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Estimating optimal salinity and temperature of chaetognaths

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Determining optimal temperature and salinity for marine organisms is a challenge for marine ecologists because not every species can be easily maintained in the laboratory for testing the influence of environmental parameters. To find a simple method to estimate the optimal temperature and salinity for marine organisms based on survey data, a reciprocal quadratic yield-density model was used for determining the optimal temperature or salinity from abundance data for six pelagic Chaetognatha species. The data for the modelling were collected in four surveys in the East China Sea (23°30′–33°N 118°30′–128°E) from 1997 to 2000. According to both survey data and results from the models, we analysed qualitatively and quantitatively the ecological characteristics of those species. Estimated optimal temperatures and salinities are 17.3°C and 14.1‰ for Sagitta nagae*, 20.3°C and 13.8‰ for* S. bedoti*, 24.9°C and 32.9‰ for* S. enflata*, 22.5°C and 16.5‰ for* S. ferox*, 24.5°C and 34.1‰ for* S. pacifica *and 17.3°C and 14.1‰ for* S. pulchra*, respectively. Three ecological groups were evident in the East China Sea: the neritic, warm temperate water species (*S. nagae*); the neritic, warm water species (*S. pulchra, S. ferox *and* S. bedoti*); and the oceanic, warm water species (*S. enflata *and* S. pacifica*). Our results validate that the model is applicable for describing the relationship between chaetognaths abundance and temperature or salinity.*

Keywords: Chaetognatha, yield density model, temperature, salinity, East China Sea

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INTRODUCTION

Chaetognaths are an important component of marine zooplankton communities, second in abundance only to copepods (Feigenbaum & Maris, 1984), and an important food for fish (Terazaki, 2005) and carnivorous zooplankton (Froneman *et al.*, 2002), i.e. they play a key role in oceanic food web. Chaetognaths are a cosmopolitan group found in all major ocean systems, from temperate to tropical waters, such as in the tropical waters of the Indian (Nair *et al.*, 2002), Atlantic (Pierrot-Bults, 1982; Daponte *et al.*, 2004), and Pacific (Bieri, 1959; Terazaki, 1996) Oceans, and the Bohai Sea (Bi *et al.*, 2001), the East China Sea (Xu & Chen, 2005), the South China Sea (Yin *et al.*, 2006), the Mediterranean Sea (Furnestin, 1979; Kehayias, 2004), the Red Sea (Durcret, 1973), the Eastern Irish Sea (Khan & Williamson, 1970), and in the Arctic and subarctic areas of the Indian (David, 1963), Atlantic and Pacific Oceans (Terazaki, 1998).

Intensive field investigations have revealed the spatial and temporal distributions of chaetognaths worldwide (e.g. Khan & Williamson, 1970; Grant, 1977; Marazzo & Nogueira, 1996; Terazaki, 1996; Pierrot-Bults & Nair, 1997; Ruiz-Boijseauneau *et al.*, 2004; Yin *et al.*, 2006). Within chaetognaths, some species are distributed worldwide, for example *Sagitta enflata*, which is distributed widely in temperate and tropical waters (e.g. Cheney, 1985; Terazaki 1993, 1996; Pierrot-Bults & Nair, 1997; Nair *et al.*, 2002; Daponte *et al.*, 2004; Kehayias, 2004; Xu & Chen, 2005; Yin *et al.*, 2006); and some are mainly confined in the Arctic and temperate waters, for example *S. elegans* (e.g. Sherman & Schaner, 1968; Tiselius & Peterson, 1986; Terazaki, 1998; Choe & Deibel, 2000; Fulmer & Bollens, 2005). Apparently the variation in distribution patterns is related to temperature, as well as other hydrographic factors, such as salinity. Generally, studies on temperature or salinity tolerance of zooplankton species should address three questions: temperature or salinity range of zooplankton distribution; optimal temperature or salinity for zooplankton; and how the zooplankton population responds to temperature or salinity fluctuation, i.e. the effect of suboptimal temperature or salinity on population density.

Although the dependence of zooplankton distribution on temperature and salinity, including chaetognaths (O'Brien, 1977; Tiselius & Peterson, 1986), is well known, previous studies are mostly qualitative descriptions based on the relationship between abundance and temperature or salinity (i.e. scatterplot between abundance and temperature or salinity); the traditional protocol can only be used for addressing temperature or salinity range of zooplankton distribution. Usually the temperature and salinity at which zooplankton abundance peaks occur can be used to represent the optimal temperature and salinity of zooplankton. Quantitative analysis, especially in determining optimal temperature and salinity for marine organisms, is still a challenge because suitable mathematical models have not been found to present the relationship between abundance and temperature or salinity. Recently, we determined successfully the optimal temperature and salinity for four Appendicularia species using a reciprocal

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quadratic yield-density model based on survey data (Xu & Zhang, 2010). The yield-density model was selected because the function has an extreme value (i.e. peak value) in quadrant I (the positive quadrants of the ordinate axes), as required by the present study. In this study, we described temperature- or salinity-related distribution of chaetognaths in the East China Sea, and used the yield-density model to define the relationship between observed abundance and temperature or salinity (measured in psu) to determine the optimal temperature or salinity for major species in Chaetognatha. Ecological characteristics of the chaetognaths in the East China Sea were analysed qualitatively and quantitatively based on the models as well.

