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RESEARCH ARTICLE

Causal analysis of the diversity of medusae in East China Sea

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Abstract Based on the maritime data collected from 23°30′–33°00′ N and 118°30′–128°00′ E of the East China Sea (ECS) in four seasons during 1997–2000, the dynamics of medusae diversity and their causes were analyzed. A total of 103 medusae species were identified, and these species mainly distributed in the southern and northern offshore areas of the ECS. Species diversity index (H') of medusae was higher in the south than those in the north, higher in summer and winter than in spring and autumn, and higher in offshore than in the nearshore areas. The species number was closely correlated with H' value, whereas the abundance of species had no significant relationship with the diversity index. The lower H' value of the nearshore in spring and autumn resulted from the aggregation of *Muggiaea atlantica* in the south nearshore and *Diphyes chamissonis* in the north nearshore. In addition, water temperature, followed by salinity, is the main environmental factor influencing the distribution of species diversity. The H' value was related to the water temperature at the 10 m layer in winter and spring, and it was associated with the surface water temperature in summer and with the 10 m-salinity-layer in autumn. In spring and summer, the isoline distribution of H' value reflected the direction of the Taiwan Warm Current and the variation of the water masses in the ECS. In winter, the isoline of the H' value indicated the incursion of Kuroshio current. In conclusion, the H' isoline is an good indicator for water masses in ECS.

Keywords East China Sea, zooplankton, medusae, diversity, causal analysis

1 Introduction

For the purpose of the present study, the term 'medusae' is used to refer to the species of the Phylum Cnidaria (hydromedusae, siphonophores and scyphomedusae). These organisms prey on zooplankton, pelagic eggs and the larvae of fish and thus they may be detrimental to fish populations (Purcell and Arai, 2001). For its significant role in marine ecosystem, the blooming of medusae often turns out to be an ecosystem catastrophe (Mills, 2001; Purcell et al., 2001). Consequently, medusae have attracted more attention than before. In China, most of the relevant studies mainly focused on the morphologic description of medusae (Gao, 1982; Lin, 1989; Ma et al., 2000; Ma and Gao, 2000; Xu et al., 2003; Zhang et al., 2003). The diversity of medusae and especially, the causal analysis of the diversity had been rarely investigated.

Due to the complexity of its nature, descriptive ecology itself is not sufficient to uncover the causes and effects behind the phenomena. Many new approaches, especially the multivariate analysis method, help provide some solutions, thereby, enriching theoretical ecology. Previously, field studies of the marine medusae were always limited to small or local areas of the East China Sea (ECS). In the present study, using the meso-scale data collected in the ECS from 23°30′–33°00′ N and 118°30′–128°00′ E during 1997–2000, the distribution of the Shannon diversity, dynamics of medusae, the abundance and number of species, as well as the aggregation of dominant species were investigated using quantitative analysis and environmental dynamic analysis. In addition, we explored the causes and effects of the medusae diversity in the ECS and its possible application as an indicator of water mass. This study could be a pilot work on the marine diversity in China.

2 Materials and methods

2.1. Sample collection and analysis

Samples were collected from the ECS (23°30′–33°00′ N, 118°30′–128°00′ E). Four seasonal surveys were conducted: in the spring of 1998 (from March to May), the summer of 1999 (from June to August), autumn of 1997 (from October

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to November), and in the winter of 2000 (from January to February). The study area was divided into five distinct zones along 29°30′ N, 25° N and 125° E (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); and zone V, the Taiwan Strait (23°30′–25°30′ N, 118°–121° E) (Fig. 1).

