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Nitrogen stable isotope composition suggests trophic differentiation in three chaetognath species (*Parasagitta elegans*, *Pseudosagitta maxima*, and *Eukrohnia hamata*) from the Barents Sea

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ABSTRACT: Chaetognaths are often considered strict predators, feeding primarily on copepods, but recent studies have shown that algae and/or marine snow may also be potential food source for some species in polar waters. The aim of this study was to investigate the relative trophic position (TP) of three chaetognath species (*Parasagitta elegans*, *Pseudosagitta maxima*, and *Eukrohnia hamata*) using nitrogen stable isotope analysis. Chaetognaths were collected at 14 stations in the Barents Sea during the polar nights in 2013 and 2014. Since natural variations of δ^{15}N values can be expected across the stations, we used filter-feeding copepods (*Calanus* spp.) as an isotopic baseline. To assess the possible effect of size on the TPs of chaetognaths, we measured all specimens and analyzed them individually. Our results showed significant differences in δ^{15}N values among the three species, indicating that *P. elegans* occupied the highest TP, followed by *P. maxima* and *E. hamata*. The variations of δ^{15}N values across the stations were positively correlated with those of copepods in *P. elegans*, but not in the other two species. In *E. hamata*, we have detected negative correlation of δ^{15}N values with depth, but it remains unknown if this trend is due to an isotopic shift in the food source or to actual changes in TP. Size was not a good predictor of TPs in these chaetognaths, as no general pattern in δ^{15}N values was observed among the three species or within a single species. Our results complement other studies suggesting that *E. hamata* and *P. maxima* are omnivorous and feed at lower trophic levels than *P. elegans*. Thus, considering chaetognaths as a single trophic group may oversimplify their actual role in marine food webs.

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KEY WORDS: Chaetognaths, Copepods, stable isotopes, trophic position, Polar night, Barents Sea.

Состав стабильных изотопов азота указывает на трофические различия у трех видов хетогнат (*Parasagitta elegans*, *Pseudosagitta maxima* и *Eukrohnia hamata*) из Баренцева моря

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РЕЗЮМЕ: Хетогнаты часто рассматриваются как облигатные хищники питающиеся преимущественно копеподами, однако последние исследования показывают, что водоросли и/или морской снег могут также быть потенциальным источником пищи для некоторых видов в полярных водах. Целью настоящего исследования было изучить относительное трофическое положение (ТП) трех видов хетогнат (*Parasagitta elegans*, *Pseudosagitta maxima* и *Eukrohnia hamata*) с использованием анализа стабильных изотопов азота. Хетогнаты были собраны на 14 станциях в Баренцевом море в течение полярной ночи 2013 и 2014 гг. Поскольку естественные вариации значений δ^{15}N ожидаемы среди станций, мы использовали копепод-фильтраторов (*Calanus* spp.) в качестве изотопного бэйзлайна. Чтобы оценить возможное влияние размеров на ТП хетогнат, мы измерили длину всех экземпляров и анализировали их индивидуально. Наши результаты показали значительные различия в значениях δ^{15}N между тремя видами, указывающие что *P. elegans* занимает самое высокое ТП, за ней следуют *P. maxima* и *E. hamata*. Вариации значений δ^{15}N среди станций положительно коррелировали с таковыми у копепод у *P. elegans*, но не у других двух видов. У *E. hamata* мы обнаружили отрицательную корреляцию значений δ^{15}N с глубиной, однако остается неясным, вызвано ли это изотопным сдвигом в источнике питания или реальными изменениями ТП. Размер не являлся хорошим предиктором ТП у этих хетогнат, поскольку общей закономерности не было обнаружено ни среди трех видов, ни в пределах отдельных видов. Наши результаты дополняют другие исследования, предполагающие, что *E. hamata* и *P. maxima* являются всеядными и питаются на более низких трофических уровнях чем *P. elegans*. Таким образом, рассмотрение хетогнат в качестве единой трофической группы может чрезмерно упрощать их реальную роль в морских пищевых сетях.

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КЛЮЧЕВЫЕ СЛОВА: щетинкочелюстные, копеподы, стабильные изотопы, трофическое положение, полярная ночь, Баренцево море.

Introduction

Different aspects of chaetognath's ecology have been studied in Arctic waters in recent decades, including their seasonal life strategies (Grigor *et al*., 2014, 2015), population structure and distribution (Kosobokova, Hopcroft, 2021), growth and reproduction (Grigor *et al*., 2017), feeding strategies (Grigor *et al*., 2020), and predation impact on zooplankton communities (Amano *et al*., 2019; Patuła *et al*., 2023). In pelagic food webs, chaetognaths are often considered among the dominant predators, with copepods being their main prey (reviews: Feigenbaum, Maris, 1984; Feigenbaum, 1991). Indeed, it has been shown that chaetognaths use special mechanoreceptors that respond to vibrations similar to those produced by copepods (Feigenbaum, Reeve, 1977). Their grasping apparatus is also adapted to piercing chitinous integuments and injecting a poison similar to tetrodotoxin (Thuesen *et al*., 1988; Thuesen, Kogure, 1989). However, the predation impact of chaetognaths on the copepod populations remains enigmatic, as many researchers have emphasized the remarkable scarcity of prey in the guts of these predators in different regions of the World's Oceans (e.g., Øresland, 1987; Falkenhaug, 1991; Kruse *et al*., 2010; Grigor *et al*., 2015, 2020).

Various microscopy techniques have been used to examine the diet of chaetognaths, allowing the detection of undigested food remains, in particular copepod mandibles and other chitinous structures (e.g., Falkenhaug, 1991; Froneman, Pakhomov, 1998; Grigor *et al*., 2015, 2020). However, this approach provides only short-term dietary observations and is subject to certain limitations, such as: 1) the rapid rate of digestion in chaetognaths and 2) cod-end feeding, prey loss due to regurgitation, and other artefacts during the sampling and preservation (Baier, Purcell, 1997). Stable isotope analysis (SIA) is an alternative approach that can provide a time-integrated measure of trophic position of an organism (review: Layman *et al*., 2012). The application of this method is based on the similarity of the isotopic composition of the consumer and its food source. For example, ratios of carbon stable isotopes ($\delta^{13}C$) undergo low changes (< 1‰) with trophic transfers and thus are commonly used to infer the sources of primary production (Post, 2002). In contrast, ratios of nitrogen stable isotopes ($\delta^{15}N$) show more pronounced trophic enrichment (3–4‰), so they are used to determine the trophic position of a consumer and the structure of the food web (Minagawa, Wada, 1984; Post, 2002).

