag{2}$$

Based on estimates of d from gill surface area and respiratory studies in 27 populations of 24 species of teleost fish ranging from guppies to tuna [18,27], we estimated d values with W_{max} in g; then, D was computed from D = 3(1 - d) to simplify things.

Table 1 presents the compiled life history traits and the resulting L_{max}^{D} and L_m^{D} values for the 207 coral reef cases that were assembled for this study. The mean ratio L_{max}^{D} vs. L_m^{D} was estimated as the slope of a regression of L_{max}^{D}

The mean ratio L_{max}^D vs. L_m^D was estimated as the slope of a regression of L_{max}^D vs. L_m^D , along with its 95% confidence interval (C.I.), by running a Bayesian regression model with the intercept forced at zero using the *brm* function in the *brms* R package in R Statistical Software (v4.3.1, [28,29]).

To test for the effect of phylogeny on the estimated value, the effect of phylogenetic biases was accounted for by associating the mean L_{max}^{D} and L_m^{D} of each species with the full phylogeny tree obtained from the *Fish Tree of Life* through the R package *fishtree* [30]. A number of species (n = 131 - 11 = 120) that were not available in the *Fish Tree of Life* were removed from further analysis. Using the *brm* function [29], we re-estimated the slope with and without the phylogenetic component.

Comparing the results of the regression models with and without the phylogenetic component should allow for testing whether the inclusion of shared evolutionary history between species is an important factor to consider in the relationship between L_{max}^{D} and L_{m}^{D} . Although the model with the phylogenetic component requires a Bayesian framework, it is comparable to the widely used phylogenetic generalized least squares regression [29]. Furthermore, by employing Bayesian methods to estimate these models, we are provided

with the advantage of generating a distribution of the slopes (i.e., a posterior distribution), which enables better comparison among slope estimates.

3. Results

In total, 207 L_{max} and L_m data pairs accounting for 131 species from 44 different families were collected. Out of the 131 species in the dataset of this study, 11 species did not have resolved phylogenetic positions on the *Fish Tree of Life*, leaving 120 species to be further analyzed separately with and without phylogeny taken into consideration.

Considering all L_{max}^{D} vs. L_m^{D} data pairs, the resulting slope was $L_{max}^{D} = 1.35 \cdot L_m^{D} \cdot (\pm 0.02)$. For species that were on the *Fish Tree of Life*, but without phylogeny, the result was similar, with $L_{max}^{D} = 1.34 \cdot L_m^{D} \cdot (\pm 0.03)$ (Figure 2a, Table 1). When phylogeny was considered, the resulting slope was $L_{max}^{D} = 1.20 \cdot L_m^{D} \cdot (\pm 0.11)$, i.e., not statistically different, but with the mean exhibiting a bias that is discussed below (Figure 2b, Table 1).



Figure 2. Plot of L_{max}^{D} vs. L_m^{D} for (**a**) all 207 cases; (**b**) 120 species on the *Fish Tree of Life* with phylogenetic affinities considered. Shaded area indicates the 95% confidence interval of slope.

Table 1. Comparison of estimated coefficients and their 95% confidence interval for different subsets in the relationship between length at first maturity and maximum length.

Dataset	Ν	Slope (95% C.I.)
All cases	207	1.35 (1.33–1.37)
Species on <i>FishTree</i> with phylogeny considered	120	1.20 (1.09–1.31)
Species on <i>FishTree</i> without phylogeny considered	120	1.34 (1.31–1.37)

Thus, L_m in coral reef fish can be estimated from $L_m = L_{max}/1.35^{1/D}$, with the D value estimated from D = 3(1 – d) and d from Equation (2). As for its C.I., it can be estimated by using the standard error of 1.35, i.e., ± 0.02 . Note, however, that the uncertainty in L_m values obtained by this relationship is likely to be an underestimate, because, while it accounts for the uncertainty in the 1.35 ratio, it does not account for the uncertainly in L_{max} and D.

4. Discussion

As was the case with previous tests, this study generated results compatible with the two-part hypotheses of Pauly [11] that in coral fish (i) the same relative individual size induces a readiness to perceive environmental stimuli that trigger maturation and spawning and (ii) that this relative size is not significantly different from $L_m = L_{max}/1.35^{1/D}$.

More precisely, the slope of the plot of L_{max}^{D} vs. L_m^{D} in Figure 2a (=1.35; 95% C.I. = 1.33–1.37) overlaps with confidence intervals reported in previous contributions dealing with other bony fish [11–16], implying that the slope estimates are not statistically different.

When phylogeny is considered (Figure 2b), the change in slope is similar to what was observed by Warren [31] for cartilaginous species, i.e., that the correlation was weak, with a wide confidence interval, which is apparently a common result when including phylogenetic signals into analyses such as ours [32,33]. While some authors have suggested that statistical analyses without phylogenetic elements are "flawed" or "biased" [32], it has also been demonstrated that "poor statistical performances" will be the result when

phylogenetic methods based on incorrect assumptions are applied to regression models [34]. Our coral reef fish dataset is phylogenetically extremely diverse, which suggests that the consideration of phylogeny in our analysis may not only be superfluous, but also result in misleading results [32]. Therefore, we are focusing our remaining discussion solely on the results derived from the data without considering phylogeny, as these are more likely to provide a reliable basis for our conclusion.