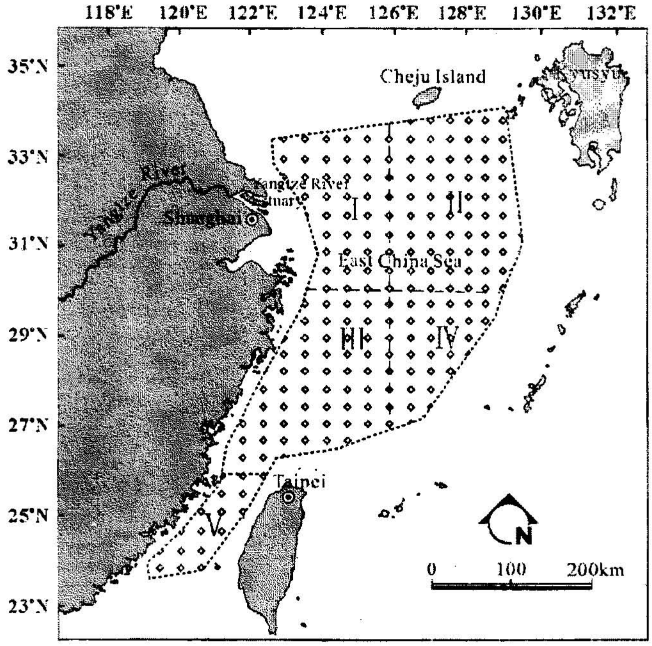

Fig. 1 Location of zooplankton sampling stations. ◇ stands for sampling station. I: North nearshore (29°30′–33°00′ N, 122°30′–125°00′ E); II: North offshore (29°30′–33°00′ N, 125°00′–128°00′ E); III: South nearshore (25°30′–29°30′ N, 120°30′–125°00′ E); IV: South offshore (25°30′–29°30′ N, 125°00′–128°00′ E); V: The Taiwan Strait (23°30′–25°30′ N, 118°00′–121°00′ E)

For zooplankton sampling, a standard large net (diameter 80 cm, length 145 cm, 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 (Fig. 2). The catch was then removed from the net and immediately preserved in 5% buffered formalin. In the laboratory, with the aid of a stereomicroscope, the medusae were counted and species were identified according to Bouillon and Boero (2000), Gao et al. (2002), Kramp (1968), Mackie et al. (1987) and Totton and Bargmann (1965). The Taiwan Strait (zone V) was not sampled in the winter for technical reasons.

2.2. Data processing

The Shannon index (H') was used to express medusa diversity. To identify environmental factors influencing the H' value of the medusae, step-wise regression analysis was carried out, with surface water temperature (t_0), 10-m water temperature (t_{10}), bottom water temperature (t_b), surface water salinity (S_0), 10-m water salinity (S_{10}) and bottom water salinity (S_b) serving as independent variables and the H' value serving as a dependent variable. The relationship between the number of medusae species, the abundance of medusae and the Shannon-Wiener index were also calculated. Important environmental or ecological factors were identified and a linear equation was formed. All these were done by SPSS 13.0 (Guo, 1999).

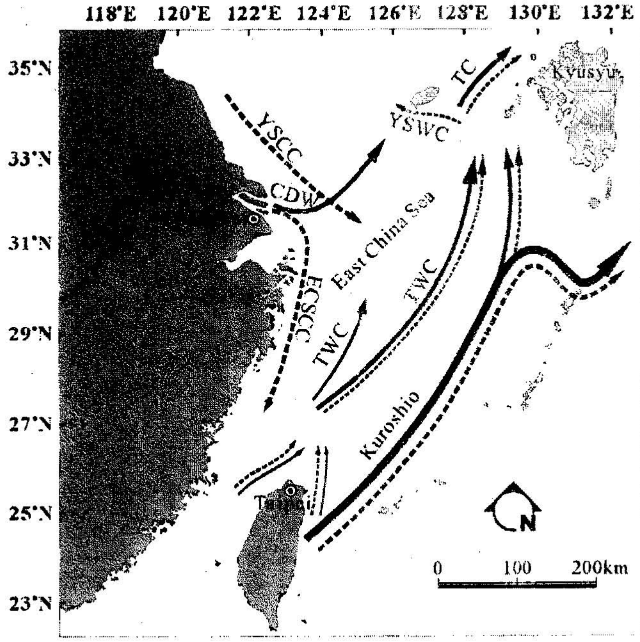

Fig. 2 Circulation pattern in the East China Sea (by Fishery Bureau of Ministry of Agriculture, 1987). ······Winter current; —— Summer current; ECSCC, East China Sea Coastal Current; CWD, Changjiang Dilute Water; TC, Tsushima Current; TWC, Taiwan Warm Current; YSWC, Yellow Sea Warm Current.