Several species of chaetognaths inhabit Arctic waters, among them *Parasagitta elegans* is most common in shelf waters and *Eukrohnia hamata* in deep-sea areas (Grigor *et al*., 2014, 2017, 2020; Kosobokova, Hopcroft, 2021). These two species are similar in size (up to 30–40 mm), but previous researchers have noted significant differences in their reproduction (Grigor *et al*., 2017; Kosobokova, Hopcroft, 2021) and feeding strategies (Grigor *et al*., 2020). Grigor *et al*. (2020) provided comprehensive data on the trophic ecology of these two chaetognaths in the Canadian Arctic, using gut contents as short-term signals and trophic markers (stable isotopes, lipids and fatty acids) as signals integrated over the longer-term. Their results indicated that *E. hamata* feeds at lower trophic levels than *P. elegans*, and it was suggested that *E. hamata* receives a substantial energy input from diatoms that make up aggregates of marine snow. Another

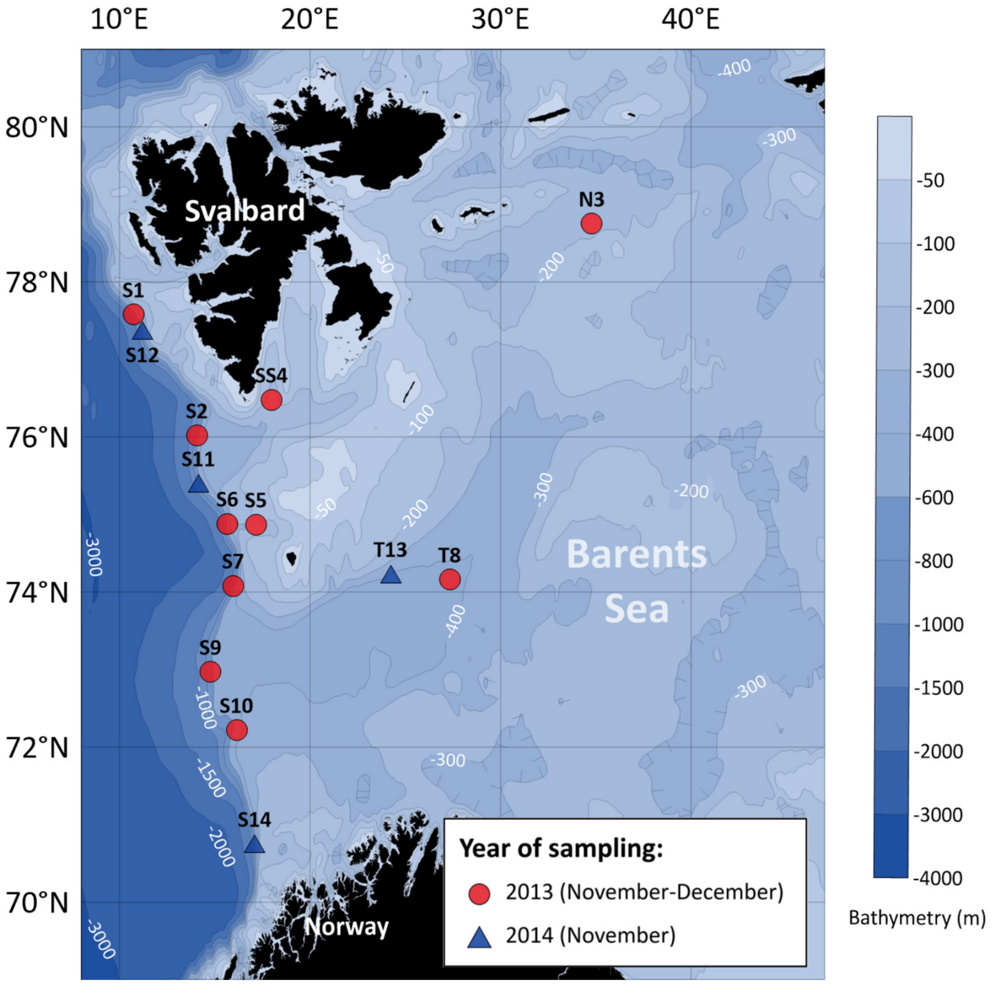

Fig. 1. Bathymetric map showing sampling stations in the Barents Sea.
Рис. 1. Батиметрическая карта, показывающая станции отбора проб в Баренцевом море.

species found in deep Arctic waters, *Pseudosagitta maxima*, reaches much larger sizes (up to 90 mm), but information on its trophic ecology is limited due to its rare occurrence (Sameoto, 1987; Øresland, 1990). Size is an important parameter determining the diet of chaetognaths, and many studies have indicated a positive relationship between the size of these predators and their prey (e.g., Pearre, 1980; Sullivan, 1980; Falkenhaug, 1991; Brodeur, Terazaki, 1999). To date, detailed studies on the chaetognath's stable isotope ecology have focused primarily on *P. elegans* and *E. hamata* (Søreide *et al.*, 2006, 2013; Connelly *et al.*, 2014; Grigor *et al.*, 2015, 2020), but size has not been considered as a potential factor influencing the trophic position of these chaetognaths.

While some studies highlight the importance of non-carnivorous feeding in chaetognaths (e.g., Casanova *et al.*, 2012; Grigor *et al.*, 2020), it remains unknown to what extent alternative food sources (marine snow, algae) contribute to the diet of these predators. In this regard, the focus of this paper was on studying the trophic position of three chaetognath species (*P. elegans*, *P. maxima*, and *E. hamata*) in the Barents Sea based on samples collected during the polar nights of 2013 and 2014. We address the following questions: 1) Do these species have differences in their trophic position? 2) Does their trophic position depend on their size? We provide indirect estimates of the trophic position of these chaetognaths by comparing their δ^{15}N values with those of filter-feeding copepods (*Calanus* spp.) collected in the same study area. To assess the possible effect of size on the trophic position of chaetognaths, we measured all specimens and analyzed them individually. Our study provides a basis for further research on the trophic ecology of chaetognaths in the Barents Sea, which is of particular importance for understanding the food web structure in marine ecosystems.

