Biomass and estimated production, and feeding pressure on zooplankton of chaetognaths in the Yellow Sea, China

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ABSTRACT

The biomass and estimated production, feeding rate of chaetognaths were studied in the Yellow Sea. *Sagitta crassa*, *Sagitta enflata*, *Sagitta bedoti*, and *Sagitta nagae* were found during the study period, and *S. crassa* and *S. nagae* were the dominant species. The mean chaetognath biomass was in the range of 2.56 - 5.57 mg DM m^{-3}, and *S. crassa* and *S. nagae* comprised 49 - 90 and 10 - 33%, respectively. The geographical distribution pattern was differed between different species. The annual average estimated feeding rate and production of chaetognaths was evaluated as 55.24 mg C m^{-3} year^{-1} and 15.90 mg C m^{-3} year^{-1}, respectively. The body length of *Sagitta* species less than 9 - 11 mm had relatively high feeding rate in August, September, and December because of their relatively high total biomass, while the body length with 8 - 16, 11 - 15, and 6 - 16 mm groups had relatively high feeding rate in March, May, and June, respectively. The average feeding pressure on zooplankton biomass and production by chaetognaths could be evaluated as 1.07 and 18.95%, respectively, and the biomass and production of small copepods, and nauplius and copepodite of large copepods would be seriously impacted during whole year.

1. INTRODUCTION

The chaetognaths are major pelagic invertebrates which are extremely abundant in marine systems, often second only to copepods in number (Feigenbaum and Maris 1984). Chaetognaths are well known as important carnivores of secondary producers in marine ecosystems (Terazaki 2001), and their predation may have a significantly impact on copepod population dynamics (Reeve 1970; Sameoto 1972), especially under conditions of low environmental productivity (Kimmerer 1984; Øresland 1990).

Biomass, production and consumption of chaetognaths and dominant chaetognath species have been reported in some sea areas. Chaetognaths had a mean biomass of 0.109 - 0.146 mg C m^{-3} in Southern Ocean (Kruse et al. 2010). The yearly production and required a prey production of *S. crassa* was estimated to be 3.8 g C m^{-2} and 13.1 g C m^{-2} year^{-1} in Tokyo Bay, respectively. Chaetognaths were identified as the second most important group composing at times up to 30% (mean 14.7%) of total zooplankton abundance in the pelagic system of the Prince Edward Islands (Froneman and Pakhomov 1998). Trophic ecology of chaetognaths or dominant chaetognath species was studied by many researchers, which could be indicated by the feeding pressure on zooplankton biomass and production. Feeding pressure of chaetognaths on zooplankton varied significantly under different environmental conditions and between different sea areas. Kehayias et al. (2005) reported that the feeding pressure of chaetognaths on zooplankton standing stocks was 0.02 - 2.76% in Aegean Sea, while Baier and Purcell (1997b)

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reported that chaetognaths could consume up to 44% d⁻¹ of standing stocks of large copepods in South Atlantic Bight. Feeding pressure of *Sagitta elegans* on zooplankton production was only 0.7 - 1.0% in St. Margaret's Bay (Sameoto 1972), while the dominant species *Sagitta tenuis* consumed up to 5 - 15% of zooplankton production in Chesapeake Bay (Canino and Grant 1985).

The Yellow Sea is a marginal sea of the northwest Pacific, surrounded by the eastern coast of China and the Korean peninsula, with a mean depth of 44 m and maximum depth of 103 m, and as a shallow shelf water, the Yellow Sea contains complex physical environments and is affected greatly by climatic conditions (Huo et al. 2012). The Yellow Sea is a major fishing ground, and the bordering countries derive a substantial part of their food from fishing in coastal waters. It is our responsibility to preserve the health of this productive ecosystem in order to sustain fishing in the future. The relationships between zooplankton and higher trophic levels in the Yellow Sea was a key scientific question, and how to describe variations of zooplankton biomass and production and make it easier to be modeled in the Yellow Sea ecosystem is the main purpose (Sun et al. 2010). The zooplankton functional groups approach, which is considered a good method of linking the structure of food webs and the energy flow in the ecosystems, is used to describe this process in the Yellow Sea ecosystem (Sun et al. 2010).

Chaetognaths is one gelatinous carnivorous zooplankton groups in the Yellow Sea (Sun et al. 2010), which seem to be opportunistically positioned to utilize secondary production that is ordinarily consumed by fish (Mills 1995). In addition, the chaetognaths group is also a food resource for fish (Sun et al. 2010). However, to our knowledge, there has few studies on chaetognaths in the Yellow Sea. Zuo et al. (2004) and Lee et al. (2016) described the relationship between distribution patterns of chaetognaths and environmental factors; Huo et al. (2010) reported that the life cycle of *S. crassa* in the Southern Yellow Sea; Kang et al. (2012) summarized that chaetognaths also showed a downward trend after the mid-1990s, but high positive anomalies were observed in 2002 and 2006 in the Eastern Yellow Sea; Choi and Park (2013) found that the abundance of chaetognaths fluctuated around the long-term mean value during the past four decades in the western waters of the Korean Peninsula in the Yellow Sea.

However, the trophic ecology of chaetognaths is unknown in the Yellow Sea. Our hypothesis is that chaetognaths would require a significant prey production in the Yellow Sea. In this present study, the biomass, and estimated production and feeding of chaetognaths as well as the feeding pressure of chaetognaths on zooplankton biomass and secondary production were evaluated based on data obtained from the six cruises during period from September 2006 to August 2007 in the Yellow Sea, which is very important for "parameterization" of food web structure models of the Yellow Sea.

2. MATERIAL AND METHODS

2.1 Study Area and Sampling Methods

The chaetognaths was sampled during six cruises on the R/V "*Beidou*" in the Yellow Sea during period from September 2006 to August 2007. Figure 1 shows the location of transects and sampling stations during these six cruises. The maximum water depth of these stations was less than 100 m. Vertical profiles of temperature and salinity were recorded at each station with a Sea-Bird (SBE 25) CTD instrument lowered and retrieved from the sea surface to near the sea bed. Seawater samples for the measurement of chlorophyll *a* (Chl *a*) were collected at different depths from the sea surface to near the sea bed, filtered onto GF/F glass-fiber filters, extracted using 90% aqueous acetone and the concentration of Chl *a* determined fluorometrically using a Turner Designs fluorometer. Bad weather prevented experiments being done at some stations in certain cruises.

The chaetognaths were sampled using the conical plankton net with 500 μm mesh size and 0.8 m mouth diameter (Wang and Wang 2003; Sun et al. 2010), which were towed vertically at ~1 m s⁻¹ from near the sea bottom of the water column to the sea surface. A TSK flow-meter and depth sensors were mounted at the mouth of the each net to measure the volume of water filtered and the sampling depth, respectively. After the nets were retrieved, the zooplankton samples were immediately preserved in 5% neutralized formalin seawater solution. In the laboratory, the abundance of chaetognaths was all counted, and were enumerated under a dissecting microscope.

