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Determining optimal temperature and salinity of *Lucifer* (Dendrobranchiata: Sergestoidea: Luciferidae) based on field data from the East China Sea

ZHAO L. XU*

East China Sea Fisheries Research Institute, Chinese Academy of Fisheries Sciences, 300 Jungong Road, Shanghai 200090, P. R. China

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Abstract: Distribution patterns and abundance of the epiplanktonic shrimp *Lucifer* were examined in the East China Sea (23°30′–33°N, 118°30′–128°E), in relation to temperature and salinity. A total of 443 samples were collected from four seasonal surveys conducted between 1997 and 2000. The yield density model was used to predict optimal temperature (OT) and optimal salinity (OS) of four *Lucifer* species: *Lucifer typus*, *L. hanseni*, *L. intermedius* and *L. penicillifer*. Thereafter, their distribution patterns were determined. The results indicated that these species are the most abundant in summer. *Lucifer typus*, with OT of 28.0°C and OS of 33.8, is considered to be an oceanic tropic water species. The species is mainly found in the northern waters off Taiwan in summer and autumn. *Lucifer hanseni*, *L. intermedius* and *L. penicillifer*, with OTs of 26.4, 28.0, 27.4°C and OSs of 33.6, 33.4, 33.2, are off-shore subtropical water species. They are mainly distributed in the south off-shore the East China Sea and north of Taiwan.

Key words: East China Sea, *Lucifer*, optimal salinity, optimal temperature, zooplankton

Introduction

Temperature and salinity are the most important factors related to the distribution of marine zooplankton (e.g. Belehràdek 1935, Kinne 1963, Heinle 1969, Huntley & Lopez 1992). Populations of zooplankton reach their maxima at their respective optimal temperatures. Low temperatures can hinder maintenance or repair, while high temperatures can result in enzyme inactivation (Huey & Kingsolver 1980). Salinity is also a fundamental factor in determining the distribution of zooplankton by affecting osmoregulation. Therefore, estimates of the optimal temperature (OT) and optimal salinity (OS), and thermal and saline tolerance ranges of species might help us to understand the relationship between zooplankton abundance and hydrological conditions.

Lucifer Thompson 1829 is a single genus belonging to the family Luciferidae of the order Decapoda (Burkenroad 1981, 1983). Seven species of *Lucifer* are widely distributed in tropical and subtropical waters (Bowman 1967, Omori 1976). All the species occur in the western North Pacific except for the Atlantic species *L. faxoni* Borradaile (Hashizume & Omori 1998). *Lucifer* species are epiplanktonic and are important in the diet of some fishes (e.g. Bowman & McCain 1967, Huang & Fang 1987). Previous studies on *Lucifer* in the East China Sea (ECS) mainly focused on taxonomy (Zheng 1954, Tsai & Cheng 1965, Cai 1986). Less attention was paid to quantitative analyses of the population distributions (Chen et al. 1978, 1980, Meng et al. 1987, Bai 1990). According to Xu (2005a, b, c), *Lucifer* species were most abundant in summer and in the southern part of the ECS and inshore waters of the Taiwan Strait.

The OT and OS of zooplankton species have been measured mainly under laboratory conditions (e.g. Lyster 1965, Roddie et al. 1984, Uye 1988, 1990, Huntley & Lopez 1992, Cervetto et al. 1999). For certain technical reasons, not all marine species can be cultured in the laboratory. Thus, I attempted to estimate the OT and OS of *Lucifer* using statistical models with field data in the ECS, and reveal how the hydrological factors affected *Lucifer*'s distribution.

Materials and Methods

Sample collection and analysis

Figure 1 shows the study area. The samples were collected from the ECS (23°30′–33°00′N, 118°30′–

