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Seasonal Population Structure of the Copepod *Temora turbinata* (Dana, 1849) in the Kuroshio Current Edge, Southeastern East China Sea

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Abstract: The abundance of adult males, females, and copepodites, and sex ratio of a *Temora turbinata* population and seawater hydrology were studied from 2018 to 2019 in waters off northeast Taiwan, northwest Pacific Ocean. The hydrological parameters showed significant differences between sampling months caused by interactions of Kuroshio, East China Sea water, and the China Coastal Current. The highest average abundance was recorded from the June 2018 cruise with 2903.92 ± 3499.47 (inds. m^{-3}), followed by a cruise in June 2019 with an average abundance of 1990.64 ± 1401.55 (inds. m^{-3}). The sex ratio ranged between 0.25 and 2.33; the records were significantly higher in samples of June 2018 than during other sampling cruises (one-way ANOVA). The spatiotemporal distribution of *T. turbinata* showed a clear pattern of seasonal changes among sampling stations and distribution zones. Abundance of females and copepodites correlated significantly positive (r = 0.755, $p < 0.001$), whereas sex ratio (r = 0.247, $p = 0.119$) did not correlate significantly. The present study revealed that the abundance of *T. turbinate* was highest in June and was positively correlated with seawater temperature; furthermore, this is the first time the in situ sex ratio of *T. turbinata* in western Pacific waters has been reported.

Keywords: *Temora turbinata*; copepod; hydrology; Kuroshio Current; Kueishan Island; Northwest Pacific Ocean

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Citation: Wang, Y.-G.; Tseng, L.-C.; Xing, B.-P.; Sun, R.-X.; Chen, X.-Y.; Wang, C.-G.; Hwang, J.-S. Seasonal Population Structure of the Copepod *Temora turbinata* (Dana, 1849) in the Kuroshio Current Edge, Southeastern East China Sea. *Appl. Sci.* **2021**, *11*, 7545. https://doi.org/10.3390/app11167545

Academic Editor: Marco F. L. Lemos

Received: 18 June 2021
Accepted: 8 August 2021
Published: 17 August 2021

1. Introduction

Zooplankton provides important trophic links in aquatic and marine trophic webs by transferring energy and materials from microbes to higher trophic levels [1]. Zooplankters are the main natural food source of larval and juvenile fishes worldwide [2]. Zooplankters are valuable indicators of ecological conditions due to their intermediate position, linking primary production with consumers at higher levels of the trophic cascade, and being sensitive to environmental characteristics [1,3,4]. Zooplankters are sensitive to changing physical and chemical properties of waters. These abiotic parameters affect the spatial distribution and abundance of zooplankton [5–7]. As such, environmental changes could also affect the geographic distribution of certain species [3,8]. At the same time, some opportunistic species could adapt to particular environmental changes [9]. The copepod assemblage is the most dominant group of the zooplankton community and is considered as a key group in the marine pelagic environment [10].

The copepod genus *Temora* belongs to the family Temoridae with broadcast-spawning representatives. It is planktonic and important as it provides one of the major groups of prey for commercially shoaling fishes [11]. To date, a total of six species belong to the genus *Temora* worldwide. According to historical records, four species of *Temora* have been reported in waters around Taiwan [12–21]. Among those, *Temora turbinata* (Dana, 1849) and *Temora discaudata* (Giesbrecht, 1889) were recorded in the waters of northern Taiwan [22]. *Temora turbinata* has been recorded as the predominant species in mesozooplankton communities in various environments around the world, such as in Korea [23], in Taiwan [21], in Brazilian coastal waters [24], and in coastal and shelf waters [11], as well as tropical and subtropical areas in general [20,25–28]. This species is widely adapted to a variety of environments, such as polluted and eutrophicated waters, eutrophic lagoons, outfall areas, and nuclear power plant discharge areas [17,20,27,29–31]. *T. turbinata* could especially cooccur with the bloom-forming *Karenia brevis* in the Gulf of Mexico, a toxic dinoflagellate [32]. The feeding behavior of *T. turbinata* is opportunistic and omnivorous and depends on the food item composition in ambient waters. Previous reports found it primarily herbivorous and rarely carnivorous [33]. In addition, *T. turbinata* as a suspension feeder prefers microscopic and non- or slow-moving plankter, such as *Thalassiosira* spp. [34], and moving prey ciliates [35].

In dioecious species, the theoretical sex ratio is balanced (1:1, female:male), whereas biased sex ratios are quite common in nature [36–38]. The sex ratio represents an internal factor that affects population dynamics and growth [39,40]. In marine copepods, sex determination and sex ratios are governed by diverse hydrological factors, such as pH, chemical composition, temperature, depth, and hydrostatic pressure, which commonly leads to an alteration of sex ratios and reproductive timing [41–43]. For example, the sex ratio of *Acartia tonsa* increased from 0.3 ± 0.1 to 1.3 ± 0.1 with a decrease of salinity from 35 to 13 PSU in the laboratory [44]. Besides such abiotic factors, previous reports revealed that biotic factors, such as metabolism, reproductive age, and life span, also play important roles that affect the sex ratios of copepods [45–47]. The scarcity of data referring to in situ sex ratios is also due to the effect of differential vertical migration of sexes, and the difficulty of identifying sexes in immature copepodites. Sex ratio is, therefore, probably the most understudied population trait in copepod ecology [43].

A few studies reported developmental time, growth, length-weight relationship, chemical content, egg production rate, biomass, and temporal variation in the population production rate of *T. turbinata* from different ocean areas [30,48–54].

The sampling area was next to Kueishan Island located at the I-Lan Bay in the coastal waters of northeastern Taiwan which is affected by the Kuroshio Current (KC) [55]. The Kuroshio originates near the bifurcation of the North Equatorial Current at about 13° N, then flows northwards along the Philippine and Taiwan eastern coastlines to Japan and off Sanriku, east coast of Honshu, Japan. It affects one of the largest marine ecosystems worldwide and represents the major current in the west as a boundary in the northwest Pacific Ocean [56–58]. It flows over the I-Lan ridge before entering the East China Sea and transports warm water masses from the north Pacific tropical and intermediate waters [59–61]. Besides the Kuroshio, several freshwater discharges also affect the hydrological characteristics around Kueishan Island (KI) [62]. The southwest monsoon prevails during May to October and the northeast monsoon prevails during November to February in this region [63]. The river run-off is affected by weather changes and precipitation. The hydrology of I-Lan Bay strongly affects the aquatic biota in this area [64–66].

To date, we have only a limited understanding of the composition of *T. turbinata* populations, such as sex ratio and the proportion of copepodites and adults. At the southern coast of the ECS, *T. turbinata* is an important zooplankton species. Therefore, a comprehensive investigation of the issues of biology and ecology of *T. turbinata* is important and necessary. In the present study, the abundance of copepodites and male and female adults of *T. turbinata* were measured, and the spatiotemporal distribution patterns in waters off Northeastern Taiwan were compared to reveal the following issues: (1) the seasonal composition of *T. turbinata* populations in the zooplankton; (2) whether the geographic distribution of *T. turbinata* is correlated with zones of seabed depth; (3) the sex structure of *T. turbinata* during different monsoon periods in waters off northeastern Taiwan.

2. Materials and Methods

2.1. Sampling Area and Field Study

Field sampling was carried out during four cruises in June (Southwest monsoon period) and September (Southwest-Northeast monsoon transition period) in 2018, and March (Northeast monsoon period) and June (Southwest monsoon period) in 2019 around Kueishan Island, in I-Lan Bay off northeastern Taiwan (Figure 1). Samples were collected from 12 selected stations distributed in three seabed depth zones [shallow depth zone (<200 m), middle depth zone (200–400 m), deep depth zone (>400 m)] during each cruise (Table 1). In the past, the research methods of copepods in this water area were to collected samples from surface zone, such as [7,55,67]. Therefore, the present study collected samples from the surface zone for do comparison with the past studies. A conical net (45 cm in diameter, 200 µm mesh size, and 180 cm length) was horizontally towed in surface waters (above the 10 m depth contour) for 10 min at each station to collect zooplankton samples. A flow-meter (Hydrobios, Germany) was fixed at the center of the net mouth to calculate the respective filtered water volumes. Zooplankton samples were immediately preserved in 5–10% neutralized seawater-formalin for identifying and counting their abundance in the laboratory. The hydrographic parameters temperature and salinity were measured by Sea-bird CTD equipment at each station.

