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SEASONAL FEEDING HABITS, REPRODUCTION, AND DISTRIBUTION OF *HARPIOSQUILLA HARPAX* (STOMATOPODA: HARPIOSQUILLIDAE) IN THE BEIBU GULF, SOUTH CHINA SEA

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ABSTRACT

Harpiosquilla harpax, a mantis shrimp, serves an important role in both commercial fisheries and benthic food webs in tropical and subtropical marine areas. Yet its population biology and ecology remain poorly understood. In this study, seasonal, independent surveys were conducted in August 2010, November 2010, February 2011 and May 2011 in the Beibu Gulf (formerly the Gulf of Tonkin), South China Sea. It was observed that *H. harpax* dominated the Stomatopoda catch, accounting for more than 80% of the total mantis shrimp caught in the survey areas. Spatial-temporal patterns of *H. harpax* trophic ecology, reproduction, and distribution were examined. The carapace length (CL), body length (BL) and body weight (BW) were compared between the sexes and among seasons and sites. The weight-length relationships of females and males were identified and allometric growth patterns were observed. Study findings showed that sex ratios varied among seasons. Half of the female specimens had a BL of 202.5 mm by sexual maturity. Crustacean, Pisces, and Cephalopoda were the three major taxonomic groups in the stomach content of *H. harpax*. The dietary patterns of *H. harpax* were significantly different among seasons, but not between sexes or across sites. Its feeding intensity peaked in fall and declined to a minimum in winter. *H. harpax* spawned year-round, peaking in summer when the gonad somatic index and sea surface temperature (SST) were highest. *H. harpax* density was positively correlated with SST and negatively correlated with salinity and phytoplankton density, respectively. Seasonal and latitudinal factors were important in determining the distribution of *H. harpax*.

KEY WORDS: *Harpiosquilla harpax*, mantis shrimp, seasonal variations, sex ratio, spatial distribution

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INTRODUCTION

Harpiosquilla harpax (de Haan, 1844), a species off mantis shrimp, is wildly distributed from the Pearl River Estuary of the South China Sea to the Philippines and Singapore (Moosa, 2000; Huang et al., 2009). Notably, it serves an important role in local commercial fisheries (Lui, 2005), and it is one of the dominant species of mantis shrimp discovered in the northern continental shelf of the South China Sea (Huang and Zhang, 2009), while Harpiosquillidae has the largest individual sizes in Stomatopoda (Liu and Wang, 1998).

Early research on mantis shrimp has focused on zoological taxonomy and phylogenetics. Gravier (1930) observed stomatopod crustaceans around Nha-Trang waters, South China Sea, as early as the 1930s, while systematic research on stomatopod around Vietnamese waters including the Western Beibu Gulf started in the 1950s (Seréne, 1954). Two decades later, the Soviet-Vietnamese expedition reported 33 species of Stomatopoda from the Beibu Gulf, including *H. harpax* and five other new species (Blumstein, 1974). In 1998, another species of Harpiosquillidae, *H. sinensis*, was discovered in the Nansha Islands (Spratly Islands), South China Sea (Liu and Wang, 1998). Subsequently, Ahyong and Harling (2000) modified and reclassified mantis shrimp families and genera. Miller and Austin (2006) also used mitochondrial sequences to investigate the complete mitochondrial genome of *H. harpax*. More recently, Ahyong et al. (2008) published a catalog of the currently known 63 species of mantis shrimp in Taiwanese waters.

Scientists have revealed that mantis shrimp feeding habits are strongly influenced by their trophic apparatus and, thus, may be inferred as evidence of resource partitioning and niche differentiation (Caldwell and Dingle, 1976; Ayhong, 2001; Patek et al., 2013). Mantis shrimp raptorial appendages fantastically vary from spears to hammers across species (Ayhong, 2001; Patek et al., 2013). Accordingly, their two primary prey capture strategies diverge from spearing to smashing (Caldwell and Dingle, 1976). As spearing mantis shrimp, *H. harpax* has an elongated, spined, toothed raptorial apparatus that is well adapted for capturing fish (Dingle and Caldwell, 1978). The effects of salinity on feeding and survival of *Oratosquilla oratoria* (De Haan, 1844)

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in the larval pseudozoea period were studied by Liu et al. (2012). Seasonal diet variation also has been tracked for *O. oratoria* in the East China Sea and Yellow Sea (Xu et al., 1996a; Sheng et al., 2009). Furthermore, diet and biochemical compositions of *Squilla mantis* (Linnaeus, 1758) have been investigated in Tunisian waters (Mili et al., 2013). However, no similar research has been done for *H. harpax*.