2.2 Biomass Determination

Only four chaetognath species, *Sagitta crassa*, *Sagitta enflata*, *Sagitta bedoti*, and *Sagitta nagae*, was found during the study period in the Yellow Sea. The biomass of each chaetognath species was determined based on the relationship between the dry weight and the body length. The biomass of *S. crassa* and *S. enflata* could be obtained based on the following equations: $W = 0.197L^{3.01}$ for *S. crassa* (Nagasawa 1984) and $W = 0.0001352L^{3.1545}$ for *S. enflata* (Feigenbaum 1979), respectively. Because the abundance of *S. bedoti* was rather low compared with other *Sagitta* species, and the body length of *S. bedoti* was similar to that of *S. crassa*, so the biomass of *S. bedoti* was evaluated according to the relationship between the dry weight and the body length of *S. crassa*. Total lengths of 170 undamaged live *S. nagae* were measured to the nearest 0.1 mm. These samples were rinsed with distilled water to remove external salts, dried at 60°C for 24 - 36 h, weighed to the nearest 0.1 μg. The range of lengths was 8.50 - 25.75 mm. The relationship between the dry weight and the body length of *S. nagae* could be described as following equation: $W = aL^b$ (Uye 1982), where *a* and *b* were the constant parameters.
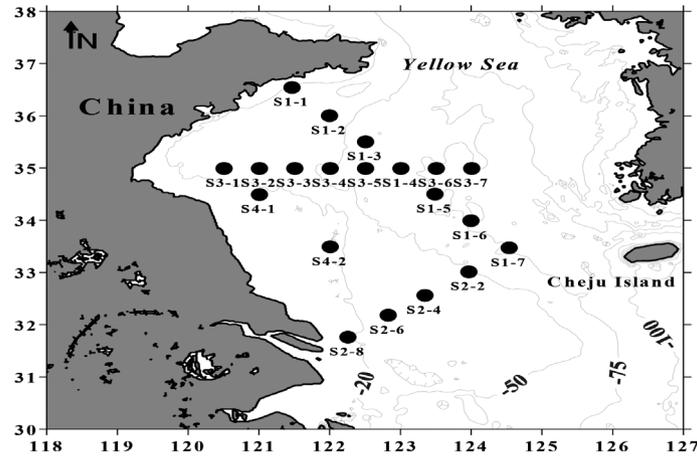
Fig. 1. Map of the study area and localities of the transects and sampling stations with isobaths of 20, 50, 75, and 100 m.

2.3 Production and Feeding Rate Evaluation

According to Huo et al. (2012), the respiration rate of each *Sagitta* species for the feeding and production estimates was calculated based on the Ikeda and Motoda's physiological model (Ikeda and Motoda 1975, 1978). Respiration was expressed as carbon units (R_C, mg C animal^{-1} h^{-1}) as the following equation, assuming an ammonia RQ of 0.97 (Gnaiger 1983): $R_C = R_{O2} \times 0.97 \times 12/1000 \times 22.4$, where 12 is the molar mass of carbon (g mol^{-1}), 22.4 is the molar volume of oxygen (L mol^{-1}) and R_{O2} is respiration rate (μl O$_2$ animal^{-1} h^{-1}) which was calculated as a function of body weight (W) and temperature (T, °C): ln R_{O2} = -0.2512 + 0.7886 ln W + 0.0490 T, where R_{O2} is respiration rate (μl O$_2$ animal^{-1} h^{-1}) and W is body dry weight (mg animal^{-1}) (Ikeda 1985). Equations of feeding and production of each *Sagitta* species were suggested as follows (Nagasawa 1991): $F = 1.6R_C$, $P = 0.46R_C$, where F is feeding and P is production. The feeding and production per day of each *Sagitta* species were obtained as F and P multiplying the abundance of each *Sagitta* species (ind. m^{-3}) and 24 h.

In the Yellow Sea, the strong stratification appeared in the summer time from June to September resulted by the Yellow Sea Cold Bottom Water (YSCBW). During the summer time at the YSCBW sea area, *S. enflata*, *S. nagae* and *S. bedoti* were mostly distributed in the upper layer and outside the cold water mass sea area, but *S. crassa* inhabited mostly inside the thermocline (Zuo et al. 2004). So in the June, August, and September, when calculating the respiration rate of *S. crassa* at the YSCBW sea area, the parameter T was the average temperature of the thermocline, while calculating the respiration rate of the other three *Sagitta* species, the parameter T was the average temperature of water column upper the thermocline. And in other months when the strong stratification disappeared, the parameter T was the average temperature of water column from sea surface to the bottom. Based on the results reported by Huo et al. (2012), we could confirm that S1-3, S1-4, S1-5, S1-6, S1-7, S3-2, S3-3, S3-4, S3-5, S3-6, S3-7 located inside the YSCBW sea area in June 2007, and S1-2, S1-3, S1-4, S1-5, S1-6, S1-7, S3-3, S3-4, S3-5, S3-6, S3-7 in August 2007, and S1-2, S1-3, S1-4, S1-5, S1-6, S1-7, S3-7 in September 2006, respectively.

2.4 Feeding Pressure on the Zooplankton Biomass and Production

Huo et al. (2012) reported the biomass (mg C m^{-3}) and estimated production (mg C m^{-3} d^{-1}) of zooplankton at the same sapling sites in the Yellow Sea. So the feeding pressure could be evaluated based on the feeding rate of each *Sagitta* species and total four *Sagitta* species divided by the biomass and production of zooplankton as follows: $F_{Biomass} = F/B_{Zooplankton}$, $F_{Production} = F/P_{Zooplankton}$, where F is feeding rate of chaetognaths, $F_{Biomass}$ is feeding pressure of chaetognaths on zooplankton biomass, $F_{Production}$ is feeding pressure of chaetognaths on zooplankton production, $B_{Zooplankton}$ is zooplankton biomass and $P_{Zooplankton}$ is zooplankton production, respectively.

2.5 Data Analysis

The sampling map and geographical distribution of chaetognath biomass were constructed using Surfer 8.0 software. Biomass, feeding rate and estimated production of chaetognaths were reported as mean values ± standard deviation (mean ± SD). Rang and average of biomass (mg DM m^{-3}), feeding rate (μg C m^{-3} d^{-1}) and production (μg C m^{-3} d^{-1}) of four *Sagitta* species and total chaetognaths were calculated as the range between the lowest and highest value, and mean value from all sampling sites, respectively. Statistical analyses were conducted using SPSS 19.0.

Multivariate ordination techniques were used to analyze the relationship of environmental variables with the

chaetognaths by CANOCO for Windows 4.5. The environmental parameters were adopted as the explanatory variables. All of these environmental parameters were log10-transformed before analysis. The chaetognath species data were log10(x + 1) transformed before analysis to obtain consecutive distributions. Detrended correspondence analysis (DCA) for the chaetognath species data was employed to decide whether linear or unimodal ordination methods should be applied in this study. DCA revealed that the maximum gradient length of the four axes was lower than 3, therefore, redundancy analysis (RDA) was used. Monte Carlo simulation was used to test the significance of the environmental parameters to explain the chaetognaths data in the RDA.