* Corresponding author: Zhao-li Xu; E-mail, xiaomin@sh163. net.cn

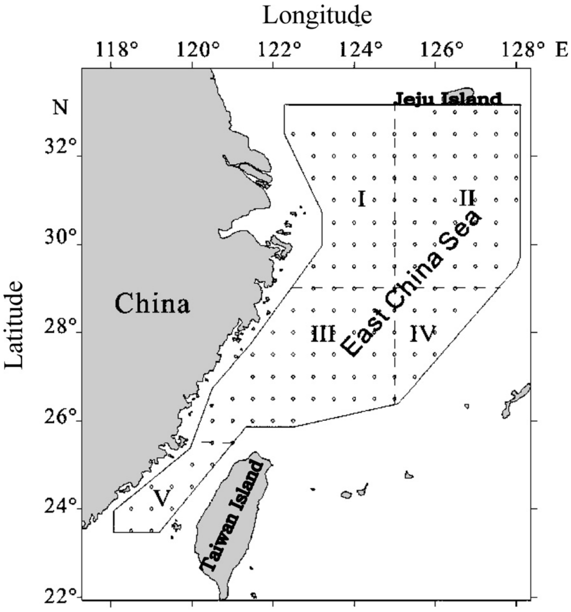

Fig. 1. Map of the study area. In the map, the dots indicate the location of sampling stations, which could be divided into five zones, zone I-north near-shore; zone II-north off-shore; zone III-south near-shore; zone IV-south off-shore and zone V-Taiwan Strait.

128°00′E). Four seasonal surveys were conducted separately in the spring of 1998 (from March to May), the summer of 1999 (from June to August), the autumn of 1997 (from October to November) and the winter of 2000 (from January to February). The study area was divided into 5 zones along 29°30′N, 25°30′N and 125°00′E, since their hydrographic conditions are clearly different from each other (Fishery Bureau of Ministry of Agriculture 1987). The five zones are zone I-north nearshore (29°30′–33°00′N, 122°30′–125°00′E), zone II-north off-shore (29°30′–33°00′N, 125°00′–128°00′E), zone III-south nearshore (25°30′–29°30′N, 120°30′–125°00′E), zone IV-south off-shore (25°30′–29°30′N, 125°00′–128°00′E) and zone V-the Taiwan Strait (23°30′–25°30′N, 118°00′–121°00′E) (Fig. 1).

A total of 443 samples, among them 128 samples in spring, 132 samples in summer, 110 samples in autumn, and 63 samples in winter, were collected during the surveys. Most of these samples were collected by vertical hauls with a standard large net (mouth diameter 80 cm, mesh size 0.505 mm) from the sea floor to the surface. In a few stations where water depth was more than 150 m, the net was towed vertically from 150 m depth to the surface. A flow-meter was mounted in the center of the net mouth to measure the volume of water filtered. The samples were immediately fixed and preserved in seawater with 5% buffered formalin. The surface water salinity and temperature were monitored using a CTD (SBE-19: Laurel Industrial Company) during each sampling session.

In the laboratory, the adult individuals of each *Lucifer* species were sorted, identified and counted with the aid of a stereomicroscope. Abundance units are in indiv. m^{-3}. Zone V was not sampled in winter for certain technical reasons.

Data analysis

The distributions of *Lucifer* species were determined by surface water temperature and surface water salinity, as *Lucifer* are mainly distributed in the surface water. In this paper, average distribution temperature (ADT) refers to the mean of surface water temperatures from all stations where *Lucifer* occurred. Average distribution salinity (ADS) was defined similarly to ADT. The optimal temperature (OT) and optimal salinity (OS) were calculated using the yield density model. The thermal range (TR) and salinity range (SR) were the ranges of temperature and salinity (max-min) respectively found in the habitat of each *Lucifer* species. The percentage of the abundance of a particular species compared to the total *Lucifer* abundance was indicated as the abundance percentage (AP).

The yield density model was first applied in an analysis of crop yield and density (Holliday 1960) and has been widely used since then (e.g. Hellis et al. 1999, Schabenberger & Pierce 2001). Here, this empirical model was employed to reveal the relationship between specific *Lucifer* abundance (y) and temperature or salinity (x). The model was expressed by the following equation:

$$y=\frac{1}{a+bx+cx^2} \tag{1}$$

The Marquardt method (Marquardt 1963, SAS Institute Inc. 1996) was used to estimate the parameters a, b and c in Eq. 1. From the point view of ecology, the OT or OS is defined as the x when y reaches a maximum in Eq.1. To acquire the maximum, Eq.1 should be taken as the origin of the following derivative equation:

$$y'=\frac{b+2cx}{\left(a+bx+cx^2\right)^2} \tag{2}$$

The x corresponding to the maximal point of y in Eq.1 is expressed as the x when $y'=0$ in Eq. 2. According to Roll's theorem (Ghosh & Haque 2004), Eq. 3 came from simplified Eq.2 when $y'=0$, that is:

$$x=-\frac{b}{2c} \tag{3}$$

Up to this point, the OT and OS can be calculated from Eq. 3 when b and c can be estimated by the Marquardt method. For a detailed treatment of calculations and process, see Christensen (1996).

