

Interannual, Seasonal, and Diurnal Variations in Vertical and Horizontal Distribution Patterns of 6 *Oithona* spp. (Copepoda: Cyclopoida) in the South China Sea

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Jiang-Shiou Hwang, Ram Kumar, Hans-Uwe Dahms, Li-Chun Tseng, Qing-Chao Chen (2010) Interannual, seasonal, and diurnal variations in vertical and horizontal distribution patterns of 6 *Oithona* spp. (Copepoda: Cyclopoida) in the South China Sea. *Zoological Studies* 49(2): 220-229. Temporal changes in abundance and distribution patterns of cyclopoid copepods belonging to the genus *Oithona* were analyzed from a 3 yr survey in the South China Sea comprising 9 sampling cruises, during spring, summer, and autumn of 2000-2002. Plankton samples were collected by oblique tows of a North Pacific zooplankton net of 100 μm mesh size including 3 different depth strata (50-0, 100-0, and 150-0 m) and provide the 1st multiscale depth study for an assemblage of *Oithona* spp. worldwide. The mean occurrence rate of *Oithona* spp. was > 85% with an average density of 45.86 ± 206.97 individuals (ind.)/ m^3 . Among the 6 most abundant species, including *O. attenuata*, *O. setigera*, *O. fallax*, *O. similis*, *O. rigida*, and *O. brevicornis*, *O. attenuata* was dominant, with an average density of 45.9 ± 133.61 ind./ m^3 (with an occurrence ratio of 47.59%) throughout the study, followed by *O. setigera* with an average abundance of 9.49 ± 34.11 ind./ m^3 . The average densities of these 2 highly abundant species were higher in samples collected from 100-0 and 150-0 m depths than those from surface samples. The intermediate-sized oceanic warm-water species, *O. setigera*, was most abundant during 2000 and 2001. During 2002, the smaller (< 1000 μm) species, *O. attenuata*, became dominant. The occurrence rate of *O. attenuata* was higher at coastal stations than at offshore stations, whereas *O. setigera* showed no significant differences in occurrence between coastal and oceanic stations. The average oithonid abundance recorded during the spring was higher than in either summer or autumn. In spring, the oithonid assemblage was dominated by *O. setigera* in 2000 and 2001, whereas *O. attenuata* was the most dominant species in 2002. *Oithona fallax* appeared in summer and autumn; in contrast, *O. similis* was not recorded in summer samples. Total oithonid densities did not significantly differ in relation to the depth layer sampled. <http://zoolstud.sinica.edu.tw/Journals/49.2/220.pdf>

Key words: Spatiotemporal distribution, Community structure, Horizontal and vertical distribution, South China Sea, *Oithona*.

Copepods commonly comprise the majority of mesozooplankton abundances in oceans (Verity et al. 1996, Kiørboe 1997, Hwang et al. 2000 2003). The role of smaller copepods, particularly of the genus *Oithona* was recently recognized in terms of their numerical contribution to the

mesozooplankton and particularly their high turnover rates (Herman 1992, Hopcroft et al. 1998, Elwers and Dahms 1999, Gallienne and Robins 2001, Pakhomov and Froneman 2004), proving to have a pivotal position in food webs, microbial loops, and in carbon cycling (Nakamura and Turner

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1997, Saiz et al. 2003, Turner 2004). The genus *Oithona* includes intermediate- to smaller-sized (< 1 mm) cyclopoid copepods. Different species of *Oithona* show differential levels of adaptability to physical and hydrological parameters, and include cosmopolitan species as well as those with narrower distribution ranges (Nishida 1985). They comprise both neritic and oceanic species (Yahia et al. 2004). They feed on smaller-sized organisms, such as heterotrophic and autotrophic protists, and copepod nauplii, and are the preferred food of fish larvae and other zooplanktivores. Oithonids, therefore, may play more-important roles in the transfer of both bacterial and algal carbon to higher trophic levels than previously thought.