MATERIALS AND METHODS

Study area and sampling method

The data were collected in waters of 23°30′–33°00′N 118°30′–128°00′E in the East China Sea (Figure 1). Four surveys were conducted at 143 stations in the autumn of 1997 (from October to November), the spring of 1998 (from March to May), the summer of 1999 (from June to August), and the winter of 2000 (from January to February, except for the Taiwan Strait due to an incident). Because *Sagitta nagae* and *S. bedoti* are mainly distributed in nearshore waters (Xu & Chen, 2005), additional surveys at 28 stations were conducted in May, August, and November of 2002, and March of 2003 in waters of 29°00′–32°00′N 122°00′–123°30′E (Figure 1) to get a more complete distribution profile for the two species in the East China Sea. Bottom depths of the sampling sites are 40–200 m, mostly 50–100 m.

In total, 411 samples were collected during those surveys. For chaetognath sampling, standard plankton net with 80 cm diameter mouth and 505 µm mesh was hauled vertically from the bottom to the surface. The volume of water filtered was measured with a flowmeter mounted at the net mouth. The samples were immediately preserved in 5% buffered formalin. Surface temperature and salinity were recorded with SBE-19 CTD at every sampling site. Water stratification rarely occurs in the sampling area. Surface (10 m depth) temperature or salinity was used for modelling because zooplankton, including chaetognaths, is mainly present in surface waters in the East China Sea (Xu *et al.*, 1995, 2004). Chaetognath samples were brought to the laboratory and identified and enumerated using a stereomicroscope. Species identifications were determined according to the guide in Mitsuo & Masaaki (1997).

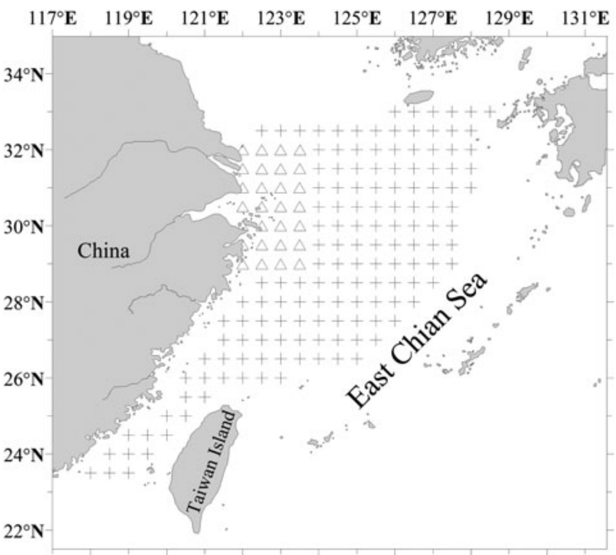

Fig. 1. Map of study location and sampling stations. +, stations for surveys during 1997–2000; △, stations for surveys in 2002 and 2003.

Modelling

Here we present abundance (*A*, simplified as abundance hereafter) as ind.m^{-3}. The relationship between chaetognath abundance and temperature or salinity was based on a yield-density model that was developed to account for yield-density relations in crops (Holliday, 1960). This reciprocal quadratic model is expressed as

$$A = \frac{1}{a + bx + cx^2} \quad (1)$$

where, *A* is abundance and *x* represents temperature or salinity. Parameters *a, b* and *c* are identified following the Marquardt method (Marquardt, 1963; SAS Institute, 1996), a method of non-linear regression analysis (curve fitting), using the observed abundance and temperature or salinity. The optimal temperature or salinity is the *x* value at which *A* is maximized. To maximize *A*, its derivative *A'* was determined from Equation 1:

$$A' = \frac{b + 2cx}{(a + bx + cx^2)^2} \quad (2)$$

According to Rolle's theorem, *A* reaches the maximum when $A' = 0$ (Silverman, 2003). When $A' = 0$, Equation 2 can be simplified as

$$x = -b(2c)^{-1} \quad (3)$$

Optimal temperature (or salinity) can be calculated from the function $x = -b(2c)^{-1}$ if *b* and *c* are known. For detailed calculations, principles and processes see Christensen (1996).

Definite integrals were used to evaluate abundance of individual species between optimum −1 and optimum +1 (AOP) of temperature or salinity and total abundance (TA) as follows:

$$A = \int_m^n \left(\frac{1}{a + bx + cx^2}\right) dx \quad (4)$$

where *A* is abundance, *m* is low limit and *n* is upper limit. For evaluating AOP, *m* and *n* are optimum −1 and optimum +1 of temperature or salinity, respectively. TA was calculated using the two ends of the distribution range of temperature or salinity as the lower and upper limits. AOP may reflect sensitivity of chaetognaths to temperature or salinity, hence we could identify their ecological characteristics with the relative abundance (A%) that refers to the percentage AOP of an individual species relative to total chaetognath abundance (A% = (AOP/TA) ×100).

