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Biogeographic distribution of the cyclopoid copepod genus *Oithona* – from mesoscales to global scales

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ABSTRACT

Abundance and productivity of smaller copepods such as the cyclopoid *Oithona* spp. have been substantially underestimated in most studies, primarily due to large mesh sizes employed during zooplankton tows. Several studies demonstrate that the assemblage structure of *Oithona* spp. shows considerable variation at temporal and spatial scales. We report here the remarkable horizontal variation in distribution as well as abundance patterns of 8 *Oithona* species off northeastern Taiwan in the southeastern East China Sea and compare this distribution pattern with community compositions worldwide. The present study provided the first explanation of a spatial distribution pattern and a relationship between species richness and area, as well as community similarities with increasing distance worldwide for the ecologically important planktonic copepod genus *Oithona*.

1. Introduction

The important role of small planktonic copepods, such as those of the genus *Oithona* Baird, 1843 has been recognized recently in terms of their numerical contribution to the mesozooplankton and particularly due to their high production turnover rates (Gallienne and Robins, 2001), providing a pivotal position in marine food webs, microbial loops, and carbon cycling (Saiz et al., 2003). Cyclopoid copepods of the genus *Oithona* include intermediate to smaller sized (<1 mm) representatives. They comprise neritic and oceanic species. They feed on smaller sized organisms, such as heterotrophic or autotrophic microbes, and copepod nauplii, and are prefered food of fish larvae and other zooplanktivores (Elwers and Dahms, 1999). Different species of *Oithona* show differential levels of adaptability to physical and hydrological parameters, and include cosmopolitan as well as species with a narrower range of distribution. Oithonids, therefore, may play a larger role in the transfer of both bacterial and algal biomass to higher trophic levels than hitherto expected.

Because of larger mesh sizes usually employed in large scale zooplankton research (>200 micrometer mesh size) and variable sampling strategies (Dahms et al., 2012, 2013), up to 92% sampling losses of *Oithona* spp. have been shown in samplings from several oceans (Gallienne and Robins, 2001). Even adult *Oithona* spp., because of their spherical diameter of <200 μm are likely to pass through a net with a mesh diameter >200 μm (Hwang et al., 2006) have thus been undersampled and underestimated (Hwang et al., 2010; Tseng et al., 2011).

To date, reliable information is still lacking regarding the abundance, seasonality, and distribution of the smaller size fraction of mesozooplankter such as *Oithona* spp. in the South China Sea (Hwang et al., 2006). *Oithona* represents the only copepod genus that occurs in all marine geographical regions. The abundance and community structure of *Oithona* exhibits considerable variation, though, at interannual, seasonal, and regional scales (Paffenhöfer, 1993). Temporal variation in copepod communities is related to strong seasonal pulses of the ambient environment. Considering the importance and unresolved distribution patterns of *Oithona* spp. and their adaptability to temperate *versus* tropical waters or oligotrophic *vs.* eutrophic waters (Gallienne and Robins, 2001), we conducted here a spatial distribution study of oithonid species abundance and distribution patterns in the coastal and oceanic water masses of the East China Sea.

It remained unexplored as yet how different *Oithona* species can be separated in their spatial distribution patterns. We investigated the differential distribution patterns of *Oithona* on the basis of a single short-term study at different spatial scales. The main objectives of the present study were to reveal the variation at horizontal meso-spatial horizontal scales (from 1 to 5000 m) in the abundance and distribution patterns of identifiable *Oithona* species around a small volcanic island off northeastern Taiwan in the summer of 2008 and compare this with patterns worldwide.

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2. Materials and Methods

2.1. Study area and sample collection

In order to reveal the distribution and community patterns of *Oithona* copepods in the waters off northeastern Taiwan (Fig. 1), we set up 6 sampling stations in a transect line at 1 kilometer south of Turtle Island of the southeastern East China Sea. The sampling stations were designed in an east to west orientation and had the following distances from each other: 1 m, 10 m, 100 m, 1 km, 2 km and 5 km (Fig. 1). The zooplankton samples of the present study were retrieved from on-board of a research diving boat at noon time on the 27th of May, 2008. Three samples were collected from each sampling station as three replicates. At 6 selected stations copepod samples were collected by surface tows (0-5 m) with a standard North Pacific zooplankton net (mouth diameter 45 cm, 1.8 m long and a mesh size of 100 μm), having a Hydrobios flowmeter (Germany) mounted at the centre of the net mouth. Zooplankton samples were preserved in seawater with 5% buffered formaldehyde immediately on-board (see Dahms et al., 2014).

2.2. Copepod enumeration and identification

In the laboratory, zooplankton samples were split by a Folsom plankton splitter until the subsample contained less than 500 specimens. Adult copepods in subsamples were identified and counted under a stereo-microscope. Species identification was done according to keys and references by Chen and Zhang (1965), Chen et al. (1974), and Chihara and Murano (1997).