Material and methods

Sample collection and preservation

The material for this study was collected during four cruises of the Polar branch of the FSBSI "VNIRO" ("PINRO" named after N. M. Knipovich) in November and December 2013 and November 2014. Sampling was carried out at 14 stations in the depth range from 252 to 753 m (Fig. 1; Table 1). Most of the stations are located along the slope of the Barents Sea (S1, S2, S5–7, S9–12, S14), one in the northern Barents Sea (N3), one south of Svalbard (SS4), and two in the Bear Island Trench (T8 and T13). An open macroplankton net (0.2 m^2 mouth opening, 0.56 mm mesh size) was mounted on the roof of a trawl to collect the zooplankton. It has been repeatedly shown that zooplankton is predominantly distributed in the hyperbenthic zone during the polar night (e.g., Hirche *et al*., 2016; Dvoretsky *et al*., 2023). Therefore, the trawl was towed horizontally within 5–10 m above the bottom; however, since the macroplankton net did not have a closing mechanism, sampling was also possible during the trawl retrieval.

Samples were fixed onboard and stored in a 10% formalin/seawater solution for 7–8 years. As the formalin and other preservatives introduce exogenous carbon, such samples are not recommended for δ^{13}C analysis (Kaehler, Pakhomov, 2001; Sarakinos *et al*., 2002; Carabel *et al*., 2009). The effect of preservation on δ^{15}N values is generally considered to be minor (Kaehler, Pakhomov, 2001; Sarakinos *et al*., 2002; Carabel *et al*., 2009), although there are also opposite opinions (e.g., Feuchtmayr, Grey, 2003; Fleming *et al*., 2011). For instance, the reliable δ^{15}N values have been shown in the works of Rau *et al*. (2003) and Ohman *et al*. (2012) for the chaetognaths and copepods stored in formalin for over 50 years. Even if we assume an effect of preservation on our material, it should have been uniform across all samples, and therefore, the comparisons within this study should be relevant. In addition, formalin preservation results in small changes in the body length of chaetognaths (Conway, Robins, 1991), but we considered these changes negligible within our study.

Laboratory processing and sample selection

Samples were examined using a stereomicroscope in the Laboratory of Hydrobiology and Molecular Systematics (Kazan Federal University) in 2021 and 2022. Since our material was not suitable for quantitative analysis, we did not consider the number of chaetognaths and copepods at the stations. In total, three species of chaetognaths (*P. elegans*, *P. maxima*, and *E. hamata*) and mixed samples of copepods (*Calanus* spp.) were collected for SIA (Table 1). *Parasagitta elegans* were not sampled from station S6 due to their damaged condition, and *P. maxima* were absent at stations N3 and SS4. *Parasagitta elegans* and *E. hamata* were abundant in the samples, so they were selected randomly from the total population (5–30 ind. per station). *Pseudosagitta maxima* were few, and all were collected for the further analysis (1–7 ind. per station). All chaetognaths used for SIA were checked for the absence of food residues in their guts and measured to the nearest millimeter from the top of the head to the tip of the tail, excluding the caudal fin.

The copepods were represented by adults and late copepodite stages of either *C. glacialis* or *C. finmarchicus*. They were not measured individually but had approximately the same size range at all stations (prosome length ≈ 2–4 mm). These copepods (10–50 ind.) were pooled into one sample per station.

Nitrogen stable isotope analysis

The final samples for SIA containing individual chaetognaths and pooled copepods were rinsed in distilled water and placed in plastic vials. They were dried in a thermostat at 60 °C for 12–24 h until complete dehydration of tissues, and then each sample was homogenized with a mortar and pestle. The SIA was carried out in the Laboratory of Isotopic and Elemental Analysis (Kazan Federal University) with a Flash HT series elemental analyzer coupled online via a ConFlo IV interface to a Delta V Plus mass spectrometer (TermoFisher Scientific, Germany). The ratios of nitrogen stable isotopes (^{15}N/^{14}N) in the samples were determined as a relative value delta (δ), which is measured in permille (‰) as the difference between the ratios of isotopes in the test object and the standard:

$$\delta^{15}\mathrm{N}\ (‰) = [(^{15}\mathrm{N}/^{14}\mathrm{N}_{\mathrm{sample}} - {}^{15}\mathrm{N}/^{14}\mathrm{N}_{\mathrm{standard}}) / {}^{15}\mathrm{N}/^{14}\mathrm{N}_{\mathrm{standard}}] \times 1000$$

The isotope ratios were expressed relative to atmospheric nitrogen (AIR). The accuracy of determining the δ^{15}N values was ± 0.2‰. Original data on the isotopic composition of chaetognaths and copepods are presented in Supplement Table 1.

Data analysis

The conventional trophic enrichment factor is assumed to be 3–4 ‰ (Minagawa, Wada, 1984; Post, 2002), but reliable estimates of trophic position (TP) require knowledge of the actual isotope fractionation

Table 1. Information on the sampling stations. The stations are numbered chronologically and abbreviated by geographic location (S — Barents Sea slope, SS — South Svalbard, T — Bear Island Trough, N — Northern Barents Sea). *n* = number of individual samples of chaetognaths and pooled samples of copepods used for stable isotope analysis at each station. For copepods, exact numbers of individuals pooled per sample are given in brackets.

Таблица 1. Информация о станциях отбора проб. Станции пронумерованы в хронологическом порядке и названы по географическому положению (S — склон Баренцева моря, SS — южный Свальбард, T — желоб острова Медвежий, N — север Баренцева моря). *n* = число индивидуальных проб хетогнат и объединенных проб копепод, использованных для анализа стабильных изотопов на каждой станции. Для копепод, точное число объединенных в пробу особей указано в скобках.