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RESULTS

Seasonal and spatial distribution

Six major chaetognath species were identified in the East China Sea. Of the six species, *Sagitta enflata*, *S. nagae* and *S. bedoti*, the first three most dominant and frequent species, were distributed throughout the surveyed area, and *S. ferox*, *S. pacifica* and *S. pulchra* were sub-dominant species (Table 1; Figure 2).

Sagitta enflata, the most abundant and frequent species, presented the highest density in summer, followed by autumn, winter and spring (Table 1). In spring, it occurred in the entire study area. In summer, its greatest abundance occurred in nearshore waters (Figure 2).

Sagitta nagae was the second most abundant and frequent species (Table 1). It was distributed almost throughout the study area, and its highest mean abundance occurred in summer and winter. However, its highest regional density appeared in spring. It was more abundant in nearshore water in spring, summer and autumn than offshore water, but more in offshore water in winter (Figure 2).

Sagitta bedoti was the third most abundant and frequent species (Table 1). It was most frequent in autumn, and occurred at only a few stations in winter. In autumn, it was distributed almost throughout the study area. Generally, higher abundance was recorded in nearshore waters in summer and autumn rather than in offshore waters. However, abundance in some patches in offshore waters was similar to that in nearshore waters (Figure 2).

The remaining species, i.e. *Sagitta ferox*, *S. pacifica* and *S. pulchra*, had a patchy distribution in the study area, and mostly in offshore waters (Figure 2).

Temperature- and salinity-related distribution

Sagitta enflata occurred at temperatures of 11.8–28.6°C and salinities of 4.8 to 34.8 (Table 1). It co-occurred most strongly with temperatures of 18–27°C, and was most abundant at about 23°C (Figure 3). Its highest abundance occurred at salinities of 31–34 (Figure 4).

Sagitta nagae was recorded at temperatures of 7.8–28.4°C and salinities of 3.3–34.8 (Table 1). *Sagitta nagae* exhibited its highest abundance at a temperature of about 17°C (Figure 3). It was able to occur in a broad salinity range (Figure 4).

Sagitta bedoti occurred at temperatures of 9.9–28.6°C (Table 1), and was most abundant at 18.5–26.5°C (Figure 3). *Sagitta bedoti* inhabited water of the broadest salinity range (0.4–34.8), and was most abundant at salinities of 15–16 (Figure 4).

Sagitta ferox occurred at temperatures of 11.8–28.6°C (Table 1), and was most abundant at 19–20°C (Figure 3). It lived in water with salinities of 4.8–34.8, and was most abundant at 15–21 (Figure 4).

Sagitta pacifica occurred at temperatures of 17.1–28.6°C, and salinity ranges from 20.7–34.8 (Table 1). It preferred temperatures of 22.5–26°C (Figure 3). Its highest abundance appeared at salinities of 34–35 (Figure 4).

Sagitta pulchra was recorded at temperatures of 12.4–28.6°C, and salinities of 13.4–34.8 (Table 1). Its highest abundance occurred at a temperature of about 23°C (Figure 3) and 'bloomed' at a salinity of 31.5 (Figure 4).

Estimated optimal temperatures and salinities

The yield-density model well estimated optimal temperatures and salinities for all species (all $P < 0.05$, Table 2; Figures 3 & 4). All estimated optimal temperatures and salinities fall in the observed ranges. Optimal temperature for *Sagitta enflata* (24.9°C) and *S. pacifica* (24.5°C) was the highest. It was lowest for *S. nagae* (17.3°C), and intermediate for *S. bedoti* (20.3°C), *S. ferox* (22.5°C) and *S. pulchra* (23.2°C) (Table 2). Optimal salinity for *S. pacifica* (34.1) was the highest. It was lower than 20 for *S. bedoti* (13.8), *S. nagae* (14.1) and *S. ferox* (16.5), and intermediate for *S. enflata* (32.9) and *S. pulchra* (31.5) (Table 2).

Three distinct curve patterns were identified according to the estimated abundance between optimum −1 and optimum +1 of temperature/salinity. Wide, narrow and intermediate peaks are defined according to the relative abundance, each of ≤30, ≥70, and between 30 and 70. For example, for species with a narrow curve peak, such as *Sagitta pulchra*, 95.9% of the individuals are distributed at temperatures of optimum ±1.0°C (Figure 3); for species with a wide curve peak, such as *S. enflata*, only 18.9% of individuals occur at temperatures of optimum ±1.0°C (Figure 3). According to the models, 95.9%, 38.3%, 33.7%, 24.5%, 18.9% and 12.9% of the individuals of *S. pulchra*, *S. pacifica*, *S. bedoti*, *S. nagae*, *S. enflata* and *S. ferox* occur at a temperature range of peak value ±1.0, respectively (Table 3), and 93.1%, 77.2%, 38.9%, 16.0%, 9.6% and 8.6% of individuals of *S. pulchra*, *S. pacifica*, *S. enflata*, *S. ferox*, *S. nagae* and *S. bedoti* occur at a salinity range of optimum ±1.0, respectively (Table 4). If the number of individuals of a species that occur at

Table 1. Mean abundance (ind.m^{-3}) of chaetognath species, surface temperature (°C) and salinity in the East China Sea during four seasons, each sampled once during one cruise in March–May 1998 (spring), June–August 1999 (summer), October–November 1997 (autumn) and January–February 2000 (winter).

