Thalassic Rotifers from the United States: Descriptions of Two New Species and Notes on the Effect of Salinity and Ecosystem on Biodiversity

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Abstract: This study shows the results of a rotifer faunistic survey in thalassic waters from 26 sites located in northeastern U.S. states and one in California. A total of 44 taxa belonging to 21 genera and 14 families were identified, in addition to a group of unidentifiable bdelloids. Of the fully identified species, 17 are the first thalassic records for the U.S., including *Encentrum melonei* sp. nov. and *Synchaeta grossa* sp. nov., which are new to science, and *Colurella unicauda* Eriksen, 1968, which is new to the Nearctic region. Moreover, a refined description of *Encentrum rousseleti* (Lie-Pettersen, 1905) is presented. During the survey, we characterized samples by different salinity values and ecosystems and compared species composition across communities to test for possible ecological correlations. Results indicate that both salinities and ecosystems are a significant predictor of rotifer diversity, supporting that biodiversity estimates of small species provide fundamental information for biomonitoring. Finally, we provide a comprehensive review of the diversity and distribution of thalassic rotifers in the United States. The results of the present study increase the thalassic rotifer record for the U.S. from about 105 (87 at species level) to 124 (106 at species level) taxa.

Keywords: marine; brackish; meiofauna; microscopic invertebrates; North America; taxonomy; ecology

1. Introduction

Phylum Rotifera is a group of micrometazoans including 2149 species (inclusive subspecies) distributed worldwide in almost every type of aquatic and semi-aquatic habitat, and containing two major groups: Bdelloidea and Monogononta; Seisonacea represents a small group of four epizoic marine species [1–6]. Most of the known rotifer taxa are freshwater, and only about 455 taxa have been reported from saline ecosystems, both thalassic and athalassic [6–11]. The relatively low richness of saltwater rotifers may reflect the actual paucity of the group; however, results might be likely misrepresented by a clear sampling bias [6,12]. In fact, the majority of rotifer investigations have been performed in freshwater biotas, with rotifers being traditionally neglected in saltwater habitats [6]. Yet, not surprisingly, the diversity of brackish and marine rotifers seems to be particularly high in areas around Europe, reflecting the geographic distribution of the investigators [10,13,14], a phenomenon known as the "rotiferologist effect" [12].

In the United States, marine biodiversity is well investigated; however, as also stated by Fautin et al. [15], the most documented and better described marine taxa appear to be the ones that are larger and of commercial importance (but see the study on marine coastal tardigrades by

Miller and Perry [16]). Most studies focusing on biodiversity include rotifers in larger groups, usually called "other invertebrates" [15]. This pattern is likely due to taxonomic inventories based on records scattered in space and time, but it also supports the perception that microscopic invertebrates are underappreciated and largely neglected in biodiversity studies [9,17].

Taxonomic investigations on thalassic rotifers, i.e., both marine and brackish, of the U.S. almost exclusively concern Monogononta. The first study dates back to 1904 when Smith described *Synchaeta bicornis* from Louisiana, Gulf of Mexico [18]. Subsequent contributions are mostly limited to the first half of the 20th century and mainly focused on the thalassic environments of Maine and New Jersey (Northeast U.S. Continental Shelf) [19–28]. Further information on the rotifers of the Gulf of Mexico was added by Ahlstrom [29,30], Koste [31], and Turner [32,33]. A single study has discussed rotifers from Alaska [34]. Occasional information on thalassic rotifers from the Hawaiian Islands was provided by Weber [35], Hauer [36], and Jersabek [37]. A new seisonid, collected off the coast of California, was more recently described by Leasi et al. [38]. Additional or occasional information is mostly included in more general ecological investigations of plankton. Ecological studies, usually treating rotifers besides other organisms, are largely restricted to the plankton of the estuaries of the Chesapeake Bay basin, and mostly refer to rotifers as a group or at the genus level only (e.g., [39–41]).

The present study shows the results of a taxonomic and ecological survey of 26 thalassic sites from the northeastern U.S. states and one in California. Rotifer communities were collected, analyzed taxonomically, and compared across different ecosystems and salinities to test for possible ecological correlations. Four species were new to science, of which two are described hereafter. During the survey, we found several specimens of *Encentrum rousseleti* (Lie-Pettersen, 1905), which allowed us to refine the description of its external morphology and masticatory hard parts. In addition, we present a comprehensive review of the diversity and distribution of thalassic rotifers reported in U.S. waters to date.

2. Materials and Methods

2.1. Sampling

A total of 27 saltwater sites were sampled across seven U.S. states between March and September 2012 (Table 1, Figure 1). Sites were mainly from the Northeast Continental Shelf, including Connecticut (two sites), Maine (two sites), Massachusetts (four sites), New Hampshire (two sites), New Jersey (13 sites), and New York (three sites); one site was from California Current. Ecosystems consisted of littoral beaches to salt and brackish channels, backshore areas, circumscribed saline ponds, and marshes. All samples were characterized by either floating or benthic green algae (gutweed, *Ulva* sp.), salt grass (*Distichlis* sp.), and wrack (*Fucus* sp.). Although samples were inevitably collected together with some surrounding water and sediment, the identified rotifers shall be considered periphytic. Samples were collected by hand with jars in three replicates, kept in refrigerated coolers at a temperature of about 10 °C, and taken to the laboratory at the Academy of Natural Sciences of Drexel University in Philadelphia, where they were processed within a few days. Each replicate was investigated separately and results were pooled together. For each site, geographical coordinates were recorded, ecosystem observed, and salinity measured in the field with a ±0.5‰ resolution VWR® International Brand Hand Held Refractometer (Table 1). For a gross general survey, we arbitrarily considered "saltwater" to be water with a salinity equal to or higher than 0.5‰. Specifically, we distinguished "brackish waters" as waters with a salinity of 20‰ or lower and "marine waters" as those with salinity above 20‰ [42,43]. For a more detailed analysis of salinity (S), we followed the Venice System [44], recognizing oligohaline (0.5‰ < S ~ 5‰), mesohaline (5‰ < S ~ 18‰), polyhaline (18‰ < S ~ 30‰), and euhaline waters (30‰ < S ~ 40‰). Ecosystems sampled (Table 1, Figure 1) were grouped into three major types: (i) Coast, including habitats that are not expected to be affected by water fluctuations. For example, coastal waters, internal harbors, exposed or sheltered beaches, backshore areas, and channels permanently connected to the ocean; (ii) Ponds, including habitats that are likely

