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History of Colonization of Jeju Island (Republic of Korea) by the Water Fleas (Crustacea: Cladocera) Is Reflected by the Seasonal Changes in Their Fauna and Species Associations

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Abstract: The aim of this paper is to study the species composition, structure and seasonal dynamics of the cladoceran fauna and species associations in inland water bodies of Jeju Island (Republic of Korea). Only 47 taxa were found in 199 samples. Such faunal paucity could be explained by the existence of only a few types of aquatic environments on Jeju Island as compared to continental China and the Far East of Russia, with their great diversity of water types. We have demonstrated a high significance of the tropical species on Jeju. Our data confirm seasonal faunistic changes in the continental waters of Jeju Island. The rate of tropical taxa is highest in September, after the monsoon season, while the Far Eastern endemic taxa are more common in winter. At the same time, the contribution of Boreal taxa to the fauna of the island is low even in winter. Species associations have been revealed based on binominal distribution; they change significantly from summer to winter. However, a contribution of Boreal taxa to the species associations also is minimal (even in winter), whereas tropical taxa contribute to them greatly (including in winter). We can propose a rough scheme of faunal formation exploring the whole set of obtained information. Initially, at the earlier stages of the island formation, its fauna was consisted of some pre-Pleistocene taxa. Then, during the Pleistocene time, Jeju Island was secondarily interconnected with more southern territories, and tropical species have colonized it. Recent Boreal cladoceran invaders arrived at the island water bodies later when they were already inhabited by formed associations, and for this reason only few of them were able to settle down there. Such a scheme is a hypothesis which needs to be checked by the future phylogeographic studies.

Keywords: zoogeography; Far East; aquatic communities; continental waters

1. Introduction

Faunistic studies are frequently regarded as outdated by some recent experts in "style" and "technological" biology. Partly, it is a reflection of the fact that faunistics is a taxonomy-dependent science, but the "traditional" animal taxonomy (= "descriptive taxonomy" by Zhang [1]) has entered a deep crisis [2–4], and the interest in such activity is continuously declining in the developed countries. To replace traditional taxonomy, some technological approaches such as barcoding and metabarcoding are proposed [5–7]. Of course, these

methods could expand our understanding of the regional and total biodiversity patterns, but their proper application is possible only by having the barcodes from all known species. Moreover, a relationship between each barcode and each described species must be properly established. Obvious incorrect identifications (e.g., deposited in the GenBank now [8,9]) greatly diminish the value of the barcoding application of such genetic data and their use in subsequent surveys (ecological, biogeographic etc.) based on the former. In many cases, we need "to decode the barcoding results" [10].

At the same time, the traditional taxonomists, molecular biologists and experts combining both methods are in the minority when compared to the number of population biologists, ecologists, toxicologists, experts in monitoring, biogeographers and experts in applied sciences [11,12]. The quality of the results of the latter depends greatly on the activity of the former. In view of the rapid progress in taxonomy of some groups (i.e., due to successful application of molecular and morphological analyses), we need to perform new faunistic studies in so-called "well-studied" regions with "well-studied fauna". This is the only way to have adequate data for any subsequent (i.e., biogeographic and ecological) analyses [13], while using old, outdated, information is vulnerable to criticism.

In contrast to some freshwater animals with a great decline (if not a collapse) of taxonomic studies, Cladocera (Crustacea: Branchiopoda) is an example of a model group with a relatively "healthy" taxonomy. Several tropical countries are intensively studying it now, such as Mexico [14,15], Brazil [16–18], Columbia [19–21] or Ecuador [22]. Unfortunately, faunistic studies have almost stopped in many western countries or are conducted by some non-professional enthusiasts [23]. Many European, North American and Australian students of the Cladocera mainly switched to solely genetic studies [24–27], although there are some exclusions from this rule [28,29].

One of the centers of recent taxonomic studies (based on either solely morphological approach or supported by molecular phylogenies) is the Far East of Asia. Many papers on the cladocerans of Far East of Russia [30–35], China [36–40], Korea [41,42] and Japan [43–46] have been published recently. Some new biogeographic generalizations were apparent after such studies [34,42], e.g., penetration of several "tropical" taxa deeply north, to the territory of Korea and even to the Far East of Russia, was revealed. Based on numerous publications on the Cladocera of East Asia, Kotov [47] proposed to divide the entire pool of taxa in Eastern Siberia and Far East of Russia into several faunistic complexes = groups of species presumably sharing origin, genesis and relatively similar recent distribution ranges [48], following the old idea of the "fauna type" by Shtegman [49]. Subsequently, Garibian et al. [50] analyzed the distribution of these complexes in a 2000 km latitudinal section (in Russian Far East—Korea) and demonstrated a change in Boreal to tropical fauna moving south along this transect. The studied region belongs to the Far Eastern zone of the cladoceran endemism existence, which was predicted by Korovchinsky [51] and then confirmed in subsequent phylogeographic publications [34,47,52].

The Republic of Korea, a country with a relatively small territory, has been studied intensively due to the realization of the program of the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea [53]. Several endemic taxa of the Cladocera were described from this country, and many new records for the country were carried out [54–57]. These results were partly summarized in several previous publications [50,56].

It should be mentioned that most samples for previous studies in South Korea were collected by the route trips: most localities were sampled at once. Some preliminary conclusions on the seasonal changes in the cladoceran fauna in the southern portion of the peninsula were made by Kotov et al. [54]. They found that the proportion of Boreal species, even in the same locality, is higher in spring and lower in autumn. Several series of samples from the Republic of Korea were collected recently, i.e., from Jeju Island, the largest island of South Korea (1.83 percent of the total area of South Korea); as a result, three endemic species were described from the latter [34,55,58]. The aim of this paper is to

study the species composition, structure and seasonal dynamics of the cladoceran fauna and species associations in inland water bodies of Jeju Island.

