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研究论文集

A COLLECTION OF RESEARCH PAPAERS

(2005)

第一辑

2006年5月

目　　录

Horizontal distribution and dominant species of heteropods in the East China Sea

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Received 18 October 2004; accepted in principle 26 January 2005; accepted for publication 1 March 2005;

This article discusses the horizontal distribution and dominant species of heteropods in the East China Sea. The ecological characteristics of heteropods and their adaptability to the environments were also considered. Oceanographic census was carried out in the East China Sea (23°30′~33° N and 118°30′~128° E) in four seasons from 1997 to 2000. It was found that the total abundance showed obvious seasonal variations. It peaked in autumn with a mean value of 21.03 ind. 10^{-2} m^{-3}, followed by summer (4.89 ind. (100 $m^3)^{-1}$). The lowest abundance occurred in winter and spring. As to the horizontal distribution, abundance in summer and autumn was higher in nearshore than in the offshore of the East China Sea. In winter and spring, heteropods were barely found in the northern nearshore. Three dominant species were observed in four investigated seasons, in which only Atlanta rosea dominated in winter, spring and summer while Atlanta peroni and Atlanta lesueuri mainly dominated in autumn. These two dominant species observed in autumn exhibited a rather higher occurrence frequency than A. rosea. Temperature was found to be a major influencing factor whereas salinity was a minor one. Comparing their adaptability, A. rosea can survive in a wider temperature range (16~28°C), which enables it to dominate in four seasons, while A. peroni survives in a relatively narrow temperature range (19~28°CC) and the range for A. lesueuri was even more narrow (21~28°CC). Moreover, A. rosea was also adapted to a wider range of salinity. However, the abundance of A. rosea in autumn was lower than those of A. peroni and A. lesueuri. It can be thereby inferred that the multiplication speed of A. rosea was lower than the other two species within the same favorable temperature range. Due to their adaptability to high salinity, the distribution of heteropods was closely related to the domain of the Taiwan Warm Current and Kuroshio. Especially for A. peroni and A. lesueuri, their high abundance areas are always indicative of the lasting existence of strong warm currents. The negative values of aggregation indices indicated relatively even distribution of heteropods in the East China Sea. The high abundance area (31°00′ N, 126°00′ E) of heteropods in autumn is on the migration pathway of the mackerel (Scomber japonicus Houttuyn). Thus, there is also a fishing ground of the mackerel. This suggested that the high abundance area of heteropods in autumn is important to the fisheries in the East China Sea. Comparing with the historical records, the abundance of heteropods appeared to increase in the past 40 years. This may be a result of strengthened warm currents due to global warming.

INTRODUCTION

Heteropoda belong to Prosobranchia subclass, Gastropoda order. They mainly consist of pelagic species and thus their distribution patterns are closely associated with the strength of ocean warm currents and global warming. So they are indicator species of water masses. In addition, heteropods are good food for fishes.

Regarding the abundance and species number, heteropods are not the major taxon in pelagic zooplankton. Thereby, the ecology of heteropods was not largely

doi:10.1093/plankt/fbi014, available online at www.plankt.oupjournals.org

studied over the world. Thiriot-Quievreux (Thiriot-Quievreux, 1973) reviewed the coetaneous studied of the heteropods on their seasonal and geographical distribution, morphology, food and digestion, and development. Later on, taxonomy, abundance distribution or species composition of heteropods were widely studied in different waters (Richter, 1972; Newman, 1990; Michel and Michel, 1991; Hernandez *et al.*, 1993; Castellanos and Suarez-Morales, 2001). Concerning the western Pacific, studies of heteropods mainly focused on taxonomy and recent researches were scarcely found. The geographical distribution of heteropods in the western Pacific Ocean and in the Kuroshio waters was investigated (Okutani, 1966; Tanaka, 1971). As a diet of fishes, it was found that heteropods were the food for the pelagic shrimps in the central part of the Indian Ocean and also the lancet fish in Hawaiian and the central equatorial Pacific waters (Moteki *et al.*, 1993; Pakhomov *et al.*, 1993). In China, reports are even fewer. Based on an oceanographic census during 1958 and 1960, the taxonomy of heteropods in coastal areas of China (Zhang and Qi, 1961; Zhang, 1954, 1966) and a very simple ecology studies (Section of Planktology, 1977) were carried out. With the data obtained in 1970s, the vertical distribution of zooplankton was investigated, in which heteropods was also involved (Gao, 1990). In 1980s, the ecology of mollusks were studied in the central of the South China Sea and in Taiwan Strait (Dai, 1989, 1995; Huang *et al.*, 1989). However, their researches were mainly related to Pteropoda and very little to heteropods. In conclusion, there have been no complete reports of heteropods in large-scale water areas in the China Seas.

With the data obtained in a large-scale census in the East China Sea (23°30~33° N, 118°30′~128° E) from 1997 to 2000, abundance and geographic distribution of heteropods in the East China Sea were studied. This article only considers the first part, namely the abundance variation of heteropods. The abundance dynamics of heteropods were revealed by analyzing changes of dominant species and their relationship with environmental factors. In addition, through the analysis of their ecology, the scientific significance of heteropods were also approached as an indicator of warm water currents.