Previous research on spearing mantis shrimp reproductive biology has been focused mainly on *O. oratoria*. Its ovarian development and basic characteristics of sperm production were observed microscopically from specimens collected along the East China Sea (Xu et al., 1996b). The annual histological changes in ovary (gonadosomatic index) and germ cell development of *O. oratoria* were also tracked in Tokyo Bay (Kodama et al., 2009) and coastal Dalian, Yellow Sea (Liu et al., 2013). Moreover, Kodama et al. (2004) studied the relationship between *O. oratoria* reproductive patterns and seasonal larval occurrence in Tokyo Bay, and Kodama et al. (2006) linked its reproductive patterns to stock abundance. Additionally, the male and female reproductive anatomies of *Squilla empusa* Say, 1818 have been described in detail using light and scanning electron microscopy (Wortham-Neal, 2002). A recent study revealed the life history of *S. mantis*, particularly the maturation development of ovary and sexual accessory glands (Vila et al., 2013). However, for Harpiosquilla, only three stages of gonad maturity of *Harpisquilla raphidea* (Fabricius, 1798) were recorded in a laboratory in Indonesia (Wardiatno and Mashar, 2010).

Former mantis shrimp studies have demonstrated that the spatial-temporal distribution varies by species, life cycle stage and environmental factors. For instance, Huang and Zhang (2009) reported the composition and distribution of mantis shrimp in the northern continental shelf of the South China Sea. The specific months that *O. oratorio* larval abundance peaks may serve as a key indicator of the following year's catch (Kawamura et al., 1997). The oxygen-deficient bottom water in October has been reported to be partially responsible for the absence of mantis shrimp larvae and juveniles in the region (Ohtomi et al., 2005). Changes in environmental conditions can also result in interannual variations in young-of-the-year juveniles abundance (Ohtomi et al., 2006). In relation to *Harpiosquilla*, the distribution of *H. raphidea* in the intertidal and subtidal areas have been compared (Wardiatno and Mashar, 2011). *H. harpax* also has been used as a biomonitor to trace metal contamination in sediment around Hong Kong waters (Ng et al., 2007).

The primary objectives of this research were to: 1) ascertain food composition of *H. harpax* in the tropical Beibu Gulf, as well as its feeding intensity seasonally; 2) assess the sex ratio, reproductive periods and gonadal development; and 3) explore the population demography, spatial-temporal distribution, and their related environmental factors.

MATERIALS AND METHODS

Field Collection

Samples of *H. harpax* were collected from fishery-independent, bottom-trawl surveys in the Beibu Gulf (formerly the Gulf of Tonkin), South China Sea (Fig. 1). The fishing vessel Beiyu 60011 was used seasonally in August 2010, November 2010, February 2011 and May 2011. A total of 31 stations located between 18°30′N, 107°15′E and 21°30′N, 109°15′E were sampled. According to preliminary investigations in the Beibu Gulf, *H. harpax* is distributed abundantly between depths of 20 to 50 m, especially around Weizhou Island and Xieyang Island. Therefore, in this study we divided the sampling locations into two parts. Fourteen stations (Stations 1 to 14) were stratified selected north to 20°30′N (north stations). The remaining stations (Stations 15 to 31) were determined using a pre-defined 30′ × 30′ (55,560 × 55,560 m) square grid (south stations). Daytime surveys were conducted using a trawler with a 514.5 kW main engine. A trawl net with a 32 m headline, 60 m net length, 200 mm mesh size in the mouth and 40 mm at the cod end was used throughout the sampling process. The trolling speed was about 3 knots (1.5 m/s). All fresh specimens captured were immediately frozen under −25°C in the fishing vessel and then transported to the laboratory for further analyses.

Laboratory Measurements and Examination

The body length (BL) of *H. harpax* samples, from the base of the rostrum to the anterior edge of the median notch of the telson, and the carapace length (CL), from the base of rostrum to the dorsal posterior edge of the carapace along the midline, were measured to the nearest 1 mm. The wet body weight (BW) and wet gutted weight (GW) were measured to the nearest 0.1 g using a G&G T500 electronic balance, and the gonad weight was measured to the nearest 0.01 g by using a G&G JJ500 electronic balance. Sex was determined macroscopically: males have penises (a pair of copulatory organs) located at the base of third pereiopods on the eighth thoracic segment, and females have a genital plate on the sixth thoracic segment sternite (Kubo et al., 1959). Sex stages were determined according to reference (Xu et al., 1996a).

All *H. harpax* stomachs were removed by opening the carapace with tweezers and immediately were frozen under −35°C. During the stomach content analyses, the prey was thawed and identified to the species level (where possible) with a binocular dissecting microscope, Zeiss Discovery V20. After thawing and surface water removal, the prey items were weighted to the nearest 0.001 g with a Shimadzu AUY220 electronic balance and enumerated in relation to the undigested parts.

Data Analysis

Relative abundance of prey taxa was calculated as the weight percentage to total stomach content. Seasonally, feeding intensity of *H. harpax* was assessed with the percentage of empty stomachs (vacuity index, VI), percentage of empty stomachs and repletion index (RI), defined as the ratio of stomach content weight to gutted weight (Morato et al., 2000; Figueiredo et al., 2005).