2. Materials and Methods

Jeju-do (=Cheju-do) is a large island (73 × 31 km) located southwest of the Korean Peninsula (33.11~34.00° N; 126.13~126.97° E) (Figure 1). The island covers an area of 1833.2 km² (Jeju Island, 2021). It was formed about 2MYA due to volcanic eruptions, its middle part is occupied by Mt. Halla volcano (altitude 1.950 m.a.s.l.), with about 360 smaller monogenetic volcanoes (scoria cones) in its vicinities [59,60]. Jeju Island has an oceanic climate because of its location. Due to the influence of warm currents, there is some fluctuation in annual temperatures, with a significant monsoon influence during the summer. The annual average temperature is about 16.1 °C and the rainfall is about 1550 mm. The climate differs on southern and northern landform, in the South it is significantly warmer and regarded as humid subtropical [55,61]. Most stagnant water bodies on the Island are dams, moreover, any "lakes" are also dams, but of a natural origin.
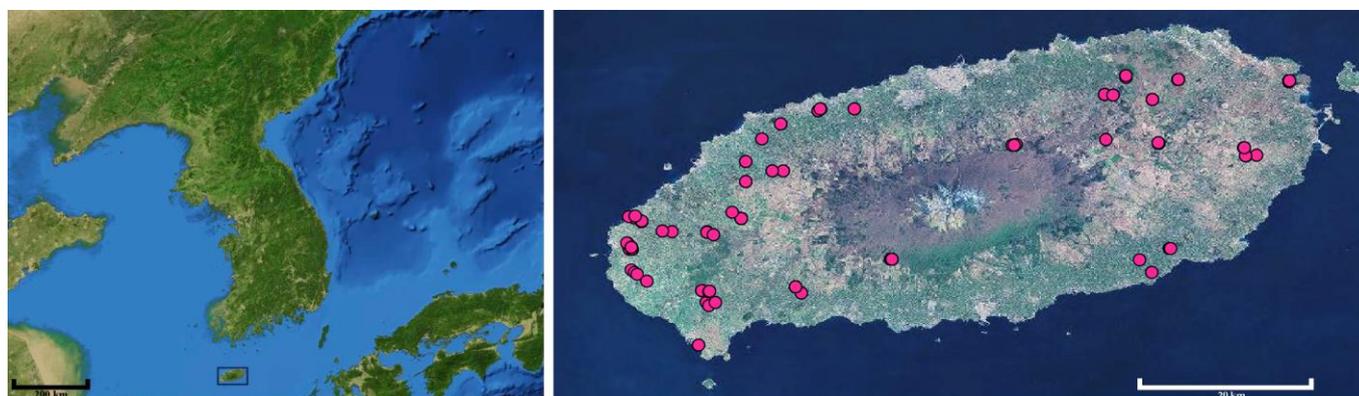

Figure 1. Geographic position of Jeju Island and its map with localities sampled here. Base map from Yandex Maps https://yandex.ru/maps/ (accessed on 1 October 2022).

Totally, 199 samples (a single large total sample from each small water body, two large total samples from each pelagic and littoral zone of each large water body) were taken: 21 samples in November of 2011; 33 samples in February of 2012; 79 samples in June of 2018; 66 samples in September of 2019 (Supplement Table S1; Figure 2, see also photos of some other localities in Jeong et al. [55]). A smaller number of samples in November and February is explained by the winter specify: at that time, a part of water bodies, i.e., in higher altitudes, was covered by a fragile ice, and attempts to collect the samples from the latter were not safe.

All samples were collected by small plankton nets or dip nets (with 50 μm mesh) and fixed with 4% formaldehyde or 96% ethanol. They were studied in the laboratory using a binocular stereoscopic microscope Leica MZ7.5. For proper taxon identification, specimens were selected from samples under binocular stereoscopic microscope and studied under an Olympus BX41 optical microscope in a drop of a glycerol-formaldehyde mixture. A few females from each sample were dissected: thoracic limbs and other body parts were detached using tungsten needles electrolytically sharpened in 10% NaOH. Each dissected portion was individually transferred to a drop of glycerol and covered by a coverslip with small model clay "legs". All drawings were made using a camera lucida.

An empirical randomized species accumulation curve, depending on the sampling effort (the number of samples analyzed), was constructed in the EstimateS 9.1 software package [62]. Using the same package, the model curves of taxa accumulation were reconstructed applying five different nonparametric species estimators: Chao1, Chao2, Jacknife1, Jacknife2, and Bootstrap. The best of the five models (Chao 1) was selected on

the basis of the minimum variance of the values predicted for each step; note that the latter estimator is effective in the case of a relatively high species richness [63].
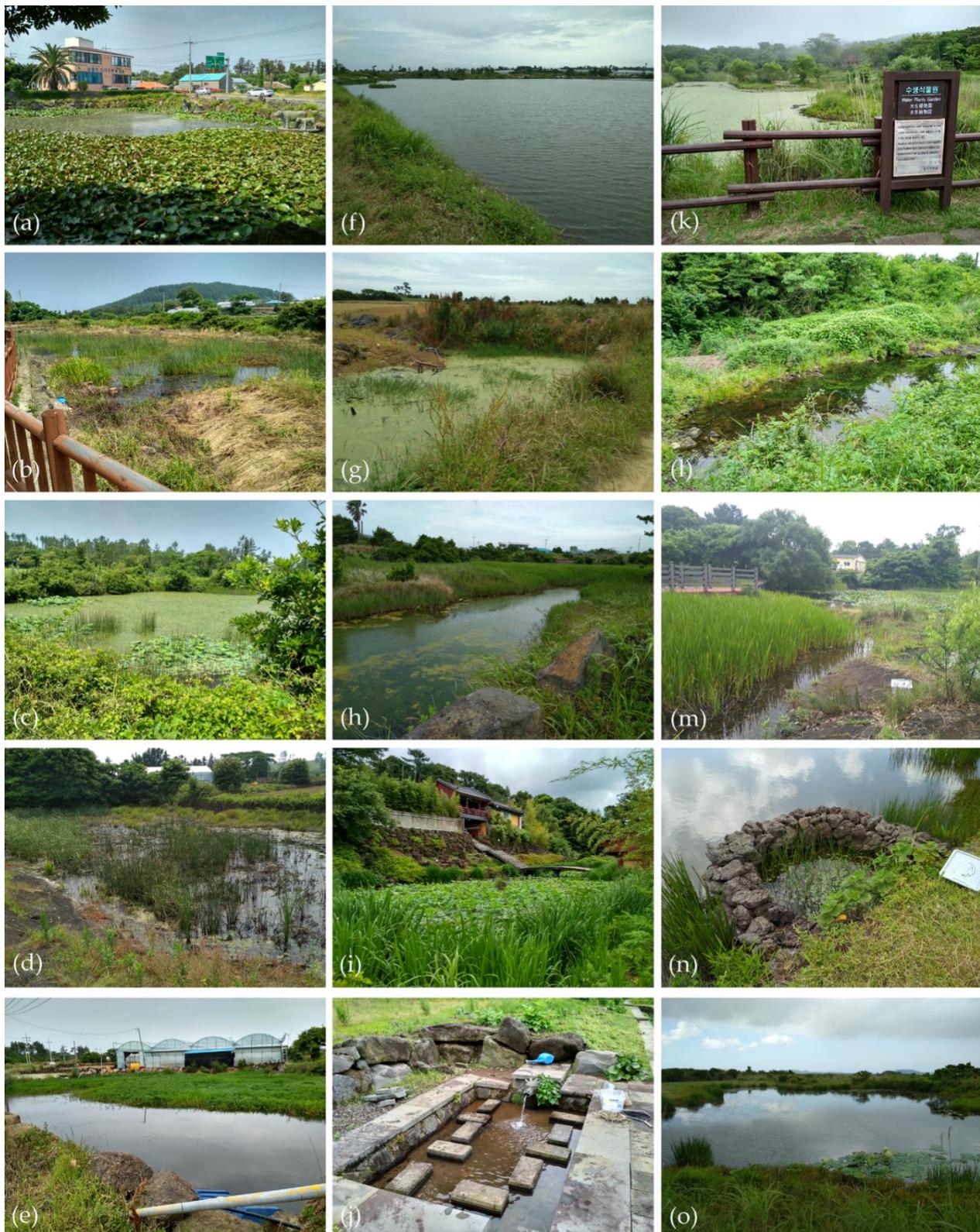