Species	Abundance (mean ± SE)				Temperature		Salinity	
	Spring	Summer	Autumn	Winter	Mean ± SE	Range	Mean ± SE	Range
Sagitta enflata	0.1 ± 0.02	1.7 ± 0.19	2.3 ± 0.18	0.6 ± 0.09	20.2 ± 0.2	11.8–28.6	19.8 ± 0.2	4.8–34.8
S. nagae	1.1 ± 0.02	0.6 ± 0.09	0.1 ± 0.02	1.4 ± 0.23	18.1 ± 0.2	7.8–28.4	19.0 ± 0.3	3.3–34.8
S. bedoti	0.1 ± 0.02	0.4 ± 0.07	2.6 ± 0.78	0.1 ± 0.03	19.2 ± 0.2	9.9–28.6	17.6 ± 0.3	0.4–34.8
S. ferox	0.0 ± 0.00	0.05 ± 0.01	0.1 ± 0.01	0.0 ± 0.00	22.2 ± 0.3	11.8–28.6	19.8 ± 0.4	4.8–34.8
S. pacifica	0.0 ± 0.00	0.03 ± 0.01	0.2 ± 0.04	0.0 ± 0.00	24.3 ± 0.2	17.1–28.6	27.8 ± 0.2	20.7–34.8
S. pulchra	0.0 ± 0.00	0.03 ± 0.01	0.2 ± 0.04	0.0 ± 0.00	24.0 ± 0.2	12.4–28.6	24.1 ± 0.2	13.4–34.8

SE, standard error.

