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Article

Invasive and Rare Aquatic Invertebrates of Taiwan with a Focus on Their Dormancy

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Abstract: Invertebrates in tropical ecosystems are generally considered to have little or no need for a dormant phase due to the stability of the habitat. However, resting stages of aquatic organisms are occasionally found here as well. This fact increases the possibility of transport of tropical organisms by ships' ballast water, which is the main vector for the spread of alien aquatic organisms between continents. During a study of resting stages in the bottom sediments of the island of Taiwan in 2006–2007, nine species of invertebrates were found, invasive or new to the fauna of the island, with some of them forming large banks of resting stages in sediments.

Keywords: resting stage; bioinvasion; marine; continental waters; mollusk; copepod; nematode

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1. Introduction

Biological invasions of aquatic organisms in tropical countries are rather poorly studied. To some extent, this is due to the fact that there is a large number of pantropical species [1]. Naval transportation carried out by large-tonnage fleets (tankers, container ships, etc.) is accompanied by the transportation of large volumes of ballast water, reaching several hundred thousand tons of water for one vessel. Uncontrolled transportation and the emptying of ballast water during the 20th century led to significant biological contamination of areas, such as the Baltic Sea, the Mediterranean Sea in Europe and large lakes in North America [2–5].

Despite its relatively small size and location in the subtropics, the island of Taiwan is also one of the regions with busy maritime traffic, especially in its southern waters where one of the largest seaports in Southeast Asia, the port of Kaohsiung, is located. Most species have become invasive as a result of direct introduction as objects of aquaculture or ornamental aquarium businesses [6,7]. For different groups of fish, the proportion of invasive fish ranges from 20 to 30% of the native fauna, which is a very high value even when compared to the Baltic Sea, which is considered to be one of the most biologically contaminated regions in the world [8]. As for aquatic invertebrates, the level of invasive penetration of organisms of this group in Taiwan, as well as the possible participation in this process of resting (dormant) stages, remain insufficiently studied. Resting stages are an almost obligatory part of the life cycle of most aquatic invertebrates of temperate and high latitudes, since this allows organisms to survive during unfavorable conditions (desiccation, freezing, lack of food, etc.) [9]. The reduced level of metabolism underlying biological dormancy causes nonspecific resistance of resting stages to toxic substances often found in ballast waters [10]. This is what determines the high efficiency of transportation of aquatic invertebrates by ship ballast waters, particularly in water bodies of temperate climates [11]. For organisms living in tropical regions, the formation of resting stages is uncommon due to the stability of the habitat (weak or complete absence of the seasonal factor). This question was examined in detail, in particular by Danilevsky, on insects, including their freshwater larvae [12]. It cannot be ruled out, however, that tropical organisms can also form resting stages under conditions of predictable environmental instability; for example, periodic drying of temporary reservoirs during a drought. In this case, possible restrictions on the dispersal by ship ballast water of tropical species forming resting stages will be removed.

The present research focuses on the level of biological pollution of Taiwan's inland waters by aquatic invertebrates and on invasive and potentially invasive or rare freshwater and marine benthic representatives of the subtropical zone.

2. Materials and Methods

Research was carried out across several seasons in 2006 and 2007, in reservoirs located throughout the territory of the island of Taiwan, as well as in marine biotopes along the western coast of the island, starting from its northern tip (Turtle Island) to the south. Along with samples of zooplankton and zoobenthos, samples of bottom sediments were collected as places of possible accumulation of resting stages. In marine biotopes, sampling by scuba divers was widely used at depths from 1 to 40 m. At greater depths, over 50 m, a bottom grab was applied to collect sediments. In inland water bodies, which included temporary water bodies, rivers, rice fields and the largest lake in Taiwan, Sun Moon Lake, tubes were applied in the collection of sediments with a sampling area of 50 to 100 cm^2. All samples at each station and at each depth were collected in 3 replicates. Zooplankton and zoobenthos samples were preserved with 70% alcohol or 4% formalin. Sediment samples were delivered to the laboratory and kept at a stable temperature of 10–12 °C and under conditions of significant saturation with organic matter, the decomposition of which quickly caused complete oxygen consumption, for 7 days to eliminate active stages. During this time, all active stages, judging by the observations, died from oxygen deficiency. To count the living resting stages after a week of storage, the sample was transferred into wide flat vessels, filled with marine or fresh water, depending on the place of collection, and placed in a thermostat at 25 °C with a photoperiod of 16 light to 8 dark, which corresponds to the summer season in Taiwan. Sediment samples were examined daily; the revived stages were immediately deposited and identified to the lowest possible taxonomic level, depending on the stage at which the organism undergoes diapause (embryos—calanoid copepods, ostracods, nematodes; late larvae—cyclopoid copepods, freshwater diaptomid copepods, insects; mature stages—harpacticoid copepods, cladocerans, mollusks). The duration of the experiment depended on the duration of reactivation and was terminated 3 days after the appearance of the last revived organism, but it was not shorter than 10 days. Reactivation of organisms from marine sediments was carried out on the island of Taiwan, at Ocean University, Keelong, and freshwater organisms—in St. Petersburg, Zoological Institute, Laboratory of Experimental Entomology, at a facility with photoperiodic and temperature control. Some groups of organisms (nematodes, mollusks) were transferred to experts in the relevant groups of the Zoological Institute of the Russian Academy of Sciences for identification.

