

## Article

# Length–Weight Relationships and Growth Parameters of Common and Leafy Seadragons (Syngnathidae) from a Public Aquarium

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**Abstract:** The length–weight relationships (LWR) of the common seadragon *Phyllopteryx taeniolatus* (Lacepède, 1804) and the leafy seadragon *Phycodurus eques* (Günther, 1865), Syngnathidae, are presented in this paper, based on specimens raised in the Birch Aquarium at Scripps, La Jolla, California. Furthermore, we used the length at known age of 40 specimens of common and 15 leafy seadragons to estimate the parameter of the von Bertalanffy growth function (VBGF) for these species. Some of the pros and cons of the newly proposed length type used, ‘scalene length’ are presented. The parameters of the LWR and the VBGF parameters are discussed, with an emphasis on the rearing conditions, the peculiar anatomy of seadragons, especially of *P. eques*, and on the Gill-Oxygen Limitation Theory (GOLT).

**Keywords:** von Bertalanffy growth function; Gill-Oxygen Limitation Theory; *Phyllopteryx taeniolatus*; *Phycodurus eques*; scalene length



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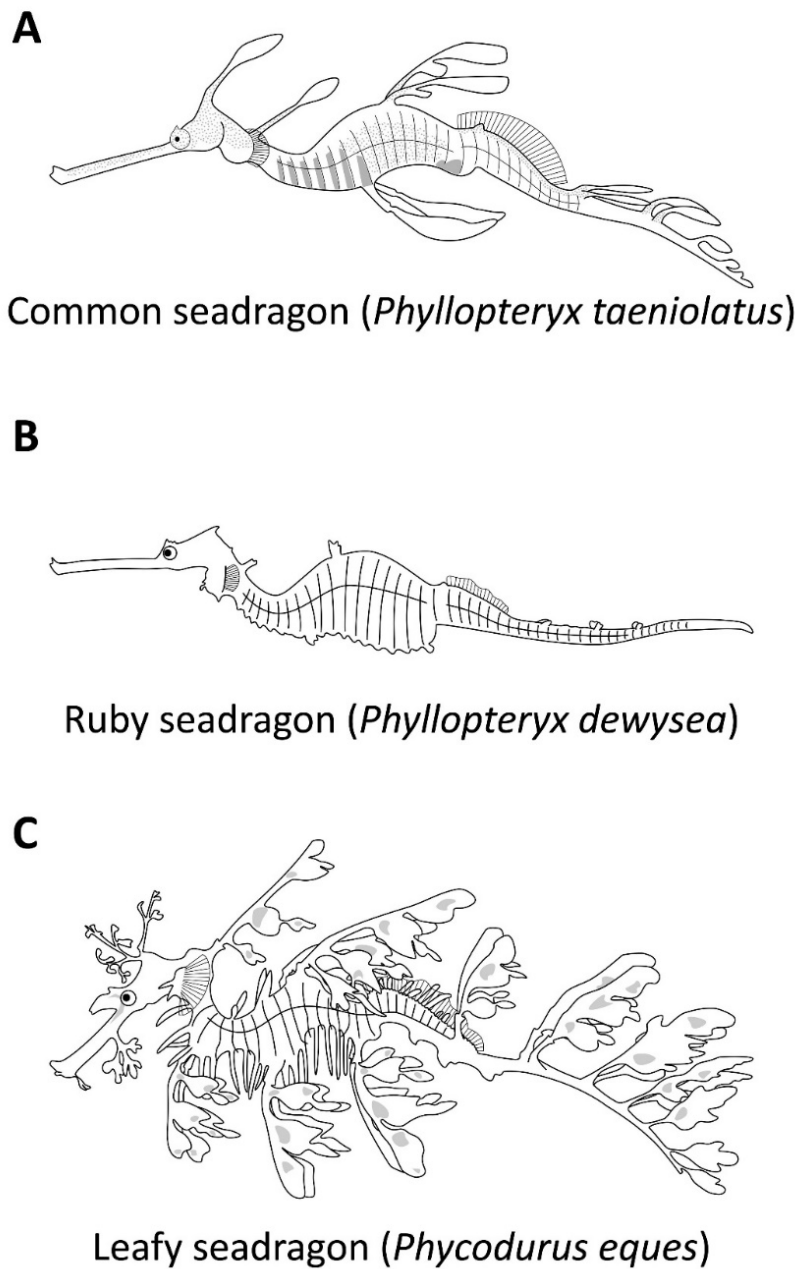
## 1. Introduction

The common seadragon *Phyllopteryx taeniolatus* (Lacepède, 1804) and the leafy seadragon *Phycodurus eques* (Günther, 1865) belong, like seahorses and pipefish, to the family Syngnathidae. Their bizarre shape (Figure 1A,C) is shared only with the ruby seadragon *Phyllopteryx deweysea* (Figure 1B), a species of seadragons described only recently [1].