To assess the gonadal development and the relationship between reproduction and feeding habits, the female gonadosomatic index (*GSI*), the percentage of stomach content weight to GW was calculated (Htun-Han, 1978).

A logistic model was used to relate the female size with gonadal maturity of mantis shrimp (Kodama et al., 2009):

$$P_{\mathrm{m}} = \left(\frac{1}{1 + \mathrm{e}^{-r(\mathrm{BL} - \mathrm{BL}_{50})}} \right), \tag{1}$$

where P_{m} is the percentage of the matured samples, BL is the body length, BL_{50} is the size at which an individual has a 50% probability of being mature, and r is a coefficient that increases with the steepness of the curve.

The catch of each haul (C_{w} in kg) was standardized to 1 km^2:

$$C_{\mathrm{w}} = \frac{c_{\mathrm{w}}}{a}, \tag{2}$$

where C_{w} is the total catch of each haul, and a is the swept area, which can be calculated as (Zhan, 1995):

$$a = h \cdot x_1 \cdot \mathrm{Dis}, \tag{3}$$

where h is the length of the headline (32 m in this case), x_1 is the ratio of the effective trawling width to the headline (assuming 0.5 in this case), and Dis is the trawling distance:

$$\mathrm{Dis} = \frac{2\pi R}{360} \sqrt{(\mathrm{Lat}_1 - \mathrm{Lat}_2)^2 + (\mathrm{Long}_1 - \mathrm{Long}_2)^2 \cdot \cos^2\left(\frac{\pi \cdot (\mathrm{Lat}_1 + \mathrm{Lat}_2)}{180} \right)}, \tag{4}$$

where Lat_1 and Lat_2 are the latitudes of the beginning and ending locations, Long_1 and Long_2 are the longitudes of the beginning and ending locations,

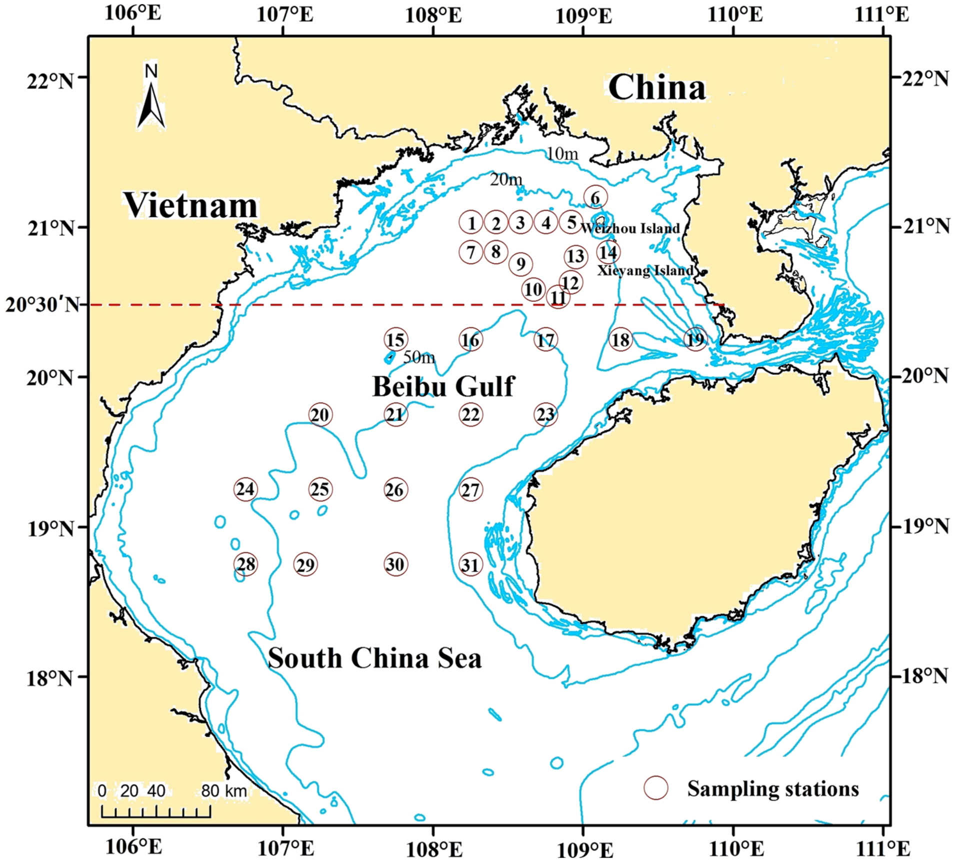

Fig. 1. Locations of *H. harpax* sampling stations in the Beibu Gulf (formerly the Gulf of Tonkin), South China Sea. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x.

and R is the mean radius of the earth (3443.9 nautical miles in this case). The resource density, D, was calculated as:

$$D = \frac{c_w}{x_2}, \quad (5)$$

where x_2 is the escaping rate (assumed 0.5 in this case).