In total, several zones of possible accumulation of resting stages were examined. In marine ecosystems, coastal ecosystems in the intertidal zone (biotopes of coral reefs and mangroves) and deep-water ones outside the intertidal zone (sulfur hot springs and along the coastline at depths of more than 50 m) were surveyed. In inland water bodies, temporary water bodies, both natural and artificial, rivers in sediment accumulation areas, and Sun Moon Lake were surveyed. In Sun Moon Lake, sediments were collected both in the littoral zone (within aquatic vegetation) and in the benthic zone (at a depth of 9–11 m). In total, 10 types of water bodies were examined for the presence of resting stages of aquatic invertebrates.

Statistical processing. All data were analyzed for the normality of the distribution of individual variants using the Kolmogorov–Smirnov test. Depending on the normality of the distribution, either the arithmetic mean (normal distribution) or the median (abnormal distribution) was used to estimate the mean. Estimates of these quantities (errors) were also calculated on the basis of parametric and nonparametric indicators using the Statistica 6 software package.

3. Results

3.1. Invasive and New Species of Aquatic Invertebrates in Water Bodies of Taiwan

Invasive species of aquatic invertebrates have been found only in inland waters. In total, nine species of aquatic invertebrates alien or new to science (at the time of sampling) were found. According to their places of origin, 3 species belong to the faunal complexes of Africa, 1 species to the Ponto–Caspian region of Eurasia, 1 species to South Asia and 1 species to the Neotropics. The 3 species found were later recognized as new to science and are now considered endemic to the island. Below are brief comments on these species and their locations.

GASTROPODA.

Lissachatina fulica (Bowdich, 1822) (Figure 1).

Figure 1. *Lissachatina fulica* (Bowdich, 1822). Taipei Park, northern Taiwan.

Lissachatina fulica is a terrestrial snail, which was found in parks and rice paddies without overlaying water. The highest density noted for this species, and only calculated for large mature individuals, was 4–6 specimens per m^2.

Pomacea canaliculata (Lamarck, 1822) (Figure 2).

Figure 2. *Pomacea canaliculata* (Lamarck, 1822). Adult specimen, Penghu, South Taiwan, identified by Chen Chuen-hui; egg clutch, collected by H.-U. Dahms, southern Taiwan.

Characteristic pink egg clutches of *Pomacea canaliculata* were observed on dense substrates above the water level and contained from several tens to 400 eggs in a state of shallow biological dormancy. Long-term storage of clutches at temperatures of 20–25 °C after 3 months leads to a gradual release of young snails. Storage at a low temperature (4 °C for a month) as well as short-term freezing (−18 °C for a day) causes 100% death. Placement of resting eggs in water led to synchronous hatching of eggs within 1–2 days. In Kaohsiung city ponds (inland reservoirs with a solid bottom and artificial shoreline) in southern Taiwan, the number of clutches of this species per m^2 reached 10–12/m^2, which corresponds to about several thousand eggs of different ages, and the biomass observed during the monsoon season was over 1 kg per m^2.

BIVALVIA.

Dreissena bugensis (Andrusov, 1897) (Figure 3).

Figure 3. *Dreissena bugensis* (Andrusov, 1897) (after [13]).

Dreissena bugensis was found in the littoral zone of Sun Moon Lake, as well as attached to floating structures in the same lake—fish tanks, gazebos for recreation, boat docks, etc. The collected specimens corresponded with the original description [13].

The density of populations varied greatly from several specimens per 1 m^2 to the maximum registered in the sample collected. Eighty-one specimens were collected from a plot of 30 cm^2 with the visually most abundant population, which amounted to 27,000 ind/m^2. However, such a density was noted only at a few points, and the density indicated above cannot be related to the area per square meter of the substrate, since a significant part of it was free from mollusks. The size–age structure of the population was estimated using the same sample and is shown in Figure 4. The weight–length ratio of the studied population is shown in Figure 5. The largest population was made up of individuals of the middle class, 10–11 mm long. As a result, small young individuals prevailed in the population. Individuals up to 11 mm with a maximum length of 22 mm provided 68% of the overall abundance, which indicates the predominance of birth processes over mortality.

