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Areal and seasonal distribution of heteropods in the East China Sea

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Abstract: This paper studies heteropods in terms of species composition, distribution and abundance, and analyzes the dominant species' contribution to the total heteropod abundance in the East China Sea by step-wise regression and other ecological indices based on data collected from four oceanographic cruises in the East China Sea (23°30′–33°N, 118°30′–128°E) during 1997 to 2000. A comparison was made between results from the present study and that of the year 1959. Eleven species were found in the above mentioned four oceanographic cruises during the research - 9 in autumn, 7 in summer, 2 in spring and only 1 in winter. Four species, namely *Atlanta rosea*, *A. peroni*, *A. lesueuri* and *Protalanta souleyeti*, are defined as 'common species' based on the fact that they were found all over the East China Sea. Others are thereby considered 'rare species', namely *A. inclinata*, *Firoloida desmaresti*, *Atlanta* sp., *Oxygyrus keraudreni*, *A. turriculata*, *A. helcinoides* and *A. depressa*. The analysis of regression contribution shows that of all heteropod species, *A. rosea* is the most important one, whereas the importance of *A. peroni* and *A. lesueuri* is revealed in autumn. By comparing data from 1959 with that from the present sampling period, an increase in the number of heteropod species could be observed. Taking into consideration the close reliance of heteropods on warm currents, they might serve as an effective indicator of warm current intrusion into the East China Sea.

Key words: East China Sea, heteropods, species alternation, species composition, zooplankton

Introduction

Heteropoda is a group of holoplanktonic gastropods with a long larval cycle (Lalli & Gilmer 1989) that spend their lives mainly in oceanic surface waters. Due to the weak swimming ability of heteropods, their distribution is strongly affected by ocean currents. Thus, studies on the relationship between their distribution and the environment is of great interest in Heteropod ecology.

Early studies mainly focused on taxonomy, but recent papers deal more with the ecological distribution of heteropods, for example, Lozano & Hernannd (1991) reported the distribution of 8 heteropod species in the Canary Islands. In recent studies, the geographical distribution, faunal composition and variations in abundance have been focused on more frequently. Castellano & Suarez (2001) analyzed the distribution, composition, and abundance of this mollusk in neritic waters of the Caribbean Sea and the southern Gulf of Mexico; Newman (1990) investigated the heteropod fauna in the Great Barrier Reef; Cummings and Seapy (2003) studied the seasonal variation of heteropods from waters overlying San Pedro Basin. In the western Pacific Ocean, very few studies have focused on heteropods except for Tanaka's (1971) investigation on the geographical distribution. It has been found that heteropods were prominent in the diets of the lancet fish in Hawaiian and central equatorial Pacific waters (Moteki et al. 1993). In the East China Sea (ECS), based on an oceanographic census from 1958 to 1959, the taxonomy of heteropods (Zhang 1964) and ecological studies on them (Zhang 1966) were carried out. After the 1980s, research on heteropods in this area was mainly carried out by Dai (1995). However, her research interests concentrated on the pteropods and neglected the heteropods. Concerning the above studies as a whole, quantitative analyses have been almost entirely neglected.

With the data obtained in a mesoscale census in the ECS (23°30′–33°N, 118°30′–128°E) from 1997 to 2000, the horizontal distribution and dominant species of heteropods were discussed (Xu & Li 2005b). The present study focuses on species composition, species distribution, species number, seasonal alternation of heteropod fauna and contributions to the abundance of heteropods analysed by the method of step-wise regression.

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Materials and Methods

The surveys were carried out in the area 23°30′–33°00′N, 118°30′–128°00′E in the ECS. Four cruises 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 locations of the sampling stations are shown in Fig. 1. The study area was divided into 5 zones according to the previous work (Fishery Bureau of Ministry of Agriculture 1987): Zone I-north nearshore (29°30′–33°N, 122°30′–125°E), Zone II-north offshore (29°30′–33°N, 125°–128°E), Zone III-south nearshore (25°30′–29°30′N, 120°30′–125°E), Zone IV-south offshore (25°30′–29°30′N, 125°–128°E), Zone V-the Taiwan Strait (23°30′–25°30′N, 118°–121°E). The first four zones were delimitated along 29°30′N and 125°E. The offshore area of the East China Sea (Zone II, IV) was dominated by the Kuroshio Current and Tsushima Current (TC) while the nearshore area was mainly affected by the Taiwan Warm Current (TWC) in summer and autumn, then by the Changjiang Dilute Waters (CDW) and the Yellow Sea Continental Current (YSCC) together from autumn to spring (Fig. 2).