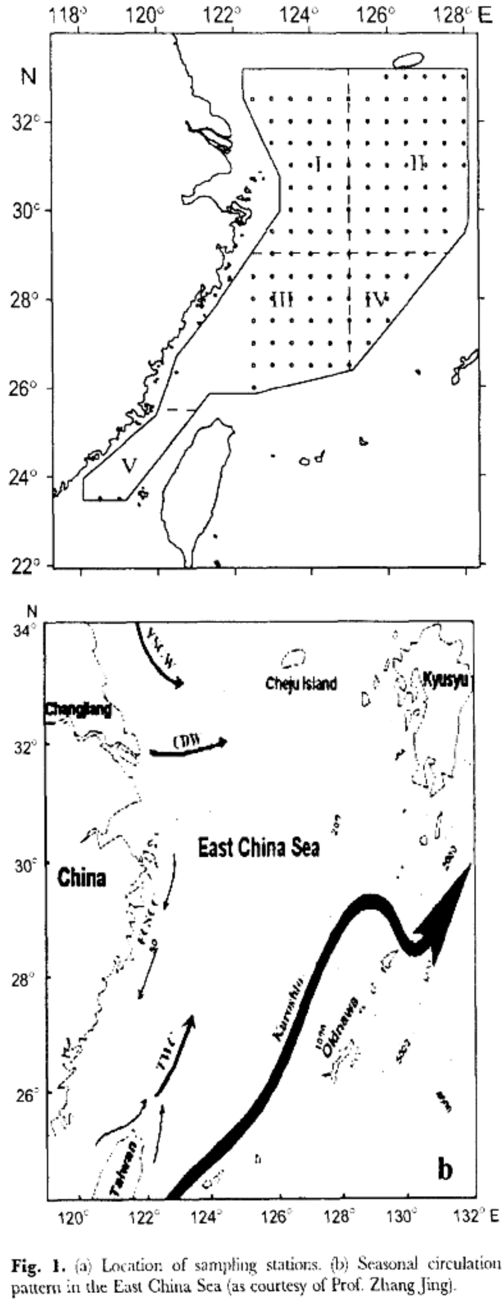

Fig. 1. (a) Location of sampling stations. (b) Seasonal circulation pattern in the East China Sea (as courtesy of Prof. Zhang Jing).

METHODS

Study area and sampling methods

The census was carried out in a large area (23°30′~33°00′ N, 118°30′~128°00′ E) in the East China Sea. 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 sampling stations were shown in Fig. 1(a). In order to examine the relationship between heteropods and their habitats, the census area was divided into 5 zones according to the reference (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, Taiwan strait (23°30′~25°30′ N, 118°~121° E). The first four zones were delimitated along 29°30′ N and 125° E. As shown in Fig. 1(b), the offshore area of the East China Sea (Zone II and Zone IV) was dominated by the Kuroshio while the nearshore area was affected by the Yellow Sea Continental Waters (YSCW), the Changjiang Dilute Waters (CDW), the East China Sea Continental Current (ECSCC) and the Taiwan Warm Current (TWC). The influence of the warm currents and water masses varied with seasons.

In total, 508 samples were collected. The sampling and laboratory processing strictly followed the Specifications of Oceanographic Survey (China State Bureau of Technical Supervision, 1991). For zooplankton sampling, a standard large net (diameter 80 cm, mesh fiber GG36, mesh size 0.505 mm) was hauled vertically from the ocean bottom to the surface. A flowmeter was mounted 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 formalin seawater. In the laboratory, each sample was divided by using a Folsom plankton splitter until the subsample contained ~500 organisms. Enumeration and determination of each species were performed with the aid of a stereomicroscope. Abundance was expressed as ind. $(100 \cdot m^3)^{-1}$. Since the water area of Taiwan Strait (Zone V) was not sampled in winter, the total abundance of Zone I, II, III and IV were averaged as the overall mean abundance in the East China Sea in the discussion below.

Data processing

In this article, occurrence frequency of a species refers to the proportion of the number of stations reporting its occurrence in the total number of the sampling stations. Dominance (Y) of a species was calculated by the following equation (Zhao and Zhou, 1984):

$$Y = \frac{n_i}{N} \cdot f_i \qquad (1)$$

in which, n_i is the abundance of species i, f_i is the occurrence frequency of species i, N is the total abundance. The dominant species was defined when $Y \geq 0.02$ (Xu and Chen, 1989)

Moreover, a series of indices were introduced to describe the aggregation characteristics of dominant species as shown below: (Zhao and Zhou, 1984).

$$\text{Index of clumping: } I = \frac{V}{\overline{X} - 1} \qquad (2)$$

$$\text{Mean crowding: } \overline{X}^* = \frac{(V - \overline{X} + \overline{X}^2)}{\overline{X}^2} \qquad (3)$$

$$\text{Index of patchiness: } \frac{\overline{X}^*}{\overline{X}} = \frac{(V - \overline{X} + \overline{X}^2)}{\overline{X}^2} \qquad (4)$$

$$\text{Index of dispresion: } I_d = \frac{(V - \overline{X} + \overline{X}^2)}{\overline{X}^2} \times \frac{N}{(N-1)} \qquad (5)$$

In the above equations, V is the variance of the samples and $\overline{X}$ is the mean. These indices are statistical variables that describe the nonrandom degree of the spatial distribution from different aspects. In a viewpoint of statistics, they are to estimate the statistical value of $V/\overline{X}$. When $V > \overline{X}$, i.e. $V - \overline{X}$ is positive, it means that the nonrandom magnitude of the spatial distribution was relatively high; or in another words, aggregation exists to some extent and vice versa. The higher the positive value is, the higher the aggregation intensity is. When the above four indices are all positive, it suggests that the distribution of a species shows an aggregation trait.

All statistical analysis was carried with the statistical package SPSS as proposed in reference (Guo, 1999).

RESULTS

Horizontal distribution of the total abundance

Figure 2 shows that the total abundance of heteropods was rather low in spring. In the north, heteropods became scarce in nearshore and were only observed in three sampling stations of the offshore area with the water temperature in the range of 17~24°C. Heteropods mainly distributed in the southern nearshore and offshore area, where water temperature ranged from 16.5 to 26.3°C. However, the abundance there was still very low. *Atlanta rosea* was found to be the main component of the heteropods, and *Atlanta lesueuri* was recorded only in one sampling station in the northern offshore.