Because the diversity of medusae was closely related to the spatial aggregation, the dominant species was defined when $Y > 0.02$ (Xu and Chen, 1989). Moreover, the index of clumping was introduced to describe the aggregation characteristics of dominant species as shown below:

Index of clumping: $I = \frac{S^2}{\bar{X}} - 1$ (David and Moore, 1954)

I is simply the variance-to-mean ratio less than 1. The rationale behind the index is that the Poisson case with the variance equaling the mean, $I = 0$; underdispersion with $I < 0$; the non-random distribution with $0 < I < 5$; the aggregation with $I \geqslant 5$ (Zhao and Zhou, 1984).

3 Results

3.1. Horizontal and seasonal distribution of the diversity

In spring, the diversity was high in the Taiwan Strait, the south nearshore, the south offshore and the north offshore (Fig. 3). From south to north and from offshore to nearshore, the H' values were generally increasing. In the summer,

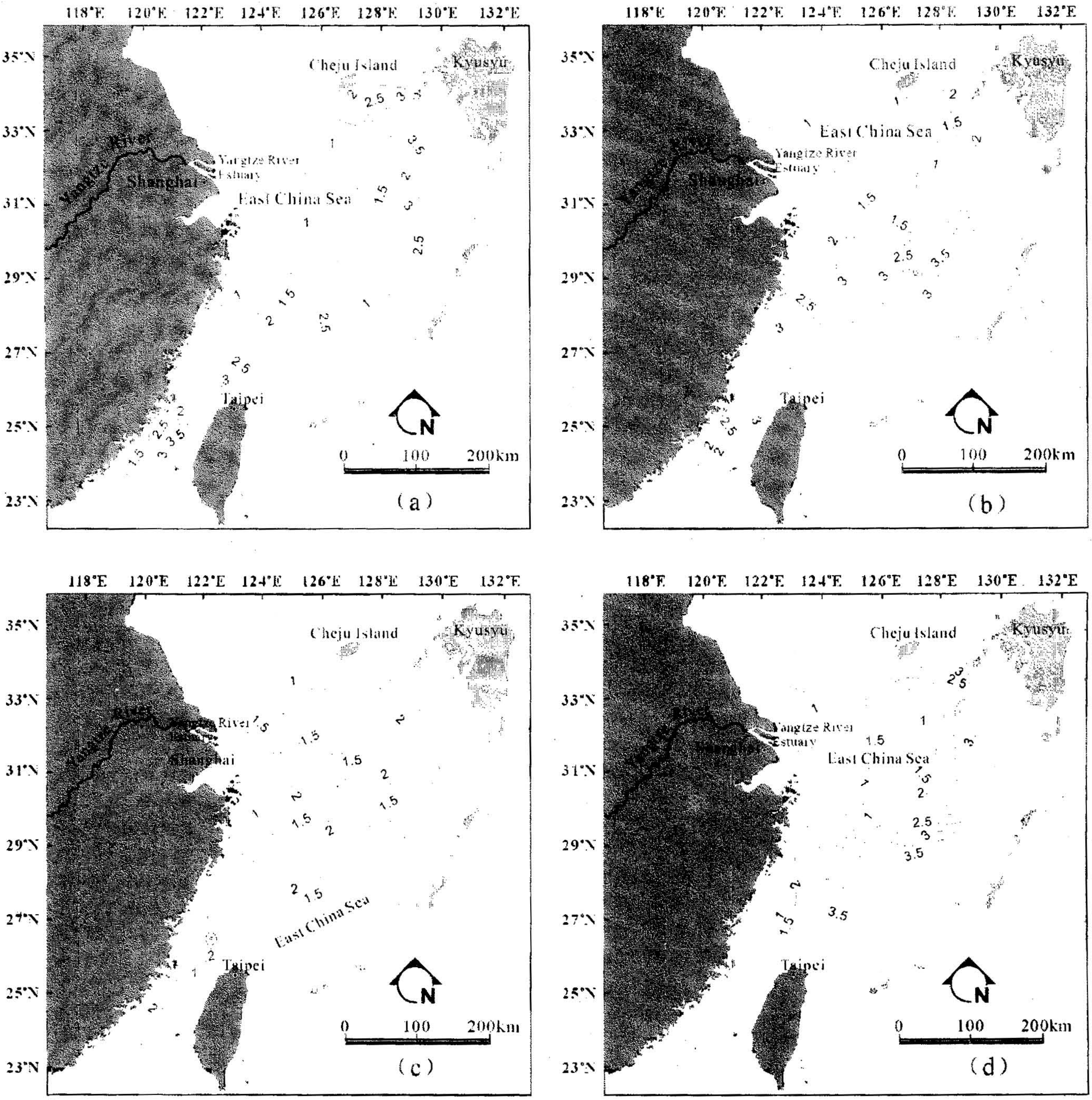

Fig. 3 Horizontal distribution of medusae diversity (H') in the East China Sea. Note: (a) spring; (b) summer; (c) autumn; (d) winter

the west-east running isolines of H' values were densely arranged near the area around 29°–30° N, with low diversity indices (< 2) in the north and high diversity indices (> 2.5) in the south. In autumn, the H' values were greater in the south than those in the north, and greater in the offshore than in the nearshore. The H' values were relatively higher in the south of the Taiwan Strait and offshore. In winter, the H' values were low in the north nearshore and the isolines were aggregated in the area around 26°–28° N in a similar fashion to the pattern found in summer.