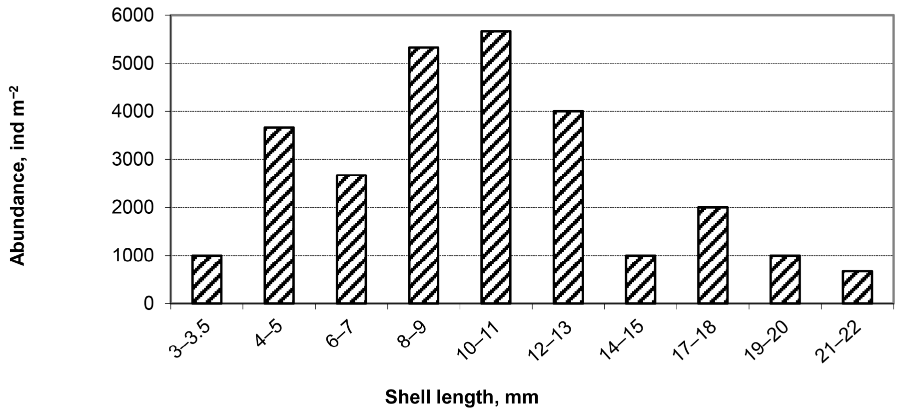

Figure 4. Length–abundance distribution of the *Dreissena bugensis* population at the sampled site in the littoral zone of Sun Moon Lake, Taiwan.

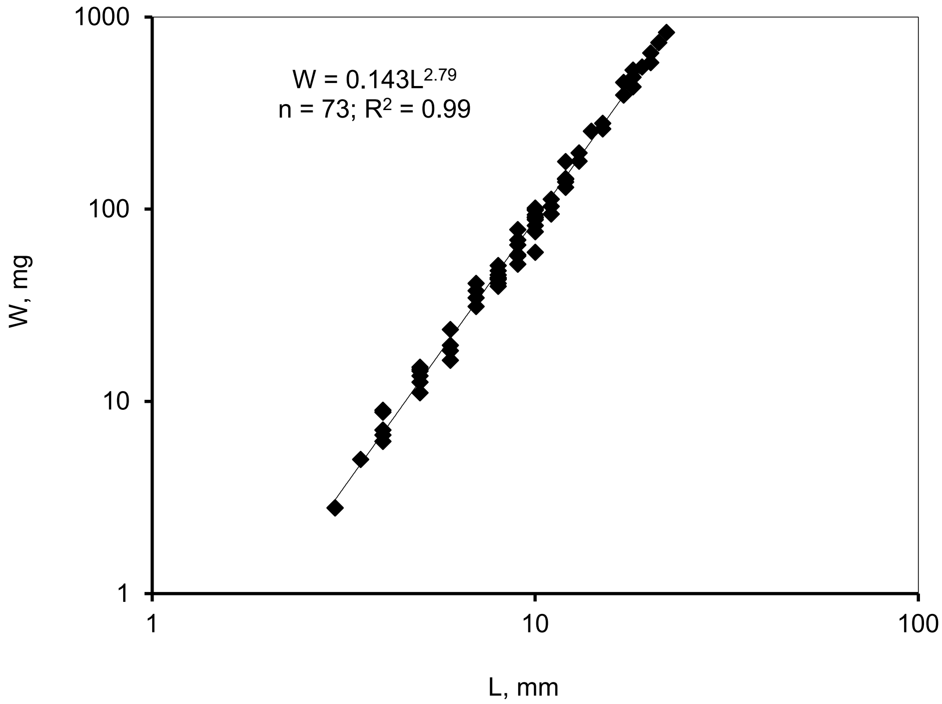

Figure 5. Length–weight distribution of a *Dreissena bugensis* population from a site in the littoral zone of Sun Moon Lake, Taiwan.

COPEPODA.
Metacyclops minutus (Claus, 1863) (Figure 6).

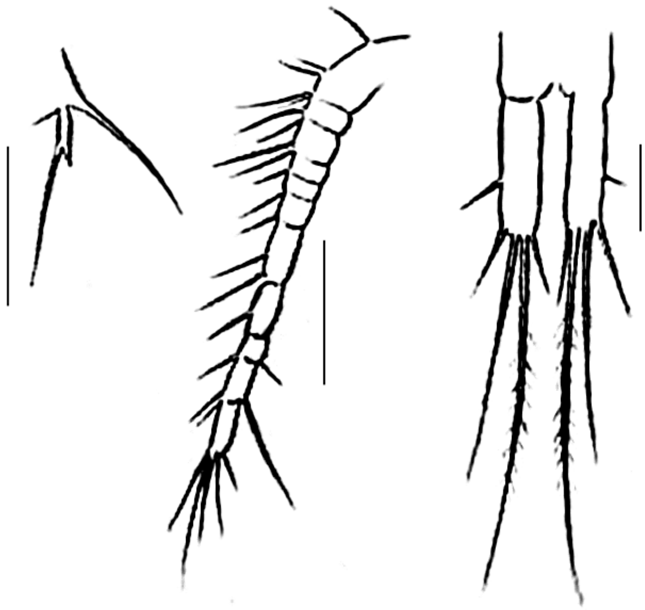

Figure 6. *Metacyclops minutus* (Claus, 1863) (after [14]). Scale bars: 50 µm.

Metacyclops minutus is a freshwater cyclopid, which was recorded in temporary reservoirs with the highest density in rice paddies, where the number of adults reached 40,000 ind/m^2.