affected by seasonal water fluctuations. For example, circumscribed basins and either natural or artificial ponds not directly connected to the ocean or not disturbed by maritime activities; (iii) Marshes, defined as temporary areas of coastal vegetation affected by regular and frequent seawater flooding and desiccation. Out of the 27 sampled sites, 12 were saline marshes, 8 sites were located on the coast or permanently connected to the open ocean, and 7 were circumscribed ecosystems or ponds (Figure 1). Nine sites were characterized by brackish and 18 by marine water, with salinity values ranging between 2‰ and 40‰: four oligohaline, four mesohaline, eleven polyhaline, and eight euhaline.
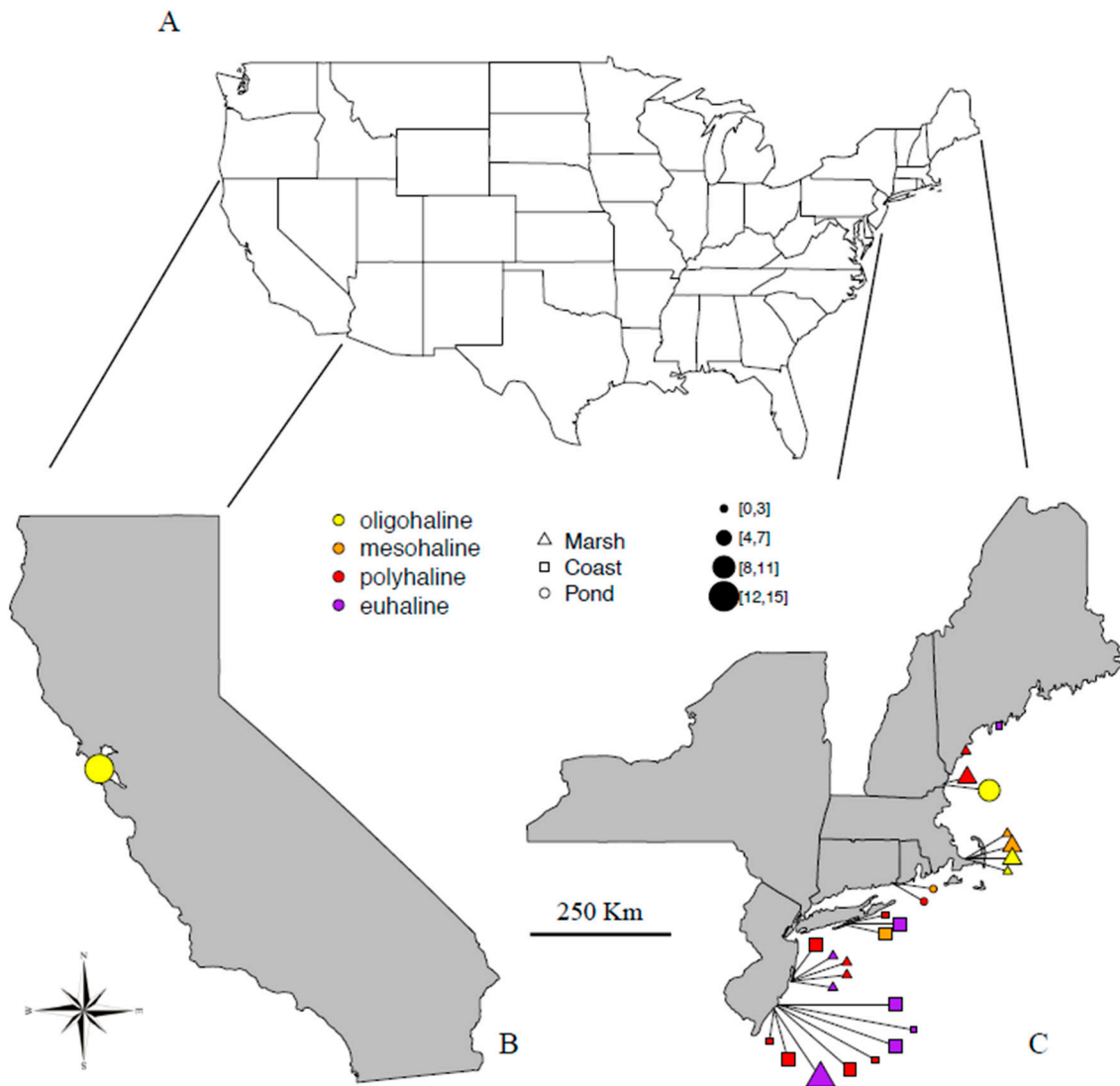
Figure 1. Map indicating sampling sites: (**A**) outline of the United States; (**B**) California. (**C**) Northeast U.S. Locations are indicated using different colors for salinities according to the Venice Classification and different shapes for the three types of ecosystem. The size summarizes the number of species found at each site.

Table 1. List of sites and ecosystems where samples were collected. Coordinates (in decimal degree format), salinity values and classifications, ecosystems, and date of sampling are shown.