Because of the larger mesh sizes usually employed in large-scale zooplankton research (> 200 μm mesh size) and variable sampling strategies, up to 92% sampling losses of *Oithona* spp. were shown in samplings from several oceans (Vannucci 1968, Gallienne and Robins 2001, Turner 2004). Because of their spherical diameter of < 200 μm , even adult *Oithona* spp., are likely to pass through a net with a mesh diameter > 200 μm (Vannucci 1968, Evans and Snell 1985, Gallienne and Robins 2001, Turner 2004, Hwang et al. 2007), and thus have been undersampled and underestimated. To date, no reliable information is available regarding the abundance, seasonality, or distribution of *Oithona* spp. in the South China Sea (SCS; Tan et al. 2004, Hwang et al. 2006). Although over a quarter of the world's population inhabits countries bordering the SCS, very little is known about the ecology and biology particularly of the smaller-sized fraction of mesozooplankton here. *Oithona* is the only copepod genus that occurs in all marine geographical regions (Paffenhöfer 1993). The abundance and community structure of *Oithona* exhibit considerable variations at interannual, seasonal, and regional scales (Paffenhöfer 1993). Temporal variations in copepod communities are related to strong seasonal pulses of the ambient environment (Peterson and Keister 2003). Considering the importance and little-known distribution patterns of *Oithona* spp. and their adaptability to temperate versus tropical waters (Paffenhöfer 1993, Uye and Sano 1998, Paffenhöfer and Flagg 2002, Turner 2004) and oligotrophic versus eutrophic waters (Uye 1994, Uye and Sano 1995), we conducted a 3 yr study of oithonid species abundances and distribution patterns in coastal and oceanic water masses of the northeastern SCS.

The SCS, a marginal sea in the western Pacific Ocean covering an area of $35 \times 105 \text{ km}^2$, borders Guangdong and Guangxi Provinces of China in the north, the Philippines in the east, and the islands of Kalimantan and Sumatra in the south. Oceanic currents are mainly influenced by the prevailing East Asian monsoonal winds, which are northeasterly (NE) in winter and southwesterly (SW) in summer (Chen 1992, Tseng and Shen 2003, Tan et al. 2004). Spring and autumn are transitional periods when the 2 monsoons alternate. Since monsoons drive water masses and their accompanying pelagic biota, a combination of organisms are relocated during the transitional seasons, by both the NE and SW monsoonal winds (Goldblatt et al. 1999, Tan et al. 2004, Hwang et al. 2006).

How different *Oithona* species are separated in spatiotemporal distribution patterns remains unexplored. We attempted to examine this here on the basis of a multiyear study. The main objectives of the present contribution were to analyze temporal (interannual, seasonal, and diurnal) and spatial variations in the abundances and distribution patterns of identifiable *Oithona* species, collected from 3 vertical depth strata in spring, summer, and autumn of 2000-2002.

MATERIALS AND METHODS

Large-scale oceanic cruises were conducted in spring (Mar. 2000, 2002, 2003), summer (June 2000 and July 2001; summer data in 2002 were not collected because a major typhoon prohibited sampling), and autumn (Nov. 2000, Oct. 2001, and Sept.-Oct. 2002), and copepod samples were collected at 23 stations throughout the SCS (Fig. 1). This study combined the results of 9 sampling cruises, covering a 3 yr period from Mar. 2000 to Oct. 2002. Details of the research vessels, sampling stations, and depths are given in table 1. Samples were collected using a modified Norpac (north Pacific) zooplankton net (1 m opening, 4.5 m in length, and 100 μm mesh size). A flow meter (Hydrobios, Kiel, Germany) was mounted in the center of the mouth opening. The zooplankton net was towed horizontal to the surface (0-5 m) for the surface sample and obliquely in order to sample 3 vertical depth strata (from 50, 100, and 150 m to the surface). Samples were immediately preserved on board in 5% buffered formalin-seawater. In the laboratory, all *Oithona* specimens were counted and identified to species level under

a microscope using keys and references by Chen and Zhang (1965), Chen et al. (1974), Shih and Young (1995), and Chihara and Murano (1997).