Eucyclops (*Denticyclops*) *taiwanensis* Sukhikh and Alekseev, 2015 (Figure 7).

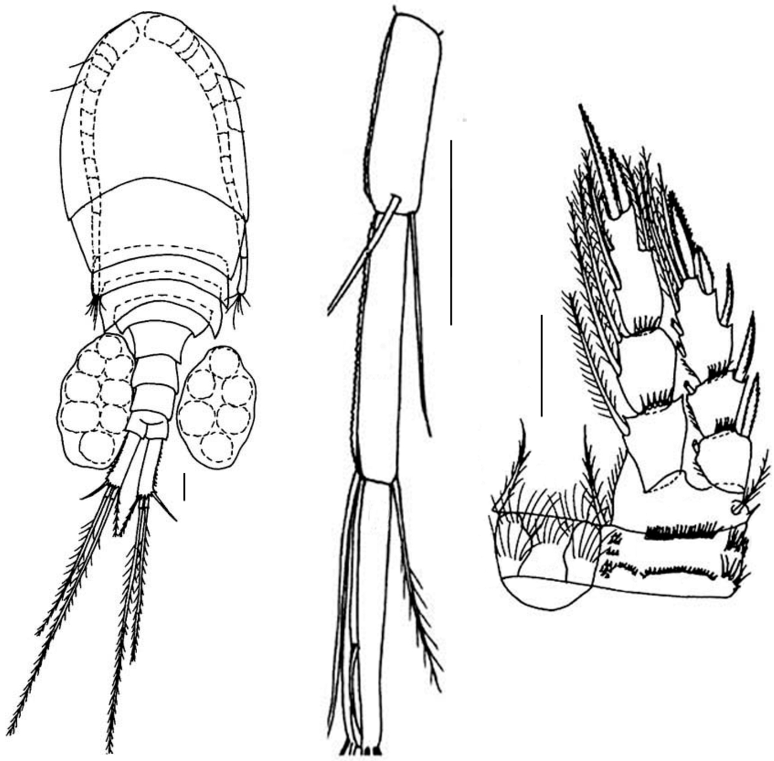

Figure 7. *Eucyclops* (*Denticyclops*) *taiwanensis* Sukhikh and Alekseev, 2015 (after [15]). Scale bars: 50 µm.

Eucyclops taiwanensis is another freshwater cyclopid, which was found in a shallow lake in northern Taiwan. The population density of adults was 260 ind/m^2. A distinctive feature of this species is the partially reduced serration of the hyaline plate of the distal segments of the antennule.

NEMATODA.

Mesodorylaimus szechenyii Andrássy, 1961 (Figure 8).

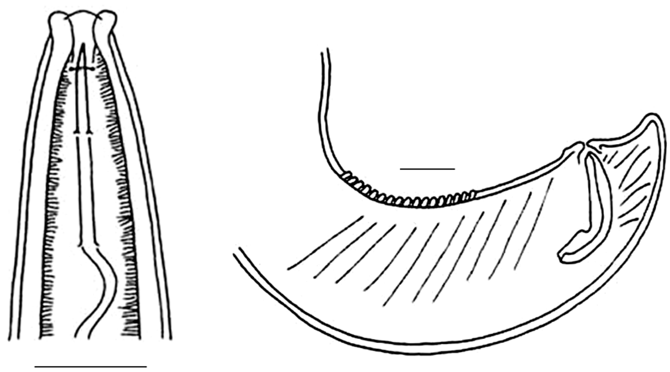

Figure 8. *Mesodorylaimus szechenyii* Andrássy, 1961 (after [16]). Scale bars: 20 µm.

Mesodorylaimus szechenyii is an African species described from East Africa (Tanzania). In Taiwan, it is found in the littoral zone of Sun Moon Lake. The population density was 10,000 ind/m^2. The Taiwanese specimens were identified and described by Professor Tsalolikhin [16], which was the first record of this species outside Africa.

Mactinolaimus typicus Andrássy, 1970 (Figure 9).

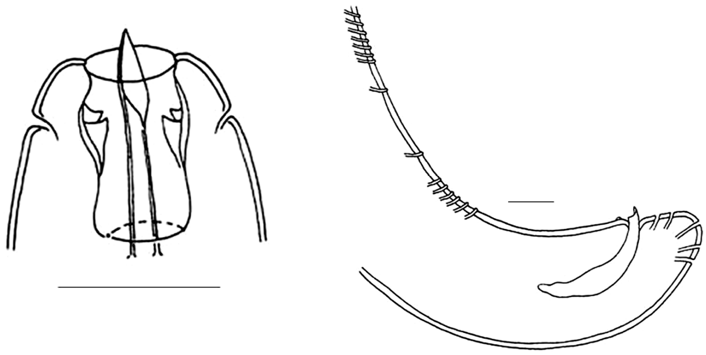

Figure 9. *Mactinolaimus typicus* Andrássy, 1970 (after [16]). Scale bars: 20 μm.