A total of 508 samples were collected in the surveys by a standard large net (diameter 80 cm, mesh size 0.505 mm) hauled vertically from the bottom to the surface. A flowmeter was set in the center of the net mouth to measure the volume of water filtered. Catches were then removed from the net and immediately preserved in 5% buffered seawater formalin. In the laboratory, enumeration and determination were performed strictly following the Specifications of Oceanographic Surveys (China State Bureau of Technical Supervision 1991) with the aid of a stereomicroscope. Abundance of heteropods was expressed as indiv. 100 m^{-3}.

The occurrence frequency (OFR) of a species refers to the percent of stations where the species occurred. The alternation fraction (R) was represented by the percent of different species among the whole between two seasons.

An index, contribution of dominant species to heteropod abundance (CHA), was used to describe the importance of a species. A stepwise multiple regression of the total abundance (the dependant variable) on the abundances (the independent variables) of individual dominant species was applied to define the regression contribution of the species to total heteropods. The species that had an obvious regression contribution to total abundance were selected by a t-test with a significant p-value. The standard regression coefficient β can be calculated by the regression formula (Christensen 1996). By removing the effect of magnitude, the standard regression coefficient β can measure CHA. Using this method, the effect on total abundance owing to each dominant species is clear.

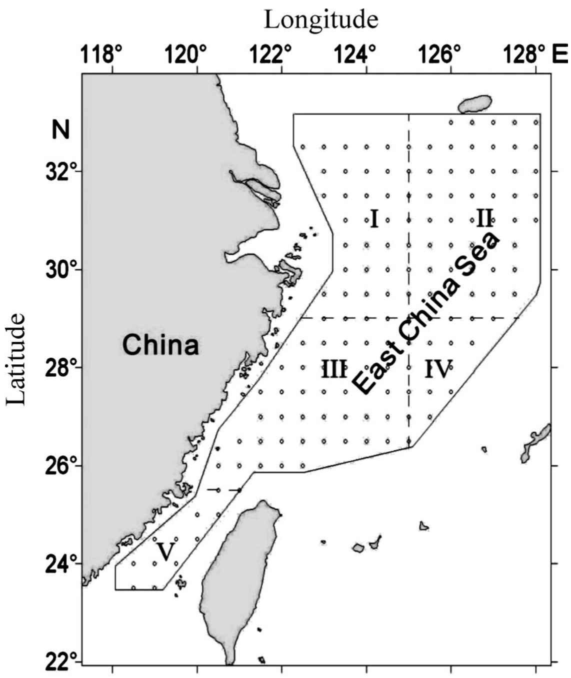

Fig. 1. Map of the study area. In the map, the dots indicate the location of sampling stations, which could be divided into five zones, zone I—north nearshore; zone II—north offshore; zone III—south nearshore; zone IV—south offshore and zone V—Taiwan Strait.