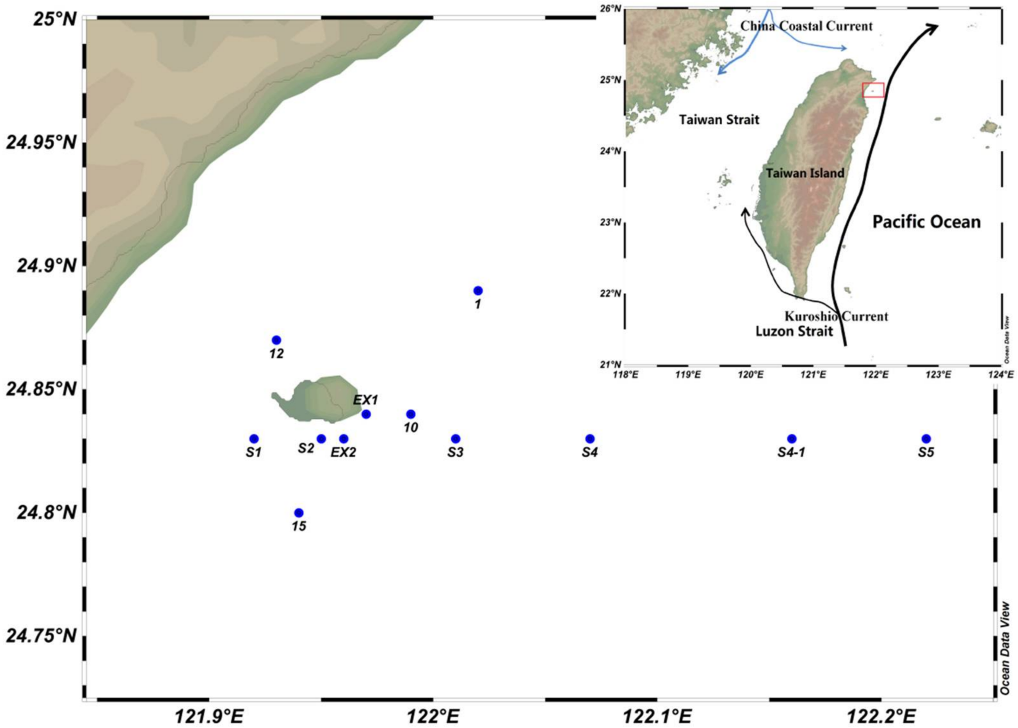

Figure 1. Sampling stations in the area of investigation along the northeastern Taiwan coast.

Table 1. Location and depth of sampling stations in waters off northeastern Taiwan, SZ = shallow depth zone (<200 m), MZ = middle depth zone (200–400 m), DZ = deep depth zone (>400 m).

Station	Longitude (E)	Latitude (N)	Seabed Depth	Grouping
St 1	24°53.42′	122°01.17′	454	DZ
St 10	24°50.46′	121°59.40′	210	MZ
St 12	24°52.33′	121°55.90′	130	SZ
St 15	24°48.01′	121°56.45′	273	MZ
St Ex1	24°50.57′	121°58.02′	123	SZ
St Ex2	24°49.81′	121°57.75′	156	SZ
St S1	24°50.06′	121°54.92′	167	SZ
St S2	24°49.67′	121°57.16′	57	SZ
St S3	24°49.93′	122°00.25′	288	MZ
St S4	24°50.10′	122°04.08′	674	DZ
St S4-1	24°50.09′	122°09.64′	536	DZ
St S5	24°50.06′	122°13.25′	878	DZ

2.2. Zooplankton Identification and Abundance Measurement

Zooplankton samples were divided by a Folsom plankton sample splitter until the subsamples contained about 300–500 individuals. *Temora turbinata* were identified with the help of related taxonomic references [68–71]. Male, female, and copepodites of *T. turbinata* were counted separately under a dissecting microscope (SMZ1500, Nikon, Tokyo, Japan). The number of each item was applied to calculate the in situ abundance of individuals per cubic meter (inds. m^{-3}).

2.3. Data Analysis

Spatial and temporal variations of *T. turbinata* populations were studied by collecting them from different monsoon throughout 4 cruises, and the PAST (Paleontological statistics [72]) software package was used to analyze the abundance and proportion of *T. turbinata* in each sample. A total of 48 samples were used to calculate similarities before clustering and nonmetric multidimensional scaling (NMDS) analyses. Euclidean distance was used to evaluate the relative similarity of populations between samples. In order to reduce the bias of samples, the functional test for transformation of data was applied prior to conducting a similarity analysis by Box and Cox [73]. The value (λ) was 0.919, therefore, the original abundance data of *T. turbinata* were using log10 (x + 1) for all samples. The value of sex ratio represents all male individuals divided by females in each sample.

One-way analysis of variance (ANOVA) with the post hoc Tukey's Honestly Significance Difference (HSD) test provided differences in population structure among sampling months and sampling zones. Pearson's correlation analysis estimated the relationship between abundance of copepods and hydrographic parameters. Statistical analysis made use of the statistical software package SPSS v24.

3. Results

3.1. Hydrological Conditions

The salinity profiles showed high variation during the four sampling cruises (Figure 2a–d), which was influenced by both the China Coastal water (CCW) and Kuroshio water (KW) in the study area. The observed salinity curves during the June 2018 and March 2019 cruises were similar to KW (Figure 2a,c). The salinity curves showed a wide variation and were mostly closed to the CCW curve during the September cruise in 2018 (Figure 2b). Most stations showed the salinity curve close to the CCW salinity curve, except station S5 which was weakly affected by the KW during the June cruise in 2019 (Figure 2d).