3 RESULTS

3.1 Biomass Distribution of Four *Sagitta* Species

The total length-dry weight relationship of *S. nagae* is described by the following equation: $W = 0.0565L^{3.3426}$, where W is dry weight (μg) and L is total length (mm). The mean total biomass of chaetognaths in the Yellow Sea peaked in May 2007 with 5.57 mg DM m^{-3}, and was lowest in August 2007 with 2.56 mg DM m^{-3}, and in other months, the biomass was in the range of 2.85 - 4.12 mg DM m^{-3} (Table 1). *S. crassa* and *S. nagae* comprised 49 - 90 and 10 - 33% of the total biomass throughout the year, respectively. High biomass of *S. crassa* was mainly distributed at the northern part of the investigated area throughout the year (Fig. 2). *S. enflata*, the oceanic species, was mainly distributed at the southern part of the study area. In March 2007, relative high biomass of *S. nagae* located at the northern part of study area, while in other investigated months, it was mainly distributed at the central and southern part of the study area. *S. bedoti* had lowest biomass compared with

other three *Sagitta* species during the study period in the Yellow Sea.

During the study period, the spatio-temporal distribution of the environmental variables varied between the investigated months. The results observed for these environmental variables were reported by Huo et al. (2012). The relationship between environmental factors and chaetognaths biomass in each month investigated was analyzed by RDA (Table 2 and Fig. 3). There were different significant environmental factors that explained the variability of the chaetognaths in the investigation months according to the RDA with forward selection. Surface salinity was found to statistically explain the variation in the composition of chaetognaths in September 2006. Bottom temperature was the significant environmental factor in December 2006, March 2007, May 2007, and August 2007, and Chl *a*, bottom salinity and surface salinity was also the significant environmental factor in December 2006, May 2007, and August 2007, respectively. During the study period in June 2007, no environmental factor was significantly correlated with chaetognaths in the Yellow Sea.

3.2 Estimated Feeding Rate and Production of Four *Sagitta* Species

The mean total feeding rate and production of four *Sagitta* species was also highest in May 2007 with 222.84 and 64.39 μg C m^{-3} d^{-1}, respectively, but was lowest in December 2006 with 115.74 and 33.28 μg C m^{-3} d^{-1}, respectively (Tables 1 and 3). In September 2006 and June, August 2007, chaetognaths also had high feeding rate and production (Huo et al. 2012), even though their body weights were relatively low in August and September (Tables 1 and 3). *S. crassa* and *S. nagae* had high feeding rate and production during the whole study period because of relatively their high biomass

Table 1. Rang and average of biomass (mg DM m^{-3}) of four *Sagitta* species and total chaetognaths in different investigated months in the Yellow Sea.

Species		Sagitta crassa	Sagitta enflata	Sagitta bedoti	Sagitta nagae	Total
September 2006	Range	0.01 - 5.49	0 - 4.89	0 - 0.86	0 - 2.80	0.44 - 6.27
	Average	1.41 ± 0.34	0.77 ± 0.31	0.14 ± 0.06	0.53 ± 0.18	2.85 ± 0.43
December 2006	Range	0.02 - 14.49	0 - 0.38	0 - 0.32	0 - 3.80	0.11 - 18.89
	Average	2.24 ± 0.84	0.05 ± 0.02	0.06 ± 0.02	0.63 ± 0.22	2.97 ± 1.08
March 2007	Range	0.01 - 27.48	0 - 0.01	0 - 0.07	0 - 1.54	0.08 - 29.03
	Average	3.73 ± 1.57	0.0007 ± 0.0007	0.01 ± 0.0042	0.38 ± 0.09	4.12 ± 1.64
May 2007	Range	0.07 - 33.16	0 - 0.15	0 - 6.10	0 - 3.71	0.52 - 33.48
	Average	4.15 ± 1.70	0.01 ± 0.01	0.47 ± 0.33	0.93 ± 0.23	5.57 ± 1.65
June 2007	Range	0 - 8.41	0 - 0.23	0 - 1.44	0 - 5.14	0.22 - 8.67
	Average	2.38 ± 0.65	0.02 ± 0.02	0.12 ± 0.08	1.22 ± 0.34	3.74 ± 0.69
August 2007	Range	0.05 - 7.25	0 - 0.03	0 - 0.13	0 - 4.08	0.14 - 11.32
	Average	1.81 ± 0.63	0.0018 ± 0.0018	0.02 ± 0.01	0.74 ± 0.27	2.56 ± 0.81
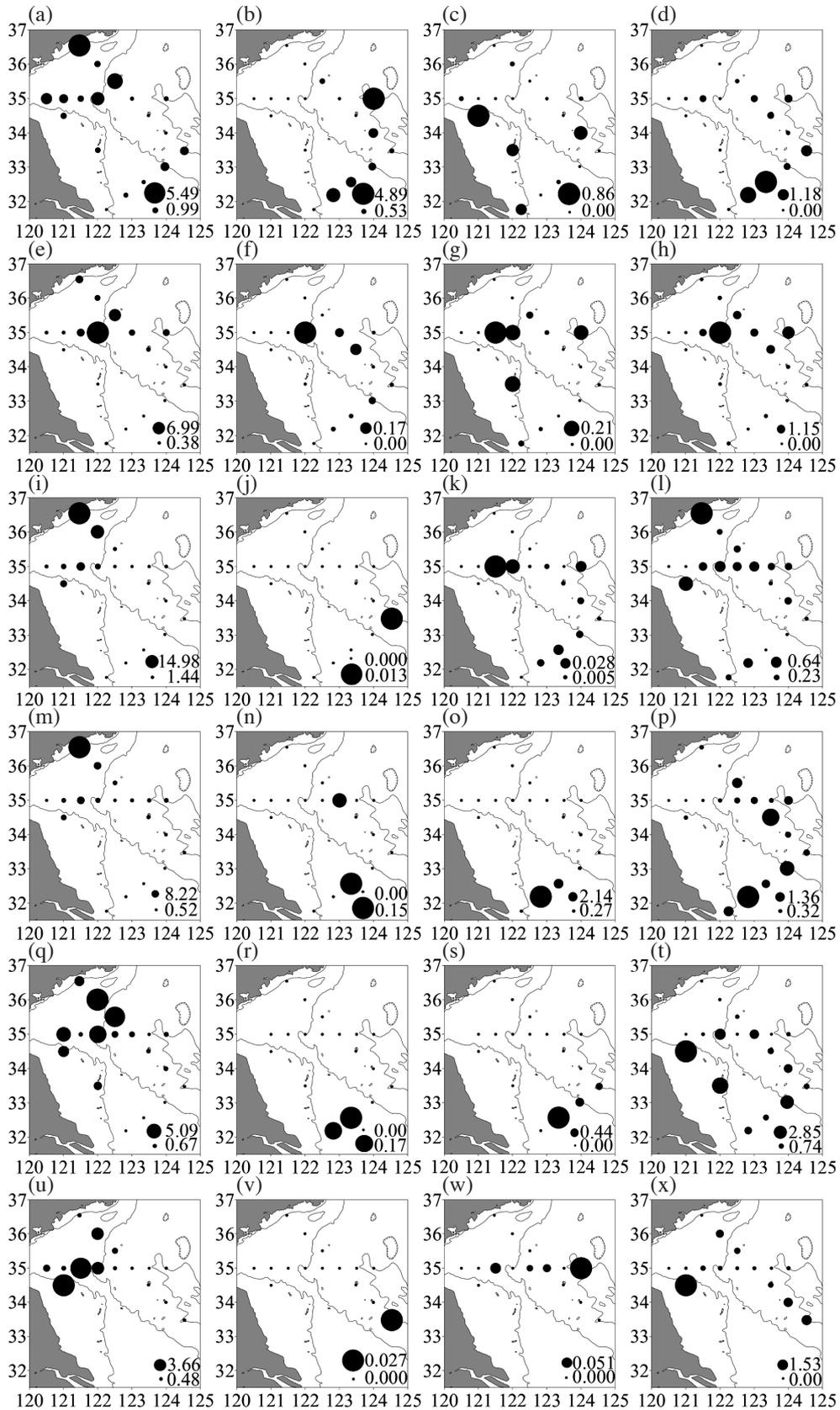
Fig. 2. Biomass (mg DM m⁻³) distribution of *Sagitta crassa* in September 2006 (a), December 2006 (e), March 2007 (i), May 2007 (m), June 2007 (q), and August 2007 (u); *Sagitta enflata* in September 2006 (b), December 2006 (f), March 2007 (j), May 2007 (n), June 2007 (r), and August 2007 (v); *Sagitta bedoti* in September 2006 (c), December 2006 (g), March 2007 (k), May 2007 (o), June 2007 (s), and August 2007 (w); *Sagitta nagae* in September 2006 (d), December 2006 (h), March 2007 (l), May 2007 (p), June 2007 (t), and August 2007 (x).