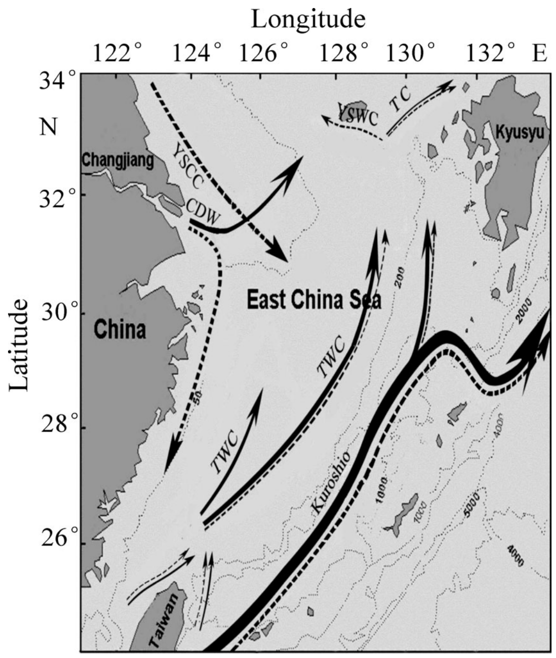

Fig. 2. Map showing the circulation patterns in the East China Sea. Dotted line indicates the currents during the winter monsoon; solid line indicates the currents during summer monsoon; YSCC indicates Yellow Sea Coast Current; YSWC indicates Yellow Sea Warm Current; CDW indicates Changjiang Dilute Waters; TWC indicates Taiwan Warm Current and TC indicates Tsushima Current (After Qv et al. 2005).

Results

A total of 11 heteropod species were identified in the ECS (Table 1), 9 in autumn, 7 in summer, 2 in spring, and only 1 in winter. Comparing species numbers among the different zones, the following order can be found: Zone II (9 species)>Zone III (7 species)>Zone IV (5 species)>Zone V (4 species)=Zone I (4 species).

Atlanta rosea was observed in all four seasons and *A. peroni*, was observed in three seasons. Three species, *A. lesueuri*, *A. turriculata* and *Protalanta souleyeti* were present in two seasons, and the remaining 6 species were present only in a single season.

Comparing the values of occurrence frequency (OFR), three species, *A. rosea*, *A. peroni* and *A. lesueuri* were had OFRs above 20%, of these, *A. rosea* mainly occurred in summer and autumn; with the two others occurring mainly in autumn. The remaining species exhibited low OFRs (Table 1).

Seasonal alternation of species composition was clearly evident, with values (R) of 77.8% in spring-summer, 54.5% in summer-autumn, 90.9% in autumn-winter and 50.0% in winter-spring.

Besides *A. rosea*, another three species *A. peroni* and *A. lesueuri*, *P. souleyeti* were observed in all zones (Table 2). However, *A. depressa* and *A. helcinoides* were observed only in two zones, and the remaining 5 species were only present in one zone (Table 2).

Atlanta rosea was mainly distributed in the south and offshore with a low abundance (Fig. 3) in spring and winter when the maximal abundance was only 10 indiv. $100\,m^{-3}$ at 26°00′N, 121°30′E. *Atlanta rosea* gradually attained a relatively high abundance in the Taiwan Strait and its adjacent waters with the increase in water temperature from spring to summer. The maximal abundance was 71 indiv. $100\,m^{-3}$ at 27°50′N, 121°30′E in summer. The area of abundance

Table 1. Heteropod species composition, occurrence frequency, salinity and temperature.

Species	Spring	Summer	Autumn	Winter	Salinity	Temperature
	OFR* (%)	OFR (%)	OFR (%)	OFR (%)	‰	°C
Atlanta depressa Souleyet			2.70		33.8	23.7
Atlanta helcinoides Souleyet			0.90		33.9	24.4
Atlanta inclinata Souleyet			0.90		33.7	23.1
Atlanta lesueuri Souleyet		1.37	36.04		32.0–35.0	21.5–28.6
Atlanta peroni Lesueur	0.76	8.90	39.64		32.0–35.0	19.4–28.6
Atlanta rosea Souleyet	9.16	29.45	23.42	7.69	31.0–35.0	16.7–27.7
Atlanta sp.		0.68			33.9	25.0
Atlanta turriculata (d'Orbigny)		1.37	0.90		33.6	24.0–26.7
Firoloida desmaresti Lesueur		0.68			33.6	27.3
Oxygyrus keraudreni (Lesueur)			0.90		33.7	24.0
Protalanta souleyeti (Smith)		0.68	0.90		32.8	23.7–24.8
Total number of species	2	7	9	1		

Note: * OFR is occurrence frequency.

Table 2. Occurrence of heteropods in different seasons and zones.