Figure 2. Some localities sampled in June 2018: (**a**) locality 6; (**b**) locality 7; (**c**) locality 8; (**d**) locality 14; (**e**) locality 19; (**f**) locality 19; (**g**) locality 23; (**h**) locality 27; (**i**) locality 39; (**j**) locality 41; (**k**) locality 44; (**l**) locality 47; (**m**) locality 52; (**n**) locality 62; (**o**) locality 63.

The Species Sampling Relationship (SSR) model [64] was also used to assess the completeness of the cladoceran fauna in the samples from the investigated water bodies. Empirical data were used to simulate the statistical distribution of the species number by the Monte Carlo method with 1000 permutations. The accumulation curve was approximated by a rational function of the first order with a finite limit [65]:

$$f(x) = \frac{a + b \cdot x}{1 + c \cdot x}$$

where the parameters a, b and c of the rational function were estimated by the nonlinear least squares regression.

A diagram of the ranked distribution of taxa by frequency of occurrence (total number of taxon records/total number of records) for whole dataset was plotted.

All the taxa (except of those identified up to the genus level only) were separated into four faunistic complexes sensu Kotov [47]:

WE, widely distributed Eurasian faunistic complex;

EAA, widely distributed in East Asia and could penetrate North America;

EA, endemics belonging to the Far Eastern zone of endemism;

ST, southern tropical;

and two artificial groups:

WS, non-revised widely distributed species;

IS, apparently non-indigenous species (donor regions of the invasions could be very different, see Kotov et al. [66]).

In a few cases, those belonging to any complex was updated using information from subsequent publications [34,50,52,67–69]. Representatives of three other faunistic complexes (circum-Arctic, mountain endemic, and Baikal endemic) are absent in the studied region. In the diagram of ranked distribution of taxa, bars for species from different faunistic complexes were marked by different colors.

For analysis of seasonality, we have selected 174 samples from water bodies which were sampled at least twice, while all water bodies sampled only during a single season were not taken into consideration. A dataset for each month (=season) was analyzed separately. We have plotted the rank distribution diagrams for each season and marked the taxa belonging to ST, WE and EA complexes on it.

Dependence of the faunistic complex occurrences on the month and the "season" (when the whole dataset was subdivided into two "summer" (June and September) and "winter" (November and February)) was carried out using a permutation analysis of variance with 5000 permutations per comparison. Tukey's HSD test was used as a post-hoc test [70] Ordination diagrams were built using the canonical correspondence analysis (CCA) method [71], which is a direct ordination method reflecting the change in species composition along the gradient of environmental factors. We used the months and the season of sampling as such a factor.

To determine the mutual association of the species of Jeju Island, a binomial distribution functions was used. The co-occurrence of the two species in a sample was considered as success in the Bernoulli process. Since we cannot know the exact probability value of that, we have used its a-posteriori estimation:

$$p = \frac{m}{N} \cdot \frac{n}{N}$$

where m, n—occurrence of two species and N—total number of specimens. Thus the probability of co-occurrence of two species in exactly x specimens is determined by the probability function of the binomial distribution. We used 95% and 99% one sided confidential interval to decide on the association or incompatibility of species pairs.

All calculations were performed in the R 3.6 statistical analysis environment [72] using vegan [73] and permuco [74] packages. The visualization of the graphs was performed in the igraph package [75].

3. Results

Among 47 taxa (Table 1) found in 199 samples (Supplement Table S1), 6 taxa could not be identified up to species level as their populations were represented by juveniles only or by ephippia only, therefore 41 taxa were identified up to species level. Our analysis of the taxon richness based on the Chao1 estimator confirmed that the region is studied relatively adequately: we have revealed 47 taxa, while Chao 1 estimation is 48 taxa (Figure 3a). SSR estimation gave a slightly higher value—53 species (Figure 3b), but still it is close to the species number we have revealed empirically in our samples.