Mactinolaimus typicus is another African species. It was previously described from West-Central Africa (Republic of the Congo). In Taiwan, this species was found in the littoral zone of Sun Moon Lake. The population density was 10,000 ind/m^2. These Taiwanese specimens were identified and described by Professor Tsalolikhin [16], which was the first record of this species outside Africa.

Neotobrilus sinensis Tsalolikhin and Shoshin, 2009 (Figure 10).

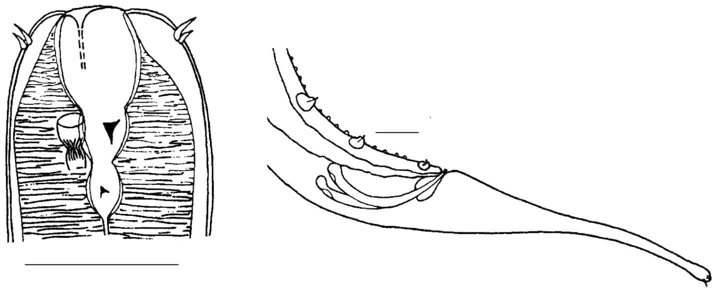

Figure 10. *Neotobrilus sinensis* Tsalolikhin and Shoshin, 2009 (after [17]). Scale bars: 20 μm.

Specimens of *Neotobrilus sinensis* were collected during this study of water bodies in Taiwan in 2007, from the muddy littoral zone of Sun Moon Lake, and described as a new species in 2009 [17]. *N. sinensis* is closely related to *N. vicinus* (Loof, 1973) from Suriname, South America [17]. This is an abundant species with population densities reaching 18,000 ind/m^2 in Sun Moon Lake.

Crassolabium alekseevi Tsalolikhin, 2017 (Figure 11).

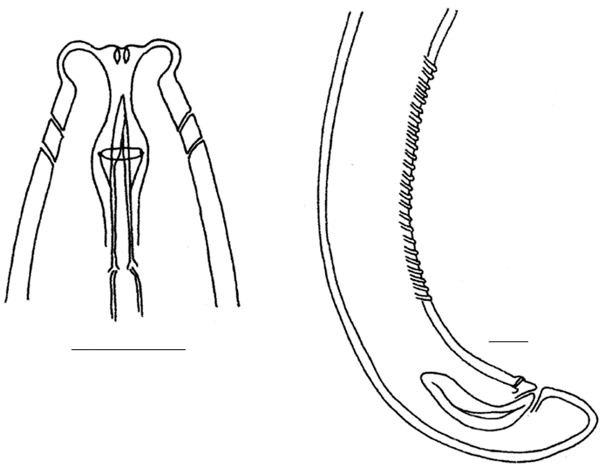

Figure 11. *Crassolabium alekseevi* Tsalolikhin, 2017 (after [18]). Scale bars: 20 μm.

Specimens of *Crassolabium alekseevi* were also collected during this survey of water bodies in Taiwan in 2006, in a pond in Taipei City, in Guine Park. It was described as a new species only in 2017 based on this material. A characteristic of this species is the extreme morphological similarity of both sexes. This species has spicules similar in size to *C. kaszabi* (Andrassy, 1959) and *C. plica* (Ciobanu, Popovici and Decraemer, 2004) [18]. The population density was 14,000 ind/m^2.

3.2. Accumulation of Resting Stages in the Sediments of Inland Water Bodies and Coastal Areas of Taiwan

3.2.1. Marine Ecosystems

A. Shallow biotopes (sediments from mangroves and shallow coral reefs)

Reactivation of sediments from these biotopes collected along the entire western coast of Taiwan (10 stations for coral reefs and 4 for mangroves) did not reveal any resting stages.

B. Deeper marine waters along the west coast

At a hot spring outlet area near Turtle Island in northern Taiwan, sediment samples collected at a depth of 37 m in the open part, as well as in an underwater cave, did not reveal the presence of resting stages of aquatic invertebrates.

Oceanic sediments sampled from a depth of 60–70 m in the vicinity of the Kaohsiung seaport in Taiwan at 2–3 km distance from the Kaohsiung River mouth contained resting stages. Samples were taken from three horizons: 0–2, 2–4 and 4–6 cm. Resting stages were found only in the surface horizon of 0–2 cm. All resting stages were represented by the eggs of several species and genera of marine calanoid copepods. The activated resting stages belonged to the following genera of calanoids: *Tortanus* sp., *Acartia* sp., *Centropages* sp. and *Calanopia* sp. (Table 1).

Table 1. Activated species from the seabed of Kaohsiung harbor (A—traverse Kaohsiung River estuary; B—port area), as of 10 March 2007.