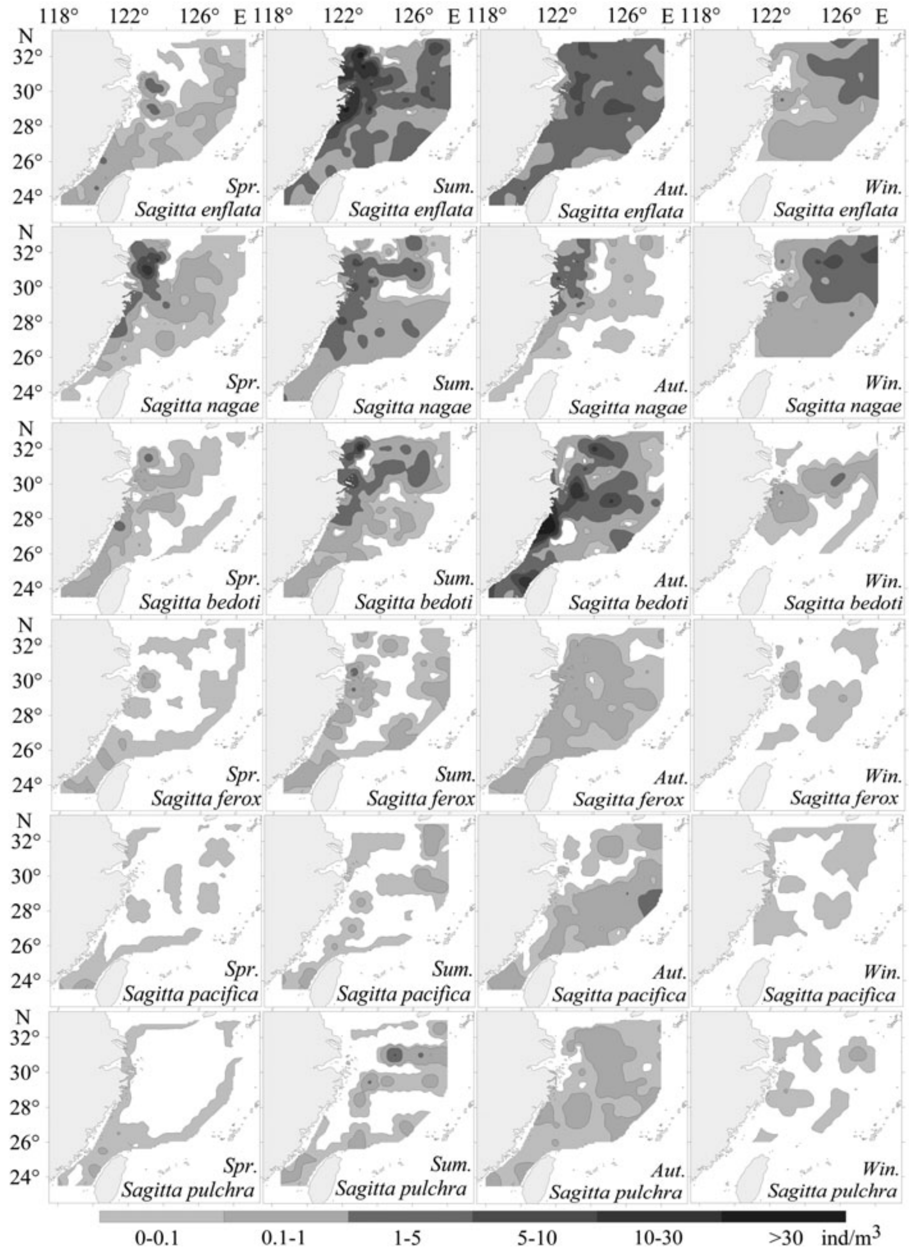

Fig. 2. Seasonal horizontal distribution of abundance of six Chaetognatha species in the East China Sea during four seasons, each sampled once during one cruise between 1997 and 2000. Note that surveys were not completed in winter in the Taiwan Strait.

temperatures of optimum $\pm 1.0^{\circ}$C is greater than that occurring at salinities of optimum ± 1, it means that temperature is more important to affect distribution of the species, and vice versa.

DISCUSSION

Traditionally, ecological characteristics of zooplankton are often determined by the relationship presented by using the data directly (i.e. scatter plots between abundance and temperature or salinity). However, it is not easy to describe the ecological characteristics precisely using this simple relationship (even if there may be a line fitting to the data), especially in determining optimal temperature and salinity for zooplankton, which only provides a range of temperatures or salinities. For example, species may be distributed in similar temperature- or salinity-ranges, however some species may aggregate at a narrow temperature- or salinity-range, and some species may be abundant in a wide temperature- or salinity-range. For the former, a range of optimal temperature or salinity is easy to identify, however it is hard to determine a range for the latter. In the present study, we resolve the problem with a yield-density model using six Chaetognatha species as cases. Previous studies have roughly recognized *Sagitta bedoti* and *S. enflata*, *S. ferox*, *S. pacifica* and *S. pulchra* as warm water species (e.g. Bieri, 1959; Terazaki, 1992), and *S. nagae* as a neritic species (Terazaki, 1992) or a mixed water (mixture of cold and warm water) species (Johnson *et al.*, 2006) based on most direct data of temperature and salinity related to their distributions, geographical distribution, and water masses inhabited. According to the

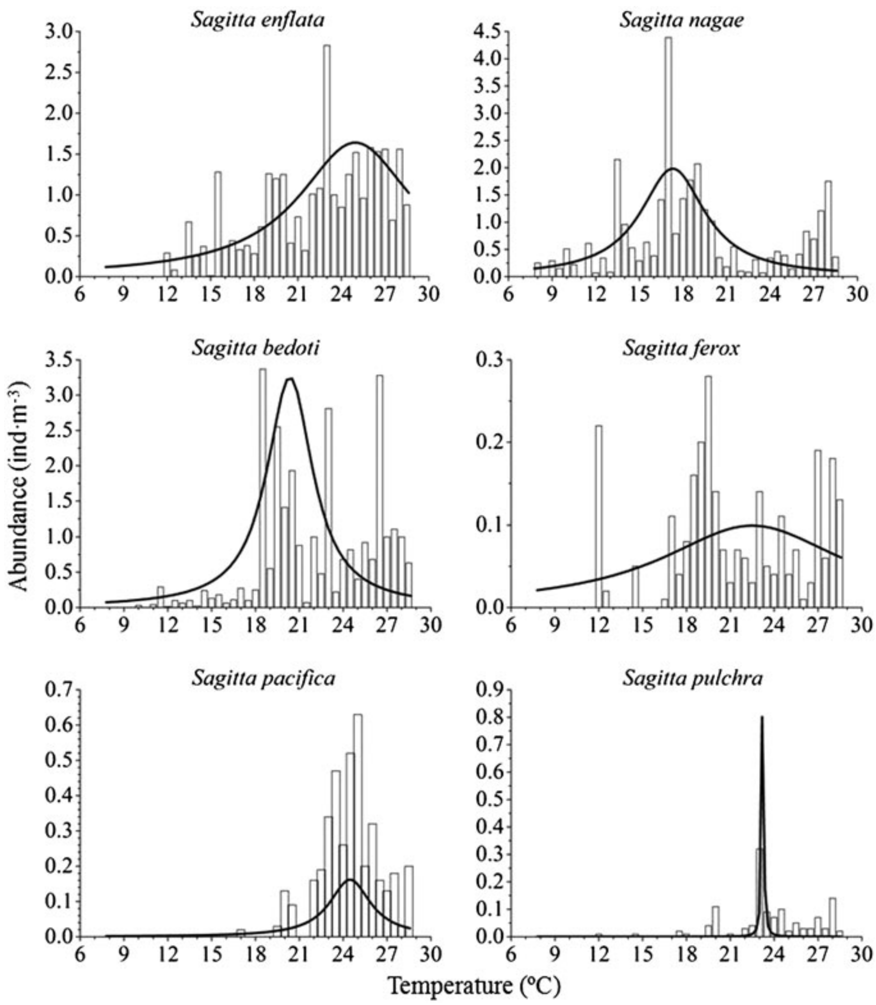

Fig. 3. Relationship between chaetognath abundance and sea surface temperature. The yield density model for each species is presented by the solid line.