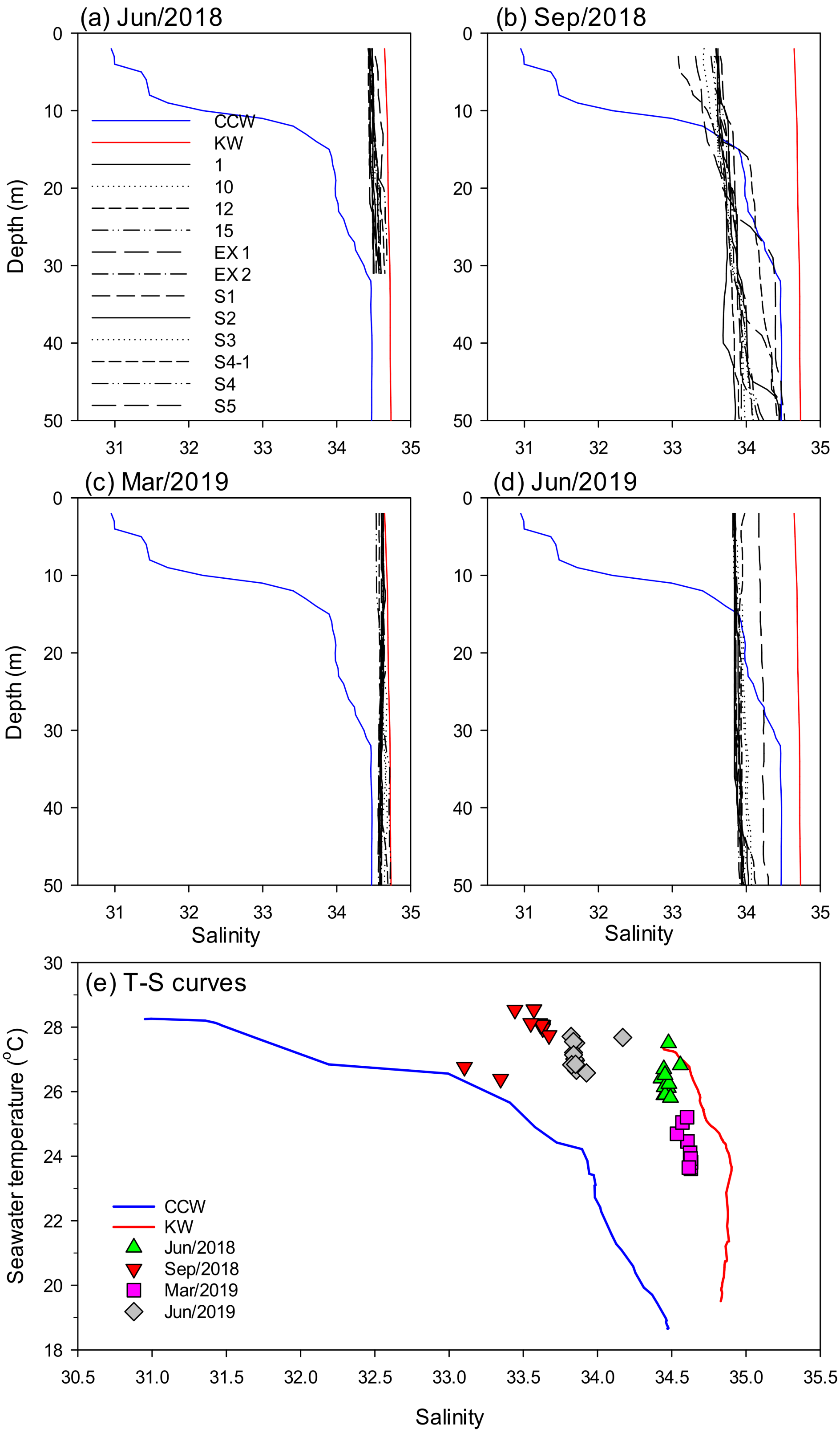

Figure 2. Salinity profile above 50 meters depth recorded at each sampling station. Data referred to 2018 in June (above 30 m depth) (**a**), September (**b**); and 2019 in March (**c**), June (**d**). The temperature (T) and salinity (S) diagram shows the distribution of averaged values of surface water (above the 10 m depth) of each sampling stations during all cruises (**e**). Two reference temperature–salinity curves were recorded from cruise OR1 618 between 15 July and 29 July 2001; the blue and red solid lines of T-S curves indicating the CCW (plume of Yangtze River; 30°30′ N 122°52′ E) and KW (Kuroshio water; 25°10′ N 123°10′ E) (adopted from Tseng et al. [30]), respectively.

Figure 2e shows at 5 m depth the correlation between salinity and temperature. The averaged surface seawater temperature (SST) was highest in September 2018 with values 27.87 ± 0.65 °C (mean ± standard deviation). During this cruise, SST varied from 26.39 °C to 28.55 °C, while the average sea surface salinity (SSS) was only 33.53 ± 0.16 PSU which was the lowest of all sampling cruises. During the cruises in June 2018 and June 2019, the average SST was 26.35 ± 0.48 °C and 27.14 ± 0.39 °C and the average SSS was 34.47 ± 0.03 PSU and 33.88 ± 0.10 PSU, respectively. The lowest average SST was 24.14 ± 0.57 °C, recorded during the cruise in March 2019, with the highest average SSS 34.61 ± 0.03 PSU. The SST limit was 23.61 to 25.21 °C in March 2019. The average SST and salinity were significantly different among the four sampling cruises ($p < 0.01$, one-way ANOVA).

3.2. Variation and Distribution of the *Temora turbinata* Population

The average abundance of *T. turbinata* showed a seasonal variation (Figure 3). The highest average abundance was recorded during the June 2018 cruise with 2903.92 ± 3499.47 (inds. m^{-3}). This was followed by the cruise in June 2019 with an average abundance of 1990.64 ± 1401.55 (inds. m^{-3}). The lowest average abundance was 96.35 ± 77.91 (inds. m^{-3}), recorded during the cruise in March 2019. During the September 2018 cruise, the abundance was 174.31 ± 176.05 (inds. m^{-3}), being a little higher than during the cruise in March 2019. Overall, the average abundance was lowered during the northeastern (March) and southwestern-northeastern monsoon transition period (September) compared to the southwestern monsoon period (June).

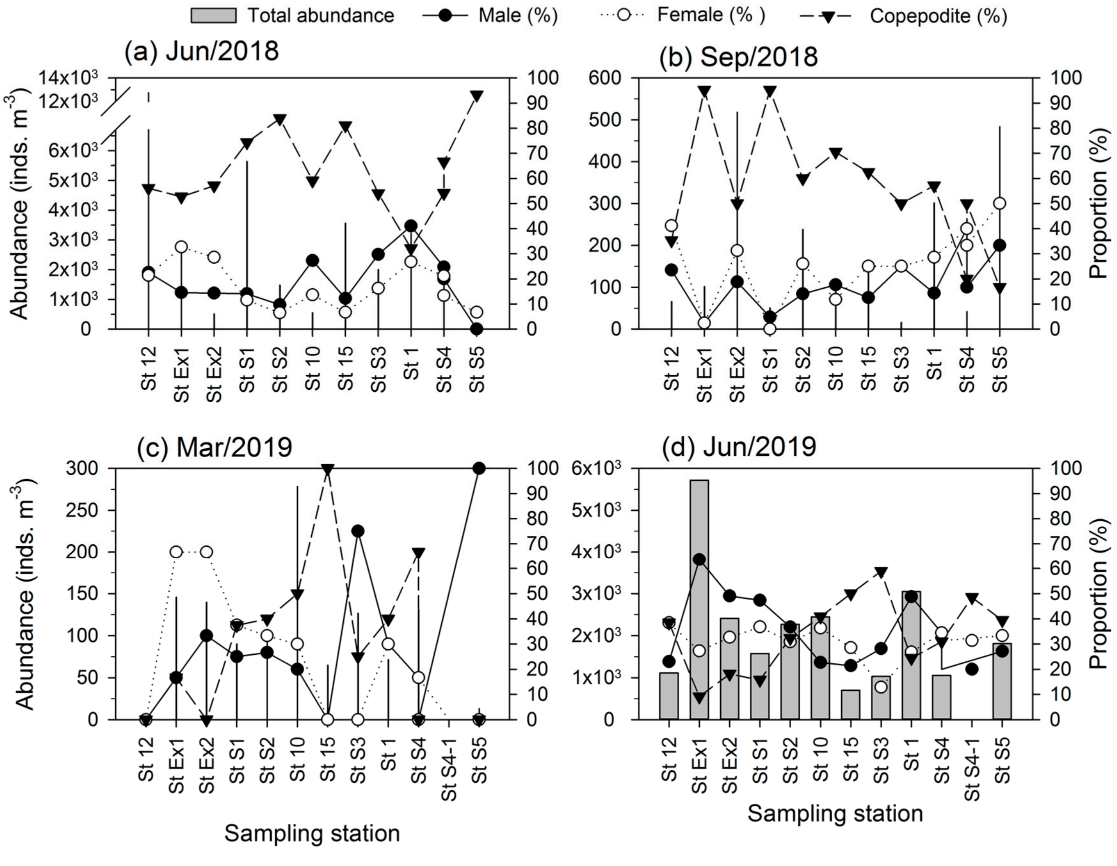

Figure 3. The variation of abundance and composition of *Temora turbinata* population during each cruise; variation in June (**a**), September (**b**) 2018; and March (**c**), June (**d**) 2019.