2.3. Data analysis

The copepod community structures were analyzed using the Paleontological Statistics (PAST) computer package (Hammer et al., 2001). Bray–Curtis similarity coefficient and average linkage routine were applied for non-metric multidimensional scaling (NMDS) analyses. NMDS was applied to test the similarities in the copepod community of *Oithona* spp. among different geographical zones obtained from the Marine Plankton Copepod website (Razouls et al., 2005–2012 - http://copepodes.obs-banyuls.fr/en [accessed February 03, 2012]). Information about *Oithona* congeners from different geographical areas worldwide were made available by Razouls's database. To evaluate similar distribution patterns of *Oithona* species, the data of 23 geographical zones comprising 40 *Oithona* species were analyzed using nonmetric multidimensional scaling (NMDS) to elucidate the variations of presence and species richness worldwide. The species richness in each geographical zone was using Bray–Curtis similarities prior to conducting the NMDS analyses. Further, Minimum Spanning Tree (MST) analysis with weights less was applied to find the smallest difference among each geographical zone.

3. Results

3.1. Hydrological structure

Monthly-averaged information derived from Advanced Very High Resolution Radiometer (AVHRR) recordings for sea surface temperature and seawater chlorophyll *a* values for May 2008 are shown in Fig. 2. The image for sea surface temperatures (Fig. 2A) shows the sea around Turtle Island with a temperature of about 24 °C. Sea surface concentration of chlorophyll *a* (Fig. 2B) shows the highest regional distribution along the coast of the mainland of China, with concentration levels higher than 5.0 mg m^{-3}. From satellite images it can be inferred that the surface water towards the area around Turtle Island could be characterized by the interplay of East China Sea waters with the Kuroshio Current (KC) during the sampling period.

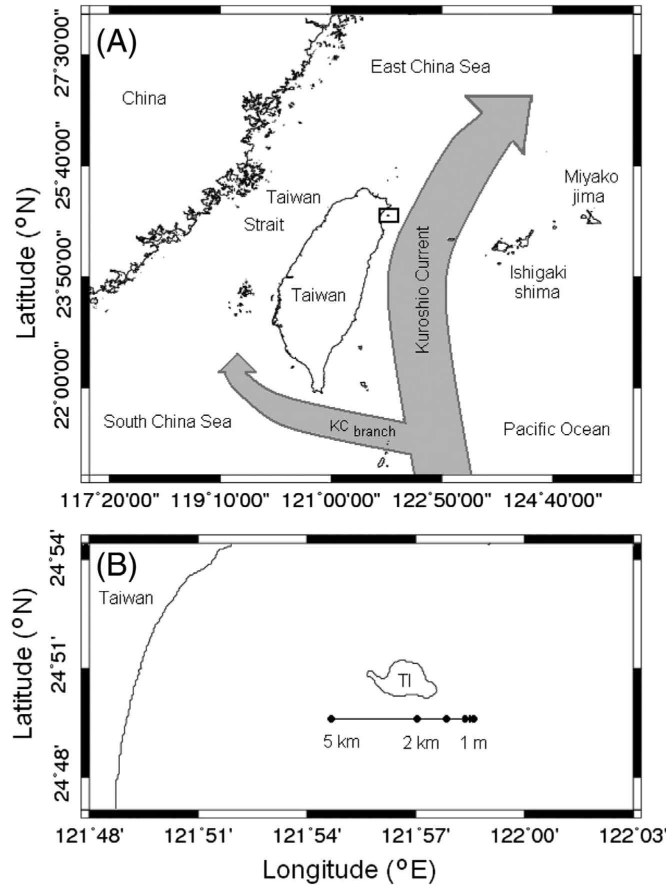

Fig. 1. Map of the study area (A) and sampling stations (B) in Turtle Island. KC is the Kuroshio Current and TI is the location of Turtle Island.

3.2. Copepod community structure

From 18 samples, which were collected in the present study, 8 *Oithona* species were identified in total: *O. attenuata*, *O. brevicornis*, *O. fallax*, *O. longispina*, *O. rigida*, *O. setigera*, *O. similis* and *O. simplex*. The average abundance, relative abundance (RA) and occurrence ratio (OR) of each species are shown in Table 1. Among all the samples, the most abundant species was *O. similis* (56.67 ± 24.24 ind. 10^{-1} m^{-3}, RA: 48.25%), *O. fallax* (25.06 ± 14.45 ind. 10^{-1} m^{-3}, RA: 21.33%) and *O. setigera* (12.39 ± 7.97 ind. 10^{-1} m^{-3}, RA: 10.55%). The three species *O. fallax*, *O. setigera* and *O. similis* have the highest OR value (100%) and were recorded in all 18 samples. These species were followed by *O. attenuata* with 83.3% OR, whereas *O. rigida* showed the lowest values of OR (11.1 %) which were identified from two samples only. The observed patterns showed that total abundance was significantly decreased with distance from east to west ($r = -0.923$, $p = 0.009$, Pearson's correlation), species richness was not significant ($r = -0.670$, $p = 0.146$, Pearson's correlation) (Fig. 3). These results indicated that a higher density of copepods were distributed in the area close to the hydrothermal vent site. We analyzed the relation between species richness and total abundance and found no significant differences ($r = 0.623$, $p = 0.186$, Pearson's correlation).

