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The Sizes, Growth and Reproduction of Arrow Worms (Chaetognatha) in Light of the Gill-Oxygen Limitation Theory (GOLT)

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Abstract: The Chaetognatha are a marine invertebrate phylum including 132 extant, carnivorous species in nine families and two orders, but with unclear protostomian affinities in the animal kingdom. We document the gradual recognition of the distinctiveness of chaetognaths by early taxonomists, with some emphasis on the often-overlooked studies by Chinese marine biologists. The carnivorous arrow worms are understudied relative to their importance in the marine zooplankton, where they rank second in abundance after the herbivorous copepods. Although arrow worms lack gills or other dedicated respiratory organs, we show that the Gill-Oxygen Limitation Theory (GOLT) can be used to explain how temperature and respiration affect their growth and related life-history traits. Notably, we present a reappraisal of evidence for size–temperature relationships between and within chaetognath species, and for the relationship between their temperature-mediated oxygen demand and their growth patterns. Von Bertalanffy weight growth curves of *Ferosagitta hispida* (family: Sagittidae) based on earlier aquarium experiments by various authors are presented, which suggest (a) a good fit and (b) that the life span of chaetognaths is much lower than suggested by the authors of several published growth curves drawn onto length–frequency samples from the wild. In addition, we show that chaetognaths attain first maturity at a fraction of the maximum length they can attain that is similar to the corresponding fraction in fishes. Overall, we suggest that the manner in which the oxygen they require enters the body of small marine invertebrates, although often neglected, is a crucial aspect of their biology. In addition, based on our result that arrow worms conform to the GOLT, we suggest that this theory may provide the theoretical framework for the study of growth in the other water-breathing ectotherms lacking gills.

Keywords: von Bertalanffy; respiration; morphometrics; growth; size–temperature relationships

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1. Introduction

The Chaetognatha (i.e., "bristle jaws"), or arrow worms (Figure 1), belong to a marine invertebrate phylum with unclear protostomian affinities in the animal kingdom, and are spread through all oceans from the surface down to 5000 m, with a 6000 m record to be confirmed. Of the 132 extant species currently recognized [1], 58% are pelagic, and 42% benthopelagic or benthic [2]. In the marine zooplankton, their biomass is about 1/3 that of copepods globally, and over 1/5 of the total zooplankton in the North Atlantic [3]. The maximum sizes of chaetognaths range over two orders of magnitude, from 1.3 mm in *Spadella boucheri* [4] to 105 mm in *Pseudosagitta gazellae* [5,6]. Arrow worms are carnivorous, feeding preferentially on copepods, but also on other small invertebrates and fish larvae [7–9]. While a few species are reported to consume bacteria and particulate or dissolved matter, e.g., in the nepheloid layer and polar areas [10–12], as an adaptative response to the scarcity of prey, more studies are required on more species to generalize these food sources for the entire phylum. In turn, chaetognaths contribute substantially to the zooplankton consumed by commercially exploited fish [13].

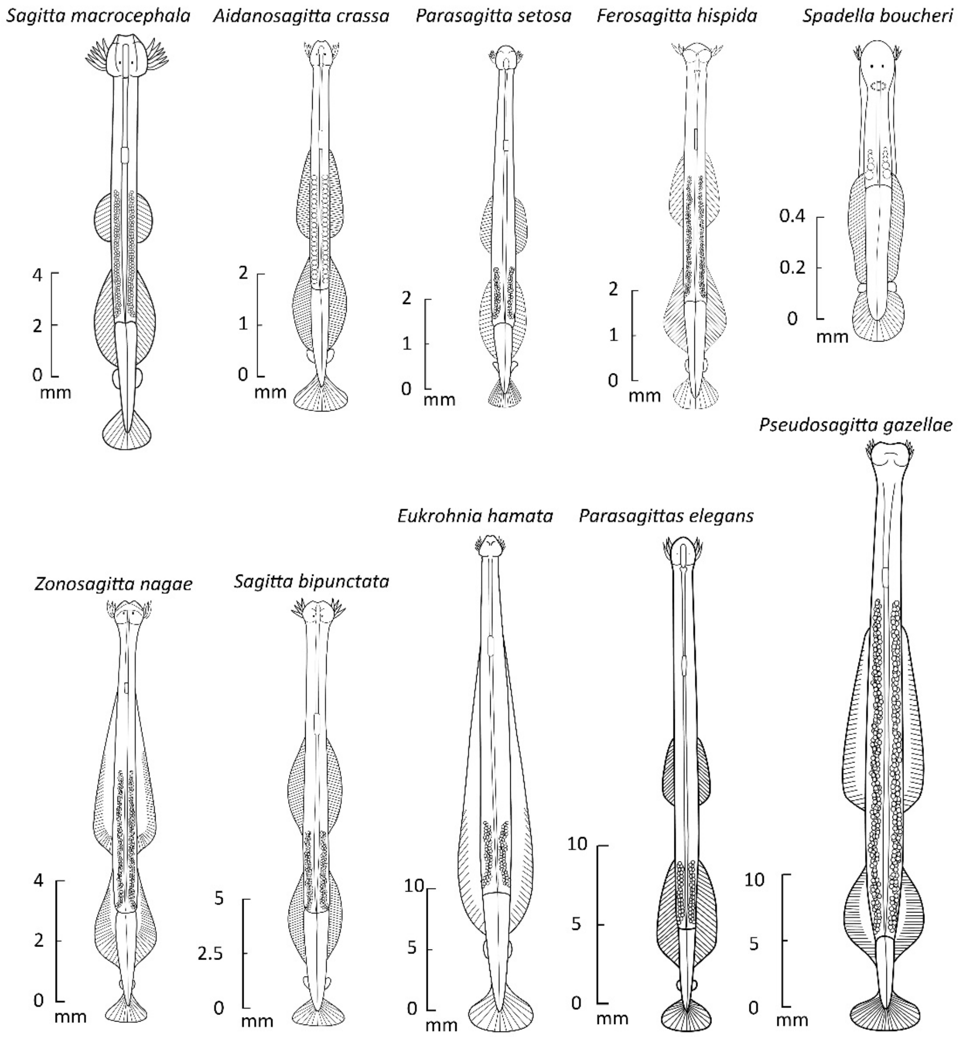

Figure 1. Illustrating the uniformity of body shapes with the phylum Chaetognatha, which includes species ranging in maximum body length from 1.3 mm in *Spadella boucheri* to 105 mm in *Pseudosagitta gazellae* (redrawn by E. Chu from multiple sources).

Here, we document, based on a brief review of the zoological literature spanning the years 1771 to 1911, the gradual recognition of the distinctiveness of chaetognaths by early taxonomists, and the establishment in 1965 of their currently accepted classification. Then, we briefly focus on the often-overlooked studies by Chinese scientists. This sets the stage for a reappraisal of the knowledge about the growth and reproduction of chaetognaths as related to oxygen consumption, as outlined in the Gill-Oxygen Limitation Theory (GOLT; [14–16]), which was developed to explain the growth of gilled marine organisms. Although chaetognaths lack gills [17], the GOLT is used here to explain thus-far neglected aspects of the biology of arrow worms, in particular their growth and reproduction, and their relationships to temperature.

The GOLT is based on the observation that water-breathing ectotherms (WBE) obtain their *supply* of oxygen through a surface (that of their gills, or through another surface in gill-less WBE), but that this surface cannot, for geometric reasons, keep up with the growth of the body whose mass generates the oxygen *demand*. Thus, as WBE grow, their oxygen supply per unit weight must decline, which impacts their growth and reproduction, both of which are oxygen-dependent [16].

When water-breathing ectotherms (WBE) have hard parts, such as bones, otoliths and scales in fish, or statoliths in squids, the age at different sizes can be estimated by counting annual rings in long-lived fish exposed to marked summer–winter differences in the temperature of their habitats, or daily rings in otoliths or statoliths [15]. Unfortunately, arrow worms do not have statoliths [18]. Thus, the growth of chaetognaths must be inferred from specimens grown in the laboratory, or from the analysis of length–frequency (L/F) data sampled in the wild. However, there are many misunderstandings about the correct way to infer growth from L/F data. Many authors place great emphasis on identifying the peaks of their various L/F samples, assumed to represent cohorts. On the other hand, they place less emphasis on the criteria they (should) use for linking the peaks of successive L/F samples with each other, although this is the very process that generates growth increments upon which growth curves can be based [19].

Increased temperatures, by increasing Brownian motion and hence the shocks between water molecules and proteins, reduce the half-life of the proteins in the bodies of WBE. The denatured proteins must be resynthesized, thus increasing O_2 consumption. When the water around WBE becomes warmer, their asymptotic length and weight should thus decline (as per the interpretation of Equation (3) below in Material and Methods). Thus, with regard to growth, the applicability of the GOLT to arrow worms can be tested via three hypotheses:

1. Species living in colder water will tend to be larger than those living in warmer temperatures, other factors being equal.
2. Within different populations of the same species, maximum size and mean size at first maturity should decline with temperature.
3. The growth of chaetognaths should conform to the VBGF.

In the absence of gills, arrow worms breathe through their integument, i.e., body walls [20]. Thus, their respiratory surface area is small and cannot be very thin because it also functions as part of their hydrostatic skeleton [21]. Therefore, as our fourth hypothesis, we expect that:

4. Arrow worms should remain small (compared, e.g., with other zooplanktivorous WBE, such as anchovies) and exhibit growth performances (requiring a high O_2 supply) that are very low (again compared to fishes).

Finally, with regards to reproduction and given the GOLT, we suggest that:

5. In a given population, chaetognaths reach maturity at a fraction of their maximum length that is similar to the fraction that would occur in fish of the same size.

2. Materials and Methods

2.1. Taxonomy and Compilation of Chaetognath Life Traits

Five main databases were primarily consulted for gathering data. WoRMS was used to provide the current chaetognath taxonomy [1], and distributions that included point data came from OBIS [22]. The Biodiversity Heritage Library [23] was used to consult the early taxonomic works. Additional taxonomic data were also extracted from information compiled in the framework of LifeWatch Greece [24]. SeaLifeBase [2] was used to obtain maximal lengths and benthic/benthopelagic/pelagic assignments, adapted mainly from the "Chaetognatha of the World" website [25]. Species authorities are given in Supplementary Materials S1.

When the required data were missing in these databases, they were mainly extracted from the original descriptions, following a search for other taxonomic and systematic literature. This was the case for species described since the mid-1980s, and for the minute species in the family Spadellidae, which generally have a restricted distribution area, both of which include many species known only from their original descriptions.

Latitudinal ranges were estimated visually from maps based on OBIS occurrence records, from the geographic coordinates of the type localities, or from the literature.

The mean latitude (*LAT*) was computed from the latitudinal range as the mean of the averages in two hemispheres, and rounded to the closest $\frac{1}{4}$ of a degree, as follows:

$$LatNRM = \text{northernmost latitude},\ LatSRM = \text{ southernmost latitude} \tag{1}$$

$$LAT = (|LatNRM - 0|\ /\ 2\ +\ |0 - LatSRM|\ /\ 2))/2 = (|LatNRM|\ +\ |LatSRM|)\ /\ 4 \tag{2}$$

The list of the 132 currently valid species of chaetognath, their mean latitude of occurrence, occurrence along China's coast (Y/N), habitat assignments (pelagic, benthopelagic, and benthic), and maximum body lengths (mm) are documented in Supplementary Materials (Table S1).

2.2. Morphometrics

To enable us to estimate the volume (and hence the weight) of individual arrow worms from their lengths, we assumed that their body is composed of successive cylinders, each with a different circumference, as estimated from successive width of the drawings representing them. For each cylinder, the maximum rectangular area (S), as well as the length of the rectangle, i.e., the height of the cylinder (h), was obtained by using the ImageJ software. Then, the width of the rectangle, i.e., the diameter of the cylinder (R), can also be calculated according to $R = S/h$, while the volume can be computed from $V = \pi r^2 h$, where $r = R/2$. The head of an arrow worm can be taken as a half-sphere. The volume of a sphere is $(4/3)\pi r^3$, and half of that is $V = (2/3)\pi r^3$. Thus, we obtained the volume of an arrow worm by adding successive cylinders to a half sphere.