According to the synchronous data, chlorophyll *a* at most of the sampling stations was $<0.5\,mg\,m^{-3}$ throughout the study period (Zheng et al. 2003). Temperature and salinity are the two main key factors left to affect *Lucifer* distribu-

Table 1. Seasonal average surface water temperature, thermal range, average surface water salinity and salinity range in different zones of the East China Sea.

			zone I	zone II	zone III	zone IV	zone V
surface water temperature (°C)	spring	average	14.9	16.9	21.3	21.4	24.2
		range	14.7–15.2	12.8–21.2	16.1–25.6	17.7–25.4	22.4–25.9
	summer	average	25.8	25.8	26.6	25.5	27.7
		range	23.0–27.0	21.3–28.6	24.3–28.0	23.9–27.5	26.6–28.4
	autumn	average	23.4	23.9	22.8	24.5	21.9
		range	22.2–24.5	22.7–24.9	20.0–25.7	23.3–25.5	19.4–23.2
	winter	average	14.2	17.4	18.4	19.9	–
		range	12.7–16.5	13.5–20.3	12.4–23.4	16.7–22.7	–
surface water salinity	spring	average	31.7	34.0	31.4	33.5	31.9
		range	29.1–33.2	32.0–34.8	27.9–34.0	32.4–34.4	30.7–32.7
	summer	average	29.6	32.5	33.5	33.5	33.7
		range	18.6–33.2	29.8–33.7	29.6–34.1	32.7–34.1	33.3–34.1
	autumn	average	32.4	33.5	33.8	34.1	33.7
		range	28.6–33.6	32.1–34.4	31.4–34.8	33.8–34.5	31.5–34.6
	winter	average	33.0	34.0	34.2	34.5	–
		range	31.8–34.5	32.0–34.7	32.3–34.6	34.4–34.7	–

Table 2. Adaptive distribution temperature (ADT), thermal range (TR), adaptive distribution salinity (ADS), and salinity range (SR) in habitats of *Lucifer* species in the East China Sea.

Species	seasons	N*	surface water temperature (°C)		surface water salinity	
			ADT±SD	TR	ADS±SD	SR
Lucifer intermedius	spring	54	20.7±3.1	14.0–26.3	32.6±1.6	28.7–34.7
	summer	111	26.2±1.4	21.3–28.6	32.3±2.5	18.6–34.1
	autumn	98	23.3±1.2	19.4–25.7	33.5±1.0	28.6–34.8
	winter	30	17.7±2.9	12.7–22.7	34.0±0.9	32.0–34.7
	entire year	293	23.4±3.4	12.7–28.6	32.9±1.9	18.6–34.8
L. hanseni	spring	20	22.4±2.5	16.4–25.4	32.4±1.6	28.9–34.6
	summer	30	26.3±1.4	23.1–28.2	33.3±1.0	29.6–34.1
	autumn	0	–	–	–	–
	winter	17	18.7±3.1	12.7–22.7	34.2±0.7	32.3–34.7
	entire year	67	23.1±3.9	12.7–28.2	33.3±1.2	28.9–34.7
L. penicillifer	spring	8	22.1±2.3	18.1–25.2	32.3±1.3	30.4–34.2
	summer	46	26.8±1.2	23.1–28.6	33.4±0.7	31.2–34.1
	autumn	0	–	–	–	–
	winter	4	18.3±2.8	14.3–21.1	34.5±0.3	34.2–34.7
	entire year	58	25.3±3.1	14.3–28.6	33.2±1.0	30.4–34.7
L. typus	spring	14	22.6±3.0	17.6–25.9	33.1±1.1	31.0–34.6
	summer	23	26.6±1.2	24.1–28.0	33.4±1.0	30.9–34.1
	autumn	4	24.7±1.0	23.4–25.6	33.6±0.3	33.2–34.0
	winter	5	20.4±2.0	19.1–23.4	34.6±0.1	34.5–34.6
	entire year	46	24.7±2.9	17.6–28.0	33.4±1.0	30.9–34.6

Notes: N*, number of sample where the species of *Lucifer* occurred; *Lucifer chacei* only occurred twice, at 16.6 ºC, 30.5, and 22.7 ºC, 31.0.

tion in the sampling area.