During the cruise in June 2018, the overall abundance ranged from 109.85 to 12,736.91 (inds. m^{-3}) (Figure 3a). The highest abundance was recorded at station 12 in the northwest of KI. During that cruise, the average abundance of males was 841.03 ± 975.37 (inds. m^{-3})

and that of females was 606.34 ± 394.21 (inds. m^{-3}); the highest average abundance of copepodites was 1751.09 ± 2080.13 (inds. m^{-3}), which was recorded during the cruise in June 2018. SST and salinity were 26.41 °C and 34.43 PSU at this station. The lowest abundance was recorded at station S5, being located in the most eastern area far away from KI. The SST and salinity were 26.82 °C and 34.56 PSU at station S5. The abundance at station S4-1 was 155.71 (inds. m^{-3}), which is near to station S5. The highest SST (27.50 °C) was recorded at station S4-1 during this cruise, where the salinity of the surface waters was 34.48 PSU. Taken together, the horizontal copepod distribution showed that the total abundance of the western inshore area was higher than in the eastern offshore area of KI.

During the cruise in September 2018, the average abundance of males and females was 34.04 ± 48.18 (inds. m^{-3}) and 54.60 ± 75.56 (inds.m^{-3}), and the copepodite average abundance was 76.18 ± 21.99 (inds. m^{-3}). The lowest total abundance was recorded at station S4 (9.80 inds. m^{-3}), which was located at the eastern offshore area with an SST of 28.12 °C. The highest abundance was recorded at station Ex2 (518.16 ind. m^{-3}), near to the east of KI with an SST of 28.07 °C. The abundance center appeared in the region of the southeastern coast of KI and the far eastern offshore area (Figure 3b). This was due to a relatively higher abundance at the offshore station S5 (483.34 inds. m^{-3}), where the SST was 26.39 °C.

A low abundance of the *T. turbinata* population appeared in March 2019 at station 12 which is located at the northwest of KI and at station S4-1 which is at the eastern offshore area of KI. During the spring cruise, the male average abundance was 27.14 ± 27.49 (inds. m^{-3}) and the female average abundance was 31.89 ± 38.13 (inds. m^{-3}), and the average abundance of copepodite stages was only 37.32 ± 42.11 (inds. m^{-3}). The horizontal distribution showed that the highest abundance (278.35 inds. m^{-3}) of the total *T. turbinata* population appeared at station 10 east of the KI area with SST 23.65 °C (Figure 3c).

The total abundance ranged from 698.98 to 5721.86 (inds. m^{-3}) during the June 2019 summer cruise. The average abundance of copepodites was 543.27 ± 229.13 (inds. m^{-3}) during the summer cruise in 2019 (Figure 3d). The highest abundance occurred at station Ex1, and was located close to the northeast coast of KI with the highest SST 27.71 °C. The lowest abundance was recorded at the eastern offshore stations S4 and 15 in the south of KI. The SST was 26.84 °C and 26.79 °C at stations S4 and 15, respectively. The horizontal distribution was similar to records during the June 2018 cruise. The population center of *T. turbinata* was in the east of KI.

3.3. Sex Ratio Differences of *Temora turbinata*

The sex ratio of *T. turbinata* demonstrated seasonal variation (Figure 4). Sex ratios were highest at station Ex1 during the cruise in June 2019, whereas the lowest recorded was 0.25 at station Ex1 in samples from March 2019. The one-way ANOVA results revealed that the sex ratio was significantly higher in samples of June 2018 (1.33 ± 0.51) than in September 2018 (0.76 ± 0.32, $p = 0.039$) and in March 2019 (0.70 ± 0.27, $p = 0.044$). The mean value for the sex ratio in June 2019 (1.23 ± 0.61) was not significantly different from other samplings ($p > 0.05$). It is worth noting that the sex ratio of *T. turbinata* showed a clear conversion phenomenon. In June, the proportion of adult males was relatively high. In contrast, the proportion of adult females was relatively high in September and March (Figure 4).

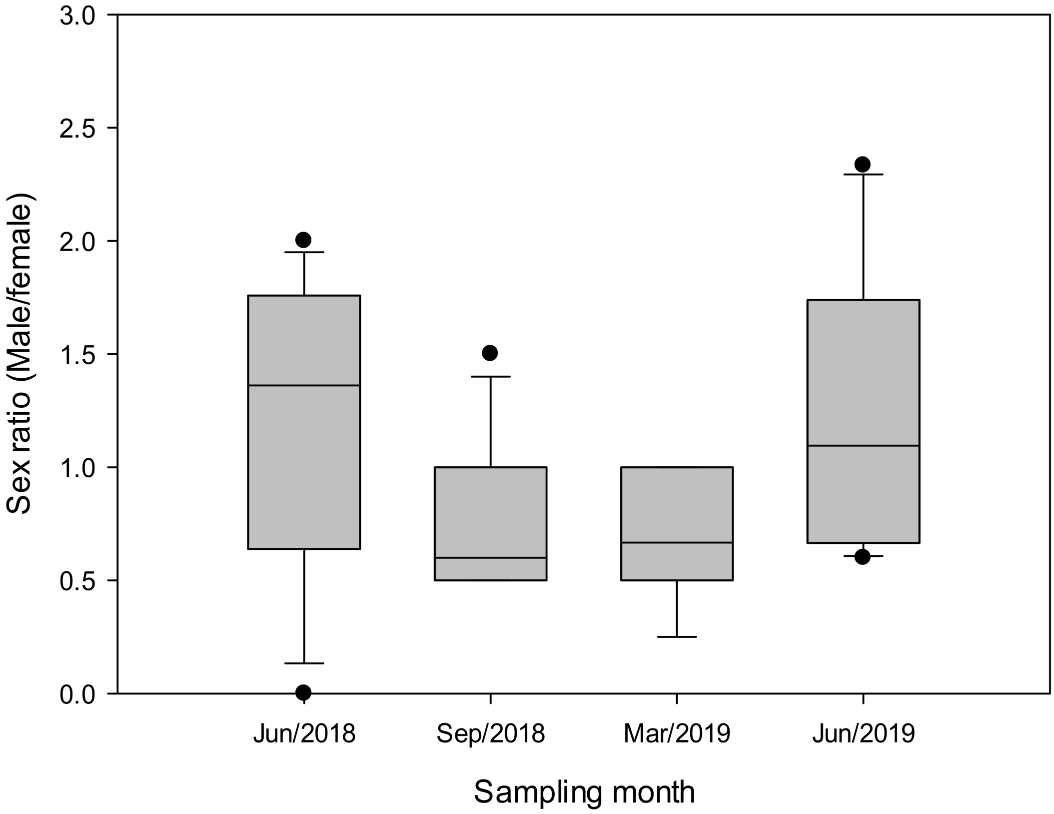

Figure 4. Male to female ratios of adult *Temora turbinata* during each cruise. The boundary of the box closest to zero and of the box farthest from zero marks the 25th percentile and the 75th percentile, respectively; a line within the box indicates the median. Whiskers (error bars) above and below the box mark the 90th and 10th percentiles.

3.4. Seasonal Population Structure of *Temora turbinata*

Cluster analysis results based on Euclidean distances are shown in Figure 5a. The cluster analysis results of the samples are mainly divided into two groups. The first group (group A) contains most samples from June 2018, June 2019, and two samples collected in September 2018. The second group (group B) contains most of the samples from September 2018, March 2019, and two samples from cruises in June 2018. The results of the cluster analysis proved that there were clear differences between the *T. turbinata* populations among seasons (Table 2). From the composition of the two groups, it can clearly be seen that the densities of adult males, adult females and copepodites in the samples of group A were higher than those of group B. A similar result is indicated by the proportion of copepodites in both groups that accounts for a relatively higher proportion of adult males compared to adult females. In contrast, the proportion of adult males in group A (29.72%) is higher than that in group B (20.19%), and the proportion of adult females in group B (26.23%) is higher than that of group A (23.76%). This phenomenon of switching proportions of adult individuals matches with the analysis of sex ratios (Figure 4).

Table 2. Composition of grouping results by cluster analysis, where numbers show abundance (inds. m^{-3}, mean ± SD) and their proportion (%) in parentheses.

