Title	Synthesis towards a global-bathymetric model of metabolism and chemical composition of marine pelagic chaetognaths
Author(s)	Ikeda, Tsutomu; Takahashi, Tomokazu
Citation	Journal of Experimental Marine Biology and Ecology, 424-425, 78-88 https://doi.org/10.1016/j.jembe.2012.05.003
Issue Date	2012-08
Doc URL	http://hdl.handle.net/2115/59730
Type	article (author version)
File Information	HUSCUP-Sagitta.pdf

[Instructions for use](#)

1 **J. Exp. Mar. Biol. Ecol. 424-425: 78–88 (2012)**

2
3 Synthesis towards a global-bathymetric model of metabolism and chemical composition
4 of marine pelagic chaetognaths

5
6 Tsutomu Ikeda*, Tomokazu Takahashi

7 Graduate School of Fisheries Sciences, Hokkaido University, Minato-cho, Hakodate,
8 041-8611 Japan

9
10
11 *Corresponding author

12 *Present address: 16-3-1001 Toyokawa-cho, Hakodate, 040-0065 Japan

13 ikeda.tutomu@sepia.plala.or.jp

14 Tel: +81-138-22-5612

15
16 Running head: Metabolism of marine pelagic chaetognaths

17
18 Keywords: chaetognaths, chemical composition, ETS activity, global-bathymetric
19 model, respiration,

ABSTRACT

Respiration (=oxygen consumption) and chemical composition [water content, ash, carbon (C) and nitrogen (N)] were determined for seven chaetognaths (*Parasagitta elegans*, *Caecosagitta macrocephala*, *Pseudosagitta scrippsae*, *Solidosagitta zetesios*, *Eukrohnia hamata*, *E. bathypelagica* and *E. fowleri*) from the epipelagic through bathypelagic zones (< 3000 m) in the western subarctic Pacific Ocean. Enzyme activities of the electron transfer system (ETS) were also determined on mesopelagic and bathypelagic chaetognaths, and ETS:respiration ratios were calculated to confirm the validity of respiration rates measured at near *in situ* temperature but under normal pressure (1 atm). These data were combined with literature data from Arctic, Antarctic, temperate and tropical waters and epipelagic through bathypelagic zones. A total of 25 data sets on 17 chaetognaths for respiration, and a total of 18–34 data sets on 18–21 chaetognaths for chemical composition were used to explore important parameters affecting their respiration rates and chemical composition. Designating body mass (dry mass, C or N), ambient temperature, oxygen saturation and sampling depth as independent variables, stepwise multiple regression analyses revealed that body mass, habitat temperature and sampling depth were significant, attributing 82–93% of the variance of respiration rates. No significant effect of sampling depth and habitat temperature was detected in the chemical composition. These results are compared with those of copepods to highlight unique features of chaetognaths.

1. Introduction

Among the various metazoan animal taxa occurring as plankton in the pelagic realm of the ocean, chaetognaths are the second most numerous taxon (2–10%; Longhurst, 1985) following copepods (55–95%). Because chaetognaths are primarily predators of copepods (cf. Feigenbaum, 1991), information about the metabolism and chemical composition of chaetognaths is of particular relevance for understanding oceanic biogeochemical cycles of carbon and other elements (Terazaki, 1995). From the viewpoint of trophodynamics, significant feeding impacts of chaetognaths on prey copepods have been estimated in the Bedford Basin, Nova Scotia (Sameoto, 1972), Bering Sea in summer (Kotori, 1976), Resolute in the Canadian high Arctic (Welch et al., 1996), off the coast of North Carolina (Coston-Clements et al., 2009), and the Lazarev Sea, Antarctica (Kruse et al., 2010a).

Metabolic rates of zooplankton living in the epipelagic zones have been documented as a function of body mass and habitat temperature (Ivleva, 1980; Ikeda, 1985). Although body mass and temperature have been regarded as two major parameters to define metabolic characteristics of marine pelagic animals, the habitat depth has emerged as an additional parameter since the observation that metabolic rates decrease rapidly with depth for large pelagic animals with developed visual perception systems (eyes) such as micronektonic fishes, crustaceans, and cephalopods (Childress, 1995; Seibel and Drazen, 2007). To date, the effect of habitat depth on metabolic rates of chaetognaths is controversial, as Kruse et al. (2010a) noted a significant negative effect while Thuesen and Childress (1993) did not.

Comparing C and N composition of diverse zooplankton taxa from tropical, subtropical, temperate and subarctic waters, Ikeda (1974) noted a general increase in C

composition toward higher latitude seas. Båmstedt (1986) compiled voluminous data on the chemical composition (proximate composition and elemental C and N) of pelagic copepods from high, intermediate and low latitude seas and from surface and deep, and confirmed higher C and lower N composition for those living in lower temperature habitats (= high latitude seas and deep waters). Higher C and lower N composition of zooplankton living in high latitude seas have been interpreted as results from an accumulation of energy reserves (lipids) to compensate for unstable food supply. According to a recent study on pelagic copepods from the surface to 5000 m depth in the subarctic Pacific where vertical change in temperature is less pronounced, the chemical composition of deeper living copepods is characterized by stable C composition but low N composition, possibly because of their reduced muscles or reduced swimming activities in dark environments (Ikeda et al., 2006a). For chaetognaths, analysis of the data to reveal global and bathymetric trends has not yet been attempted.

In order to evaluate global-bathymetric patterns of metabolism and chemical composition of chaetognaths, we determined the respiration rates (=oxygen consumption) and chemical composition of the body (water content, ash, carbon and nitrogen) of live chaetognaths retrieved by shipboard sampling from the epipelagic through bathypelagic zones in the western subarctic Pacific. As another measure of respiration potential, enzyme activities of the Electron Transfer System (ETS) were also measured using frozen specimens to ensure the validity of the respiration data. These data were combined with literature data of chaetognaths from polar, temperate and tropical/subtropical seas, and significant parameters attributing the variance were explored. Body mass, habitat temperature, sampling depth and ambient oxygen

saturation are used as determinants of respiration rates as in the global-bathymetric respiration model for pelagic copepods by Ikeda et al. (2007). As parameters affecting chemical composition, habitat temperature and sampling depth are considered. Finally, the present results are compared with those of copepods to highlight some unique features of chaetognaths.

2. Materials and methods

2.1. Chaetognaths

Specimens were collected at Site H (41°30'N 145°50'E) and Station Knot (44°00'N 155°00'E) in the western Pacific (cf. Fig. 1) during several T.S. Oshoro-Maru Cruises: 112 (March) in 2001; 133D (March) and 136A (June) in 2003; 144A (March) and 154B (December) in 2004; and 155 (March) and 165 (December) in 2005. Additional specimens were obtained during the T.S. Hokusei-Maru Cruise 91(3) (August) in 2001. A vertical closing net [80 cm diameter, as modified from Kawamura (1968)] equipped with a large cod-end (1–2 l capacity) was used to retrieve live zooplankton from the epipelagic through bathypelagic zones. The depth intervals between 500–1000 m (mesopelagic zone) and 2000–3000 m (bathypelagic zone) were sampled most frequently in the present study. The closing net was towed from the bottom to the top of designated depth stratum at $1 \text{ m} \cdot \text{s}^{-1}$, closed and retrieved to the surface at $2 \text{ m} \cdot \text{s}^{-1}$. The depth the net reached was read from the record of an RMD depth meter (Rigosha Co. Ltd.) attached to the suspension cable of the net. After closing the mouth of the net at the designated depth, the time required to retrieve the net to the surface was 17 min at most (when closed at 2000 m depth).

Upon retrieval of the net, undamaged specimens were sorted immediately. Sorted

specimens were placed in 1 liter glass containers filled with seawater from the mid-depth range of their collection (e.g. 750 and 2500 m for the specimens collected respectively from 500–1000 and 2000–3000 m depth zones). The seawater was collected with 20-l Niskin bottles immediately before zooplankton collection for each experiment. Temperature and salinity profiles were determined using a CTD system.

The nomenclature of chaetognaths proposed by Bieri (1991) was used throughout this study.