In general, in ECS, the H' values of medusae were higher in winter and summer than in spring and autumn (Table 1). According to the horizontal distribution, the H' values were greater in the south than those in the north

Table 1 Seasonal change of diversity (H') and species number of medusae in the East China Sea

season	diversity (H')						species number					
	I	II	III	IV	V	mean	I	II	III	IV	V	total
Spring	1.17	2.00	1.72	1.66	3.23	1.95	12	53	46	35	39	68
Summer	2.23	3.03	3.82	3.93	3.73	3.35	14	24	64	35	40	75
Autumn	1.83	1.64	2.97	2.59	3.02	2.41	22	31	36	22	30	50
Winter	2.28	2.96	3.22	3.96	–	–	17	51	41	39	–	66
mean/total	1.88	2.41	2.93	3.04		–	37	73	84	58	61	114

and greater offshore than nearshore, except in autumn when in the south nearshore (2.97), the H' values were higher than in the south offshore (2.59).

3.2 Horizontal and seasonal distribution of medusae abundance

In spring, the medusae were aggregated around 27°30′–30°30′ N, 122°00′–126°00′ E with a concentration above 500 ind./100 m^3. From spring to summer, the medusae concentration in the south was greater than in the north, and greater in the nearshore than in the offshore, and the former trend was particularly obvious in summer, the latter was more evident in spring. In autumn, the high density areas are located in the north nearshore not far from the Yangtze River Estuary. The abundance of medusae in the north was greater than in the south and greater in the nearshore than in the offshore areas, which were different from that in spring and summer. In winter, the concentration was still larger in the north than in the south, but there were no significant differences between the nearshore and the offshore areas. Linear regression analysis shows no significant correlation between the total abundance of medusae and the H' value during four seasons.