Site ID	State *	Site	Salinity ‰	Salinity Group	Ecosystem	Lat N	Long W	Venice Classification	Date of Sampling mm/dd/2012
100	NJ	Barnegat Bay	34	Marine	Marsh	39.7917	74.113	euhaline	03/30
101	NJ	Barnegat Bay	40	Marine	Marsh	39.7904	74.1150	euhaline	03/30
102	NJ	Barnegat Bay	30	Marine	Marsh	39.7905	74.1171	polyhaline	03/30
103	NJ	Barnegat Bay	30	Marine	Marsh	39.7909	74.1171	polyhaline	03/30
104	NJ	Barnegat Bay	24	Marine	Marsh	39.8718	74.0822	polyhaline	03/30
118	NJ	Brigantine	34	Marine	Coast	39.4192	74.3796	euhaline	06/05
119	NJ	Brigantine	34	Marine	Coast	39.4191	74.3800	euhaline	06/05
120	NJ	Brigantine	34	Marine	Coast	39.4191	74.3800	euhaline	06/05
121	NJ	Brigantine	30	Marine	Coast	39.3947	74.4030	polyhaline	06/05
122	NJ	Brigantine	30	Marine	Coast	39.3949	74.4026	polyhaline	06/05
123	NJ	Calvert	30	Marine	Coast	39.3459	74.4765	polyhaline	06/05
124	NJ	Calvert	30	Marine	Coast	39.3460	74.4761	polyhaline	06/05
125	NJ	Calvert	34	Marine	Marsh	39.3526	74.4790	euhaline	06/05
126	CA	San Francisco	4	Brackish	Pond	37.7803	122.5139	oligohaline	07/09
130	NY	Fire Island	30	Marine	Pond	40.6927	72.9882	polyhaline	07/31
131	NY	Fire Island	32	Marine	Pond	40.6939	72.9868	euhaline	07/ 31
132	NY	Fire Island	8	Brackish	Pond	40.6915	72.9863	mesohaline	07/ 31
139	ME	Boothbay	32	Marine	Coast	43.8422	69.6545	euhaline	09/28
140	ME	Biddeford	20	Brackish	Marsh	43.4395	70.3654	polyhaline	09/28
141	NH	Hampton	30	Marine	Marsh	42.9295	70.8405	polyhaline	09/28
142	NH	Hampton	2	Brackish	Pond	42.9078	70.8667	oligohaline	09/28
143	MA	Cape Cod Barnstable	6	Brackish	Marsh	41.7338	70.3794	mesohaline	09/30
144	MA	Cape Cod Barnstable	10	Brackish	Marsh	41.7333	70.3794	mesohaline	09/30
145	MA	Cape Cod Barnstable	3	Brackish	Marsh	41.7332	70.3794	oligohaline	09/30
146	MA	Cape Cod Barnstable	4	Brackish	Marsh	41.7333	70.3794	oligohaline	09/30
147	CT	Mystic	10	Brackish	Pond	41.3563	71.9644	mesohaline	09/30
148	CT	Mystic	30	Marine	Pond	41.3562	71.9648	polyhaline	09/30

* CA, California; CT, Connecticut; MA, Massachusetts; ME, Maine; NH, New Hampshire; NJ, New Jersey; NY, New York.

2.2. Taxonomic Analysis

Specimens were extracted by siphoning off the water just above the residue sediment and vegetation [45]. Live material was studied using dissecting (Leica M125) and light microscopes (Leica DM6B), followed by fixation with formalin. The major works used for identification of rotifer species were by Koste [46], Nogrady et al. [47], Segers [48], De Smet [49,50], Nogrady and Segers [51], and Fontaneto et al. [7]. The nomenclature of the rotifers followed the proposal of Segers et al. [52] and Jersabek et al. [53]. Fixed specimens were drawn using a Leitz Orthoplan microscope equipped with camera lucida. Preparation of the rotifer trophi was done following De Smet [54], and scanning electron microscopy (SEM) was performed with a Philips SEM 515 operated at 20 kV. The terminology of the trophi elements of *Synchaeta* followed De Smet (in prep.); elements are indicated in the figures of the species description.

2.3. Data Analysis

We expected that type of ecosystem, as well as salinity, might affect species composition and species distribution. Therefore, we tested for the statistical significance of rotifer communities across (1) the three types of ecosystems, broadly defined and described above as coast, ponds, and marshes, and (2) salinity values. Differences in community structure (β-diversity) between samples were measured using the Jaccard dissimilarity index, therefore, we partitioned differences in community composition among variables using a permutational multivariate analysis of variance (PERMANOVA) approach and tested significance by permuting the data (999 permutations, function *adonis* in the R package Vegan 2.4–5 [55]). Pairwise comparisons between group levels were performed with the function *pairwise.perm.manova* (package RVAideMemoire 0.9–72 [56]). Moreover, we performed a two-dimensional non-metric multidimensional scaling ordination (nMDS) to investigate community dissimilarities. The Jaccard dissimilarity index was used to generate a rank dissimilarity matrix, which was converted into an nMDS [55,57]. Rotifers of each site were considered as a unique assemblage using the R package Vegan 2.4–5 [55]. Furthermore, we used analysis of variance (ANOVA), implemented in R, to test whether the type of ecosystem is a significant predictor of salinity [58].

A few taxa could only be identified to the genus level and are included in the analyses as such. Six bdelloid specimens were not identified because of their contracted body resulting from fixation in formalin, and not allowing for any diagnostic investigation. Therefore, they were not included in the analyses, although we are aware they might represent further species. Biological units were organized in presence/absence (incidence) datasets. To test the effect of the sample size, a linear model was used to correlate the number of investigated samples from each of the three ecosystems, as well as from each of the four salinity groups according to the Venice System, with species diversity measured in both richness (α-diversity) and community structure (β-diversity).