Results

The investigations covered most of the area and four seasons of the ECS. The surface water temperature and salinity ranged from 9.2° to 28.6°C and 18.6 to 34.9 respectively during the period. Hydrographic measures exhibited a seasonal pattern (Table 1). Average surface water temperature was the lowest in winter, and peaked in summer. Average surface water salinity was the highest in winter. The salinities in offshore waters (zones III, IV) were general higher than nearshore (zones I, II).

Five species of Lucifer were found in present study. However, as *L. chacei* Bowman, which is known to inhabit only coastal waters (Bowman 1967), has rarely been collected, it was not included in the present analysis. Among the remaining four species, the ADT of *L. penicillifer* Hansen (25.3°C) was the highest, followed by *L. typus* (H. Milne Edwards) (24.7°C), *L. intermedius* Hansen (23.4°C) and *L. hanseni* Nobili (23.1°C) (Table 2). These species were mainly found in summer when the surface water temperature was the highest in the year (Table 2). The TRs of *L. penicillifer* and *L. typus* were narrower compared with those of *L. hanseni* and *L. intermedius* (Table 2, Fig. 2).

As to the salinity adaptations of *Lucifer* species, ADS of *L. intermedius* (32.9) was lower than those of *L. typus* (33.4), *L. penicillifer* (33.2) and *L. hanseni*, (33.3), particularly in summer (Table 2). *Lucifer intermedium* and *L. hanseni* were distributed over a wider salinity range than *L. typus* and *L. penicillifer*. Particularly *L. intermedius* occurred in waters of any salinity within the ECS (Table 2, Fig. 2).