Table 2 Abundance ($\overline{X}$) and clumping index (I) of medusae dominant species (ind./100 m^3)

dominant species	Spring		Summer		Autumn		Winter	
	$\overline{X}$	I	$\overline{X}$	I	$\overline{X}$	I	$\overline{X}$	I
Diphyes bozani	4.0	−0.5	8.0	1.0	1.0	−0.6	3.0	−0.9
Lensia subtiloides	2.0	−0.7	10	1.3	51.0	3.4	1.0	−0.9
Bassia bassensis	3.0	−0.8	2.0	−0.8	1.0	−1.0	9.0	0.2
Diphyes chamissonis	3.0	−0.4	7.0	−0.3	130.0	5.3	51.0	2.9
Muggiaea atlantica	308.0	12.6	10.0	10.6	16.0	9.1	49.0	3.2
Aglaura hemistoma	13.0	−0.6	2.0	−0.08	21.0	0.2	15.0	0.2
Liriope tetraphylla	5.0	−0.8	4.0	−0.6	3.0	−0.1	4.0	−0.7
Abylopsis eschscholtzi	17.0	44.8	3.0	−0.3	1.0	−0.9	6.0	−0.8

3.3 The abundance of dominant species and their aggregation

Muggiaea atlantica show a clear trend of aggregation in the south nearshore from spring to autumn. *Abylopsis eschscholtzi* were mainly aggregated during spring. *Diphyes chamissonis* were aggregated in the nearshore areas of the Yangtze River Estuary in autumn. As to the other species, they were evenly or non-randomly distributed (Table 2).

3.4 Relationship between species number and the H' values

A total of 103 species of medusae were identified (Table 3). As shown in Tables 1 and 3, there was no difference between the numbers of species during the different seasons. However, the H' values changed greatly during the different seasons. The species number of the south nearshore was larger than that of the north nearshore areas. The species numbers in the north offshore areas were greater than in the south nearshore all-year long except in summer. For the horizontal distribution, the number of species in the north nearshore was lowest among all the five zones in spring. In summer, the species number decreased markedly in the north offshore. In autumn, except for the north nearshore areas, the number of species in all the other four zones declined greatly. In winter, the distribution pattern of species numbers was similar to that in spring. A linear relationship was found between the number of medusae species and the H' values, *viz.* $H' = 0.3604 + 0.1708x$ ($n = 453$, $r = 0.8653$, $p = 0.0001$).

3.5 Relationship between Shannon index (H') and environment factors

Step-wise regression analysis indicated that there was a strong linear correlation between the diversity index (H') and the correspondent 10-meter sea water temperature during the spring and winter. During summer, the H' value was linearly correlated with the sea surface temperature. During autumn, the H' value was correlated with the 10-meter sea water salinity (Table 4).

4 Discussion

The Shannon index was higher in winter and summer than those in spring and autumn, similar to the pteropods (Xu, 2005a), euphausiids (Xu and Li, 2005) and decapods (Xu, 2005b), but totally different from chaetognaths (Xu et al., 2004).

4.1 Number of species and species diversity (H')

The seasonal changes in species number and the H' value were not parallel. Therefore, in spring, the species number was larger than in autumn. The value of H' in spring was lower than in autumn. According to the definition of the Shannon index (Shannon, 1948), a low H' value accompanied a large species number when high concentrations were confined to a few species while most of the other species were at low concentrations. For example, only *Muggiaea atlantica* or *Abylopsis eschscholtzi* aggregated in the nearshore during spring and hence the diversity index was low there. The linear correlation between the number of species and the H' values was significant. Therefore, the species number was the main factor affecting the H' value in the ECS.