The variation of species number (Fig. 3A) and copepod abundance (Fig. 3B) at each sampling station are demonstrated in Fig. 3. The average number of *Oithona* species identified at each station ranged between 4.67 (station 2 km) and 5.67 (station 1 m) (Fig. 3A). The lowest average abundance of total *Oithona* copepods in the present study was 52.00 ± 21.70 (ind. 10^{-1} m^{-3}) at station 5 km, whereas the highest record of abundance was 136.67 ± 59.20 (ind. 10^{-1} m^{-3}) at station

1 m (Fig. 3B). Abundance patterns were showing a decreasing trend from the eastern station (1 m) towards the western station (5 km).

The average abundance of every *Oithona* copepod at each sampling station is shown in Fig. 4. In Figs. 4A-H the distribution of each species is ranked by its average abundance. The variation of abundance among 8 *Oithona* species was different at each station. *O. simplex*, *O. fallax*, *O. setigera*, *O. attenuata* and *O. brevicornis* demonstrated similar distribution curves with the lowest density at the 5 km station (Figs. 4A-E). *O. rigida* was found only at station 100 m (Fig. 4F). *O. longispina* was recorded at the two stations 1 m and 5 km (Fig. 4G). *O. simplex* showed the highest values at station 5 km (Fig. 4H).

The variation of proportion of each *Oithona* species at different sampling stations indicated changing patterns with distance between stations (Table 4). The proportion of *O. similis* shows an increasing trend from station 1 m to 5 km (eastern to western). *O. attenuata* and *O. brevicornis* were found at stations 1 m to 2 km.

4. Discussion

Even though the important role of *Oithona* spp. in oceanic ecosystems is well documented (Gallienne and Robins, 2001), a distribution study of representatives of *Oithona* spp. has never been undertaken before. This is the first study dealing with the occurrence and abundance of this copepod taxon retrieved from a 100 μm mesh net in the area off northeastern Taiwan. The two dominant oithonid species, *O. attenuata* and *O. setigera* are coastal warm water species (Tan et al., 2004). They are perennially found in appreciable densities in the South China Sea.

These species are also observed in the Danshuei River estuary in the northwest of Taiwan and in other coastal waters of Taiwan (Hwang et al., 2006). Representatives of *Oithona* have been recorded from the Atlantic and the Indian Ocean. A wide range of salinity and temperature allows a number of *Oithona* spp. to occur. An unprecedented adaptability of *Oithona* spp. with respect to predator avoidance and with varying trophic conditions has been discussed earlier (Tan et al., 2004). Hwang et al. (2006) recorded a fluctuation of *O. rigida* density in some of the samples, and densities were fluctuating an order of magnitude for *O. attenuata*, accompanied by high spatial patchiness in this latter species (coefficient of variability >90%). The authors explained the extreme density variability in *O. attenuata* by swarming aggregations. Hwang et al. (2006) found a replacement of oceanic oithonid species by an estuarine group of oithonids, particularly by *O. rigida* and *O. setigera* in the Danshuei estuary that were explained by river discharges (Tan et al., 2004). The seasonal variation 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 will need further studies into the causal mechanisms of its patchy distribution. Future studies need also to explore the proximate and ultimate causes that modify oithonid community structures and population dynamics. This may hold for emigration movements of individuals within and between populations, stage-related mortality schedules, and also for species-specific differences of intrinsic rates of increase. Scale-dependent differences in horizontal distribution patterns will also be affected by species- and stage-specific behavior patterns, such as in different performances of Diel Vertical Migration (DVM) that would affect horizontal assemblage compositions (Lo and Hwang, 2000).

4.1. Observed spatial patterns of the copepod Oithona

Newly established databases have promoted the knowledge of geographical distribution on a global scale. Later, we used the database of *Oithona* copepods from Marine Plankton Copepods (Razouls et al., 2005–2012) for the verification of a community similarity–distance relationship.