2.2. Respiration

A sealed-chamber method (Ikeda et al., 2000) with small glass bottles (40–70 ml capacity) was used to determine the respiration rates of chaetognaths. It is noteworthy that 500–2000 m depth in the western North Pacific is characterized by moderately low oxygen (1.0–2.0 ml O₂ l⁻¹, or 10–30% saturation; Favorite et al., 1976). To obtain respiration rates under near natural oxygen concentrations, seawater was filtered gently through 10 µm mesh netting before use to remove large particles. The oxygen concentration of seawater thus prepared for the chaetognaths from 500–2000 m was 1.5–2.0 ml O₂ l⁻¹. Experiments started within 1–3 h of the collection of the specimens. Experimental bottles containing specimens (mostly single individuals) and control bottles without specimens were prepared simultaneously, and kept in the dark for 24 h at *in situ* temperatures, e.g. 3°C for the mesopelagic zone and 1.5°C for the bathypelagic zone under normal pressure (1 atm). During the experiment, bottles containing the specimens were laid down in order to provide enough space to stretch the bodies of individuals. The lack of *in situ* hydrostatic pressure at 1000 m depth (= 100 atm) was shown to affect the respiration rates of some bathypelagic chaetognaths only slightly

(Childress and Thuesen, 1993). At the end of each experiment, the dissolved oxygen concentration was determined using a Winkler titration method on subsamples siphoned from the bottles into two small oxygen vials (7 or 14 ml capacity). For chaetognaths from low oxygen habitats (500–2000 m), the oxygen concentration at the end of experiments was $>1.0 \text{ ml O}_2 \text{ l}^{-1}$ (= 21 mm Hg), which is well above the critical oxygen pressure (P_c) of ca. 10 mmHg in the three copepods inhabiting oxygen-deficient zones off California (Childress, 1975). Based on replicate measurements on a homogenous water sample, the precision, expressed as the coefficient of variation (CV), was estimated as 0.2%.

2.3. ETS activity

Freshly collected specimens were identified to species under a dissecting microscope. They were subsequently preserved immediately in liquid nitrogen onboard the ship and brought back to the land laboratory for ETS assay. Within one month after their collection, the frozen specimens were homogenized together with a small piece of glass fiber filter in a glass-teflon tissue homogenizer. The method described by Owens and King (1975) was used for this assay, but the final reaction volume was reduced from 6 ml to 1.5 ml. One-milliliter homogenized samples in ETS-B solution were centrifuged. The resultant cell-free extract was used for ETS assay. Preliminary tests indicated that the ETS activities of single specimens were too low to measure at *in situ* temperatures (1.5–3°C). All assays were made at a fixed temperature of 10°C to overcome this problem. The ETS activities were determined from two 0.25 ml aliquots of cell-free extract of each sample. The effect of hydrostatic pressure on ETS activities of crustacean plankton has been demonstrated to be insignificant at least to 265 atm (=

2650 m depth)(King and Packard, 1975a). Protein concentrations were determined on each homogenate to define the body mass of the specimens analyzed. Protein was determined in duplicate using the method of Lowry et al. (1951) using bovine serum albumin as a standard. In order to compare with respiration rates, ETS activity was finally expressed per mg N, by using a conversion factor of $N = 0.2 \times \text{protein}$ (Ikeda, unpublished).

2.4. Chemical composition

All specimens used for respiration experiments were rinsed briefly with small amounts of chilled distilled water, blotted on filter paper, and frozen at -60°C onboard the ship for later determination of the wet mass (WM), dry mass (DM), and carbon (C) and nitrogen (N) compositions at a land laboratory. Frozen specimens were weighed (WM) and freeze-dried to obtain DM. Water content was calculated from the difference between WM and DM of the same specimens. A microbalance (MT5; Mettler Toledo International Inc.) was used for weighing to a precision of $1\text{ }\mu\text{g}$. Specimens of the same species from the same depth stratum were pooled in each cruise and finely ground with a ceramic motor and pestle. They were used for C and N composition analyses using a CHN elemental analyzer (Elementar vario EL) with acetanilide as a standard. Weighed fractions of the ground samples were incinerated at 480°C for 5 h and reweighed for ash determination. All measurements were made in duplicate, and the general precision (CV) was 3% for C, 7% for N and 10% for ash.

2.5. Global-bathymetric model for respiration

In addition to the 2 conventional independent variables (X_1 : body mass; and X_2 :

habitat temperature) used in the previous global respiration model for marine epipelagic copepods (Ivleva, 1980; Ikeda, 1985), 2 new independent variables (X_3 : mid-sampling depth, and X_4 : oxygen saturation) were introduced to the present analyses. X_4 was expressed as a fraction of saturation (full saturation = 1.00). It is noted that X_3 thus defined is for the specimens used in this study and not necessarily consistent to the depth of occurrence for the populations reported in the subarctic Pacific by previous workers such as Kotori (1976), Terazaki and Miller (1986) and Ozawa et al. (2007). X_1 was expressed as DM, nitrogen mass (N) or carbon mass (C) since the choice of the body mass unit is known to cause somewhat different results (Ivleva, 1980; Ikeda, 1985).

Two regression models were adopted according to the mathematical form of the temperature and body mass effects. One was a theoretical model characterized by the Arrhenius relationship ($R = R_0 M^{3/4} e^{-E/kT}$, where R is respiration rate, M is body mass, T is absolute temperature, $3/4$ is theoretical body mass exponent, E is an average activation energy for the rate-limiting enzyme-catalyzed biochemical reactions of metabolism, k is Boltzmann's constant and R_0 is a normalization constant (cf. Gillooly et al., 2001) and the other was empirical (or log/linear) model characterized by the Van't Hoff rule (Q_{10}) (Ikeda, 1985);

$$\text{Theoretical model: } \ln Y = a_0 + a_1 \ln X_1 + a_2 (1000 X_2^{-1}) + a_3 \ln X_3 + a_4 X_4$$

$$\text{Empirical model: } \ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_4$$

It is noted that a_1 was 0.75 (= 3/4) for the theoretical model. The attributes of these variables were analyzed simultaneously by using stepwise multiple regression (backward selection) method (Sokal and Rohlf, 1995). Independent variables were added if $p < 0.10$ and removed if $p > 0.10$. The calculation was conducted using

SYSTAT version 10.2.

3. Results

3.1. ETS

Across epipelagic (*Parasagitta elegans*) and three mesopelagic/bathypelagic chaetognaths (*Eukrohnia bathypelagica*, *E. fowleri*, and *E. hamata*), ETS activities at 10°C ranged from 2.28 (*E. bathypelagica*) to 5.86 $\mu\text{O}_2 \text{ mgN}^{-1} \text{ h}^{-1}$ (*P. elegans*) (Table 1). In order to compute the ETS:Respiration (= ETS:R) ratio, respiration rates of respective species determined at *in situ* temperatures (Table 2) were adjusted to the rates at 10°C based on the temperature coefficients derived from the two regression models (see below). Resultant ETS:R ratios fell within the range of 1.2–1.9 (Table 1).

3.2. Respiration

Of a total of 7 chaetognaths studied, the smallest and largest species were *Eukrohnia hamata* (1.24 mgDM) and *Pseudosagitta scrippsesae* (13.91 mgDM), respectively (Table 2). Respiration rates at *in situ* temperature ranged from 0.13 $\mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*Eukrohnia hamata*) to 1.18 $\mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*Solidosagitta zetesios*) (Table 1, Data set A).

Literature data (Table 2, Data set B) of *Aidanosagitta neglecta*, *Ferosagitta hispida*, *F. robusta*, *Flaccisagitta enflata*, *Mesosagitta minima*, *Parasagitta elegans*, *P. tenuis*, *Pseudosagitta gazellae*, *Sagitta bipunctata*, *Zenosagitta bedoti* forma *minor*, *Eukrohnia hamata* and *E. bathypelagica* from various geographical locations (Fig. 1) were combined with the present results on the basis that the respiration rates were measured with similar methodology (sealed-chamber method coupled with Winkler

titration for dissolved oxygen determination, cf. Ikeda et al., 2000) with the exception of the use of a Gilson differential respirometer by Coston-Clements et al. (2009). Sampling depths being reported as “surface” or “surface layer” in the literature were designated arbitrarily as 2 m. Temperatures and oxygen saturations were represented by ambient values reported in the same literature (if not available, they were substituted by those in the World Ocean Atlas of the National Oceanography Data Center (NODC) Homepage by knowing location, season and depth. As a result, these data sets on 16 chaetognaths altogether extend the ranges of independent variables from 13 to 100% for oxygen saturation, from 0.084 to 35.33 mgDM for body mass, and from 0.06 to 4.68 μLO_2 ind.⁻¹ h⁻¹ for respiration rates. In the case of species for which no C and N composition data was available, literature values from similar species and habitat were used. Treating the data on the same species from different regions or workers as independent, 25 data sets on 17 chaetognaths were available for the present analyses (Data sets A and B, Table 2,).