present models, three ecological groups were evident in the East China Sea: the neritic, warm-temperate water species (*Sagitta nagae*); the neritic, warm water species (*S. pulchra*, *S. ferox* and *S. bedoti*); and the oceanic, warm water species (*S. enflata* and *S. pacifica*). Characterization of chaetognaths in the East China Sea agrees well with the observed data and the previous recognition, suggesting that the proposed model can be used to determine the relationship between abundance and temperature or salinity in chaetognaths. Although R^2 values are small (e.g. 0.01) for some cases, the low statistical correlations are still biologically meaningful with large number of data (Table 2).

Sagitta bedoti is recognized as a typical species of the Indo-Pacific warm neritic waters and is abundantly distributed in the Indo-Pacific (Bieri, 1959; Pierrot-Bults & Nair, 1991), such as in the western tropical Indian Ocean (Nair & Madhupratap, 1984), in a tidal creek of Sagar Island, Sunderbans, West Bengal (Sarkar *et al.*, 1985), in Bahía de Banderas, Mexico (Ruiz-Boijseauneau *et al.*, 2004), and in the Pearl River estuary, China (Li *et al.*, 2009). Estimated optimal temperature (20.3°C) and salinity (13.8) in combination with curve pattern (intermediate for temperature curve, and wide for salinity curve) for *S. bedoti* in the East China Sea suggest that the species supports the previous conclusion (Pierrot-Bults & Nair, 1997). *Sagitta bedoti* prefers lower salinity (optimal salinity of 13.8), and temperature seems more important than salinity to affect its distribution (Tables 3 & 4).

Sagitta enflata has been characterized as a warm-water species, or an oceanic or semi-neritic species (McLelland, 1989); globally it is distributed in waters worldwide between 45°N and 40°S (Bieri, 1959; Pierrot-Bults & Nair, 1997). Hence, it is also recognized as a eurythermal and euryhaline species due to its occurrence in environments with great temperature and salinity variations (e.g. Almeida Prado, 1961; McLelland, 1989). It has been found in both temperate waters, such as in the lower Chesapeake Bay, USA (Grant, 1977), the western North Atlantic (Pierrot-Bults, 1982; Cheney, 1985), and in the Bay of Fundy, Canada (Hurley *et al.*, 1983), and tropical waters, such as in the western tropical Indian Ocean (Nair & Madhupratap, 1984), in a tidal creek of Sagar Island, Sunderbans, West Bengal (Sarkar *et al.*, 1985), and in the Guanabara Bay, Brazil (Marazzo & Nogueira, 1996). Its distribution in the East China Sea mostly supports the previous recognition. Estimated optimal temperature (24.9°C) and salinity (32.9) for *S. enflata* indicate that it is an oceanic warm-water species, not a semi-neritic species as McLelland (1989) suggested. It might be brought into neritic environments occasionally by currents. Moreover, the curve pattern of the yield-density model for the species also

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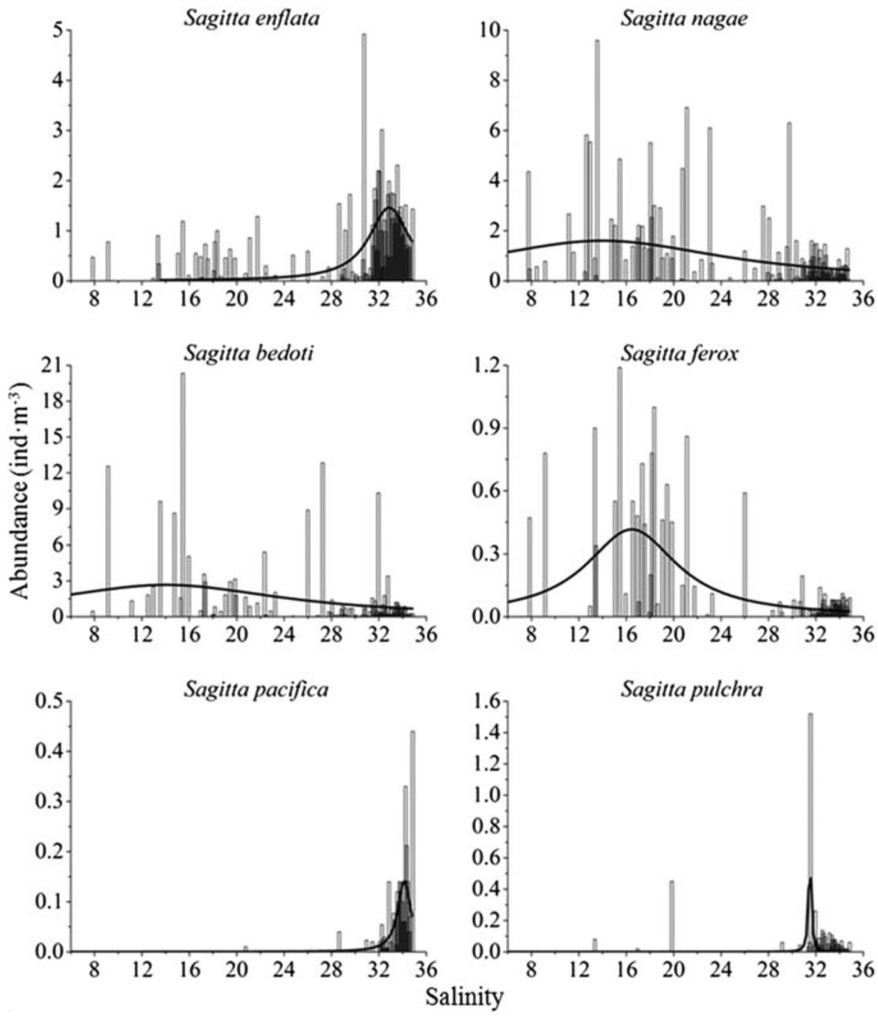