All three species are on IUCN Red List ([www.iucnredlist.org](http://www.iucnredlist.org), accessed on 15 December 2021), with the common and leafy seadragons assessed as being of ‘Least Concern’, although their populations are declining [2,3], and the ruby seadragon was assessed as being ‘Data Deficient’ [4].

As seadragons are extremely fragile (MW, pers. obs.) and protected in southern Australia [5], the only place where they occur naturally, their study has been limited (although see [6–10] and references therein), and basic information on their morphometric and biology is still lacking, notably on their length–weight relationships (LWR). However, LWR are necessary to convert lengths to weights, i.e., to convert growth in length (which cannot be interpreted physiologically, nor be compared between taxa), to growth in weight, which enables such interpretations and comparisons. This applies particularly to seadragons, which, due to their odd shapes, cannot be straightforwardly compared to other bony fish.

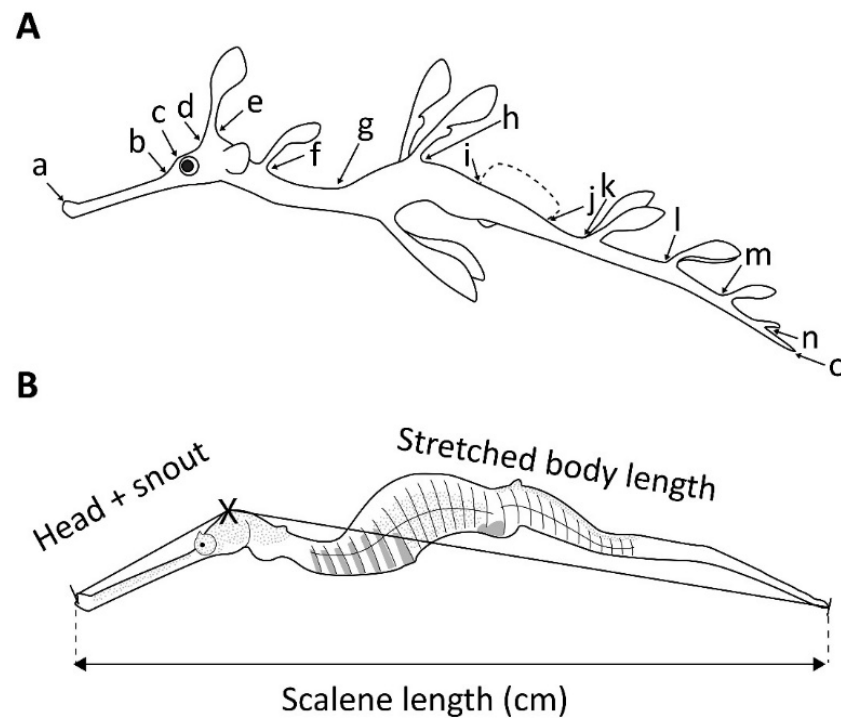
Based on newly estimated LWR, this contribution thus aims to show that, while they are oddly shaped, seadragons grow in the same fashion as other bony fish, although they grow relatively slowly, as can be expected given the design of their respiratory apparatus.



**Figure 1.** Illustrating the three extant seadragon species ((**A**): common seadragon; (**B**): ruby seadragon; (**C**): leafy seadragon), all endemic to Southern Australia (drawings by Elaine Chu).

## 2. Materials and Methods

Figure 2 illustrates the manner in which the length of seadragons may be measured; Figure 1A documents the step-by-step measurements defined in Figure 1 of Forsgren and Lowe [10], that need to be added to yield a length that may be called ‘cumulative length’ (CL). Figure 1B documents a more practical ‘scalene length’ (ScL), so named as it refers to the longest side of a scalene triangle, where the other sides are formed by the head (including the snout) and the (gently) stretched body and tail. To facilitate comparisons between these two length types, four specimens each of common and leafy seadragons were measured using both length types and the mean ratios of the measurements were calculated.



**Figure 2.** Approaches for defining the ‘length’ of seadragons: (A), modified from Figure 1 of Forsgren and Lowe [10], identifies the successive 14 body segments (a–b; b–c; etc. until n–o) whose lengths are added to obtain what may be called ‘cumulative length’ (CL); (B) documents a practical ‘scalene length’ (ScL), so named as it refers to the longest side of a scalene triangle, whose other sides are formed by the head and the stretched body.

The bulk of the data used for this study are presented in Table 1 for the common (also ‘weedy’) seadragon and in Table 2 for the leafy seadragon. Scalene lengths were measured to the nearest millimeter, and the corresponding weight measurements to the nearest hundredth of a gram; both measurements were taken on dead specimens preceding a necropsy.

These data were used to estimate length–weight relationships (LWR) of the form  $W = a \cdot L^b$ , where  $W$  is the weight (in g) and  $L$  the scalene length (in cm) of individual fish in Tables 1 and 2, and  $a$  and  $b$  are based on the intercept ( $\alpha$ ) and the slope ( $b$ ) of a regression of  $\log(W)$  on  $\log(L)$  [11,12], i.e.,

$$\log(W) = \alpha + b \cdot \log(L) \quad (1)$$

where  $10^\alpha = a$ , the multiplicative term of an LWR, and  $b$  its exponent.