Although these *Lucifer* species can tolerate wide salinity

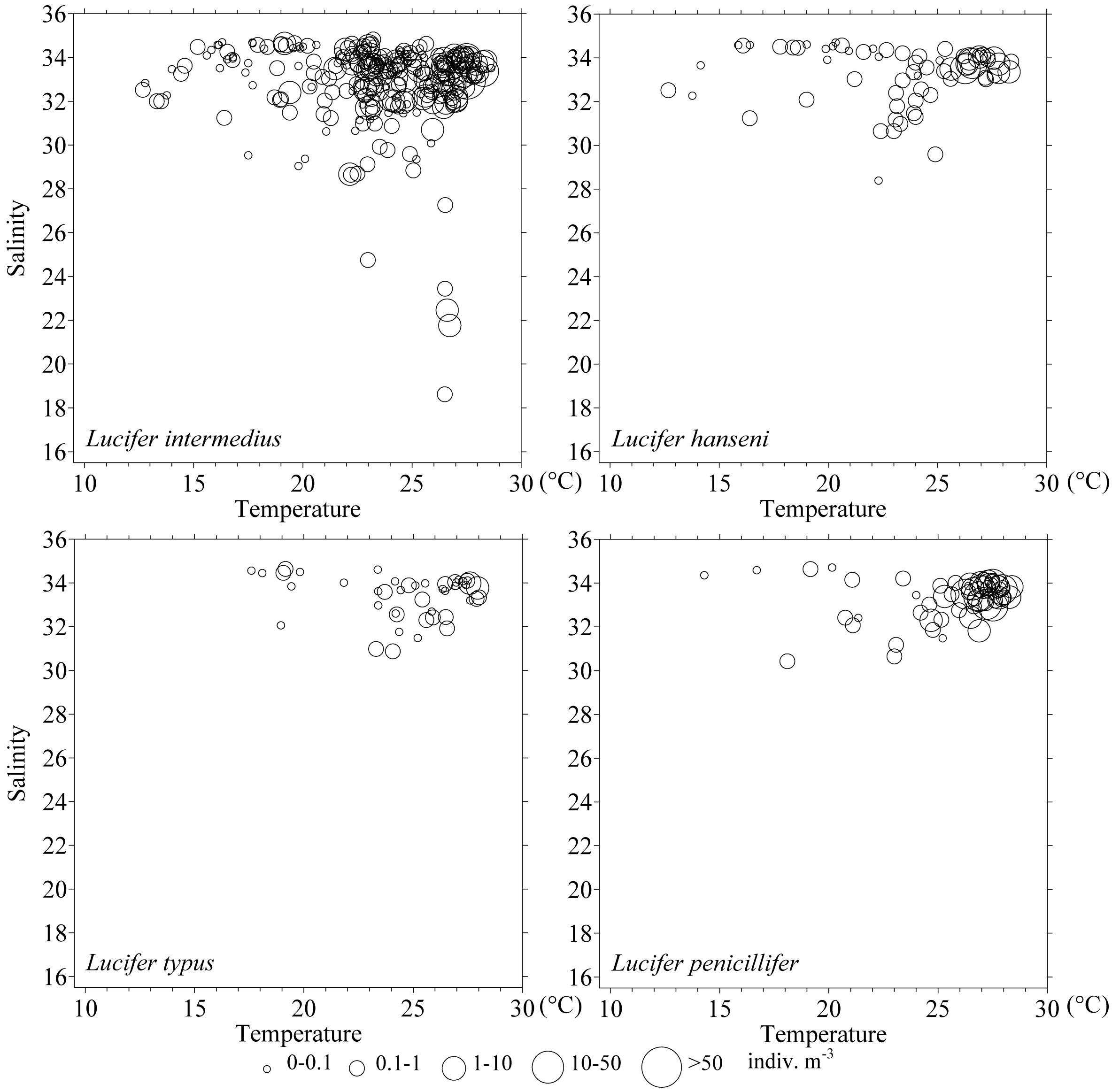

Fig. 2. Temperature and salinity conditions of the habitats of four species of *Lucifer* in the East China Sea.

and temperature ranges, they were mainly distributed in waters with high temperatures and high salinities (Fig. 2). For example, even though *L. penicillifer* occurred in waters with a temperature of 14.3°C; it was mainly distributed in waters warmer than 24.0°C (Fig. 2). Similarly, *L. typus* was collected at a salinity of 22.5, yet it was mainly found at salinities higher than 30.5 (Fig. 2).

The OT and OS values of four *Lucifer* species are shown in Table 3. The OTs of *L. penicillifer* and *L. typus* were highest (28.0°C), whereas only the OS of *L. typus* was the highest (33.8). *Lucifer typus* was mainly distributed in zone V during summer (Table 4). *Lucifer hanseni* was abundant in zone III. Both *L. intermedius* and *L. penicillifer* reached peak abundances in summer (Table 5). All the estimated OTs were in good accord with the field temperatures with the highest densities in the ECS (Fig. 2, Tables 3, 4).

The hyperhaline Taiwan Warm Current, strengthening northwards to zone III during summer, causes the high salinities in this zone, ranging from 33.5 to 34.0 (Zheng et al. 2003). High abundances of *Lucifer* species were located there, and the OSs of them were therefore thought to be reasonable. In short, the estimated OTs and OSs corresponded well with geographical distribution (Table 4) and seasonal abundance (Table 5) from the field data.

Lucifer intermedius, the predominant species, was widely distributed in the ECS all year round and was most abundant in summer. The remaining species, however, were mainly distributed in zones III, IV and V, which had high salinities, compared with zones I and II (Table 4).

In the graph showing the relationship between abundance and temperature or salinity, high abundance columns of *Lucifer* were usually limited to narrow intervals for both temperature and salinity. Within these intervals, peak abundances were specifically around a certain value. For example, the graphs for *L. intermedius* and *L. penicillifer* showed peak abundance near a temperature about 27°C and salinity about 33.3 (Fig. 3).

Table 3. Optimal temperature and optimal salinity.

species	optimum		*R*	*F*	*p*
Lucifer intermedius	*t*	27.4°C	0.33	25.64	0.0001
	S	33.2	0.17	6.17	0.0023
L. hanseni	*t*	26.4°C	0.31	22.99	0.0001
	S	33.6	0.20	9.06	0.0001
L. penicillifer	*t*	28.0°C	0.29	19.96	0.0001
	S	33.4	0.15	4.92	0.0077
L. typus	*t*	28.0°C	0.42	46.98	0.0001
	S	33.8	0.19	8.07	0.0004

Notes: *t* signifies surface water temperature (°C); *S* signifies surface water salinity in the equation, *R* is the goodness of fit of the model. *F* and *p* are the results of the *F*-test, which was used to analyze the statistical significance of the estimated parameters.

Table 4. Geographical distribution of *Lucifer* in the East China Sea.

Species	spring					summer					autumn					winter			
	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV
L. intermedius	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
L. hanseni		+	+	+	+	+		+	+	+						+	+	+	+
L. penicillifer			+	+	+	+	+	+	+	+							+	+	+
L. typus		+	+	+	+	+	+	+	+	+		+	+				+	+	
L. chacei			+		+														

Note: "+" means occurrence. I: the north near-shore, II: the north off-shore, III: the south near-shore, IV: the south off-shore, V: the Taiwan Strait.