In order to identify depth- and station-related distribution and abundance patterns of the 6 most abundant oithonid copepod species in the SCS, we performed principal component analyses (PCAs) with log-transformed data using PRIMER 5 (Plymouth Routines In Multivariate Ecological Research (Clarke and Gorley 2001). A two-way ANOVA (analysis of variance) was used to evaluate the effect of mean number of plankton taxa and their abundance, with 'season' and 'depth' as factors. Based on similarities and differences, a scatterplot was created. To gain further insights into our data using a two-factor F -test of the general linear model univariate procedure, we tested null hypotheses that means of abundances of the 6 most abundant oithonid copepod species in the SCS were not affected by seasonal and depth variations. The effects of depth, season, and their interaction on the abundances of copepods were statistically tested with the two-factor F -test using SPSS vers. 13.0 for Windows software package (SPSS, Chicago, IL, U.S.A.). To evaluate

differences among specific means the F -test was followed by post-hoc range tests and multiple comparisons using Tukey's honest significant difference (HSD). In order to reduce higher heteroscedasticity observed in the original species abundance data for copepods, a transformation power by maximizing the log likelihood function (Zar 1999) was generated. Accordingly, data were $\log(X+1)$ -transformed before being subjected to the parametric statistical tests.

RESULTS

Our hydrological data indicated remarkable interannual variations in temperature and salinity. The average temperature recorded during Mar. 2002 was significantly lower than the springtime surface water temperature of previous years (Mann Whitney U -test, $p < 0.05$; Fig. 2). During autumn, surface temperatures of about 27°C were similar between 2001 and 2002, but they were cooler in 2000. Salinity followed a reverse trend in spring, with the lowest value recorded in 2000 and the highest in 2002. However, we found no significant correlations between oithonid abundances and either salinity or temperature values.

Six identifiable *Oithona* species were examined during the present study. *Oithona attenuata* and *O. setigera* were the most abundant species (Table 2, Fig. 3). However, different

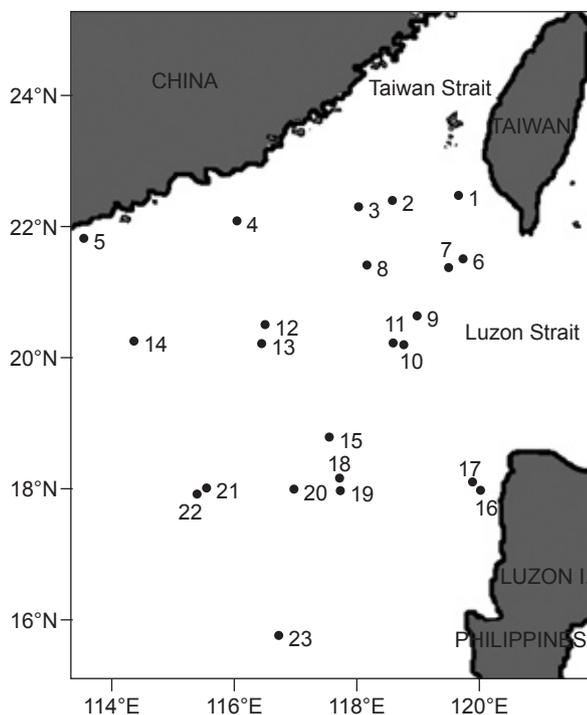


Fig. 1. Map showing the study area and sample stations in the South China Sea.