The length ( $L_x$ ) and weight ( $W_x$ ), at which two LWRs cross each other (i.e., have a point in common), was estimated by setting two log-linear equations corresponding to two LRWs (1, 2) equal to each other, i.e.,

$$\log(W_x) = \alpha_1 + b_1 \cdot \log(L_x) = \alpha_2 + b_2(L_x) \quad (2)$$

which, rearranged, gives

$$\log(L_x) = (\alpha_2 - \alpha_1) / (b_1 - b_2) \quad (3)$$

The weight of the conspicuous appendages and their supporting stalks in our two species of seadragons was evaluated by cutting up one each of preserved specimens in the Australian Museum in Sydney. These specimens were originally fixed in formalin; however, they were kept in 70% ethanol for long-term preservation. They were measured, patted dry and weighed, the leaf-like soft appendages were removed and weighed; then the exoskeleton’s stalks were removed and weighed.

**Table 1.** Hatching and death dates (day/month/year), ages, ‘scalene’ lengths (see text) and weights of common seadragons (*Phyllopteryx taeniolatus*) kept at the Birch Aquarium at Scripps, La Jolla, CA.

Hatching Day	Death Day	Age (Days)	Sex	Length (mm)	Weight (g)
1/9/2013	6/12/2013	96	–	85	0.75
19/9/2013	25/11/2013	67	–	91	0.66
19/9/2013	3/12/2013	75	–	92	0.63
19/9/2013	1/12/2013	73	–	92	0.70
19/9/2013	12/1/2013	73	–	96	0.76
9/1/2013	8/12/2013	98	–	98	0.77
21/3/2020	11/4/2020	228	–	152	5.04
15/12/2009	7/4/2011	478	♀	155	4.69
1/8/2012	25/7/2013	358	–	210	14.71
–	20/1/2020	–	♂	324	35.62
15/12/2018	12/1/2020	393	♂	226	12.05
15/12/2018	18/12/2019	368	♂	230	12.89
10/12/2018	19/2/2020	436	♀	239	10.00
–	15/1/2020	–	♂	351	48.56
10/12/2018	17/2/2020	434	–	245	–
1/8/2012	13/8/2013	377	♀	247	14.02
15/12/2009	18/5/2015	980	♀	273 <sup>1</sup>	23.04 <sup>1</sup>
15/12/2014	13/6/2017	911	♂	284	27.24
1/3/2016	30/1/2018	700	♀	285	22.84
15/12/2015	9/1/2019	1121	♀	294	29.91 <sup>2</sup>
15/12/2005	2/2/2015	3336	♀	299	28.17
–	14/5/2016	–	♂	327	32.63
–	5/5/2016	–	♀	330	35.65
15/12/2005	2/7/2014	3121	♀	300	28.16
15/12/2011	23/6/2015	1286	♀	301	37.05
15/12/2015	18/1/2020	1495	♀	302	32.90
15/12/2011	24/9/2020	3206	♀	310	38.25
15/12/2015	23/1/2020	1500	♀	312	36.55
15/12/2015	23/5/2020	1621	♀	315	41.77
15/12/2014	15/3/2016	456	♂	315	29.52
19/9/2013	19/1/2020	2313	♀	316	41.60
–	2/2/2016	–	♀	320	31.90
15/12/2011	12/8/2015	1336	♂	320	40.65
15/12/2012	73//2018	1908	♂	324	39.19
15/12/2012	21/8/2020	2806	♂	325	36.79
15/12/2011	20/2/2015	1163	♂	330	33.15
1/12/2011	28/12/2016	1854	♂	330	33.70
15/12/2014	18/1/2020	1860	♀	332	42.99
1/12/2011	25/4/2015	1241	♂	333	38.90
15/12/2011	19/1/2014	766	–	338	27.68
15/12/2014	13/12/2020	2190	♂	344	41.45
15/12/2014	23/5/2020	1986	♀	345	51.27
15/12/2009	1/4/2015	1933	♂	362	44.00
–	22/5/2011	–	–	266	17.00
15/12/2011	20/2/2015	1163	♂	391	51.54

<sup>1</sup> The length was measured and the weight was reconstructed after some internal organs were dissected. <sup>2</sup> The weight is without dorsal and ventral appendages.

**Table 2.** Hatching and death dates (day/month/year), ages, ‘scalene’ lengths (see text) and weights of leafy seadragons (*Phycodurus eques*) kept at the Birch Aquarium at Scripps, La Jolla, CA.