In summer, the distribution areas were located mainly in the southern nearshore of the East China Sea and the northern part of the Taiwan Strait as shown in Fig. 2,

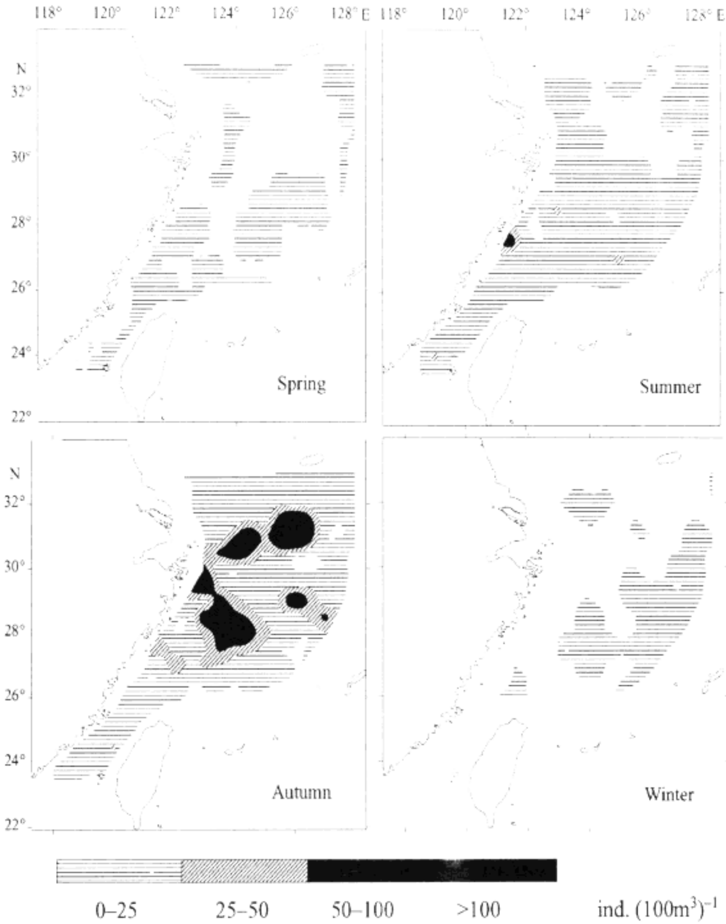

Fig. 2. Horizontal distribution of heteropods abundance in the East China Sea.

where the water temperature was around 27°C. Likewise *A. lesueuri* only occurred in one sampling station in the northern offshore. *Atlanta peroni* was recorded in the Changjiang estuary and in the northern nearshore area off the estuary (123°30′ E), where the water temperature was around 26~27°C. In the northern offshore of the East China Sea, heteropods consisted of *A. peroni* and *A. rosea* while in the southern offshore it consisted of only *A. rosea.*

In Fig. 2, it shows that the total abundance of heteropods was relatively uneven in autumn. There was a high-abundance distribution area to the east of Chanjiang estuary (31°00′ N, 122°30′~128°00′ E), which spread from southwest to the northeast. In this area, the highest abundance (195 ind.$\cdot$(100 m^3)$^{-1}$) occurred in 31°00′ N, 126°00′ E with the local temperature of 23~24°C, and heteropods were composed of *A. peroni.* Another high-abundance area was located in the edge of the southern nearshore, stretching from the northwest to the southeast with the water temperature ranging from 22 to 25°C. The main species were *A. peroni* and *A. lesueuri.*

In winter, heteropods were hardly observed in other water areas except in five sampling stations in the south. In these stations, the water temperature was 17.5~22.3°C, and the abundance was very low.

Seasonal changes of the total abundance

In Table I, the total abundance exhibited an obvious seasonal variation. It peaked in autumn (21.03 ind. (100·m^3)$^{-1}$), declined in summer (4.89 ind. (100·m^3)$^{-1}$) and reached the lowest in winter and spring. In summer and autumn, the abundance was higher in the nearshore (Zone I and III) than in the offshore (Zone II and IV) at the same latitude. In winter and spring, heteropods were not found in the northern nearshore. In the offshore area, the abundance was always higher in summer than in winter, no matter in northern part or in the southern part.

Table I: Seasonal variation of heteropods abundance in the East China Sea (individuals (100 m^3)$^{-1}$)

Season	Zone I	Zone II	Zone III	Zone IV	Zone V	Overall mean
Spring	0.00	0.55	0.91	0.27	0.38	0.56
Summer	2.87	1.77	8.90	5.25	9.83	4.89
Autumn	22.30	16.22	24.05	19.45	7.55	21.03
Winter	0.00	1.05	0.40	2.25	—	0.75
Year-round mean	6.29	4.90	8.57	6.81	—	6.81

Dominant species of heteropods

Ecological characteristics

Totally three dominant species ($Y \geq 0.02$) occurred in four investigated seasons. They were *A. rosea*, *A. peroni* and *A. lesueuri*. In winter and spring, although its occurrence frequency was rather low (7.7% in Winter and 9.2% in Spring), *A. rosea* was almost the sole species of heteropods, because its abundance accounted for all the heteropods. In summer, *A. rosea* remained dominant and its occurrence frequency increased drastically to 29.5%. Its abundance still covered 82.2% of the total abundance of heteropods. In autumn, *A. peroni* and *A. lesueuri* replaced the first place of *A. rosea* as the major dominant species. The abundance and dominance were only 2.9 ind. (100·m^3)$^{-1}$ and 0.03 respectively for *A. rosea*, while 10.0 ind. (100·m^3)$^{-1}$ and 0.20 respectively for *A. peroni* and 5.73 ind. (100·m^3)$^{-1}$ and 0.10 respectively for *A. lesueuri*. Their occurrence frequency were 23.4, 39.6 and 36.0% respectively.

Temperature and salinity adaptability of dominant species

In order to show their temperature adaptability, the abundance of each dominant species was plotted against temperature and salinity as shown in Figs. 3, 4 and 5. It shows that *A. rosea* developed in the temperature of 16~28°C with the highest abundance found in the range of 23~28°C. Meanwhile, the salinity range for *A. rosea* was 31~35 and the range for high abundance was 33~35. Likewise the temperature range for *A. peroni* was 19~28°C, and its high abundance occurred around 23°C. Its adapted salinity range was 32~35, and the range for highest abundance was 33~34. *A. lesueuri* grew as temperature ranged from 21~28°C and showed high abundance at temperature of ~23°C. The salinity range for *A. lesueuri* was 32~35, and the range was 33~34 for high abundance.