Table 1. Species found in the continental water bodies in Jeju Island during four seasons (month number is marked by a Roman letter: 2—February, 6—June, 9—September, 11—November. See abbreviations for faunistic complexes in the text.

| No.	Taxon	2	6	9	11	Total Number of Records	Faunistic Complex	Reference
1	*Acroperus africanus* Neretina & Kotov, 2015				+	5	ST	[47]
2	*Alona guttata* Sars, 1862	+	+	+	+	16	WS	[47]
3	*Alonella* cf. *excisa* (Fischer, 1854)			+	+	16	EA	[52]
4	*Biapertura herricki* (Sinev, 2013)	+			+	2	IS	[67]
5	*Biapertura* sp.	+	+	+		7		
6	*Bosmina longirostris* (O. F. Müller, 1776)	+	+	+	+	29	WS	[47]
7	*Camptocercus uncinatus* Smirnov, 1971		+		+	2	EAA	[47]
8	*Ceriodaphnia* cf. *quadrangula* (O.F. Müller, 1785)		+		+	5	WS	[47]
9	*Ceriodaphnia cornuta* Sars, 1885			+		3	ST	[47]
10	*Ceriodaphnia reticulata* (Jurine, 1820)		+	+	+	37	WS	[47]
11	*Ceriodaphnia* sp.	+	+			6		
12	*Chydorus* cf. *sphaericus* (O.F. Müller, 1776) (clade A3)	+	+	+	+	97	EAA	[69]
13	*Coronatella jejuana* Sinev, Lee & Kotov, 2022	+	+			7	EA	This study
14	*Coronatella rectangula* (Sars, 1862)	+	+	+	+	36	WS	[47]
15	*Daphnia* cf. *obtusa* Kurz, 1875 emend. Scourfield, 1942	+	+			6	WS	[47]
16	*Daphnia galeata* Sars, 1864	+			+	10	WE	[47]
17	*Daphnia jejuana* Kotov et al., 2021	+	+		+	19	EA	[34]
18	*Daphnia sinensis* Gu, Xu, Li, Dumont, Han, 2013		+			6	WE	[47]
19	*Daphnia (Daphnia)* sp.		+	+		16		
20	*Diaphanosoma* cf. *amurensis* Korovchinsky & Sheveleva, 2009			+		1	EA	[47]
21	*Diaphanosoma* cf. *brachyurum* (Liévin, 1848)		+	+		2	WE	[47]
22	*Diaphanosoma dubium* Manujlova, 1964			+		7	EA	[47]
23	*Diaphanosoma sarsi* Richard, 1894		+			3	ST	This study
24	*Diaphanosoma* sp.			+		3		
25	*Disparalona ikarus* Kotov & Sinev, 2011		+			1	ST	[68]
26	*Dunhevedia crassa* King, 1853			+		4	ST	[47]
27	*Flavalona costata* (Sars, 1862)	+	+	+	+	33	WS	[47]
28	*Ilyocryptus* cf. *raridentatus* Smirnov, 1989		+			2	ST	[47]
29	*Ilyocryptus spinifer* Herrick, 1882	+	+	+		10	ST	[47]
30	*Leberis diaphanus* (King, 1853)			+		1	ST	This study
31	*Leydigia ciliata* (Gauthier, 1939)		+			1	ST	[47]
32	*Macrothrix rosea* (Jurine, 1820)			+		2	WE	[47]
33	*Macrothrix triserialis* Brady, 1886			+		5	ST	[47]
34	*Macrothrix vietnamensis* Silva-Briano, Dieu & Dumont, 1999			+		3	ST	[47]
35	*Moina* cf. *macrocopa* (Straus, 1820)			+		2	WE	[47]
36	*Moina* cf. *micrura* Kurz, 1875		+	+		6	WS	[47]
37	*Moina* sp.			+		1		
38	*Pleuroxus quasidenticulatus* (Smirnov, 1996)	+	+	+	+	77	ST	[47]
39	*Pleuroxus jejuensis* Jeong, Kotov & Lee, 2013	+			+	6	EA	[47]
40	*Pseudosida szalayi* (Daday, 1898)			+		3	ST	[47]
41	*Scapholeberis smirnovi* Garibian, Neretina, Taylor & Kotov, 2020		+	+	+	52	ST	[50]
42	*Sida ortiva* Korovchinsky, 1979			+		2	EAA	[47]
43	*Simocephalus congener* (Koch, 1841)	+				1	WS	[47]
44	*Simocephalus mixtus* Sars, 1903	+	+	+		34	WS	[47]
45	*Simocephalus serrulatus* (Koch, 1841)		+	+		8	WS	[47]
46	*Simocephalus vetulus* (O.F. Müller, 1776)	+		+		7	WS	[47]
47	*Simocephalus* sp.	+		+		5		
	Total number of taxa	19	26	31	16			
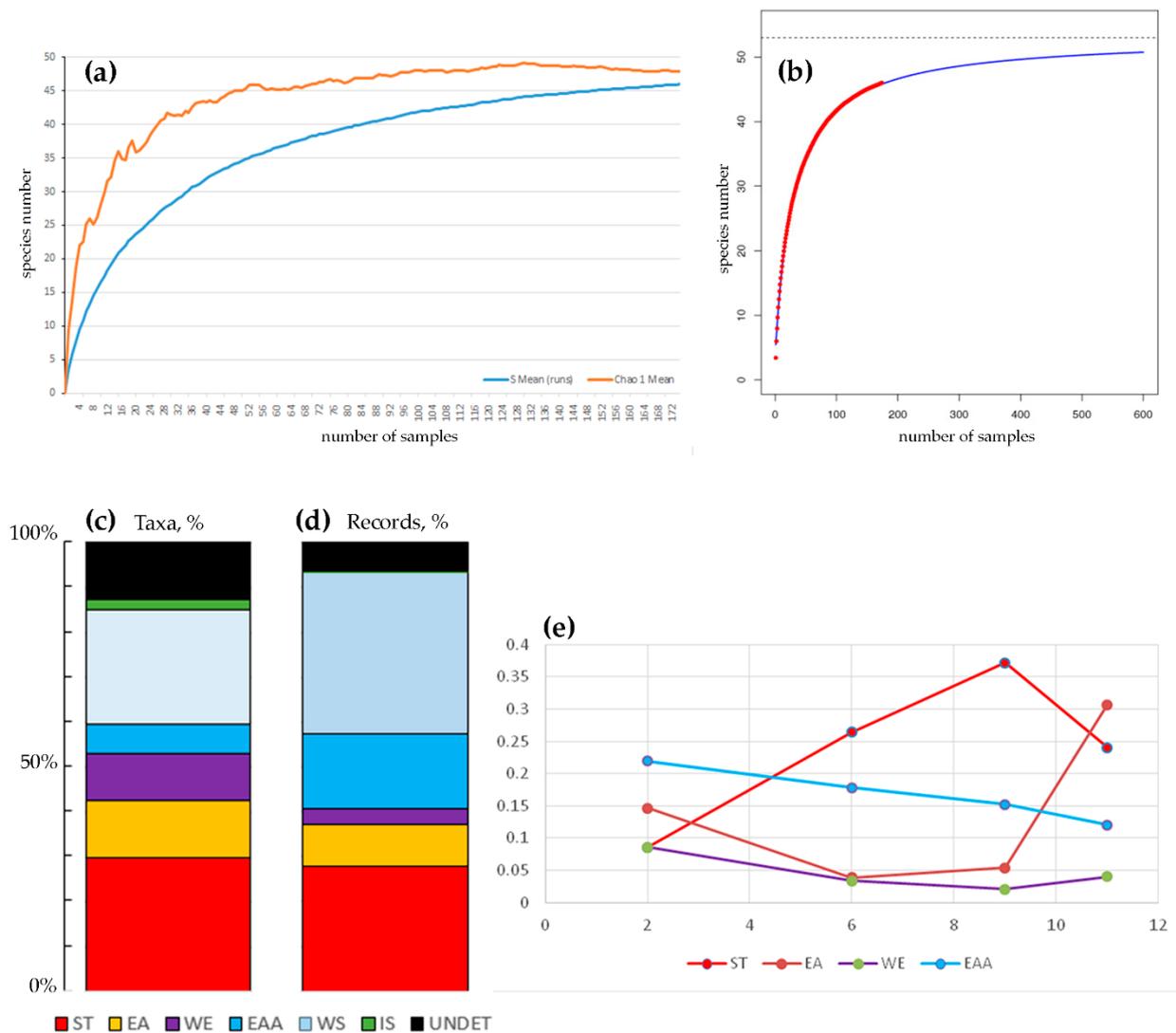
Figure 3. Analysis on the whole dataset of the cladoceran records in Jeju Island: (**a**) Sample-based rarefaction curve (S Mean) and estimator curve (Chao 1 Mean) for the water bodies/season. (**b**) The Species Sampling Relationship (SSR) model. Red dots—simulated species accumulation curve, blue line—rational function approximation, (**c**) All revealed taxa belonging to different faunistic complexes. (**d**) Total records of taxa belonging to different faunistic complexes. (**e**) Rate of records belonging to three faunistic complexes in general pool during four different months.