Hatching Day	Death Day	Age (Days)	Sex	Length (mm)	Weight (g)
15/12/2011	22/3/2012	98	–	109	2.80
13/12/2010	7/4/2011	115	–	124	3.90
13/12/2010	2/5/2011	140	–	160	3.43
15/12/2009	25/3/2011	465	♀	180	4.00
27/11/2017	31/3/2019	489	♀	217	15.44
27/11/2017	25/1/2019	424	♂	223	13.25 <sup>1</sup>
27/11/2017	14/2/2019	444	♂	225	13.59 <sup>2</sup>
15/12/2018	11/3/2020	452	♂	230	21.70
15/12/2018	2/4/2020	474	♀	234	24.32
15/12/2009	19/8/2011	612	♂	255	40.84
15/12/2011	19/6/2018	2378	♂	280	49.83
23/12/2012	19/6/2019	2369	♀	282	54.36
23/12/2012	25/9/2019	2467	♂	302	61.27
15/12/2011	14/5/2020	3073	♂	310	65.92
23/12/2012	23/3/2015	820	♀	324	55.38

<sup>1</sup> Four appendages were cut off prior to weighing. <sup>2</sup> A few appendages were cut off before weighing.

The growth of fishes is usually conceived as the result of two processes with opposite signs, i.e.,

$$dw/dt = Hw^d - kw \quad (4)$$

where  $dw/dt$  is the growth rate,  $Hw^d$  is the rate of synthesis of proteins (which uses oxygen provided by the gills,  $kw$  is the rate at which proteins are being spontaneously denatured [13] and  $d$  relates the gill surface area to body mass [14]. This equation implies that fish reach their maximum weight ( $W_{max}$ ) when the two terms on the right side of Equation (4) become equal, i.e., when their metabolic rate ( $Q$ ), or oxygen supply per unit weight, is just sufficient to meet the demand for their maintenance ( $Q_{maint}$ ), which must occur at some point if  $d < 1$ . For small fishes, e.g., seadragons, a value of  $d \sim 2/3$  is to be expected [14,15].

Integrating Equation (4) with  $d = 2/3$  yields the von Bertalanffy Growth Function (VBGF), which has the form:

$$L_t = L_{\infty} \cdot (1 - e^{-K \cdot (t - t_0)}) \quad (5)$$

where  $L_t$  is the mean length at age  $t$  of the fish in question,  $L_{\infty}$  their asymptotic length, i.e., the mean length that would be attained after an infinitely long time, and  $K$  a growth coefficient expressing how fast the asymptotic size is approached (here in year<sup>−1</sup>);  $K$  is equal to  $k/3$  in Equation (4), and thus can also be conceived as expressing the level of stress that is experienced by the fish [15]. Finally,  $t_0$  is a parameter adjusting for the fact that VBGF usually fails to describe the growth of the earliest stages (larval and early juvenile) of fish growth [15].

Here, the dates at hatching and death are recorded for most of the individuals in Tables 1 and 2, and thus their precise age in days could be used to estimate the parameters of the VBGF for length. The corresponding equation for growth in weight is

$$W_t = W_{\infty} \cdot (1 - e^{-K \cdot (t - t_0)})^b \quad (6)$$

where  $W_{\infty}$  is the asymptotic weight, as derived from an LWR whose  $b$  value is also used, and the other parameters are defined above.

The advantage of a growth curve in weight is that it allows for comparing the growth performance of fishes of widely different shapes through the index

$$\emptyset = \log(K) + 2/3 \log(W_{\infty}) \quad (7)$$

This was based on the analysis of a multitude of  $W_{\infty}$  and  $K$  data pairs in a wide variety of fish species [15,16].

Furthermore, one should note that other growth equations could be fitted to the data in Tables 1 and 2; the VBGF was chosen here both as its wide use allows straightforward comparisons with the growth of other fishes, and as its parameters are easy to interpret biologically.

Finally, we computed the ratio  $L_{max}^D/L_m^D$  of seadragons from literature data, with  $L_{max}$  being the maximum length in a given population,  $L_m$  the mean length at first maturity and  $D = 3(1 - d)$ . This ratio has the interesting property of being equivalent to the ratio of  $Q_m$ , the metabolic rate at first maturity to  $Q_{maint}$ , as defined above.

### 3. Results

Table 3 presents the stepwise measurements of four specimens each of common and leafy seadragons, their sum (i.e., cumulative length or CL) and the ratios of CL to ScL (or scalene length). The resulting mean ratio of ScL to CL is 0.93 for the common, and 0.82 for the leafy seadragon.

**Table 3.** Data for computing the ratio of two different ‘length types’ in two species of seadragons. The ‘length steps’ refer to Figure 2A; ScL refers to scalene length, as defined in Figure 2B.