2.4. Compilation of Checklist of U.S. Thalassic Rotifer Taxa

The checklist of thalassic rotifers from the United States (Supplementary Table S1) was based on a compilation of all published records known to us [3,18–41,59–79], in addition to information available in the Frank J. Myers Rotifera Collection at the Academy of Natural Sciences of Drexel University [79], the Rotifer World Catalog [3], a few hitherto unpublished occasional records by one of us (W.H.D.S.), and the species found in the present survey. We must emphasize that many literature reports concern unverifiable records. The biogeographical system for marine regions of the U.S. of Fautin et al. [15] was used to summarize rotifer distribution.

3. Results

3.1. Taxonomic Analysis

Two species, new to science, are described below. *Encentrum melonei* sp. nov. was found in euhaline waters from New Jersey and Maine. *Synchaeta grossa* sp. nov. was present in mesohaline,

polyhaline, and euhaline waters from New Jersey, Maine, and Massachusetts. Moreover, a refined description of the external morphology and masticatory hard parts of *Encentrum rousseleti* is presented.

Systematics

Class EUROTATORIA De Ridder, 1957
Subclass MONOGONONTA Plate, 1889
Order PLOIMA Hudson and Gosse, 1886
Family Dicranophoridae Harring, 1913
Genus *Encentrum* Ehrenberg, 1838
Encentrum melonei De Smet and Leasi, new species

Diagnosis: Large-sized *Encentrum* about 205–210 μm long (slightly contracted); trophi subgenus *Encentrum* type; rostrum small, rounded; corona oblique; tail very short, somewhat straight-cut; toes conical, indented near mid-length, bases swollen, tubuli distinct; rami very weakly asymmetrical, median rami opening wedge-shaped with two marginal slightly asymmetrical teeth, left tooth fairly acute, right one blunt; intramallei with small additional platelet medio-laterally.

Material examined: Six females collected from New Jersey (sites 124 and 125; Table 1) and one from Maine (site 139, Table 1).

Type locality: New Jersey, Calvert Ventnor City, 39.346071 N, −74.476131 E; site 124; collected 5 June 2012, salinity = 30‰. Lagoon in estuarine system surrounded by wetland in close proximity to salt marsh islands and connected to the Atlantic Ocean by a channel. Samples characterized by a variety of benthic seaweeds, viz. sea lettuce (*Ulva lactuca*), wrack (*Fucus* sp.), and gutweed (*Ulva* sp.).

Holotype: An adult female in a permanent glycerin glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (R.B.I.N.S.), Brussels, Belgium, IG. 34111, RIR.283

Paratypes: An adult female in R.B.I.N.S (IG. 34111, RIR.284), and one in the Department of Biology, University of Antwerp; four stubs, each with trophi preparation for SEM in the Department of Biology, University of Antwerp.

Etymology: The species is named after Prof. Dr. Giulio Melone (University of Milan, Italy), in recognition of his contributions to rotiferology. http://zoobank.org:act:476BBF80-33AD-4F33-B01C-A5E69EF212F1.

Description of female: Body (Figure 2A,B) stout fusiform in dorsal view, broadest near mid-length, in lateral view weakly arched. Head *c.* 1/3 total length, offset from trunk by distinct neckfold, almost in line with trunk; weak longitudinal furrows dorso-laterally. Dorsal antenna at 1/3 from neckfold. Rostrum small, rounded. Corona oblique. Trunk with distinct distal pseudosegment and weak longitudinal dorso-lateral furrows terminating in shallow dorso-lateral expansions near posterior 1/3. Lateral antennae near distal margin of main trunk pseudosegment. Tail very short, somewhat straight-cut in dorsal view. Foot short, broad, a single pseudosegment, with small caudal antenna between toes. Toes (Figure 2C,D) *c.* 1/8 total length, in dorsal view conical, symmetrically indented near mid-length, terminating in distinct tubuli; in lateral view dorsal medial indentation less pronounced. Brain saccate, with distinct retrocerebral sac. Proventriculus present. Gastric glands large, spherical, stalks apparently absent. Bladder spherical. Pedal glands extending into trunk, elongated bean-shaped with small spherical reservoirs. Vitellarium with eight spherical nuclei.

Trophi (Figures 2E and 3) of subgenus *Encentrum* type; large, elongated, fairly slender. Rami very weakly asymmetrical, rami outline longer than wide, ratio length: width of closed rami ~1.6; dorsal outer margin of rami straight laterally, angular postero-laterally, forming short blunt alulae; ventral outer margins, in particular of subbasal chambers, converging towards fulcrum; rami laterally fairly concave, with distinct ridge between subbasal and basal chambers (Figure 3F: r); carina rami absent; median rami opening wedge-shaped with two marginal slightly asymmetrical teeth formed by the protruding distal ends of the subbasal chambers, left tooth fairly acute, right one blunt; basal chambers dorsally with small ellipsoid basifenestrae; subbasal chambers caudally with small, rounded subbasifenestrae. Each ramus with single, slightly offset apical tooth set at almost right angle to trophi