The estimated critical threshold of the L_{max}^{D} vs. L_{m}^{D} ratio (1.35) varies slightly between populations and species because it is a heuristic [35] used by individual fish to determine when to start perceiving the external stimuli that make them start their maturation process [23]. As such, this heuristic can generate predictions (i.e., values of L_{m}) that are too low (thus leading to an egg production that is lower than would have been possible by allowing more growth before first maturity) or too high (thus exposing the individual to an elevated risk of being predated upon before having spawned at least once). This explains some of the differences between the lines and the dots in Figure 2a,b, the rest of these differences being mostly caused by imprecisions in the estimation of L_m and L_{max} .

What this study establishes, however, is that coral reef (bony) fish, for all the specificities associated with the singular ecosystems within which they evolved, initiate their maturation and reproduction under the same respiratory constraints as other teleosts. Notably, our results add to the evidence against the "Reproductive Drain Hypothesis", and in favor of the alternative hypothesis as presented in Pauly and Liang [4]; see also refs. [11–16]. Our results, thus, also suggest that generalizations concerning other aspects of the biology of coral reef fish, e.g., their respiratory physiology, would also benefit from being compared with the respiratory physiology of well-studied temperate fish, including freshwater species, rather than being a priori assumed to be different from other fish.

Some studies have shown that reef-associated fish have evolved a relatively high hypoxia tolerance, probably due to the fact that coral reefs go through daily cycles of oxygen levels [36–38]. However, the above considerations lead one to predict that the increased stress of ocean deoxygenation and increased temperatures [39] will not only lead to smaller maximum sizes in coral reef fish, but also to smaller sizes at first maturity, generally associated with fewer and smaller eggs [40] and, thus, with reduced fitness.

5. Conclusions

The Gill Oxygen Limitation Theory (GOLT) as proposed by Pauly [11] suggests that the triggering of maturation in fish occurs when the growth-induced reduction in gill surface area relative to body weight (and hence oxygen supply) reaches a critical level. This study confirms that this triggering effect also occurs in coral reef fish and that its level is the same as in other fish populations. Understanding the size and age of maturity of fish is an important aspect of effective fisheries management. The results of this study suggest that with increasing temperature and deoxygenation, coral reef fish will mature at smaller sizes and, as a result, will produce smaller eggs. These changes will influence the factors that must be considered in the management of coral reef fisheries.

Author Contributions: Conceptualization, D.P.; Data curation, E.C.; Formal analysis, E.C.; Investigation, E.C.; Methodology, E.C. and D.P.; Resources, E.C.; Software, E.C.; Supervision, D.P.; Validation, E.C. and D.P.; Visualization, E.C. and D.P.; Writing—original draft, E.C.; Writing—review and editing, D.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: The research that we have done in our manuscript does not involve direct research on humans or animals. The data we used was assembled by compiling the results from various published literature sources. Therefore, the requirement for ethical committee approval does not apply to our manuscript.

Data Availability Statement: Data are contained within the article and Appendix A.

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table 1. Assembled data on reef-associated species for the analysis of the relationship between length at first maturity (L_m) and maximum length (L_{max}) , arranged alphabetically by family and by species names. Lengths are in fork lengths. L_{max} values in brackets were estimated from L_{inf} using $L_{max} = 0.95 \times L_{inf}$. W_{max} estimated from L_{max} using length–weight relationship coefficients from FishBase. (F = female; M = male; U = unsexed).