2.3. Growth, Growth Comparisons, and Longevity

The concepts to be presented below apply to animals that breathe in water (i.e., WBE), and thus can be applied to arrow worms. The growth of WBE can be represented by

$$\mathrm{d}W/\mathrm{d}t = HW^d - kW \tag{3}$$

where $\mathrm{d}W/\mathrm{d}t$ is the rate of growth in terms of weight—W (or more precisely mass), d is a scaling factor <1, and H and k are coefficients expressing the synthesis of the body's proteins ("anabolism") and the denaturation of the same proteins ("catabolism"), respectively. As defined here (see Pauly [15,16] for details), anabolism is proportional to the oxygen (O_2) supply to the body because O_2 and, hence, ATP are required for synthesis. On the other hand, catabolism is weight-proportional because all protein molecules in the body, due to thermal noise, lose the quaternary structure required for their specific functions at rates that determine their half-lives [26–28].

If the scaling factor d in Equation (3) is assumed to be equal to 2/3, this equation can be integrated into a growth curve known as the von Bertalanffy growth function (VBGF), which has the following form:

$$L_t = L_\infty\left(1 - \mathrm{e}^{-K\cdot(t-t_0)}\right) \tag{4}$$

where L_t is the mean length at age t of the animals in question, L_∞ their asymptotic size, i.e., the mean size attained after an infinitely long time, K expresses how fast L_∞ is approached (herein, year^{-1}), with longevity $\approx 3/K$, and t_o is a parameter adjusting for the fact that the VBGF usually fails to describe the growth of the earliest (larval) stages of WBE. Thus, t_o, by representing the age WBE would have at a size of zero, if they had always grown in the manner predicted by the equation, allows the VBGF to correctly represent length-at-age in post-larval stages [19].

The VBGF for length growth can be straightforwardly transferred into an equation for growth in weight by combining a length–weight relationship (LWR) of the form: $W = a \cdot L^b$ with Equation (4). The VBGF for growth in weight is, thus,

$$W_t = W_\infty \left(1 - e^{-K\cdot(t-t_0)}\right)^b \tag{5}$$

where W_∞ is the weight corresponding to L_∞, b is the allometry coefficient, and all other parameters are defined as above.

The literature on the growth of chaetognaths includes many examples of growth curves whose author(s) presupposed slow growth. This has resulted in "cohorts" being subjectively created whose growth curves extended to well over a year, sometimes two [29,30], and including long periods of near-zero growth at minuscule sizes (see, e.g., Zo [31]).

Here, rather than tracing our own growth curves and adding to the confusion, we analyzed a set of previously published "mass-at-age" data generated by Hirst and Foster [32] based on aquarium experiments (see Supplementary Materials, Table S2). We fitted Equation (5) with $b = 3$, using Microsoft Excel's Solver routine after removing the data point representing larval growth (the deleted data points are documented in Table S2).

For comparisons of growth performance within and between different chaetognaths species, and between chaetognaths and other WBE, one can use the index

$$\varnothing\prime = \log(K) + 2\cdot\log(L) \tag{6}$$

which is relatively constant within species (and higher taxa with similar shapes), as assessed by studying and relating hundreds of L_∞–K data pairs (see Pauly [15,19], Binohlan and Pauly [33]; see also "Life history" in FishBase [13]). However, to allow for comparisons that take into account the different shapes that different clades of WBE can have, we use the index

$$\varnothing\prime = \log(K) + 2/3\cdot\log(W) \tag{7}$$

which assumes LWRs with slopes b = 3, as commonly occurs in WBE.

2.4. Oxygen, Temperature, and Arrow Worms

The total amount of O_2 which can diffuse into the body of a WBE per unit time follows Fick's law of diffusion:

$$Q\prime = \mathrm{d}P\cdot U\cdot G\prime\cdot WBD^{-1} \tag{8}$$

where Q' is the oxygen uptake ($\mathrm{mL\cdot h^{-1}}$); dP is the difference between the oxygen partial pressure on either side of the respiratory membrane (in atm); U is Krogh's diffusion constant, that is, the amount of oxygen (in mL) which diffuses through an area of 1 mm^2 in one minute for a given type of tissue (or material) when the pressure gradient is one atmosphere (1013.25 hPa) of oxygen per μ (micron); G' is the total respiratory surface, and WBD is the water–blood distance, that is, the thickness of the tissue between the surrounding water and the interior of the body in μ [34].

Of the four parameters of Equation (8), which determine the value of Q', only G' may be assumed to vary greatly as body size increases, thus making the respiratory surface area the key factor limiting oxygen uptake in WBE. The GOLT is structured around the fact that gills, because they have to function as a 2D surface in contact with the water that delivers oxygen, cannot keep up with the growing 3D bodies they have to supply with oxygen.

2.5. Reproduction

In fishes, mean length at first maturity (L_m, i.e., the length at which 50% of the individuals are mature) occurs at ${L_{max}}^D/{L_m}^D \approx 1.35$, with $D = 3(1\text{-}d)$ [16,35,36].

Here, we also tested whether chaetognaths reach maturity and spawn at a fraction of their maximum length (L_{max}) that is similar to that of fishes. Note that since post-larval chaetognaths maintain their basic shape as they grow, their integument (i.e., their respiratory surface) should grow in proportion to 2/3 of their weight, i.e., d ~ 0.67. Given its definition, this means that, for chaetognaths, D = 1, and, hence, $L_{max}{}^{D}/L_{m}{}^{D} = L_{max}/L_{m}$.

3. Results

3.1. Early Illustrative and Taxonomic Work on the Chaetognatha, or Arrow Worms

The first published record and drawing of an arrow worm, from the North Sea, are in Slabber [37] (46–48; Pl. 6, S4), where it was described as a "sea-worm". Slabber coined the Latin name *Sagitta* (arrow) and the Dutch name "*pyl*" ("*pijl*" = arrow) for his sea-worm. For the precise dates of Slabber's publication, see Hoeven [38], Benthem Jutting [39], and Welter-Schultes [40]. *Sagitta* Slabber, 1771 is not "available" as a generic name in nomenclatural terms because he did not describe a species or refer to an existing one. The drawing was later identified as *Parasagitta setosa* (J. Müller, 1847) [41].

In 1825, Blainville mentions a genus within a family of pelagic mollusks as "G. Sagitelle Lesueur" [42] (T1:492), noticing that Lesueur described that genus and one species from "warm seas", but that it may represent several species. In a complementary note dated from 1827 [42] (T2:656), he explained that Lesueur had described *Sagitella aequipinnis* and two other species (whose names were not cited) from the Caribbean Sea, in a manuscript, "Monog. des Ptérop. Pl. 11, Figures 1–3", that was apparently never published ([43], p. 645). In another publication dated from the same year, Blainville [44], who obviously had access to that manuscript, detailed the description of the three species under the French common and Latin scientific names coined by Lesueur: *Sagitella aequipinnis*, *Sagitella tuberculata*, and *Sagitella inaequipinnis*.

Blainville also listed *Sagitta* (with the species name *Sagitta bipunctata* Quoy & Gaimard [45]) with this comment: "*MM. Quoy et Gaimard viennent d'établir sous cette dénomination un petit genre de malacozoaires, qui semble être extrêmement rapprochés des sagittelles de M. Lesueur.*" (MM. Quoy and Gaimard just established under that name a small genus of malacozoa, which seems very close to the sagitelles of M. Lesueur). This has been overlooked by most of the subsequent authors, except Eydoux and Souleyet [43]. The possible nomenclatural anteriority within the year 1827 remains to be investigated since only a French vernacular generic name was mentioned without a species in 1825, along with the homonymies of the genus.

The first valid description of a chaetognath species currently recognized is from 1827, and pertains to *Sagitta bipunctata* from Gibraltar (Quoy and Gaimard [45] (232, Pl. 8C, S4). Shortly thereafter, Charles Darwin sketched an arrow worm in his *"H.M.S. Beagle"* field notes [46] and later wrote about their abundance and biology [17], citing d'Orbigny [47] and Forbes [48] who had meanwhile described three and two new species, respectively (see also Barrett et al. [49], p. 78 and 479).

The name Chaetognathi ("bristle jaws"), was coined by Leuckart when he proposed that the genus *Sagitta* should be separated from the other groups of "Vermes": "At the moment, it seems most natural to regard the Sagittas as representatives of a small group of their own that makes the transition from the real annelids (first of all the lumbricines) to the nematodes, and may not be unsuitably named [Chaetognathi]." ([50], p. 335; translated from German).

This settled the issue of the identity of chaetognaths, which until then had been viewed as mollusks, annelids (oligochaetes), nematodes, gordians, gephyreans, and tardigrades. Eventually, Leuckart ([51], p. 117) emended Chaetognathi to Chaetognatha in a short note reiterating his conclusions. Hertwig [52] endorsed that name: "Gegenbaur ([53], p. 138) called the newly created division the Oesthelminthes, Harting ([54], p. 617) the Pterhelminthes and Leuckart ([50], p. 335) the Chaetognaths [Chaetognathen]. I keep this latter name for the description of the order, since it has priority and it has become common in literature." ([52], p. 8; translated from German).

After Leuckart [50], and before "phylum" was commonly used as a taxonomic rank, the chaetognaths were variously listed as an order or a class in Vermes. This ended when Grassi ([55], p. 5) separated them as a group with unknown affinities. Today, molecular studies have clearly demonstrated that they have protostomian rather than deuterostomian affinities (e.g., [56,57]) as was long thought because of their peculiar ontology. However, these studies have failed so far to firmly establish their sistership in that lineage. Several hypotheses were tested for the past 25 years without a clear consensus, although the latest analyses related them to the Gnathifera (e.g., [58]). Barthélémy and Casanova [59] even provided a reappraisal of the molluscan sistership hypothesis, ironically their first placement by Blainville ex Lesueur [42,44] and Quoy et Gaimard [45], based on morphoanatomical and other zoological methods. Under both hypotheses, however, the chaetognaths would remain within the Spiralia clade.

After 1844 and until 1910, 66 species and five genera were described. Ritter-Záhony [60] published the first and only exhaustive revision of the group together with two new species, but reduced the number of valid species to 27 in six genera, and 16 *incertae sedis* species. No family was defined.

After 1911 and until 1965, 52 species and six genera were described. Tokioka [61] reviewed the classification by establishing two classes, two orders (and two suborders), four families, and six genera, validating 58 species (and seven infraspecific taxa) in 15 genera and five families (of which four were new ones), and 11 *incertae sedis* species. The class Archisagittoidea contained the fossil *Amiskwia sagittiformis* Walcott, 1911 (now seen as a stem group of Chaetognatha but a crown group of Gnathifera [62], or a stem group of the Gnathostomulida or the Gnathifera [63], both hypotheses remain in the Gnathifera clade). He divided the class Sagittoidea established for the extant species into two orders, Aphragmophora and Phragmophora. Several further attempts to establish new subclasses, orders, or suborders (including those of Tokioka) failed to survive subsequent morphoanatomical and molecular analyses.

Tokioka's general classification (with adaptations by Bieri [64,65]) is still in use with the additional taxa described since, and today contains 132 valid species in 26 genera, nine families, and two orders [1] (Table S1). Several unequivocal fossil chaetognaths have been described (e.g., [66,67]), but placed each in their own family without ordinal classification. Gasmi et al. [68] proposed some adjustments based on their most comprehensive molecular phylogeny so far, but their suggestions have not yet been integrated in a proper taxonomic framework.

3.2. Chinese Studies on Arrow Worms

A total of 37 chaetognath species are reported from China's waters [69] (see also Table S1), where they are distributed over a wide range of depths.

Research on the chaetognaths of China began in 1919 with the investigation of the "Albatross" [70]. However, with the exception of Hsü [71] reporting chaetognaths from China's coastal areas, and Sproston [72] from the waters of the Zhoushan Archipelago, there was no follow-up until the late 1950s, when China launched successive surveys of marine systems and fishery resources. These surveys included zooplankton studies, especially the national comprehensive marine survey from 1958 to 1960, which laid the foundation for China's research on chaetognaths.