axis; cardal apophyses very small to absent. Prior to apical teeth a preuncinal tooth set at a right angle to trophi axis; preuncinal teeth with elongated triangular head and short shaft forming right angle; base of head very weakly swollen; distal end of shaft with small cardal apophysis. Fulcrum long, slightly longer than ramus, in dorsal/ventral view distal end slightly widening, widening indented distally; in lateral view with broader base, gradually tapering, continuing parallel-sided. Unci medium long, composed of single uncinus, slightly curved, head as long as shaft, with small dorsal and ventral apophyses. Intramallei long (Figure 3E: im), sock-shaped, with relatively long, rounded medio-lateral basal expansion showing opening at the inner median side, and bearing fused additional platelet medially (Figure 3E: ap) at anterior margin; inner side expanded, fitting lateral concavity of rami. Supramanubria apparently absent. Manubria slightly less incus length, stout, rod-shaped, proximal 2/3 straight, distal 1/3 incurving with crutched cauda, head short, with small triangular expansion showing fairly large median opening.
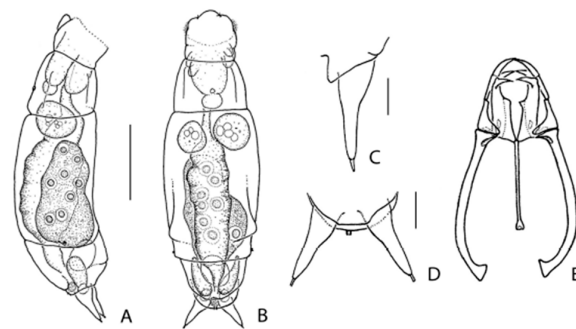
Figure 2. *Encentrum melonei* sp. nov. (**A**) Female, lateral. (**B**) Female, dorsal. (**C**) Toe, lateral, right. (**D**) Toes, dorsal. (**E**) Trophi, ventral. Scale bars: (**A,B**): 50 μm; (**C–E**): 10 μm.
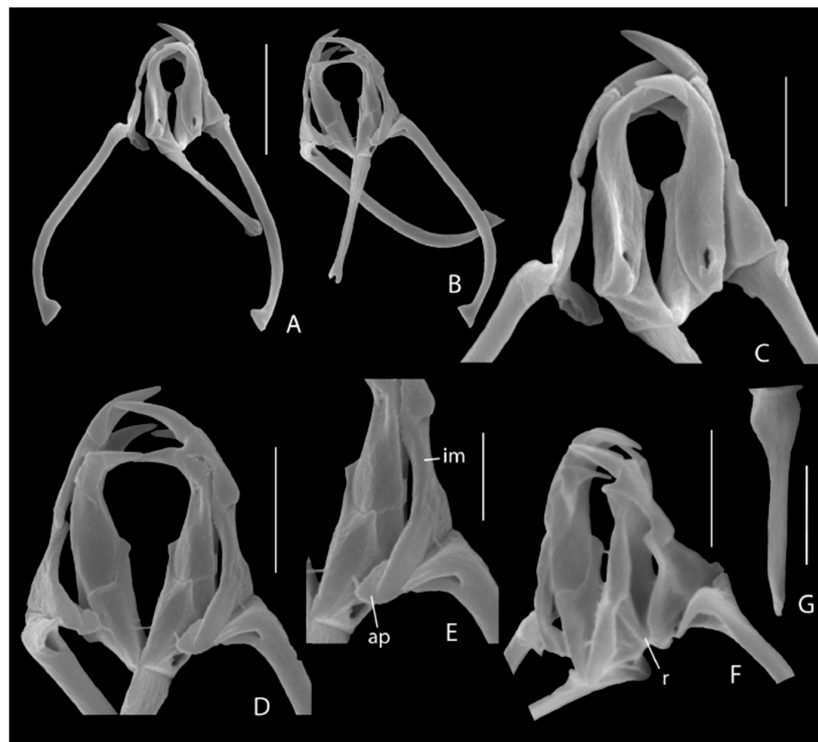
Figure 3. *Encentrum melonei* sp. nov., scanning electron microscopy (SEM) photographs of trophi. (**A**) Complete set, dorsal. (**B**) Complete set, ventral. (**C**) Detail, dorsal. (**D**) Detail, ventral. (**E**) Left intramalleus, ventro-lateral. (**F**) Detail, ventro-lateral. (**G**) Fulcrum, lateral. ap: additional platelet; im: intramalleus; r: ridge between subbasal and basal chamber. Scale bars: (**A,B**): 10 μm; (**C–G**): 5 μm.

Measurements: Total length (slightly contracted) (N = 5): 205–210 µm, toe 23–27 µm; trophi (N = 4): length 26.8–29.0 µm (mean 27.7 µm), ramus 9.6–10.2 µm (mean 9.9 µm), fulcrum 10.3–11.5 µm (mean 11.2 µm), uncus 6.4–7.1 µm (mean 6.8 µm), preuncinal tooth (tooth × shaft) 2.1–3.4 × 2.1–2.6 µm (mean 2.3 × 2.9 µm), intramalleus ~5–6.3 µm, manubrium 19.4–20.3 µm (mean 19.6 µm).

Distribution and ecology: *Encentrum melonei* sp. nov. is, to date, only known from New Jersey (Atlantic County, Ventnor City) and Maine (Lincoln County, Boothbay). Sample sites are located either backshore, although connected to the open Atlantic Ocean (New Jersey, site 124), in marshes (New Jersey, site 125), or directly on the coast (Maine, site 139). Samples were collected in June and September at salinities ranging from 30‰ to 34‰, indicating that it may be a truly marine (euhaline) species.

Comments: The new species superficially resembles the larger species belonging to the subgenus *Encentrum* [50], but is easily differentiated by its characteristic toes and the presence of slightly asymmetrical median rami teeth. Judging from the shape of the species-specific trophi, the next related species of *E. melonei* sp. nov. is *Encentrum limicola* Otto, 1936, which lacks median rami teeth, and *E. algente* Harring, 1922, showing rather pronounced symmetrical median rami teeth. The small additional platelet fused to the intramallei present in the new species have not been demonstrated in the 12 *Encentrum* (*Encentrum*) species studied to date by SEM [50,80,81]. Their medio-lateral position at the antero-proximal end of the intramallei suggest that it may be vestigial supramanubria.