Table 2. Variation partitioning analysis of the significant environmental factors on the chaetognaths assemblages in different investigated months in the Yellow Sea.

Month	Environmental factor	Eigenvalues	Variation explains solely/%	F	p
September 2006	Surface salinity	0.269	26.9	5.894	0.002
December 2006	Bottom temperature	0.209	20.9	4.227	0.046
	Chl *a*	0.186	18.6	4.597	0.040
March 2007	Bottom temperature	0.700	70.0	39.698	0.002
May 2007	Bottom temperature	0.239	23.9	5.332	0.008
	Bottom salinity	0.277	27.7	9.147	0.004
August 2007	Surface salinity	0.424	42.4	9.569	0.004
	Bottom temperature	0.175	17.5	5.229	0.010
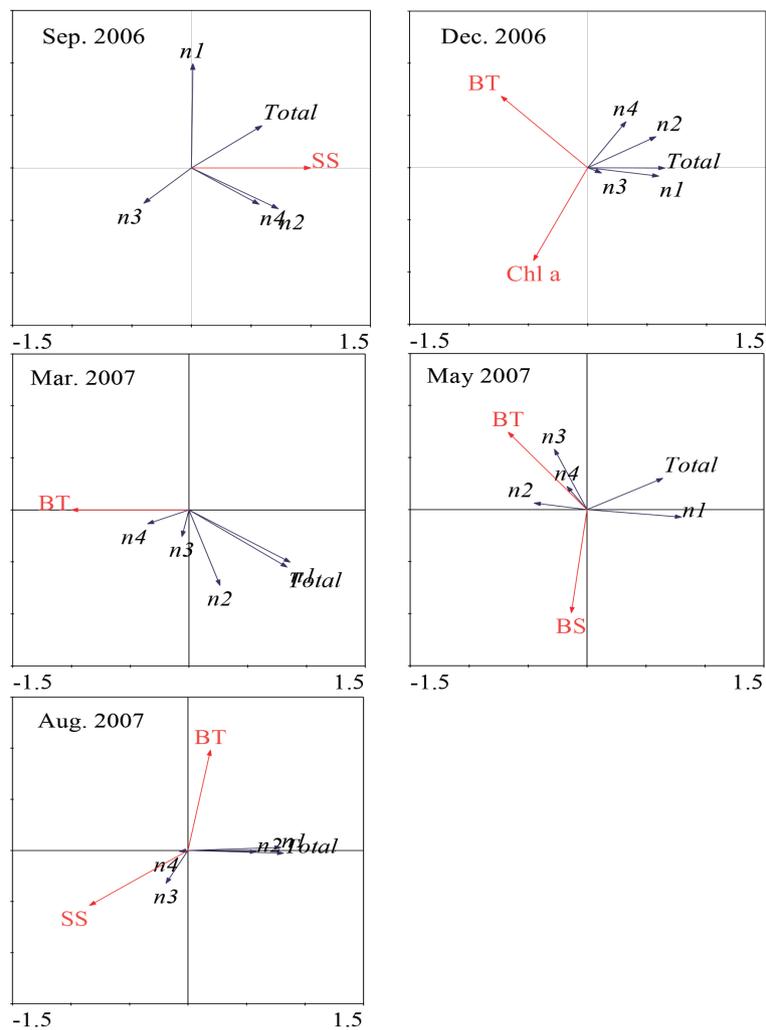
Fig. 3. Correlation plots of the redundancy analysis (RDA) for the relationship between the environmental variables and chaetognath species. The numbers with letters represent the following species: *n1* represents *Sagitta crassa*, *n2 Sagitta nagae*, *n3 Sagitta bedoti*, *n4 Sagitta enflata*, *n5* represents total chaetognath biomass.

Table 3. Rang and average of feeding rate (µg C m⁻³ d⁻¹) and production (µg C m⁻³ d⁻¹) of four *Sagitta* species and total chaetognaths in different investigated months in the Yellow Sea.

Species	Items	Sagitta crassa		Sagitta enflata		Sagitta bedoti		Sagitta nagae		Total	
		Feeding	Production	Feeding	Production	Feeding	Production	Feeding	Production	Feeding	Production
September 2006	Range	1.74 - 479.73	0.50 - 137.92	0 - 204.10	0 - 58.68	0 - 65.22	0 - 18.75	0 - 132.94	0 - 38.22	33.32 - 479.73	9.58 - 137.92
	Average	104.01 ± 27.34	29.90 ± 7.86	37.94 ± 14.84	10.91 ± 4.27	10.55 ± 4.36	3.03 ± 1.25	21.90 ± 7.86	6.30 ± 2.26	174.39 ± 27.83	50.14 ± 8.00
December 2006	Range	1.37 - 614.50	0.39 - 176.67	0 - 12.39	0 - 3.56	0 - 8.31	0 - 2.39	0 - 115.96	0 - 33.34	4.49 - 751.16	1.29 - 215.96
	Average	93.38 ± 35.49	26.85 ± 10.20	1.77 ± 0.75	0.51 ± 0.22	2.12 ± 0.76	0.61 ± 0.22	18.48 ± 6.67	5.31 ± 1.92	115.74 ± 42.65	33.28 ± 12.26
March 2007	Range	0.47 - 732.95	0.14 - 210.72	0 - 0.56	0 - 0.16	0 - 2.21	0 - 0.64	0 - 28.77	0 - 8.27	2.68 - 761.72	0.77 - 218.99
	Average	107.25 ± 41.99	30.84 ± 12.07	0.03 ± 0.03	0.01 ± 0.01	0.41 ± 0.14	0.12 ± 0.04	8.54 ± 1.76	2.46 ± 0.50	116.24 ± 43.09	33.42 ± 12.39
May 2007	Range	5.64 - 1127.10	1.62 - 324.04	0 - 5.61	0 - 1.61	0 - 395.43	0 - 113.69	0 - 256.02	0 - 73.60	22.14 - 1136.91	6.37 - 326.86
	Average	147.88 ± 57.87	42.52 ± 16.64	0.54 ± 0.35	0.15 ± 0.10	28.81 ± 21.38	8.28 ± 6.15	45.60 ± 17.47	13.44 ± 4.99	222.84 ± 62.05	64.39 ± 17.86
June 2007	Range	0 - 341.44	0 - 98.16	0 - 13.60	0 - 3.91	0 - 93.72	0 - 26.94	0 - 203.45	0 - 58.49	9.42 - 437.69	2.71 - 125.84
	Average	116.03 ± 29.17	33.36 ± 8.39	1.35 ± 0.93	0.39 ± 0.27	8.02 ± 5.42	2.31 ± 1.56	49.22 ± 13.77	14.15 ± 3.96	174.63 ± 31.56	50.21 ± 9.07
August 2007	Range	0 - 630.52	0 - 181.28	0 - 1.89	0 - 0.54	0 - 8.18	0 - 2.35	0 - 202.99	0 - 58.36	7.99 - 833.51	2.30 - 239.63
	Average	114.84 ± 42.93	33.02 ± 12.34	0.13 ± 0.13	0.04 ± 0.04	1.06 ± 0.59	0.31 ± 0.17	38.55 ± 13.39	11.08 ± 3.85	154.58 ± 53.79	44.44 ± 15.47