The initial research on chaetognaths in Chinese coastal areas mainly focused on their taxonomy and occurrence. In the 1980s, the research interest began to shift to chaetognath ecology, such as species composition [73,74], species diversity [75], quantitative distribution [76,77], vertical movement [78], ecology, including the relationship with oceanographic features [79–82], and feeding ecology [83].

However, most of these studies were based on survey data, and experimental research on the ecology of chaetognath is still rare. Liu et al. [84] conducted preliminary studies on the tolerance to temperature and salinity in *Aidanosagitta crassa*, which established that their survival rates were higher at lower temperatures. Liu et al. [85] also studied the effects of different temperature and salinity on the oxygen consumption rate of *A. crassa*. Based on monthly sampling data at a station in Jiaozhou Bay in the Yellow Sea in 2006, Huo et al. [86] demonstrated a negative relationship between body length and average water temperature in *A. crassa* (see below).

3.3. Body Length in 132 Species: Relation to Temperature and Habitat

The maximum recorded body lengths (*BL*, in mm) for the 132 species of chaetognaths currently recognized were related to the mean latitude of their distribution range (LAT, in degrees north or south; a proxy for temperature [87,88]) and their habitat through the multiple regression

$$\log(BL) = 0.616 + 0.445 \cdot \log(LAT) - 0.580 \cdot B - 0.354 \cdot BP \quad (9)$$

where *B* is a dummy variable (*B* = 1 for benthic and 0 for pelagic and benthopelagic species), and *BP* is another dummy variable (*BP* = 1 for benthopelagic and 0 for pelagic and benthic species).

The multiple correlation coefficient R = 0.573, which implies that this model, with $R^2 = 0.329$, explains more than 30% of the variance in the dataset in Supplementary Table S1. In addition, its partial slopes have the expected signs and are significantly $\neq 0$ ($p < 0.001$; see Table 1). Equation (9) implies that chaetognath species tend to be smaller the closer they are to the equator, but also that the 14 benthic speces are, on average, 3.8 times smaller than the 77 pelagic species, while the 41 benthopelagic species tend to be 2.3 times smaller than the pelagic species, i.e., intermediate, as may be expected (Figure 2). Figure 2 also suggests that some species are misclassified, e.g., benthopelagic species labelled as pelagic or benthic species.

Table 1. Estimated coefficients of a multiple regression of log(body length) against log(latitude) and two dummy variables defining the habitat of three groups of chaetognath species [a].

Parameter	Coeff.	SE	t-stat.	*p*-Value	Lower 95%	Upper 95%
Intercept	0.632	0.153	4.124	0.000066	0.329	0.936
log(LAT)	0.445	0.114	3.880	0.000166	0.218	0.672
B (benthic)	−0.580	0.086	−6.711	< 0.00001	−0.752	−0.408
BP (benthopelagic)	−0.354	0.062	−5.726	< 0.00001	−0.477	−0.232

[a] There are 77 pelagic species (with B and BP = 0), 14 benthic, and 41 benthopelagic species.

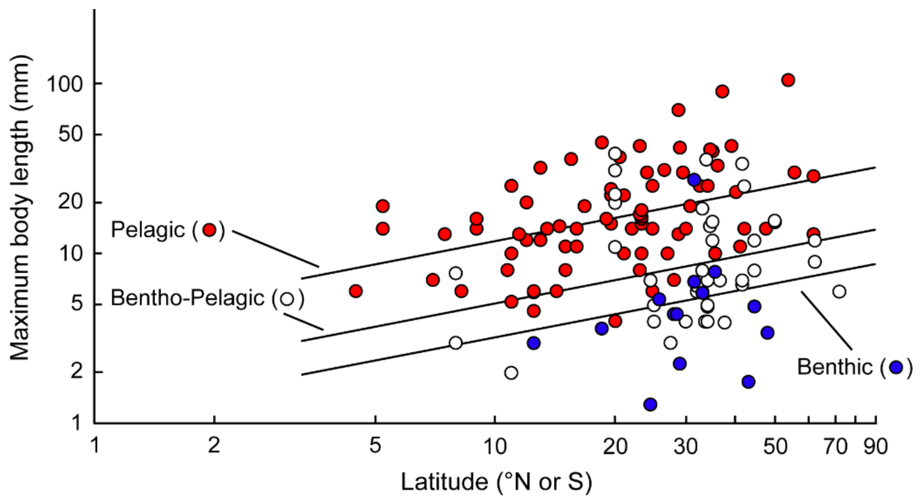

Figure 2. Relationship between the maximum body length of the 132 species of extant chaetognaths and the mean latitudes of their distribution ranges (as proxy for sea surface temperature); see also Equation 9 and Table S1. On average, pelagic species (n = 77) are 2.3 times longer than benthopelagic species (n = 41) and 3.8 times longer that benthic species (n = 14). This figure also suggests that the habitat of some of the species in Table S1 may have been wrongly assigned.

3.4. Body Lengths in Three Chaetognath Species Experiencing Different Water Temperatures

Figure 3 presents size–temperature relationships in three chaetognath species, *Parasagitta elegans*, *Aidanosagitta crassa*, and *Ferosagitta hispida*, based on data published by McLaren [89], Zo [31], Huo et al. [86], Reeve [3], Reeve and Walter [90], and Reeve and Baker [91].

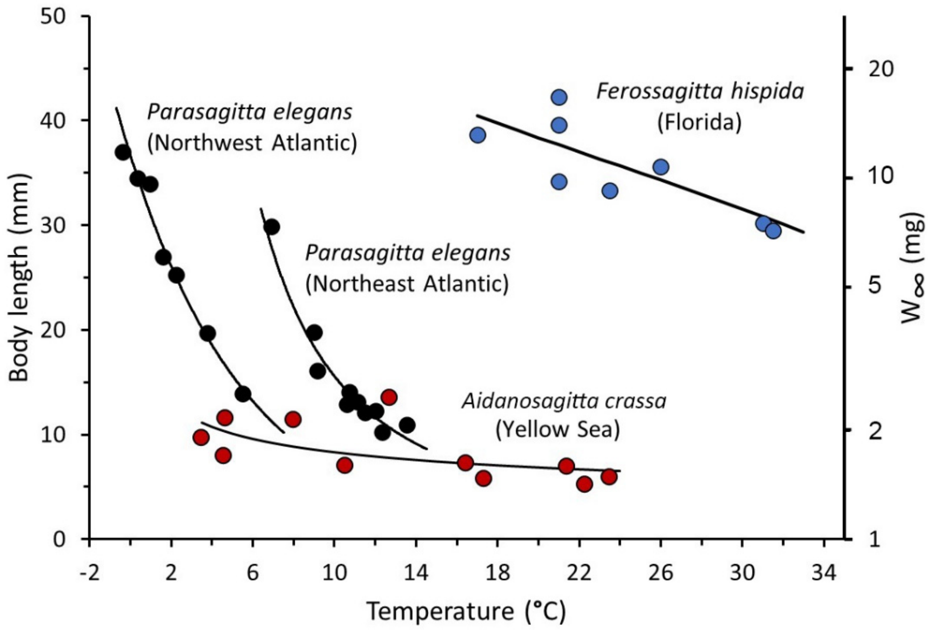

Figure 3. Relationship between the size (body length or W_∞, i.e., asymptotic weight) of 3 species of chaetognaths and the mean temperature of the water in which they live or were raised. The body lengths and the curves for *Parasagitta elegans* (black dots) in the North Atlantic were redrawn from Figure 1 in McLaren [89], and the (red dots) points for *Aidanosagitta crassa* in the Yellow Sea are from Huo et al. [86], with a curve replacing their straight line. The blue dots refer to *Ferosagitta hispida* from coastal waters in Florida (based on data from Reeve [3], Reeve and Baker [91], and Reeve and Walter [90]), see text.

As might be seen, body size in these three species and, by extension, in other chaetognaths as well, decreases with temperature, as predicted by the GOLT.

3.5. Morphometrics and Growth of Chaetognaths

Table S3 presents estimates of the surface area of the body of six species of chaetognaths (excluding fins), and the corresponding volume of their bodies, based on published drawings of adult specimens. These data allowed two general patterns to be established (Figure 4). One is that the surface area of the body of chaetognaths (S) can be predicted from their body length (L), using $S = 0.232 \cdot L^{1.92}$ when the surface is in mm^2 and the length in mm (Figure 4A). The other is that the relative surface of the body (i.e., the respiratory surface per unit volume) declines with volume (S/V; Figure 4B) according to $S/V = 511 \cdot L^{-0.90}$ when S/V is expressed in cm$^2 \cdot$g^{-1} and length in mm. In both cases, the relationships are near isometric, with the former relationship not significantly lower than 2, and the latter not significantly higher than -1.

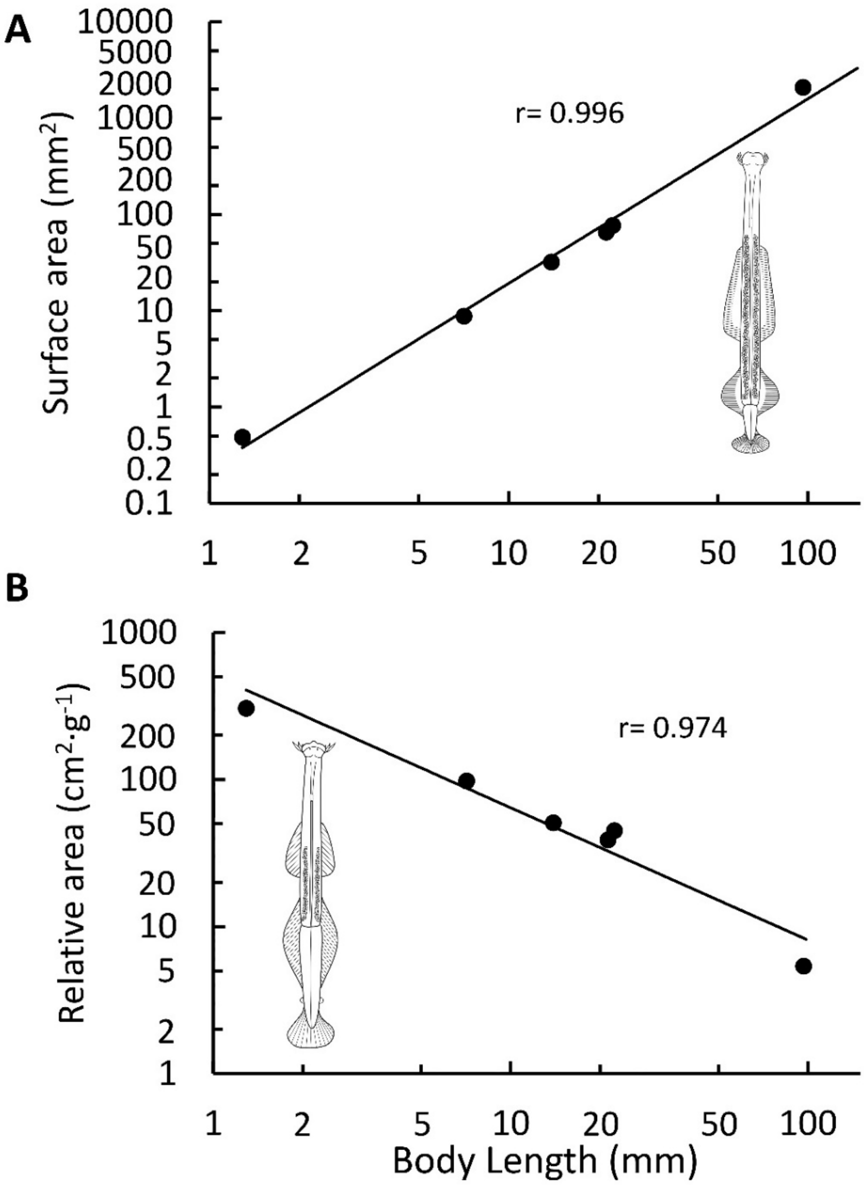

Figure 4. Demonstrating the relationships between the body length of 6 individual chaetognaths representing 6 species, (**A**) the surface area of their bodies (fins excluded), and (**B**) their surface area/volume (based on the measurements in Table S3).