Species	Spring					Summer					Autumn					Winter			
	Zone					Zone					Zone					Zone			
	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV
Atlanta depressa												+	+						
Atlanta lesueuri						+	+				+	+	+	+	+				
Atlanta rosea		+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+
Atlanta peroni		+				+	+				+	+	+	+	+				
Atlanta sp.									+										
Atlanta turriculata							+					+							
Atlanta inclinata													+						
Atlanta helcinoides												+	+						
Oxygyrus keraudreni												+							
Firoloida desmaresti							+												
Protatlanta souleyeti						+	+				+	+	+	+	+				

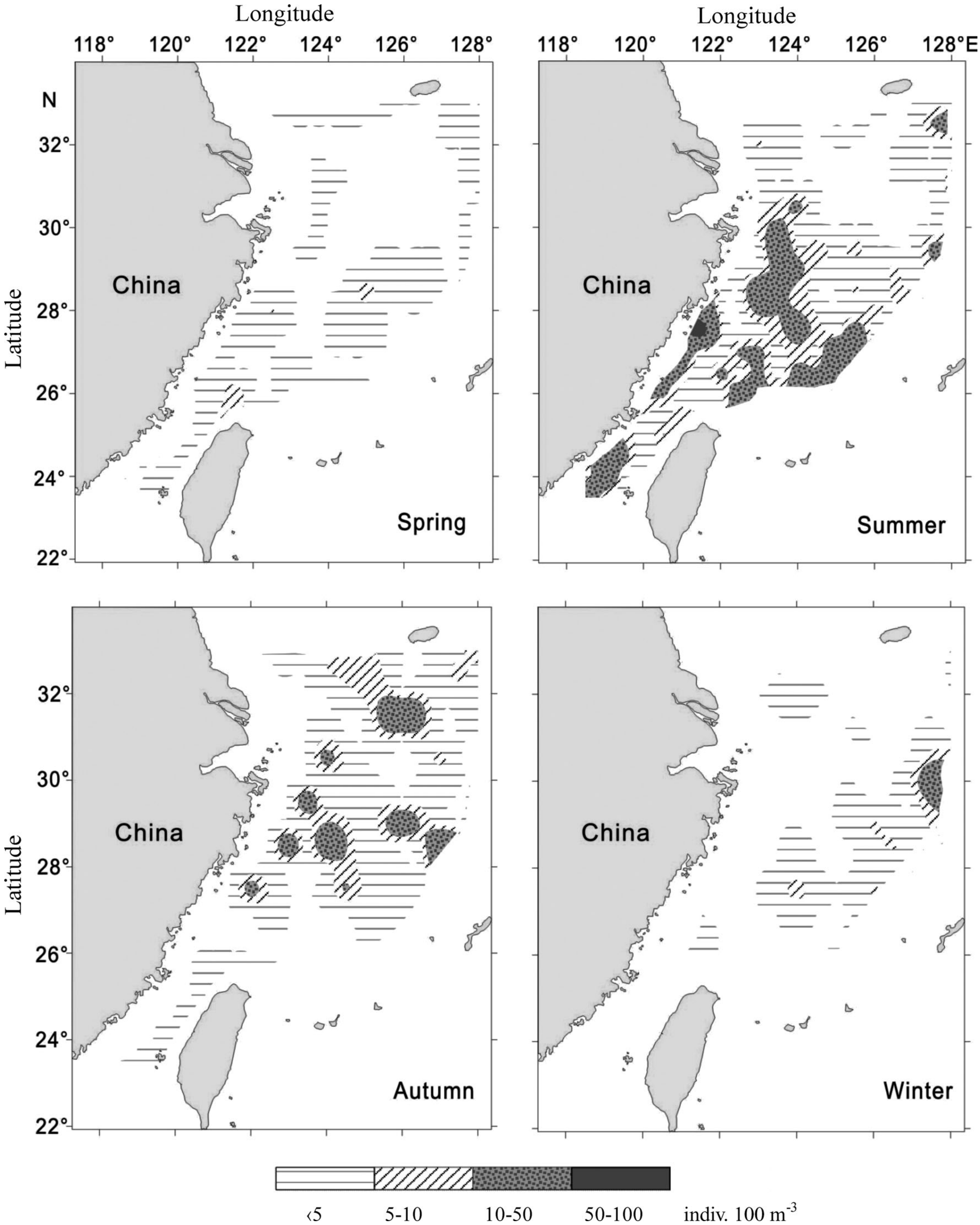

Fig. 3. Horizontal variation in abundance of *Atlanta rosea*.