Cluster Grouping	Group A	Group B
Adult male	736.4 ± 876.08 (29.72%)	23.05 ± 22.33 (20.19%)
Adult female	588.81 ± 575.61 (23.76%)	30.11 ± 32.87 (26.37%)
Copepodite	1152.73 ± 1569.72 (46.52%)	61.03 ± 50.65 (53.45%)

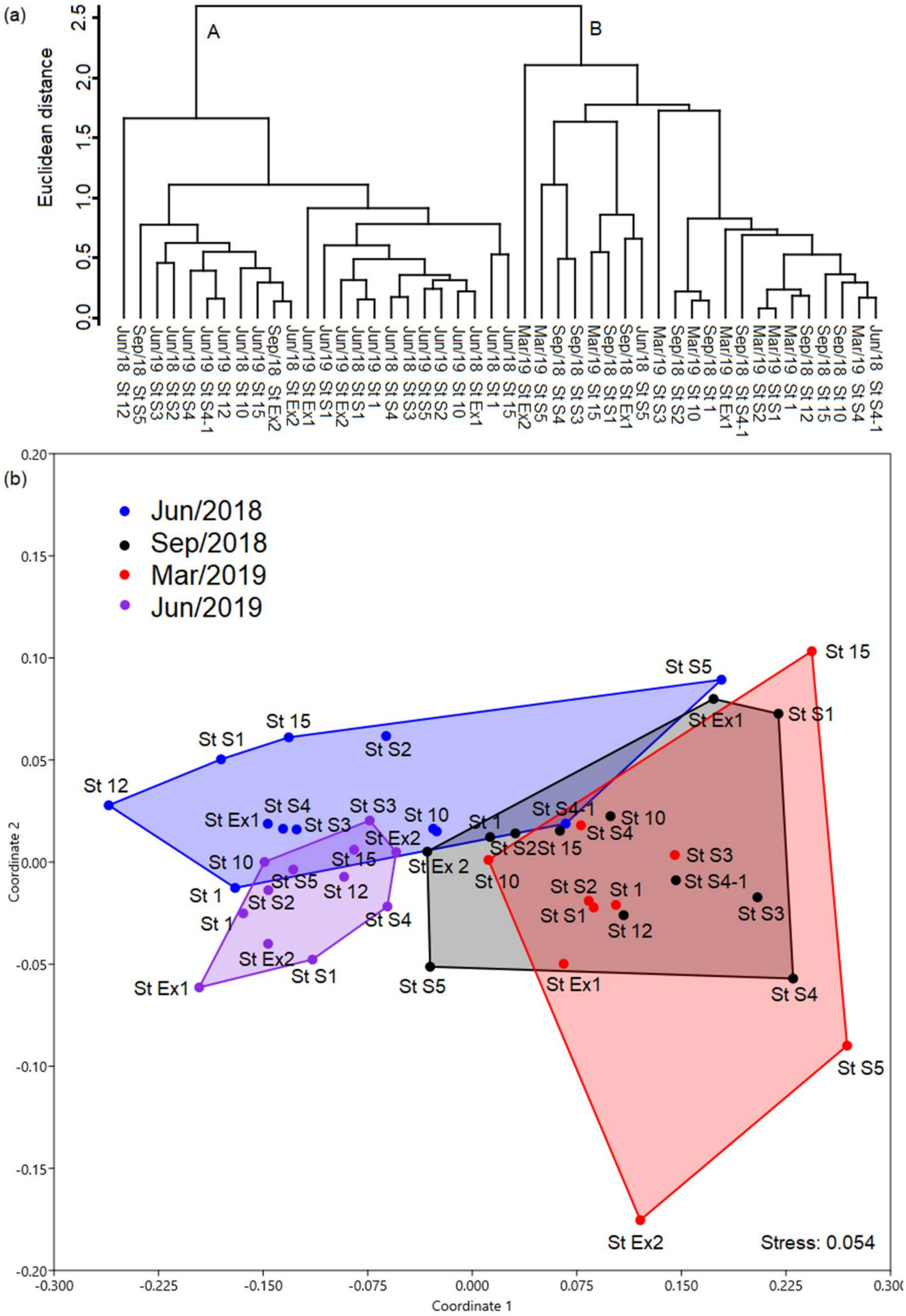

Figure 5. Clustering dendrogram of different *Temora turbinata* samples using Euclidean distances and clustering strategy of flexible links in the area off Northeastern Taiwan (**a**), and nonmetric multidimensional scaling of all samples (**b**).

The NMDS data of *T. turbinata* are shown in Figure 5b. The figure also indicates that the close distribution of *T. turbinata* having a similar population structure in samples collected in June 2018 and 2019 was apparently different from those collected in September 2018 and March 2019. Compared to the other months, variations in March 2019 were higher. The samples in September 2018 were distributed between the samples in June 2018 and March 2019, which is consistent with the characteristics of the monsoon transition period in September. The dynamic proportion of adult males, adult females, and copepodites in each sampling month indicated a seasonal succession.

3.5. Statistical Analysis of the Spatiotemporal Distribution of Temora turbinata

Among four sampling cruises, multiple comparisons of mean values for abundance of all adult males and females, as well as the copepodites of *T. turbinata*, were conducted using ANOVA, followed by a Tukey post hoc test. First, the temporal patterns of total *T. turbinata* abundances showed variations among sampling cruises (Figure 6). The abundance of all adult *T. turbinata* was significantly higher in June 2019 (1447.37 ± 1342.86 inds. m^{-3}) than in September 2018 (88.64 ± 123.5 inds. m^{-3}, $p = 0.012$) and March 2019 (59.03 ± 53.29 inds. m^{-3}, $p = 0.01$; Figure 6a). Similarly, the abundance of male *T. turbinata* was significantly higher in June 2019 (841.03 ± 975.37 inds. m^{-3}) than in September 2018 (34.04 ± 48.18 inds. m^{-3}, $p = 0.016$) and March 2019 (27.14 ± 27.49 inds. m-3, $p = 0.015$) (Figure 6b). The abundance of female *T. turbinata* was significantly higher in June 2018 (539.99 ± 752.99 inds. m^{-3}) and June 2019 (606.34 ± 394.21 inds. m^{-3}) than in September 2018 (54.6 ± 75.56 inds. m^{-3}, $p < 0.04$) and March 2019 (31.89 ± 38.13 inds. m^{-3}, $p < 0.03$) (Figure 6c). Furthermore, the abundance of copepodites of *T. turbinata* was significantly higher in June 2018 (1751.09 ± 2080.13 inds. m^{-3}) than in September 2018 (85.67 ± 76.18 inds. m^{-3}, $p = 0.002$), March 2019 (37.32 ± 42.11 inds. m^{-3}, $p = 0.001$), and June 2019 (543.27 ± 229.13 inds. m^{-3}, $p = 0.034$) (Figure 6d). In contrast, the abundance of all adult, male, female, and copepodite of *T. turbinata* were not significantly different to the location of stations across the three sampling depth zones ($p > 0.05$, one-way ANOVA) (Figure 7). The average abundance of *T. turbinata* showed no significant differences among the 12 selected stations ($p > 0.05$, one-way ANOVA). Similarly, there was no significant distribution pattern among sampling stations and depth zone during each sampling cruise ($p > 0.05$, one-way ANOVA).