No.	Family	Species	Location	Sex	L _{max} (cm)	L _m (cm)	W _{max} (g)	D	L _{max} D	L_m^D	Reference
1	Acanthuridae	Acanthurus chirurgus	Pedro Bank, Jamaica	М	35.0	17.0	978.3	0.66	10.33	6.43	[41]
2	Acanthuridae	Acanthurus lineatus	Tutuila Isl. Amer.	U	28.9	18.0	670.2	0.67	9.66	7.02	[42]
3	Acanthuridae	Acanthurus lineatus	Pohnpei State, Micronesia	F	20.5	16.8	250.3	0.72	8.81	7.63	[43]
4	Acanthuridae	Acanthurus nigricauda	Pohnpei State, Micronesia	F	22.6	18.4	311.2	0.71	9.15	7.91	[43]
5	Acanthuridae	Acanthurus nigrofuscus	Coil reef, Northern Queensland	U	15.5	10.5	85.7	0.77	8.26	6.12	[44]
6	Acanthuridae	Acanthurus nigrofuscus	Yankee reef, N. Queensland	U	17.9	10.5	108.7	0.76	8.95	5.96	[44]
7	Acanthuridae	Acanthurus triostegus	Lakshadweep lagoons, India	U	17.5	7.3	154.3	0.74	8.36	4.38	[45]
8	Acanthuridae	Naso lituratus	Terengganu, Malaysia	U	38.1	19.9	1331.2	0.64	10.36	6.82	[46]
9	Albulidae	Albula vulpes	Florida Keys, US	F	70.0	48.8	5534.2	0.58	11.56	9.39	[47]
10	Albulidae	Albula vulpes	Florida Keys, US	Μ	70.2	41.8	5584.8	0.58	11.56	8.57	[47]
11	Apogonidae	Cheilodipterus artus	Terengganu, Malaysia	U	17.7	11.2	112.6	0.76	8.80	6.21	[46]
12	Apogonidae	Cheilodipterus macrodon	Terengganu, Malaysia	U	23.6	15.1	306.8	0.71	9.46	6.89	[46]
13	Apogonidae	Cheilodipterus quinquelineatus	Terengganu, Malaysia	U	11.9	8.2	26.8	0.82	7.69	5.68	[46]
14	Apogonidae	Ostorhinchus compressus	Terengganu, Malaysia	U	11.1	7.4	24.2	0.83	7.34	5.24	[46]
15	Apogonidae	Pterapogon kauderni	Banggai Archipelago	U	7.6	4.9	10.4	0.87	5.79	3.99	[48]
16	Balistidae	Balistapus undulatus	Kavieng, PNG	F	20.2	15.7	217.6	0.73	8.89	7.40	[49]
17	Balistidae	Balistes capriscus	Ghana	F	34.0	14.5	679.5	0.67	10.76	6.06	[50,51]
18	Balistidae	Balistes vetula	Pedro Bank, Jamaica	F	39.0	23.5	1936.2	0.62	9.87	7.19	[52]
19	Balistidae	Balistes vetula	Pedro Bank, Jamaica	Μ	44.0	26.5	2738.9	0.61	10.01	7.35	[52]
20	Belonidae	Tylosurus acus	Suez Canal, Egypt	Μ	74.5	45.9	727.3	0.67	18.00	13.02	[53]
21	Belonidae	Tylosurus acus	Suez Canal, Egypt	F	74.5	45.3	727.3	0.67	18.00	12.91	[53]
22	Belonidae	Tylosurus crocodilus	Suez Canal, Egypt	Μ	94.4	50.1	1759.7	0.63	17.51	11.75	[53]
23	Belonidae	Tylosurus crocodilus	Suez Canal, Egypt	F	94.4	49.5	1759.7	0.63	17.51	11.66	[53]
24	Carangidae	Alepes djedaba	Kerala, India	U	(26.2)	16.0	339.0	0.71	10.03	7.08	[54]
25	Carangidae	Alepes kleinii	SW Coast, India	U	(14.2)	11.3	58.9	0.79	8.09	6.75	[54]
26	Carangidae	Atule mate	Kerala, India	U	(29.0)	15.4	360.9	0.70	10.68	6.85	[54]
27	Carangidae	Carangoides bajad	Shathleen, Egypt	U	56.4	34.8	2970.5	0.61	11.47	8.56	[55]
28	Carangidae	Carangoides bajad	Coast of Abu Dhabi, UAE	U	(38.4)	24.7	697.7	0.67	11.62	8.64	[56]
29	Carangidae	Carangoides equula	Northern South China Sea	U	(28.1)	18.7	513.0	0.69	9.88	7.48	[57]
30	Carangidae	Caranx heberi	South Africa	U	100.0	50.0	19,887.8	0.52	10.79	7.54	[58,59]