Aggregation characteristics of dominant species

As shown in Table II, the aggregation indices of heteropods were all negative, showing relatively even distribution pattern. However, comparing with the other two dominant species, *A. peroni* showed relatively higher aggregation intensity.

DISCUSSION

Horizontal abundance distribution and its seasonal changes

For low-temperature seasons, the abundance and the occurrence frequency of heteropods were both rather low. For example, the occurrence frequency was only 7.7% in winter and 10.0% in spring. Heteropods were mainly distributed in areas with a relatively high

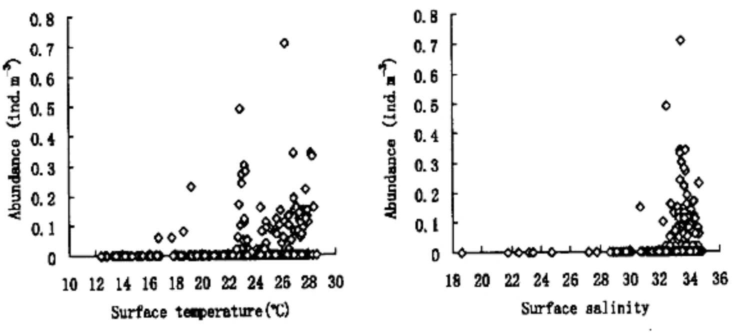

Fig. 3. Relationship between *Atlanta rosea* abundance and surface temperature and salinity.

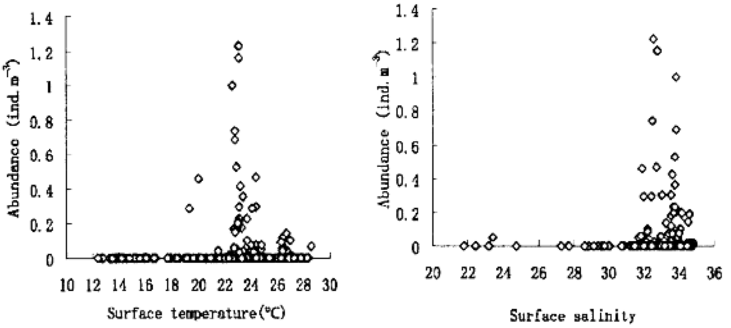

Fig. 4. Relationship between *Atlanta peroni* abundance and surface temperature and salinity.

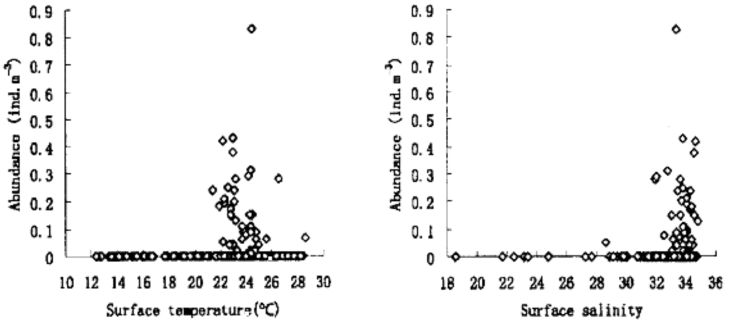

Fig. 5. Relationship between *Atlanta lesueuri* abundance and surface temperature and salinity.

Table II: Aggregation indices of dominant species of heteropods

Dominant species	Spring				Summer			
	I	$X^*/\bar{X}$	I_δ	X^*	I	$X^*/\bar{X}$	I_δ	X^*
Atlanta peroni	—	—	—	—	-0.77	-128.09	-129.09	-0.76
Atlanta rosea	-0.75	-144.43	-145.43	-0.75	-0.68	-14.62	-15.62	-0.64
	Autumn				Winter			
Atlanta peroni	-0.12	-0.17	-1.17	-0.02	—	—	—	—
Atlanta lesueuri	-0.58	-9.05	-10.05	-0.52	—	—	—	—
Atlanta rosea	-0.43	-13.76	-14.76	-0.40	-0.41	-53.95	-54.95	-0.41

temperature, such as the offshore and the southern part of the East China Sea and northern part of the Taiwan Strait. This suggested that temperature was a major factor influencing the seasonal changes of the total abundance. Namely, the abundance of heteropods increased with increasing temperature. Thus, the occurrence frequency increased drastically when it changing from spring to summer. The abundance of each station increased likewise. However, regarding the absolute values, the abundance was still very low in the northern nearshore, while it was a little higher in the other areas and ranged from 0 to 25 ind. $(100.m^3)^{-1}$. When it turned from summer to autumn, the high-abundance area expanded gradually from the south to the north, with heteropods presenting all over the East China Sea. The seasonal variation of total abundance was rather remarkable. For example, the abundance in the autumn was 35 times that in winter. Such a tremendous difference was rarely observed for other zooplanktons in the East China Sea (Xu *et al.*, 2003a,b,c, 2004a,c; Xu and Chen, 2004d). Therefore, it can be concluded that heteropods populations are very sensitive to temperature.

Relationship between abundance variation and ocean currents

Besides minor species, the three dominant species of heteropods were all pelagic warm water species (Zheng *et al.*, 1984). Therefore, ocean currents would have some impact on the abundance variation. As shown in Fig. 2, in winter and spring, heteropods are only distributed in Kuroshio and the southern part of the East China Sea, where the temperature was relatively high. In summer, the distribution area of heteropods expanded from the south to the north and from the offshore towards the nearshore. As it turned from summer to autumn, the nearshore temperature maintained high for a period of time, and thus heteropods transported by the warm currents were able to multiply rapidly. Meanwhile, with the expansion of the warm current, high-abundance areas were formed in areas where the Taiwan Warm Current converged with Changjiang Dilute Waters, coastal water masses in Fujian and Zhejiang provinces and Yellow Sea Water Masses. Synchronous observations showed that the abundance of phytoplankton in these areas was also high in autumn. Therefore, it can be concluded that the ocean currents firstly brought heteropods to the nearshore of the East China Sea, and they then quickly grew into high abundance in the nearshore rather than in the offshore with abundant phytoplankton as food and favorable high temperature. In a word, ocean currents played an important role in the abundance variation and the specific distribution of heteropods.