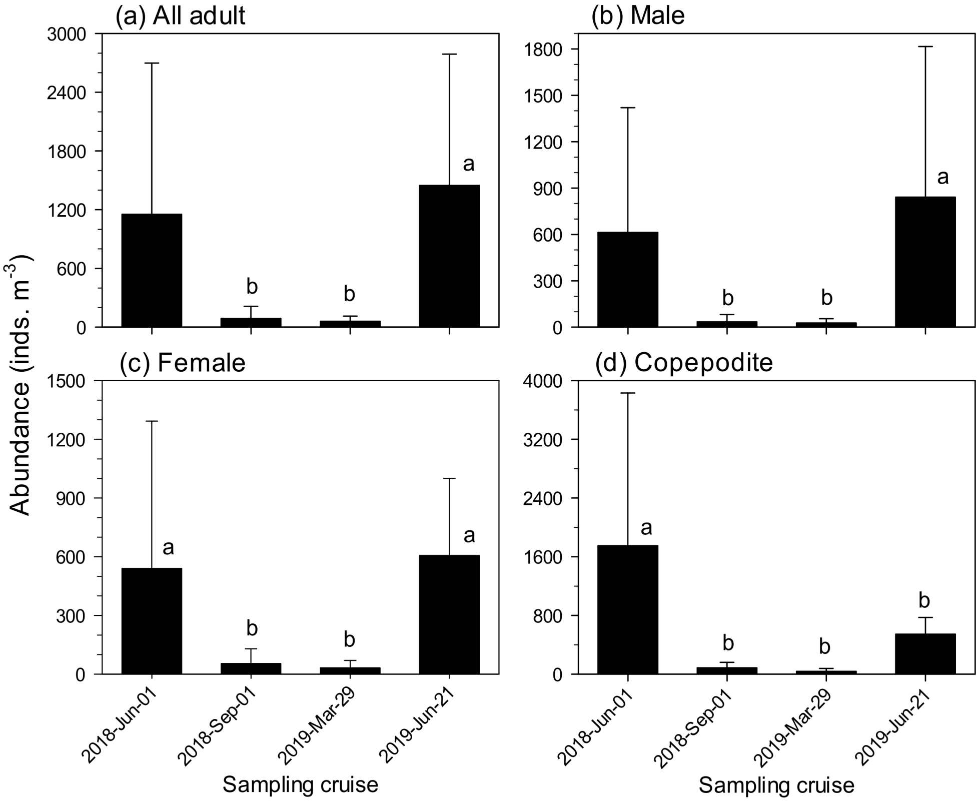

Figure 6. The abundance of all adults (**a**), males (**b**), females (**c**), and copepodites (**d**) of Temora turbinata throughout four samplings from June 2018 to June 2019 by using one-way analysis of variance, followed by Tukey test. Significant differences are indicated by different superscripts ($p < 0.05$) among the sampling months in the waters off Northeast Taiwan.

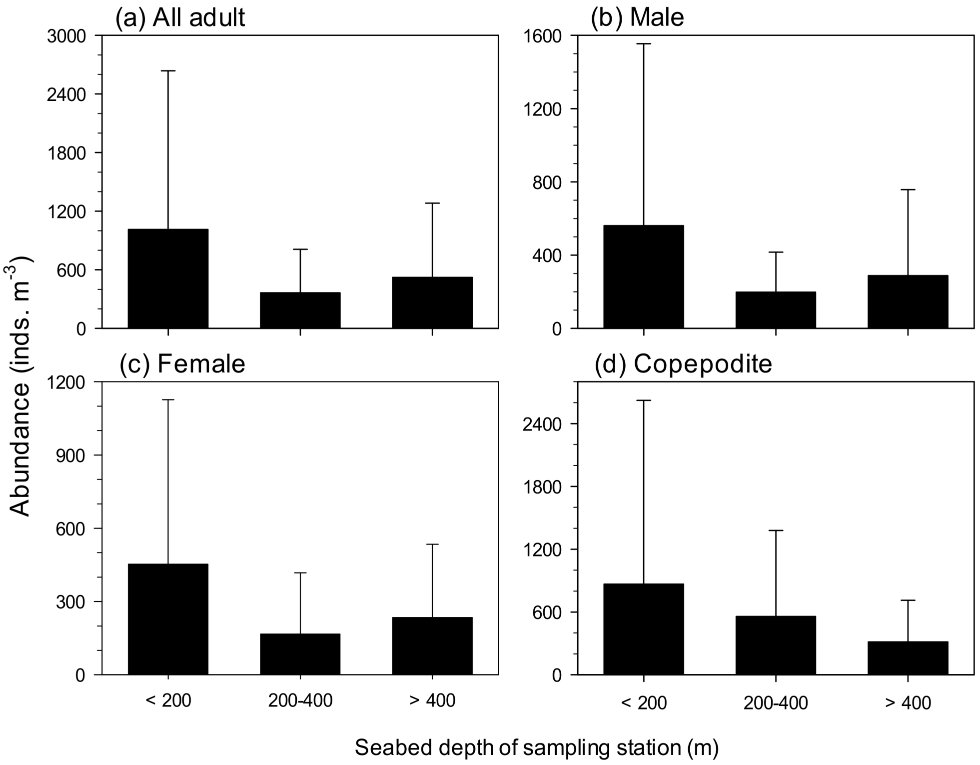

Figure 7. The abundance of all adults (**a**), males (**b**), females (**c**), and copepodites (**d**) of *Temora turbinata* among three seabed-depth zones from June 2018 to June 2019.

Abundance of all adult males and females, the copepodites, and the sex ratio (male/female) of *T. turbinata* were not significantly correlated with salinity and seawater temperature ($p > 0.05$) (Table 3). The abundance of all adult *T. turbinata* was significantly positive correlated with sex ratio (r = 0.405, $p = 0.009$). It is worth noting that there was a significantly positive correlation between the abundance of females and the abundance of copepodites (r = 0.755, $p < 0.001$), whereas this was not significantly correlated with sex ratio (r = 0.247, $p = 0.119$) (Table 3).

Table 3. Correlation results of all adult abundance (individuals m^{-3}), male abundance, female abundance, copepodite abundance, and sex ratio (male/female) according to Pearson's correlation analysis. The value represents the correlation (r), and the value in parentheses represents p.

	All Adult Abundance	Male Abundance	Female Abundance	Copepodite Abundance	Sex Ratio
Salinity	−0.014 (0.923)	−0.027 (0.854)	0.005 (0.972)	0.197 (0.180)	0.106 (0.511)
Temperature	0.175 (0.233)	0.181 (0.219)	0.157 (0.286)	0.025 (0.866)	0.194 (0.223)
All adult abundance		0.983 ** (<0.001)	0.964 ** (<0.001)	0.661 ** (<0.001)	0.405 ** (0.009)
Male abundance			0.899 ** (<0.001)	0.569 ** (<0.001)	0.496 ** (0.001)
Female abundance				0.755 ** (<0.001)	0.247 (0.119)
Copepodite abundance					0.196 (0.218)

**. Correlation is significant at the 0.01 level (2-tailed).

4. Discussion

4.1. Hydrography off Northeastern Taiwan Waters

In the northwestern Pacific, the seasonal monsoon, impinging eddies, and typhoons affect the Kuroshio Current (KC) and shift its path [74,75]. During the northeast monsoon in winter, the southward cold current (such as the China Coast Current marked with blue arrows in Figure 1) increased and the Kuroshio Current (the pathway was marked with black arrows in Figure 1) shifted closer to the eastern shore of Taiwan, whereas during the southwest monsoon in summer, fall and spring, the KC moved seawards [74,76]. Where the KC encountered the continental shelf of China in the ECS, the I-Lan ridge northeast of Taiwan, its mainstream was forced to turn northeastwards [77]. A small branch of the KC maintained its momentum towards the shelf, mixing the waters of the ECS and the KC, providing a complex oceanographic environment [78,79] which subsequently greatly affected the biota [16,17,55,66,80]. The Kuroshio waters transport tropical and subtropical fauna, and transport neritic fauna towards offshore, this way increasing the diversity of the mesozooplankton assemblage in I-Lan Bay [55,80]. The present study investigated the seasonal distribution and variation of *T. turbinata* populations in the area around KI, revealing remarkable differences in spatiotemporal variability throughout the developmental cycles of its populations.

4.2. Biology and Ecology of *Temora turbinata*

Temora turbinata is a warm water epipelagic, neritic species. It can tolerate wide ranges of temperature (5–35 °C) and salinity (20–45 ppt). The ideal temperature and salinity for its culture was 25–28 °C and 30–35 ppt, respectively [81]. It is more frequent and more abundantly recorded in the northern hemisphere compared to the southern hemisphere [82]. *Temora turbinata* was more dominant at low salinity waters in the Indus Delta of Pakistan [81]. Ara reported that the most dominant *Temora stylifera* was substituted by *T. turbinata* along the southern border of São Paulo State [27,83].