In Jeju Island, we have found the representatives of six faunistic groups: those of four true faunistic complexes: ST, EA, EAA, WE and those of two artificial groups: IS (invasive species are represented by a single taxon) and WS (Figure 3c,d). Unfortunately, we need to put many taxa (25%) and records (35%) to the group of non-revised widespread species (WS), which makes our analysis more complicated. The contribution of southern tropical complex (ST) is also strong: 30% of species and 28% of records. Endemics of the Far East make 13% of taxa and 9% of records. The contribution of WE and EAA is less strong. Note that most records of EAA belong to a single taxon, *C.* cf. *sphaericus*, which was identified genetically by Karabanov et al. [69].

Rate of the species belonging to different complexes varies with the season (Figure 3e). Statistical analysis confirms that the occurrence of ST species decreases in November and February (significance level $p < 0.001$ both by months and seasons), while the occurrence of EA species increases in the same months ($p < 0.001$ both by months and seasons). The occurrence of WE and EAA species fluctuates insignificantly, see Figure 3e.

Rank distribution of revealed taxa is represented in Figure 4. Totally during all the seasons, two species of ST and a single species from EAA dominated. During different seasons, different species dominated: in February the only single species of EAA (*Chydorus* cf. *sphaericus*), in June and September it was accompanied by two species of ST (*Pleuroxus quasidenticulatus* and *Scapholeberis smirnovi*), in contrast, in November two species of EA (*Alonella* cf. *exisa* and *Daphnia jejuana*) are most common in the water bodies of Jeju Island.
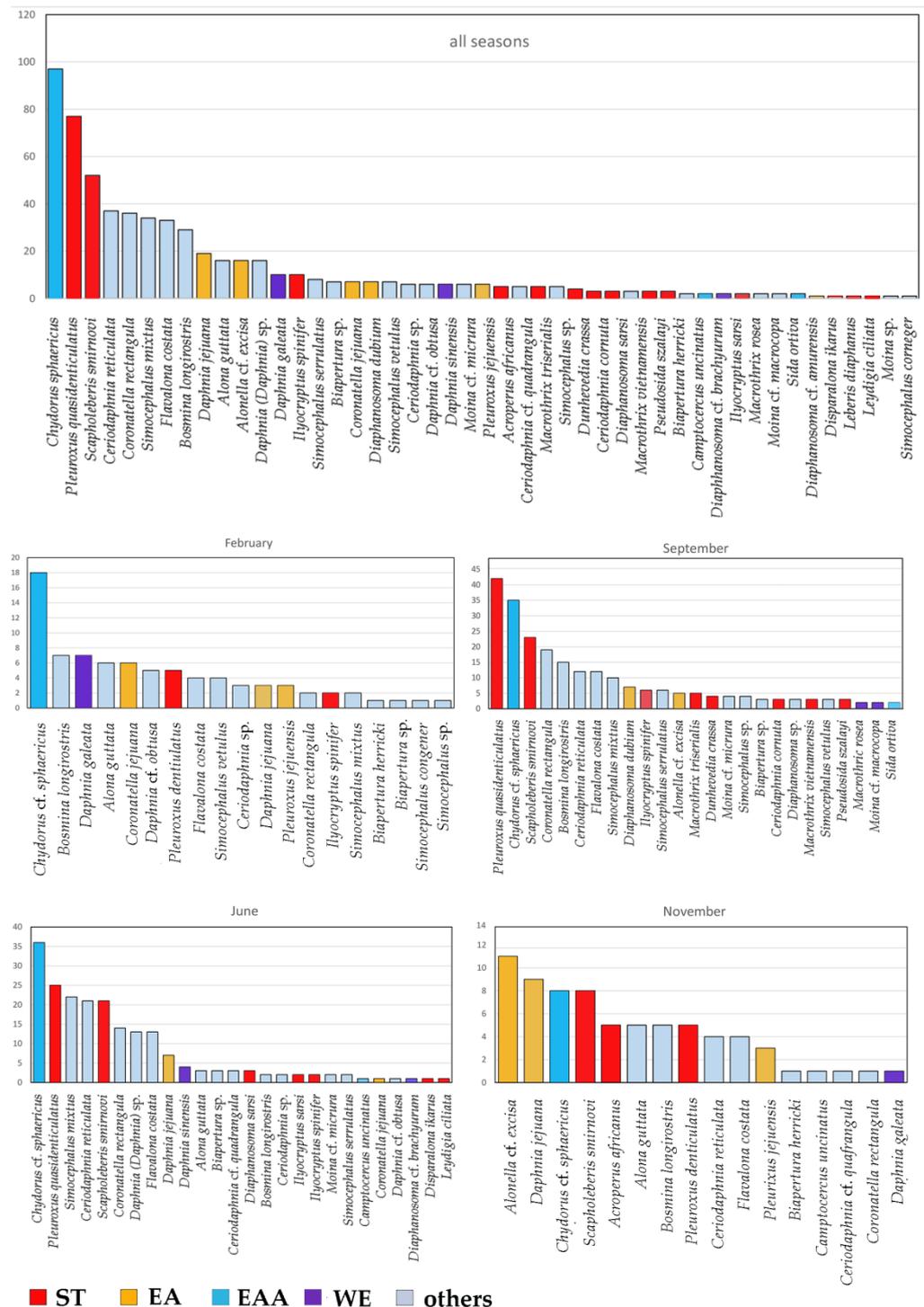
Figure 4. Rank distribution of the cladoceran taxa in the continental water bodies of Jeju Island based on the number of records during all seasons (**top** panel) and each season separately (**bottom** panels). Colors mean belonging to different faunistic complexes.