The latter trend establishes that large chaetognaths will be challenged in acquiring, by diffusion through their integument, the oxygen they need to sustain their activity and growth. This is the reason why the largest chaetognath, *Pseudosagitta gazellae*, reaching 10.5 cm, occurs only in Antarctic water, where the low temperature keeps its oxygen requirement low, and perhaps also why the water content of chaetognaths appears to increase with their size (Table 2).

Table 2. Dry weight of chaetognaths in % of their wet weight.

Species	BL [a]	Location	% Dry Weight	Source
P. gazellae	105	Antarctica	5.3	Ikeda and Kirkwood [6] (Table 2)
P. elegans	30	NS, Canada	9.0–10.9	Pearre [92] (Table 4); Harrison [93]
Z. nagae	25	East China Sea	7.7	Feng [94], p. 56
P. setosa	14	Off Plymouth	9.3	Harrison [93] (Table I)
F. hispida	11	Near Miami	15.2	Reeve et al. [95] (Table 1)
A. crassa	10	Yellow Sea	14.4	Feng [94], p. 51
12 species	–	Various	9.3	Kiørboe [96] (Table 1)
Several spp.	–	Various	10.0	Thuesen and Childress [97] (Table 1)

[a] Maximum body length, in mm.

Sameoto [98], working with *Pseudosagitta elegans*, obtained a mean slope of 0.69 for the relation between the logarithm of their metabolic rate and their (dry) weight (see Ikeda and Kirkwood [6]); similarly, Kruse [99] (p. 119/120) obtained a mean slope of 0.664. This justifies the use of the VBGF not only to describe empirically the growth of arrow worms, but also as a "physiologically correct" model of their growth, because the parameter d in Equation (3), which is assumed to be 2/3 in the VBGF, actually took values near 0.667 in chaetognath respiration studies.

On the other hand, the data in Table 2 show that the chaetognaths with dry weights that are about 10% of their wet weights are intermediate between the jellyfish, with 5 to 2% [100] and other WBE with 20–30% [101,102]. Note the tendency for large species to have a higher water content, confirming Kiørboe [96].

Fitting the "mass-at-age" data for *Sagitta hispida* in Table S2 and the observed size-at-age data of Reeve [3] with Equation (5) yielded the growth parameters in Table 3 and the growth curves in Figure 5.

Table 3. Growth parameters of *Ferosagitta hispida* raised in aquaria and estimated from "mass-at age" data of Hirst and Foster [32], as documented in Tables S2A and S2B (panels A–G in Figure 5) and size-at-age data in Figure 2 of Reeve [3], as documented in Table S2B (panel H in Figure 5). All samples originated from coastal water in Florida, USA.

Case	Temp (°C)	W_∞ (mg) [a]	K (year^{-1})	t_0 (year)	Ø [b]	Data Sources
A	21	16.7	31.09	0.0045	0.308	Reeve and Baker [91] (Figure 1)
B	31	7.5	88.07	0.0024	0.528	Reeve and Baker [91] (Figure 1)
C	17	13.1	41.75	0.0072	0.367	Reeve and Walter [90] (Figure 3)
D	21	14	43.79	0.0077	0.406	Reeve and Walter [90] (Figure 3)
E	23.5	9.2	72.51	0.0037	0.504	Reeve and Walter [90] (Figure 3)
F	26	10.7	83.67	0.0035	0.609	Reeve and Walter [90] (Figure 3)
G	31.5	7.1	97.00	0.0027	0.556	Reeve and Walter [90] (Figure 3)
H	21	9.8	53.37	0.0033	0.387	Reeve [3] (Figure 2)

[a] Converted to wet weight by multiplying by 10 (see Table 2) the values in Table S2, and computed from lengths via $W = 0.001 \cdot L^3$ (see text).
[b] Computed with W_∞ in g, facilitate comparison with fishes; mean Ø = 0.458.

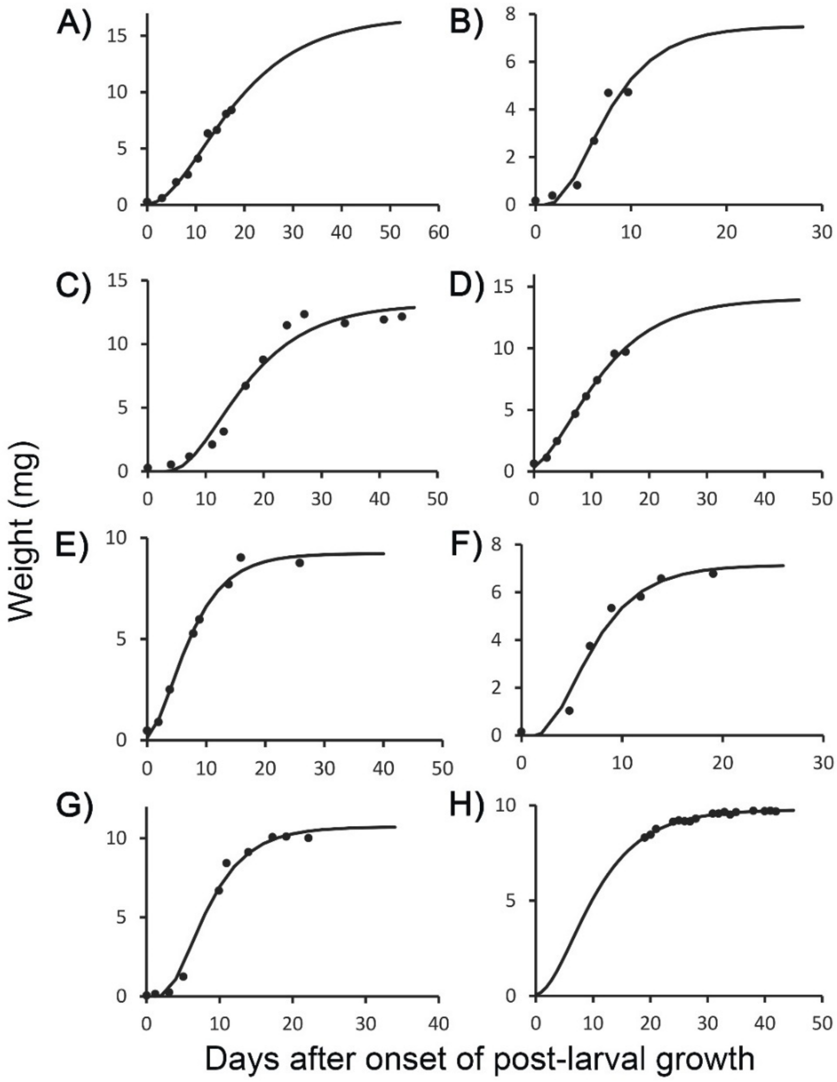

Figure 5. Weight growth curves of *Ferosagitta hispida* based on the "mass-at-age" or length-at-age data converted to wet weight by multiplying by 10 the values in dry weight documented in Table S2. Case (**A**–**H**) (see also Table 3).

Table 4 compares the growth of *Ferosagitta hispida* (and the inferred growth of *Pseudosagitta gazellae*) to that of a few fish species, illustrating how limited the growth performance of chaetognaths is, compared to even slow-growing fishes.

Table 4. Comparison between the growth performance of 6 species of fish and 2 species of chaetognaths.

Species [a]	W_∞ (g)	K (year $^{-1}$)	Ø (logK+ 2/3logW_∞)
Thunnus albacares	198,940	0.250	2.93
Morone saxatilis	17,543	0.186	2.10
Mugil cephalus	13,890	0.110	1.80
Trigla gurnardus	534	0.312	1.31
Callionymus lyra	53	0.490	0.84
Cottus bubalis	102	0.230	0.70
Pseudosagitta gazellae [b]	≈1	(4.86)	(0.458)
Ferrosagitta hispida [c]	≈0.01	55	0.458

[a] The 6 species of fish are documented in Pauly (1981). [b] Assuming that the mean Ø estimates from Table 3 also applies to *P. gazellae*. [c] See Table 3.

3.6. Reproduction in Chaetognaths

Figure 6, based on Table 5, shows that in chaetognaths, L_{max}, when plotted vs. L_m in a regression with zero intercept, leads to a slope of 1.30, which is close to the estimate of 1.35 for teleosts [35,36], and well within its 95% confidence interval of 1.22–1.53 (see Pauly [16]). This suggests that maturity, in chaetognaths, is triggered by the oxygen supply to their tissues dropping, as they grow and their surface area/volume ratio declines, to a level near 1.3 times their maintenance metabolism, as also occurs in fish [16,35].

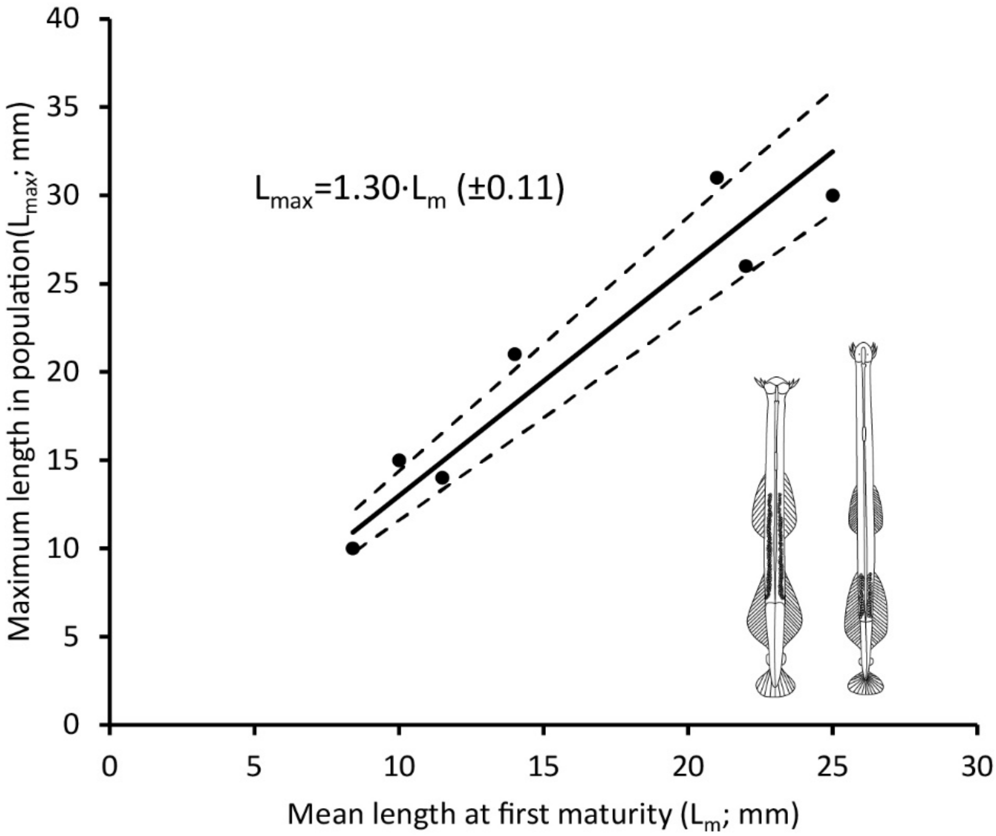

Figure 6. Maximum lengths (L_{max}) vs. lengths at maturity (L_m) of 4 species chaetognaths (n= 7; from Table 5), fitted with a linear regression with a zero intercept. The estimated slope is 1.30, with a 95% confidence interval (C.I.) of 1.19–1.41, which overlaps with the slope of $L_{max}{}^D$ vs. $L_m{}^D$ in fishes (1.35; C.I. = 1.22–1.53); see text.

Table 5. Approximate length at maturity (L_m) and maximum length (L_{max}) of chaetognaths (in mm).