Station	Date	Latitude (°N)	Longitude (°E)	Depth (m)	Species	*n*
S1	18.11.2013	77.58	10.75	740	*P. elegans*	15
					P. maxima	4
					E. hamata	25
					Calanus spp.	1 (50)
S2	20.11.2013	76.02	14.08	660	*P. elegans*	5
					P. maxima	2
					E. hamata	15
					Calanus spp.	1 (20)
N3	21.11.2013	78.75	34.79	271	*P. elegans*	30
					P. maxima	–
					E. hamata	10
					Calanus spp.	1 (10)
SS4	23.11.2013	76.48	17.98	252	*P. elegans*	25
					P. maxima	–
					E. hamata	5
					Calanus spp.	1 (22)
S5	27.11.2013	74.87	17.17	280	*P. elegans*	10
					P. maxima	1
					E. hamata	20
					Calanus spp.	1 (50)
S6	28.11.2013	74.88	15.67	434	*P. elegans*	–
					P. maxima	1
					E. hamata	10
					Calanus spp.	1 (20)
S7	30.11.2013	74.08	15.97	742	*P. elegans*	10
					P. maxima	3
					E. hamata	10
					Calanus spp.	1 (30)
T8	01.12.2013	74.16	27.33	407	*P. elegans*	10
					P. maxima	2
					E. hamata	5
					Calanus spp.	1 (50)

Table 1 (continued).
Таблица 1 (окончание).

Station	Date	Latitude (°N)	Longitude (°E)	Depth (m)	Species	*n*
S9	04.12.2013	72.97	14.78	663	*P. elegans*	10
					P. maxima	7
					E. hamata	10
					Calanus spp.	1 (50)
S10	09.12.2013	72.22	16.15	559	*P. elegans*	10
					P. maxima	5
					E. hamata	10
					Calanus spp.	1 (20)
S11	10.11.2014	75.40	14.15	753	*P. elegans*	10
					P. maxima	1
					E. hamata	15
					Calanus spp.	1 (50)
S12	12.11.2014	77.37	11.22	641	*P. elegans*	15
					P. maxima	2
					E. hamata	15
					Calanus spp.	1 (30)
T13	20.11.2014	74.23	24.23	396	*P. elegans*	15
					P. maxima	1
					E. hamata	15
					Calanus spp.	1 (10)
S14	25.11.2014	70.75	17.10	658	*P. elegans*	10
					P. maxima	4
					E. hamata	10
					Calanus spp.	1 (40)

between the consumer and its diet, which in most cases can only be determined experimentally. As far as we know, there are no experimental studies on the isotope fractionation in chaetognaths. Therefore, we do not report direct estimates of their TPs, but provide indirect estimates by presenting δ^{15}N data and comparing them with filter-feeding copepods (*Calanus* spp.), which were used as an isotopic baseline in accordance with previous studies (e.g., Hobson *et al*., 2002; Agersted *et al*., 2014; Grigor *et al*., 2015).

To consider the possible effects of different variables on the δ^{15}N values of chaetognaths, we used Spearman's rank correlation, which is more robust when applied to the limited number of observations. First, we tested whether the mean δ^{15}N values of chaetognaths (calculated for each station where applicable, see Table 2) were correlated with copepod δ^{15}N values and station parameters (depth, latitude, and longitude). Although we acknowledge the limitations of using correlations due to the highly unbalanced sample size among the stations (especially for *P. maxima*), it is the only feasible approach for statistical analysis in our study. In addition, we tested whether δ^{15}N values of chaetognaths were correlated with their size within individual stations. To account for the multiple comparisons, *p*-values for correlations were adjusted using Holm's method.

Comparing all three species of chaetognaths at all stations was not possible, as they were not always present in sufficient numbers. Therefore, we had to use a two-way ANOVA in two cases: 1) first, we compared two species (*P. elegans* and *E. hamata*) at 13 stations (except for S6, where *P. elegans* was absent), 2) then we compared all three species at stations S9 and S10 (where the sample size for *P. maxima* was 5 individuals or more). To account for the unbalanced design and

Table 2. Nitrogen stable isotope ratios ($\delta^{15}N$, ‰) of the three species of chaetognaths and copepods at different stations. *n* = total number of samples for each species (for detailed information on the stations and sample size, see Table 1). For stations where multiple samples were analyzed, means and standard deviations are shown.

Таблица 2. Соотношения стабильных изотопов азота ($\delta^{15}N$, ‰) у трех видов хетогнат и копепод на разных станциях. *n* = общее число проб для каждого вида (для подробной информации по станциям и размеру выборки, см. табл. 1). Для станций, где было проанализировано несколько проб, приведены средние и стандартные отклонения.

Station	*Parasagitta elegans* *n* = 175	*Pseudosagitta maxima* *n* = 33	*Eukrohnia hamata* *n* = 175	*Calanus* spp. *n* = 14
S1	10.2 ± 1.2	8.4 ± 0.4	7.9 ± 1.0	6.2
S2	11.3 ± 0.9	10.7 ± 0.1	8.5 ± 0.7	8.8
N3	10.9 ± 0.6	–	9.7 ± 0.7	9.0
SS4	11.3 ± 0.7	–	9.8 ± 1.3	8.7
S5	11.4 ± 0.5	8.7	8.6 ± 0.7	9.0
S6	–	10.0	8.6 ± 0.6	7.9
S7	11.5 ± 0.7	9.9 ± 0.2	8.6 ± 0.5	9.4
T8	10.6 ± 0.6	9.6 ± 0.4	9.0 ± 1.4	8.5
S9	11.1 ± 0.6	9.1 ± 0.4	7.4 ± 0.7	9.1
S10	10.4 ± 0.6	9.0 ± 1.1	8.1 ± 1.0	7.6
S11	10.2 ± 1.0	11.1	8.3 ± 0.8	7.1
S12	10.5 ± 0.5	8.7 ± 0.4	8.7 ± 0.7	7.9
T13	10.8 ± 0.8	11.5	9.0 ± 0.7	8.7
S14	10.1 ± 1.0	9.7 ± 0.8	7.3 ± 0.6	8.1
All	10.8 ± 0.9	9.4 ± 0.9	8.4 ± 1.0	8.3 ± 0.9

interaction effect of the two factors (species:station), we used the two-way ANOVA with type III sum of squares ("car" package, Fox *et al.*, 2012). The data were checked for normality ($p > 0.05$) and homogeneity ($p > 0.05$) using the Shapiro-Wilk test and Levene's test and met the assumptions of ANOVA. The estimated marginal means (EMMs) were calculated for each chaetognath species within each analyzed station for the further post-hoc comparisons ("emmeans" package, Lenth *et al.*, 2023), and *p*-values were adjusted using Tukey's method. A package "ggplot 2" was used to visualize the data (Wickham, 2016).