Thuesen and Childress’s (1993) data (Data set C, Table 2) were treated separately from the other published data sets because their “minimum-depth of occurrence” (MDO; below which 90% of the population can be found) is difficult to translate to the sampling depth because of the broad vertical distribution of each chaetognath. This, together with their standardization of respiration data to WM only (as against to DM, C and N of the present analysis), makes direct comparison of their data with others not possible in the light of the wide between-species variations in body composition of chaetognaths (see “Chemical composition” section below). For comparative purposes only, MDO was assumed to be equivalent to mid-sampling depth, and body WM was converted to N by using mean conversion factors of non-*Pseudosagitta* spp. or

Pseudosagitta spp. (see “Chemical composition” section below).

By using the theoretical model in which the scale coefficient of body mass is preset as 0.75, preliminary analysis was made for the effect of temperature on the respiration rates by plotting the respiration rate standardized to the rate (R_0) of specimens weighing 1 mg DM ($R_0 = R \times DM^{-0.75}$) against temperature ($1000/K$ or $^{\circ}C$) (Fig. 2). It is clear that the rate values for the species below 550 m distribute well below the rate values above 150 m at equivalent inverse temperature or temperature. From this result, only the data of < 150 m were used for the analysis of temperature effect on R_0 . The resultant slope (-7.528) of the regression line was used to compute respiration rate at a given temperature (designated as $10^{\circ}C$) of the chaetognaths from these sampling depths (< 150 m + > 550 m), which was plotted against the mid-sampling depth (Fig. 3). The standardized respiration rates (R_0) at $10^{\circ}C$ of these chaetognaths were correlated negatively with the sampling depth ($p < 0.01$), and this result was not affected with or without the addition of the data set C of Thuesen and Childress (1993).

The overall results of stepwise multiple regressions showed that the variable X_4 (oxygen saturation) was not significant (F -test, $p = 0.25$ – 0.27 for the theoretical model, and $p = 0.41$ – 0.86 for the empirical model), but the rest of independent variables (F -test, $p < 0.001$ for the theoretical and empirical models) were significant attributing 91.5–92.5% (theoretical model) or 82.3–88.8% (empirical model) of the variance in the respiration rates (Table 4). As body mass unit, N yielded the best fit followed by C and DM as judged by adjusted R^2 values. Relative importance of the significant variables as estimated by the standardized partial regression coefficients (Std a_x) indicated the greatest importance of body mass (X_1), followed by temperature (X_2) or depth (X_3) for

the empirical model and near equal importance of X_2 and X_3 for the theoretical model. Judging from the variation inflation factors (VIF), which were all less than 5, multicollinearity was not high among the significant variables of the present analyses (cf. Kutner et al., 2004).

3.3. Chemical composition

Excepting *Pseudosagitta scrippsae* which showed high extreme water content (94.4% of WM) and ash (50.4% of DM) but low extreme C (22.8% of DM) and N (5.9% of DM), the results of the rest of 6 species fell into narrow ranges of 89.8–92.9% for water content, 14.0–27.1% for ash, 7.8–12.1% for N and 32.6–41.1% for C (Table 3, Data set A). C:N ratios calculated were 3.3–5.1 across the seven chaetognaths including *P. scrippsae*.

Literature data (Table 3, Data set B) of *Aidanosagitta neglecta*, *Ferosagitta hispida*, *Flaccisagitta enflata*, *F. hexaptera*, *Mesosagitta minima*, *Parasagitta elegans*, *P. setosa*, *P. tenuis*, *Pseudosagitta gazellae*, *Sagitta bipunctata*, *Solidosagitta marri*, *Zenosagitta bedoti* forma *minor*, *Z. nage*, *Eukrohnia bathypelagica*, *E. bathyantartica* and *E. hamata* from various locations of the world's oceans (Fig. 1) were added to those of the present study for the following analyses. For a total of 21 chaetognaths including “chaetognaths” by Beers (1966) altogether (Data sets A and B, Table 3), habitat temperatures ranged from –1 to 28°C, water content from 83.7 to 94.7%, ash from 6.7 to 50.4%, C from 20.1 to 52.0%, N from 5.7 to 15.1%, and C:N ratio from 2.6 to 5.1.

Water content, ash, C, N and C:N ratio data of chaetognaths inhabiting < 5°C were selected first and separated into two depth groups (< 500 m and ≥ 500 m) to examine the effect of habitat depths by *U*-tests. The test showed that chemical

composition was not affected by habitat depth ($p > 0.15$). Then, the chemical composition data were pooled disregarding dissimilar habitat depths and plotted against habitat temperatures (Fig. 4). Habitat temperature was chosen as an independent variable since it relates closely to either the latitudes or depth of habitats of chaetognaths. As judged by the correlation coefficients, only significant correlation was found in the water content (Fig. 4A), which decreased with the increase of habitat temperature.

Apart from the effects of habitat depth and temperature, the three *Pseudosagitta* spp. data were conspicuous by extremely high water content and ash, and extremely low C and N composition as compared with respective values of non-*Pseudosagitta* spp. (*U*-test, $p < 0.01$, Table 3, Data set A + B). However, removal of these extreme data of *Pseudosagitta* spp. did not alter the significant correlation between water contents and habitat temperatures noted above ($p < 0.05$).

4. Discussion

One might argue that the lower respiration rates of chaetognaths from greater depths in this study (Fig. 3) reflect damage that the specimens incurred during sampling from deeper layers. Enzyme assay of the intermediary metabolism is another measure of respiration rates: a measure that is almost free from the problems associated with recovery of copepods from great depths. This follows from the premise that the amounts of enzymes in a specimen do not vary appreciably over a short time (see Ikeda et al., 2000). Activities of ETS are measured under saturating conditions of substrates and cofactors so that they estimate potential respiration rates ($V_{\max}$ of the Michaelis-Menten equation). On the premise that damage during sampling is minimal for epipelagic

species, similar ETS:Respiration (ETS:R) ratios of mesopelagic/bathypelagic species to those of epipelagic species are indicative of the lack of the damage of specimens retrieved from depth. The theoretical ETS:R ratio is 2 (Owens and King, 1975) and shows little effect of temperature or the body mass of zooplankton (King and Packard, 1975b). From these criteria, the ETS:R ratio of 1.2–1.9 (Table 1) for *Eukrohnia hamata*, *E. bathypelagica* and *E. fowleri* from mesopelagic/bathypelagic zones is somewhat lower than the theoretical value, but is consistent with the values of 1.4–1.8 of *P. elegans* and 1.3 of *Flaccisagitta enflata* from the epipelagic zone. The similar ETS:R ratios between epipelagic and mesopelagic/bathypelagic chaetognaths observed in this study suggest that possible damage of chaetognath specimens retrieved from depth are unlikely in this study.