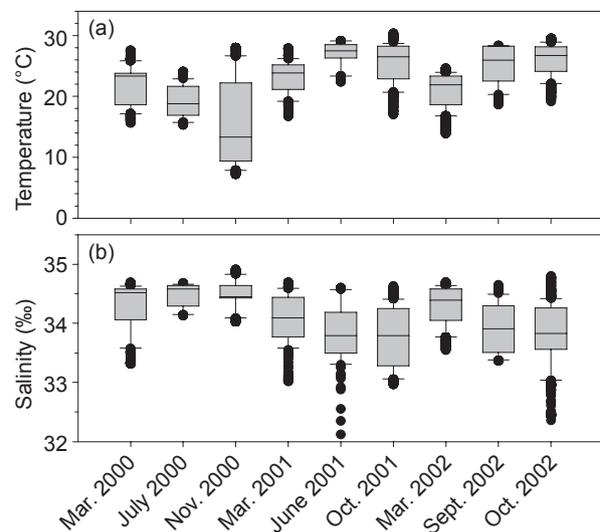


Fig. 2. Box and whisker plots (median values with quartiles) for sea surface water temperatures (a) and salinities (b) in the South China Sea from Mar. 2000 to Oct. 2002. Outlying values are shown as points.

higher in samples collected from 150 m deep to the surface, than in either the surface layer or the 50-0 m stratum. The mean abundances of *O. setigera* in deeper samples (150-0 m) were significantly higher than those from either the 0-100 m depth stratum (one-way ANOVA, $p = 0.006$) or surface (0 m) samples (one-way ANOVA, $p = 0.019$). In contrast, *O. rigida* was present in surface samples as well as in samples collected from the 50-0 m depth stratum (Fig. 4) but in neither the 100 m surface nor the 150 m surface depth stratum. These 2 otherwise abundant oithonid species were conspicuously absent from stations 5, 10, and 17 (Fig. 4).

The top 2 highly abundant species showed differential spatial distribution patterns. Mean abundances of *O. attenuata* were significantly higher at coastal than offshore stations (Fig. 5), whereas *O. setigera* showed no significant difference between coastal station 5 and the remaining oceanic stations.

Most discernible differences in copepod abundances related to day/night shifts were only apparent at the surface. If the ranges of daytime and nighttime were defined as 06:00-18:00 and 18:00-06:00 h, respectively, the following 3 species were found in both daytime and nighttime: *O. attenuata*, *O. fallax*, and *O. setigera*, whereas *O. rigida* and *Oithona* sp. were exclusively found at night (Fig. 6).

A PCA did not resolve differences in abundances with depth or station, probably because we only examined Oithonidae copepods, and the species richness was relatively low in most

samples (Fig. 7).

DISCUSSION

Significant seasonal variations found in the present study are indicative of monsoon-driven changes in oithonid abundances. Monsoon-driven currents are powerful physical forces in the SCS. During the NE monsoon period in winter, the southwestward driven current prevails and causes a part of the Kuroshio Current to intrude into the SCS through the Bashi Channel (Chen 1992). During the same period, the partial long-shore current of the East China Sea (ECS) enters the SCS through the Taiwan Strait (Chuang and Liang 1994, Chiu and Chen 1997 1998). The spring data in the present study recorded higher abundances of species from relatively warmer waters, i.e., from the Kuroshio intrusion and from the warm temperate ECS, resulting in higher occurrence ratios of the 6 dominant oithonid species. A confluence of different water masses resulting in higher abundances and diversities of zooplankton species was previously recorded in other boundary waters of the ECS and from the Taiwan Strait, adjacent to the SCS (Chiu and Hsyu 1994, Chiu and Chen 1998, Hwang et al. 2000). An avoidance of visually preying fish by several oithonid species resulting in the migration of these copepods to deeper water layers beyond the photic zone, particularly during daytime, was previously recorded (e.g., Ohlhorst 1982, Ohman 1990). Our data reaffirm those observations. The higher abundance of *O. fallax* over all depths