Results

High variations of $\delta^{15}N$ values were detected in copepods *Calanus* spp. and the three species of chaetognaths across the stations (Table 2; Fig. 2a). Because the isotope data for copepods were obtained from a single sample per station, it was not possible to consider their isotopic variation within individual stations, as was done for chaetognaths. Due to this, we used mean $\delta^{15}N$ values of chaetognaths (where applicable, see Table 2) and a single $\delta^{15}N$ value of copepods to test whether their variations followed a common trend across the stations (Fig. 3). Among the three chaetognath species, only *P. elegans* had a significant positive correlation of $\delta^{15}N$ values with those of *Calanus* spp. ($r_{s(11)} = 0.86, p < 0.001$), while *E. hamata* had a negative correlation with station depth ($r_{s(12)} = -0.72, p = 0.016$). None of the species analyzed had a significant correlation with latitude or longitude (Fig. 3).

The three species of chaetognaths differed in size, with *P. maxima* being considerably larger (51 ± 13 mm [mean ± SD]) than *P. elegans* (23 ± 6 mm) and *E. hamata* (22 ± 7 mm) (Fig. 2b). However, interspecific differences in their $\delta^{15}N$ values were not related to size, as the highest values were typically observed in *P. elegans* (10.8 ± 0.9‰), medium in *P. maxima* (9.4 ±

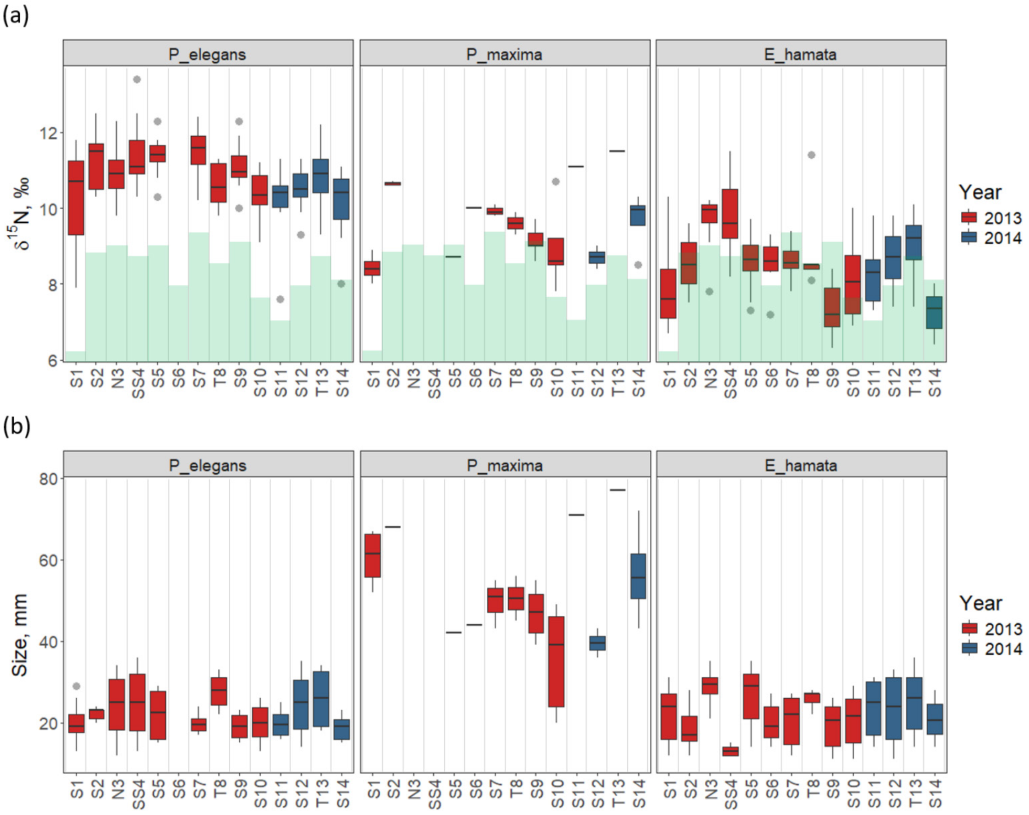

Fig. 2. Distribution of δ^{15}N values (a) and size (b) in the three species of chaetognaths at different stations. Green color indicates δ^{15}N values of copepods *Calanus* spp. at respective stations. Boxplots indicate the median value, the first and third quartiles, the total range of the data, and outliers (defined as the data points falling outside the 1.5 interquartile range).

Рис. 2. Распределение значений δ^{15}N (a) и размера (b) у трех видов хетогнат на разных станциях. Зеленый цвет показывает значения δ^{15}N у копепод на соответствующих станциях. Боксплоты обозначают медиану, первый и третий квартили, общий диапазон данных и выбросы (определены как данные, выходящие за пределы 1.5 межквартильного размаха).

0.9‰), and the lowest in *E. hamata* (8.4 ± 1.0‰). Since we had a limited number of samples for *P. maxima*, we did not test the effect of size on their δ^{15}N values. For *P. elegans* and *E. hamata*, correlations were made within each station with $n \geq 10$ for a species. No consistent pattern was observed in either *P. elegans* or *E. hamata* across the stations, and most correlations were not significant (Fig. 4).

Comparisons of δ^{15}N values for *P. elegans* ($n = 175$) and *E. hamata* ($n = 165$) were made at all stations except for S6. The two-way ANOVA revealed significant effects of species ($F_{(1)} = 81.6, p < 0.001$) and stations ($F_{(12)} = 8.8$, $p < 0.001$), as well as their interaction ($F_{(12)} = 4.3, p < 0.001$). Post-hoc comparisons of EMMs confirmed significant differences between these two species at all analyzed stations. When we compared *P. elegans* ($n = 20$), *P. maxima* ($n = 12$), and *E. hamata* ($n = 20$) at stations S9 and S10, the two-way ANOVA also revealed significant effects of species ($F_{(2)} = 22.6$, $p < 0.001$) and stations ($F_{(1)} = 4.8, p = 0.033$), and their interaction ($F_{(2)} = 4.9, p = 0.012$). In this case, post-hoc comparisons of EMMs confirmed significant differences between *P. maxima* and *P. elegans* at both stations, and between *P. maxima* and *E. hamata* at station S9 only.