Temora turbinata was reported to be associated with the KBC in the Taiwan Strait [3,21,84,85] and was also commonly found around coastal waters of Taiwan [7,20,85–87]. Hwang et al. [3] and Dur et al. [88] found that *T. turbinata* occurred in waters of >28 °C temperature and was considered as a warm-water indicator species in the northwest of Taiwan. Tseng et al. [20] reported about the decadal data of *T. turbinata* and found that it was an important copepod species, abundant in the southwestern monsoon prevailing period from waters adjacent to nuclear power plants along the northeast coast of Taiwan. In their research, peak of abundance was recorded in summer, indicating a possible temperature effect, and was followed by a second peak in autumn. The lowest record of abundance was 96.35 ± 77.91 (inds. m^{-3}) in spring when the northeastern monsoon prevails. Previous studies confirmed that *T. turbinata* has strong adaptability and could survive in various environments. Therefore, it represents the most dominant copepod species and is representative of the mesozooplankton in coastal Taiwan waters.

Copepods account for the majority of mesozooplankton abundance in the open seas of the tropics and can comprise 70% or more of the zooplankton community in abundance and about 30% of its biomass [89]. However, copepod populations in the field are dominated by juvenile stages. The abundance of copepodites usually outnumbers those of adults [90]. For example, copepodites account for 27–41% of total zooplankton abundance in the southeastern Baltic Sea [91]. McKinnon and Duggan [90] reported copepodite percentages ranging between 59.77% and 90.82% of the total copepod numbers in Bathurst Island, Indonesia, Darwin Harbour, the Arafura Sea, Kimberley, the Great Barrier Reef, Northwest Cape, and Scott Reef. In this research, the percentage of copepodite limits was 27.29% to 60.30%, which is relatively lower than reported from other areas. The copepodite percentage may be closely related to the differences in life strategies and life spans of different species. For example, *T. turbinata* spawned about 15–30 eggs per day almost without diapause or dormant eggs. At optimal temperature conditions, about 80% eggs hatched after 15–20 h and it would take about 15 days from the naupliar phase to metamorphose into adults.

The life span of the adults was reported to be about 20–25 days [81], while the longevity of *A. tonsa*, which belongs to the Acartiidae Family, was about (29.31 ± 5.9) to (32.52 ± 6.1) days in laboratory cultures under different salinity conditions [44]. The longevity of *T. turbinata* was obviously longer than *A. tonsa*.

4.3. Sex Ratio of Copepods

Unbalanced sex ratios were discovered at the beginning of the 20th century by Sewell [92]. Kiørboe [40] reviewed the sex ratio of 12 copepod families and pointed out that the values varied between 0.15 and 1.1. The general sex ratios were higher and had a wider range of variation in broadcast spawners than in sac spawners (Table 4). Hirst and Kiørboe [93] reported that the sex ratio of *Temora longicornis* was lowest with 0.75 during February to October in 1947 and the highest number was recorded with 1.63 during March to September in 1993. The sex ratio of *Temora stylifera* ranged from 0.32 (from September 1971 to August 1973) to 1.27 (during September 1986 to June in 1988). The present study found that *T. turbinata* and the other two congener species (*T. longicornis* and *T. stylifera*) show similar changes in sex ratio.

Table 4. Field adult sex ratio of planktonic copepods (adopted from Hirst and Kiørboe [93]).

Species	Sex Ratios	Period	Location	References
Family Acartiidae				
Acartia bifilosa	0.59	January/1970–October/1971	Kiel Bay, Baltic	Schnack [94]
A. bifilosa	0.35	January–December/1993	Southampton Water, UK	Hirst et al. [95]
Acartia clausi	0.72	April–December/1993	Southampton Water, UK	Hirst et al. [95]
A. clausi	0.2	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
A. clausi	0	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
A. clausi	0.75	January–October/1933	Loch Striven, Scotland	Marshall [96]
A. clausi	0.56	January–November/1947	Plymouth Area, English Channel	Digby [97]
A. clausi	0.75	November/1971–December/1972	Damariscotta River estuary, USA	Lee and McAlice [98]
Acartia discaudata	0.89	March–December/1993	Southampton Water, UK	Hirst et al. [95]
A. discaudata	0.45	January/1970–October/1971	Kiel Bay, Baltic	Schnack [94]
Acartia longiremis	0.67	January/1970–October/1971	Kiel Bay, Baltic	Schnack [94]
A. longiremis	0.18	October/1985–October/1986	Balsfjorden, Norway	Norrbin [99]
A. longiremis	0.39	November/1971–December/1972	Damariscotta River estuary, USA	Lee and McAlice [98]
Acartia omori	0.79	November/1986–July/1987	Fukuyama Harbor, Inland Sea of Japan	Liang and Uye [100]
Acartia tonsa	0.39	January/1970–October/1971	Kiel Bay, Baltic	Schnack [94]
A. tonsa	1.44	November/1971–December/1972	Damariscotta River estuary, USA	Lee and McAlice [98]
Family Calanidae				
Calanus finmarchicus	0	August/1950–August/1961	Scoresby Sound, East Greenland	Digby [101]
C. finmarchicus	0.23	February–August/1933	Scottish Waters	Gibbons [102]
Calanus finmarchicus	0.25	June/1933–May/1934	Oslo Fjord, Norway	Wiborg [103]
C. helgolandicus	0.18	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
C. helgolandicus	0.08	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
C. helgolandicus	0.04	3 seasons	North Aegean Sea	Moraitou-Apostolopoulou [104]
Calanus minor	0.28	3 seasons	North Aegean Sea	Moraitou-Apostolopoulou [104]
Calanus tenuicornis	0.01	3 seasons	North Aegean Sea	Moraitou-Apostolopoulou [104]

Table 4. *Cont.*

Species	Sex Ratios	Period	Location	References
Undinula vulgaris	0.33	September/1971–August/1973	St Vincents, Barbados	Moore and Sander [105]
Family Candaciidae				
Candacia armata	0.39	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
C. armata	0.75	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
Family Centropagidae				
Centropages hamatus	1.78	March–October/1933	Loch Striven, Scotland	Marshall [96]
C. hamatus	1.04	January/1970–October/1971	Kiel Bay, Baltic	Schnack [94]
C. hamatus	0.37	March–December/1993	Southampton Water, UK	Hirst et al. [95]
C. hamatus	1.13	June/1933–May/1934	Oslo Fjord, Norway	Wiborg [103]
Centropages typicus	0.81	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
C. typicus	0.79	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
C. typicus	0.85	January–October/1947	Plymouth Area, English Channel	Digby [97]
C. typicus	0.72	3 seasons	North Aegean Sea	Moraitou-Apostolopoulou [104]
C. typicus	0.72	February/1965–December/1965	North Aegean Sea	Moraitou-Apostolopoulou [106]
Centropages violaceus	0.59	3 seasons	North Aegean Sea	Moraitou-Apostolopoulou [104]
Family Clausocalanidae				
Clausocalanus spp.	0.15	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
Clausocalanus spp.	0.18	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
Microcalanus pygmaeus	1.4	January–October/1933	Loch Striven, Scotland	Marshall [96]
M. pygmaeus	0.03	August/1950–August/1951	Scoresby Sound, East Greenland	Digby [101]
M. pygmaeus	0.25	June/1933–May/1934	Oslo Fjord, Norway	Wiborg [103]
Pseudocalanus acuspes	0.43	October/1985–October/1986	Balsfjorden, Norway	Norrbin [99]
Pseudocalanus elongatus	0.27	January–December/1947	Plymouth Area, English Channel	Digby [97]
P. minutus	0.28	January–October/1933	Loch Striven, Scotland	Marshall [96]
P. minutus	0.03	August/1950–August/1951	Scoresby Sound, East Greenland	Digby [101]
P. minutus	0.25	June/1933–May/1934	Oslo Fjord, Norway	Wiborg [103]
Pseudocalanus sp.	0.39	January/1970–October/1971	Kiel Bay, Baltic	Schnack [94]
Family Euchaetidae				
Euchaeta marina/acuta	0.22	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
E. marina/acuta	0.19	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
Euchaeta norvegica	0.12	September/1971–April/1972	Loch Etive, Scotland	Hopkins [107]
Family Metridiidae				
Metridia longa	0	August/1950–September/1950	Scoresby Sound, East Greenland	Digby [101]
M. longa	0.54	June/1933–August/1938	Oslo Fjord, Norway	Wiborg [103]
Pleuromamma gracilis	0.52	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
P. gracilis	0.41	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]