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No.	Family	Species	Location	Sex	L _{max} (cm)	L _m (cm)	W _{max} (g)	D	L _{max} D	L _m D	Reference
31	Carangidae	Caranx ignobilis	Northwestern Islands, Hawaii	U	162.6	56.0	83,360.9	0.45	9.87	6.12	[60]
32	Carangidae	Caranx melampygus	Northwestern Islands, Hawaii	U	70.8	32.7	10,551.0	0.55	10.23	6.71	[60]
33	Carangidae	Caranx melampygus	Shathleen, Egypt	U	73.9	44.3	652.8	0.68	18.30	12.96	[55]
34	Carangidae	Caranx sexfasciatus	South Africa	U	80.0	50.0	9456.4	0.55	11.19	8.64	[58,59]
35	Carangidae	Decapterus macrosoma	Java Sea, Indonesia	М	20.1	13.7	75.6	0.78	10.27	7.61	[61,62]
36	Carangidae	Decapterus macrosoma	Java Sea, Indonesia	F	20.1	14.3	75.6	0.78	10.27	7.88	[61,62]
37	Carangidae	Decapterus maruadsi	East China Sea	U	20.8	17.5	133.1	0.75	9.74	8.55	[63,64]
38	Carangidae	Decapterus maruadsi	Gulf of Tonkin/Beibu Gulf	U	24.2	17.1	100.1	0.76	11.38	8.74	[65]
39	Carangidae	Decapterus punctatus	South Atlantic Bight	U	21.0	11.0	125.3	0.75	9.88	6.08	[66,67]
40	Carangidae	Elagatis bipinnulata	Pernambuco, Brazil	F	97.0	64.6	7563.3	0.56	13.05	10.39	[68]
41	Carangidae	Megalaspis cordyla	SW coast, India	U	(33.6)	22.5	502.2	0.69	11.22	8.50	[54]
42	Carangidae	Megalaspis cordyla	East Coast, India	U	(35.0)	22.5	517.0	0.69	11.47	8.46	[54]
43	Carangidae	Megalaspis cordyla	NW Coast India	U	(44.8)	22.5	837.5	0.66	12.48	7.89	[54]
44	Carangidae	Parastromateus niger	Taiwan Strait, Taiwan	U	30.5	19.1	1131.1	0.65	9.22	6.80	[69]
45	Carangidae	Scomberoides commersonnianus	Weipa region, Queensland, Australia	М	(108.3)	38.5	11,888.7	0.54	12.58	7.19	[70]
46	Carangidae	Scomberoides commersonnianus	Weipa region, Queensland, Australia	F	(122.6)	63.5	16,788.9	0.52	12.45	8.82	[70]
47	Carangidae	Selar crumenophthalmus	Caribbean coast, Colombia	U	(27.8)	19.6	342.3	0.71	10.45	8.18	[71]
48	Carangidae	Selaroides leptolepis	Tamil Nadu/Pondicherry, India	U	(17.0)	8.9	69.0	0.78	9.12	5.53	[54]
49	Carangidae	Selaroides leptolepis	Inner Gulf of Thailand	U	(16.8)	8.9	80.4	0.77	8.87	5.44	[72]
50	Carangidae	Seriola dumerili	Pelagie Islands, Italy	F	157.2	114.3	43,955.9	0.48	11.31	9.70	[73]
51	Carangidae	Seriola dumerili	Pelagie Islands, Italy	М	157.2	118.4	43,009.6	0.48	11.37	9.92	[73]
52	Carangidae	Trachinotus falcatus	Florida Keys/Tampa Bay, US	Μ	85.5	48.6	13,816.4	0.53	10.73	7.94	[74]
53	Carangidae	Trachinotus falcatus	Florida Keys/Tampa Bay, US	F	91.6	54.7	16,760.5	0.52	10.69	8.16	[74]
54	Carangidae	Trachurus lathami	Southern region, Brazil	U	21.4	11.8	118.8	0.75	10.10	6.43	[75]
55	Centriscidae	Centriscus scutatus	Terengganu, Malaysia	U	15.0	10.0	4.2	0.91	11.78	8.14	[46]
56	Chaenopsidae	Acanthemblemaria paula	Carrie Bow Cay, Belize	U	2.0	1.3	0.0	1.12	2.17	1.31	[76]
57	Chaetodontidae	Chaetodon auriga	Lakshadweep lagoons, India	U	14.9	13.0	86.3	0.77	8.00	7.20	[45]
58	Dorosomatidae	Amblygaster sirm	Lagoons, New Caledonia	U	21.0	14.6	71.3	0.78	10.72	8.06	[77]
59	Dorosomatidae	Herklötsichthys quadrimaculatus	Seychelles	U	12.8	10.1	31.2	0.82	8.03	6.62	[78]
60	Dorosomatidae	Opisthonema oglinum	Ceará, Brazil	М	17.0	11.0	69.3	0.78	9.12	6.49	[79,80]