ArcGIS 10.0 software was used to map the seasonal resource density of *H. harpax*, which was then compared the correlation to the corresponding seasonal sea surface temperatures (SST), salinity and average phytoplankton density. The synchronized environmental data were obtained from CATSAT fisheries GIS (Collecte Localisation Satellite, France).

The seasonal SST of the Beibu Gulf oscillated from 15.7 to 30.4, and the seasonal salinity fluctuated from 31.56 to 33.49. The seasonal phytoplankton density varied from 0 to 14.4 mg/m^3. The average seasonal SST decreased from 29.7°C in summer to 18.7°C in winter, and then increased to 24.9°C in spring. The average seasonal salinity increased from 32.11 in summer to 33.23 in winter, and then slightly increased to 33.28 in spring. The average seasonal phytoplankton density was lowest in summer (0.6 mg/m^3), increased to 1.7 mg/m^3 in fall, and then maximized to 2.0 mg/m^3 in winter.

Statistical Analysis

The sex ratio, as the female proportion of the total, was calculated for all seasons. Spatial and sexual variations of BL, CL, BW and GW were tested by the analysis of covariance (ANOVA) using factors: sex (♀ and ♂), sampling sites (“north stations” and “south stations”), and season (spring: March-May; summer: June-August; fall: September-November; winter: December-February) (Zar, 1999). Pearson correlation coefficients were used to test for relationships between the *H. harpax* density and environmental variables, i.e., SST, salinity and phytoplankton density. The percentage contribution of each dominant food category to the total stomach content by weight ($W\%$) (Hyslop, 1980) was compared to determine if the dietary pattern is significantly different between sexes and among sites or seasons. Analysis of similarity (ANOSIM) was applied, in which a similarity matrix was calculated using the Bray-Curtis distance (Bray and Curtis, 1957) and seriation was tested to detect the sequence change of dominant food categories in different sex, site, or season groups (Clarke, 1993). All statistical analyses were performed in R V3.1.1 (R Development Core Team, 2009).

Results

Sample Composition and Body Weight-Length Relationship

A total of 754 *H. harpax* individuals were caught during the surveys, including 426 females and 328 males (Table 1). The average BLs and CLs of females were larger than males in all seasons. Similarly, females had greater BW relative to males.

Based on the ANOVA results, sexual and seasonal differences were significant in CL ($p_{CL}^{sex} < 0.05$, $p_{CL}^{season} < 0.05$), BL ($p_{BL}^{sex} < 0.05$, $p_{BL}^{season} < 0.05$), and BW ($p_{BW}^{sex} < 0.05$, $p_{BW}^{season} < 0.05$); site difference was significant in CL ($p_{CL}^{site} < 0.05$) and BL ($p_{BL}^{site} < 0.05$), but not in BW ($p_{BW}^{site} = 0.0769$). In addition, the interaction effect was detected between sites and season for all CL ($p_{CL}^{site\cdot season} < 0.05$), BL ($p_{BL}^{site\cdot season} < 0.05$), and BW ($p_{BW}^{site\cdot season} < 0.05$), and between season and sex in BW ($p_{CL}^{sex\cdot season} < 0.05$).

Table 1. Sample number, carapace length (mean ± SD), body length (mean ± SD) and body weight (mean ± SD) of female and male *Harpiosquilla harpax* in the Beibu Gulf, South China Sea.

Survey date	Sex	No.	Carapace length (mm)		Body length (mm)		Body weight (g)	
			Range	Average	Range	Average	Range	Average
Aug. 2010	♀	165	31-56	44.5 ± 5.1	114-209	167.1 ± 18.7	12.8-82.9	39.2 ± 13.2
	♂	176	29-58	39.5 ± 3.6	110-205	146.6 ± 12.9	12.5-57.8	28.9 ± 8.1
Nov. 2010	♀	166	21-67	43.7 ± 9.2	78-221	156.7 ± 32.1	4.4-98.3	37.5 ± 19.4
	♂	83	22-49	38.2 ± 6.6	79-178	136.0 ± 23.1	4.7-50.6	24.6 ± 10.7
Feb. 2011	♀	24	22-61	39.5 ± 11.6	78-212	144.3 ± 41.8	4.1-73.5	31.6 ± 22.5
	♂	18	24-52	33.2 ± 8.0	81-192	125.1 ± 27.3	4.0-58.4	20 ± 3.1
May 2011	♀	71	25-57	44.5 ± 8.7	96-212	169.0 ± 32.2	7.0-84.5	48.7 ± 22.0
	♂	51	25-49	37.4 ± 6.2	100-197	140.8 ± 21.9	4.6-49.7	27.8 ± 13.1
Total	♀	426	21-67	43.9 ± 8.0	78-221	162.2 ± 29.1	4.1-98.3	39.4 ± 18.2
	♂	328	22-58	38.6 ± 5.3	79-205	141.8 ± 19.2	4.0-58.4	27.1 ± 10.1

The length-weight relationship was calculated separately for each sex:

$$\begin{cases} BW_{female} = 2.091 \cdot 10^{-5} \cdot BL^{2.823}, \\ BW_{male} = 5.199 \cdot 10^{-5} \cdot BL^{2.648}. \end{cases} \quad (6)$$

The exponent (b) of the weight-length relationship function indicates the growth pattern of the organism (Zhan, 1995). The b values for male and female *H. harpax* were both smaller and significantly different from 3 ($p_{isomatric,male} < 0.05$, and $p_{isomatric,female} < 0.05$), which indicate negative allometric growth patterns for both sexes.