So far, no clear pattern between the species richness of *Oithona* spp. and a given sampling area has been established. A hypothetical spatial pattern of diversity for species richness–area correlations of *Oithona* copepods is shown in Fig. 5A. The estimated trend of change by the spatial increase, the rate of richness follows a slow rise from a local area to a larger geographical zone. A shift takes place in community assemblages in a species richness–area correlation slope between smaller and worldwide geographical scales. We expect measures of species richness (or copepod diversity) to be scale-dependent. This means that we can encounter local diversity (called alpha diversity) as well as regional diversity or large scale diversity. The changes of the diversity level according spatial scales are very important in ecology. Unfortunately, the intermediate scale level was not sampled during our study.

The current species richness of *Oithona* spp. worldwide is shown in Fig. 5B and Table 2. Species richness is commonly correlated with area, and this is also demonstrated by the species richness of *Oithona* which is increasing with exploration area as well. The geographical zones of the Arctic Ocean, southern Iceland, southern Greenland (E & W), Davis Strait, Labrador Sea, Antarctic and Central South-Atlantic showed lower richness compared to other regions of the world's oceans (Fig. 5B).

4.3. Community similarity-distance relationships

The species number of *Oithona* copepods found in the waters around Taiwan varied in different reports according to the experimental location and sampling period (Table 3). From the known *Oithona* species, 15 species have been recorded from the area. We found 8 *Oithona* species in the Kuroshio region representing more than half of the known

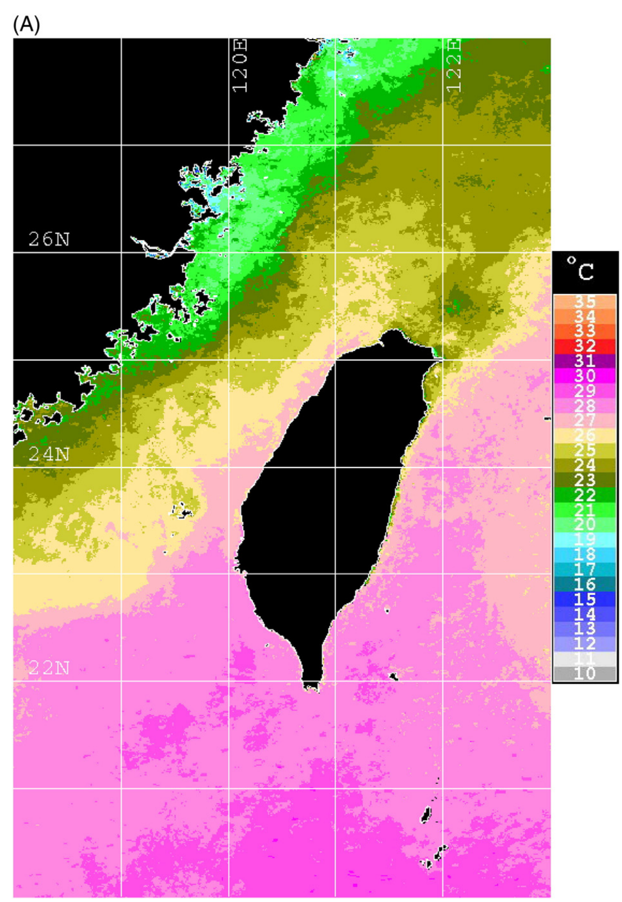

Fig. 2. Monthly-averaged information derived from NOAA for sea surface temperature (A) and chlorophyll *a* (B) of May 2008.

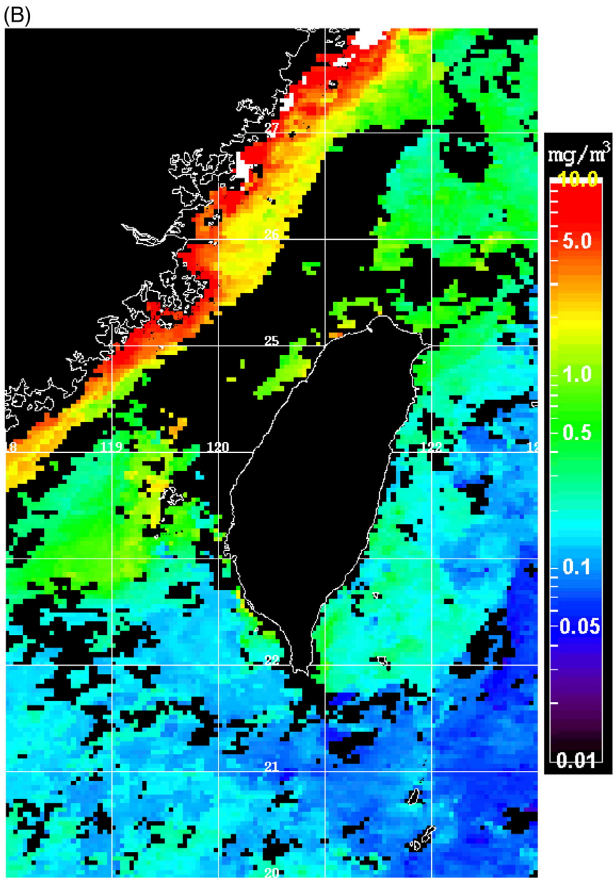

Fig. 2 (*continued*).