compared with other two species. The annual average feeding rate and production of chaetognaths in the study area was evaluated as 55.24 and 15.90 mg C m⁻³ year⁻¹, respectively. Chaetognaths had relatively high feeding rate and production at sampling stations of northern part and along the transect near Yangtze estuary in September 2006; in the central part of Yellow Sea in December 2006; at the coast of Shandong peninsula in March and May 2007; and along the coast of Yellow Sea in June and August 2007 (Fig. 4).

3.3 Feeding Rate of Different Body Length of Chaetognaths

Feeding rate of different body length of chaetognaths was analyzed at the interval of 1 mm which was showed in Fig. 5. The feeding rate of 5 - 9 mm body length of chaetognaths was relatively higher than those of other chaetognath body length groups in September 2006 and August 2007. In December 2006, the 7 - 11 mm body length of chaetognaths had relatively high feeding rate than other chaetognath body length groups. And in the March, May, and June of 2007, the relatively high feeding rate of chaetognaths was in the body length of 8 - 16, 11 - 15, and 6 - 16 mm groups, respectively.

3.4 Feeding Pressure on Zooplankton Biomass and Production

Based on the results of zooplankton biomass and production obtained from the same sampling sites of the Yellow Sea reported by Huo et al. (2012), the feeding pressure on zooplankton biomass and production by four *Sagitta* species in the Yellow Sea could be evaluated as Table 4 showed. Feeding pressure on zooplankton biomass and production was lowest in May 2007 with 0.80 and 13.54%, respectively. Feeding pressure on zooplankton production was as high as 26.90%, but was only 0.99% on zooplankton biomass in March 2007. In other investigated months, the feeding pressure was in the range of 1.05 - 1.22 and 14.50 - 21.21% on zooplankton biomass and production, respectively. Based on these data, the annual average feeding pressure on zooplankton biomass and production was evaluated as 1.07 and 18.95%, respectively, in the Yellow Sea. *S. crassa* and *S. nagae* contributed most to the feeding pressure on zooplankton biomass and production during the whole study period because of their relatively high biomass compared with other two species (Table 4).

4. DISCUSSION

4.1 Methods of Evaluating the Feeding Rate of Chaetognaths

Feeding rate of chaetognaths can be evaluated as the following equation proposed by Bajkov (1935): $FRi = NPC \times 24/DT(h)$, where FRi is daily feeding rate (mean number
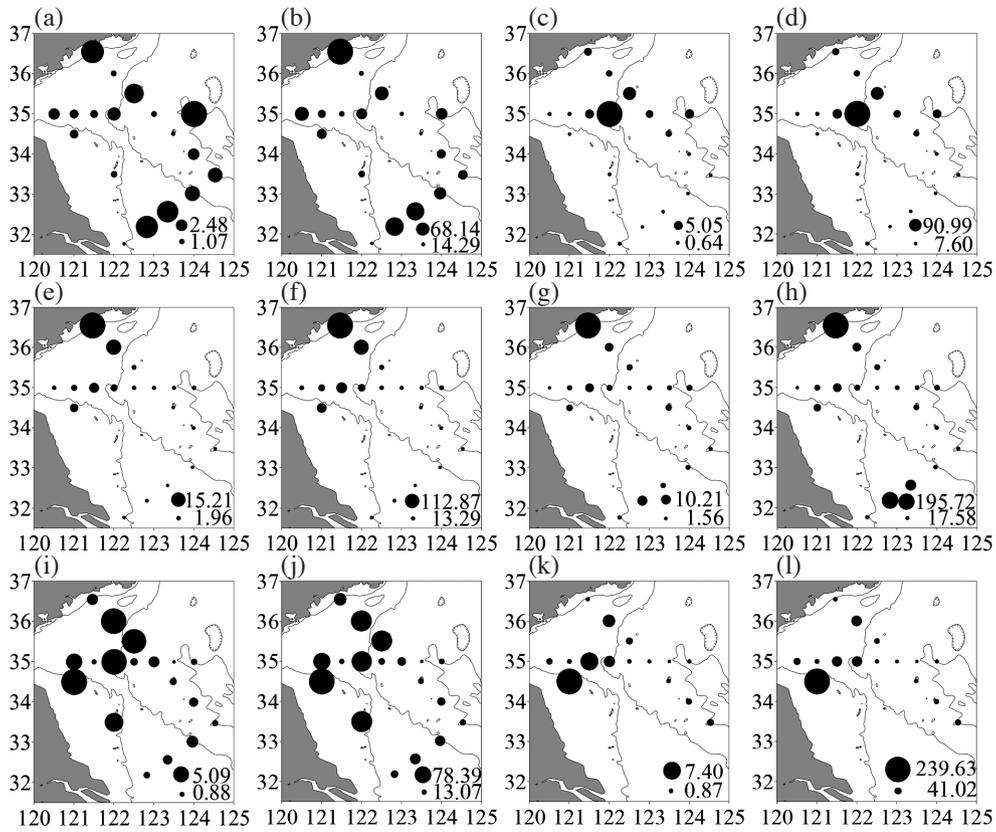
Fig. 4. Geographical distribution of biomass (mg DM m⁻³ d⁻¹) and production (μg C m⁻³ d⁻¹) for the total four *Sagitta* species in September 2006 (a) and (b), December 2006 (c) and (d), March 2007 (e) and (f), May 2007 (g) and (h), June 2007 (i) and (j), August 2007 (k) and (l), respectively.
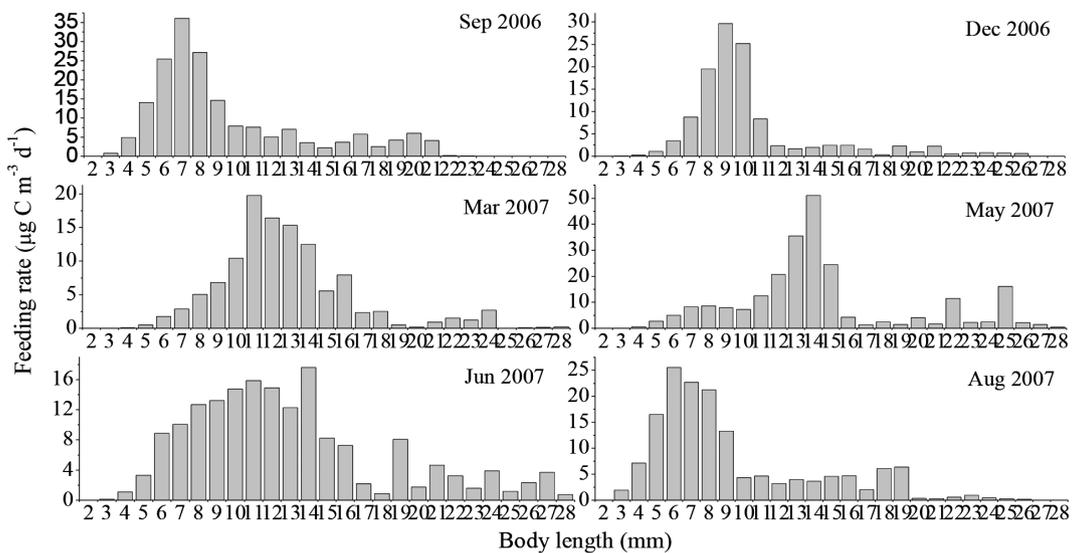
Fig. 5. Relationship between feeding rate and different body length of chaetognaths in investigated months in the Yellow Sea.