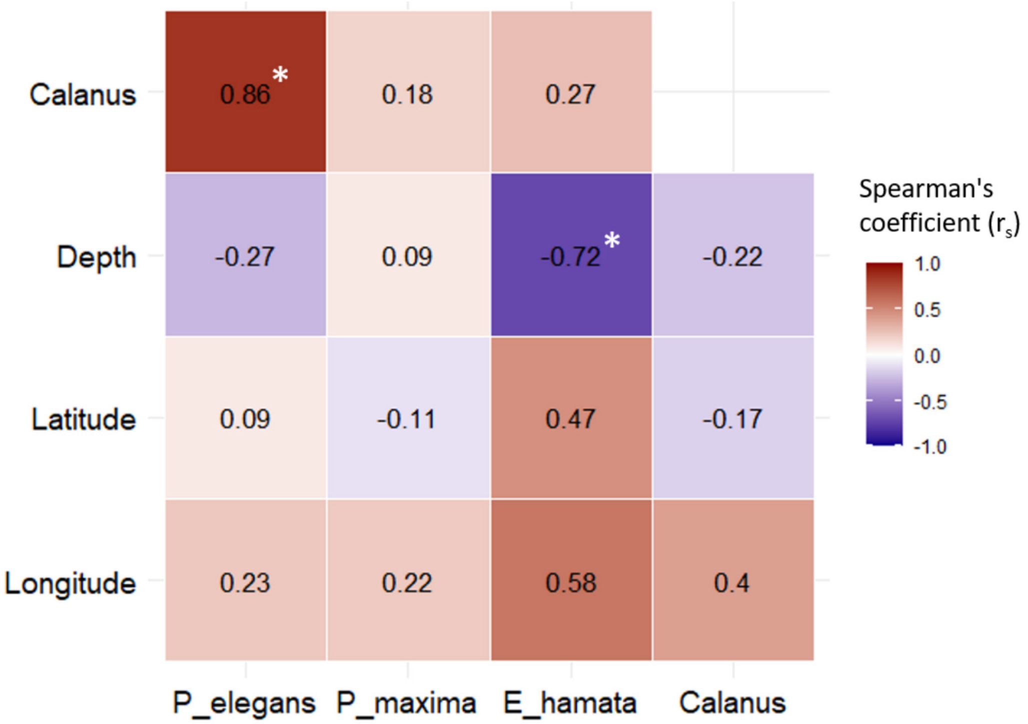

Fig. 3. Heatmap of Spearman's correlation coefficients (r_s) calculated for $\delta^{15}N$ values of chaetognaths and copepods and different variables. Correlations are based on the mean $\delta^{15}N$ values of chaetognaths (where applicable, see Table 2) and the single $\delta^{15}N$ value of copepods at each station. Significant results ($p < 0.05$ after Holm's adjustment) are indicated with asterisks.

Рис. 3. Тепловая карта коэффициентов корреляции Спирмена (r_s), рассчитанных для значений $\delta^{15}N$ хетогнат и копепод с разными переменными. Корреляции основаны на средних значениях $\delta^{15}N$ у хетогнат (где применимо, см. табл. 2) и единственном значении $\delta^{15}N$ у копепод на каждой станции. Значимые результаты ($p < 0,05$ после поправки Холма) отмечены звездочкой.

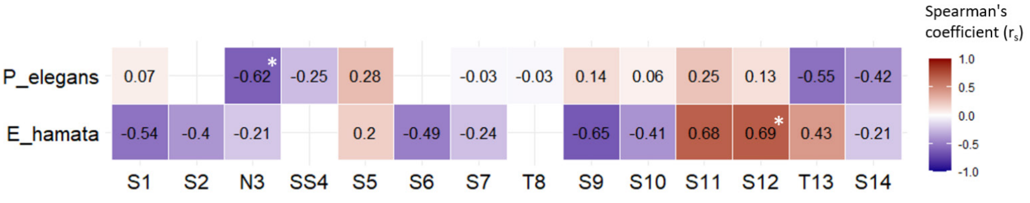

Fig. 4. Heatmap of Spearman's correlation coefficients (r_s) calculated for $\delta^{15}N$ values and size of two chaetognath species at individual stations. Significant results ($p < 0.05$ after Holm's adjustment) are indicated with asterisks.

Рис. 4. Тепловая карта коэффициентов корреляции Спирмена (r_s), рассчитанных для значений $\delta^{15}N$ и размеров у двух видов хетогнат на отдельных станциях. Значимые результаты ($p < 0,05$ после поправки Холма) отмечены звездочкой.

Discussion

Limitations associated with the calculation of trophic position

Over the course of the seasonal production cycle, high δ^{15}N fluctuations can be observed in zooplankton (Jennings *et al*., 2008; Kürten *et al*., 2013). During the polar night, the contribution of fresh primary production is expected to be lower compared to microbial-detrital material, and this may result in a shift in δ^{15}N values at the base of the food web. Interpretations of isotopic data thus require a robust baseline that can integrate spatial and temporal isotopic variations. Filter-feeding copepods (*Calanus* spp.) are traditionally used as a baseline for pelagic primary production pathway (e.g., Hobson *et al*., 2002; Agersted *et al*., 2014; Grigor *et al*., 2015). With the onset of the polar night, these copepods migrate to greater depths and enter a diapausing state to utilize their wax esters (Berge *et al*., 2020). Although *Calanus* spp. are often assigned a second trophic level (i.e., herbivorous), many studies suggest that they may consume detritus, bacteria, and other alternative food when phytoplankton is scarce (Ohman, Runge, 1994; Levinsen *et al*., 2000; Basedow, Tande, 2006; Cleary *et al*., 2017). According to Søreide *et al*. (2008), in Svalbard waters only *C. glacialis* exhibited seasonal shift in δ^{15}N values (from 7.6‰ in May to 9.6‰ in December), indicating opportunistic feeding in winter months (mean TP = 2.5). This was not the case for *C. finmarchicus*, which retained herbivorous signals (mean TP ≈ 2) and apparently were not feeding during the polar night. Thus, the uneven distribution of the two copepod species (*C. glacialis* and *C. finmarchicus*) across the stations may be one of the reasons for the variations in the baseline.