Species	Place/Time	L_m	L_{max}	Source
P. elegans	Bedford Basin, May–June 1968	21	31	Zo [31] (Figure 2)
P. elegans	Plymouth, September 1930	10	15	Russell [103] (Plate I)
P. elegans	Plymouth, May 1930 & 1931	14	21	Russell [103] (Plate I)
F. hispida	Laboratory, at ~30 °C,	8.4	10	Reeves and Walters [90] (Figures 3 and 4A)
F. hispida	Laboratory, at ~17 °C,	11.5	14	
E. bathypelagica	Lazarev Sea, Antarctica	22	26	Kruse [99] (Figure 1, p. 68)
E. bathyantarctica	Lazarev Sea, Antarctica	25	30	Kruse [99] (Figure 2, p. 69)

4. Discussion

The distribution of the chaetognaths of both orders, the Aphragmophora and Phragmophora, is different between the two hemispheres; the former has 58 species in the Northern vs. 36 in the Southern Hemisphere, while for the Phragmophora, the corresponding numbers are 56 species in the Northern vs. 15 in the Southern Hemisphere (see Table S1). However, we think that this imbalance is due to a sampling bias rather than a phylogeographic signal. The Aphragmophora are mainly planktonic, and thus have been easily sampled during oceanographic campaigns or surveys, while the Phragmophora are mainly benthopelagic (Heterokrohniidae), and benthic (Krohnitellidae, Spadellidae), i.e., require the targeted and dedicated samplings that have been historically more frequent in the Northern than the Southern Hemisphere.

This becomes more evident when the planktonic Eukrohniidae are added to the Aphragmophora, resulting in 68 species in the Northern and 41 species in the Southern Hemisphere, vs. 48 species in the Northern and 10 species in the Southern Hemisphere for the Phragmophora without the Eukrohniidae.

Benthic chaetognaths are largely understudied around the world. It is symptomatic that many of the minute spadellid species are known only from the type specimens, and that the most recent one (*Spadella kappae*) was described near the "Station Biologique de Roscoff" [104,105], a French marine station established in 1872 on the coast of the English Channel, i.e., in one of the most intensively studied parts of the world's oceans.

The sampling bias hypothesis could be tested by checking the type localities; however, the time since the Spadellidae diverged from more generalized chaetognaths would have to be known. The hypothesis would be rejected if the Spadellidae arose recently in the Northern Hemisphere, and thus did not have time to radiate into much of the Southern Hemisphere. Unfortunately, Gasmi et al. [68] did not provide a time resolution which can be used for such a test.

While all the partial slopes of Equation (9) are significant (Table 1), Figure 2 makes it evident that it is only the pelagic chaetognaths that show a clear tendency toward increased size with increased latitude and the correspondingly higher sea surface temperature. Indeed, for deep benthic species, we should not expect marked changes of size with latitude, because deep-sea temperatures do not change much with latitude, if at all [106]. The observed pattern of size decline with latitude reflects a temperature trend that is well documented in other WBE, including fishes [15,87,88], and it is commonly attributed to the direct impact of temperature on fish metabolism [16]. While other mechanisms could be hypothesized (see, e.g., [107]), they would need to also correlate with temperature and thus would be inherently be less parsimonious than the GOLT, which states that increasing temperatures themselves are the causes for size reduction in WBE [16].

What Figure 2 also suggests is that the habitat assignment of some species may have been erroneous, due to the fuzzy limits between "benthic" and "benthopelagic" modalities, and to uncertainty about the distance from the bottom where the specimens were collected. Habitat assignments, especially for the deep-sea species, while derived by experts, still require confirmation.

It is likely that the temperature–size relationship among chaetognath species in Figure 2 has the same cause as the temperature–size relationship within the three species in Figure 3. However, this relationship works at evolutionary scale in Figure 2, and at ontogenetic scale in Figure 3. The respiratory surface of chaetognaths, which grows approximately with length squared (Figure 4) and limits their oxygen supply (Equation (8)), cannot keep up with their oxygen demand, which grows approximately with length cubed and, similar to in other WBE, must increase when temperatures are high.

In captivity, fish and other WBE usually grow rapidly toward a smaller size than they reach in nature, resulting in lower asymptotic size (length and weight) and higher values of the parameter K when von Bertalanffy growth curves are fitted to their size-at-age data. This may also be the case for the growth curves in Figure 5 and the parameters in Table 3. In any case, these growth curves provide a realistic alternative to many of the hand-traced growth curves found in the literature, some of which suggest longevities as high as 2–3 years.

Indeed, the growth curves in Figure 5 may be realistic despite an early phase of larval growth having been assumed, i.e., the first data points in Table S2 were not used. At least some of the omitted points may correspond to the period between hatching and first feeding that is characteristic of chaetognath larvae, and which can last up to 10 days [108].

Even if preceded by a larval period, the growth curves in Figure 5 suggest that, at least for *Ferosagitta hispida,* the emergence and disappearance of a cohort would occur in a matter of about 2 months, which is possible given the small body length they reach ($\approx$ 1 cm) and the high temperatures to which they were exposed. Thus, our results are compatible with Russell [109] who suggested 5–6 generations per year near Plymouth, and with the four, and six or seven generations per year reported by Murakami [110] and Nagasawa and Marumo [111], respectively, i.e., from areas in the U.K. and Japan that are cooler than Florida.

The Ø-values in Table 3 have a mean of Ø = 0.458. Thus, the largest extant chaetognath, *P. gazellae*, with an asymptotic weight of $W_\infty \approx 1$ g, would have a value of K of 4–5 year $^{-1}$ (see Table 4), which is compatible with having a single cohort per year, as reported by Pearre [108], based on David [112].

Chaetognaths have always posed problems as to their identity and biology, mainly because of their bizarre anatomy, which is unrelated to that of other invertebrate phyla. However, we hope to have shown that concerning some of their physiological traits, they behave similar to other, better-studied WBE. Thus, we could demonstrate that chaetognaths behave as hypothesized, i.e.,

1. Species occurring in colder waters are generally larger than those in warmer waters.
2. Individual chaetognaths reach larger sizes in colder than in warmer waters.
3. The growth of chaetognaths can be described by the VBGF.
4. Chaetognaths remain small and exhibit low growth performance.
5. Chaetognaths mature at a fraction of their maximum size that is similar to that of fish of the same size.

Therefore, we conclude that the chaetognaths conform to the Gill-Oxygen Limitations Theory (GOLT), even though they lack gills.

While there are numerous studies on metabolic rate (i.e., O_2 consumption) of chaetognaths [30,97,98,113,114], very little thought has been devoted to how they breathe, i.e., how they transfer oxygen dissolved in the water surrounding them into their bodies. For example, there is no mention of breathing, respiration, or oxygen in the otherwise wonderfully detailed 12 chapters in the book *The Biology of Chaetognaths* [115].

One author [116] wrote about the long, flagella-like cilia in the gut of chaetognaths that these cilia "*maintain a current in the gut lumen. This may be concerned with respiration or with the removal of dissolved excretory matter liberated by the intestinal cells. Neither circulation of body fluids nor excretory organs have been described in* Spadella *so it may be concluded that the intake of oxygen and the excretion of katabolites takes place at the surface of the body. If these processes occur at the surface of the gut, then some mean would be necessary to renew the water in the lumen. The cilia would provide this means*." However, this is not realistic because it would require either a rapid throughflow (through the vent?) of ingested water or nearly constant swallowing and regurgitation of oxygen-depleted water, none of which has ever been observed.

We think it is unavoidable to infer that the integument of chaetognaths serves as their respiratory organ. However, the integument may be thinner (and thus, given Equation (8), more efficient for respiratory purposes) near the "corona", a group of "*cilia arranged around a depression on the dorsal side of the head and/or neck*" [117] (citing Kapp [118]). The corona is where the cilia generate a flow which contributes "*2 to 3 times more to the oxygen transport than diffusion does*" [117].

However, Bleich et al. [117] conclude, "*While the corona (. . .) may incidentally support respiration, especially for the oxygen supply of brain, eyes and head muscles, this is most probably not its main function.*" They also note that *"the continuous activity of the cilia of the corona* *means a considerable energy investment* [119]. *It lets us conclude that the corona and the generated flow are important to chaetognaths*."

We cannot imagine a function more important for a small organism (which must acquire all the oxygen it needs by diffusion from the boundary layer of water adjacent to its integument) than to induce a flow that would renew the water surrounding them. Indeed, this is necessary if a high O_2 gradient is to be maintained between the surrounding water and its integument.

The GOLT is built around the assumption that animals that must extract the oxygen they require from the water surrounding them will have increasing difficulties breathing as their size increases because the volume of their bodies grows in three dimensions, i.e., faster than the surface area of the gills or other organ through which the required O_2 enters the body.

This "dimensional tension" not only affects growth, but causes the maximum size of WBE to be strongly dependent on temperature, because it not only limits the O_2 content of water, but also increases their O_2 requirements [120].

Demonstrating the limiting effect of size on growth itself and that high temperatures are associated with lower maximum sizes in WBE are both tests of the GOLT's generality. If positive, these tests suggest that the GOLT applies to the WBE in question.

Moreover, if the GOLT applies to a clade of WBE, other inferences can be drawn that may explain some of their other traits. For example, given the estimation of likely von Bertalanffy growth parameters illustrated in Table 4, their food consumption and food conversion efficiency can be estimated [14], as can their productivity, or P/B ratios [121].

These various inferences should facilitate the inclusion of chaetognaths into trophic models of marine ecosystems [122] as an explicit group, rather than an undifferentiated component of "zooplankton" as is currently carried out in most cases; see repository of the nearly 500 such models described by Colléter et al. [123]. They would also allow chaetognaths, despite their taxonomic isolation, to be perceived as responding to the influence of physical constraints in a manner similar to other small marine metazoans.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/jmse9121397/s1. Table S1A: List of the 66 currently valid extant species of chaetognath belonging to the order Aphragmophora. Table S1B: List of the 66 currently valid species of chaetognath belonging to the order Phragmophora. Table S2: Weight-at-age data derived by Hirst and Forster [32] from aquarium growth experiments with *Ferosagitta hispida* by Reeve and Walter [90] and Reeve and Baker [91]. Table S3: Surface area (excluding fins) and volume of the body estimated from drawings of adult specimens of 6 species of chaetognaths. The relative area is in $cm^2 \cdot g^{-1}$ to enable comparisons with other groups. Supplementary Materials S4: Detailed citation for old references.

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Supplementary material S1
List of all the 132 currently valid extant species of Chaetognatha in the classification of WoRMS as of 10 October 2021 [1] with their habitat, maximum length, mean latitude, and presence in China

Supplementary material to:

Pauly, D.; Liang, C.; Xian, W.; Chu, E.; Bailly, N. The sizes, growth and reproduction of arrow worms (Chaetognatha) in light of the Gill-Oxygen Limitation Theory (GOLT). *Journal of Marine Science and Engineering, 9,* doi.org/10.3390/jmse912197.

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Table S1A. List of the 66 currently valid extant species of chaetognath belonging to the Order Aphragmophora.