Feeding Habits

Among the 754 sampled mantis shrimp individuals, 245 had non-empty stomachs. Feeding intensity varied across seasons (Fig. 2). RI increased from spring to fall, and then decreased in winter. It reached the highest in fall (0.85) and lowest in spring (0.38). VI reflected a similar pattern, in which it peaked in spring (80.43%) and reached a minimum in fall (37.5%), with a high annual average value of 57.3%.

Due to the feeding structures and pyloric stomach (Kunze, 1981) of this species, most prey items observed were broken down in their stomachs. Prey identification to species level could only be attained for seven prey species, while the rest were identified to family or genus level (Table 2). *H. harpax* dietary composition was mainly based on three major taxonomic groups (Crustacea, Pisces and Cephalopoda), while Pisces and Cephalopoda were the main food sources. Cannibalism was observed frequently in spring, with a high prey weight percentage of 57.41%. Food compositions were diverse in summer and fall but more similar in winter. In summer, *Uroteuthis duvaucelii* was the primary component among the identified species of the diet (20.91% of the whole prey weight). While in winter, unidentified Pisces comprised 43.01% of the total prey weight. Unidentified Pisces and *Uroteuthis* sp. were the main dietary components of mantis shrimp for both sexes. In general, *Uroteuthis* sp. and unidentified Pisces dominated in *H. harpax* prey throughout the whole gulf, but the dietary composition for the north was more diverse than that of the south. One-way ANOSIM results indicated that the dietary pattern of mantis shrimp were significantly different among seasons ($p^{season}_{Diet} < 0.05$), but not between sexes ($p^{sex}_{Diet} = 0.743$) or among sites ($p^{site}_{Diet} = 0.062$).

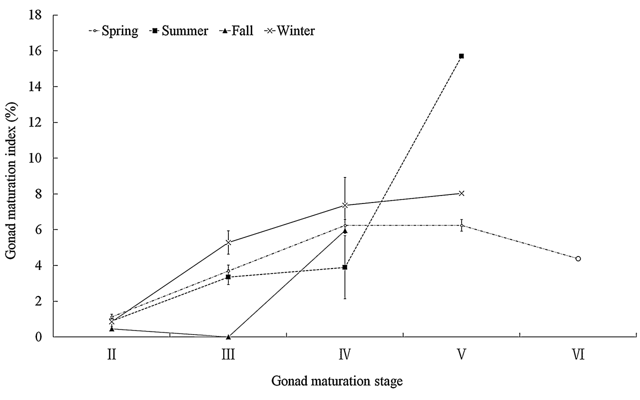

Fig. 2. Gonad maturation index versus gonad maturation stage for the *H. harpax* samples obtained during the survey.

Reproduction

Mature female *H. harpax* individuals were observed in all seasons in the Beibu Gulf. The female maturity, indicated by GSI, varied across maturation stages and among seasons. Summer had the highest GSI, so it can be deduced that fall is the main spawning season of *H. harpax* (Fig. 3). The BL_{50} was calculated to be 202.5 mm.

Sex ratios were calculated as: 0.48 (Aug. 2010), 0.65 (Nov. 2010), 0.54 (Feb. 2011) and 0.58 (May 2011), with an annual value of 0.56.

As for the maturity stages, it is difficult to directly classify males without histological slides. Accordingly, only the females were observed in this study. A total of 50% female *H. harpax* achieved at BL of 202.5 mm at sexual maturity. The smallest mature female captured was 132 mm in BL and 26 mm in CL, larger than those (CL 21.4 mm) found in Hong Kong waters (Lui, 2005).

Seasonal Distribution

The seasonal distributions of *H. harpax* are plotted in Fig. 4. For the north sites, the density was relatively high in summer (Fig. 4b) but low in winter (Fig. 4d). This indicates that *H. harpax* was mainly distributed in the northern part of the bay in summer and fall. In winter, it was more evenly distributed in the northern and southern bay. The average seasonal

Table 2. *H. harpax* food compositions (weight percentage) by season, sex and site (North stands for north of 20°30′N; South stands for south of 20°30′N) in the Beibu Gulf, South China Sea. + The ratio was <0.01%.