Relationship between abundance and environmental factors

The environmental factors, which influenced the total abundance of heteropods, were selected from the stepwise regression. The results (shown in Table III) were

Table III: Regression analysis between abundance of heteropods and temperature and salinity

Season	Regression equation	*n*	*r*	*F*	*p*
Spring	$Y = -0.0097 + 0.0007t_0$	127	0.216	6.11	0.0148
Summer	$Y = -0.0820 + 0.0070t_b$	131	0.266	9.85	0.0021
Year-round	$Y = -0.5347 + 0.0144\,t_0 + 0.0103\,S_{10}$	426	0.277	17.64	0.0000

y is the total abundance of heteropods; t_0 and t_b is/are the surface and bottom temperature, respectively; S_{10} is the 10-m salinity; *n*, *r*, *F*, *p* are statistical parameters related to the step-wise regression.

consistent with those found in the seasonal variation pattern. Concerning the year-round regression result, temperature was a major influencing factor ($\beta = 0.26$), and salinity was a minor factor ($\beta = 0.10$). As the temperature changed drastically from spring to summer, the abundance of heteropods also increased remarkably, showing a significant correlation. In winter heteropods were only present in five stations, which were all within the Kuroshio, and thus the temperature of every station differed little. In autumn the whole area of the East China Sea exhibited little temperature variation as well. Therefore, the total abundance of heteropods in winter and autumn was not significantly related to temperature, as it was in spring and summer.

Comparison of the adaptability of dominant species

Comparing the results shown in Figs. 3, 4 and 5, it can be found that *A. rosea* was able to survive in winter and spring when water temperature was rather low, indicating that this species is adapted to a lower temperature than the other two species. Thus, it has a temporal superiority, which enables it to multiply earlier than the others when summer arrives. This explained its domination in summer and its highest abundance in four seasons as well. Moreover, from Fig. 3, it can be seen that *A. rosea* can survive at temperature ranging from 16 to 28°C. So it remained dominant in four seasons. On the contrary, *A. peroni* was adapted to a relatively narrow temperature range (19~28°C), and the temperature range for *A. lesueuri* was even more narrow (21~28°C). Therefore, the order of survival superiority was *A. rosea* > *A. peroni* > *A. lesueuri*.

In autumn, *A. peroni* and *A. lesueuri* were able to grow to high abundance in the areas where Changjiang Dilute Waters and Yellow Sea Water Masses converged with the Taiwan Warm Current. This indicated that they were warm water species, which can grow to a large amount in the nearshore areas. However, *A. peroni* distributed in both nearshore and offshore areas, while *A. lesueuri* mainly distributed in the nearshore and scarcely in the offshore. In Figs. 3, 4 and 5, it showed that the abundance of *A. rosea* in autumn was lower than those of *A. peroni* and *A. lesueuri*, though it was adapted to wider ranges of temperature and salinity. It can be thereby inferred that under favorable temperature, the growth of *A. rosea* population was slower than those of *A. peroni* and *A. lesueuri*. Though the temperature in autumn favored the growth of all these three dominant species, different growth speeds of their populations eventually resulted in the difference in their abundance.

These three dominant species were all found adapted to high salinity likewise, though *A. rosea* is adapted to a relatively wider salinity range. This feature is quite distinct from other zooplanktons in the East China Sea, whose dominant species usually exhibit diverse adaptabilities. Euryhalinous and eurythermous species are acclimatized to a variety of environments, and coastal species are somewhat adapted to the low salinity of estuary. For example, *Calanus sinicus* is euryhalinous and eurythermous species (Xu *et al.*, 2003b, 2004a; Xu, 2004b), and *Muggiaea atlantica* is coastal temperate water species (Xu *et al.*, 2003c). *Sagitta bedoti* (Xu and Chen, 2004d, 2005) and *Pseudeuphausia sinica* (Xu *et al.* 2003d, 2004c) are coastal warm water species. As shown in Fig. 1(b), the nutrients brought by the East China Sea Continental Currents boosted the growth of phytoplankton. Therefore, when they meet Taiwan warm current, they provide sufficient food for the flourish of zooplanktons. Thus, owing to their varied adaptabilities, the abovementioned dominant species were able to grow into high abundance in this area. This increased their total biomass as well. Therefore, compared with other zooplankton, the poor adaptability of heteropods explained their low abundance in the East China Sea.

The above discussion also indicated that the dominant species of heteropods were adapted to high temperature and high salinity. Thus, their distribution patterns were closely associated with the strength of the Taiwan Warm Current and Kuroshio. This is particularly true for *A. peroni* and *A. lesueuri*, whose high abundance areas often indicate the presence of lasting intensified warm currents.

Comparison of the aggregation characteristics of dominant species

The aggregation indices of the Heteropod dominant species were all negative, suggesting a relatively even distribution of these species in the East China Sea. This feature was totally different from what were observed for Copepods (Xu *et al.*, 2004a), Siphonophores (Xu *et al.*, 2003b), Chaetognaths (Xu and Chen, 2004d), Pteropods and Euphausiids (Fishery bureau of Ministry of Agriculture, 1987). Since heteropods are adapted to relatively narrow temperature and salinity ranges, their high abundance occurred in limited areas and seasons. Even though the conditions are favorable, the growth of the same dominant species in different water areas will not differ much, owing to their relatively low growth speed. So their distribution showed a random pattern rather than an aggregated pattern. The low abundance of dominant species was another evidence.