Family	**Species**	**Habitat assignment**	**Maximum length (mm)[a]**	**Mean latitude[b] of occurrence**	**Occurring in China's seas[c]**
Bathybelidae	*Bathybelos typhlops* Owre, 1973	pelagic	17	23 (N)	No
Krohnittidae	*Krohnitta balagopali* Nair, Panampunnayil, Pillai & Gireesh, 2008	pelagic	6	12.5 (N)	No
Krohnittidae	*Krohnitta pacifica* (Aida, 1897)	pelagic	8	23 (N)	Yes
Krohnittidae	*Krohnitta subtilis* (Grassi, 1881)	pelagic	16.5	23.25 (NS)	Yes
Pterokrohniidae	*Pterokrohnia arabica* Srinavasan, 1986	pelagic	11	15 (N)	No
Pterosagittidae	*Pterosagitta draco* (Krohn, 1853)	pelagic	16	23.25 (NS)	Yes
Sagittidae	*Aidanosagitta alvarinoae* (Pathansali, 1974)	pelagic	19	5.25 (NS)	No
Sagittidae	*Aidanosagitta bedfordii* (Doncaster, 1902)	pelagic	4	20 (N)	Yes
Sagittidae	*Aidanosagitta crassa* (Tokioka, 1938)	pelagic	10	35.5 (N)	Yes
Sagittidae	*Aidanosagitta delicata* (Tokioka, 1939)	pelagic	7	28 (N)	Yes
Sagittidae	*Aidanosagitta demipenna* (Tokioka & Pathansali, 1963)	pelagic	14	30 (N)	No
Sagittidae	*Aidanosagitta erythraea* (Casanova, 1985)	pelagic	10	21 (N)	No

Sagittidae	*Aidanosagitta guileri* (Taw, 1974)	pelagic	14	42 (S)	No
Sagittidae	*Aidanosagitta johorensis* (Pathansali & Tokioka, 1963)	pelagic	5.9	12.5 (N)	Yes
Sagittidae	*Aidanosagitta meenakshiae* (Nair, Panampunnayil, Pillai & Gireesh, 2008)	pelagic	4.6	12.5 (N)	No
Sagittidae	*Aidanosagitta nairi* (Casanova & Nair, 2002)	pelagic	5.2	11 (N)	No
Sagittidae	*Aidanosagitta neglecta* (Aida, 1897)	pelagic	10	23.25 (NS)	Yes
Sagittidae	*Aidanosagitta oceania* (Grey, 1930)	pelagic	8	10.75 (N)	Yes
Sagittidae	*Aidanosagitta ophicephala* (Pathansali, 1974)	pelagic	14	5.25 (NS)	No
Sagittidae	*Aidanosagitta regularis* (Aida, 1897)	pelagic	6	24.75 (NS)	Yes
Sagittidae	*Aidanosagitta septata* (Doncaster, 1903)	pelagic	6	8.25 (N)	Yes
Sagittidae	*Aidanosagitta tropica* (Tokioka, 1942)	pelagic	7	7 (N)	No
Sagittidae	*Caecosagitta macrocephala* (Fowler, 1904)	pelagic	22	21 (NS)	Yes
Sagittidae	*Decipisagitta decipiens* (Fowler, 1905)	pelagic	14	22 (NS)	Yes
Sagittidae	*Decipisagitta sibogae* (Fowler, 1906)	pelagic	30	29.5 (N)	No
Sagittidae	*Ferosagitta americana* (Tokioka, 1959)	pelagic	8	15 (NS)	No
Sagittidae	*Ferosagitta ferox* (Doncaster, 1902)	pelagic	18	23.25 (NS)	Yes
Sagittidae	*Ferosagitta galerita* (Dallot, 1971)	pelagic	14	13.5 (S)	No
Sagittidae	*Ferosagitta hispida* (Conant, 1895)	pelagic	11	41 (N)	No
Sagittidae	*Ferosagitta madhupratapi* (Casanova & Nair, 1999)	pelagic	10	11 (N)	No
Sagittidae	*Ferosagitta robusta* (Doncaster, 1902)	pelagic	22	19.5 (NS)	Yes
Sagittidae	*Ferosagitta siamensis* (Casanova & Goto, 1997)	benthopelagic	7.7	8 (N)	No
Sagittidae	*Flaccisagitta adenensis* (Casanova, 1985)	pelagic	32	13 (N)	No
Sagittidae	*Flaccisagitta enflata* (Grassi, 1881)	pelagic	25	24.75 (NS)	Yes
Sagittidae	*Flaccisagitta hexaptera* (d'Orbigny, 1836)	pelagic	70	28.75 (NS)	Yes
Sagittidae	*Mesosagitta minima* (Grassi, 1881)	pelagic	10	27 (NS)	Yes
Sagittidae	*Parasagitta chilensis* (Villenas & Palma, 2006)	pelagic	15.3	50 (S)	No
Sagittidae	*Parasagitta elegans* (Verrill, 1873)	pelagic	30	56 (N)	No
Sagittidae	*Parasagitta euneritica* (Alvariño, 1961)	pelagic	16	19 (NS)	No
Sagittidae	*Parasagitta friderici* (Ritter-Záhony, 1911)	pelagic	15	19.5 (NS)	No
Sagittidae	*Parasagitta megalophthalma* (Dallot & Ducret, 1969)	pelagic	20	12 (N)	No
Sagittidae	*Parasagitta peruviana* (Sund, 1961)	pelagic	13	7.5 (S)	No
Sagittidae	*Parasagitta popovicii* (Sund, 1961)	pelagic	6	4.5 (S)	No

Sagittidae	*Parasagitta setosa* (J. Müller, 1847)	pelagic	14	47.5 (N)	No
Sagittidae	*Parasagitta tenuis* (Conant, 1896)	pelagic	11	16 (NS)	Yes
Sagittidae	*Pseudosagitta gazellae* (Ritter-Záhony, 1909)	pelagic	105	54 (S)	No
Sagittidae	*Pseudosagitta lyra* (Krohn, 1853)	pelagic	42	29 (NS)	Yes
Sagittidae	*Pseudosagitta maxima* (Conant, 1896)	pelagic	90	37 (NS)	No
Sagittidae	*Sagitta bipunctata* Quoy & Gaimard, 1827	pelagic	19	30.75 (NS)	Yes
Sagittidae	*Sagitta bombayensis* Lele & Gae, 1936	pelagic	13	11.5 (N)	No
Sagittidae	*Sagitta helenae* Ritter-Záhony, 1911	pelagic	14	16 (NS)	No
Sagittidae	*Serratosagitta bierii* (Alvariño, 1961)	pelagic	19	16.75 (NS)	No
Sagittidae	*Serratosagitta pacifica* (Tokioka, 1940)	pelagic	14	24.75 (NS)	Yes
Sagittidae	*Serratosagitta pseudoserratodentata* (Tokioka, 1939)	pelagic	6	14.25 (N)	Yes
Sagittidae	*Serratosagitta serratodentata* (Krohn, 1853)[d]	pelagic	13	28.75 (NS)	No
Sagittidae	*Serratosagitta tasmanica* (Thompson, 1947)	pelagic	30	24 (NS)	No
Sagittidae	*Solidosagitta abyssicola* (Chidgey, 1989)	pelagic	33	36 (N)	No
Sagittidae	*Solidosagitta marri* (David, 1956)	pelagic	28.5	62.5 (S)	No
Sagittidae	*Solidosagitta planctonis* (Steinhaus, 1896)	pelagic	37	20.5 (NS)	Yes
Sagittidae	*Solidosagitta zetesios* (Fowler, 1905)	pelagic	45	18.5 (N)	Yes
Sagittidae	*Zonosagitta bedoti* (Béraneck, 1895)	pelagic	15	23.25 (NS)	Yes
Sagittidae	*Zonosagitta izuensis* (Kitou, 1966)	pelagic	41	34.5 (N)	No
Sagittidae	*Zonosagitta littoralis* (Dallot & Laval, 1974)	pelagic	12	13 (S)	Yes
Sagittidae	*Zonosagitta lucida* (Casanova, 1985)	pelagic	36	15.5 (N)	No
Sagittidae	*Zonosagitta nagae* (Alvariño, 1967)	pelagic	25	32.5 (N)	Yes
Sagittidae	*Zonosagitta pulchra* (Doncaster, 1902)	pelagic	24	19.5 (NS)	Yes

a) Maximum body length, i.e., excluding the caudal fin.
b) Mean latitudes are rounded to the nearest ¼ degree (see Material and Methods for details); N: North; S: South, NS: North and South.
c) Based on Xiao (2008); note that an additional species belonging to the Order Aphragmophora, Zonosagitta sinica Xiao, 2004 may be added here which was published and cited in Chinese publications, but which is not mentioned in WoRMS.
d) Worms list two valid subspecies: *Serratosagitta serratodentata serratodentata* (Krohn, 1853) and *Serratosagitta serratodentata atlantica* (Thompson, 1947) that we have not considered in that paper.

Table S1B. List of the 66 currently valid species of chaetognath belonging to the Order Phragmophora.

Family	Species	Habitat assignment	Maximum length (mm)[a]	Mean latitude[b] of occurrence	Occurring in China's seas[c]
Eukrohniidae	*Eukrohnia bathyantarctica* David, 1958	pelagic	31	26.5 (NS)	Yes
Eukrohniidae	*Eukrohnia bathypelagica* Alvariño, 1962	pelagic	23	40 (N)	Yes
Eukrohniidae	*Eukrohnia calliops* McLelland, 1989	pelagic	43	23 (N)	No
Eukrohniidae	*Eukrohnia flaccicoeca* Casanova, 1986	pelagic	14	9 (S)	No
Eukrohniidae	*Eukrohnia fowleri* Ritter-Záhony, 1909	pelagic	40	35 (N)	Yes
Eukrohniidae	*Eukrohnia hamata* (Möbius, 1875)	pelagic	43	39 (NS)	Yes
Eukrohniidae	*Eukrohnia kitoui* Kuroda, 1981	pelagic	25	34 (N)	No
Eukrohniidae	*Eukrohnia macroneura* Casanova, 1986	pelagic	16	9 (S)	No
Eukrohniidae	*Eukrohnia minuta* Silas & Srinivasan, 1969	pelagic	12	12 (N)	No
Eukrohniidae	*Eukrohnia proboscidea* Furnestin & Ducret, 1965	pelagic	25	11 (S)	No
Eukrohniidae	*Eukrohnia sinica* Zhang & Chen, 1983	pelagic	14.5	14.5 (N)	Yes
Heterokrohniidae	*Archeterokrohnia docrickettsae* Thuesen & Haddock, 2013	benthic	28.5	28 (N)	No
Heterokrohniidae	*Archeterokrohnia longicaudata* (Hagen & Kapp, 1986)	pelagic	12.9	62.5 (S)	No
Heterokrohniidae	*Archeterokrohnia palpifera* Casanova, 1986	benthopelagic	7.1	41.5 (N)	No
Heterokrohniidae	*Archeterokrohnia rubra* Casanova, 1986	benthopelagic	22.5	20 (N)	No
Heterokrohniidae	*Heterokrohnia alvinae* Casanova, 1992	benthopelagic	8	33 (N)	No
Heterokrohniidae	*Heterokrohnia angeli* Casanova, 1994	benthopelagic	6	33 (N)	No
Heterokrohniidae	*Heterokrohnia bathybia* Marumo & Kitou, 1966	benthopelagic	14.6	34.5 (N)	No
Heterokrohniidae	*Heterokrohnia biscayensis* Casanova, 1994	benthopelagic	12	44.5 (N)	No
Heterokrohniidae	*Heterokrohnia curvichaeta* Casanova, 1986	benthopelagic	10,8	20 (N)	No
Heterokrohniidae	*Heterokrohnia davidi* Casanova, 1986	benthopelagic	30.6	20 (N)	No
Heterokrohniidae	*Heterokrohnia discovery* Casanova, 1994	benthopelagic	7	24.5 (N)	No
Heterokrohniidae	*Heterokrohnia fragilis* Kapp & Hagen, 1985	benthopelagic	8.7	63 (S)	No
Heterokrohniidae	*Heterokrohnia furnestinae* Casanova & Chidgey, 1987	benthopelagic	34	41.5 (N)	No
Heterokrohniidae	*Heterokrohnia heterodonta* Casanova, 1986	benthopelagic	20	20 (N)	No
Heterokrohniidae	*Heterokrohnia involucrum* Dawson, 1968	benthopelagic	15.7	50 (N)	No
Heterokrohniidae	*Heterokrohnia longidentata* Kapp & Hagen, 1985	benthopelagic	12.2	63 (S)	No