An analysis of the ordination diagram by months (Figure 5a) shows that if the samples from June and September differ slightly from each other and form relatively compact clouds grouped approximately near $(-1, 0)$ point, the samples from November and February have a significantly stronger dispersion. The November samples are mainly located in negative values along the ordinate axis, and February samples are in positive values along the abscissa axis. With ordination by season (Figure 5b), most of the "winter" samples are in the positive region of the abscissa axis, and most of the "summer" samples are in the negative one.
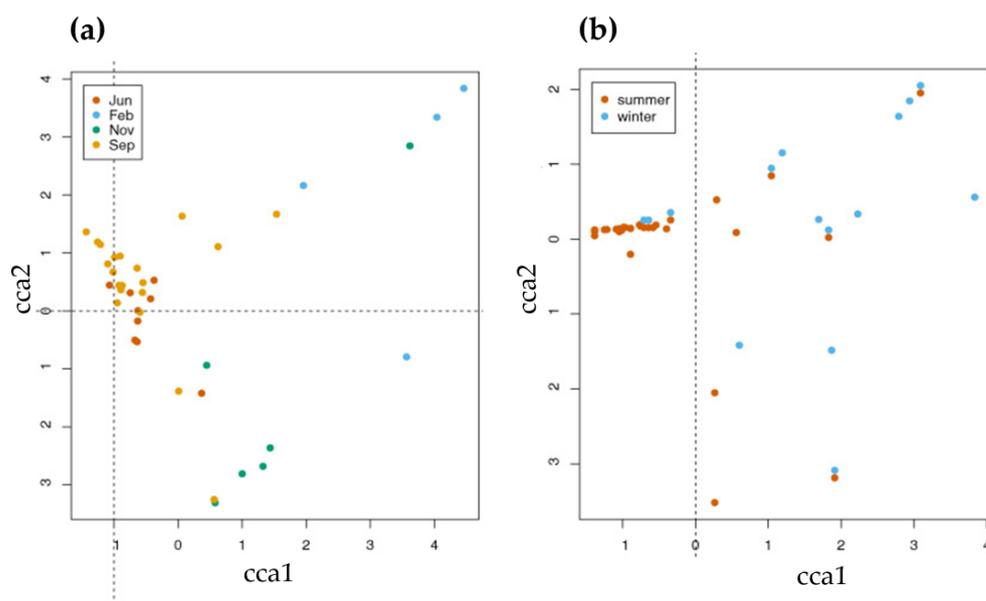

Figure 5. CCA ordination diagrams. As an environmental factor: (**a**) sampling months; (**b**) sampling season.

We can draw a conventional boundary between the "winter" and "summer" samples along the line x = 0 and select the species that are most common in the "winter" samples in the area x > 0. These are: *Daphnia jejuana* (19 occurrences; EA), *Alonella* cf. *excisa* (12; EA), *Daphnia galeata* (10; WE), *Coronatella jejuana* (7; EA), *Pleuroxus jejuensis* (6; EA), *Pleuroxus quasidenticulatus* (6; ST), *Scapholeberis smirnovi* (6; ST), and *Acroperus africanus* (5, ST). Note that specific winter species include only EA and ST members (endemics and species of southern origin).

Species associations revealed based on binominal distribution are visualized in Figure 6. The number of species involved in associations was higher in summer (27 taxa at $p = 0.05$; 10 at $p = 0.01$) than in winter (12 at $p = 0.05$; 5 at $p = 0.01$). Note that less than half of all revealed taxa are significantly involved in associations, and few species form cores of the associations (at $p = 0.01$).

Three main associations were detected in summer (1–3), we do not discuss small-sized associations 4–6 as the association strength is low and the involved taxa are frequently rare. The association 1 included phytophylous species (*Pleuroxus quasidenticulatus*, *Coronatella rectangula*, *Flavalona costata*) and neustonic *Scapholeberis smirnovi*, it was characteristic for a littoral zone of different water bodies. The association 2 included planktonic *Bosmina longirostris*, *Ceriodaphnia cornuta* and *Diaphanosoma dubium*, it was a predominantly planktonic association, while such species as *Macrothrix triserialis* penetrated this association probably from the benthos. The association 3 included the species of open littoral (*Pseudosida szalayi* and *Macrothrix vietnamensis*), while at $p = 0.05$ this cluster was added to by different other taxa, but the strength of this association was low. Interestingly, at $p = 0.01$, more than half of the species making the association core belonged to ST.