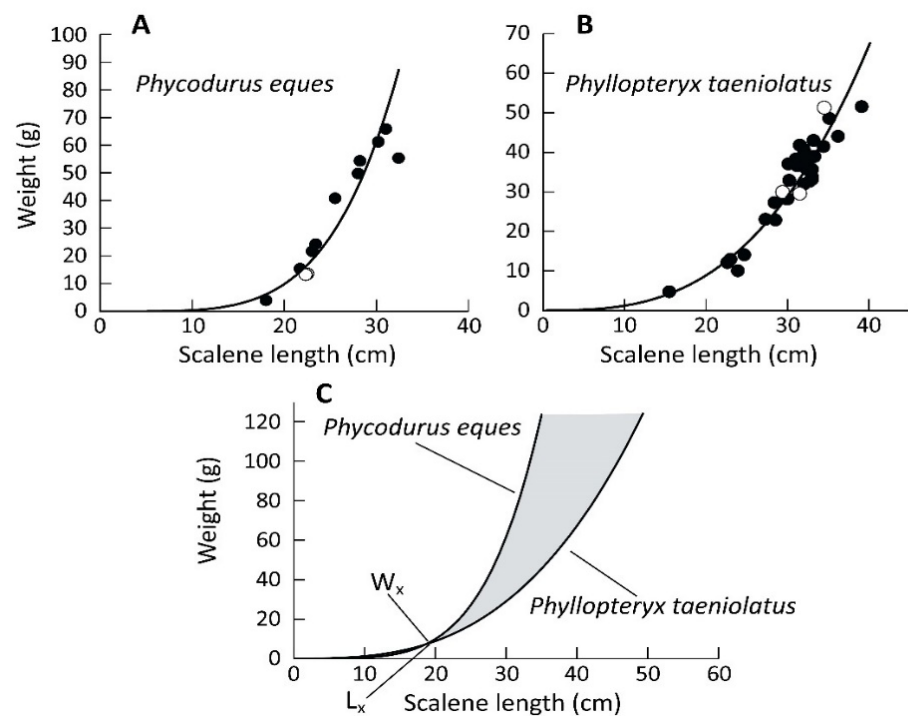
Item Number	Length Step (mm)	<i>Phyllopteryx taeniolatus</i>					<i>Phycodurus eques</i>		
		A	B	C	D	E	F	G	H
1	a–b	49.6	50.6	55.6	35.6	37.5	15.5	40.1	33.5
2	b–c	9.4	10.3	11.9	8.0	7.3	3.9	10.4	9.5
3	a–d	9.4	10.3	11.2	7.7	13.0	9.4	12.7	11.1
4	d–e	9.4	11.9	14.4	7.5	12.0	5.7	12.7	13.7
5	e–f	14.2	14.7	18.1	12.0	15.8	4.8	17.6	15.5
6	f–g	23.5	31.9	31.8	21.0	22.6	14.0	25.4	26.0
7	g–h	47.0	51.8	56.6	33.7	28.6	6.8	30.0	29.3
8	h–i	32.3	39.2	50.8	25.8	31.3	10.3	33.6	31.1
9	i–j	35.4	39.9	41.5	29.7	46.0	23.5	51.9	46.2
10	j–k	16.0	19.5	20.3	15.4	30.2	9.2	28.6	23.6
11	k–l	30.6	30.8	37.4	27.5	30.7	12.3	29.8	25.7
12	l–m	25.7	30.0	34.7	26.4	20.2	9.4	19.7	23.3
13	m–n	31.3	21.1	22.8	17.5	27.9	6.0	14.4	18.0
14	n–o	11.0	19.9	26.3	15.3	7.7	7.4	18.1	18.3
15	Sum	345	377	433	282	331	132	345	325
16	ScL	320	360	392	260	260	115	275	265
17	Ratio	0.928	0.955	0.904	0.921	0.785	0.871	0.797	0.815

A: Australian Museum specimen: AMS I.20223-013 (weight = 34.15 g); B: AMS IB.856, N.S.W., Bondi, Sydney (33° 53′ S, 151° 17′ E), 1909 (62.79 g); C: AMS IB.855, N.S.W., Wollongong (34° 26′ S, 150° 53′ E), 1909 (90.42 g); D: AMS I.20223-008, W.A., Cape Le Grande, Lucky Bay (34° 1′ S, 122° 14′ E), 1978 (18.25 g); E: AMS I.20223-012 (18.25 g); F: AMS I.20223-009, same as D (2.56 g); G: same as F (37.59 g); H: AMS E.2376 S.A., Investigator Strait, South of Kangaroo Island (35° 50′ S, 138° 3′ E), 1909 (40.9 g).

The LWR for common and leafy seadragons are shown in Table 4 and Figure 3A,B, while Figure 3C documents the scalene length at which the two LWR cross each other, i.e.,  $Lx = 18.9$  cm, corresponding to 7.43 g in both species.

**Table 4.** Parameters of the length–weight relationship (LWR) and of the von Bertalanffy growth function (VBGF) estimated for the data in Tables 1 and 2, with both sexes combined.

Item (Definition; Units)	<i>Phyllopteryx taeniolatus</i>	<i>Phycodurus eques</i>
$n$ (number of fishes used in LMR)	31	10
$a$ (multiplicative term of LWR; cm and g)	0.000139	0.0000135
$b$ (exponent of LWR)	2.92	4.51
$r^2$ (coefficient of determination of linear LWR)	0.930	0.912
$N$ (number of fishes used for the VBGF)	40	15
$L_\infty$ (asymptotic ‘scalene’ length, in cm)	32.4	29.9
$W_\infty$ (asymptotic weight, in g)	36.3	60.4
$K$ (growth coefficient; year <sup>−1</sup> )	1.09	0.93



**Figure 3.** Length–weight relationships (LWR) of the common (A) and leafy (B) seadragons of both sexes (see also Table 3). The open dots refer to non-intact specimens (see Tables 1 and 2), which were not used in computing the LWR. Panel (C) shows where the two LWR cross and highlights (in grey) the weight-at-length difference between the two species.