In our study, reliable calculations of TPs are further complicated by the fact that the copepod δ^{15}N data were obtained from a single (pooled) sample within a station, which does not allow us to consider their variability in the same way as was done for chaetognaths. Previous attempts to determine TPs in chaetognaths and copepods in the Barents Sea were made in studies by Søreide *et al*. (Table 3). These authors used two isotopically distinct sources of primary production (ice-POM and pelagic-POM) as a baseline and analyzed pooled samples of both chaetognaths and copepods. Similar to ours, their results show that the difference corresponding to one trophic level (≈ 3–4‰) is not always evident between chaetognaths and copepods, as might be expected between pure herbivores and carnivores. As already noted, we are not aware of any experimental studies on the isotopic fractionation in chaetognaths, which could theoretically differ from the generally accepted one. In addition, it is known that the isotopic composition of a consumer may be affected by its physiology (Layman *et al*., 2012). Ikeda and Skjoldal (1989) reported that daily losses of body nitrogen were higher in *P. elegans* than in the three *Calanus* species in the Barents Sea in early summer, which suggests shorter turnover in this chaetognath compared to copepods. It remains unknown to what extent these metabolic differences influence their isotopic fractionation, so further experimental studies are highly recommended.

Evidence for differences in the trophic position of chaetognaths

We have shown that differences in δ^{15}N values of *P. elegans*, *P. maxima* and *E. hamata* were evident across the stations, indicating differences in their TPs. Similar results were previously reported for *P. elegans* and *E. hamata* in different seasons and areas, with the former having consistently higher δ^{15}N values than the latter (Table 3; Connelly *et al*., 2014; Grigor *et al*., 2020). Unlike previous studies, we analyzed samples of individual chaetognaths rather than pooled samples, which contributed to the observed isotopic variability. Information on the stable isotopes of *P. maxima* is limited to isolated reports (Wada *et al*., 1987; Pomerleau *et al*., 2011; Stasko *et al*., 2017; Kohlbach *et al*., 2023), so our study represents the first detailed examination of this species, one of the largest among chaetognaths.

Chaetognaths are non-visual predators and can feed throughout the year, but their feeding activity may decrease during the polar night, as has been shown for *P. elegans* in Svalbard waters (Grigor *et al*., 2015). However, previous studies did not find any evidence of seasonal shift in δ^{15}N values of *P. elegans* (Grigor *et al*., 2015; McGovern *et al*., 2018; Choi *et al*., 2020), while information on the other two species remains lacking. Many studies have indicated a positive relationship between the size of these predators and their prey (e.g., Pearre, 1980; Sullivan, 1980;

Table 3. Previous reports of isotopic composition and trophic position (TP) calculations for chaetognaths and copepods from the Barents Sea and adjacent waters. *n* = number of samples. Note that unlike the present study, the isotopic data are reported for pooled samples of chaetognaths (i.e., several individuals were combined per sample).

Таблица 3. Предыдущие сообщения изотопного состава и вычисления трофической позиции (ТП) хетогнат и копепод из Баренцева моря и прилегающих вод. *n* = число проб. Обратите внимание, что в отличие от настоящего исследования, изотопные данные представлены для объединенных проб щетинкочелюстных (т.е. несколько экземпляров было включено в одну пробу).

Source	Sampling area and date	Species	*n*	Size/stage	δ^{15}N, ‰	TP
Søreide *et al.* (2006)	Barents Sea, June 1995	*Parasagitta elegans*	2	n. m.	12.0 ± 0.0	3.7 ± 0.0
	Barents Sea, May 1999	*Parasagitta elegans*	3	30–40 mm	11.9 ± 0.2	3.8 ± 0.1
		Calanus glacialis	4	CVIF	7.1 ± 0.3	1.9 ± 0.1
		Calanus finmarchicus	3	CVIF	7.4 ± 0.4	2.0 ± 0.4
	Barents Sea, March 2000	*Eukrohnia hamata*	2	15–30 mm	9.4 ± 0.0	3.0 ± 0.0
		Parasagitta elegans	3	30–40 mm	12.2 ± 0.1	3.7 ± 0.0
		Calanus glacialis	3	CVIF	9.7 ± 0.2	2.9 ± 0.1
		Calanus finmarchicus	2	CVIF	9.7 ± 0.3	3.1 ± 0.0
	East Greenland, October 1999	*Eukrohnia hamata*	5	15–30 mm	8.6 ± 0.2	2.6 ± 0.1
		Parasagitta elegans	1	26–30 mm	12.6	3.8
		Calanus glacialis	6	CVIF	9.1 ± 0.1	2.8 ± 0.0
		Calanus glacialis	3	CV	10.2 ± 0.3	3.1 ± 0.1
		Calanus finmarchicus	5	CVIF	6.4 ± 0.2	2.0 ± 0.1
Søreide *et al.* (2013)	Northeastern Svalbard, August 2003	*Eukrohnia hamata*	9	17–30 mm	9.9 ± 0.1	2.6 ± 0.0
		Parasagitta elegans	3	35–45 mm	11.7 ± 0.3	3.2 ± 0.1
		Calanus glacialis	9	CV	9.4 ± 0.5	2.5 ± 0.1
	Northwestern Svalbard, August 2003	*Eukrohnia hamata*	3	17–25 mm	8.5 ± 0.2	2.2 ± 0.1
		Calanus glacialis	3	CV	9.5 ± 0.1	2.5 ± 0.0
		Calanus finmarchicus	6	CV	7.5 ± 0.2	1.9 ± 0.0

Falkenhaug, 1991; Brodeur, Terazaki, 1999). Although one might expect larger chaetognaths (e.g., *P. maxima*) to feed at higher trophic levels, we do not see such a pattern in δ^{15}N values either among the three species or within a single species. This means that interspecific differences in δ^{15}N values cannot be explained by differences in their size. At the same time, when considering a single species (either *P. elegans* or *E. hamata*), the absence of a pronounced size trend may indicate a significant overlap in the diet of small and large individuals.