Table 5. The average abundance of *Lucifer* in the East China Sea in different seasons.

Species	spring		summer		autumn		winter	
	y	AP	y	AP	y	AP	y	AP
L. intermedius	0.1372	67.94	2.4470	57.68	0.5885	99.47	0.0948	62.92
L. hanseni	0.0360	17.81	0.3711	8.75			0.0380	25.23
L. typus	0.0098	4.84	0.0558	1.32	0.0032	0.53	0.0074	4.90
L. penicillifer	0.0147	7.26	1.3688	32.26			0.0105	6.95
L. chacei	0.0044	2.16						

Note: *y* is the average abundance (indiv. m^{-3}) in a season; AP refers to the percentage of the abundance of a particular species compared to the total *Lucifer* abundance.

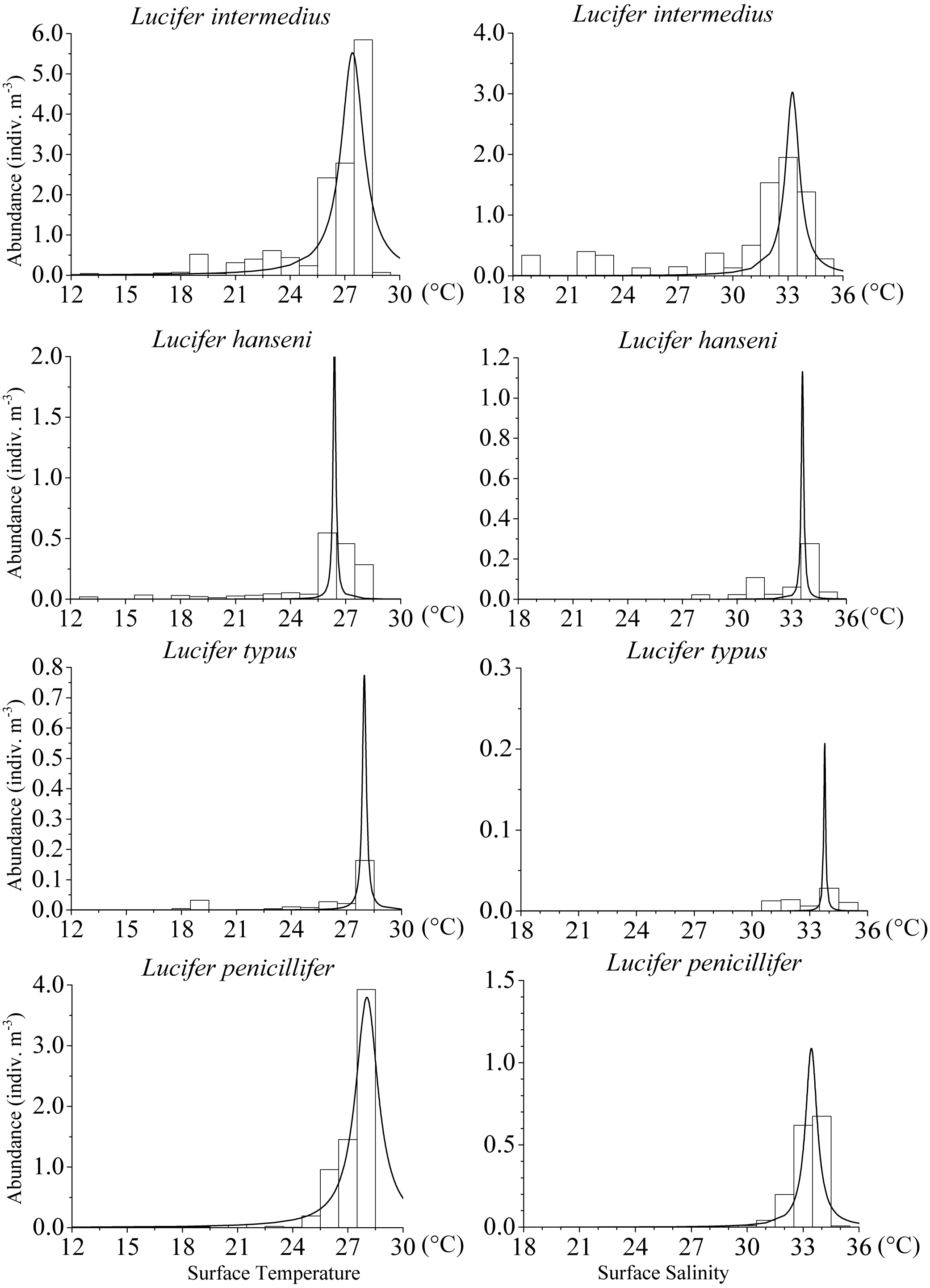

Fig. 3. Relationship between *Lucifer* species abundance and surface water temperature or salinity. The yield density model for each species is represented by the solid line.