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No.	Family	Species	Location	Sex	L _{max} (cm)	L _m (cm)	W _{max} (g)	D	L _{max} D	L _m D	Reference
61	Dorosomatidae	Opisthonema oglinum	Ceará, Brazil	F	17.0	11.5	69.3	0.78	9.12	6.72	[79,80]
62	Dorosomatidae	Opisthonema oglinum	Pernambuco, Brazil	U	22.4	12.5	126.4	0.75	10.35	6.69	[81]
63	Dorosomatidae	Sardinella albella	Mandapam, India	U	(10.9)	7.8	16.7	0.85	7.56	5.67	[82]
64	Engraulidae	Encrasicholina devisi	Ysabel Passage, PNG	U	(6.2)	3.6	1.9	0.95	5.67	3.40	[83]
65	Engraulidae	Encrasicholina devisi	Karnataka, India	U	9.6	6.0	5.3	0.90	7.64	5.04	[84]
66	Engraulidae	Encrasicholina heteroloba	Singapore Strait	U	(8.9)	5.3	7.4	0.88	6.92	4.36	[85]
67	Engraulidae	Stolephorus insularis	Singapore Strait	U	(10.0)	5.3	8.1	0.88	7.56	4.33	[85]
68	Fistulariidae	Fistularia commersonii	Mediterranean Sea, Lebanon	F	113.0	65.4	1969.1	0.62	19.12	13.59	[86]
69	Fistulariidae	Fistularia commersonii	Mediterranean Sea, Lebanon	М	100.0	54.7	1368.0	0.64	19.16	13.01	[86]
70	Gerreidae	Gerres filamentosus	Manila Bay, Philippines	Μ	14.3	8.4	50.9	0.79	8.25	5.43	[87]
71	Gerreidae	Gerres filamentosus	Manila Bay, Philippines	F	12.7	7.9	35.6	0.81	7.84	5.35	[87]
72	Gerreidae	Gerres longirostris	Southern Arabian Gulf	М	(17.9)	16.3	1680.6	0.63	6.18	5.83	[88]
73	Gerreidae	Gerres longirostris	Southern Arabian Gulf	F	(20.1)	20.6	2404.1	0.61	6.34	6.43	[88]
74	Gobiidae	Eviota melasma	Lizard Island, Australia	Μ	2.7	1.1	0.1	1.07	2.91	1.10	[89]
75	Gobiidae	Eviota melasma	Lizard Island, Australia	F	2.7	1.2	0.1	1.07	2.91	1.16	[89]
76	Gobiidae	Eviota queenslandica	Lizard Island, Australia	М	2.6	1.3	0.1	1.08	2.77	1.34	[89]
77	Gobiidae	Eviota queenslandica	Lizard Island, Australia	F	2.6	1.4	0.1	1.08	2.77	1.43	[89]
78	Gobiidae	Eviota sigillata	Lizard Island, Australia	Μ	1.8	1.1	0.0036	1.13	1.94	1.13	[89]
79	Gobiidae	Eviota sigillata	Lizard Island, Australia	F	1.8	1.1	0.0036	1.13	1.94	1.14	[89]
80	Gobiidae	Exyrias belissimus	Terengganu, Malaysia	U	15.0	10.0	31.8	0.82	9.12	6.55	[46]
81	Gobiidae	Istigobius decoratus	Terengganu, Malaysia	U	13.0	9.0	22.4	0.83	8.46	6.23	[46]
82	Gobiidae	Istigobius goldmanni	Terengganu, Malaysia	U	6.0	5.0	2.3	0.94	5.37	4.53	[46]
83	Haemulidae	Diagramma pictum	Southern Arabian Gulf	Μ	(57.6)	30.7	1832.3	0.63	12.72	8.58	[90]
84	Haemulidae	Diagramma pictum	Southern Arabian Gulf	F	(60.6)	31.8	2137.0	0.62	12.76	8.55	[90]
85	Haemulidae	Diagramma pictum	Arabian Gulf, Kuwait	U	(69.1)	52.3	4963.3	0.58	11.72	9.97	[91]
86	Haemulidae	Haemulon aurolineatum	Pernambuco, Brazil	Μ	23.5	15.3	178.1	0.74	10.21	7.45	[92]
87	Haemulidae	Haemulon aurolineatum	Pernambuco, Brazil	F	23.5	15.0	178.1	0.74	10.21	7.34	[92]
88	Haemulidae	Haemulon plumierii	Ceará State, Bazil	F	34.3	16.9	843.6	0.66	10.45	6.53	[93]
89	Haemulidae	Haemulon plumierii	Ceará State, Brazil	Μ	27.7	18.6	446.9	0.69	10.00	7.59	[93]
90	Haemulidae	Pomadasys stridens	Gulf of Suez	F	18.3	10.3	104.9	0.76	9.13	5.90	[94]
91	Haemulidae	Pomadasys stridens	Gulf of Suez	Μ	18.3	9.1	104.9	0.76	9.13	5.36	[94]
92	Hemiramphidae	Hemiramphus brasiliensis	Pernambuco, Brazil	М	29.9	18.6	229.7	0.72	11.71	8.31	[95]
93	Hemiramphidae	Hemiramphus brasiliensis	Pernambuco, Brazil	F	29.9	19.3	229.7	0.72	11.71	8.53	[95]
94	Hemiramphidae	Hemiramphus far	Bardawil lagoon, Egypt	Μ	27.6	21.1	128.3	0.75	12.10	9.87	[96]
95	Hemiramphidae	Hemiramphus far	Bardawil lagoon, Egypt	F	28.1	21.3	127.9	0.75	12.25	9.94	[96]