Our conclusion that habitat depth, together with body mass and habitat temperature, is an important parameter to affect respiration rates of pelagic chaetognaths is consistent with that of Kruse et al. (2010a) but not with that of Thuesen and Childress (1993). Our results (Fig. 3) suggest that while the data of deeper living chaetognaths of Thuesen and Childress (1993) are comparable to ours, there may be too few data of shallow-living chaetognaths to detect the depth-related pattern. It is noted that 9 out of 12 literature data sets used by Kruse et al. (2010a) were common to the present analysis but two data sets for deep-sea chaetognaths used by Kruse et al. (2010a) [those of Thuesen and Childress (1993) off California, cf. Table 2] were not used in the present analysis because of the reasons mentioned above (different definitions and units of parameters). Instead, we used our own respiration data for deep-sea chaetognaths collected from the western subarctic Pacific (Table 2). Because of this difference in the source of respiration data for deep-sea chaetognaths, it is interesting to compare the

outputs of the model of Kruse et al. and those of ours. The original description of Kruse
 et al. (2010a)'s model is; $\log R = 10.0264 + 0.6643 \times \log M - 2956.8576/T - 0.3870 \times$
 $\log D + X_{\text{taxon}}$, where R is respiration rate ($\text{J ind.}^{-1}\text{d}^{-1}$), M is body mass (J ind.^{-1}), T is
 absolute temperature (K), D is habitat depth (m), and X_{taxon} is +0.1212 for Eukrohniidae
 and -0.1212 for Sagittidae. By using conversion factors of $1 \text{ ml O}_2 = 20.100 \text{ J}$ for R and
 $1 \text{ mgC} = 45.7 \text{ J}$ for M in Kruse et al. (2010a) and C:N ratio = 4 of this study (Table 3),
 the model can be translated to the equation of a theoretical model in which body mass
 was expressed by N units as; $\ln Y = 27.2757 + 0.6643 \ln X_1 - 6.8107(1000X_2^{-1}) -$
 $0.3870 \ln X_3 + 2.3026X_{\text{taxon}}$. Since the coefficients of X_2 (-6.8107) and X_3 (-0.3870)
 are much greater than those of our theoretical model expressed by the same body mass
 unit (-4.859 and -0.216, respectively, cf. Table 4), Kruse et al.'s (2010a) model (named
 as K-model) is anticipated to be more sensitive to the change of these two independent
 variables than ours (IT-model). In order to investigate the magnitude of differences in
 the output between these two models, respiration rates of a chaetognath standardized to
 a body size of 1 mgN (R_0) and living in the surface (2 m depth) through 3000 m depth
 at a hypothetical site in the subarctic Pacific in summer were computed (Fig. 5). As a
 result, K-model yielded respiration rates 3.2 times greater than that predicted by
 IT-model for the chaetognath living in the surface layer, the difference reduced
 gradually with increasing depth, and reached 0.7 times at 3000 m. Thus, the discrepancy
 between the predicted respiration rates from the two models was greatest for
 shallow-living chaetognaths.

For marine zooplankton taxa other than chaetognaths, the effect of habitat depth
 on respiration rates has already been demonstrated on copepods (Ikeda et al., 2006b). As
 an explanation for the phenomenon applicable to both copepods and chaetognaths, it

might be considered to reflect low selective pressure for high activity in these animals in the deep-sea (the predation-mediated selection hypothesis, cf. Ikeda et al., 2006b). According to this hypothesis, copepods and chaetognaths living in the illuminated epipelagic zone have the advantage of a rich diet, but they must also be sufficiently active to avoid predation by micronekton for which biomass decreases exponentially with depth (Mauchline, 1991). For copepods, the following evidence was raised in support of the hypothesis: 1) body N (= muscle) decreases from the epipelagic to the abyssopelagic zone (Ikeda et al., 2006a); 2) as a predator avoidance behavior, diel vertical migration (DVM), which is characterized by nocturnal ascent, is frequently observed in shallow-living species but is lacking in deeper-living ones (cf. Yamaguchi et al., 2004); 3) fecundity of deep-living species (Yamaguchi et al., 2004) is lower than that of shallow-living counterparts. Compared to copepods, chaetognaths exhibit less marked depth-related features: 1) a decrease in body N is not detectable (Fig. 4); 2) DVM behavior is infrequent among epipelagic species (Sameoto, 1987; Terazaki, 1998); and 3) lowered fecundity has been demonstrated in few deeper-living species (Terazaki, 1991). These less pronounced depth-related patterns in chaetognaths suggest that the predation pressure on chaetognaths is not as high as that on copepods because of the transparent bodies of the former.

In contrast to respiration rates, no significant effects of sampling depth and habitat temperature on ash, C and N composition and C:N ratios of chaetognaths were detected in the present study (Fig. 4B–E). As the only exception, water content was correlated negatively with habitat temperature (Fig. 4A). For fishes and crustaceans, the decrease in water content is often associated with the increase in lipid content or C composition (Ikeda et al., 2004; Love, 1970) but this is not the case for chaetognaths in this study. At

present, no immediate explanation is available for this phenomenon of chaetognaths. Since C and N composition reflect lipid and protein contents in zooplankton materials (Postel et al., 2000), the lack of correlation between C and N composition and habitat temperature suggest that there are no consistent patterns in lipid contents in chaetognaths inhabiting high/low latitude seas and shallow/deep layers. Presently available data from seasonal survey on lipid contents in chaetognaths are in support of this hypothesis: 11.1–17.7% of DM for mesopelagic *Eukrohnia bathypelagica* and *E. bathyantartica* in the Weddel Sea, Antarctica (Kruse et al., 2010b), 24–40% for *E. hamata* from Korsfjorden, western Norway (Båmstedt, 1978), < 16% for epipelagic *Parasagitta elegans* from Conception Bay, Newfoundland (Choe et al., 2003), and 9–27% for epipelagic *Ferosagitta hispida* from Biscayne Bay, Miami (Reeve et al., 1970). Compared with these values (max: 40%) for chaetognaths, lipids as high as 50–70% of DM (Båmstedt, 1986; Lee et al., 2006) have been reported on copepods from high latitude seas and deep-seas as energy reserves for the seasonally unstable food supply. In terms of C composition and C:N ratios, the maximum values as large as 64% for C (versus 52% for chaetognaths, Table 3) and 11 for C:N ratios (versus 5.1) have been reported on overwintering copepods in the subarctic Pacific (Ikeda, 1974; Ikeda et al., 2004). All these results for lipid contents, C or C:N ratios of chaetognaths imply that their food supply is stable relative to that of copepods in the same habitats.

Terazaki (1993) observed developed intestinal tissue containing small lipid droplets in *Parasagitta elegans* from the mesopelagic zone of the Japan Sea characterized by Japan Sea Proper Water at near zero temperature. Accumulation of small lipid droplets around the intestine has also reported on mesopelagic *Eukrohnia* spp. of the Arctic and Antarctic waters (Kruse et al., 2010b). Lee and Hirota (1973) also

reported the presence of wax esters (a lipid energy reserve) in deep-water chaetognaths but not in epipelagic chaetognaths. Nevertheless, the C:N ratio of the specimens containing small lipid droplets was measured as 4.7, which is somewhat greater than 3.5 of the same species with no-lipid droplets collected from the epipelagic zone of the North Pacific (Terazaki, 1993). This, combined with the lack of any remarkable variation among chaetognaths from diverse habitats (Fig. 4C, D), suggests that the contribution of the lipid droplets in deep-sea chaetognaths to the C and N composition of the whole body is small and masked by the interspecific variation in body composition (Fig. 3).

Acknowledgements

We are grateful to an anonymous referee for comments, which improved the manuscript. We thank D.A. McKinnon for reading the earlier manuscript and valuable comments. Thanks are due to the captain, officers and crew members of T.S. Oshoro-Marui and T.S. Hokusei-Marui for their help in field sampling, and H. Matsumoto and A. Maeda of the Center for Instrumental Analysis of Hokkaido University for CHN elemental analysis. Part of this study was supported by a grant from JSPS KAKENHI 14209001 to T.I.

References

- Båmstedt, U., 1978. Studies on the deep-water pelagic community of Korsfjorden, western Norway. Seasonal variation in weight and biochemical composition of *Chiridius armatus* (Copepoda), *Boreomysis arctica* (Mysidacea), and *Eukrohnia hamata* (Chaetognatha) in relation to their biology. *Sarsia* 63, 145–154.
- Båmstedt, U., 1979. Seasonal variation in the respiratory rate and ETS activity of deep-water zooplankton from the Swedish west coast. In: Naylor, E., Hartnoll, R.G. (Eds.), *Cyclic Phenomena in Marine Plants and Animals*. Pergamon Press, Oxford, pp. 267–274.
- Båmstedt, U., 1986. Chemical composition and energy content. In: Corner, E.D.S., O'Hara, S.C.M. (Eds.), *The Biological Chemistry of Marine Copepods*. Clarendon Press, Oxford, pp. 1–58.
- Beers, J.R., 1966. Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. *Limnol. Oceanogr.* 11, 520–528.
- Bieri, R., 1991. Systematics of chaetognaths. In: Bone, Q., Kapp, H., Pierrot-Bolts, A.C. (Eds.), *The Biology of Chaetognaths*, Oxford Univ Press, Oxford, pp. 122–136.
- Childress, J.J., 1975. The respiratory rates of midwater crustaceans as a function of depth occurrence and relation to the oxygen minimum layer off Southern California. *Comp. Biochem. Physiol. A* 50, 787–799.
- Childress, J.J., 1995. Are there physiological and biochemical adaptation of metabolism in deep-sea animals? *Trends Ecol. Evol.* 10, 30–36.
- Childress, J.J., Thuesen, E.V., 1993. Effects of hydrostatic pressure on metabolic rates

480 of six species of deep-sea gelatinous zooplankton. *Limnol. Oceanogr.* 38,
 481 665-670.