4.2 The abundance and diversity of medusae

The relationship between the abundance and diversity of medusae was divided into three types: first, low abundance

Table 3 List of the species of Cnidaria in the East China Sea

species	Spring	Summer	Autumn	Winter
Hydroidomedusae				
Bougainvillia platygaster (Haeckel, 1879)	−	−	+	+
Bougainvillia ramosa (Van Beneden, 1844)	−	+	+	−
Bougainvillia niobe Mayer, 1894	−	+	−	−
Koellikerina diforficulata Xu and zhang, 1878	+	−	−	−
Cytaeis tetrastyla Eschscholtz, 1829	−	−	−	+
Podocoryne apicata Kramp, 1959	−	+	−	−
Podocoryne minima (Trinci, 1903)	−	−	−	+
Podocoryne similex Kramp, 1928	−	+	−	−
Pseudotiara tropica (Bigelow, 1912)	−	+	−	−
Leuckartiara octona (Fleming, 1823)	+	−	−	−
Merga tergestina (Neppi and Stiasny, 1912)	+	+	−	+
Merga sp.	+	−	−	−
Sarsia nipponica Uchida, 1927	+	−	−	−
Euphysora bigelowi Maas, 1905	+	+	+	+
Vannuccia forbesi (Mayer, 1894)	+	+	+	−
Pennaria grandis Kramp, 1928	−	+	−	−
Pennaria vitrea Agassiz and Mayer, 1899	−	+	−	−
Euphysa aurata Forbes, 1848	+	−	−	−
Ectopleura latitaeniata Xu and Zhang ?	+	+	−	−
Ectopleura minerva Mayer, 1900	−	−	−	+
Zanclea costata Gegenbaur, 1857	+	−	−	−
Aequorea australis Uchida, 1947	−	+	−	−
Aequorea macrodactyla (Brandt, 1834)	−	+	−	−
Malagazzia carolinae (Mayer, 1900)	−	+	−	−
Malagazzia curviductum (Xu and zhang, 1978)	−	−	+	−
Sugiura chengshanense (Ling, 1937)	+	−	−	−
Dichotomia cannoides Brooks, 1903	−	+	−	−
Eirene hexanemalis (Goette, 1886)	−	+	+	−
Eirene menoni Kramp, 1953	+	−	−	−
Eirene tenuis (Browne, 1905)	−	+	−	−
Eirene sp.	+	−	−	+
Eutima levuka (Agassiz and Mayer, 1899)	−	+	−	−
Laodicea indica Browne, 1905	+	+	+	+
Toxorchis polynema Kramp, 1959	−	−	+	−
Paralovenia bitentaculata Bouillon, 1984	−	−	−	+
Eucheilota menoni Kramp, 1959	−	−	+	−
Eucheilota sp.	−	+	−	−
Lovenella assimilis (Browne, 1905)	+	+	−	−
Clytia folleata (McCrady, 1859)	+	+	+	+
Clytia hemisphaerica (Linnaeus, 1767)	+	−	−	−
Clytia sp.	+	+	−	−
Obelia dichotoma (Linnaeus, 1758)	−	−	+	−
Obelia spp.	+	+	−	+
Phialucium mbenga (Agassiz and Mayer, 1899)	−	−	+	−
Proboscidactyla ornata (McCrady, 1859)	+	−	−	+
Liriope tetraphylla (Chamisso and Eysenhardt, 1821)	+	+	+	+
Petasiella asymmetrica Uchida, 1947	+	+	+	+
Aglantha elata (Haechel, 1879)	−	+	−	−
Aglaura hemistoma Péron and Lesueur, 1810	+	+	+	+
Rhopalonema funerarium Vanhöffen, 1902	+	+	−	+
Rhopalonema velatum Gegenbaur, 1857	+	+	+	+
Solmundella bitentaculata (Quoy and Gaimard, 1833)	+	+	+	+
Aeginura grimaldii Maas, 1904	+	+	+	+
Solmaris leucostyla (Will, 1844)	+	−	−	+
Solmissus marshalli Agassiz and Mayer, 1902	−	−	+	−
Cunina octonaria McCrady, 1859	−	−	+	+
Cunina peregrina Bigelow, 1909	−	−	+	−
Haliscera sp.	−	−	−	+
Dipleurosoma pacificum Agassiz and Mayer, 1902	−	−	+	−
Other Hydromedusae	+	+	−	+
Siphonophorae				
Agalma elegans (Sars, 1846)	+	+	−	+