Significance in fishing grounds

In winter, spring and summer, the abundance of heteropods was too low to benefit the fishing grounds. However, as the abundance increased drastically in autumn, the high-abundance distribution area overlapped the high-abundance areas of other zooplanktons, such as Copepods (Xu *et al.*, 2004a), Siphonophores (Xu *et al.*, 2003b), Chaetognaths (Xu and Chen, 2004d), Pteropoda and Euphausiids (unpublished data). These areas were not only the localities, where the Taiwan Warm Current mixed with the Changjiang Dilute Waters, the Continental Currents and Yellow Sea Water Masses, but also the grazing grounds of many commercial fishes. In particular, the high abundance area of heteropods (31°00′ N and 126°00′), where *A. peroni* dominated, was on the migration pathway of the mackerel (*Scomber japonicus*). So the high-abundance area of heteropods in Changjiang estuary and in the nearshore area of the East China Sea will be of some significance to fisheries.

Significance as indicator species

There were many studies on the indicator species in marine environment. Johnson and Terazaki (2003) found that Chaetognaths showed lower abundance but higher species diversity in the Kuroshio Warm-Core Ring (KWCR) than in the Oyashio waters. For example, *Sagitta. elegans* accounts for a large proportion of individuals in the Oyashio water and presents in deep water in Sagami. Thereby, it can be regarded as a cold water indicator. Similarly, *Sagitta pacifica* and *Krohnitta pacifica* are Kuroshio water indicator species. The high abundance of *S. scrippsae* occurred in the place where the Kuroshio and the Oyashio currents meet. Thus, it is a mixed-water species. Kang *et al.* (Kang *et al.*, 2004) studied the influence of physical parameters on the distribution of indicator species in the Ulleung Basin, which is characterized by the northward-flowing East Korean Warm Current. Benovic *et al.* ((Benovic *et al.*, 2005) investigated the distribution of medusae in the open waters of the middle and south Adriatic Sea during spring 2002, and revealed the indicative role of hydromedusa in different water depth. More discussion can be found elsewhere (Stylianos *et al.*, 2002; Delphine *et al.*, 2004). All these studies applied different ecological indices and analysis methods.

The indicator species in the East China Sea can be categorized into two different groups, according to their abundance and aggregation characteristics. One is marked by the occurrence of the species, and the other is marked by the presence of their high abundance area. As an important indicator species in the East China Sea, heteropods fall into the first group. Zooplanktons in this group are mostly pelagic warm water species, which was adapted to a narrow range of temperature and salinity and thus usually very sensitive to the changes of aquatic environments. They can hardly survive the low temperature in winter and spring. Even though the environmental conditions are favorable, they will not show high aggregation intensity because of their low growth speed and abundance. Therefore, although their aggregation indices listed in Table II were all negative, showing an even distribution pattern, heteropods can still be used as indicator of warm currents. The second group of indicator species can be represented by some coastal warm water species, such as *Eucalanus subcrassus* (X. Zhao-li, unpublished results), *S. bedoti* (Xu and Chen, 2004d, 2005) and *P. sinica* (Xu, 2003d, ; Xu *et al.*, 2004c). In the East China Sea, the presence of their high abundance area indicated the expansion of high- temperature-and-low-salinity coastal currents in summer and autumn. Different from heteropods, these zooplanktons species are relatively less sensitive to the changes of aquatic environments and show high aggregation intensity in favorable conditions due to their fast growth. So their high abundance area can indicate the convergence of different water masses. Aggregation characteristics are important ecological features to differentiate these two groups.

Comparing the results of this study with historical records, the abundance of heteropods showed an increasing trend during the past 40 years. In the earliest oceanographic census in 1959, the abundance of heteropods seldom exceeded 1 ind. m^{-3} in the nearshore areas of the East China Sea (Zhang, 1966). However, in this study, the highest abundance was observed up to 1.95 ind.$\cdot m^{-3}$ as shown in Fig. 2. As to *Atlanta* genus, their mean abundance in September was 0.15 ind. m^{-3} (Zhang, 1966), while the mean value in autumn in this study was 0.20 ind.$\cdot m^{-3}$ plus, much higher than previously reported data. Meanwhile, a similar trend can be found in the central part of the South China Sea when comparing the observations in 1997 2000 (unpublished data) with the results found in 1980s (Dai, 1995). The increased abundance of heteropods may be explained by the strengthened warm currents due to global warming.

ACKNOWLEDGEMENTS

This study was funded by National Key Science Foundation Research "973" Project of the Ministry of Science and Technology of China under contract No. 2001CB409700-07. We thank Prof. Chen Yuan-quan, Mr. Wang Yun-long, Ms. Yuan Qi, Ms. Jiang Mei, Ms. Han Jin-di and Mr. Zhun Jiang-xing for sampling, in-door sample processing and data processing. We also express our gratitude to Prof. He De-hua and Prof. Yang Guan-min, Prof. Yang Yuan-li of the Second Institute of Oceanography, SOA, for in-door sample processing. Special thanks are due to Prof. Shen Xiao-ming for his insightful suggestion and great efforts in the preparation of the draft copy.

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Aquat. Living Resour. 18, 187–192 (2005)

DOI: 10.1051/alr:2005020
www.edpsciences.org/alr

Aquatic Living Resources

Morphological differences between close populations discernible by multivariate analysis: A case study of genus *Coilia* (Teleostei: Clupeiforms)

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Received 9 April 2005; Accepted 10 June 2005

Abstract – In order to understand the morphological differences between four populations of genus *Coilia* (Teleostei: Clupeiforms) and identify them conveniently, truss network data were used to conduct multivariate analysis. Nineteen morphometric measurements were made for each individual. Burnaby's multivariate method was used to obtain size-adjusted shape data. The cluster analysis and discriminant analysis were used to discriminate among populations. The results indicated that 1) the four populations were clustered into three distinct groups; the first group included Changjiang *C. mystus* and Taihu *C. ectenes*, the second one included Zhujiang *C. mystus*, the last one included Changjiang *C. ectenes*, and 2) discriminant analysis with selected 4 morphological parameters showed that the identification accuracy was between 88% and 100%, and global identification accuracy was 95%. Our result showed that populations of different *Coilia* species living in geographic proximity to one another are more similar than conspecifics living farther apart. Separation and adaption are important to morphological difference. The taxonomy of genus *Coilia* should be reconsidered. This study also showed that the method to obtain size-adjusted data is important to acquire right conclusion.