Table 4. Rang and average of estimated feeding pressure on zooplankton biomass (%) and production (%) per day of four *Sagitta* species and total chaetognaths in different investigated months in the Yellow Sea.

Species	Items	*Sagitta crassa*		*Sagitta enflata*		*Sagitta bedoti*		*Sagitta nagae*		Total	
		%Biomass	%Production	%Biomass	%Production	%Biomass	%Production	%Biomass	%Production	%Biomass	%Production
September 2006	Range	0.04 - 2.56	1.15 - 23.65	0 - 0.76	0 - 15.30	0 - 0.42	0 - 6.26	0 - 0.62	0 - 7.19	0.19 - 2.56	6.01 - 38.41
	Average	0.77 ± 0.17	9.17 ± 1.87	0.19 ± 0.07	3.23 ± 1.22	0.06 ± 0.03	0.95 ± 0.45	0.12 ± 0.04	1.91 ± 0.51	1.14 ± 0.14	15.26 ± 2.09
December 2006	Range	0.01 - 5.16	0.17 - 91.74	0 - 0.10	0 - 1.85	0 - 0.14	0 - 3.00	0 - 0.97	0 - 17.31	0.05 - 6.31	0.57 - 112.15
	Average	0.92 ± 0.31	16.79 ± 5.43	0.02 ± 0.01	0.36 ± 0.13	0.02 ± 0.01	0.49 ± 0.19	0.18 ± 0.06	3.57 ± 1.09	1.15 ± 0.36	21.21 ± 6.51
March 2007	Range	0.01 - 6.20	0.15 - 234.55	0 - 0.02	0 - 0.22	0 - 0.02	0 - 0.45	0 - 0.65	0 - 24.46	0.01 - 6.85	0.22 - 259.01
	Average	0.86 ± 0.32	23.52 ± 12.06	0.0009 ± 0.0009	0.01 ± 0.01	0.0050 ± 0.0015	0.10 ± 0.03	0.12 ± 0.04	3.27 ± 1.26	0.99 ± 0.35	26.90 ± 13.21
May 2007	Range	0.01 - 1.97	0.12 - 31.47	0 - 0.04	0 - 0.73	0 - 0.75	0 - 9.95	0 - 0.48	0 - 6.37	0.11 - 1.98	1.97 - 31.75
	Average	0.58 ± 0.16	9.71 ± 2.62	0.0033 ± 0.0026	0.07 ± 0.05	0.07 ± 0.05	1.01 ± 0.71	0.15 ± 0.04	2.75 ± 0.58	0.80 ± 0.15	13.54 ± 2.24
June 2007	Range	0 - 2.72	0 - 43.57	0 - 0.11	0 - 0.96	0 - 0.31	0 - 2.30	0 - 1.03	0 - 11.35	0.15 - 3.01	1.53 - 52.94
	Average	0.66 ± 0.23	9.65 ± 3.84	0.01 ± 0.01	0.09 ± 0.07	0.04 ± 0.02	0.38 ± 0.21	0.34 ± 0.08	4.37 ± 1.00	1.05 ± 0.25	14.50 ± 4.14
August 2007	Range	0.05 - 3.10	0.76 - 33.31	0 - 0.01	0 - 0.25	0 - 0.11	0 - 1.86	0 - 1.00	0 - 10.84	0.13 - 4.10	2.17 - 42.94
	Average	0.90 ± 0.25	11.04 ± 2.94	0.0006 ± 0.0006	0.02 ± 0.02	0.01 ± 0.01	0.20 ± 0.13	0.30 ± 0.07	4.70 ± 1.04	1.22 ± 0.28	15.96 ± 3.20

of prey taken per 24 h), and *DT* is digestion time (h), and *NPC* represents mean number of prey ingested per chaetognath. *NPC* can be obtained based on the abundance of copepod mandible or chaetognath hooks or other zooplankton detected from the gut content analysis. *DT* can be evaluated using two methods. The first method is that chaetognaths which contain food in their guts are cultured *in situ* environmental conditions, and then the digestion time is observed (Feigenbaum and Maris 1984). The other method is that the digestion time is calculated using the empirical equation: $DT = 10.96e^{-0.086T}$ derived for the *Sagitta* species by Stuart and Verheye (1991).

The accuracy of the quantitative analysis of gut contents in samples collected by planktonic nets can be affected by various factors. Among the main factors that can cause uncertainties in the estimates is the cod-end feeding and also the regurgitation and evacuation of prey during the handling and preservation processes (Kehayias 2003). Baier and Purcell (1997a) indicated that tow duration should be minimized and prey in the foregut from gut content analysis should be excluded in order to reduce errors due to cod-end feeding, and they also reported that prey loss due to evacuation can be as much as 50% of the total prey in tows of greater than 2 min duration, so some researcher suggest that the NPC values in the above feeding rate equation were multiplied by two (Baier and Purcell 1997b; Kehayias et al. 2005). In addition, the possibility of chaetognaths regurgitating their prey during sampling can't be discounted (Feigenbaum and Maris 1984). Feigenbaum and Maris (1984) reviewed digestion times of some chaetognath species evaluated in laboratory or *in situ* environmental conditions. However, it is evident that digestion time at any temperature can be extremely variable because of the size, type, abundance, chemical composition of prey, as well as the size, development stage of chaetognath species, and that variation between species may not be as great as within species (Stuart and Verheye 1991; Øresland 2000).