In our study, *P. elegans* was the only chaetognath 1) to show a positive correlation of δ^{15}N values with copepods and 2) to have an average increase about 2.5‰ relative to copepods, which is close to the conventional trophic enrichment factor. This provides strong evidence that this species is more dependent on *Calanus* spp. than the other two chaetognaths. *Parasagitta elegans* is primarily an epipelagic species and occurs in the upper 100–150 m of the water column (Terazaki, 2004), but seasonal migrations of this chaetognath to mesopelagic zone have been observed in the Arctic (Grigor *et al*., 2014, 2017). It was suggested that *P. elegans* follows the seasonal migrations of *Calanus* spp. to overwintering depths (Grigor *et al*., 2014, 2015). In the Barents Sea, the gut content of *P. elegans* was investigated by Falkenhaug (1991) in the summer period, and the author demonstrated that copepodites of *Calanus* spp., nauplii and smaller copepods (*Pseudocalanus*, *Oithona*) were indeed the dominant prey for these predators. Similar results have been shown for other Arctic and Subarctic areas, suggesting that this chaetognath feeds on the most abundant copepod species (Terazaki, 2004). Interestingly, Sullivan (1980) reported that *P. elegans* generally consumed larger copepods than *E. hamata* in the subarctic Pacific, and its vertical distribution was related to high prey densities in the upper water column.

Pseudosagitta maxima and *E. hamata* are eurybathic species typical for mesopelagic zone in Arctic waters (Sameoto, 1987; Grigor *et al*., 2017, 2020; Kosobokova, Hopcroft, 2021). Compared to *P. elegans*, these two chaetognaths seem to be less active predators, as suggested by their lower metabolic rates (Thuesen, Childress, 1993; Ikeda, Takahashi, 2012). Little is known about the diet of *P. maxima* (Sameoto, 1987; Øresland, 1990), and trophic ecology of *E. hamata* has been better studied in Antarctic waters (Øresland, 1990, 1995; Froneman, Pakhomov, 1998; Froneman *et al*. 1998; Kruse *et al*., 2010; Giesecke, González, 2012), and less in the Arctic and Subarctic (Sullivan, 1980; Sameoto, 1987; Grigor *et al*., 2020). For both species, copepods were also noted as an important food source. However, Grigor *et al*. (2020) demonstrated that captured *E. hamata* can use their hooks to ingest marine snow in a petri dish, and similar feeding behavior was mentioned for *P. maxima* in the Canadian Arctic (Grigor *et al*., 2015). These authors suggested that *E. hamata* may feed on algae and/or marine snow in their natural habitat, because green detritus was frequently observed in the guts of these chaetognaths sampled in different seasons. Specific fatty acids (FAs) (16:1(n − 7)) also indicated that *E. hamata* relied on diatom source pathway more than *P. elegans* in the Canadian Arctic (Grigor *et al*., 2020). We have shown that *E. hamata* had the lowest δ^{15}N values among the studied chaetognaths, almost the same as in *Calanus* spp., supporting the idea of non-carnivorous feeding for this species. In addition, *E. hamata* was the only species in which δ^{15}N values negatively correlated with station depth. It is difficult to explain whether this trend was due to an isotopic shift in the food source of these chaetognath or to actual changes in their TP (e.g., a more carnivorous diet at shallow stations and a more omnivorous diet at deep stations).

In this study, there was a highly unbalanced sampling for *P. maxima*, but at most stations this species occupied an intermediate TP between *P. elegans* and *E. hamata*. We did not find any trends in δ^{15}N values of *P. maxima* in relation to copepods or station parameters, although these trends may have been obscured by the limited sample size. Thuesen and Childress (1993) hypothesized that *P. maxima* must be an ambush predator using the “sit-and-wait” feeding strategy because of its extremely low metabolic rates and reduced body musculature. However, analysis of several lipid markers made by Kohlbach *et al*. (2024) suggested low carnivory indices for *P. maxima* in the Barents Sea, which complements our results. For example, this species had a lower concentration of *Calanus*-associated FAs relative to *P. elegans*, while higher dinoflagellate/*Phaeocystis* FAs (22:6 ($n-3$)) indicated a possible contribution of phytoplankton to its diet. Some authors suggest that the presence of algal-associated FAs in chaetognaths is the result of their transfer along the food chain, i.e., from phytoplankton to copepods and further to chaetognaths (e.g., Connelly *et al*., 2014). However, we believe it is reasonable to assume that not only *E. hamata* but also other species of chaetognaths may optionally feed on marine snow. Both *E. hamata* and *P. maxima* apparently do not exhibit active seasonal migrations following copepods, unlike the more carnivorous species *P. elegans* (Grigor *et al*., 2014, 2017, 2020). Although all three species can certainly feed on copepods that overwinter in the hyperbenthic zone, marine snow may serve as an important alternative food source, especially for non-migrating *E. hamata* and *P. maxima*.

It is known that chaetognaths use special mechanoreceptors that respond to vibrations similar to those produced by copepods (Feigenbaum, Reeve, 1977). To better understand the trophic ecology of chaetognaths, it is necessary to know whether the disturbance produced by marine snow is sufficient to elicit their feeding response, and to what extent this response varies among different species. The chaetognaths studied in this work also differ in the morphology of their grasping apparatus and toxicity levels, with *P. elegans* having a higher number of hooks and teeth (Pierrot-Bults, 2017), and higher values of tetrodotoxin production (Thuesen *et al*., 1988). These characteristics may be important in explaining the differences in trophic ecology among the three species, so further research is needed to clarify this issue.

Conclusions

Understanding the trophic ecology of chaetognaths is important for modelling marine food web structure. In this paper, we have presented the first detailed study of the relative trophic position (TP) of three chaetognath species in the Barents Sea during the polar night. Nitrogen stable isotope analysis confirmed previously known differences in TP between *P. elegans* and *E. hamata* and provided the first insight for *P. maxima*, one of the largest chaetognath species. We have discussed the limitations of calculating their TPs using the filter-feeding copepods (*Calanus* spp.) as a baseline. The variations of δ^{15}N values across the stations were positively correlated with those of copepods in *P. elegans*, but not in the other two species. In *E. hamata*, we have detected negative correlation of δ^{15}N values with depth, but it remains unknown if this trend is due to an isotopic shift in the food source of these chaetognath or to actual changes in their TP. We have shown that size is not a good predictor of TPs in these chaetognaths, as no general pattern in δ^{15}N values was observed among the three species or within a single species. Our results indicates that *P. elegans* occupies the highest TP, followed by *P. maxima* and *E. hamata*. This complements other studies that have suggested that marine snow plays an important role in the diet of the latter two species. For this reason, we recommend a more careful consideration of their role in marine food webs, particularly with regard to their predation impact on zooplankton communities.

Electronic supplements.

The following materials are available online.

Supplement Table 1. Original data on the isotopic composition of chaetognaths and copepods.

Compliance with ethical standards

The authors declare that they have no conflicts of interest.

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