482 Choe, N., Deibel, D., Thompson, R.J., Lee, S.H., Bushell, V.K., 2003. Seasonal
 483 variation in the biochemical composition of the chaetognath *Parasagitta*
 484 *elegans* from the hyperbenthic zone of Conception Bay, Newfoundland. *Mar.*
 485 *Ecol. Prog. Ser.*, 251, 191–200.

486 Coston-Clements, L., Waggett, R.J., Tester, P.A., 2009. Chaetognaths of the United
 487 States South Atlantic Bight: Distribution, abundance and potential interactions
 488 with newly spawned larval fish. *J. Exp. Mar. Biol. Ecol.* 373, 111–123.

489 Curl, H. Jr., 1962. Standing crops of carbon, nitrogen, and phosphorus and transfer
 490 between trophic levels, in continental shelf waters of New York. *Rapp. Proc.*
 491 *Verb. Cons. Int. Explor. Mer* 153, 183–189.

492 Donnelly, J., Torres, J.J., Hopkins, T.L., 1994. Chemical composition of Antarctic
 493 zooplankton during austral fall and winter. *Polar Biol.* 14, 171–183.

494 Favorite, F., Dodimead, A.J., Nasu, K., 1976. Oceanography of the subarctic Pacific
 495 region, 1960–1971. *Bull. Int. Pacif. Fish. Commn.* 33, 1–187.

496 Feigenbaum, D., 1991. Food and feeding. In: Bone, Q., Kapp, H., Pierrot-Bolts, A.C.
 497 (Eds), *The Biology of Chaetognaths*. Oxford Univ Press, Oxford, pp. 45–54.

498 Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of
 499 size and temperature on metabolic rate. *Science* 293, 2248–2251.

500 Gorsky, G., Dallot, S., Sardou, J., Fenaux, R., Carré, C., Palazzoli, I., 1988. C and N
 501 composition of some northwestern Mediterranean zooplankton and
 502 micronekton species. *J. Exp. Mar. Biol. Ecol.* 124, 133–144.

503 Ikeda, T., 1974. Nutritional ecology of marine zooplankton. *Mem. Fac. Fish. Hokkaido*

Univ. 22, 1–97.

Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Mar. Biol.* 85, 1–11.

Ikeda, T., Hirakawa, K., 1998. Metabolism and body composition of zooplankton in the cold mesopelagic zone of the southern Japan Sea. *Plankton Biol. Ecol.* 45, 31–44.

Ikeda, T., Kirkwood, R., 1989. Metabolism and elemental composition of a giant chaetognath *Sagitta gazellae* from the Southern Ocean. *Mar. Biol.* 100, 261–267.

Ikeda, T., Mckinnon, D.A. 2012. Metabolism and chemical composition of zooplankton and hyperbenthos from the Great Barrier Reef waters, North Queensland, Australia. *Plankton Benthos Res.* 7, 8–19.

Ikeda, T., Skjoldal, H.R., 1989. Metabolism and elemental composition of zooplankton from the Barents Sea during early arctic summer. *Mar. Biol.* 100, 173–183.

Ikeda, T., Torres, J.J., Hernández-León, S., Geiger, S.P., 2000. Metabolism. In: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds), *ICES Zooplankton Methodology Manual*. Academic Press, San Diego, pp. 455–532.

Ikeda, T., Sano, F., Yamaguchi, A., 2004. Metabolism and body composition of a copepod *Neocalanus cristatus* (Crustacea) from bathypelagic zone of the Oyashio region, western subarctic Pacific. *Mar. Biol.* 145, 1181–1190.

Ikeda, T., Yamaguchi, A., Matsuishi, T., 2006a. Chemical composition and energy content of deep-sea calanoid copepods in the western North Pacific Ocean. *Deep-Sea Res. I* 53, 1791–1809.

- 528 Ikeda, T., Sano, F., Yamaguchi, A., Matsuishi, T., 2006b. Metabolism of mesopelagic
529 and bathypelagic copepods in the western North Pacific Ocean. Mar. Ecol. Prog.
530 Ser. 322, 199–211.
- 531 Ikeda, T., Sano, F., Yamaguchi, A., 2007. Respiration in marine pelagic copepods: a
532 global-bathymetric model. Mar. Ecol. Prog. Ser. 339, 215–219.
- 533 Ivleva, I.V., 1980. The dependence of crustacean respiration rate on body mass and
534 habitat temperature. Int. Revue ges. Hydrobiol. 65, 1–47.
- 535 Kawamura, A., 1968. Performance of Peterson type closing net. Bull. Plankton Soc.
536 Jpn 15, 11–12.
- 537 King, F.D., Packard, T.T. 1975a. The effect of hydrostatic pressure on respiratory
538 electron transport system activity in marine zooplankton. Deep-Sea Res. 22,
539 99–105.
- 540 King, F.D., Packard, T.T., 1975b. Respiration and the activity of the respiratory
541 electron transport system in marine zooplankton. Limnol. Oceanogr. 20,
542 849–853.
- 543 Kotori, M. 1976. The biology of Chaetognatha in the Bering Sea and the northern
544 North Pacific Ocean, with emphasis on *Sagitta elegans*. Mem. Fac. Fish.
545 Hokkaido Univ. 23, 95–183.
- 546 Kruse, S., Brey, T., Bathmann, U., 2010a. Role of midwater chaetognaths in Southern
547 Ocean pelagic energy flow. Mar. Ecol. Prog. Ser. 416, 105–113.
- 548 Kruse, S., Hagen, W., Bathmann, U., 2010b. Feeding ecology and energetic of the
549 Antarctic chaetognaths *Eukrohnia hamata*, *E. bathypelagica* and *E.*
550 *bathyantartica*. Mar. Biol. 157, 2289–2302.
- 551 Kutner, M.H., Nachtsheim, C., Neter, J., 2004. Applied Linear Regression Models, 4th

552 edition, McGraw-Hill, Irwin.

553 Lee, H.F., Hirota, J., 1973. Wax esters in tropical zooplankton and nekton and the
554 geographical distribution of wax esters in marine copepods. *Limnol. Oceanogr.*
555 18, 227–239.

556 Lee, R.F., Hagen, W., Kattner, G. 2006. Lipid storage in marine zooplankton. *Mar. Ecol.*
557 *Prog. Ser.* 307, 273–306.

558 Longhurst, A.R., 1985. The structure and evolution of plankton communities. *Prog.*
559 *Oceanogr.* 15, 1–35.

560 Love, R.M., 1970. *The Chemical Biology of Fishes*. Academic Press, London

561 Lowry, O.H., Rosebrough, N.J., Farr, A.L., Randall, R.J., 1951. Protein measurement
562 with the Folin Phenol reagent. *J. Biol. Chem.* 193, 265–275.

563 Mauchline, J., 1991. Some modern concepts in deep-sea pelagic studies: patterns of
564 growth in the different horizons. In: Mauchline, J., Nemoto, T. (Eds), *Marine*
565 *Biology, its Accomplishment and Future Prospect*. Hokusen-sha, Tokyo, pp.
566 107–130.

567 Mayzaud, P., Martin, J.L.M., 1975. Some aspects of the biochemical and mineral
568 composition of marine plankton. *J. Exp. Mar. Biol. Ecol.* 17, 297–310.

569 Omori, M., 1969. Weight and chemical composition of some important oceanic
570 zooplankton in the North Pacific Ocean. *Mar. Biol.* 3, 4–10.