(10–50 indiv. 100 m^{-3}) gradually shifted towards the north in autumn, with the highest density of 71 indiv. 100 m^{-3} being located at approximately 31°00′N, 126°00′E.

Atlanta peroni was present at one station in Zone II (31°30′N, 128°00′E) with a density of 3 indiv. 100 m^{-3} in spring, but none occurred in winter. In summer, *A. peroni* was collected from waters off the Changjiang Estuary of Zone I (123°30′E) and other waters in Zone II with a maximum abundance of 14 indiv. 100 m^{-3}. The high abundance areas in autumn were located in a similar position to in summer, but the population size was significantly larger (Fig. 4).

The distribution pattern of *A. lesueuri* was similar to *A. peroni*, but the population size was significantly lower than the former. In summer, the species occurred in the north at only two stations. However, in autumn the species was

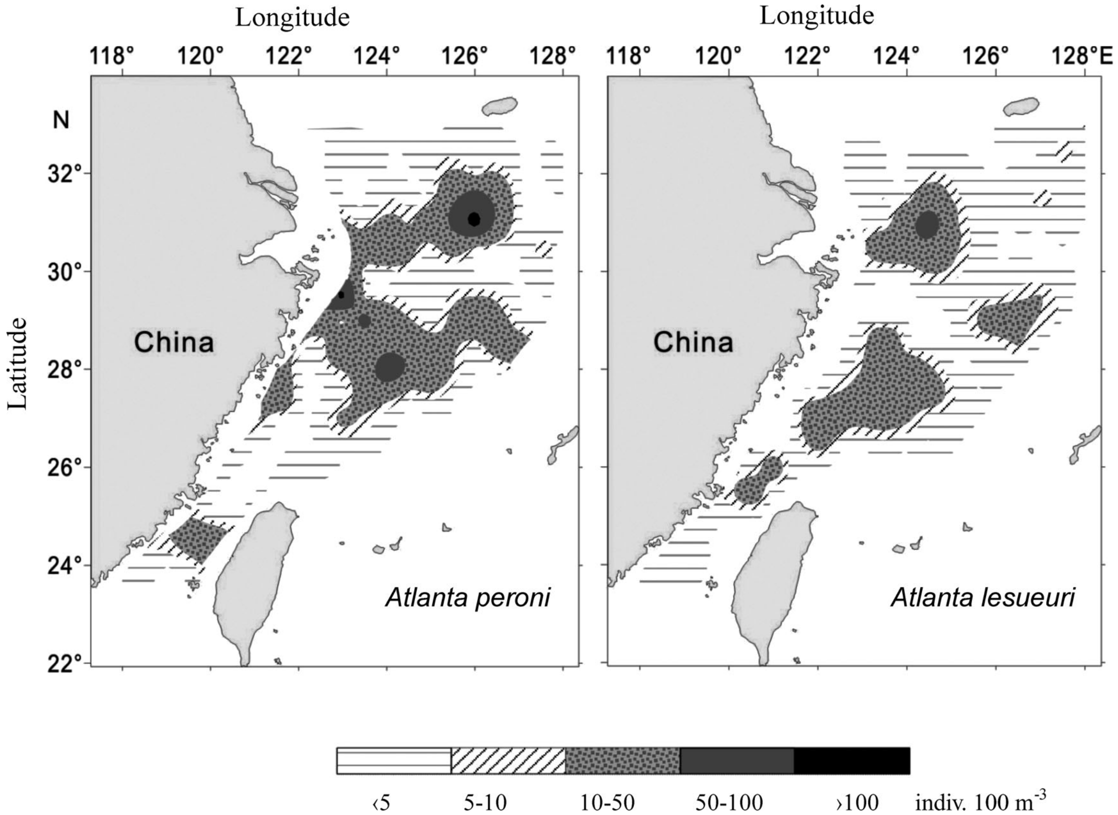

Fig. 4. Horizontal variation in abundance of *Atlanta peroni* and *A. lesueuri* in autumn.

widely distributed from Zones I to III with the highest density of 123 indiv. 100 m^{-3} at 31°00′N, 126°00′E (Fig. 4).