Fig. 4. Relationship between chaetognath abundance and sea surface salinity. The yield density model for each species is presented by the solid line.

implies that *S. enflata* is a eurythermal species (wide curve peak), however, it may not be a euryhaline species (intermediate curve peak).

Sagitta ferox is characterized as a species associated with warm-water masses (Bieri, 1959), such as in Toyama Bay, the southern Japan Sea (Terazaki, 1993), in the Celebes and Sulu Seas (Johnson *et al.*, 2006), and in the Pearl River estuary, China (Li *et al.*, 2009). Recognition resulting from the yield-density model (optimal temperature: 22.5°C, optimal salinity: 16.5; both temperature and salinity curves are wide) indicates that *S. ferox* is a semi-neritic warm-water species. Moreover, it is a eurythermal and euryhaline species.

Table 2. Yield-density models to present relationship between abundance (A) and temperature (t, °C) or salinity (s) and estimated optimal value for individual chaetognath species in the East China Sea, data collected during four seasons, each sampled once during one cruise in March–May 1998, June–August 1999, October–November 1997 and January–February 2000.

Species	Model	Optimum	R	F	*P*
Sagitta enflata	$A = 1/(17.3858 - 1.3450t + 0.026956t^2)$	24.9	0.33	33.57	0.0001
	$A = 1/(171.4408 - 10.3911s + 0.1581s^2)$	32.9	0.24	16.73	0.0001
S. nagae	$A = 1/(21.0138 - 2.3707t + 0.0685t^2)$	17.3	0.23	14.59	0.0001
	$A = 1/(1.1375 - 0.1073s + 0.0038s^2)$	14.1	0.28	24.13	0.0001
S. bedoti	$A = 1/(35.0803 - 3.4172t + 0.0840t^2)$	20.3	0.17	8.02	0.0004
	$A = 1/(0.8781 - 0.0717s + 0.0026s^2)$	13.8	0.11	3.43	0.0330
S. ferox	$A = 1/(97.6075 - 7.7831t + 0.17298t^2)$	22.5	0.13	4.35	0.0133
	$A = 1/(31.6002 - 3.5482s + 0.1078s^2)$	16.5	0.37	43.60	0.0001
S. pacifica	$A = 1/(1276.1473 - 103.7904t + 2.1206t^2)$	24.5	0.29	25.10	0.0001
	$A = 1/(18907.6709 - 1107.3626s + 16.2197s^2)$	34.1	0.26	19.64	0.0001
S. pulchra	$A = 1/(101487.1091 - 8741.2899t + 188.2280t^2)$	23.2	0.29	25.20	0.0001
	$A = 1/(85176.5784 - 5408.0182s + 85.8427s^2)$	31.5	0.23	14.60	0.0001

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Table 3. Estimated abundance (ind.m^{-3}) of chaetognath species in the East China Sea between optimum −1 and optimum +1 of temperature. See 'Materials and Methods' for detail about the evaluation process.

Species	TA	AOP	A%	Peak pattern
Sagitta enflata	17.17	3.24	18.9	Wide
S. nagae	14.94	3.80	24.5	Wide
S. bedoti	17.72	5.98	33.7	Intermediate
S. ferox	1.53	0.20	12.9	Wide
S. pacifica	0.77	0.29	38.3	Intermediate
S. pulchra	0.23	0.22	95.9	Narrow

TA, total abundance; AOP, abundance between optimum −1 and optimum +1; A%, (AOP/OA) ×100.

Table 4. Estimated abundance ((ind.m^{-3}) of chaetognath species in the East China Sea between optimum −1 and optimum +1 of salinity. See 'Materials and Methods' for detail about the evaluation process.

Species	TA	AOP	A%	Peak pattern
Sagitta enflata	7.01	2.73	38.9	Intermediate
S. nagae	53.88	5.16	9.6	Wide
S. bedoti	61.53	5.98	8.6	Wide
S. ferox	5.15	5.32	16.0	Wide
S. pacifica	0.23	0.18	77.2	Narrow
S. pulchra	0.28	0.26	93.1	Narrow

TA, overall abundance; AOP, abundance between optimum −1 and optimum +1; A%, (AOP/TA) ×100.