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No.	Family	Species	Location	Sex	L _{max} (cm)	L _m (cm)	W _{max} (g)	D	L _{max} D	L _m D	Reference
96	Holocentridae	Holocentrus adscensionis	Pernambuco, Brazil	F	17.8	12.1	211.0	0.73	8.13	6.13	[97,98]
97	Holocentridae	Holocentrus rufus	Jamaica	F	23.0	13.5	206.8	0.73	9.84	6.67	[99]
98	Holocentridae	Myripristis murdjan	Lakshadweep lagoons, India	U	19.2	15.6	212.9	0.73	8.59	7.39	[45]
99	Holocentridae	Sargocentron rubrum	Terengganu, Malaysia	U	29.1	18.2	571.9	0.68	9.94	7.22	[46]
100	Kyphosidae	Kyphosus bigibbus	Northwest Kyushu, Japan	F	57.4	36.0	3327.5	0.60	11.35	8.58	[100]
101	Kyphosidae	Kyphosus bigibbus	Northwest Kyushu, Japan	Μ	50.6	28.4	2320.0	0.62	11.24	7.87	[100]
102	Kyphosidae	Kyphosus cinerascens	Kavieng, Papua New Guinea	F	34.0	22.6	935.2	0.66	10.21	7.80	[49]
103	Kyphosidae	Kyphosus cinerascens	Kavieng, Papua New Guinea	М	30.0	20.1	647.3	0.68	9.97	7.60	[49]
104	Labridae	Halichoeres hortulanus	Lakshadweep lagoons, India	U	28.9	12.8	356.2	0.70	10.67	6.02	[45]
105	Labridae	Halichoeres marginatus	Lakshadweep lagoons, India	U	17.9	7.0	99.6	0.76	9.04	4.42	[45]
106	Lethrinidae	Lethrinus borbonicus	Southern Arabian Gulf	Μ	28.7	22.1	366.8	0.70	10.57	8.80	[101]
107	Lethrinidae	Lethrinus borbonicus	Southern Arabian Gulf	F	28.7	21.3	366.8	0.70	10.57	8.57	[101]
108	Lethrinidae	Lethrinus borbonicus	Gulf of Suez, South Sinai coast	U	27.6	19.4	426.8	0.70	10.05	7.88	[102]
109	Lethrinidae	Lethrinus borbonicus	Foul Bay, Egypt, Red Sea	U	28.9	19.3	501.9	0.69	10.11	7.65	[103]
110	Lethrinidae	Lethrinus lentjan	Southern Arabian Gulf	Μ	(29.2)	24.6	446.9	0.69	10.36	9.21	[104]
111	Lethrinidae	Lethrinus lentjan	Southern Arabian Gulf	F	(32.4)	27.7	604.7	0.68	10.61	9.54	[104]
112	Lethrinidae	Lethrinus microdon	Southern Arabian Gulf	М	(32.6)	27.4	512.8	0.69	10.94	9.72	[101]
113	Lethrinidae	Lethrinus microdon	Southern Arabian Gulf	F	(32.0)	29.1	487.2	0.69	10.90	10.21	[101]
114	Lethrinidae	Lethrinus nebulosus	Southern Arabian Gulf	Μ	54.1	28.6	2230.2	0.62	11.80	7.95	[90]
115	Lethrinidae	Lethrinus nebulosus	Southern Arabian Gulf	F	55.7	27.6	2423.5	0.61	11.82	7.68	[90]
116	Lethrinidae	Monotaxis grandoculis	Pohnpei state, Micronesia	F	33.0	27.5	858.7	0.66	10.15	9.00	[43]
117	Lutjanidae	Aphareus rutilans	South China Sea	U	(67.2)	41.7	5356.0	0.58	11.36	8.62	[105]
118	Lutjanidae	Aprion virescens	Hawaii, US	F	102.8	44.9	15,361.5	0.53	11.57	7.47	[106]
119	Lutjanidae	Apsilus dentatus	Jamaica	F	54.0	40.0	2346.2	0.62	11.67	9.70	[107,108]
120	Lutjanidae	Apsilus dentatus	Jamaica	Μ	56.0	44.0	2634.2	0.61	11.68	10.08	[107,108]
121	Lutjanidae	Etelis coruscans	Hawaii, US	F	96.9	66.3	13,830.8	0.53	11.47	9.37	[106]
122	Lutjanidae	Lutjanus apodus	Great Barrier Reef, Australia	М	92.8	34.3	11,905.6	0.54	11.57	6.76	[109]
123	Lutjanidae	Lutjanus apodus	Jamaica	F	57.0	25.0	3764.4	0.59	11.04	6.77	[107]
124	Lutjanidae	Lutjanus bohar	Great Barrier Reef, Australia	F	67.5	42.9	5932.5	0.57	11.17	8.61	[110]
125	Lutjanidae	Lutjanus buccanella	Jamaica	F	49.0	24.0	1741.2	0.63	11.61	7.40	[107,108]
126	Lutjanidae	Lutjanus buccanella	Jamaica	Μ	49.0	26.0	1494.1	0.64	11.93	7.97	[107,108]
127	Lutjanidae	Lutjanus carponotatus	Palm Island, GBR, Australia	F	33.7	19.0	558.5	0.68	11.05	7.47	[111]
128	Lutjanidae	Lutjanus carponotatus	Lizard Island, Australia	F	35.4	19.0	646.4	0.68	11.15	7.32	[111]
129	Lutjanidae	Lutjanus ehrenbergii	Southern Arabian Gulf	U	(23.0)	20.4	199.1	0.73	9.89	9.06	[104]
130	Lutjanidae	Lutjanus ehrenbergii	Southern Arabian Gulf	М	(20.8)	19.9	148.0	0.74	9.59	9.27	[104]