Apart from *A. rosea* and *A. peroni*, other species did not occur in the spring and winter. In summer, *Atlanta* sp. was collected at 29°00′N, 126°30′E in Zone II. *Atlanta turriculata*, *Firoloida desmaresti* and *P. souleyeti* were found at 31°30′N–33°30′N, 128°00′E in Zone II near Jeju Island. Compared with summer, the distribution areas of many species moved towards the south and nearshore waters in autumn. For example, *P. souleyeti* occurred at 31°30′N, 123°30′E in Zone II, *A. depressa* and *A. inclinata* at 28°00′N–29°00′N, 123°00′E–124°00′E in Zone III, *Oxygyrus keraudreni*, *A. turriculata* and *A. helcinoides* at 29°30′N, 126°00′E–127°00′E in Zone II (Fig. 5).

Atlanta rosea, *A. lesueuri* and *A. peroni* occurred at lower temperatures (16.7°C, 21.5°C and 19.4°C respectively) than other species which all occurred only in waters over 23°C. The salinity values for the water in which these species occurred was also higher than that for the three dominant species (Table 1).

Since only *A. rosea* occurred in winter, and its abundance represented nearly all heteropod abundance in spring and summer, the β values were 1.00 in winter, 0.99 in spring and 0.96 in summer. In autumn, *A. peroni* contributed to most of the heteropod abundance with a β value of 0.80 (Table 3).

Discussion

R values suggested a clear seasonal alternation of the heteropod fauna from spring to summer (77%) or autumn to winter (90%). The species number changed distinctly during these two alternate seasons (Table 1). The seasonal variation of species composition actually depended on species number increases and decreases rather than species replacement. This result is similar to our previous results from a study of Pteropoda in the same area (Xu 2005), but was distinctly different from that for euphausiids (Xu & Li 2005a). The phenomenon of seasonal succession of heteropods was closely related with seasonal changes in water temperature as well as with fluctuations of the warm currents.

Common species are usually defined by three factors: OFR, seasonal numbers, and zone numbers of occurrence. In this paper, a common species is defined as a species with an OFR above 20% or alternatively when it appeared in at least four zones or in all four seasons. According to this criterion, the four species, *Atlanta rosea*, *A. peroni*, *A. lesueuri* and *Protalanta souleyeti*, which appeared in five zones, were defined as "common species". The rest, *A. turriculata*, *Firoloida desmaresti*, *Atlanta* sp., *F. desmaresti*, *Oxygyrees keraudreni*, *A. turriculata* and *A. helcinoides* were "rare species".

Geographical distribution and occurrence of species in different environments in the ECS could be interpreted ac-