(*Continued*)

species	Spring	Summer	Autumn	Winter
Agalma okeni Eschscholtz, 1825	+	+	+	+
Nanomia bijuga (Chiaje, 1841)	+	+	+	+
Halistemma rubrum (Vogt, 1852)	-	+	+	+
Physophora hydrostatica Forskal, 1775	+	+	+	+
Forskalia sp.	-	+	-	-
Amphicaryon acaule Chun, 1888	+	+	-	-
Amphicaryon sp.	+	-	-	-
Rosacea plicata Quoy and Gaimard, 1827?	-	-	+	+
Hippopodius hippopus Forskål, 1776	+	+	-	+
Vogtia glabra Bigelow, 1918	+	+	-	-
Sulculeolaria bigelowi (Sears), 1950	-	+	-	+
Sulculeolaria chuni (Lens and van Riemsdijk, 1908)	+	+	+	+
Sulculeolaria quadrivalvis Blainville, 1834	+	+	-	-
Sulculeolaria tropica Zhang	-	+	-	+
Sulculeolaria turgida (Gegenbaur, 1853)	-	+	-	+
Diphyes bojani (Eschscholtz, 1829)	+	+	+	+
Diphyes chamissonis Huxley, 1859	+	+	+	+
Diphyes dispar Chamisso and Eysenhardt, 1821	+	+	+	+
Lensia campanella (Moser, 1925)	+	+	+	+
Lensia conoidea (Keferstein et Ehlers, 1860)	+	-	+	+
Lensia cossack Totton, 1941	+	+	+	+
Lensia hotspur Totton, 1941	+	+	+	+
Lensia subtilis (Chun, 1886)	+	+	+	+
Lensia subtiloides (Lens and van Riemsdijk, 1908)	+	+	+	+
Muggiaea atlantica Cunningham, 1892	+	+	+	+
Chelophyes appendiculata (Eschscholtz, 1829)	+	+	+	+
Chelophyes contorta (Lens and van Riemsdijk, 1908)	+	+	+	+
Eudoxoides mitra (Huxley, 1859)	+	+	+	+
Eudoxoides spiralis (Bigelow, 1911)	+	+	+	+
Eudoxia macra Totton, 1954	+	+	+	+
Sphaeronectes gracilis (Claus, 1873)	+	+	+	+
Ceratocymba leuckarti (Huxley, 1859)	-	-	-	+
Abyla haeckeli Lens and van Reimsdijk, 1908	+	+	-	+
Abyla schmidti Sears, 1953	-	-	-	+
Abyla trigona Quoy and Gaimard, 1827	-	-	-	+
Abyla sp.	-	+	-	-
Abylopsis eschscholtzi (Huxley, 1859)	+	+	-	+
Abylopsis tetragona (Otto, 1823)	+	+	-	+
Bassia bassensis (Quoy and Gaimard, 1833)	+	+	-	+
Enneagonum hyalinum (Quoy and Gaimard, 1827)	+	+	-	+
Desmophyes annectens Haeckel, 1888	-	+	-	+
Other Siphonophorae	+	+	-	+
Scyphomedusae				
Tetraplatia volitans Bush, 1851	-	-	-	+
Nausithoe punctata Kölliker, 1853	+	+	-	-
Pelagia noctiluca (Forskål, 1775)	-	+	-	-