Prey category	Summer (Aug. 2010)	Fall (Nov. 2010)	Winter (Feb. 2011)	Spring (May 2011)	Male	Female	North	South
Pisces								
Apogon striatus	0.99				0.60	0.45	0.52	
Unidentified Pisces	28.37	27.29	43.01	17.11	33.37	25.09	27.67	21.94
Crustacea								
Acetes chinensis		0.25				0.14	0.10	
Liagore rubromaculata		1.13				0.66	0.50	
Unidentified shrimps		1.57	32.26		4.09		0.54	13.29
Unidentified crabs	1.04	6.87			0.75	3.72	3.04	
Unidentified mantis shrimps	0.83			57.41	0.60	4.86	3.86	
Echinoidea	7.54			4.57	7.33	3.44	4.75	
Bivalvia		2.85				1.66	1.26	
Gastropoda		+				+	+	
Cerithidea rhizophorarum	0.03					0.01	0.01	
Cephalopoda								
Uroteuthis duvaucelii	20.91	11.55			6.19	18.80	13.40	53.59
Uroteuthis chinensis	5.92	14.33			13.27	9.12	10.77	
Uroteuthis edulis	0.99	1.91			3.02	0.76	1.40	1.05
Uroteuthis sp.	31.10	29.45		5.32	30.42	26.7	29.10	
Sepia sp.		2.80	24.73			1.98	1.00	10.13
Totally unidentified	3.27			15.59	0.96	3.06	2.60	

densities were 13.34 kg/km^2, 209.83 kg/km^2, 33.12 kg/km^2 and 6.61 kg/km^2 from spring to winter, respectively. The density of *H. harpax* showed a positive relationship with the SST (Pearson correlation coefficient $r = 0.8187$). In contrast, *H. harpax* density had a negative relationship both with salinity (Pearson correlation coefficient $r = -0.8836$) and phytoplankton density (Pearson correlation coefficient $r = -0.6971$).

Discussion

Population Demography

In this study, we found that the average BL of female *H. harpax* was greater than that of the males despite seasonal variations. This result is consistent with that of *H. raphidea* in the vicinity of Sumatera Island (Wardiatno and Mashar, 2011). The maximum BL of *H. harpax* that we observed in the surveys was 221 mm, which was significantly smaller than the 234 mm specimens found in Indian waters (Antony

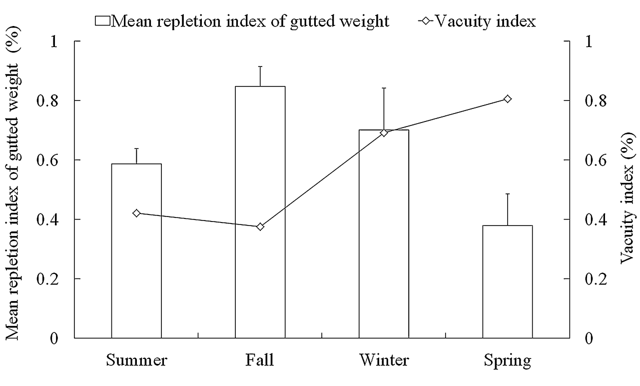

Fig. 3. Seasonal variation of the mean repletion index of gutted weight and the vacuity index in *H. harpax*.

et al., 2004) and 262 mm recorded in an Australian Museum specimen (Ahyong, 2001); *H. harpax* is typically smaller than *H. raphidea*; the maximum BL of the latter was recorded 335 mm in South China Sea (Moosa, 2000), 354 mm in Banten Bay waters, Indonesia (Mulyono et al., 2013), and 366 mm in Sumatera Island waters, Indonesia (Wardiatno and Mashar, 2011).

A similar weight-length relationship of *H. harpax* was reported in Parangipettai waters, India (Antony et al., 2004):

$$\begin{cases} \log \mathrm{BW} = -3.4826 + 2.3024 \log \cdot \mathrm{BL}, \\ \log \mathrm{BW} = -3.6479 + 2.3758 \log \cdot \mathrm{BL}, \end{cases} \quad (7)$$

where exponents were less than 3. The differences between parameter values might due to the large distance between the studied populations.

Ontogenetic and Seasonal Diet Shifts

Mantis shrimp is a common predator in regional shallow coastal waters. In this study, *H. harpax* consumed more Pisces and Cephalopoda in weight than other mantis shrimp species. Based on observations of feeding behavior in the laboratory, unlike *O. oratoria*, *Miyakea nepa* (Latreille, 1828), *Erogosquilla woodmasoni* (Kemp, 1911), and *Cloridopsis scorpio* (Latreille, 1828), *H. harpax* was capable of catching and consuming live fishes (Dingle and Caldwell, 1978). This behavior corresponds well with the relatively longer propodal spines in the raptorial appendages (second maxillipeds) and demonstrates that the tactic of prey capture was mainly spearing. Furthermore, the optic sensory structure and the length of antennules of *H. harpax* were much larger and longer than other mantis shrimp species (Dingle and Caldwell, 1978).