Class EUROTATORIA De Ridder, 1957
Subclass MONOGONONTA Plate, 1889
Order PLOIMA Hudson and Gosse, 1886
Family Dicranophoridae Harring, 1913
Genus *Encentrum* Ehrenberg, 1838
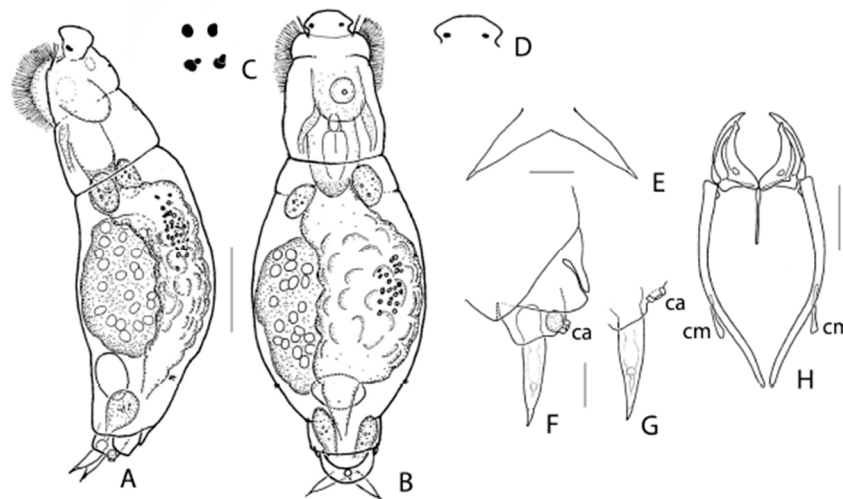*Encentrum rousseleti* (Lie-Pettersen, 1905)

Diglena rousseleti Lie-Pettersen 1905; 34–35, text Figure 3, pl. 2, Figures 9–11.

Material examined: New Jersey (site 125; marsh; S = 34‰) and Massachusetts (site 144; marsh; S = 10‰); additional material: several specimens from a brackish puddle at Ambleteuse, the Channel, France.

The species was rather poorly described by Lie-Pettersen [62] from a brackish puddle at Radö, Bergen, Norway. Remane ([13]: 138, Figure 162; 1933: 301, Figure 23a) presented more detailed figures, but without giving descriptions of the specimens, apparently collected in the Kieler Bucht, Germany. Althaus ([82]: 136–137, Figure 32) provided an extensive description, based on animals collected from an inland saline ditch at Burgliebenau, near Merseburg, Germany. The present study of specimens from U.S. and material from France allows for some corrections and additions to the description of *E. rousseleti*, as presented in the revision by De Smet [50], which was based on the above-mentioned studies. The morphology of the small trophi, at the limit of light microscopy, is redescribed based on SEM.

Emendations to female morphology: (Figure 4A–G). The rostrum (Figure 4D) is not broadly rounded uniformly but weakly flattened in the middle. A large caudal antenna (Figure 4F,G: ca), not mentioned before, is present dorsally between the bases of the toes. The toes (Figure 4E–G) are in both ventral/dorsal and lateral view almost parallel-sided for about 2/3 of their basal part, whereupon the inner, respectively ventral, margins continue in a straight way, and the outer, respectively dorsal, margins curve to continue in a straight line towards a motile acute tip, shaped as a pseudoclaw. The toes show distinct round reservoirs at *c.* 1/3 from the tip. Two red eyespots (Figure 4C), in dorsal view reniform to rounded, laterally at the base of the rostrum; each of them occasionally accompanied by a small roundish red eyespot. The number of nuclei in the vitellarium vary between 16 and 34 (18–20 in literature).

Figure 4. *Encentrum rousseleti* (Lie-Pettersen, 1905). (**A**) Female (slightly contracted), lateral. (**B**) Female, dorsal. (**C**) Eyespots (left), different shapes. (**D**) Rostrum, detail, dorsal. (**E**) Toes, dorsal. (**F**,**G**) Toes, lateral left. (**H**) Trophi, dorsal. ca: caudal antenna; cm: calcar manubrii. Scale bars: (**A**,**B**): 50 μm; (**E**–**G**): 10 μm.

Redescription of the trophi by S.E.M.: (Figure 5). Major differences to former descriptions are indicated between square brackets. Rami outline oboval with blunt dorsal postero-lateral alulae (alulae absent) and short latero-dorsal projection at the outer margin of basifenestrae (Figure 5F); median rami opening broad lenticular. Rami curved, broad and high at base, tapering to slightly outcurved blunt tips, prior to tips a short, blunt medio-lateral tooth (rami with simple acute tip). Rami lateral margins concave, showing pronounced dorsal and ventral edges (not mentioned). Basifenestrae and subbasifenestrae small. Preuncinal teeth absent. Fulcrum *c.* 4/5 ramus length (*c.* $^1/_2$ ramus length), narrow and almost parallel-sided in dorsal/ventral view, its proximal 1/3 with additional layer of lateral sclerofibrillae responsible for weak thickening (anterior half expanded); in lateral view broad at base, only weakly narrowing towards the more or less rounded distal end (posterior edge straight). Unci long, *c.* 4/5 ramus length, each composed of two slender, slightly curved uncini (Figure 5I) with long shafts and weakly offset heads (unci single-toothed); ventral uncini largest with large more or less acute head *c.* 1/5 uncus length, shaft showing sutura uncini; dorsal uncini with small rounded head *c.* 1/8 shaft length, shaft without sutura uncini. Intramallei small, thin, more or less triangular in lateral view. Supramanubria (Figure 5J,K) conical, distal tips pointing towards trophi axis, bases somewhat swollen with dorsal projection and proximal opening opposite to medio-lateral opening of head of manubria. Manubria long, *c.* 1.5 incus length, rod-shaped, slightly curved, weakly tapering and outcurving distally, bearing ventral sclerite element near midpoint of curvation: the manubrial spur or calcar manubrii (Figure 5A,B: cm); head of manubria only weakly enlarged with proximal medio-lateral opening; calcar manubrii (Figure 5L–N: cm) a narrow elongated element with slightly expanded distal end, its ventral surface smooth, the dorsal one with shallow irregular groove. Epipharynx consists of two very thin elongated lamellar structures of unclear shape, bearing two to three strongly sclerified projections distally at median margin (e.g., Figure 5D,H,I: e).