Table 4 Regression analysis between medusae diversity (H') and temperature

season	regression equation	n	r	F	P
spring	$H' = -1.3056+0.1520\,t_{10}$	124	0.624	79.02	0
summer	$H' = -8.6102+0.3862\,t_0$	134	0.410	28.06	0
autumn	$H' = -7.0159+0.2503\,S_{10}$	104	0.216	6.06	0.015
winter	$H' = -3.0724+0.2890\,t_{10}$	63	0.682	54.85	0

with a low diversity index simultaneously. There were a few species of medusae in the north offshore and nearshore during the spring and summer (Xu, 2006) and species diversity was also low. Second, high abundance accompanied by a high H' value at the same time. In the south of the Taiwan Strait, the species number increased from spring to autumn accompanied by the increase of H' values because of an even distribution of the amount in different species. Third, the trend of the H' value distribution was contrary to that of the abundance. The H' value with low abundance occurred offshore and conversely, low H' value with high abundance occurred in the nearshore. A combination of the species number and the abundance defines species diversity. With species unevenness, dominant species aggregated in certain areas. Consequently, the diversity nearshore was low in the spring and autumn. With a high species richness and a high species evenness, the diversity index was high offshore. The effect of abundance on diversity was subtle and hence the correlation between these two factors was not significant.

4.3 Effects of seasonal circulation on the diversity index (H')

The seasonal circulation pattern was responsible for the temporal and spatial distribution of the H' value. In spring, the Taiwan Warm Current (TWC) mainly flows from the Taiwan Strait and north of Taiwan, crossing the continental shelf to the north-east and finally merges into the Tsushima Current (TC) (Fig. 2). At the same time, the Yellow Sea Warm Current (YSWC) flows from the south of Jeju Island north-westwards to the Yellow Sea (Fig. 2). The dense isoline distribution of the H' values corresponded with the trochoid pattern of the warm currents (Fig. 3a). On the west side of the trochoid, the H' values were much lower than that on the east side. In summer, the TWC moves northward. The nearshore branch of the TWC flows strongly and meets with other water masses in the north areas. The dense isolines of the H' values aggregated at around 29°00′–30°00′ N, ranging from the low in the north to the high in the south because the southern waters were dominated by the TWC, which was characteristic of high species richness and evenness (Fig. 2 and 3b). This was verified by the fact that the species number in the south nearshore was as high as 77. In the north, the mixed water mass, an assemblage of TWC and Changjiang Dilute Water (CDW), as well as YSWC, was the characteristic of low species diversity (Fig. 2 and 3).

In autumn, the prevailing warm water mass lasted for a certain period. The species numbers in each region were not different significantly (Table 1). According to previous studies, warm water species would develop rapidly in this period, even in the north. The aggregation of the *Diphyes chamissonis* in the north nearshore resulted in the low diversity there (Table 1).

Although the isoline pattern in winter was similar to that in summer (Fig. 3d), its location was further south and the mechanism was different. After the Kuroshio ran into the ECS, a branch of the Kuroshio surface water intruded onto the continental shelf (Su, 2001). The isolines extended to the north-west from the south-east to produce a clear front of the diversity (Fig. 3d) which was coordinated by the temporal and spatial intrusion of the Kuroshio. The Kuroshio brought many warm species to the south nearshore. As a result, the diversity was high, which was consistent with the large species number in the south nearshore (Table 1).

4.4 Effect of hydrology on the species diversity of medusae

From winter to spring, the H' value was larger in the south than in the north and larger offshore than nearshore. Due to the rather low temperature, the warm water species were limited to the warm waters and cannot extend to the nearshore. In summer, water temperature was highest among the four seasons. In the north, with the influence of the Yellow Sea Cold Water Mass, the temperature was obviously lower than that in the surrounding waters (Zheng et al., 2003). Meanwhile, the diversity was low (Fig. 3b). In autumn, *Diphyes chamissonis* was burgeoning in the north nearshore affected with low salinity by the CDW. As a result, the diversity was low. In short, water temperature in the ECS is the most important factor for the diversity of medusae, while the influence of salinity is also crucial.

4.5 Diversity of medusae as an indicator of water mass

The diversity index of medusae is closely related to sea circulation and temperature in the ECS. The aggregated diversity isolines in Fig. 3 indicated the path of the TWC on the shelf in spring and summer and the incursion of the Kuroshio onto the shelf in winter. Consequently, medusae, especially the diversity isoline patterns, are a good indicator of the movement of water mass in the ECS.

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