The Ikeda-Motoda's physiological methods is convenient to be used to calculate feeding and production of chaetognaths if body weight and water temperature were obtained (Ikeda and Motoda 1978; Ikeda 1985). However, the gross growth efficiency and assimilation efficiency of 0.3 and 0.7 (Hirst and Sheader 1997; Ikeda 1985; Runge and Roff 2000) may vary greatly due to different species (Alldredge 1984; Omori and Ikeda 1984). And the coefficient between the feeding rate, and production and respiration rate is also affected by various factors, such as chaetognath species, water temperature, size and type of prey.

In the present study, we checked the gut contents of four *Sagitta* species on board during the investigated period, but few *Sagitta* had food in their gut, and these few *Sagitta* had hardly excreted over long time mainly because of environmental change. The choice of which of the methods mentioned above depends on the research questions and in

some cases, a global model of growth may be a sufficient approximation of growth and reproductive rates of zooplankton (Runge and Roff 2000). Therefore, Ikeda and Motoda's physiological model was selected to estimate feeding rate and production of chaetognaths based on the body weight and water temperature in the present study, which has been applied in other several studies (Nagasawa 1991).

4.2 Biomass and Production of Chaetognaths in the Yellow Sea

Table 5 showed proportions of biomass and production of chaetognaths to total biomass and production of zooplankton (Huo et al. 2012) in the Yellow Sea. Even though chaetognaths had highest biomass in May 2007, but only contributed 6.63% to total biomass of zooplankton in the Yellow Sea. The biomass of chaetognaths occupied as high as 13.61% of total zooplankton biomass even though they had relatively low biomass in December 2006. And in other months, chaetognaths contributed 6.73 - 12.73% to total zooplankton biomass. Contributions of chaetognaths to total zooplankton production were lower compared with those to total zooplankton biomass in the Yellow Sea. It was indicated that *S. crassa* and *S. nagae* dominated the chaetognath community whole year based on their biomass and production in the Yellow Sea. *Sagitta crassa* has five generations in the Yellow Sea and in adjacent sea areas (Nagasawa 1991; Huo et al. 2010). And these five generations of *S. crassa* overlapped during whole year in the Yellow Sea and in Tokyo Bay (Nagasawa 1991; Huo et al. 2010), which indicated that *S. crassa* can reproduce and grow under environmental conditions of whole year in the Yellow Sea. This was the main reason that *S. crassa* had relative high biomass compared with other *Sagitta* species in the Yellow Sea, especially from December to next June. *Sagitta nagae* had six cohorts throughout the year in Suruga Bay and peak numbers of all stages occurred between May and August (Nagasawa and Marumo 1978). In the present study, *S. nagae* also had relative high biomass during the period from May to August.

Carbon content was considered as 36.7% of dry weight in chaetognaths group (Kiørboe 2013). So average production rate (P/B) of chaetognaths can be calculated based on the average biomass and production in different investigated months in the Yellow Sea (Fig. 6). Average production of chaetognaths was highest with 64.39 µg C m^{-3} d^{-1} in May 2007, but the average production rate was only 3.15% d^{-1} because of relatively low water temperature (Huo et al. 2012). The average production rate of chaetognaths was as high as 4.79 and 4.73% d^{-1} in September 2006 and August 2007, respectively, because of relatively high water temperature even though their low standing stock in the Yellow Sea. Chaetognath production occupied 6.58% of total zooplankton production in December 2006, and only contributed 3.17% to total zooplankton production in May 2007 (Table 5).

The YSCBW had a vital role in zooplankton biomass and production distributions from June to September in the Yellow Sea (Huo et al. 2008, 2012). *Sagitta enflata*, *S. nagae*, and *S. bedoti* were not impacted by the YSCBW because they mostly distributed in the upper layer, but *S. crassa* was impacted because it inhabited mostly inside the thermocline in the Yellow Sea (Zuo et al. 2004). Therefore, *S. crassa* production was strongly impacted by the YSCBW in September 2006, June and August 2007. In these sampling months, the production rate of *S. crassa* ranged from 3.57 - 4.69% d^{-1} inside the YSCBW sea area, while 5.09 - 6.74% d^{-1} outside the cold water mass sea area (data not shown).

The distribution patterns of chaetognaths were mainly impacted by some environmental factors in the Yellow Sea. *Sagitta crassa* was considered as a coastal species which had abilities to suit to wild temperature and salinity ranges (Nagai et al. 2006), and the spatial-geographical distribution patterns of *S. crassa* were also affected by food availability. Liu et al. (2003) reported that the high biomass of every development stages of *Calanus sinicus* was found at the same area of *S. crassa* distribution, and Zuo et al. (2006) also reported that the as much as 1.80 - 3.52 × 10^5 ind m^{-2} of small copepod distributed at these sea areas. It was showed that the relatively high biomass of *S. nagae* was distributed in the central and southern part of the study area in the Yellow Sea. Xiao (2004) renamed *S. nagae* as *Sagitta sinica* which was a new species in the Yellow Sea. *Sagitta sinica* was described as a warm-temperate neritic species and was wildly distributed in the Yellow Sea and East China Sea (Xiao 2004). It is necessary to confirm whether it is a new species based on combinations of morphological, molecular and other methods in the future. The distribution mechanism of *S. enflata* and *S. bedoti* was different between warm seasons and cold seasons in the Yellow Sea. In warm seasons, the expansion of these two *Sagitta* species was mainly caused by water temperature rise and was not by current transportation (Wang et al. 2003). While in cold seasons, they were mainly impacted by physical transportation and could be transported up to 36 degree north latitude into northern Yellow Sea by the Yellow Sea Warm Current (Wang and Zuo 2004).

4.3 Feeding Pressure on the Zooplankton in the Yellow Sea

Feeding pressure on biomass and production of zooplankton by specific species of chaetognaths in different sea areas was summarized in Table 6. Feeding pressure of chaetognaths on zooplankton biomass in the Yellow Sea was lower than that in Kaneohe Bay (Kimmerer 1984), in Aegean Sea (Kehayias et al. 2005) and in Mediterranean (Kehayias 2003), but was similar with that in Southern Ocean (Froneman et al. 1998). *Sagitta friderici*, *Sagitta setosa*, *Sagitta tenuis*, and *S. enflata* exerted the high feeding pressure on zooplankton biomass in South Africa, Black Sea,

Chesapeake Bay, and Chile Sea than those of *Sagitta* species in the Yellow sea (Canino and Grant 1985; Drits and Utkina 1988; Stuart and Verheye 1991; Giesecke and González 2004). Feeding pressure on zooplankton production by chaetognaths was different from those on biomass (Table 6). *Sagitta elegans* and *Sagitta hispida* feed 36 and 100% on zooplankton production in Bedford Basin and Card Sound, respectively, which were higher than those of chaetognaths in the Yellow Sea (Sameoto 1973; Reeve and Baker 1975). While the feeding pressure of *S. crassa* on zooplankton production in the Yellow Sea was higher than that of *S. crassa* in Tokyo Bay (Nagasawa 1991), and higher than other *Sagitta* species in other sea areas (Sameoto 1972; Feigenbaum 1977; Canino and Grant 1985; Froneman et al. 1998).