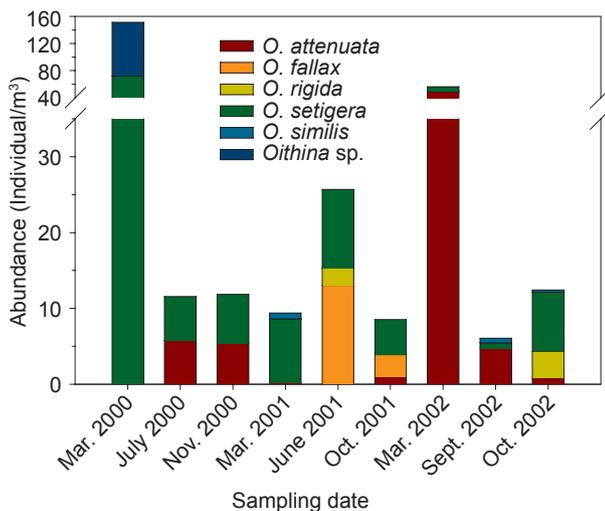


Fig. 3. Average abundances of 6 *Oithona* species recorded in the South China Sea from Mar. 2000 to Oct. 2002.

Table 2. Mean abundances (mean number of individuals \pm S.D.) and occurrence ratios of oithonid copepods collected with a 100 μ m mesh net in the South China Sea from Mar. 2000 to Oct. 2002

Species	Abundance (mean \pm S.D.)	Occurrence ratio (%)
<i>Oithona attenuata</i>	45.86 \pm 133.61	47.59
<i>O. brevicornis</i>	0.05 \pm 0.57	0.69
<i>O. fallax</i>	0.98 \pm 4.5	8.28
<i>O. rigida</i>	0.58 \pm 6.19	2.07
<i>O. setigera</i>	9.49 \pm 34.11	40.69
<i>O. similis</i>	0.84 \pm 7.02	6.21
<i>Oithona</i> sp.	2.75 \pm 20.97	3.45