Sampling Sites	Resting Stages Density (ind/m^2)	Taxon
St. 1 Port area, 66 m	2222 ± 2890 (0–5000)	*Acartia* cf. *negligens* Dana, 1849 *Tortanus* cf. *forcipatus* (Giesbrecht, 1889) *Centropages* cf. *calaninus* (Dana, 1849) C3
St. 2 Kaohsiung River estuary, 63 m	4442 ± 3852 (1666–8330)	*Tortanus* cf. *forcipatus* (Giesbrecht, 1889) *Acartia* cf. *negligens* Dana, 1849
St. 3 Kaohsiung River estuary, 68 m	2776 ± 2889 (0–4998)	*Tortanus* cf. *forcipatus* (Giesbrecht, 1889) *Calanopia* cf. *elliptica* (Dana, 1849) C2 *Acartia* cf. *negligens* Dana, 1849

At the port area station (st. 1), the density of dormant stages of calanoids varied from 0 to 5000, with a mean value of 2222 ind/m^2, and was provided by three species of marine calanoids. At the first station in the Kaohsiung River estuary (st. 2), the largest number of resting stages was noted, represented by two species of marine calanoids. At the second station in the Kaohsiung River estuary (st. 3), located at the greatest distance from the mouth of the river, the number of resting stages was less than at the previous station but represented by a higher number of species. The accumulation of resting stages at all three stations differed insignificantly and corresponded to several thousand individuals per m^2.

3.2.2. Freshwater Biotopes

In river ecosystems, no resting stages were found in the sediments (Table 2).

Table 2. Resting stage reactivation from inland sites of Taiwan.

Locality and Depth	Resting Stages Density (ind/m^2)	Taxon
Sun Moon Lake, Kaohsiung River system (9–11 m)	1000 ± 714 (500–1500)	Copepoda
Taipei River (2 m)	0	–
Temporary water body, Keelong vicinity (0.15 m)	32,000 ± 23,265 (1250–41,500)	Cladocera Ostracoda Rotifera Nematoda
Rice field near Kaohsiung (0.2 m)	87,500 ± 67,341 (3500–120,000)	Copepoda Cladocera Ostracoda Rotifera Nematoda
Agricultural canal near Kaohsiung (1 m)	45,000 ± 45,664 (1000–80,000)	Copepoda Cladocera Rotifera

In natural temporary reservoirs (deeper rain pools), a high number of resting stages was noted. The biodiversity of resting stages was quite large and was represented by nematodes, rotifers, ostracods and cladocerans, which have not been identified to species level due to the difficulty of identification by morphological methods at early stages of development, when these taxa undergo dormancy. Besides resting stages, the sampling revealed a possibly endemic species, *Eucyclops taiwanensis*, which was subsequently described in 2015 [15].

In artificial temporary reservoirs, the most significant presence of resting stages of aquatic invertebrates was noted, among which the invasive copepod *Metacyclops minutus* was dominant. Other groups of aquatic invertebrates were represented by nematodes, rotifers, ostracods and cladocerans.

A high density of resting stages was also noted in the irrigation canals associated with rice paddies, but there the leading abundance belonged to the resting stages of the cladoceran genera *Moina* and *Alona*.

In the central part of Sun Moon Lake, at a depth of 9–11 m, where the oxygen content was below 1 mg/L, excluding the presence of fish and predatory aquatic invertebrates (amphipods), the total concentration of resting stages was low. The resting stages were represented by older copepodites of cyclopids and diaptomids.

4. Discussion

Lissachatina fulica (Bowdich, 1822), a giant African land snail, is often found in shallow water bodies, in particular in rice fields, where it can become a pest, feeding on rice shoots. By the nature of nutrition, the mollusk is considered polyphagous and is indicated as a pest that eats the bark of woody plants cultivated in the tropics—citrus, papaya, rubber and cacao [19], but also actively consuming cultivated vegetables, preferring members of the genus *Brassica* [20]. However, the composition of the diet depends primarily on the cultivated species in its habitat. Preying of *L. fulica* on veronicellid slugs has been observed in Hawaii [21]. It was introduced to Southeast Asia in the 20th century from Africa for human consumption, through transportation of plant material and as duck feed [22]. In Taiwan, it was first registered in 1932 [23] where it is widely distributed for the time being. This mollusk scatters its eggs in small portions directly on the ground (see Figure 1). Judging from its rapid increase in abundance, it has few natural enemies in Taiwan. The negative effect of its introduction into ecosystems of Taiwan includes being a pest of various plant species and presenting a risk to public health as a vector of parasitic diseases [24]. With mass development, damage to cultivated plants from vegetables to fruit trees is possible.

Pomacea canaliculata (Lamarck, 1822) was also introduced intentionally as a food item in the early 1980s from Argentina [25]. It is now widely distributed in the tropical parts of all continents except Australia. High fecundity and high protection from possible aquatic enemies determine its wide ubiquitous distribution. It is an intermediate host of some helminths, but their harm to humans and farm animals has not been proven [26]. It is known as a pest of rice plantations, especially in the early stages of cultivation. The greatest harm can be caused primarily in the south of Taiwan, since, at present, its advance to the north is constrained by low temperatures in winter [27]. Mollusk eggs are well protected from potential enemies, located above the water edge and exhibit a certain form of biological dormancy, which requires a drying phase (dehydration) and subsequent watering—the beginning of the rainy period. Such a change of seasons leads to optimal hatching and the entry of young stages of the mollusk in the most favorable period into the shallower parts of reservoirs, from where they move to moist terrestrial environments.