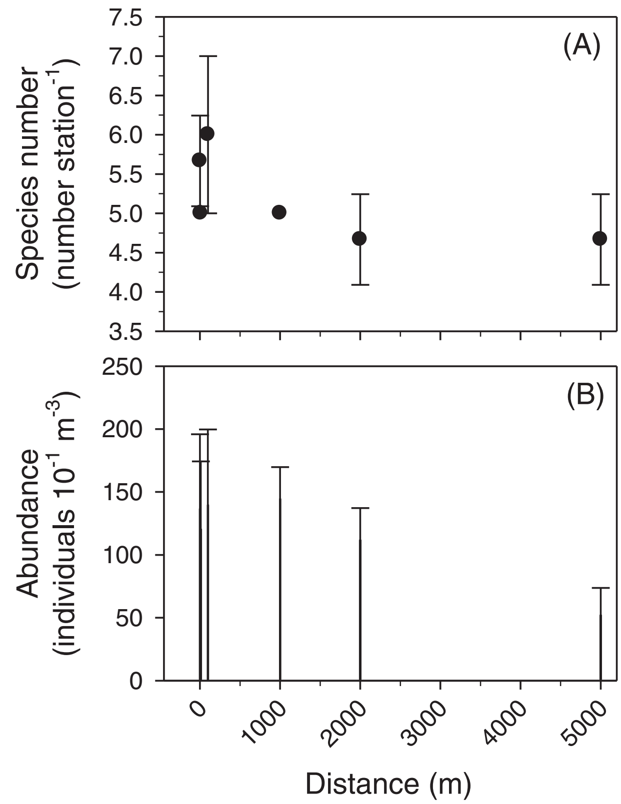

Fig. 3. Variation of averaged species number (A) and abundance (B) of *Oithona* copepods in each sampling station (sampling 3 replicates around noon on 27 May 2008 at Turtle Island).

records at present. *O. atlantica* Farran 1908 was firstly recorded in the Kuroshio area (Hsiao et al., 2011a). The remaining species can be found in waters around Taiwan. We could not find clear distribution patterns of the different *Oithona* species. The available records used different mesh sizes for sampling which might have caused the missing record of small sized representatives of *Oithona* (Tseng et al., 2011).

Spatial changes in the abundance and distribution patterns of cyclopoid copepods of the genus Oithona were analyzed during a snapshot study at Turtle Island in the southeastern East China Sea during the early summer of 2008 are shown in Fig. 6. The relationship between community similarity and distance (the community similarity–distance relationship) provides a critical issue in field ecology. The hypothetical patterns of correlations between community similarity and distance for *Oithona* copepods are demonstrating distribution patterns where the expected community similarity is higher in closer than in distant assemblages. The non-metric multidimensional scaling (NMDS) and minimum spanning tree was used to assess the community similarity of *Oithona* spp. among geographical zones in the world (Fig. 6B). Our resulting graph reveals that community similarity is highly varied among different geographical zones at low similarity of *Oithona* communities at a global scale. Examples include the Arctic Ocean (zone 1),

Table 1
Abundance (mean ± SD, individuals 10^{-1} m^{-3}) of each *Oithona* species, the values of relative abundance (RA, %) and occurrence ratio (OR, %) sampled from surface waters around Turtle Island. SD: standard deviation.

Species	Abundance	RA	OR
O. attenuata Farran, 1913	17.22 ± 13.41	14.66	83.3
O. brevicornis Giesbrecht, 1891	4.11 ± 4.56	3.50	72.2
O. fallax Farran, 1913	25.06 ± 14.45	21.33	100.0
O. longispina Nishida, Tanaka & Omori, 1977	0.5 ± 1.15	0.43	22.2
O. rigida Giesbrecht, 1896	0.44 ± 1.46	0.38	11.1
O. setigera Dana, 1852	12.39 ± 7.97	10.55	100.0
O. similis Claus, 1866	56.67 ± 24.24	48.25	100.0
O. simplex Farran, 1913	1.06 ± 2.29	0.90	27.8
Total	120.94 ± 48.53	100.0	---

Table 2
Code for geographical zone and its name [compiled after Razouls et al., 2005–2012].