Heterokrohniidae	*Heterokrohnia mirabilis* Ritter-Záhony, 1911	benthopelagic	36	33.75 (NS)	No
Heterokrohniidae	*Heterokrohnia mirabiloides* Casanova & Chidgey, 1990	benthopelagic	25	42 (N)	No
Heterokrohniidae	*Heterokrohnia murina* Casanova, 1986	benthopelagic	38.5	20 (N)	No
Heterokrohniidae	*Heterokrohnia wishnerae* Casanova, 1992	benthopelagic	8	33 (N)	No
Heterokrohniidae	*Xenokrohnia sorbei* Casanova, 1993	benthopelagic	8	44.5 (N)	No
Krohnittellidae	*Krohnittella boureei* Germain & Joubin, 1912	benthic	33	31.5 (N)	No
Krohnittellidae	*Krohnittella tokiokai* Bieri, 1974	benthic	7	31.5 (N)	No
Spadellidae	*Bathyspadella edentata* Tokioka, 1939	benthopelagic	12	35 (N)	No
Spadellidae	*Bathyspadella oxydentata* Miyamoto & Nishida, 2011	benthopelagic	15.5	35 (N)	No
Spadellidae	*Calispadella alata* Casanova & Moreau, 2005	benthopelagic	3.95	37.5 (N)	No
Spadellidae	*Hemispadella dauvini* Casanova, 1996	benthopelagic	18.5	33 (N)	No
Spadellidae	*Paraspadella anops* Bowman & Bieri, 1989	benthopelagic	4	25 (N)	No
Spadellidae	*Paraspadella caecafea* (Salvini-Plawen, 1986)	benthopelagic	4.9	34 (N)	No
Spadellidae	*Paraspadella gotoi* Casanova, 1990	benthopelagic	6	32 (N)	No
Spadellidae	*Paraspadella johnstoni* (Mawson, 1944)	benthopelagic	5	34 (S)	No
Spadellidae	*Paraspadella legazpichessi* (Alvariño, 1981)	benthopelagic	2	11 (N)	No
Spadellidae	*Paraspadella nana* (Owre, 1963)	benthic	3	12.5 (NS)	No
Spadellidae	*Paraspadella pimukatharos* (Alvariño, 1987)	benthopelagic	4	33.5 (N)	No
Spadellidae	*Paraspadella pulchella* (Owre, 1963)	benthopelagic	3	8 (N)	No
Spadellidae	*Paraspadella schizoptera* (Conant, 1895)	benthopelagic	5	25 (N)	No
Spadellidae	*Paraspadella sheardi* (Mawson, 1944)	benthopelagic	7	34 (S)	No
Spadellidae	*Spadella angulate* Tokioka, 1951	benthic	6	33 (N)	No
Spadellidae	*Spadella antarctica* Casanova, 1991	benthopelagic	6	72.5 (S)	No
Spadellidae	*Spadella birostrata* Casanova, 1987	benthic	8	35.5 (N)	No
Spadellidae	*Spadella boucheri* Casanova & Perez, 2000	benthic	1.3	24.5 (N)	No
Spadellidae	*Spadella bradshawi* Bieri, 1974	benthopelagic	6.5	32 (N)	No
Spadellidae	*Spadella cephaloptera* (Busch, 1851)	benthic	5.5	25.75 (NS)	Yes
Spadellidae	*Spadella duverti* Hernández, De Vera & Casanova, 2009	benthic	4.5	28 (N)	No
Spadellidae	*Spadella equidentata* Casanova, 1987	benthopelagic	7	36.5 (N)	No
Spadellidae	*Spadella gaetanoi* Alvariño, 1978	benthopelagic	3	27.5 (N)	No
Spadellidae	*Spadella interstitialis* Kapp & Giere, 2005	benthic	1.8	43 (N)	No
Spadellidae	*Spadella japonica* Casanova, 1993	benthopelagic	4	34 (N)	No

Spadellidae	*Spadella kappae* Schmidt-Rhaesa & Vieler, 2020	benthic	3.5	48 (N)	No
Spadellidae	*Spadella lainezi* Casanova, Hernández & Jiménez, 2006	benthic	4.5	28.5 (N) (N)	No
Spadellidae	*Spadella ledoyeri* Casanova, 1986	benthopelagic	6.6	41.5 (N)	No
Spadellidae	*Spadella moretonensis* Johnson & Taylor, 1920	benthopelagic	4	30 (S)	No
Spadellidae	*Spadella nunezi* Casanova & Moreau, 2004	benthic	2.3	29 (N)	No
Spadellidae	*Spadella valsalinae* Winkelmann, Gasmi, Gretschel, Müller & Perez, 2012	benthic	5	44.5 (N)	No
Spadellidae	*Spadella xcalakensis* Tovar & Suárez-Morales, 2007	benthic	3.7	18.5 (N)	No

a) Maximum body length, i.e., excluding the caudal fin.

b) Mean latitudes are rounded to the nearest ¼ degree (see Material and Methods for details); N: North; S: South, NS: North and South.

c) Based on Xiao (2008); note that an additional species belonging to the Order Phragmophora, *Spadella plana* Xiao, 2004, may be added here which was published and cited in Chinese publications, but which is not mentioned in WoRMS.

Supplementary material S2
Weight-at-age data from aquarium growth experiments with Ferosagitta hispida

Supplementary material to:

Pauly, D.; Liang, C.; Xian, W.; Chu, E.; Bailly, N. The sizes, growth and reproduction of arrow worms (Chaetognatha) in light of the Gill-Oxygen Limitation Theory (GOLT). *Journal of Marine Science and Enginering* 9, doi.org/10.3390/jmse912397.

Table S2A. Weight-at-age data[a] derived by Hirst and Forster [32] from aquarium growth experiments with *Ferosagitta hispida* by Reeve and Walter [90] and Reeve and Baker [91]. The ages are in days, and the (dry) weights in mg.

Fig. 3 panel	**A**	**A**	**B**	**B**	**C**	**C**	**D**	**D**
Counter	**Age**	**Weight**	**Age**	**Weight**	**Age**	**Weight**	**Age**	**Weight**
1	2.2	0.000345	2.0	0.000711	10.8	0.00702	12.7	0.00637
2	5.8	0.000544	3.3	0.000979	14.8	0.00968	14.9	0.00686
3	8.2	0.000676	5.5	0.00205	17.9	0.0116	18.0	0.0140
4	9.8	0.00113	8.6	0.00529	22.0	0.0209	**24.8**	**0.0648**
5	12.7	0.00234	**10.4**	**0.0168**	**25.0**	**0.0279**	**27.1**	**0.113**
6	14.5	0.00348	**12.2**	**0.0383**	**29.0**	**0.0544**	**28.8**	**0.2470**
7	16.1	0.00597	**14.7**	**0.0813**	**32.1**	**0.117**	**32.0**	**0.468**
8	17.6	0.0102	**16.5**	**0.268**	**36.1**	**0.211**	**33.9**	**0.610**
9	19.5	0.0194	**18.0**	**0.469**	**38.1**	**0.313**	**35.8**	**0.741**
10	**21.2**	**0.0275**	**20.1**	**0.472**	**41.9**	**0.672**	**38.8**	**0.956**
11	**24.2**	**0.0600**	--	--	**44.9**	**0.877**	**40.8**	**0.972**
12	**27.1**	**0.201**	--	--	**49.0**	**1.15**	--	--
13	**29.6**	**0.268**	--	--	**52.0**	**1.23**	--	--
14	**31.7**	**0.412**	--	--	**59.0**	**1.16**	--	--
15	**33.6**	**0.634**	--	--	**65.7**	**1.19**	--	--
16	**35.5**	**0.665**	--	--	**68.9**	**1.22**	--	--
17	**34.7**	**0.807**	--	--	--	--	--	--
18	**38.5**	**0.841**	--	--	--	--	--	--

a) Only the age-weight data pairs in bold were used for fitting growth curves (see text).

Table S2B. Weight-at-age data[a] derived by Hirst and Forster [32] from aquarium growth experiments with *Ferosagitta hispida* by Reeve and Baker [91] and Reeve [3].
The ages are in days, and the (dry) weights in mg.

Fig. 3 panel	**E**	**E**	**F**	**F**	**G**	**G**	**H**	**H**
Counter	**Age**	**Weight**	**Age**	**Weight**	**Age**	**Weight**	**Age**	**Weight**
1	9.3	0.0183	**9.7**	**0.00588**	**8.9**	**0.0155**	**19.0**	**8.31**
2	10.8	0.0120	**10.9**	**0.0153**	**13.7**	**0.103**	**20.0**	**8.46**
3	**15.0**	**0.0472**	**12.8**	**0.0262**	**15.7**	**0.375**	**21.0**	**8.76**
4	**16.9**	**0.0902**	**14.7**	**0.125**	**17.9**	**0.534**	**24.0**	**9.14**
5	**18.8**	**0.251**	**19.6**	**0.668**	**20.8**	**0.581**	**25.0**	**9.21**
6	**22.8**	**0.528**	**20.7**	**0.842**	**22.8**	**0.657**	**26.0**	**9.17**
7	**23.8**	**0.597**	**23.6**	**0.911**	**28.0**	**0.677**	**26.9**	**9.15**
8	**28.8**	**0.771**	**26.9**	**1.01**	--	--	**27.9**	**9.30**
9	**30.8**	**0.902**	**28.8**	**1.01**	--	--	**30.9**	**9.57**
10	**40.8**	**0.876**	**31.9**	**1.00**	--	--	**31.9**	**9.57**
11	--	--	--	--	--	--	**32.9**	**9.65**
12	--	--	--	--	--	--	**33.9**	**9.52**
13	--	--	--	--	--	--	**34.9**	**9.65**
14	--	--	--	--	--	--	**38.0**	**9.72**
15	--	--	--	--	--	--	**40.0**	**9.70**
16	--	--	--	--	--	--	**40.9**	**9.72**
17	--	--	--	--	--	--	**41.9**	**9.69**

a) Only the age-weight data pairs in bold were used for fitting growth curves (see text).

Supplementary material S3
Surface area and volume of the body of adult specimens of 6 species of chaetognaths

Supplementary material to:

Pauly, D.; Liang, C.; Xian, W.; Chu, E.; Bailly, N. The sizes, growth and reproduction of arrow worms (Chaetognatha) in light of the Gill-Oxygen Limitation Theory (GOLT). *Journal of Marine Science and Engineering*, *9*, doi.org/10.3390/jmse912397.

Table S3. Surface area (excluding fins) and volume of the body estimated from drawings of adult specimens of 6 species of chaetognaths[a]. The relative area is in $cm^2 \cdot g^{-1}$ to enable comparisons with other groups.

Species	**Length (mm)**	**Surface (mm^2)**	**Volume (mm^3)**	**Relative area ($cm^2 \cdot g^{-1}$)**
Spadella cephaloptera	1.29	0.486	0.0157	306
Ferosagitta hispida	7.1	8.8	0.90	98
Sagitta setosa	13.9	32.1	6.46	51
Eukrohnia hamata	22.3	77.1	23.2	45
Parasagitta elegans	21.2	65.6	17.0	39
Pseudosagitta gazellae	96.5	2096	3856	5.4

a) Rieger et al. [124] (Figure 1); Øresland [125] (Figure 1); Grigor et al. [29] (Figure 2); David [112] (Figure 27).

Additional references (not cited in the text):

124. Rieger, V.; Perez, Y.; Müller, C.H.G.; Lacalli, T.; Hansson, B.S.; Harzsch, S. Development of the Nervous System in Hatchlings of *Spadella cephaloptera* (Chaetognatha), and Implications for Nervous System Evolution in Bilateria. *Dev. Growth Differ.* **2011**, *53*, 740–759, doi:10.1111/j.1440-169X.2011.01283.x.
125. Øresland, V. Feeding of the Chaetognaths *Sagitta elegans* and *S. setosa* at Different Seasons in Gullmarsfjorden, Sweden. *Mar. Ecol. Prog. Ser.* **1987**, *39*, 69–79, doi:10.3354/meps039069.

Supplementary material S4
Detailed citation for old references

Supplementary material to:

Pauly, D.; Liang, C.; Xian, W.; Chu, E.; Bailly, N. The sizes, growth and reproduction of arrow worms (Chaetognatha) in light of the Gill-Oxygen Limitation Theory (GOLT). *Journal of Marine Science and Engineering, 9*, doi.org/10.3390/jmse912397.