571 Ozawa, M., Yamaguchi, A., Ikeda, T., Watanabe, Y., Ishizaka, J., 2007. Abundance
572 and community structure of chaetognaths from the epipelagic through
573 abyssopelagic zones in the western North Pacific and its adjacent seas.
574 *Plankton Benthos Res.* 2, 184–197.

575 Owens, T.G., King, F.D., 1975. The measurement of respiratory electron-transport
576 system activity in marine zooplankton. *Mar. Biol.* 30, 27–36.

577 Postel, L., Fock, H., Hagen, W., 2000. Biomass and abundance. In: Harris, R.P., Wiebe,
 578 P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds), ICES Zooplankton
 579 Methodology Manual. Academic Press, San Diego, pp. 83–192.
 580 Reeve, M.R., Raymont, J.E.G., Raymont, J.K.B., 1970. Seasonal biochemical
 581 composition and energy sources of *Sagitta hispida*. Mar. Biol. 6, 357–364.
 582 Sameoto, D.D., 1972. Yearly respiration rates and estimated energy budget for *Sagitta*
 583 *elegans*. J. Fish. Res. Bd Canada 29, 987–996.
 584 Sameoto, D.D., 1987. Vertical distribution and ecological significance of chaetognaths
 585 in the Arctic environment of Baffin Bay. Polar Biol. 7, 317–328.
 586 Seibel, B.A., Drazen, J.C., 2007. The rate of metabolism in marine animals:
 587 environmental constraints, ecological demands and energetic opportunities.
 588 Phil. Trans. R. Soc. B 362, 2061–2078.
 589 Sokal, R.R., Rohlf, F.J., 1995. Biometry. The Principles and Practice of Statistics in
 590 Biological Research. Freeman, New York.
 591 Terazaki, M., 1995. The role of carnivorous zooplankton, particularly chaetognaths in
 592 ocean flux. In: Sakai, H., Nozaki, Y. (Eds), Biogeochemical Processes and
 593 Ocean Flux in the Western Pacific, TERRAPUB, Tokyo, pp. 319–330.
 594 Terazaki, M., 1998. Life history, distribution, seasonal variability and feeding of the
 595 pelagic chaetognath *Sagitta elegans* in the subarctic Pacific: A review. Plankton
 596 Biol. Ecol. 45, 1–17.
 597 Terazaki, M., 1991. Deep sea chaetognaths. In: Bone, Q., Kapp, H., Pierrot-Bolts, A.C.
 598 (Eds), The Biology of Chaetognaths. Oxford Univ Press, Oxford, pp. 117–121.
 599 Terazaki, M., 1993. Deep-sea adaptation of the epipelagic chaetognath *Sagitta elegans*
 600 in the Japan Sea. Mar. Ecol. Prog. Ser. 98, 79–88.

- 601 Terazaki, M., Miller, C.B., 1986. Life history and vertical distribution of pelagic
602 chaetognaths at Ocean Station P in the subarctic Pacific. *Deep-Sea Res.* 33A,
603 323–337.
- 604 Thuesen, E.V., Childress, J.J., 1993. Enzymatic activities and metabolic rates of
605 pelagic chaetognaths: lack of depth-related declines. *Limnol. Oceanogr.* 38,
606 935–948.
- 607 Welch, H.E., Siferd, T.D., Bruecker, P., 1996. Population densities, growth, and
608 respiration of the chaetognath *Parasagitta elegans* in the Canadian high Arctic.
609 *Can. J. Fish. Aquat. Sci.* 53, 520–527.
- 610 Yamaguchi, A., Ikeda, T., Watanabe, Y., Ishizaka, J., 2004. Vertical distribution patterns
611 of pelagic copepods as viewed from the predation pressure hypothesis. *Zool.*
612 *Stud.* 43, 475–485.

Figure captions

Fig. 1. Geographical distribution of study sites of respiration (summarized in Table 2) and/or chemical composition (Table 3) of pelagic chaetognaths of the world's ocean. The sites of respiration of epipelagic (shallow) chaetognaths are separated from those of mesopelagic/bathypelagic (deep) chaetognaths.

Fig. 2. Relationship between the respiration rate standardized to a body size of 1 mg body DM (R_0) and temperature (T^{-1} : 1000/K, or T : °C) of chaetognaths from epipelagic (< 150 m) and mesopelagic/bathypelagic zones (> 550 m)(Data sets A+ B, Table 2). The data points represent means, and the regression line is derived from epipelagic species only. Data set C is for comparative purpose only. See text for details. **: $p < 0.01$.

Fig. 3. Relationship between respiration rates standardized to a body size of 1 mgDM (R_0) at 10°C and mid-sampling depth. The data points represent means derived from the data sets in Table 2. Regression lines derived from Data sets A+B (solid line) and A+B+C (hatched line) are superimposed. **: $p < 0.01$.

Fig. 4. Relationships between habitat temperature (T) and water contents (A), ash (B), C (C), N (D) and C:N ratios (E) of chaetognaths at various regions of the world's oceans. The data points represent means of each chemical composition components in Table 3. The data of chaetognaths collected from 500 m depth or below are separated from those from above 500 m. Solid regression lines show significant relationships ($p < 0.05$), while those with hatched lines were not ($p > 0.05$).

Fig. 5. Hypothetical vertical profiles of water temperature (T) in the western subarctic Pacific Ocean in early summer (left), predicted respiration rates of chaetognaths

standardized to a body size of 1 mgN (R_0) from K-model (Kruse et al., 2010a) and
IT-model (this study)(middle), and the differences between the outputs from the two
models (right). See text for details.

Table 1. ETS activities of mesopelagic and bathypelagic chaetognaths determined at 10°C and respiration rates (R) at *in situ* temperature (Table 1) then converted to R at 10°C (by using the temperature coefficients of the theoretical and empirical models of this study) to compute ETS:R ratios. ETS:R ratios of epipelagic *Parasagitta elegans* and *Flaccisagitta enflata*, both determined on the same batches of specimens at the same temperature (7°C and 27°C, respectively) are included for comparison. Values are means $\pm$ SD on N replicates. See text for details.

Species	ETS at 10°C			R at 10°C		ETS:R	Reference
	N	[μO ₂ (mg N) ⁻¹ h ⁻¹]		T: Theoretical model E: Empirical model	N		
Epipelagic							
<i>Parasagitta elegans</i>	37	5.86 ± 1.89		10	3.27 ± 0.71	1.79 ± 0.70	This study
	11					1.41 ± 0.27	Ikeda (unpublished)
<i>Flaccisagitta enflata</i>	10					1.28 ± 0.42	Skjoldal & Ikeda (unpublished)
Mesopelagic/bathypelagic							
<i>Eukrohnia hamata</i>	39	3.27 ± 1.20	T	5	2.16 ± 0.41	1.51 ± 0.63	This study
			E		2.36 ± 0.45	1.38 ± 0.57	This study
<i>Eukrohnia bathypelagica</i>	17	2.28 ± 0.88	T	16	1.83 ± 0.52	1.25 ± 0.60	This study
			E		1.98 ± 0.57	1.15 ± 0.55	This study
<i>Eukrohnia fowleri</i>	22	2.57 ± 0.89	T	32	1.33 ± 0.42	1.94 ± 0.90	This study
			E		1.46 ± 0.46	1.76 ± 0.82	This study

Table 2. Respiration rates of pelagic chaetognaths determined in this study (data set A) and by previous workers (data sets B and C) together with the data of the study site, season, sampling depth, ambient temperature (=experimental temperature) and oxygen saturation. Previous data expressed in the form of regression equations were converted to the respiration rate of a specimen at mid-body mass range (in parenthesis). Data set C was separated from data sets B by dissimilar definition of depth (MDO: Minimum Depth of Occurrence, *italic*) and body mass by WM only. Values are means $\pm$ SD on N replicates. See text for details.