Zone code	Area of geographical zone
1	Arctic Ocean
2	Southern Iceland, southern Greenland (E & W), Strait of Davis, Labrador Sea
3	Antarctic
4	Central South-Atlantic
5	Cape Cod, Nova Scotia, Island of Newfoundland
6	North East Pacific
7	North West Pacific
8	Sub-Antarctic
9	Ireland, English Channel, Faroe, Norway, North Sea, Baltic Sea
10	Chile
11	Gulf of Thailand, Malaysia-Indonesia-Philippines
12	South Africa (E & W), Namibia
13	California-Gulf of California
14	Red Sea
15	Australia (E), Great Barrier Reef, Tasman Sea, New Zealand, New Caledonia
16	Central Tropical Pacific
17	Eastern Tropical Pacific
18	Cape Verde Is., Canary Is., Madeira Is., Azores, Bay of Biscay, Ibero-Moroccan Bay
19	Japan Sea, Japan
20	Mediterranean Sea, Black Sea
21	Venezuela, Caribbean Sea, Gulf of Mexico, Caribbean, Florida, Sargasso Sea
22	China Seas, Vietnam
23	Indian Ocean

Table 3
Review of published records of *Oithona* representatives from waters around Taiwan. 1, Shih and Young, 1995; 2, Shih and Chiu, 1998; 3, Hwang et al., 2004; 4, Zuo et al., 2006; 5, Hwang et al., 2006; 6, Hwang et al., 2007a; 7, Hwang et al., 2007b; 8, Tseng et al., 2008b; 9, Tseng et al., 2008c; 10, Tseng et al., 2008d; 11, Tseng et al., 2008a; 12, Lee et al., 2009; 13, Tseng et al., 2009; 14, Chang et al., 2010; 15, Hwang et al., 2010; 16, Kâ and Hwang, 2011; 17, Hsiao et al., 2011a; 18, Hsiao et al., 2011b; 19, Tseng et al., 2011; 20, Present study. ECS, East China Sea; KC, Kuroshio Current; SCS, South China Sea; TS, Taiwan Strait; YS, Yellow Sea.

Species\study region	Checklist around Taiwan	ECS	ECS, TS	ECS, YS	ECS, KC	TS	SCS	SCS, KC	KC
O. atlantica Farran, 1908									17
O. attenuata (Farran, 1913)	1	3, 9, 10	5	4	16		7, 11, 15, 19	6	17, 20
O. brevicornis Giesbrecht, 1891	1	9					7, 15		20
O. decipiens Farran, 1913	1						11		
O. fallax (Farran, 1913)	1	3, 9, 10	5	4			7, 15		12, 17, 20
O. longispina Nishida, 1976	1	2							12, 20
O. nana (Giesbrecht, 1892)	1	10		4					17
O. plumifera (Baird, 1843)	1	2	5, 18	4			14	6	12, 17
O. rigida Giesbrecht, 1896	1	3, 9, 10	5, 18			8	7, 11, 15		12, 20
O. robusta Giesbrecht, 1891	1								12, 17
O. setigera Dana, 1849	1	2, 3, 9, 10, 13	5, 18		16		7, 11, 15, 19	6	12, 17, 20
O. similis (Claus, 1866)	1	2, 3, 9, 10	5	4			7, 14, 15, 19		17, 20
O. simplex (Farran, 1913)	1			4					17, 20
O. tenuis Rosendorn, 1913	1	2			16				12
O. vivida (Farran, 1913)	1			4					17