The growth parameters in length for common and leafy seadragons are given in Table 5 and Figure 4A,B. These growth curves are for both sexes combined, as the data in Tables 1 and 2 did not allow for estimating the parameters of sex-specific growth curves. These LWR allowed for re-expressing the length growth parameters in Table 5 in the form of growth equations in weight, i.e.,

$$W_t = 36.3 \cdot (1 - e^{-1.09 \cdot (t+0.08)})^{2.92} \quad (8)$$

for the common seadragon, and

$$W_t = 60.4 \cdot (1 - e^{-0.93 \cdot (t+0.27)})^{4.51} \quad (9)$$

for the leafy seadragon (see Figure 4C).



**Table 5.** Contributions of the appendages and their supporting spines to the weight of two species of seadragons, based on two preserved specimens.

Item (Units)	<i>Phyllopteryx taeniolatus</i> <sup>1</sup>	<i>Phycodurus eques</i> <sup>2</sup>
Scalene length (cm)	32.0	27.0
Whole specimen weight (g)	34.3	25.6
Weight of appendages (g)	0.04	1.44
Weight of stalks (g)	0.42	2.40
Appendages and stalks in total weight (%)	1.35	15.0

<sup>1</sup> Specimen: AMS I.20223-013—Australia, Western Australia, Cape Le Grande: Lucky Bay, (34° 1' S, 122° 14' E), 21 March 1978. <sup>2</sup> Specimen: AMS I.20223-012—Australia, Western Australia, Cape Le Grande: Lucky Bay, (34° 1' S, 122° 14' E), 21 March 1978.

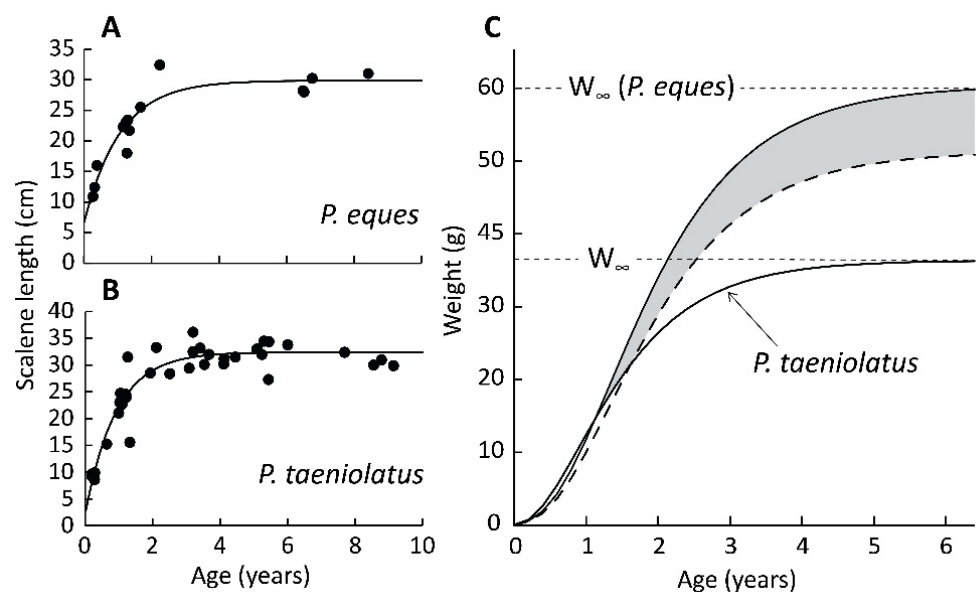
**Figure 4.** Von Bertalanffy growth curves in ‘scalene’ length of common (A) and leafy (B) seadragon of both sexes (see also Table 4), and weight growth curves for both species (C). Note the contribution of the appendages and their supporting spines to the weight of the leafy seadragon (grey area and Table 5).

Table 5 presents the contributions of appendages and their supporting spines to the weight of two species of seadragons. The 15% contribution of the appendages and supporting spines of the leafy seadragon are shown (in grey) in Figure 4C, although the 1.4% that they contribute to the weight of common seadragon is not shown. However, the latter figure was considered when assessing that 37% of the weight difference between adult common and leafy seadragons is due to the latter’s more exuberant appendages.

Table 6 shows a comparison between the growth performance of the seadragon with that of other fishes, based on Equation (7).

However, some of the estimates are tentative, due to the uncertainty inherent in converting the asymptotic length measurements of other authors to scalene lengths, and the approximate methods that generated their growth curves.

Finally, a  $L_{max}^D/L_m^D$  ratio of 1.34 for the common seadragon was estimated, assuming  $d = 2/3$  and hence  $D = 1$ , from the ratio of length at first maturity and maximum length ( $L_m/L_{max}$ ) of 0.71–0.80 published by Sanchez-Camara et al. [8]. This is very close to the mean  $L_{max}^D/L_m^D$  ratio so far estimated for over 500 populations in 234 species of bony fishes, i.e., ~1.35 [17].