Discussion

According to the principle of environmental biology, OT or OS should be the temperature or salinity at which populations can thrive and attain maximal abundance (Uye 1988, Lalli & Parsons 1997, Shen & Shi 2002). To ensure data authenticity, the sampled data need to include a wide range of temperatures and salinities from different seasons and zones (Hubert 2003). The data used in this study were collected from hundreds of stations all over the ECS in four seasons; a large scale area ranging from tropic to temperate water areas and from nearshore where coastal waters dominated to off-shore where warm currents dominated. The water temperature ranged from 9.2° to 28.6°C and the salinity from 18.6 to 34.9. The average surface water temperature was highest in summer and lowest in winter (Zheng et al. 2003). Spatially, the surface water temperature of zones III, IV and V was higher than that in zones I and II.

Based on the hydrographical features of the ECS, Shen & Shi (2002) divided marine species into the following ecological groups: subtropical species with an OT from 20° to 25°C and tropical species, with an OT over 25°C. However, with respect to the salinity adaptations, *Lucifer* species may also be divided into off-shore species with an OS from 32 to 34, and oceanic species with an OS over 34. Thus, in the ECS, the off-shore species are mainly distributed in mixed waters; whereas oceanic species are mainly distributed in the waters affected by warm currents, particular the Kuroshio Current.

Lucifer typus, *L. hanseni*, *L. intermedius*, and *L. penicillifer* are all eurytherms. This is because their TRs are all greater than 10°C (Table 2) and all these species are distributed widely from the Yellow Sea to the South China Sea (Huang 1994), the western Pacific Ocean (Hashizume & Omori 1998), and the Indian Ocean (Karuppasamy et al. 2006). As to salinity tolerances, *Lucifer* species, however, could be divided into two different ecological groups. *Lucifer typus* and *L. penicillifer* are considered stenohaline species (Table 2), whereas *L. intermedius* and *L. hanseni* are considered euryhaline (Table 2).

In conclusion, both *L. intermedius* and *L. penicillifer* are subtropical off-shore species with adaptation to high temperatures. They were abundant in zones II-IV, but rarely found in zone I (Table 4). Their highest abundances were mainly found in waters with high temperatures, particular in summer (Figs 2, 3, Table 5). *Lucifer hanseni* was abundant in zones III-IV, by high salinity and high temperature compared with zones I-II. In summer, the species was widely distributed from nearshore to offshore. Although it was also collected in the coastal waters, bays or estuaries (Lin et al. 1998, Tan et al. 2004, Zhou & Xu 2009), yet *L. hanseni* was most abundant in the south nearshore and south off-shore of the ECS in summer (Xu 2005c). Thus, the species was thought to be an off-shore subtropical species. *Lucifer typus* is considered to be an oceanic tropical species within the ECS. According to Xu (2005c), during summer its area of highest abundance lay south of 26°30′N, where the Kuroshio and Taiwan Warm Currents prevail. In winter and spring, this species was found in zone II where it was influenced profoundly by the Kuroshio Current and Tsushima Current (Su 2001). According to studies from the NW Pacific, the species is considered to be an oceanic species that is mainly distributed in waters influenced by the Kuroshio Current (Omori 1976, Ma & Song 1992, Hashizume & Omori 1998). *Lucifer typus* was also abundant in the tropical water of the Indian Ocean (Roger 1993, Karuppasamy et al. 2006).

By employing empirical models and field data, an attempt was made in this article to reveal the relationship between the OT or OS of *Lucifer* species and their distribution. Is only a pilot, and obviously further work is needed. For example, by analyzing the curves of empirical models, the eury- or steno-thermal adaptations of the species might also be determined. The analysis of OT or OS using field data, with a proper reification through laboratory work, will enrich our understanding of species-environment relationships.

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