Copepod is commonly reported as being the most abundant food item found in chaetognath guts because of its abundance in the marine habitat (Feigenbaum 1991). It was reported that the feeding of chaetognaths was more serious for the copepod community in their lower production period (Baier and Purcell 1997b). Sameoto (1973) indicated that the average feeding pressure of *S. elegans* on copepod production was 1%, but increased up to 50% during winter time in Bedford Basin. Øresland (1990) discovered that *Eukrohnia hamata* averagely feed on 0.03 - 0.06% of copepod biomass, but 12% of copepod biomass was fed during their diapause stages during winter time in Southern Ocean. In the present study, the feeding pressure of chaetognaths on zooplankton production was also highest during cold seasons in December 2006 and March 2007 with 21.21 and 26.90%, respectively, which indicated that the feeding of chaetognaths had important impacts on zooplankton community structure and production, especially on copepod.

4.4 Feeding Impacts of Chaetognaths on Different Body Length of Zooplankton

Body size of zooplankton was an important factor on determining the composition of food item fed by chaetognaths (Rakuza-Suszczewski 1969; Sullivan 1980), which indicated that feeding pressure of chaetognaths on different

Table 5. Contributions of chaetognaths to total the biomass (mg DM m^{-3} d^{-1}) and production (mg C m^{-3} d^{-1}) of zooplankton in different months in the Yellow Sea.

Months	Items	Chaetognaths	Total zooplankton	Proportion (%)
September 2006	Biomass	2.85	42.34	6.73
	Production	0.050	1.44	3.49
December 2006	Biomass	2.97	21.83	13.61
	Production	0.033	0.51	6.58
March 2007	Biomass	4.12	32.37	12.73
	Production	0.033	0.67	4.98
May 2007	Biomass	5.57	84.03	6.63
	Production	0.064	1.97	3.27
June 2007	Biomass	3.74	38.36	9.75
	Production	0.050	1.37	3.68
August 2007	Biomass	2.56	27.17	9.42
	Production	0.044	0.81	5.48
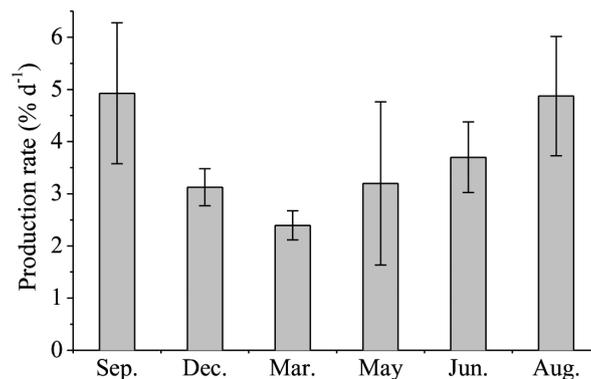
Fig. 6. Production rate (mean ± SD) of chaetognaths in different investigated months in the Yellow Sea.

Table 6. Feeding pressure by the different species of chaetognaths on biomass and production of zooplankton in different seas.

Species	Sea area	Feeding Pressure		Literature
		%Biomass	%Production	
Sagitta crassa	Tokyo Bay		10	Nagasawa 1991
Sagitta elegans	Bedford Basin		36	Sameoto 1973
Sagitta elegans	St. Margaret's Bay		0.7 - 1.0	Sameoto 1972
Chaetognaths	Kaneohe Bay	4 - 12		Kimmerer 1984
Sagitta friderici	South Afirica	1.0 - 5.3		Stuart and Verheye 1991
Sagitta setosa	Black Sea	0.3 - 6		Drits and Utkina 1988
Sagitta tenuis	Chesapeake Bay	1 - 4	5 - 15	Canino and Grant 1985
Sagitta enflata	Gulf Stream		6.1	Feigenbaum 1977
Sagitta hispida	Card Sound		100	Reeve and Baker 1975
Sagitta enflata	Zanzibar Channel	1		Øresland 2000
Chaetognaths	Aegean Sea	0.02 - 2.76		Kehayias et al. 2005
Chaetognaths	Mediterranean	0.3 - 7.8		Kehayias 2003
Sagitta enflata	Chile Sea	0.4 - 6		Giesecke and González 2004
Eukrohnia hamata and Sagitta gazellae	Southern Ocean	0.3 - 1.2	7 - 16	Froneman et al. 1998
Sagitta crassa	Yellow Sea	0.58 - 0.92	9.17 - 23.52	Present study
Sagitta nagae	Yellow Sea	0.12 - 0.34	1.91 - 4.70	Present study
Sagitta enflata	Yellow Sea	0.0006 - 0.19	0.01 - 3.23	Present study
Sagitta bedoti	Yellow Sea	0.005 - 0.07	0.10 - 1.01	Present study
Chaetognaths	Yellow Sea	0.80 - 1.22	13.54 - 26.90	Present study

body length of zooplankton was obvious distinct. There was a positive relationship between body length of chaetognaths and their food: $H = aP^b$ (Pearre 1980), but Sullivan (1980) indicated that chaetognaths did not have directly food selection. *S. nagae* did not showed food selection when the body width of copepod was in the range of 0.2 - 1.2 mm in Suruga Bay (Nagasawa and Marumo 1976). Yang and Li (1995) reported that the body length of zooplankton from 0.7 mm (e.g., *Paracalanus parvus*) to 2.3 mm (e.g., *Calanus sinicus*) was the main food of *S. crassa* in the Yellow Sea. Although adults of chaetognaths can feed on wide size spectrum of zooplankton, there exactly occurred difference on food size ranges at their different development stages (Sullivan 1980). Saito and Kiørboe (2001) demonstrated that feeding rates of *S. elegans* were affected by prey size, prey swimming behavior and small-scale turbulence, and it had highest feeding rates when the prey size was 6 - 10% of their body length. So in the present study, effects of feeding on different size spectrum of zooplankton by chaetognaths were evaluated in the Yellow Sea based on 6 - 10% of prey size to body length of chaetognaths. Based on this assumption, chaetognaths had highest feeding rate on the body length with 0.6 - 1.6 mm of zooplankton in March, May, and June 2007, which indicated that chaetognaths mainly feed on small copepod, such as *Paracalanus parvus*, *Cen-*

tropages mcmurrichi, *Oithona similis*, and individuals of large copepod at their development stages, such as *Calanus sinicus* (Sun et al. 2010; Huo et al. 2012), and in September 2006, December 2006, and August 2007, chaetognaths mainly fed on small copepod and nauplius and copepodite of large copepod due to the highest feeding rate on the body length with 0.5 - 1.1 mm of zooplankton in the Yellow Sea. Therefore, the biomass and production of small copepods, and nauplius and copepodite of large copepods would be impacted during whole year in the Yellow Sea. *Calanus sinicus* was the absolute dominant species in the Yellow Sea (Sun 2005; Sun and Zhang 2005). *Calanus sinicus* was in the diapause stage in the summer time in the Yellow Sea (Pu et al. 2004), and had lowest production in this period (Zhang et al. 2005, 2007; Huo et al. 2008), which indicated that *C. sinicus* would be impacted seriously by the feeding of chaetognaths in the summer time in the Yellow Sea.

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