Key words: *Coilia ectenes* / *Coilia mystus* / Cluster analysis / Discriminant analysis / Stock identification

Résumé – Différences morphologiques entre populations proches, et déterminées par analyse multivariée : une étude de cas du genre *Coilia* (Téléostéens : Clupéiformes). Afin de comprendre les différences morphologiques entre quatre populations du genre *Coilia* (Téléostéens : Clupéiformes) et de les identifier de façon pratique, un réseau de données a été utilisé pour conduire l'analyse multivariée. Dix-neuf mesures morphométriques ont été faites sur chaque individu. La méthode multivariée de Burnaby's a été utilisée pour obtenir des ajustements des données. L'analyse par groupes (clusters) et l'analyse discriminante ont été utilisées. Les résultats montrent que : 1) les quatre populations sont regroupées en trois groupes distincts ; le premier groupe inclut le « changjiang » *C. mystus* et le « taihu » *C. ectenes*, le deuxième inclut le « zhujiang » *C. mystus*, le dernier le « changjiang » *C. ectenes*, et 2) l'analyse discriminante avec 4 paramètres morphologiques sélectionnés montre que la précision d'identification se situe entre 88 et 100 %, et la précision globale d'identification est de 95 %. Nos résultats montrent que les populations de différentes espèces de *Coilia* vivant à proximité géographique des unes des autres ont davantage de caractères communs que des individus de la même espèce mais plus éloignés géographiquement. La séparation et l'adaptation importent beaucoup dans les différences morphologiques. La taxonomie du genre *Coilia* devrait être reconsidérée. Cette étude montre aussi que la méthode d'ajustement est déterminante pour obtenir un résultat correct.

Introduction

Genus *Coilia* (Gray 1831) fishes are distributed mainly in the northwest and western Pacific, extending southward toward Canton in the north of southern China and northward to the Ariake Sound of southwestern Japan, including all of the Yellow Sea and the area off the western coast of Korea (Whitehead et al. 1988). In China, four kinds of *Coilia* fishes were found (Zhang 2001). Two of them, namely, *C. ectenes* (Jordan et Seale 1905) and *C. mystus* (Linnaeus 1758), are of higher economic value (East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences and Shanghai Fisheries Research Institute 1990).

Due to great similarity, the taxonomic relationship between two ecotypes of *C. ectenes*, i.e., migrating Changjiang *C. ectenes* and resident Taihu *C. ectenes*, is controversial

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Table 1. Sampling details of *Coilia* fishes in this study. Range of standard length (SL), mean standard length (MSL), and standard deviations of MSL.

Population	Sampling location	Date of capture	Range of SL (cm)	MSL ± S.D. (cm)
DJ	Yangtze river estuary, Shanghai (N31° 37', E121° 80')	April 2003	16.9–24.7	21.09 ± 2.06
HJ	Taihu lake, Wuxi, Jiangsu province (N31° 38', E120° 10')	Dec. 2002	10.1–19.4	14.02 ± 2.45
CJ	Yangtze river estuary, Shanghai (N31° 37', E121° 90')	Mar. 2004	11.2–16.8	13.56 ± 1.51
ZJ	Pearl river estuary, Guangzhou (N22° 51', E113° 82')	Mar. 2004	8.6–16.9	12.17 ± 1.47

(Yuan et al. 1976; Yuan 1980; Liu 1995). Though they can be discriminated according to their physiological and ecological differences, it is very difficult to identify them with meristic index for they have many overlapping characters (Yuan et al. 1976). The physiological and ecological differences can be easily observed in spawning seasons. For example, the mature Changjiang *C. ectenes* has a longer standard length and larger diameter of mature eggs than does Taihu *C. ectenes* (East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences and Shanghai Fisheries Research Institute 1990). These differences are not consistently useful for they can be found only in spawning seasons and are not evident in other seasons. Different populations of *C. mystus*, such as, Changjiang *C. mystus* and Zhujiang *C. mystus*, are also difficult to identify with meristic index.

Moreover, only two meristic indices, i.e., numbers of anal spines and lateral lines, can be used to discriminate *C. ectenes* from *C. mystus* in traditional taxonomy (Cheng and Zheng 1987). In *C. ectenes*, anal spines number above 90 and lateral lines above 68 while in *C. mystus* anal spines number from 73 to 86 and lateral lines from 58 to 65. Given the difficulty in counting the numbers of anal spines and lateral lines to differentiate these two species they are not practical for use in everyday identification. Between February and April, *C. ectenes* is expensive, and delicious and tasteful at this season (East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences and Shanghai Fisheries Research Institute 1990); therefore due to the tremendous pressure to capture *C. ectenes* an illegal mix *C. ectenes* with *C. mystus* are often sold to consumers. This phenomenon not only damages the interests of the consumer, but is also very harmful to the protection and sustainable utilization of these two important fishery resources. Thus, it is necessary to discern their morphological differences and develop a convenient and practical method to identify them accurately. For the sake of convenience, Changjiang *C. ectenes*, Taihu *C. ectenes*, Changjiang *C. mystus* and Zhujiang *C. mystus* are coded in the text as DJ, HJ, CJ and ZJ, respectively.

Morphometric characters are continuous characters describing aspects of body shape. Morphometric variation between stocks can provide a basis for stock structure, and may be more applicable for studying short-term, environmentally induced variation and thus perhaps more applicable for fisheries management (Begg et al. 1999). Morphometric characters have been successfully used for stock identification. Traditional measurements tended to concentrated along the body axis with only sampling from depth and breadth, and most measurements were taken from the head. Another system of morphometric measurements called the truss network system (Strauss and Bookstein 1982) has been increasingly used for stock identification (Corti et al. 1988; Junquera and Perez-Gandaras 1993; Silva 2003; Tzeng 2004; Turan 2004; Turan et al. 2004).