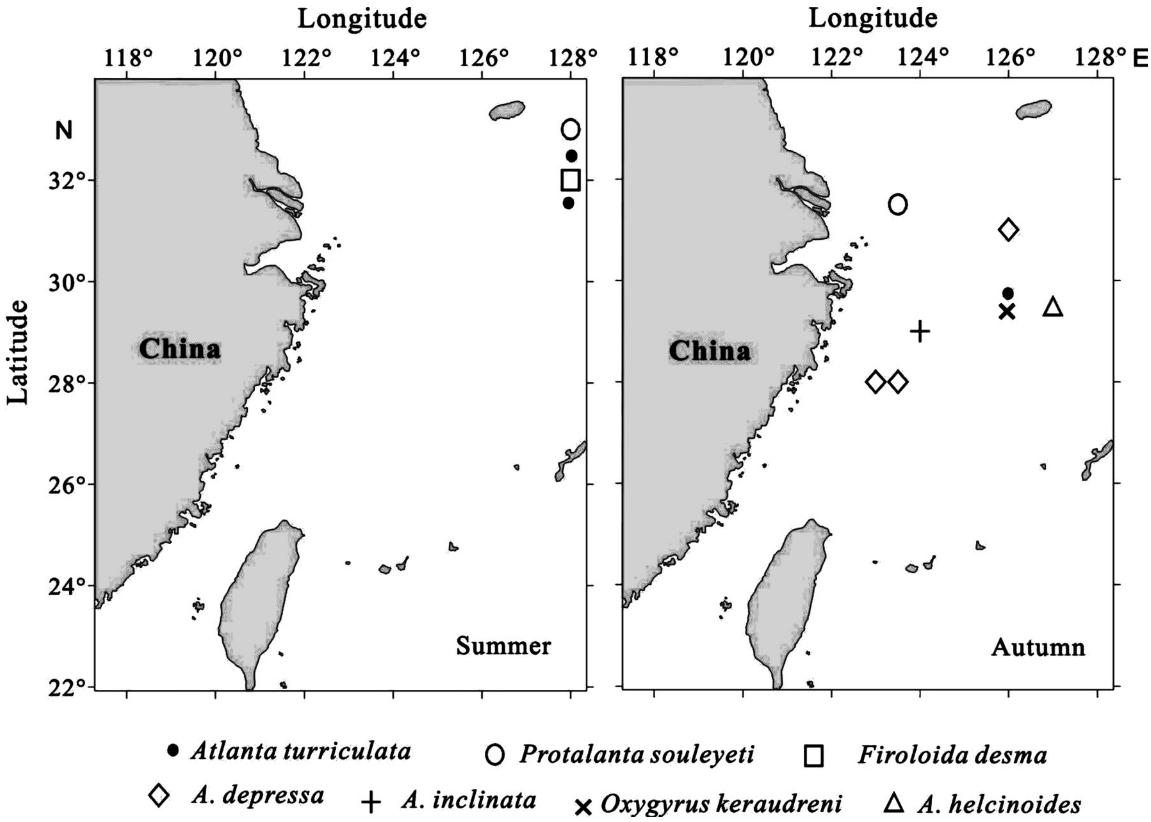

Fig. 5. Geographical distribution of heteropod species in autumn (not including *Atlanta rosea*, *A. peroni* or *A. lesueuri*).

Table 3. Contribution of dominant species to total abundance of heteropods.

Dominant species	Spring				Summer			
	Y	*β*	*t*	*p*	*Y*	*β*	*t*	*p*
Atlanta peroni					0.01	0.24	11.15	<0.001
Atlanta rosea	0.09	0.99	84.97	<0.001	0.24	0.96	44.42	<0.001
Dominant species	Spring				Summer			
	Y	*β*	*t*	*p*	*Y*	*β*	*t*	*p*
Atlanta peroni	0.20	0.80	41.22	<0.001				
Atlanta lesueuri	0.10	0.35	18.77	<0.001				
Atlanta rosea	0.03	0.20	10.47	<0.001	0.08	1.00	—	<0.001

Notes: *β*—standard regression coefficient, *Y*—dominance, *t*—*t* value, *p*—confidence

cording to the following (Figs. 3–5, Tables 1 & 2).

Atlanta rosea, the dominant "common species", was widely distributed all over the ECS in all four seasons. The area of its highest abundance varied according to seasonal shifting of TWC. Because of its extensive adaptability to lower temperatures e.g. 16.7°C, this species was the only species to occur in winter and the dominant species in spring and summer.

Atlanta peroni was distributed in Zone II in small numbers in spring. Between spring and autumn, its distribution area shifted from offshore to nearshore in accordance with a Kuroshio Current onshore intrusion along the shelf of the ECS (Chuang & Liang 1994). In nearshore areas, it maintained the largest population of all heteropods during autumn, showing that this species could live at temperatures as low as 19.4°C and possessed a greater ability to inrease its population numbers than *A. rosea* (Xu & Li 2005b).

Atlanta lesueuri, like *A. peroni*, occurred in Zone I and

Zone II in summer and flourished in autumn. However, its distribution range was smaller and abundance was lower than that of *A. peroni*. This may be due to a lower its adaptability to low temperatures than the above two dominant species (Table 1), indicated by the fact that it only inhabited waters where the temperature was 21.5°C–28.6°C, higher than that recorded for *A. peroni* and *A. rosea* habitats.