Measurements: Total length (N = 5): 265–285 μm; toe: 21–24 μm; trophi (N = 5): length 37.0–44.0 μm (mean 40.4 μm), ramus 10.0–11.7 μm (mean 11.0 μm), fulcrum 6.8–8.9 μm (mean 7.9 μm), ventral uncinus 8.2–9.7 μm (mean 9.1 μm), dorsal uncinus 6.2–7.6 μm (mean 7.0 μm), intramalleus 2.9–3.4 μm (mean 3.2 μm), supramanubrium 5.3–6.5 μm (mean 6.0 μm), manubrium 29.0–33.9 μm (mean 31.2 μm), calcar manubrii 6.8–9.2 μm (mean 7.4 μm).

Figure 5. *Encentrum rousseleti* (Lie-Pettersen, 1905), SEM photographs of trophi. (**A**) Complete set, dorsal. (**B**) Complete set, ventral. (**C**) Detail, dorsal. (**D**) Detail, ventral. (**E**) Detail dorso-lateral. (**F**) Detail, dorso-frontal. (**G**) Detail, ventro-caudal. (**H**) Detail left ramus tip and epipharynx, dorsal. (**I**) As Figure H, dorso-lateral. (**J**) Right supramanubrium, caudal. (**K**) Left supramanubrium, ventral. (**L,M**) Calcar manubrii, ventral. (**N**) Calcar manubrii, dorsal. ca: caudal antenna; cm: calcar manubrii; e: epipharynx; m: manubrium. Scale bars: (**A–G**): 10 µm; (**H–K**): 1 µm, (**L**): 5 µm; (**M,N**): 2 µm.

Comments: *Encentrum rousseleti* cannot be classified into one of the subgenera of the genus [50,80]. Its close relative is apparently *Encentrum salsum* Myers, 1936. However, the latter has been insufficiently described, and due to confusion with Myer's *E. salsum* and *E. rousseleti* specimens in the collection of the Academy of Natural Sciences of Drexel University, as well as by the condition of the slide and specimen position of the type material of *E. salsum* in the collection of the American Museum of Natural History (C. Jersabek pers. comm.), the value of the discriminating features needs to be taken with caution. Currently, *E. rousseleti* is distinguished from *E. salsum* by a different shape of the toes and a higher number of vitellary nuclei (16–34) versus 4(?) in *E. salsum*. A detailed description of the trophi of *E. salsum* is lacking, but from the photograph of the trophi preparation (ANSP 740) attributed to the species (see [3,83]), it looks that calcares manubriorum and lamellar epipharynges bearing strongly sclerified projections may be present. Both structures, in combination with the absence of preuncinal teeth and unci composed of two distinct uncini, distinguish *E. rousseleti* (and *E. salsum*) from

the congeners studied in detail. Calcares manubriorum were not described formerly in *E. rousseleti* but only indicated by Remane ([13]: Figure 162B) as small semi-circular structures in his trophi picture. To date, such calcares have not been reported in any other monogonont rotifer.

Encentrum rousseleti is a strictly haline, benthic-periphytic, and interstitial species known from marine coastal habitats, estuaries, and inland saline waters [6,50,84]. Salinities at which the species is found range from 10‰ to 34‰. It has been reported at several occasions from the Palaearctic region (Europe, Japan), and was once mentioned from U.S.A., New Jersey [3] and Puerto Rico [85].

Class EUROTATORIA De Ridder, 1957
Subclass MONOGONONTA Plate, 1889
Order PLOIMA Hudson and Gosse, 1886
Family Synchaetidae Hudson and Gosse, 1886
Genus *Synchaeta* Ehrenberg, 1832
Synchaeta grossa De Smet and Leasi, new species

Diagnosis: Medium-sized *Synchaeta* up to 250 μm; body plump, vase-shaped; auricles small to medium; foot medium, stout; ventral sensory pit/caudal antenna at some distance from base of toes; toes double, equal, small, bulbous; pseuduncinal plate with comb of five to six lamellar teeth; fimbriae pseuduncinal sinus and fimbriae ramus fibrillary.

Type locality: New Jersey, Barnegat Bay, flat marshes, 39,790567 N, 74,117133 E; site 102, collected 30 March 2012, salinity = 30‰.

Material examined: Several females collected from saline marshes located in New Jersey, Maine, and Massachusetts.

Holotype: An adult female in a permanent glycerin glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (R.B.I.N.S.), Brussels, Belgium, IG. 34112, RIR. 285.

Paratypes: Two adult females from type locality in R.B.I.N.S (IG. 34112, RIR. 286), and XX in the Department of Biology, University of Antwerp; 10 stubs each with trophi preparation for SEM in the Department of Biology, University of Antwerp.

Additional material: Several specimens from New Jersey (sites 100, 102–104, 125), Maine (site 140), and Massachusetts (site 143)

Etymology: The Latin *grossa,* plump, fat, is an adjective referring to the habitus of the species. http://zoobank.org:act:F32F381B-11C6-42E8-B8F3-C757DAFE3BCC.