**Table 6.** Comparison between the growth performance of two species of seadragon and four species of other bony fishes (from Pauly 1981), using the growth performance index  $\emptyset = \log(K) + 2/3\log(W_{\infty})$ .

Species	$W_{\infty}$ (g)	$K$ (Year <sup>-1</sup> )	$\emptyset$	Source
<i>Katsuwonus pelamis</i>	55,200	0.179	2.41	Table 7 in Pauly (1981) [15]
<i>Pollachius virens</i>	11,331	0.141	1.85	
<i>Labrus merula</i>	990	0.234	1.36	
<i>Blennius pholis</i>	102	0.746	1.21	
<i>Phycodurus eques</i>	60.4	0.930	1.16	This study
<i>Phyllopteryx taeniolatus</i>	36.3 <sup>1</sup>	1.113	1.09	Kuiter (1988) [7] and FishBase
	36.3	1.090	1.08	This study
	29.9 <sup>2</sup>	2.20	1.32	Forsgren and Lowe (2006) [11]
	40.3 <sup>2</sup>	1.52	1.25	Sanchez-Camara et al. (2011) [9]

<sup>1</sup> Obtained by multiplying the  $L_{\infty}$  estimate in FishBase (32.5 cm) by 0.82, then applying the LWR in Table 4 (see [www.fishbase.org](http://www.fishbase.org), accessed on 15 December 2021). <sup>2</sup> Obtained by multiplying the  $L_{\infty}$  estimates in Forsgren and Lowe (2006; 28.5 cm) and Sanchez-Camara et al. (2011; 36.3 cm) by 0.93, then applying the LWR in Table 4.

#### 4. Discussion

The LWR proposed here apply to scalene length (ScL) as defined in Figure 1B. This length type was selected over possible alternatives (e.g., cumulative lengths, or CL, as defined in Figure 1A, or digital image processing) for two practical reasons. The first is that digital image processing was not available to L.M. when she performed the necropsies, which generated the length data reported here. The second reason, which refers to CL, is the fact that the time that can be devoted to necropsies in a public aquarium is limited. This is similar to the field sampling of protected and/or rare fish species, where length measurements must be performed quickly, i.e., before individual fish die. Other length measurements may be more precise than scalene length; however, the CL/ScL ratios in Table 3 will allow future workers to compare their results, if expressed as CL, with the results presented here.

Another issue is the possible shrinkage of the specimens prior to necropsies. Limited shrinkage occurs in preserved specimens [12], however, this should be minimal in seadragons, particularly in *P. eques*, whose shape and dimensions are largely determined by external body structures.

As can be seen from Table 6, the growth of both common and leafy seadragons in captivity is relatively slow when compared to that of other bony fishes, and it can be assumed that this will be the case for the ruby seadragon, as well. This is not likely to be an artefact, as food was abundant. Indeed, there has been a tendency to overfeed seadragons and other syngnathid in captivity, which causes them to develop fatty liver and excess visceral fat (L.M. and W.M., pers. obs.).

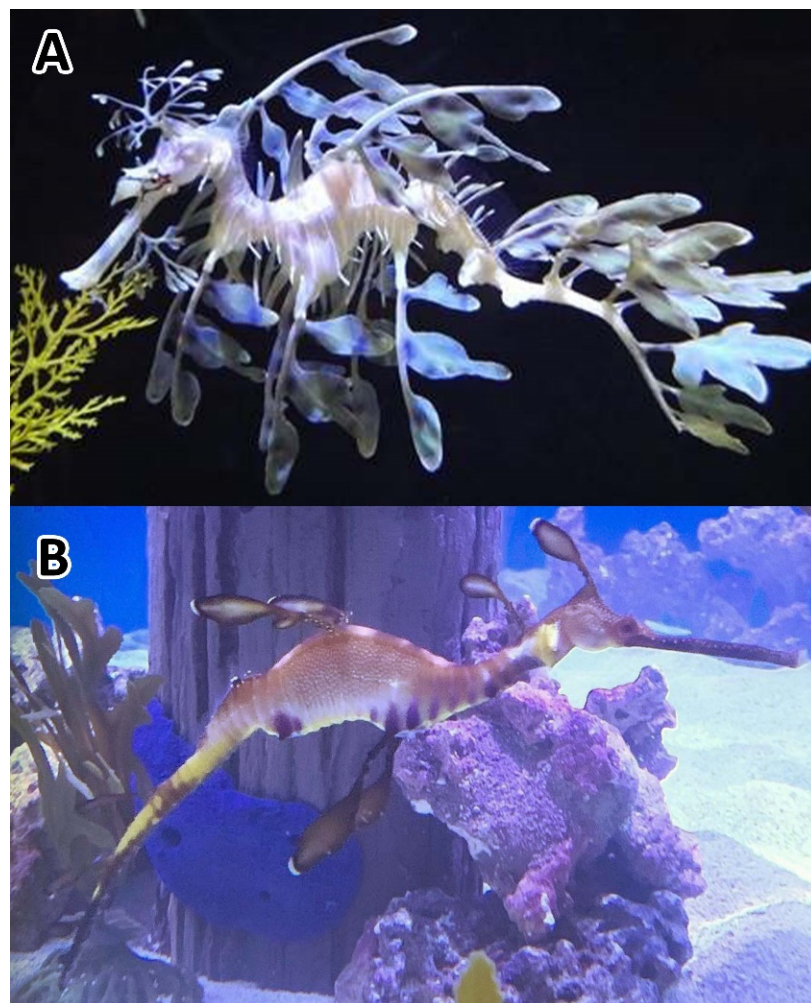
Depending on the size and configuration of the aquaria, in which there are kept, the growth of fishes in public aquaria can be very close to their growth in the wild [18]. This applies particularly to small coral and other benthic fishes [19], such as syngnathids.