The current reference formatting of the journal *J. Mar. Sci. Engin*. does not permit to include details that are often essential to quickly find the information cited from the old references. Often, the fascicles or different parts of a volume or opus published at different dates are bound without their title page, which makes the retrieval of information difficult.

The numbers before the references refer to their position in the main text (and then in the list of references).

Note that here, we do not follow the reference format of the journal *J. Mar. Sci. Engin*.

[42] **Blainville, H.-M.D. de (1825-1827).** *Manuel de malacologie et de conchyliologie*. Paris (France): F.G. Levrault, Edit.
Opus: www.biodiversitylibrary.org/bibliography/14060. doi: 10.5962/bhl.title.14060
T1:1825, 1-647 + 1 Tab;
Page 492: citation of the genus sagitelle as a vernacular name. Sagittelle should have been written with 2 ‘t’.
www.biodiversitylibrary.org/page/27344402
T2: 1827, 648-664 + 109 Pls.
Page 656: citation of *Sagitella aequipinnis*. *Sagittella* should have been written with 2 ‘t’.
www.biodiversitylibrary.org/page/27342181

[44] **Blainville, H.-M.D. de (1827).** “[Accounts for] *Sagitta*, Flèche; *Sagittella*, Sagittelle,” in: *Dictionnaire des sciences naturelles*, T47. Paris (France): F.G. Levrault, Edit., and Strasbourg (France): Le Normant.
Opus: www.biodiversitylibrary.org/bibliography/42219. doi: 10.5962/bhl.title.42219
T47: www.biodiversitylibrary.org/page/25311612
Pages 4-5: Account of *Sagitta* (Note: there are several entries for the word “Sagitta”).
https://www.biodiversitylibrary.org/page/25311617
Pages 5-8: Detailed account of *Sagittella* (entry ‘Sagittelle’) and the 3 species.
https://www.biodiversitylibrary.org/page/25311618

[47] **d'Orbigny, A.D. (1836).** Mollusques. *Voyage dans l'Amérique méridionale*, 5(3):1-758. Paris (France): Bertrand; Strasbourg (France): F.G. Levrault, Edit.
Opus: www.biodiversitylibrary.org/bibliography/110540. doi: 10.5962/bhl.title.110540
T5: www.biodiversitylibrary.org/page/49211253
Pages 140-144: “*Genre Flèche*”, *Sagitta*, with description of new species.
www.biodiversitylibrary.org/page/46822717

Note: The publication of the “Voyage” spanned between 1835 and1843 with Additions et Corrections in 1846.

[17] **Darwin, C. (1844).** Observations of the structure and propagation of the genus *Sagitta*. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology*. 13: 1-6. doi: 10.1080/03745484409442559
www.biodiversitylibrary.org/page/22067957
Note: Current publishers: London (UK): Taylor & Francis.

[43] **Eydoux, F.; Souleyet, M. (1852).** Vers, p. 645-657 *In : Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette La Bonite, Zoologie*, 2. Paris (France): A. Bertrand, 645-657
Opus: www.biodiversitylibrary.org/bibliography/10814. doi: 10.5962/bhl.title.10814
T2: www.biodiversitylibrary.org/page/12192060
Page 645: Account for *Sagitta*.
www.biodiversitylibrary.org/page/12192663.

[48] **Forbes, E. (1844).** On the addition of the order Nucleobranchia to the British molluscous fauna. *Report of the 13th meeting British Association for the Advancement of Science; held at Cork in August 1843.* London (UK): John Murray. Notices and Abstracts of Miscellaneous Communications to the Sections: 72-73.
Proceedings series: www.biodiversitylibrary.org/bibliography/2276
Report of 13th meeting: www.biodiversitylibrary.org/page/12920618
Notices and Abstracts: www.biodiversitylibrary.org/page/12920964
Page 72: Species description.
www.biodiversitylibrary.org/page/12921035
Note: The citation of this reference is difficult to establish, because the Notices and Abstracts have their proper pagination, which the pages 72-73 refer to and not to the report itself.

[53] **Gegenbaur, C. (1859).** *Grundzüge der vergleichenden Anatomie.* Leipzig (Germany): Wilhelm Engelmann, 606 p.
Opus: www.biodiversitylibrary.org/bibliography/51366. doi: 10.5962/bhl.title.51366
Page 138: Oestelminthes.
www.biodiversitylibrary.org/page/35090457
Note: Oestelminthes replaced by Chätognathen in the 2nd ed. (1870).
books.google.ca/books?id=689RAAAAcAAJ&pg

[55] **Grassi, B.J. (1883).** *I chetognathi. Anatomia e sistematica con aggiunte embriologiche. Fauna und Flora des Golfes von Neapel, 5, Monographie: Die Chaetognathen*: 1-126. Leipzig (Germany): W. Engelmann.
Opus: www.biodiversitylibrary.org/bibliography/10552. doi: 10.5962/bhl.title.10552
Page 5: Chaetognaths as an independent group.
www.biodiversitylibrary.org/page/11042794
Note: this reference is variously cited under different parts of the complete citation above.

[54] **Harting, P. (1869).** Wormen. In *Leerboek van de grondbeginselen der dierkunde in haren geheelen omvang*. III. Ongewervelde dieren. 1. Natuurhistorisch overzigt. 5. Tiel (Netherlands): H.C.A. Campagne, 489-796.
Opus: books.google.ca/books?id=_KsfAQAAIAAJ
Page 617: Pterhelminthes section.
books.google.ca/books?id=_KsfAQAAIAAJ&pg=PA617#v=onepage&q&f=false
Note: Apparently not in BHL yet, this reference is particularly difficult to find and to cite. Hertwig just gave the pages where Pterhelminthes are described (correctly pp.617-621), not even the year. Now the *Leerboek* is divided in many parts, volumes, fascicles and sections that are paginated continuously although they were not published in chronological order. Apparently, the section on Pterhemimthes was published in 1869.

Note: The name Pterhelmintes can be found in another edition from 1871:
Opus: books.google.ca/books?id=N69lAAAAcAAJ
Page 369: Pterhelminthes (*Sagitta*).
books.google.ca/books?id=N69lAAAAcAAJ&pg=PA369#v=onepage&q&f=true

[52] **Hertwig, O. (1880).** "Die Chaetognathen. Ihre Anatomie, Systematik und Entwicklungsgechichte. Eine Monographie," in: *Studien zur Blättertheorie*, Heft 2, eds O Hertwig and R. Hertwig (Jena, Germany): G. Fischer, 1vi + 111 p. + Pls. 9-14.
Opus: www.biodiversitylibrary.org/bibliography/15245. doi: 10.5962/bhl.title.15245
Page 8: Selection of the name Chaetognatha over Oesteleminthes and Pterelminthes.
www.biodiversitylibrary.org/page/15077445
Note: Also in *Jenaische Zeitschrift für Naturwissenschaft*, 14: 196-311 + Pls. 1-6, www.biodiversitylibrary.org/page/8629109

[38] **Hoeven, J. van der (1862).** Eenige aanteekeningen over Martinus Slabber's Natuurkundige Verlustigingen; benevens opgave der systematische namen van de daarin afgebeelde diersoorten. *Verslagen en mededeelingen der Koninklijke Akademie van Wetenschappen (Afd. Natuurk.)* 14: 270-285.
Series: www.biodiversitylibrary.org/bibliography/2526
Article: www.biodiversitylibrary.org/page/39138797

[50] **Leuckart, R. (1854).** Bericht über die Leistungen in der Naturgeschichte der niederen Thiere thiere während des Jahres 1848-1853. *Archiv für Naturgeschichte*, 20(2), 289-473.
Series: www.biodiversitylibrary.org/bibliography/6638
Article: www.biodiversitylibrary.org/page/7072729
Page 335: The name Chaetognathi is coined.
www.biodiversitylibrary.org/page/7072774

[51] **Leuckart, R. (1856).** *Nachträge und Berichtigungen zu dem ersten Bande von J. van der Hoeven's Handbuch der Zoologie. Eine systematisch geordnete Übersicht der Hauptsächlichste neueren Leistungen über die Zoologie der wirbellosen Thiere*. Leipzig (Germany): L. Voss, 148 p., 9 Pl.
J. van der Hoeven's Opus: www.biodiversitylibrary.org/bibliography/3983. doi: 10.5962/bhl.title.3983
Addendum by Leuckart: www.biodiversitylibrary.org/page/3168542

Page 117: Emendation in Chaetognatha.
www.biodiversitylibrary.org/page/3169487
Note: The addendum is presented following the J. van der Hoeven's book, so the citation is difficult to establish. It may be considered as a book section / chapter, although it has a different pagination. Difficult to find.

[70] **Michael, E.L. (1919).** Report on the chaetognatha collected by the United States fisheries steamer "Albatross" during the Philippine expedition, 1907-1910. *U.S. National Museum Bulletin, 100(1)[4]:235-277*.
Series: www.biodiversitylibrary.org/bibliography/7548
Article: www.biodiversitylibrary.org/page/7628551. doi: 10.5962/bhl.title.17878

[45] **Quoy, J.R.C. and Gaimard, J.P. (1827).** Observations zoologiques faites à bord de l'Astrolabe, en mai 1826, dans le Détroit de Gibraltar (suite et fin). Description des genres Biphore, Carinaire, Hyale, Flèche, Cléodore, Anatife et Briarée. *Annales des Sciences Naturelles.* 10: 225-239; Pl. 8C: Figs. 1, 2, 6, 9.
Series: www.biodiversitylibrary.org/bibliography/6343
T10: www.biodiversitylibrary.org/page/6008482
Page 232: Description of *Sagitta* and *Sagitta bipunctata*.
www.biodiversitylibrary.org/page/6008492
Plate 8C www.biodiversitylibrary.org/page/32238237
Note: the "Observations zoologiques" are divided in 3 parts in the same volume: pp. 5-21, 172-193 (Suite), 225-239 (Suite et fin), with different subtitles. Only the third part contains the description of *Sagitta bipunctata*.

[5] **Ritter-Záhony, R. (1909).** Die Chaetognathen der Gazelle Expedition. *Zoologischer Anzeiger* 34: 787-793.
Series: www.biodiversitylibrary.org/bibliography/8942
Article: www.biodiversitylibrary.org/page/30144790

[60] **Ritter-Záhony, R. 1911.** Revision der Chätognathen, in *Deutsche Südpolar-Expedition, 1901-1903, im Auftrage des Reichsamtes des Innern, hrsg. von Erich von Drygalski*. Berlin (Germany): G. Reimer,1905-1931, Band 13 (Zool. Band 5), Heft 1: 1-71.
Series: 10.5962/bhl.title.2166
Article: www.biodiversitylibrary.org/page/2138867

[37] **Slabber, M. (1769-1775).** *Natuurkundige verlustigingen, behelzende microscopise waarneemingen van de in- en uitlandse water- en land-dieren*. Haarlem (Netherlands): J. Bosch, 166 p.
Bound opus: books.google.ca/books?id=f8rDmjs4abkC
Pages 46-48, Figs. 3, 4: Description of *Sagitta*.
books.google.ca/books?id=f8rDmjs4abkC&pg=PA46#v=onepage&q&f=false
plate 6: books.google.ca/books?id=f8rDmjs4abkC&pg=PA44-IA3#v=onepage&q&f=false
Note: This reference is often cited with the dates 1769, 1771, 1775, that correspond to the dates of publication of various fascicles actually. See [40] for the correct publication date for all fascicles.

As explained by Welter-Schultes (2011)[40], full versions available online are dated either 1769 or 1778. While 1778 corresponds to a complete final edition containing all fascicles, it is most likely that full versions dated 1769 correspond to a (or several different) bonding of all fascicles without their title page, save the first one that then retain the year 1769 in the title page misinterpreted as the date of the full version.

Google Books, dated 1769, but apparently with pages not well ordered:
books.google.ca/books?id=9wgOAAAAQAAJ
Google Books, dated 1769:
books.google.ca/books?id=5AePmm2d6PAC
Google Books, dated 1778:
books.google.ca/books?id=fxUOAAAAQAAJ
Biodiversity Heritage Library, dated 1778:
doi: 10.5962/bhl.title.47657