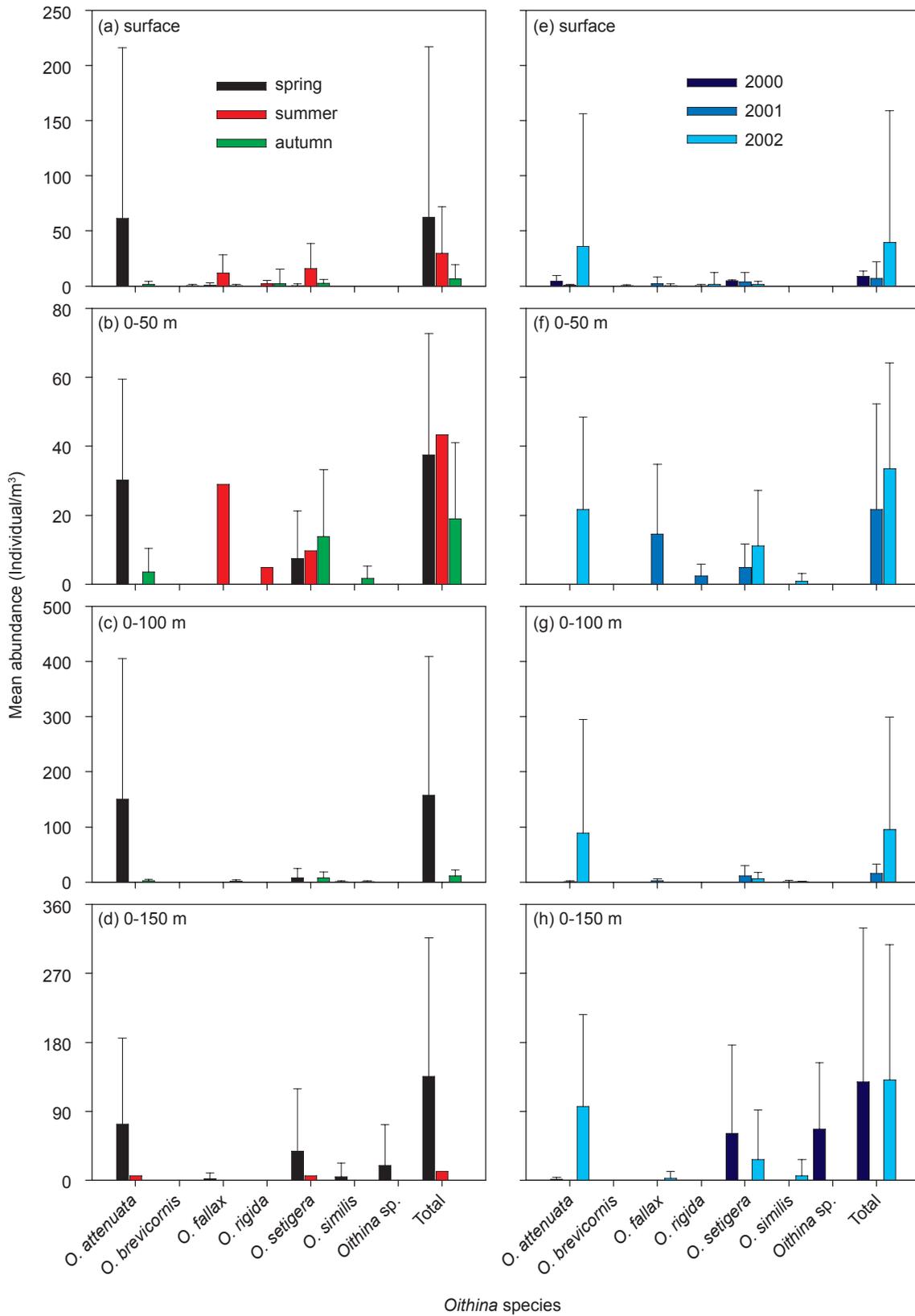


Fig. 4. Interannual and seasonal abundances of 6 *Oithona* species in relation to depth strata sampled in the South China Sea from Mar. 2000 to Oct. 2002.

Table 3. Results of the two-factor ANOVA showing sampling depth- and season-related differences in abundances of each *Oithona* species and that of total *Oithona* abundances from all cruises in the South China Sea from Mar. 2000 to Oct. 2002

Source	Sum of squares	d.f.	Mean square	F value	p value
<i>O. fallax</i>					
depth	377318564	3	125772854.7	7.917	< 0.001
season	920653044.7	2	460326522.4	28.977	< 0.001
depth × season	508119320.7	4	127029830.2	7.996	< 0.001
Error	1556847334	98	15886197.28		
Total	3057309315	108			
<i>O. attenuata</i>					
depth	42753813768	3	14251271256	0.692	0.559
season	1.02475E+11	2	51237527373	2.488	0.088
depth × season	38985018139	4	9746254535	0.473	0.755
Error	2.01795E+12	98	20591281486		
Total	2.8756E+12	108			
<i>O. brevicornis</i>					
depth	184382.728	3	61460.909	0.132	0.941
season	112666.016	2	56333.008	0.121	0.886
depth × season	554543.017	4	138635.754	0.298	0.878
Error	45553386.67	98	464830.476		
Total	47831056	108			
<i>O. rigida</i>					
depth	32774482.78	3	10924827.59	0.203	0.894
season	26234738.39	2	13117369.19	0.244	0.784
depth × season	75508663.5	4	18877165.88	0.351	0.843
Error	5267520857	98	53750212.83		
Total	5572110280	108			
<i>O. setigera</i>					
depth	1273469287.129	3	424489762.376	0.291	0.832
season	28042204.357	2	14021102.179	0.010	0.990
depth × season	2464954593.306	4	616238648.327	0.422	0.793
Error	143170508655.808	98	1460923557.712		
Total	180574874310.000	108			
<i>O. similis</i>					
depth	30042193.28	3	10014064.43	0.145	0.933
season	12308413.89	2	6154206.944	0.089	0.915
depth × season	26267440.79	4	6566860.197	0.095	0.984
Error	6768546887	98	69066804.97		
Total	7199710869	108			
Total <i>Oithona</i> abundance					
depth	23428196267	3	7809398756	0.324	0.808
season	1.01752E+11	2	50875759857	2.11	0.127
depth × season	50914850994	4	12728712749	0.528	0.715
Error	2.36277E+12	98	24109932914		
Total	3.59026E+12	108			