Data set	Species	Region	Season	Mid-sampling depth (range), MDO(<i>italic</i>) (m)	O ₂ saturation (I = 100%)	Expt. (°C)	N	DM(mg)	Respiration rate (μO_2 ind. ⁻¹ h ⁻¹)	Reference
A	<i>Caecosagitta macrocephala</i>	WN Pacific Ocean	Mar/Dec	1500(1000–2000)	0.2	2	3	6.39 $\pm$ 4.48	0.70 $\pm$ 0.68	This study
	<i>Parasagitta elegans</i>	WN Pacific Ocean	Mar	150(100–200)	1	2	10	3.24 $\pm$ 1.16	0.77 $\pm$ 0.24	This study
	<i>Pseudosagitta scrippsae</i>	WN Pacific Ocean	June	750(500–1000)	0.13	3	7	13.91 $\pm$ 3.02	1.15 $\pm$ 0.28	This study
	<i>Solidosagitta zetesios</i>	WN Pacific Ocean	Mar/Jun	1500 (1000–2000)	0.2	2	7	8.89 $\pm$ 2.42	1.18 $\pm$ 0.49	This study
	<i>Eukrohnia bathypelagica</i>	WN Pacific Ocean	Mar/Dec	750(500–1000)	0.13	3	16	1.61 $\pm$ 0.28	0.15 $\pm$ 0.06	This study
	<i>Eukrohnia fowleri</i>	WN Pacific Ocean	Mar/Dec	2500(2000–3000)	0.32	1.5	32	8.08 $\pm$ 3.53	0.50 $\pm$ 0.21	This study
	<i>Eukrohnia hamata</i>	WN Pacific Ocean	Mar/Dec	750(500–1000)	0.13	3	5	1.24 $\pm$ 0.14	0.13 $\pm$ 0.04	This study
B	<i>Aidanosagitta neglecta</i>	GBR inshorewater	Jul	2(surface)	1	23	6	0.29 $\pm$ 0.13	0.79 $\pm$ 0.45	Ikeda & McKinnon (2012)
	<i>Ferosagitta hispida</i>	Biscayne Bay, Miami	Dec	2(surface)	1	24	5	0.33 $\pm$ 0.06	1.08 $\pm$ 0.32	Ikeda (unpublished)
		Biscayne Bay, Miami		2(surface)	1	26	27	(0.10)	(0.40)	Reeve et al. (1970)
	<i>Ferosagitta robusta</i>	Eq. Indian Ocean	Oct/Nov	2(surface)	1	27	2	0.75 $\pm$ 0.51	4.68 $\pm$ 0.83	Ikeda (1974)
	<i>Flaccisagitta enflata</i>	GBR inshorewater	June	2(surface)	1	27	10	0.71 $\pm$ 0.29	1.67 $\pm$ 0.48	Ikeda (unpublished)
	<i>Mesosagitta minima</i>	SE Japan Sea	Jul	2(surface)	1	15	2	0.094 $\pm$ 0.058	0.27 $\pm$ 0.08	Ikeda (1974)
	<i>Parasagitta elegans</i>	WN Pacific Ocean	May/Jun	2(surface)	1	9	5	1.03 $\pm$ 0.83	1.04 $\pm$ 0.61	Ikeda (1974)
		Barents Sea	May/Jun	50(0–100)	1	–0.4	12	4.5 $\pm$ 0.9	1.41 $\pm$ 0.36	Ikeda & Skjoldal (1989)
		S. Japan Sea	Sep	550(400–700)	0.6	0.5	10	3.56 $\pm$ 0.74	0.98 $\pm$ 0.32	Ikeda & Hirakawa (1998)
		Canadian High Arctic	Feb/Nov	50(0–100)	1	–1.3(–1 to –1.5)		(1.41)	(0.38)	Wekch et al. (1996)
		Bedford Basin	All seasons	25(0–50)	1	7.5(0–15)	14	(1.8)	1.09 $\pm$ 0.51	Sameoto (1972)
		off the coast of North Carolina	?	2(surface)	1	22	15	0.24	0.78 $\pm$ 0.06	Coston-Clements et al. (2009)
	<i>Parasagitta tenuis</i>									
	<i>Pseudosagitta gazellae</i>	Southern Ocean	Oct	100(0–200)	1	–1	40	35.33 $\pm$ 20.54	2.68 $\pm$ 1.74	Ikeda & Kirkwood (1989)
	<i>Sagitta bipunctata</i>	Eq. Indian Ocean	Nov	2(surface)	1	27.5	2	0.45 $\pm$ 0.07	2.62 $\pm$ 0.78	Ikeda (1974)
	<i>Serratiasagitta serratodentata</i>	Eq. Indian Ocean	Nov	2(surface)	1	27	2	0.73 $\pm$ 0.24	3.97 $\pm$ 1.25	Ikeda (1974)
	<i>Zenosagitta beddii</i> L minor	GBR inshorewater	Jul	2(surface)	1	24	10	0.084 $\pm$ 0.022	0.28 $\pm$ 0.08	Ikeda & McKinnon (2012)
	<i>Eukrohnia hamata</i>	Swedish fjord	All seasons	1000(0–200)	1	5.5(5–6)	8	6.21	0.86	Björnstedt (1979)
	<i>E. hamata</i> /bathypelagica	Weddel Sea	Summer/winter	750(500–1000)	0.5	0	117	2.5	0.38 $\pm$ 0.20	Kruse et al. (2010b)
C	<i>Caecosagitta macrocephala</i>	off California	Sep/Jun/Feb	700	0.05	5	9	2.1	0.39	Thuesen & Childress (1993)
	<i>Decipisagitta decipiens</i>	off California	Sep/Jun/Feb	250	0.5	5	1	0.52	0.21	Thuesen & Childress (1993)
	<i>Flaccisagitta hexaptera</i>	off California	Sep/Jun/Feb	10	1	5	1	18.5	2.53	Thuesen & Childress (1993)
	<i>Parasagitta euneritica</i>	off California	Sep/Jun/Feb	10	1	15	2	0.22	0.21	Thuesen & Childress (1993)
	<i>Pseudosagitta lyra</i>	off California	Sep/Jun/Feb	10	1	5	4	28.6	1.73	Thuesen & Childress (1993)
	<i>Pseudosagitta maxima</i>	off California	Sep/Jun/Feb	200	0.6	5	12	26.8	1.78	Thuesen & Childress (1993)
	<i>Solidosagitta zetesios</i>	off California	Sep/Jun/Feb	300	0.4	5	12	8.2	1.34	Thuesen & Childress (1993)
	<i>Eukrohnia fowleri</i>	off California	Sep/Jun/Feb	700	0.05	5	10	10.5	0.85	Thuesen & Childress (1993)
	<i>Eukrohnia hamata</i>	off California	Sep/Jun/Feb	400	0.2	5	3	2.1	0.39	Thuesen & Childress (1993)
	<i>Heterokrohnia murina</i>	off California	Sep/Jun/Feb	1900	0.2	5	1	19.6	2.18	Thuesen & Childress (1993)

Table 3. Sampling data (region, depth, water temperature) and chemical composition (water content, ash, C, N and C:N ratios) of pelagic chaetognaths of the present study (data set A) and those of the previous workers (data set B). Data sets A and B are pooled and differences in the composition between *Pseudosagitta* and non-*Pseudosagitta* spp. are tested. Means $\pm$ SD with the number of replicates in parenthesis for water contents, or means and ranges in parenthesis for ash, C, N and C:N ratios. ND = no data. *NS* = not significant