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No.	Family	Species	Location	Sex	L _{max} (cm)	L _m (cm)	W _{max} (g)	D	L _{max} D	L _m D	Reference
131	Lutjanidae	Lutjanus erythropterus	Great Barrier Reef, Australia	U	62.4	48.5	34,639.3	0.49	7.60	6.72	[112]
132	Lutjanidae	Lutjanus fulviflamma	Southern Arabian Gulf	М	(21.2)	16.7	254.6	0.72	8.99	7.58	[113]
133	Lutjanidae	Lutjanus fulviflamma	Southern Arabian Gulf	F	(22.4)	18.7	301.0	0.71	9.14	8.04	[113]
134	Lutjanidae	Lutjanus fulviflamma	Okinawa island	F	34.2	19.6	931.8	0.66	10.25	7.11	[114]
135	Lutjanidae	Lutjanus fulvus	Yaeyama Isl., Okinawa, Japan	Μ	31.4	20.7	495.9	0.69	10.73	8.05	[115]
136	Lutjanidae	Lutjanus fulvus	Yaeyama Isl., Okinawa, Japan	F	33.2	22.5	585.6	0.68	10.85	8.32	[115]
137	Lutjanidae	Lutjanus gibbus	Pohnpei State, Micronesia	F	33.5	21.5	756.8	0.67	10.47	7.78	[43]
138	Lutjanidae	Lutjanus lutjanus	Persian Gulf and Sea of Oman	U	25.5	17.2	31.5	0.82	14.08	10.19	[116]
139	Lutjanidae	Lutjanus malabaricus	Great Barrier Reef, Australia	F	81.0	59.5	6923.8	0.57	12.01	10.09	[117]
140	Lutjanidae	Lutjanus sebae	Great Barrier Reef, Australia	F	72.0	54.8	7956.9	0.56	10.93	9.38	[117]
141	Lutjanidae	Lutjanus synagris	Jamaica	F	43.0	26.8	1288.8	0.64	11.27	8.31	[118]
142	Lutjanidae	Lutjanus griseus	Florida, US	F	72.4	23.0	6463.8	0.57	11.43	5.95	[119,120]
143	Megalopidae	Megalops atlanticus	Santa Fe, Ceará State, Brazil	Μ	153.6	120.0	23,369.2	0.51	12.97	11.44	[121,122]
144	Megalopidae	Megalops atlanticus	Santa Fe, Ceará State, Brazil	F	181.6	160.0	30,615.0	0.50	13.23	12.42	[121,122]
145	Menidae	Mene maculata	Taiwan	U	23.0	15.3	263.8	0.72	9.49	7.10	[123]
146	Monacanthidae	Aluterus monoceros	Veraval, India	U	58.9	48.5	2031.2	0.62	12.66	11.22	[124]
147	Mugilidae	Mugil curema	Sergipe State, Brazil	Μ	29.6	25.1	317.9	0.71	11.04	9.82	[125]
148	Mugilidae	Mugil curema	Sergipe State, Brazil	F	34.3	22.5	496.6	0.69	11.39	8.52	[125]
149	Mullidae	Mulloidichthys flavolineatus	Lakshadweep lagoons, India	U	24.2	16.0	200.7	0.73	10.27	7.58	[45]
150	Mullidae	Mulloidichthys martinicus	Jamaica	F	28.0	18.0	410.8	0.70	10.21	7.50	[126]
151	Mullidae	Mulloidichthys martinicus	Jamaica	Μ	28.0	19.0	332.3	0.71	10.55	8.02	[126]
152	Mullidae	Pseudupeneus maculatus	Pernambuco, Brazil	U	29.2	20.0	634.3	0.68	9.82	7.60	[127]
153	Mullidae	Pseudupeneus maculatus	Jamaica	F	24.9	18.0	232.5	0.72	9.97	8.10	[126,128]
154	Mullidae	Pseudupeneus maculatus	Jamaica	Μ	26.4	18.5	344.9	0.71	9.95	7.83	[126,128]
155	Muraenidae	Muraena augusti	Canary Islands	U	90.0	55.8	1750.1	0.63	17.00	12.58	[129]
156	Muraenidae	Muraena helena	Adriatic Sea, Croatia	Μ	121.0	79.0	3541.7	0.60	17.50	13.57	[130]
157	Muraenidae	Muraena helena	Adriatic Sea, Croatia	F	113.1	76.0	2679.8	0.61	17.88	14.03	[130]
158	Muraenidae	Muraena helena	Canary Island	U	134.0	75.1	5714.9	0.57	16.68	11.96	[129]
159	Nemipteridae	Nemipterus japonicus	Manila Bay, Philippines	F	16.2	9.2	69.2	0.78	8.79	5.66	[87,131]
160	Platycephalidae	Platycephalus indicus	Hong Kong, China	М	44.2	23.5	624.1	0.68	13.03	8.50	[132]
161	Platycephalidae	Platycephalus indicus	Hong Kong, China	F	62.2	45.7	1862.0	0.63	13.31	10.98	[132]
162	Pomacanthidae	Pomacanthus maculosus	Southern Arabian Gulf	F	33.3	21.6	1070.9	0.65	9.85	7.43	[101]
163	Pomacentridae	Abudefduf vaigiensis	Lakshadweep lagoons, India	U	16.8	10.7	146.4	0.75	8.18	5.83	[45]
164	Pomacentridae	Chromis viridis	Lakshadweep lagoons, India	U	9.7	4.9	21.4	0.83	6.65	3.78	[45]
165	Pomacentridae	Dascyllus trimaculatus	Terengganu, Malaysia	U	13.1	8.4	79.3	0.77	7.33	5.21	[46]