layers studied here during summer indicates its adaptation to warmer waters. In contrast, the absence of *O. similis* in summer indicates its adaptation to temperate waters, providing a reasonable explanation for *O. similis* being among the dominant species in neritic temperate seas (Sabatini and Kiørboe 1994, Nakamura and Turner 1997, Saiz et al. 2003, Turner 2004) and waters of the Southern Ocean (Elwers and Dahms 1999).

By its extension along the west coast of

Taiwan, the SCS is one of the most important marginal seas in the western Pacific Ocean. Although more than a quarter of the world's population lives in countries bordering the SCS, few studies have tackled copepod ecology, particularly that of *Oithona*. Although the importance of *Oithona* spp. in oceanic ecosystems is well documented (Böttger-Schnack 1988 1994, Nakamura and Turner 1997, Arashkevich et al. 2002, Turner 2004), a distributional gradient of *Oithona* spp. in the SCS was not reported before the present account. This is the 1st study dealing with abundances and occurrences of this copepod taxon, retrieved from a 100 μm mesh net in the SCS. The 2 dominant oithonid species, *O. attenuata* and *O. setigera*, are coastal warm-water species (Tseng 1975 1976, Tseng and Shen 2003). They are perennially found in appreciable densities (40-120 ind./m³) in the SCS (Chen 1992). These species are also observed in the Danshuei River

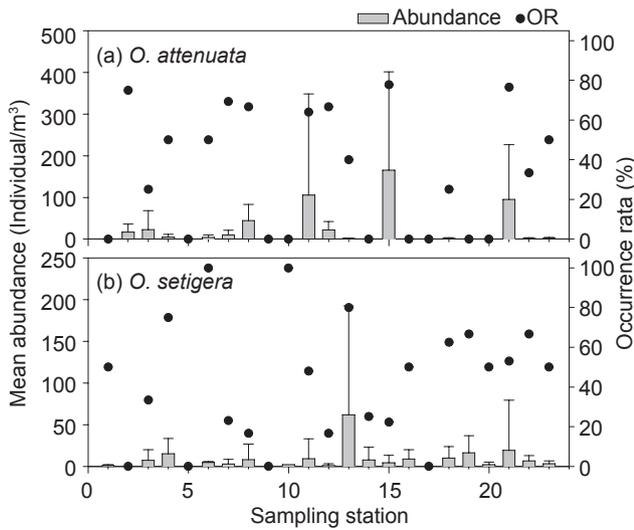


Fig. 5. Average abundances (mean \pm S.D.) and occurrence ratios (OR in percent) of the top 2 highly abundant species, *Oithona attenuata* and *O. setigera*, recorded in the South China Sea from Mar. 2000 to Oct. 2002.

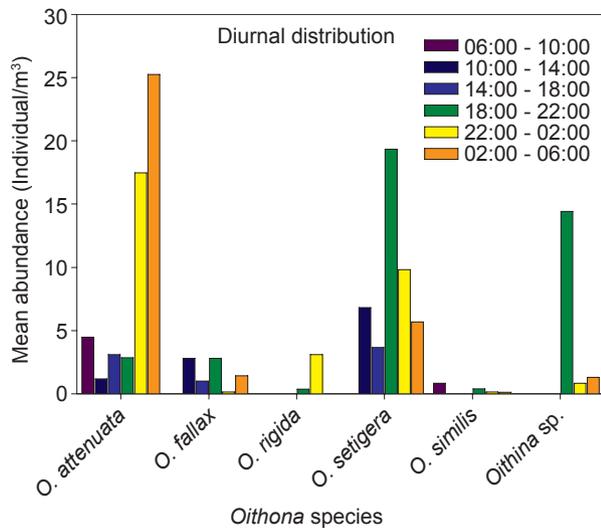


Fig. 6. Diurnal average abundance distributions of *Oithona* species recorded from surface waters in the South China Sea from Mar. 2000 to Oct. 2002.