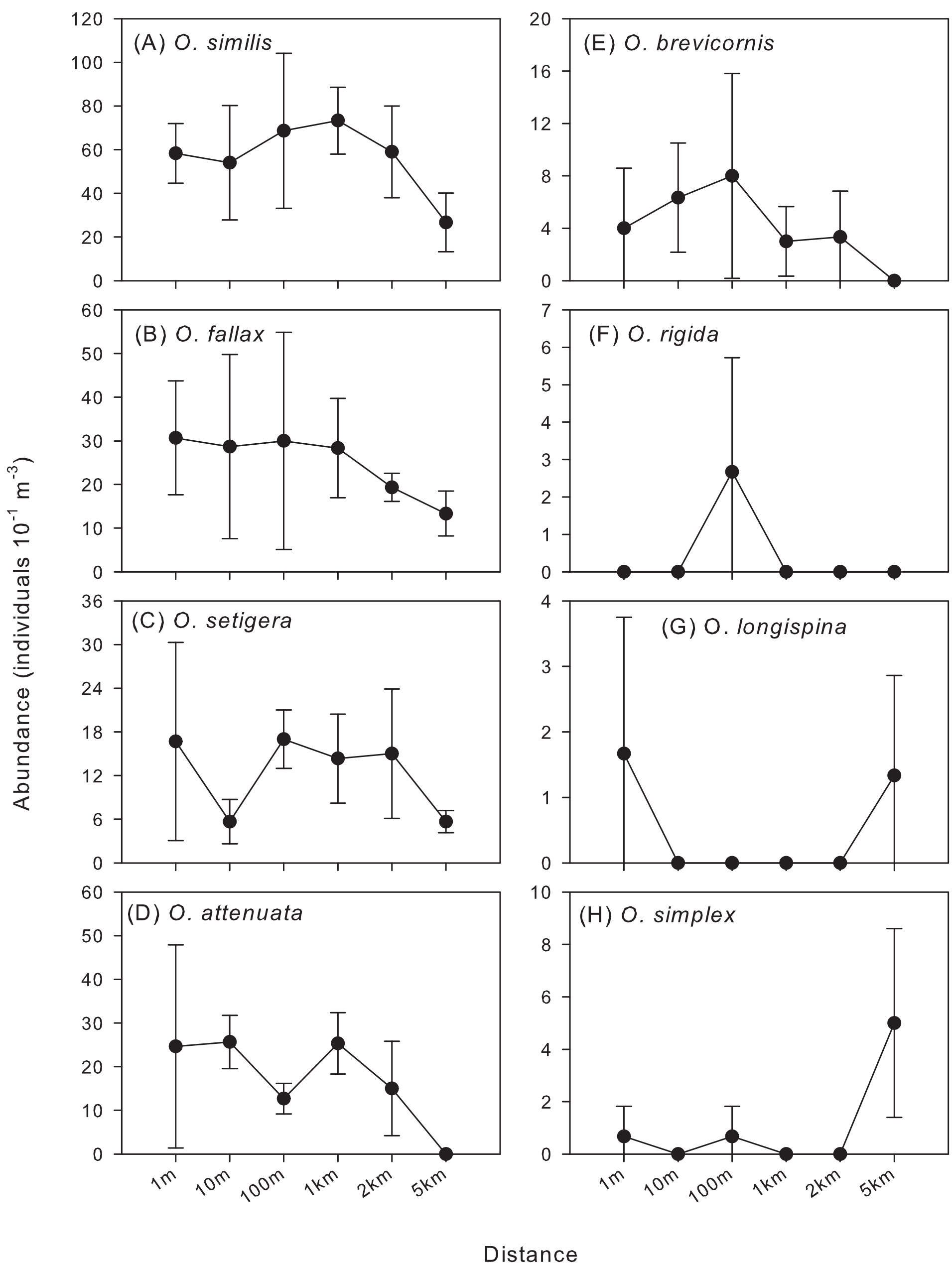

Fig. 4. Variation of abundance of *Oithona* spp. from Turtle Island.

Table 4
The proportionate abundances (%) of all *Oithona* spp. at different distant stations (see Fig. 5).

	Sampling station					
	1 m	10 m	100 m	1000 m	2000 m	5000 m
O. attenuata	18.05	21.33	9.07	17.55	13.43	0
O. brevic.	2.93	5.26	5.73	2.08	2.99	0
O. fallax	22.44	23.82	21.48	19.63	17.31	25.64
O. longisp.	1.22	0	0	0	0	2.56
O. rigida	0	0	1.91	0	0	0
O. setigera	12.20	4.71	12.17	9.93	13.43	10.90
O. similis	42.68	44.88	49.16	50.81	52.84	51.28
O. simplex	0.49	0	0.48	0	0	9.62

southern Iceland, southern Greenland (E & W), Strait of Davis, Labrador Sea (zone 2), Antarctic (zone 3), and the Central South-Atlantic (zone 4), Central Tropical Pacific (zone 16) and Eastern Tropical Pacific (zone 17). They demonstrate high community similarities between adjacent areas at short distance. In contrast, the *Oithona* copepod communities are low in abundance and similar between regions of the China Seas, Vietnam (zone 22), and the Indian Ocean (zone 23) (long distance), also between the Arctic Ocean (zone 1) and the Southern Ocean (zone 3).

The NMDS results cannot explain why the nearby zones (short distance) Arctic Ocean (zone 1) and Central South-Atlantic (zone 4) show a low similarity of *Oithona*. However, we want to point out the current dataset of identified *Oithona* copepods in each geographical zone was not collected from a standardized sampling strategy and/or equal sampling frequency (Antacli et al., 2010; Dur et al., 2007; Hwang et al., 2007b). The predictability of a correlation of community similarity-distances between each geographical zone are expected to become clear once more data will be added to the database (Dahms, 2014).

5. Conclusions

Inadequate considerations of small mesozooplankton such as the diverse species group *Oithona* underestimate its abundance, biomass, production, and the grazing impact of mesozooplankton on phytoplankton primary production, zooplankton-mediated fluxes of chemicals and materials, and marine trophic interactions in general. This is primarily due to the large mesh sizes employed during sampling. We demonstrate that the assemblage structure of *Oithona* spp. shows considerable variation at spatial scales. We report here about the remarkable horizontal variation in distribution on mesoscale as well as on global scale. We provide a first explanation of a spatial distribution pattern and a relationship between species richness and area, and community similarity and distance for the ecologically important free-living planktonic copepod *Oithona*.