Dreissena bugensis (Andrusov, 1897), like other *Dreissena* members, is one of the potentially dangerous species of aquatic invertebrates in terms of the impact on ecosystems it invades [28,29]. In Taiwan, this species has so far been found only in the littoral zone of Sun Moon Lake. A high proportion of medium- and small-sized individuals indicated that active reproduction is taking place recently, as well as a low consumption of individuals of medium and small size (which are most accessible to fish), which indirectly indicates the absence of natural enemies (consumers) in the ichthyofauna of this lake. Another possible regulatory factor preventing the mass dispersal of this species in other continental water bodies of Taiwan is its relatively low temperature tolerance. The upper temperature limit of the *Dreissena bugensis* can be as low as 25 °C [30]. In Taiwan, water bodies with such a temperature regime are very rare and are found only in mountainous regions. It is possible that Sun Moon Lake will remain the only large water body in Taiwan where this species will become part of the benthic community. For mollusks, the main way invasive species enter Taiwan is through the intentional or accidental introduction by humans.

The world distribution of representatives of *Metacyclops minutus* (Claus, 1863) covers primarily the countries of Africa, Southern Europe and a number of Asian countries where China is the closest to Taiwan [31]. There are no references to findings in the literature for the island of Taiwan, which, of course, does not exclude its possible presence in some water bodies. Nevertheless, in the course of our study, it was established that it is confined to rice fields and related hydraulic structures (canals, storage ponds) and its complete absence in natural reservoirs with a similar environment (puddles, small swamps, etc.). This is an indirect confirmation that *M. minutus* appeared on the island more recently, quite possibly due to the spread of the culture of rice production. In most other countries that are included in its natural range (desert regions of Eurasia), this species lives primarily in temporary natural reservoirs, to which it is adapted, being able to complete its full life cycle from egg to the formation of resting stages in three days at a temperature of 25 °C. It is recommended that further studies verify the above arguments by molecular methods. *Metacyclops minutus* has an extremely high growth rate, the highest among the studied species of continental copepods. The full development cycle from egg to sexually mature female at a temperature of 20 °C is only 96 h and shortens with an increase in temperature [32]. From this point of view, the species is of interest as live food in freshwater aquaculture, especially for consumption by small larvae of fish and crustaceans, since the sizes of the various stages of this species are in the range of 60–800 μm. The species, not previously recorded in Taiwan, is meanwhile a mass form of zooplankton on rice paddies, along with thermophile representatives of the cladocerans *Moina*, whose juveniles it feeds on. It forms banks of dormant resting stages dense in number, which easily tolerate prolonged drying and even cooling to temperatures unusual for the tropics. Our finding of resting stages C4–C5 for *Metacyclops minutus* in rice fields of Taiwan at densities up to 40,000 ind/m^2 is several times higher than could be found in temporary lagoons and other desiccated water bodies reported from higher latitudes and observed in our study in the Gulf of Finland area [11].

Eucyclops (*Denticyclops*) *taiwanensis* Sukhikh and Alekseev, 2015 has been described as a new species for science from Taiwan [15]. The population size is relatively small. It is found in temporary reservoirs, where it could meet, and where *M. minutus* can penetrate. In this case, as a rapidly growing and aggressive species, it can displace this endemic, which raises the question of measures to conserve the endemic. However, before that, it should be established with the help of molecular studies whether there are other populations of this species outside Taiwan, for example, in the southern regions of China.

Two new species of nematodes, *Neotobrilus sinensis* Tsalolikhin and Shoshin, 2009 and *Crassolabium alekseevi* Tsalolikhin, 2017, were also described based on the materials of this research [17,18].

Mesodorylaimus szechenyii Andrássy, 1961 and *Mactinolaimus typicus* Andrássy, 1970 were described from Africa [16]. Their presence in Taiwan may be associated with bioinvasion due to the introduction of ballast water and, in particular, sediments by sea vessels operating between Southeast Asia and Africa. Another possible explanation for the species common to Africa and Taiwan could be the existence of water links between the Pacific and Adriatic regions through the Paratethys millions of years ago [33]. This is indicated by the repeatedly noted faunistic commonality of both existing and extinct species of mollusks, trematodes, planarians and copepods common to these faunas [34–36]. To fully address the issue of the ways of formation of the nematode fauna of Taiwan, it is necessary to conduct comparative molecular studies of these species from Africa and Taiwan.