Only two associations (1' and 2') were detected in winter at $p = 0.01$. The association 1' grouped phytophylous and neustonic taxa, whereas the association 2' was clearly planktonic. At $p = 0.05$, the association 3' was also detected, this was also a group of

phytophylous taxa. The association 4' was characterized by a weak strength. Only a single taxon of winter association cores belongs to Boreal taxa (WE), only few taxa of EA (most common just in winter) were included in the association cores, while even in winter the rate of ST was high.
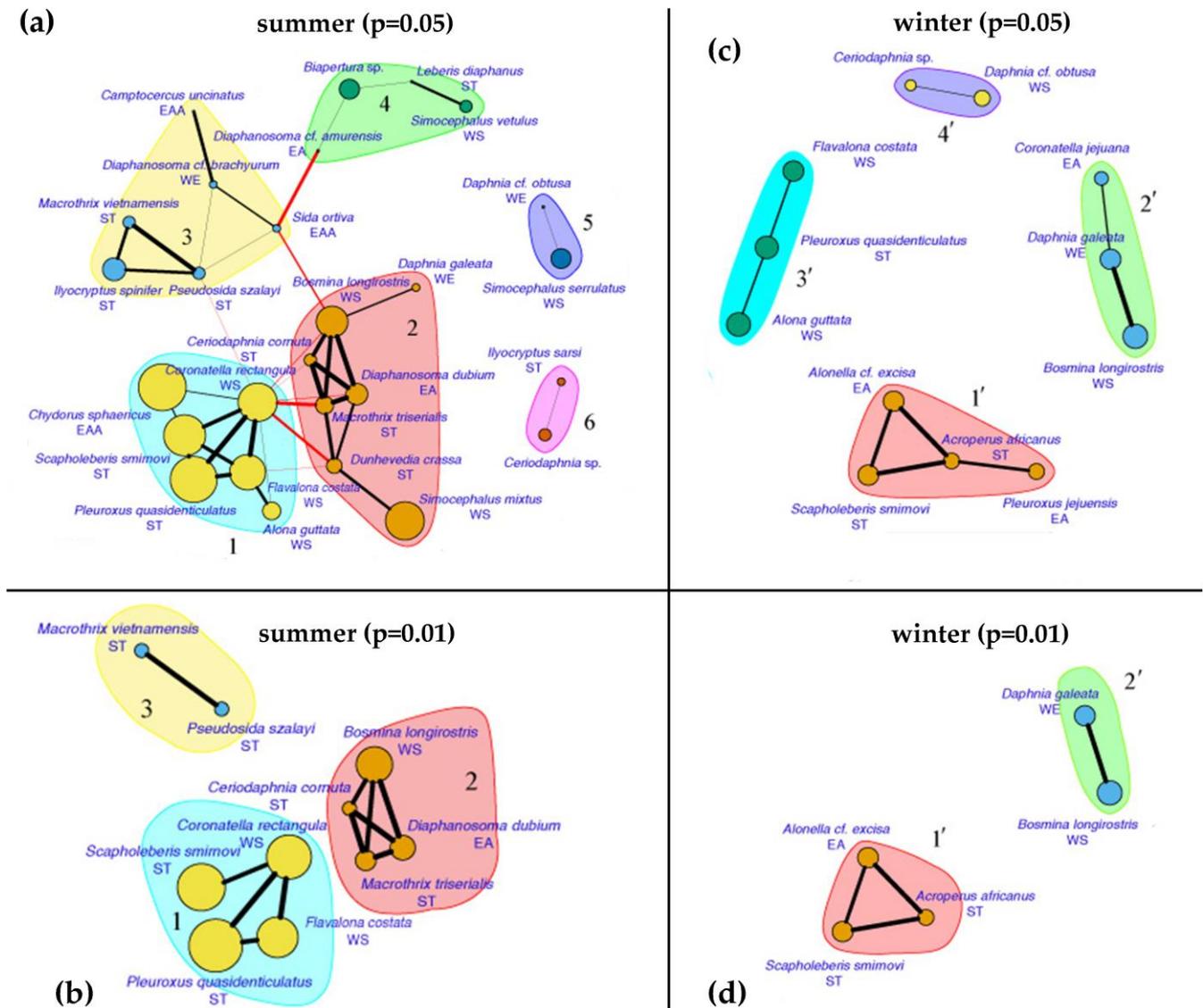

Figure 6. Clusters of positively associated cladoceran species: (**a**) in summer (*p* = 0.05); (**b**) in summer (*p* = 0.01); (**c**) in winter (*p* = 0.05); (**d**) in winter (*p* = 0.01). The node size is proportional to the frequency of the species occurrence. Internode thickness is proportional to association strength.

4. Discussion

4.1. Impoverished Island Cladoceran Fauna

As we specifically tested above, the revealed species list of 41 species is almost complete. Note that the chance to find some specific water bodies in Jeju Island, non-sampled by us, is minimal (not taking into consideration the crater lake of Mt. Halla volcano and the ground waters which are out of our scope). We can confidently conclude that the number of cladoceran species is remarkably low on Jeju Island. To date, we can say that Jeju Island does not belong to the cladoceran biodiversity hotspots in contrast, for example, to some terrestrial animals such as ants [76]. Moreover, previous studies of some other freshwater groups in Jeju water bodies also revealed few taxa [77].

It is known that island species richness increases with habitat diversity [78], also the age of island impacts the species richness [79]. Although Jeju Island is a relatively large land portion, its species list with 41 taxon is remarkably impoverished as compared to the mainland Korea with at least 95 species (85 taxa listed by Jeong et al. [56] plus at least 9 species found by Kotov et al. [67] and Jeong et al. [57]), at least 122 species in southern Far East of Russia and at least 199 species in China [36,37]. The number of the cladocerans of Hainan Island (53 species [80]) is also small as compared to that of continental China. At the same time, the Japanese Archipelago is rich of species [81] and endemic taxa [34].

A remarkable trait of the cladoceran fauna of Jeju Island is the absence of any species from two predatory orders, Haplopoda and Onychopoda which also are absent in most archipelagoes, with a few exceptions such as the British Islands, Faroes [82] and Japan [81]. Resting eggs of the predatory cladocerans are not so resistant against unfavorable environments, i.e., drying and salinization, as compared to the anomopods such as *Daphnia* [83]. Representatives of the genera *Polyphemus* and *Leptodora* are common in the adjacent continental regions of China [30,84]. However, even in South Korea *Polyphemus* is absent, although it is recorded from North Korea and the Far East of Russia [56], while *Leptodora* is recorded from several localities in South Korea [42].