Unfavorable rearing conditions, which generate stress, usually increase the metabolic rate of fish, which reduces the maximum sizes they can reach [14], as well as decreasing their asymptotic length and weight and increasing their estimates of  $K$  when the VBGF is used to describe their growth [15–17], which is the reason for the relative within-species constancy of  $\emptyset$  in Equation (7). Thus, the fact that the common and leafy seadragon both reach, at the Birch Aquarium at Scripps Institution of Oceanography, sizes similar to what they would reach in the wild strongly suggests that they experienced rearing conditions free of obvious stresses. Other public aquaria may, in the future, report different results, which may allow the determination of the biotic and abiotic factors, which have the most impact on the growth of seadragons.

Overall, the low growth performance of the seadragon is not surprising, as it has been shown elsewhere that the growth performance of fish is closely related to the size of their gills, which supply the oxygen required for the synthesis of proteins [14,15]. Fishes of the

syngnathid family have gills that are not capable of providing their owner with a high oxygen supply [20]. Indeed, the only published gill surface area estimate available for a syngnathid (*Hippocampus* sp.; [21]), is  $5.8 \text{ cm}^2$  for a specimen of 5.5 g, i.e.,  $1.08 \text{ cm}^2 \cdot \text{g}^{-1}$ , which is about one order of magnitude lower than fish of fusiform shape would have at the same weight (see [22]).

The growth curves of the common and leafy seadragons resemble each other in that they reach a similar fraction of the asymptotic weight ( $W_\infty$ ) at the same time (Figure 4), which is due to their estimates of the growth parameter  $K$  being similar. Thus, most of the difference between the growth curves of common and leafy seadragons is due to  $W_\infty$  being higher in the latter species, which, one could assume, would be due to their extravagant appendages (Figures 1 and 5). However, Table 5 shows that these appendages and their supporting spines contribute to only 37% of the weight difference. Thus, we conclude that their stouter bodies are the main reason why leafy are heavier than common seadragons.



**Figure 5.** Live photos of captive seadragons. (A): leafy seadragon *Phycodurus eques* in the Birch Aquarium, La Jolla (photo by L. Matsushige). (B): common seadragon *Phyllopteryx taeniolatus* in the Ripley's Aquarium of Canada, Toronto (photo by M. Warren).

Moreover, the appendages of seadragons appear to consist of tissues that are metabolically inert or nearly so, i.e., not requiring the development of a dedicated oxygen supply. Indeed, as noted by one of us (L.M.; pers. obs.) in multiple necropsies, while capillaries are clearly visible in the fins of common and leafy seadragons, blood vessels are not visible in the appendages' 'leaves' and supporting spines (see also Figure 4). Furthermore, W.M.

(pers. obs.) during her previous employment at Ripley's Aquarium of Canada in Toronto, noted that a common seadragon with a massive tear in one of its appendages did not bleed.

This corroborates the hypothesis that, while obviously requiring oxygen for the initial synthesis of their tissues, the multiple appendages of leafy seadragon (and the fewer appendages of common seadragon) do not require (much) oxygen for their maintenance. Note also that the added weight of these appendages is irrelevant in water, when gravity does not matter and their hydrodynamic drag is also negligible, as seadragons, and especially leafy seadragons, protect themselves from predators by hiding behind and mimicking macroalgae.

Thus, overall, our examination of the various aspects of the anatomy, growth and reproduction of seadragons, in spite of their aberrant body shape and habits, led to results that are compatible with the Gill-Oxygen Limitation Theory, or GOLT [14].

## 5. Conclusions

Overall, this article demonstrates that data from a public aquarium, combined with measurements on preserved museum specimens and published field data, could be combined such as to derive a number of important biological traits for seadragons, i.e., species with bizarre shapes that had until now precluded comparison with other bony fishes. We suggest that a similar approach, applied to other little studied species, could help fill the gaps in ichthyological knowledge, as represented, e.g., in FishBase ([www.fishbase.org](http://www.fishbase.org); accessed on 15 December 2021).

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