In a multivariate sense, morphology has two independent components: size and shape (Bookstein et al. 1985). Most of the variability in a set of multivariate characters is due to size (Junquera and Perez-Gandaras 1993). Thus, shape analysis should be free from the effect of size to avoid misinterpretation of the results (Strauss 1985).

Based on geographic variation in ontogenetic rates, morphometric differences are expected among *Coilia* populations. The objective of this study is to understand the morphological difference between four populations of genus *Coilia* fishes and identify them conveniently using multivariate statistical techniques. The results can provide a scientific basis for effective management and sustainable exploitation of *Coilia* fishes resources, optimizing their yield, and avoiding fraud.

Materials and methods

Sampling

A total of four populations of genus *Coilia*, two populations of *C. ectenes* and two populations of *C. mystus*, was collected between December 2002 and March 2004 (Table 1, Fig. 1). The sampling location and relative information are presented in Table 1. Forty animals were collected at each site, based on Reist's (1985) recommendation that at least 25 animals be used for morphological analyses. All samples were collected strictly following classification standard (Cheng and Zheng 1987).

Data collection

Nineteen morphological measurements were made on each specimen following the Truss method (Strauss and Bookstein 1982). They consisted of 18 morphological distances between

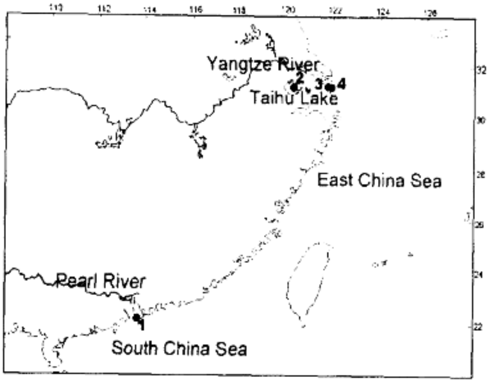

Fig. 1. Locations of sampling sites (numbers): 1. Pearl river (Zhujiang) estuary, Guangzhou; 2. Taihu lake, Wuxi, Jiangsu province; 3. Yangtze river (Changjiang) estuary, Shanghai; 4. Yangtze river estuary, Shanghai.

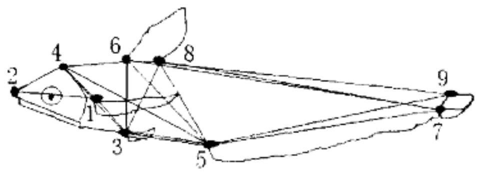

Fig. 2. Truss network of *Coilia* fish; 18 truss parameter measurements are the distances between the two of 9 landmark points. For example, D(1-2) denotes the distance between landmark points 1 and 2. Landmark points: 1. most posterior point of maxilla, 2. tip of snout, 3. origin of pelvic fin, 4. most anterior of scales on skull, 5. origin of anal fin, 6. origin of dorsal fin, 7. tremunus of anal fin, 8. tremunus of dorsal fin, 9. dorsal origin of caudal fin.

9 truss network landmark points plus standard length (SL). The morphological measurements were collected according to the method described by Elliott et al. (1995). Truss network of *Coilia* fish was shown in Figure 2.

Data analysis

To remove size-dependent variation, the data were adjusted prior to the analysis. Data were adjusted using Burnaby's multivariate size adjustment to test for shape differences among groups (Burnaby 1966; Rohlf and Bookstein 1987). The size-adjusted data were used in sequent analysis. Statistical analysis were performed with Statistica 6.0 software.

Dendrogram of four populations was constructed by hierarchical clustering of single linkage (nearest neighbor) by using Euclidean distance to assess the degree of similarity between the populations. The other linkage rules (i.e., complete linkage, unweighted pair-group average, unweighted pair-group centroid) and distance measures (i.e., Manhattan distance and Chebychev distance) were also tested to see if the results are robust to clustering method.

Table 2. The Euclidean distances between four *Coilia* fishes derived from size-free shape matrix.

Population	DJ	HJ	CJ	ZJ
DJ	0.00			
HJ	10.8	0.00		
CJ	11.3	1.2	0.00	
ZJ	13.5	3.3	2.5	0.00

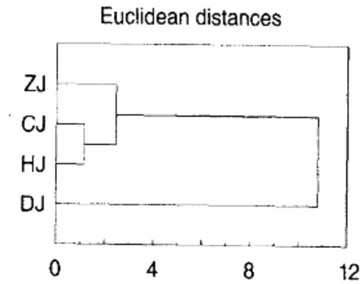

Fig. 3. Cluster dendrogram of four *Coilia* fishes derived from Euclidean distances.

A stepwise multivariate discriminant analysis was used to identify the combination of variables that best separate *Coilia* fishes. The relative importance of morphometric characters in discriminating populations was assessed using the F-to-remove statistic. Collinearity among variables used in the discriminant model was evaluated using the tolerance statistic. Accuracy of classifications was evaluated using extrinsic jackknife cross-validation, in which each specimen is removed from a discriminant function and classified to group (Marcus 1990). The proportion of individuals correctly reallocated was taken as a measure of the honesty of that population. In such a case the proportion of individuals that are misclassified is low if all groups discriminated by cluster analysis does not derived by chance alone (Soriano et al. 1988).

Results

Cluster analysis

18 characters were used to perform the cluster analysis. Different linkage rules (single linkage, complete linkage, unweighted pair-group average, unweighted pair-group centroid) and distance measures (Euclidean distance, Manhattan distance and Chebychev distance) were all tested and the results are robust to clustering method. That is to say, they produced the same cluster patterns (data not shown).

The Euclidean distance values between four samples derived from size-adjusted morphometric data were shown in Table 2. The Euclidean distance (13.5) between samples of DJ and ZJ was least similar, but the one (1.2) from the data sets of HJ and CJ was most similar. Figure 3 shows the Euclidean dendrogram of four samples.

Four samples were clustered into three distinct groups. The first group included HJ and CJ; the second group included ZJ.