At the same time, most available large water bodies in Jeju Island are newly constructed man-made reservoirs, potentially good targets for colonization from the nearest small water bodies, or from distant localities of the Asian continent. Moreover, Jeju Island is located in the zone of the East Asian Flyway, main route of the bird migrations [69,85], with many species of waterfowl involved [86]. Just the waterfowls are regarded as the main vector for the cladoceran resting egg dispersal [87,88].

Few species are found on Jeju as compared to different adjacent continental regions. We believe that such faunal poverty could be explained by the existence on Jeju Island of only a few types of the water bodies compared to continental China or Far East of Russia with a great diversity of the water types: large natural lakes, strong rivers with numerous oxbows, forest lakes and *Sphagnum* bogs with very specific chemistry, etc. Moreover, it is known that a volcanic origin of an island leads to a specific soil chemistry [89,90]. Significant climatic oscillations in this region [91] could also have a negative impact on the freshwater fauna. Finally, several strong eruptions of the Mt Halla volcano, including that ca. 2KYA [92] could have a negative effect on the island freshwater biota, including its extirpation in some water bodies and drastically changed chemistry of the surviving water bodies.

While island and mainland regions suffered equally from past habitat loss, the human impact is significantly higher on islands [93]. It is also necessary to note that, in general, recent anthropogenic influence on the water bodies in Jeju-do is quite remarkable, and such pressure could also "support" a low diversity of the hydrobionts on the island. Although Jeju Island has a high habitat quality, its natural habitats had rapidly decreased in area, i.e., by 24.9% from 1989 to 2019 [94], and now the local government performs different actions in the environment protection and restoration. Moreover, a low cladoceran diversity could be explained partly by a harmful influence of non-native fishes. No native fish taxa were found in the island freshwater localities, all species were introduced by men, and introduction of many taxa is well-documented [95]. We cannot expect a selective influence of fish to a particular faunistic complex, but we can expect a seasonality in such influence: it should be more destructive in summer as compared to winter.

4.2. Notes on Faunistic Structure

Kotov [47] separated eight faunistic complexes and artificial faunistic groups in the North-East Asia, while we found four faunistic complexes and two artificial groups on Jeju Island. Subsequent revisions could improve our ideas on exact biogeographic status of the taxa belonging to WS. However, in general, more detailed study usually leads to acceptance of a higher level of endemism as compared to a non-revised state [10,96]. The

chance that further studies will demonstrate a significantly high representation of Boreal taxa on Jeju Island, compared to the present, is minimal.

We have demonstrated a high significance of the tropical species (both number of species and records of ST are higher than those of WE+EAA), but, unfortunately, a history of tropical species dispersion towards the north is not studied adequately, and we have no ideas on the age of this penetration. To date, the idea on their late Pleistocene expansion towards the north [54] is just hypothetical.

In contrast, we already have preliminary ideas on the time of other complex differentiation and expansion, although such ideas are still based on few taxa. Two complexes (WE, EAA) have dispersed through most part of North Eurasia during the Pleistocene: WE has mainly dispersed eastward from Western Eurasia while EAA has dispersed southward from the Beringian zone [97–99]. In contrast, the Far Eastern endemic complex (EA) is of old, pre-Pleistocene origin, and the aforementioned zone of the cladoceran endemism is also a zone inhabited by pre-Pleistocene relicts [34,51].

To date, the level of local Jeju Island endemism seems to be relatively low. At the same time, the number of endemics may increase significantly after detailed molecular studies of the local cladoceran populations, and this is a prospective direction for the future.

4.3. Seasonal Changes in Fauna and Species Associations

All data above confirm seasonal faunistic changes in the continental waters of Jeju Island. The rate of tropical taxa (ST) is highest in September, after the monsoon time, while the Far Eastern endemic taxa (EA) are not numerous in summer (Figure 5). Moreover, just endemic taxa dominate in November, while ST taxa dominate in June and September (together with *C.* cf. *sphaericus* belonging to EAA). At the same time, the contribution of Boreal taxa (WE and EAA) to the fauna is low (except for the aforementioned *C.* cf. *sphaericus*) even in winter. Paradoxically, the monsoon has a limited effect on the species composition of cladocerans of the island water bodies (see clouds of dots for June and September in Figure 5a), possibly because most sampled water bodies were permanent.

It is important that the species associations also change significantly from summer to winter; moreover, some species (first of all, *Scapholeberis smirnovi* and *Bosmina longirostris* which made associations with other taxa even at $p = 0.01$) are present both in summer and winter associations, but during seasons they are involved in different associations. Such a phenomenon requires a special study on several water bodies sampled monthly. However, to date, we can conclude that a contribution of Boreal taxa (WE and EAA) to the stable species associations is minimal (even in winter), whereas tropical taxa contribute to them greatly (including winter).

We can propose a rough scheme explaining the whole set of obtained information. Initially, at earlier stages of the island formation its fauna was consisted of some pre-Pleistocene taxa (EA), which survived on the island when it was isolated from the continent by the ocean. Then, during Pleistocene time, Jeju Island was secondarily interconnected with more southern territories (mainland China and Japan [100–102]) and ST species have penetrated it. A few Boreal taxa have appeared on the island very recently, and their appearance could be explained by a waterfowl-mediated dispersion from the Korean Peninsula, or by some accidental anthropogenic introduction with fishes, which were fully absent from the island during its formation. Recent cladoceran invaders have arrived at the island water bodies which were already inhabited by already formed associations, and for this reason only a few of them were able to settle down there. We suppose that the earlier monopolization (sensu De Meester et al. [103]) of the water bodies of Jeju Island by endemic and tropical species prevented further penetration of Boreal taxa, which are very common on closest Korean Peninsula. Such scheme is a hypothesis which needs to be checked by the phylogeographic studies in the future.

Abell et al. [104] placed Jeju Island in their Freshwater Ecoregion 639 ("South of Korean Peninsula"), but our data strongly contradict this opinion: in reality, the island is

strongly different from South Korea in respect of its cladoceran fauna, because the former is historically connected with more southern continental regions.

5. Conclusions

Jeju Island is a region with a poor cladoceran fauna compared to continental Asia, in particular, with continental South Korea. The unexpectedly low contribution of the taxa of Boreal origin reflects the geological history of the region which was in the Pleistocene interconnected predominantly with the southern mainland, while Boreal taxa represent more recent colonizers.

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