Present findings showed that the main foods of *H. harpax* in the Beibu Gulf were Crustacea, Pisces, and Cephalopoda,

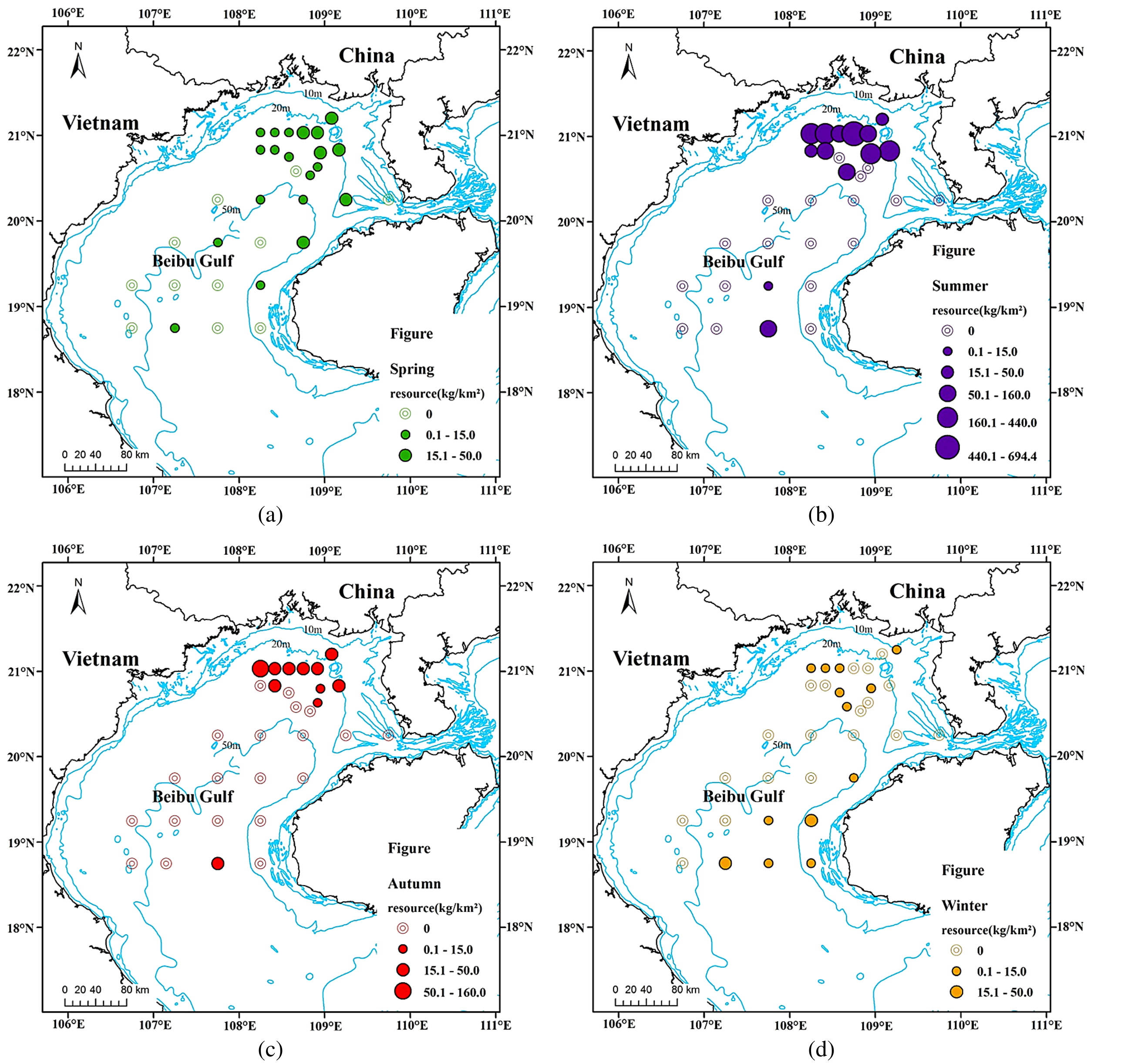

Fig. 4. The seasonal distributions of *H. harpax*: (a) Spring, (b) Summer, (c) Autumn, (d) Winter. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x.

but their weight percentages varied among seasons. Cephalopoda, mostly *U. duvaucelii* and *U. chinensis*, comprised almost 60% of the prey in summer and fall. Pisces, shrimp and cuttlefish *Sepia* sp. accounted for 43, 32 and 25%, respectively, in winter. Such variations can be potentially explained by the higher abundance of Cephalopoda in summer and fall, and higher abundance of Pisces in winter in the Beibu Gulf. The strong preference for these prey taxa reflects a balance among low handling time, high energy, nutritional values and digestibility content (Alcorlo et al., 2004). Cannibalism was relatively high in spring, with a prey percentage of 57.4%, but rather low in other seasons. This phenomenon was similar to *O. oratoria* in the Yellow Sea when there was insufficient food during winter (Sheng et al., 2009). *H. harpax* presumably exhibited opportunistic and omnivorous predatory strategies according to prey availability and abundance in the surrounding habitat.