Tab	le	1.	Cont.
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No.	Family	Species	Location	Sex	L _{max} (cm)	L _m (cm)	W _{max} (g)	D	L _{max} D	Lm ^D	Reference
166	Pomacentridae	Pomacentrus coelestis	Terengganu, Malaysia	U	8.3	5.6	11.5	0.86	6.24	4.39	[46]
167	Priacanthidae	Priacanthus hamrur	Saurashtra, India	F	29.2	18.5	409.8	0.70	10.51	7.65	[133]
168	Rachycentridae	Rachycentron canadum	Northwest Coast, India	U	(176.0)	66.9	53,225.4	0.47	11.40	7.23	[134]
169	Sciaenidae	Pennahia aneus	Manila Bay, Philippines	Μ	21.1	13.1	128.9	0.75	9.89	6.89	[87,135]
170	Sciaenidae	Pennahia aneus	Manila Bay, Philippines	F	20.0	12.6	112.7	0.76	9.67	6.81	[87,135]
171	Scombridae	Scomberomorus brasiliensis	Maranhâo	F	79.5	41.1	3804.2	0.59	13.42	9.08	[136]
172	Scombridae	Scomberomorus brasiliensis	Maranhâo, Brazil	Μ	76.5	44.3	3405.3	0.60	13.42	9.68	[136]
173	Scombridae	Scomberomorus brasiliensis	Rio Grande do Norte, Brazil	Μ	72.7	31.2	3943.7	0.59	12.64	7.66	[137]
174	Scombridae	Scomberomorus brasiliensis	Rio Grande do Norte, Brazil	F	54.0	25.3	1675.4	0.63	12.43	7.70	[137]
175	Scombridae	Scomberomorus cavalla	Ceará State, Brazil	F	100.5	63.0	7535.8	0.56	13.32	10.25	[138]
176	Scombridae	Scomberomorus cavalla	Ceará State, Brazil	F	113.6	77.0	10,910.2	0.54	13.15	10.64	[139]
177	Scombridae	Scomberomorus maculatus	Ceará, State, Brazil	F	65.5	41.0	2304.0	0.62	13.19	9.88	[138]
178	Scombridae	Scomberomorus maculatus	Ceará State, Brazil	F	78.0	46.0	3878.6	0.59	13.22	9.67	[140]
179	Scorpaenidae	Pterois russelii	Terengganu, Malaysia	U	30.0	19.0	249.1	0.72	11.59	8.34	[46]
180	Siganidae	Siganus canaliculatus	Southern Arabian Gulf	М	33.2	21.5	731.9	0.67	10.46	7.82	[141]
181	Siganidae	Siganus canaliculatus	Southern Arabian Gulf	F	36.9	25.7	1004.9	0.66	10.65	8.40	[141]
182	Sillaginidae	Sillago sihama	Gulf of Mannar, India	U	(26.2)	12.8	137.7	0.75	11.52	6.73	[142]
183	Sillaginidae	Sillago sihama	Pulicat Lake, India	U	(38.0)	22.1	327.3	0.71	13.13	8.95	[143]
184	Sparidae	Archosargus rhomboidalis	Terminos Lagoon, Mexico	U	24.6	8.5	491.0	0.69	9.07	4.38	[144]
185	Sparidae	Rhabdosargus sarba	Southern Arabian Gulf	М	29.3	23.5	513.5	0.69	10.17	8.74	[104]
186	Sparidae	Rhabdosargus sarba	Southern Arabian Gulf	F	29.3	23.7	513.5	0.69	10.17	8.79	[104]
187	Sparidae	Rhabdosargus sarba	South-eastern Australia	U	(25.1)	19.4	325.1	0.71	9.79	8.17	[145]
188	Sparidae	Sparus aurata	North Island, New Zealand	U	(55.9)	24.0	3388.1	0.60	11.13	6.71	[146]
189	Sparidae	Sparus aurata	Western North Island, N.Z.	U	(63.4)	24.0	4818.1	0.58	11.21	6.37	[146]
190	Sparidae	Sparus aurata	Western South Island, N.Z.	U	(66.1)	24.0	5426.2	0.58	11.23	6.26	[146]
191	Sphyraenidae	Sphyraena barracuda	Florida, USA	F	141.8	65.6	60,587.5	0.46	9.99	6.98	[147]
192	Synanceiidae	Inimicus didactylus	Terengganu, Malaysia	U	25.0	16.0	231.4	0.72	10.28	7.44	[46]
193	Synodontidae	Saurida tumbil	East China Sea	U	(54.7)	25.7	2664.8	0.61	11.50	7.25	[148]
194	Synodontidae	Saurida tumbil	Manila Bay, Philippines	Μ	28.0	23.9	192.5	0.73	11.48	10.22	[87]
195	Synodontidae	Saurida tumbil	Manila Bay, Philippines	F	29.2	24.7	218.9	0.73	11.59	10.27	[87]
196	Synodontidae	Saurida undosquamis	off Visakhapatnam, India	U	(34.1)	20.9	364.2	0.70	11.96	8.48	[149]
197	Synodontidae	Synodus variegatus	Terengganu, Malaysia	U	36.8	15.6	659.8	0.68	11.40	6.40	[46]
198	Synodontidae	Trachinocephalus myops	Minnan-Taiwan Bank	U	(41.0)	16.5	804.7	0.67	11.86	6.47	[150]
199	Tetraodontidae	Canthigaster valentini	Lizard Island, Australia	F	8.8	5.8	22.3	0.83	6.14	4.33	[151]
200	Tetraodontidae	Canthigaster valentini	Lizard Island, Australia	М	10.7	6.7	39.5	0.81	6.77	4.63	[151]

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No.	Family	Species	Location	Sex	L _{max} (cm)	L _m (cm)	W _{max} (g)	D	L _{max} D	L _m D	Reference
201	Tetraodontidae	Lagocephalus sceleratus	Suez Canal, Egypt	F	76.5	42.2	5076.6	0.58	12.38	8.77	[152]
202	Tetraodontidae	Lagocephalus sceleratus	Suez Canal, Egypt	М	76.5	41.0	5076.6	0.58	12.38	8.63	[152]
203	Tetraodontidae	Lagocephalus sceleratus	Rhodes, Greece	U	61.5	35.1	2646.6	0.61	12.36	8.77	[153]
204	Tetraodontidae	Lagocephalus sceleratus	Lebanon	U	71.6	39.0	5439.2	0.58	11.75	8.27	[154]
205	Tetraodontidae	Lagocephalus sceleratus	Southwest Cyprus	UI	71.2	40.8	4454.7	0.59	12.18	8.80	[155]
206	Tetraodontidae	Lagocephalus sceleratus	Southeast Cyprus	U	78.0	47.6	5872.6	0.57	12.15	9.15	[155]
207	Tetraodontidae	Lagocephalus sceleratus	Cyprus	F	75.0	19.4	5355.1	0.58	12.11	5.54	[156]

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