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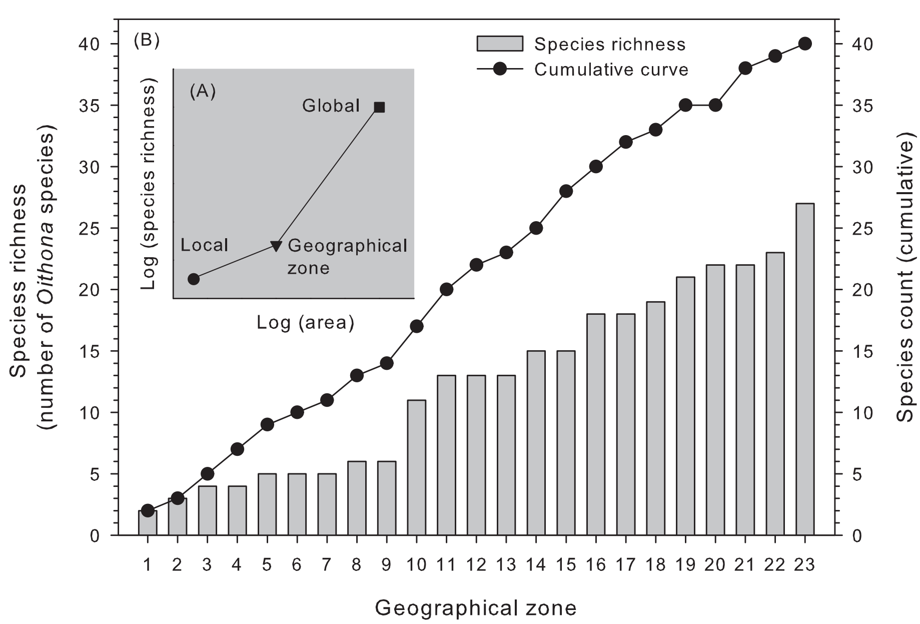

Fig. 5. Hypothetical spatial patterns of species richness–area on *Oithona* spp. diversity, the richness correlation of local (solid circle)-global (solid square) on *Oithona* spp. is estimated with the area (X-axis) by the species richness (Y-axis) (A). The current species richness of *Oithona* spp. at different scales - worldwide and smaller scale geographical zone relationships for copepods of *Oithona* spp. (B). The number represents the code for the geographical zone and the included areas are shown in Table 2.

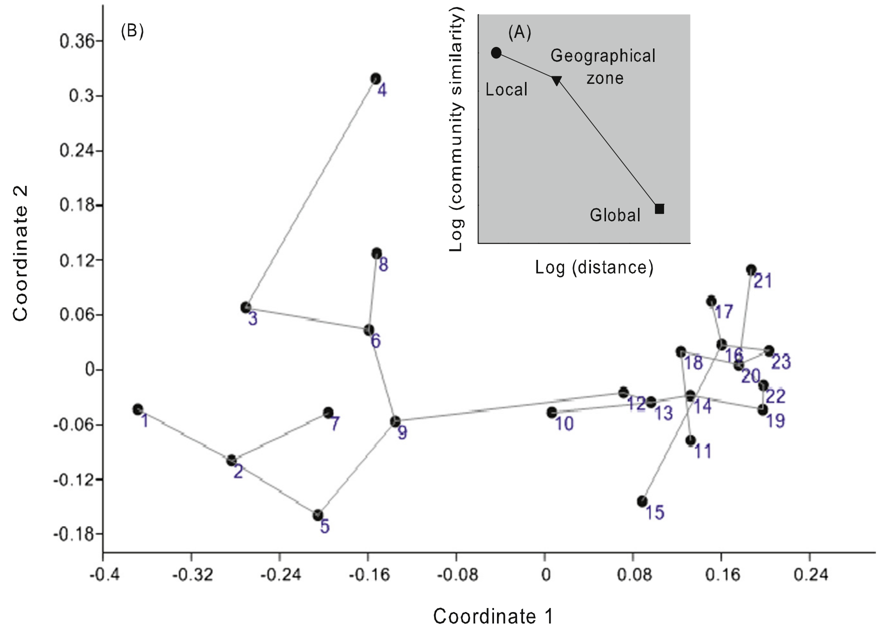

Fig. 6. Hypothetical spatial patterns of community similarity–distance on *Oithona* spp. distribution, the similarity correlation of local (solid circle)-global (solid square) on *Oithona* copepods is estimated with the distance (X-axis) by the community similarity (Y-axis) (A). The results of non-metric multidimensional scaling (NMDS) analysis demonstrating that currently community similarity and minimum spanning tree of *Oithona* spp. of each geographical zone in the world (B). The number represents a code for each geographical zone and their included area is demonstrated in Table 2.

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