H. harpax exhibited distinct feeding habits compared with other mantis shrimp species, supporting the existence of niche or resource partitioning among different species of Stomatopods in the same habitat (Lui, 2005). Feeding intensity was highest in fall, which is possibly because *H. harpax* needs to replenish its energy after the principal spawning season (summer). Fall is another main recruitment season of *H. harpax* in the Beibu Gulf. High energy foods are important to mantis shrimp during the reproductive periods as well as the high activity and growth periods (Alcorlo et al., 2004). The spring VI was high, with a value of more than 80%, reflecting that *H. harpax* can reduce its feeding activities and stay longer in burrows for mating and spawning.

Seasonal Variations of Reproduction

In this study, the spawning peaks of *H. harpax* can be identified according to the GSI. *H. harpax* spawned year-round across seasons but peaked in summer with the highest GSI. Such observations agreed with those of *H. harpax* in Hong Kong waters (Lui, 2005) and Pisces such as *Trichiurus margarites* and *T. lepturus* in the Beibu Gulf (Yan et al., 2011, 2012). During the summer, the mean SST in the Beibu Gulf reached its maximum 29.7°C, suggesting that the gonadal development of *H. harpax* is closely associated with temperature.

Study findings revealed that the sex ratio of *H. harpax* in the Beibu Gulf varied through the year. The number of females (166) was almost double the males (83) in fall, while typically less in summer (Table 1). Similarly, the sex ratio of *H. raphidea* reported in an Indonesian estuary was female-biased in November, which was an expected result from combatant behavior of the mature males (Wardiatno and Mashar, 2011). This seasonal variation of the female-biased sex ratio may be explained by the burrowing behavior during the reproductive periods. Typically, females spend more time within their burrows laying and brooding eggs until hatching thereby being less vulnerable to capture, while males have a higher mortality due to the cost of finding new burrows before breeding (Steger and Caldwell, 1983; Hamano and Matsuura, 1987; Lui, 2005). The higher sex ratio in fall may also result from different mortality rates between males and females after maturity (Rockett et al., 1984).

Changes of Spatial-Temporal Distribution

There were obvious aggregations and higher densities of *H. harpax* in summer and fall around the Weizhou Island (109°05′-109°13′E, 20°54′-21°05′N) in the Beibu Gulf, where the depth ranged from 21.5 to 44.5 m, with an average of 33.0 m. This was slightly deeper than those of the 18 mantis shrimp species previously reported in the East China Sea, which were generally found in waters less than 30 m (Mei, 1999). Most of the bottom areas around Weizhou Island are characterized as mud and muddy sands. The density of *H. harpax* was low in stone or sand gravel bottom. Similar habitat preferences have also been reported for *H. raphidea* and *H. harpax* as well as other mantis shrimp that inhabit mudflats at the mouth of the Tungkal River, Indonesia (Moosa, 2000; Wardiatno and Mashar, 2010).

Most stations with *H. harpax* surveyed year-round had depths less than 50 m, except for a few locations where this species was reported at depths of 60 to 80 m in winter. This is consistent with findings that *H. harpax* often has been recorded in much deeper waters (from 2 to 90 m) compared to other mantis shrimp species in the South China Sea (Moosa, 2000). Notably in winter, there was an apparent trend that the density in the southern gulf was significantly greater than that in the northern area, opposite to what we found in other seasons. It is possible that *H. harpax* migrate to southern, deeper and warmer waters during winter, or they remain in the burrows when water is too cold. As it has been observed that *H. harpax* has a life span of more than 16 months (Lui, 2005), we can deduce that these southern migrants may return to the northern part and prepare for mating and spawning in the next year.

Environmental factors changed with season and latitude, which were both important in determining species assemblages of Stomatopods (Wenner and Wenner, 1989). In this study, the negative relationships between *H. harpax* density and phytoplankton density and salinity, respectively, and positive correlations between density and SST were confirmed. Both the highest density and peak of spawning of *H. harpax* were found in summer, with the highest SST of the year. This is consistent with the hypotheses that higher abundance and biomass of *H. harpax* in summer are correlated with its peak reproductive periods (Lui, 2005) and the increased catchability are associated with burrow emergence (Atkinson et al., 1997). The resource density in winter was the lowest, when the minimum SST was found throughout the year. Such findings are different than those in the East China Sea, where the highest catch rate and biomass of the mantis shrimp were found in winter (Lu et al., 2013). Yet, the positive relationship between *H. harpax* density and SST agreed with the observations of *S. mantis* larval abundance (Vila et al., 2013). In addition, low levels of dissolved oxygen (Lui, 2005) and hydrographical differences especially hypoxia (Lui et al., 2007; Kodama et al., 2014) may also lead to spatial-temporal differences in biodiversity of benthic communities and in the early stage of mantis shrimp abundance.

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