The accumulation of resting stages in the sediments of inland waters and the coast of Taiwan is closely related to the possibility of dispersal of species of tropical origin by ship ballast water, but it only slightly overlaps with invasive species found in Taiwan (reactivation of *M. minutus* from rice paddies in southern Taiwan and nematodes from Sun Moon Lake). Nevertheless, the obtained materials are of importance for resolving the issue of the movement of species from Taiwan to other regions, where they may turn out as unwanted invaders. Buried eggs may remain viable, although they do not hatch unless they are resuspended into the water column or return to the water–sediment interface due to physical and biological resuspension [37]. For the dynamics of the planktonic populations, as well as for the transfer of these species with ballast water in case they were captured by the pumps of the ship's ballast system, it is critical that resting eggs maintain their viability and the ability to reactivate when exposed to favorable conditions.

Reactivated species of calanoids from sediments collected in Taiwan marine environments also provide mass forms of marine coastal zooplankton of Indochina. Their capture and transport across zoogeographical barriers (for example, through the Panama Canal to the Atlantic coast of the United States and Mexico) can lead to the bioinvasion of these forms and the formation of invasive populations that compete with local species. A similar transfer has already been noted for a number of species of oithonids and pseudocalanids [38].

According to Marcus et al. [39], subitaneous eggs of some calanoid species remain viable for only days or weeks. Hence, they are providing recruits to planktonic populations only for short periods of time, for one season at most. Diapause eggs, on the other hand, can remain viable for many years [40]. Hence, the production of diapause eggs will be important for the persistence of populations that regularly disappear from the plankton seasonally [41]. Surveys of resting eggs, as far as their distribution and abundance in the field are concerned, have primarily been conducted in northern temperate waters. Only a few studies are known from subtropical waters, and there are none from tropical regions. Most of the investigated habitats were in shallow (<20 m) water depths. Marcus [42] noted that only three studies have examined the occurrence of eggs in deeper waters down to a depth of 120 m. As has been substantiated by the present study, concentrations of eggs in sediments are reported to be variable in previous studies. According to Marcus [42], the highest numbers were generally found in muddy sediments characteristic of depositional environments, e.g., estuaries and lagoons. Marcus and Fuller [43] suggested that this distributional pattern reflected the physical characteristics and settling velocities of eggs being similar to silt particle sizes. Positive correlations between egg abundance and the proportion of silt-sized particles in the seabed have also been reported by Lindley [44]. This author concluded that eggs would be most abundant in areas of the open sea that were 20 to 80 m deep and where bottom stress due to tidal currents was <10 dynes cm^{-2}. In areas where bottom stress was greater, e.g., shallow waters, bottom sediments are suspended more often, resulting in the onset of hatching.

Off the coast of California, resting eggs occur in greater numbers inshore at 60 m depth than offshore at 90 and 120 m. This happens despite the fact that muddy sediments are accumulating offshore [42]. Considering development time and sinking rates of the eggs, nondiapause eggs will have a greater probability of reaching the sea floor prior to hatching at 60 m than at 90 or 120 m.

Local and geographical differences in the abundance of resting eggs can be influenced by the distribution of adult females and their reproductive output. Uye et al. [45] found the females of *Tortanus forcipatus* from Fukuyama Harbor (Japan) most abundant in autumn (September 1978). The abundance of the females was remarkably reduced in later investigations, while they tended to be concentrated in the innermost area of that harbor. The survival of resting eggs may have a direct effect on the initial development of planktonic populations in the next season. If the eggs were dying over a considerably wide area, the next planktonic generation might no longer appear in that area if there was no immigration from other locations. This provides invasive species with an additional chance to establish their own populations in a new place.

5. Conclusions

Nine invasive and/or previously unknown (before this study, 2006–2007) species of mollusks, nematodes and copepods were found in the aquatic fauna of Taiwan's inland waters. *Eucyclops* (*Denticyclops*) *taiwanensis* Sukhikh and Alekseev, 2011, *Neotobrilus sinensis* Tsalolikhin and Shoshin, 2009, and *Crassolabium alekseevi* Tsalolikhin, 2017 were subsequently described as new to science based on the results of the analysis of current material and probably belong to the original fauna of the island.

More than half of the nine species are clearly invasive which recently appeared in the fauna and show a tendency to active dispersal (three species of mollusks—*Pomacea canaliculata* (Lamarck, 1822), *Lissachatina fulica* (Bowdich, 1822) and *Dreissena bugensis* (Andrusov, 1897)), and the copepod *Metacyclops minutus* (Claus, 1863).

Two more species (nematodes *Mesodorylaimus szechenyii* Andrássy, 1961 and *Mactinolaimus typicus* Andrássy, 1970), originally described from water bodies of East and West Africa, appeared in the hydrofauna of Taiwan island in two ways: due to human-mediated dispersal with ballast water in recent centuries, or due to natural settlement along the water connections of the Tethys/Paratethys Sea. The solution to the question of the nature and ways of penetration of these species into the fauna of the island should be investigated by applying molecular methods.

Despite the tropical nature of the climate of the island of Taiwan, accumulations of resting stages of aquatic invertebrates were found both in marine and continental ecosystems. The most significant banks of resting stages in terms of density were noted for temporary artificial reservoirs (rice fields dominated by *M. minutus*, a supposed invader to Taiwan).

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