Protalanta souleyeti occurred in the same zones and seasons as *A. lesueuri*, but its abundance was lower than that of the latter. It was found that the OCR of *P. souleyeti* was the same as that of *A. lesueuri* in summer whereas it was much lower than the latter in autumn (Table 1). It has been shown that the temperatures at most of the sampling stations in the northern areas decreased down to 23.0°C in autumn (Zheng et al. 2003). Moreover, *P. souleyeti* could not survive at temperatures below 24.0°C (Table 1) so that low temperature was a limiting factor this species. The common species of heteropods in the area can be regarded as warm water species due to their occurrence in areas of high temperature and high salinity.

Most of the "rare species" existed offshore (Zone II and IV) in summer, for example, *A. turriculata*, *F. desmaresti* and *Atlanta* sp. More species, such as *O. keraudreni* and *A. helcinoides*, occurred in these zones in autumn (Fig. 4). Comparing the locations between the two seasons, the distribution range in autumn usually lay to the south-west of the summer regions. Some species, like *A. depressa* and *A. inclinata*, even entered Zone III. The shift in geographical distribution of rare species may be due to seasonal variation in the Kuroshio Current path. On the other hand, all "rare species" were typical warm water species as they inhabited a narrow range of high temperatures and salinities.

The regression results (Table 3) revealed that *A. rosea* dominated the heteropod community in winter, spring and summer, based on the dominance index, average abundance, and proportion of overall heteropod abundance (Xu & Li 2005b). In autumn, the heteropod assemblages were dominated by *A. peroni* and *A. lesueuri*, evident from by their high β values (Table 3). *Atlanta rosea* was the most important heteropod species while the importance of *A. peroni* and *A. lesueuri* increased in autumn.

Based on data from monthly surveys in 1959, Zhang (1966) described the geographical distribution of heteropods in the ECS at that time. In comparing the previous data with the present research, the maximum relative abundance of *Atlanta*, 15.2 indiv. $100\,m^{-3}$, occurred in September of 1959 whereas the maximum abundance was 21.3 indiv. $100\,m^{-3}$ in November in 1997. Furthermore, recently heteropod fauna have become more diverse than in 1959 in the same area. *Protalanta souleyeti* was found in the nearshore area in the present survey, though it has hitherto been thought to be an inhabitant of areas with high temperatures and salinities. In fact, the water temperature in the ECS has increased 1.2–1.5°C since 1959 (Cai et al. 2006). These phenomena may be related to global warming over several decades and suggest that distribution patterns of heteropod may be a good indicator of warming trends in the sea.

Heteropod distribution was significantly affected by temperature and salinity. The distribution patterns may also be due to species adaptability and the flow patterns of ocean currents. In the ESC, TWC primarily dominated the southern waters, while the Kuroshio Current influenced the offshore waters (Fig. 2), Most nearshore areas are affected during winter by the currents of the CDW and YSCC with low temperatures under the North-West Monsoon. Furthermore, heteropods are animals that are adapted to high water temperature and high salinity within the ECS, while CDW and YSCC have low water temperatures and salinities in winter. These two currents may cause heteropod density to decrease in this season. The force of the TWC expanded from south to north from summer to autumn (Fig. 2) under the South-east Monsoon. The warm current, constantly results in flourishing of several species in the north in autumn. However, with the decline of TWC after autumn (Fig. 2), it may have become harder and harder for hereropods to survive in Zone I. The TWC, CDW and YSCC were the main currents that affected the seasonal alternations in the heteropod fauna in nearshore area.

The species number was higher in the offshore rather than nearshore areas because the Kuroshio Current dominates there. Most of the "rare species", such as *A. turriculata*, *F. desmaresti*, *P. souleyeti*, *O. keraudreni*, *A. turriculata* and *A. helcinoides*, existed in Zone II, where the TC branches from the Kuroshio Current during the prevailing South-East Monsoon with its characteristically high water temperatures (Isobe 1999). It is inferred that the influence of the Kuroshio Current and the TC on heteropod distribution is such that their distribution is closely related with this ocean current. Their main area of high density are the same as those of other zooplankton such as Pteropoda (Xu & Li 2006), Chaetognatha (Xu et al. 2004a) and Copepoda (Xu et al. 2004b) in Zone II. It is suggested that heteropods are good warm current indicators in the ECS.

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