Table 4. *Cont.*

Species	Sex Ratios	Period	Location	References
Family Oithonidae				
Oithona nana	0.27	August–December/1947	Plymouth Area, English Channel	Digby [97]
Oithona similis	0.18	January–October/1933	Loch Striven, Scotland	Marshall [96]
O. similis	0.18	January–December/1947	Plymouth Area, English Channel	Digby [97]
O. similis	0.06	August/1950–August/1951	Scoresby Sound, East Greenland	Digby [101]
Family Oncaeidae				
Oncaea borealis	0.45	August/1950–August/1951	Scoresby Sound, East Greenland	Digby [101]
O. borealis	0.32	June/1933–May/1934	Oslo Fjord, Norway	Wiborg [103]
Oncaea mediterranea	0.75	September/1971–August/1973	St Vincents, Barbados	Moore and Sander [105]
Family Paracalanidae				
Paracalanus parvus	0.15	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
P. parvus	0.1	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
P. parvus	0.15	July–October/1933	Loch Striven, Scotland	Marshall [96]
P. parvus	0.18	August/1970–October/1971	Kiel Bay, Baltic	Schnack [94]
P. parvus	0.1	January–December/1947	Plymouth Area, English Channel	Digby [97]
Paracalanus sp.	0.45	November/1986–October/1987	Fukuyama Harbor, Inland Sea of Japan	Liang and Uye [108]
Family Pseudodiaptomidae				
Pseudodiaptomus binghami	0.22	June–September of 1971–1973	Mandovi Estuary, India	Goswami [109]
P. binghami	0.22	June–September of 1971–1973	Zuari Estuary, India	Goswami [109]
P. binghami	0.2	June–September of 1971–1973	Cumbarjua Canal, India	Goswami [109]
Pseudodiaptomus marinus	0.64	November/1986–November/1987	Fukuyama Harbor, Inland Sea of Japan	Liang and Uye [110]
Family Temoridae				
Temora longicornis	1.08	March–October/1933	Loch Striven, Scotland	Marshall [96]
T. longicornis	0.75	February–October/1947	Plymouth Area, English Channel	Digby [97]
T. longicornis	1.04	January/1970–October/1971	Kiel Bay, Baltic	Schnack [94]
T. longicornis	1.63	March–September/1993	Southampton Water, UK	Hirst et al. [95]
Temora stylifera	1.27	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
T. stylifera	0.85	September/1986–June/1988	Golfe du Lion, Mediterranean	Kouwenberg [47]
T. stylifera	0.75	3 seasons	North Aegean Sea	Moraitou-Apostolopoulou [104]
T. stylifera	0.75	February/1965–December/1965	North Aegean Sea	Moraitou-Apostolopoulou [106]
T. stylifera	0.32	September/1971–August/1973	St Vincents, Barbados	Moore and Sander [105]
Temora turbinata	1.13	June/2018	Kueishan Island	Present study
T. turbinata	0.62	September/2018	Kueishan Island	Present study
T. turbinata	0.85	March/2019	Kueishan Island	Present study
T. turbinata	1.39	June/2019	Kueishan Island	Present study

The sex ratio of pelagic copepods is typically female biased. Species of the copepod families Oithonidae and Paracalanidae were often recorded with extremely female-skewed sex ratios [40,111,112]. Hirst et al. [112] estimated that predation contributed to more than 69% of the field mortality rate in adult males, whereas in adult females it was about 36%.

This suggests that the male to female ratio skews in pelagic copepods were primarily caused by differential predation mortality of the sexes in the adult stage [112]. Lack of food can cause female-skewed sex ratios and if females have low physical fitness, this would result in a decrease of population size [113]. In contrast, the low survival rate of males in an environment lacking food leads to a change in sex ratios [114]. A female-biased sex ratio due to the higher mortality of males to females was found during cyanobacteria blooms in an open sea area near to Storfjärden, Baltic Sea [115]. Moreover, a harmful dinoflagellate bloom was reported to decrease the abundance of male copepods [116,117]. Male life span is shortened [38]. Further investigations should be carried out to clearly understand the interaction of sex ratio with the dynamics of populations.

5. Conclusions

The hydrographic environment across our survey area was dominated by the mixing of water masses of the Kuroshio Current with near shore waters. The water masses showed an obvious seasonal successional variation indicating possible temperature effect during our research. The abundance of *T. turbinata* was mainly linked to hydro-parameters such as seawater temperature. The results confirmed that *T. turbinata* showed significant seasonal changes as indicated by previous studies in coastal areas of Taiwan. The present study revealed for the first time the in situ sex ratio of *T. turbinata* in western Pacific waters. Population dynamics are as yet very little studied in the area, and they are worth investigating in more detail in the future. Furthermore, information about food supply, mortality, and high spatiotemportal sampling resolution will be needed to comprehensively understand the population dynamics of *T. turbinata* in these understudied waters.

Author Contributions: Conceptualization, Y.-G.W., J.-S.H. and C.-G.W.; methodology, Y.-G.W. and L.-C.T.; software, J.-S.H. and B.-P.X.; validation, Y.-G.W., L.-C.T. and R.-X.S.; formal analysis, L.-C.T. and Y.-G.W.; investigation, Y.-G.W. and J.-S.H.; resources, J.-S.H. and X.-Y.C.; data curation, Y.-G.W. and L.-C.T.; writing—original draft preparation, Y.-G.W. and L.-C.T.; writing—review and editing, J.-S.H., C.-G.W., B.-P.X., R.-X.S. and X.-Y.C.; visualization, Y.-G.W., B.-P.X., R.-X.S. and X.-Y.C.; supervision, J.-S.H. and C.-G.W.; project administration, J.-S.H. and X.-Y.C.; funding acquisition, J.-S.H. All authors have read and agreed to the published version of the manuscript.

Funding: We are grateful for the financial support from the Ministry of Science and Technology (MOST) of Taiwan through grants from MOST 107-2811-M-019-004, MOST 108-2811-M-019-504, MOST 109-2811-M-019-504, and MOST 110-2811-M-019-504 to L.-C.T. The grants MOST 105-2621-M-019-001, MOST 106-2621-M-019-001, MOST 107-2621-M-019-001, MOST 108-2621-M-019-003, MOST 109-2621-M-019-002, and MOST 110-2621-M-019-001, and grants from the Center of Excellence for Ocean Engineering through Grant no. 109J13801-51 to J.-S.H. This work was also supported by the Monitoring and Protection of the Seamount Ecosystem in the Western Pacific Ocean (DY135-E2-2-04), Bilateral Cooperation of Maritime Affairs, The Marine Biological Sample Museum Upgrade And Expansion (GASI-01-02-04) and Biological classification system research of the Global climate change and ocean atmosphere interaction research. The authors are grateful to members of J.-S. Hwang's laboratory for their assistance during the field works during cruises to the waters off northeastern Taiwan.

Institutional Review Board Statement: Ethical review and approval were waived for this study, due to the involvement (=sampling) of invertebrates that were not protected nor harmed during sampling.

Informed Consent Statement: Not applicable.

Data Availability Statement: The authors confirm that the data supporting the findings of this study are available within the article.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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