Data set	Species	Region	Season	Mid-sampling depth (m)	Habitat temp. (°C)	Water (% of WM)	Ash (% of DM)	C (% of DM)	N (% of DM)	C:N (by mass)	Reference
A	<i>Caecosagitta macrocephala</i>	WN Pacific Ocean	Mar/Dec	1500	2	86.7 $\pm$ 4.7(3)	17.4	44.9	9.9	4.5	This study
	<i>Parasagitta elegans</i>	WN Pacific Ocean	Mar	150	2	91.0 $\pm$ 0.2(10)	10.3	40.4	12.1	3.3	This study
	<i>Pseudosagitta scrippsae</i>	WN Pacific Ocean	June	750	3	94.4 $\pm$ 0.6(6)	50.4	22.8	5.9	3.9	This study
	<i>Solidosagitta zetesii</i>	WN Pacific Ocean	Mar/Jun	1500	2	89.8 $\pm$ 1.0(5)	14	41.1	10.5	3.9	This study
	<i>Eukrohnia bathypelagica</i>	WN Pacific Ocean	Mar/Dec	750	3	92.2 $\pm$ 0.9(16)	27.1	37.7	8	4.7	This study
	<i>Eukrohnia fowleri</i>	WN Pacific Ocean	Mar/Dec	2500	1.5	90.3 $\pm$ 1.5(30)	21.4	43.2	8.5	5.1	This study
	<i>Eukrohnia hamata</i>	WN Pacific Ocean	Mar/Dec	750	3	92.9 $\pm$ 0.3(4)	31.7	32.6	7.8	4.2	This study
B	<i>Aidanosagitta negrecta</i>	GBR inshorewater	Jul	2	23	91.1 $\pm$ 1.2(6)	ND	31.3	8.9	3.5	Ikeda & McKinnon (2012)
	<i>Ferosagitta hispida</i>	Bermuda water	Mar/Apr	2	20	ND	ND	ND	8.7	ND	Beers (1966)
		Off the coast of North Carolina		2	22	ND	ND	40.6	11.3	3.6	Coston-Clements et al. (2009)
	<i>Flaccisagitta enflata</i>	Eg. Indian Ocean	Feb	2	28	ND	ND	35.0	7.9	4.4	Ikeda (1974)
		NW Mediterranean	Mar/May	15	14	ND	ND	43.7	9.1	5	Gorsky et al. (1988)
	<i>Flaccisagitta hexaptera</i>	off NW Africa	Jan	2	20	ND	ND	33.5	7.8	4.3	Ikeda (1974)
	<i>Mesosagitta minima</i>	NE Japan Sea	Jul	2	15	ND	ND	35.9	10.9	3.3	Ikeda (1974)
		NW Mediterranean	Mar/May	15	19	ND	ND	51.0	11.8	4.3	Gorsky et al. (1988)
	<i>Parasagitta elegans</i>	off New York	All seasons?	2	10	89.4	21.6	ND	7.8	ND	Curl (1962)
		WN Pacific Ocean		275	4	85.9	4.8*	47.7	10.7	4.4	Omori (1969)
		WN Pacific Ocean	May/Jun	2	9	ND	ND	40.8	11.7	3.5	Ikeda (1974)
		St. Margaret Bay, Nova Scotia	Nov	25	10	ND	6.7	39.0	15.1	2.6	Maynard & Martin (1975)
		Barents Sea	May/Jun	50	-0.4	89.4 $\pm$ 0.5(12)	10.2	38.4	10.4	3.7	Ikeda & Skjoldal (1989)
		S Japan Sea	Sep	550	0.5	91.1 $\pm$ 0.6(10)	13.4	38.3	12.7	3.0	Ikeda & Hirakawa (1998)
		Conception Bay, Newfoundland	All seasons	235	-1	ND	11.8(9.5-17.58)	41.3(40-43)	9.4(9.1-10.0)	4.4(4-4.7)	Choe et al. (2003)
	<i>Parasagitta setosa</i>	NW Mediterranean	Mar/May	15	14	ND	ND	39.1	10.0	3.9	Gorsky et al. (1988)
	<i>Parasagitta tenuis</i>	Off the coast of North Carolina		2	22	ND	ND	37.9	9.9	3.8	Coston-Clements et al. (2009)
	<i>Pseudosagitta gozellae</i>	Southern Ocean	Oct	100	-1	94.7 $\pm$ 0.1(4)	53	20.1	5.7	3.5	Ikeda & Kirkwood (1989)
		Scotia/Weddell Sea	Fall/winter	500	0	94.3(93.5/95.1)	45.6(54.7/36.4)	23.2(19.7/26.6)	6.1(5.4/6.8)	3.8(3.7/3.9)	Donnelly et al. (1994)
	<i>Sagitta bipunctata</i>	NW Mediterranean	Mar/May	15	14	ND	ND	52.0	12.9	4.0	Gorsky et al. (1988)
	<i>Solidosagitta mauri</i>	Scotia/Weddell Sea	Winter	500	0	90.8	13.5	40.4	9.8	4.1	Donnelly et al. (1994)
	<i>Zenosagitta bedori</i> L. minor	GBR inshorewater	Jul	2	24	83.7 $\pm$ 4.1(10)	ND	38.4	12.3	3.1	Ikeda & McKinnon (2012)
	<i>Zenosagitta nuae</i>	WN Pacific Ocean		50	23	88.4	4.2*	43.5	11.1	3.9	Omori (1969)
	<i>Eukrohnia bathypelagica</i>	Weddel Sea	Summer/winter	750	0	ND	ND	27.9(24.6/31.3)	6.3(5.7/6.9)	4.4(4.3/4.5)	Kruse et al. (2010b)
	<i>Eukrohnia bathypelagica</i>	Weddel Sea	Summer/winter	750	0	ND	ND	37.4(32.4/42.4)	7.7(6.9/8.4)	5.0(4.8/5.1)	Kruse et al. (2010b)
	<i>Eukrohnia hamata</i>	Scotia/Weddell Sea	Winter	500	0	91.8	20.5	37.5	9.1	4.1	Donnelly et al. (1994)
		Weddel Sea	Summer/winter	750	0	ND	ND	34.9(30.4/39.4)	7.3(6.8/7.8)	4.9(4.6/5.1)	Kruse et al. (2010b)
	"Chaetognaths"	Sargasso Sea	All seasons	250	18	85.3(83.4-86.6)	ND	28.3(21.9-34.3)	7.8(6.3-9.4)	3.6	Beers (1966)
A + B	Grand mean (excluding <i>Pseudosagitta</i> spp. and "Chaetognaths" data)					89.6 $\pm$ 2.5	16.9 $\pm$ 7.2	39.5 $\pm$ 5.3	9.9 $\pm$ 2.0	4.0 $\pm$ 0.6	
	N					15	13	29	31	29	
	Grand mean (<i>Pseudosagitta</i> spp. data only)					94.5 $\pm$ 0.2	46.6 $\pm$ 8.9	22.0 $\pm$ 1.7	5.9 $\pm$ 0.2	3.7 $\pm$ 0.2	
	N					3	3	3	3	3	
Null hypothesis: No difference between the two means (U-test)					p	0.007	0.009	0.005	0.005	0.332^{NS}	

*Excluded in the present analysis because of high combustion temperature (800°C)

Table 4. Multiple regression statistics of theoretical and empirical models of respiration rates (Y : $\mu\text{l O}_2 \text{ ind.}^{-1}\text{h}^{-1}$) of pelagic chaetognaths on body mass (X_1 : mg ind. $^{-1}$), habitat temperature (X_2 : 1000/K for the former, $^{\circ}\text{C}$ for the latter), depth sampled (X_3 : m) and oxygen saturation (X_4 : 1.00 for full saturation) derived from backward stepwise regression analyses. Italic figures denote standardised partial regression coefficients (Std ax) and variation inflation factors (VIF) calculated for the best fit equation (Step 1).

Regression model	Body mass unit	N	Step No.	Regression equation: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 \ln X_4$					R ² (adjusted R ²)
				a ₀	a ₁	a ₂	a ₃	a ₄	
Theoretical	DM	25	0		0.75	-5.558	-0.145	0.593	0.928
			1	16.27	0.75	-4.488	-0.254		0.922 (0.915)
						-0.466	-0.528		
						3.973	3.973		
	C	25	0		0.75	-5.217	-0.156	0.564	0.932
			1	16.04	0.75	-4.201	-0.259		0.928 (0.921)
						-0.446	-0.551		
						3.937	3.937		
	N	25	0		0.75	-5.813	-0.119	0.529	0.936
			1	19.21	0.75	-4.859	-0.216		0.931 (0.925)
						-0.529	-0.470		
						3.937	3.937		
Empirical	DM	25	0		0.805	0.068	-0.184	0.458	0.852
			1	-0.173	0.833	0.06	-0.274		0.846 (0.823)
					1.464	0.743	-0.832		
					2.915	4.348	4.464		
	C	25	0		0.891	0.065	-0.250	0.249	0.882
			1	0.81	0.909	0.06	-0.300		0.880 (0.863)
					1.539	0.746	-0.909		
					3.077	4.329	4.587		
	N	25	0		0.928	0.074	-0.228	0.127	0.903
			1	1.792	0.937	0.072	-0.253		0.903 (0.889)
					1.546	0.888	-0.768		
					3.021	4.566	4.329

Ikeda & Takahashi Fig. 1

Ikeda & Takahashi Fig. 2

Ikeda & Takahashi Fig. 3

Ikeda & Takahashi Fig. 4

Ikeda & Takahashi Fig. 5