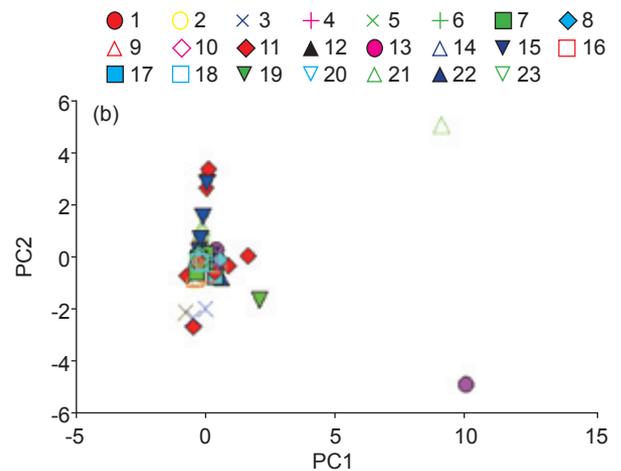
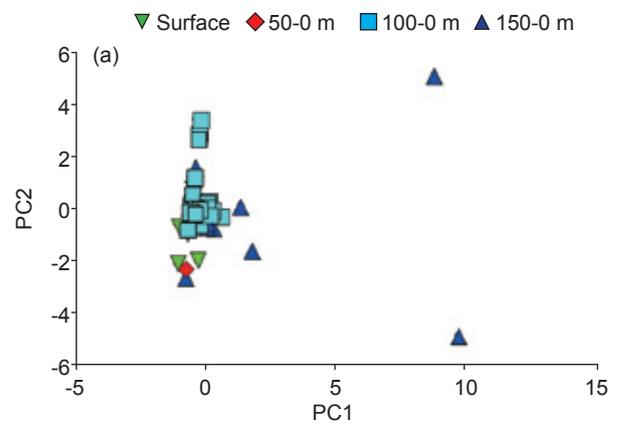


Fig. 7. Principal component analysis (PCA) showing a comparison of depths (a) and stations (b).

estuary of northern Taiwan and in other coastal waters of Taiwan (Tseng 1975 1976, Hwang et al. 2006). The present study demonstrates that the SCS perennially accommodates a combination of tropical and subtropical oithonid species. Wide ranges of salinity and temperature allow a number of *Oithona* spp. to occur here. The unprecedented adaptability of *Oithona* spp. to predator avoidance (Turner 2004) and to varying trophic conditions (Uye 1994) was discussed earlier.

We recorded fluctuations in *O. rigida* density in some of our samples, and densities that fluctuated an order of magnitude for *O. attenuata*, accompanied by high spatial patchiness (coefficient of variability > 90%). This may have been due to swarming performances (see Kimoto et al. 1988, Nielson and Sabatini 1996). A lesser oithonid abundance can be explained by replacement of oceanic oithonid species by an estuarine group of oithonids, particularly by *O. rigida* and *O. setigera*, attributable to river discharges into the SCS (Chen 1992, Tang et al. 2003, Tan et al. 2004).

Seasonal fluctuations and swarming behavior of estuarine oithonid copepods such as *O. rigida* in the South China Sea (Tan et al. 2004) and in other shallow waters of tropical and subtropical regions (Kimoto et al. 1988) require further investigations. Future studies are also needed to explore the proximate and ultimate causes that modify the oithonid community structure and population dynamics in the South China Sea.

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