Sagitta pacifica is distributed in the Indo-Pacific from 40°N–40°S (Pierrot-Bults & Nair, 1997). It is reported mainly from equatorial waters (Bieri, 1959), such as in the western tropical Indian Ocean (Nair & Madhupratap, 1984), in Bahía de Banderas, Mexico (Ruiz-Boijseauneau *et al.*, 2004), and in Pearl River estuary, China (Li *et al.*, 2009). According to results of the yield-density model (optimal temperature: 24.5°C, optimal salinity: 34.1; intermediate temperature curve and narrow salinity curve), *S. pacifica* is an oceanic warm-water species. Salinity is more restrictive than temperature in distribution of the species.

Sagitta pulchra mainly occurs in equatorial waters (Bieri, 1959), such as in the western tropical Indian Ocean (Nair & Madhupratap, 1984), and in the Pearl River estuary, China (Li *et al.*, 2009). Results from the yield-density model (optimal temperature: 23.2°C, optimal salinity: 31.5; both temperature and salinity curves are narrow) suggest that *S. pulchra* is an oceanic warm-water species as recorded usually in the literature. This species is sensitive to fluctuations of both temperature and salinity.

Sagitta nagae is mainly present in neritic temperate waters of Japan (e.g. Terazaki, 1992) and China (e.g. Xu & Chen, 2005). Results from the yield-density model (optimal temperature: 17.3°C, optimal salinity: 14.1; both temperature and salinity curves are wide) suggest that *S. nagae* is a neritic temperate water species.

In the previous study, we used the yield-density model to estimate optimal temperature or salinity from abundance with four appendicularians (Xu & Zhang, 2010). In the present study, applicability of the model in determining optimal temperature or salinity of zooplankton was further validated. This study provides a simple and informative alternative method to characterize zooplankton quantitatively and qualitatively. However, the relationship may need to be remodelled for individual species in different geographical locations because optimal temperature or salinity for chaetognaths may be different at different physical and biological environments (Table 5). For example, the temperature at which peak abundance occurs for *Sagitta enflata* in temperate waters (15°C in the Chesapeake Bay, Grant, 1977; 19°C in the Japan Sea, Nagai *et al.*, 2006) is lower than that in tropical waters (30°C on south-west coast of India, George *et al.*, 1998) (Table 5).

Although copepod abundance has been recognized as a key factor influencing spatial and temporal distribution of

Table 5. Comparison between estimated optimal temperature (EOT) and salinity (EOS) in the East China Sea and published surface temperature (PST) and salinity (PSS), and published temperature and salinity range (PTR and PSR) associated with peak abundance for each species elsewhere.

Species	EOT (°C)	PST (°C)	PTR (°C)	EOS	PSS	PSR	Habitat	Reference
Sagitta enflata	24.9		22–28	32.9		30–34.8	TEW	This study
		15			23		TEW	Grant, 1977
		19	18–20		33.9	33.8–34	TEW	Nagai *et al.*, 2006
		23			31	30–32	TRW	Marazzo & Nogueira, 1996
		30	26–30		35		TRW	George *et al.*, 1998
		31					TRW	Ruiz-Boijseauneau *et al.*, 2004
S. nagae	17.3	14.1	17–20	14.1		13–30	TEW	This study
		15	15–18		34.2	33.9–34.4	TEW	Nagai *et al.*, 2006
S. bedoti	20.3		19–27	13.8		10–32	TEW	This study
		27	27–31				TRW	Ruiz-Boijseauneau *et al.*, 2004
		30.5	28–31.5			17–23	TRW	Bhunia and Choudhury, 1983
		30			35		TRW	George *et al.*, 1998
S. ferox	22.5	19–29		16.5		8–26	TEW	This study
		30			35		TRW	George *et al.*, 1998
S. pacifica	24.5		23–26	34.1		32–36	TEW	This study
		18	16–20		33.9	33.8–34.3	TEW	Nagai *et al.*, 2006
		31					TRW	Ruiz-Boijseauneau *et al.*, 2004
		30			35		TRW	George *et al.*, 1998
S. pulchra	23.2	23–24		31.5		31–32	TEW	This study
					31.3		TRW	Srinivasan, 1971

TEW, temperate waters; TRW, tropical waters.

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chaetognaths in some waters (Sun, 1989; Marazzo & Nogueira, 1996), it seems there is no close relationship between the distributions of copepods and chaetognaths in the East China Sea (Xu *et al.*, 2003). Additionally, patterns of spatial and temporal distribution of the six species are not consistent, suggesting that food may not affect significantly their distribution in the East China Sea. Therefore food might not be a factor causing bias models in the present study, i.e. salinity tolerance characterizes oceanic species, and temperature is important for general distribution. It would be interesting to determine the effect of food on the distribution of chaetognaths in the East China Sea and on the models.

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