Description of female: Body plump (Figure 6A,B), in dorsal view vase-shaped, more or less strongly constricted behind head, in lateral view appearing less constricted, constriction with several delicate transversal wrinkles. Trunk ovate in dorsal view, with greatest width near its transversal midline, tapering to short tubular end with varying number (1–3) of transversal rows of very small and narrow U-shaped marks (Figure 6E); in lateral view ventral margin weakly arched, dorsal margin strongly arched and somewhat bulging in posterior half; lateral antennae near posterior fourth of trunk. Head tilted ventrally; auricles rather small to medium; apical field of corona in dorsal view fairly convex, in lateral view apical field strongly convex; apical field with central undivided row of cilia; the four styli characteristic of the genus absent, instead four tufts of sensory setae; dorso-lateral part of corona two prominent ciliated arches, ventral part less prominent; dorsal antenna short. Eyespot(s) absent. Foot medium, stout, slightly pointing ventral, flexible, in dorsal view (Figure 6C,D) varying from elongate conical (with in its most extended state showing weak lateral expansions near its base), to shorter conical and contracted near its base (integument of this basal zone of varying width weakly cuticularized); in lateral view (Figure 6E) with straight ventral margin and weakly arched dorsal margin; apparently a single pseudosegment, but often very delicate transversal folds near midlength and posterior third; a distinct round ventral sensory pit/caudal antenna(?) distally at some distance from base of toes. Two equal small bulbous toes, with long tip and minute offset tubulus. Pedal glands large, foot length or extending into trunk, with very large reservoirs in distal half. Proventriculus present. Gastric glands large, stalks absent. Vitellarium weakly lobed, eight large spheroid nuclei.
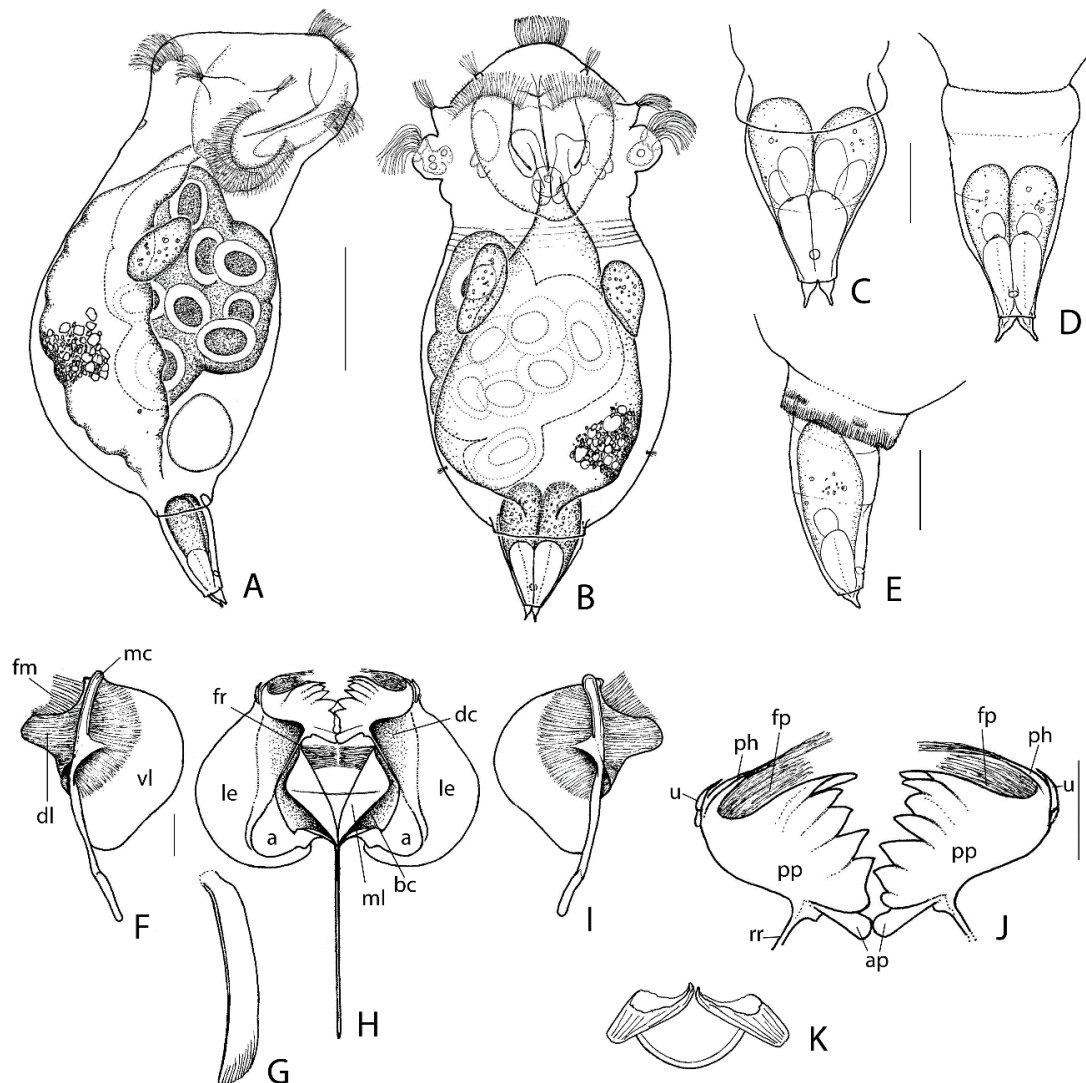
Figure 6. *Synchaeta grossa* sp. nov., (**A**) Female, lateral. (**B**) Female, dorsal. (**C**) Foot, slightly contracted, dorsal. (**D**) Foot, extended, ventral. (**E**) Foot, extended, lateral right. (**F**) Manubrium, left, outer view. (**G**) Fulcrum, lateral left. (**H**) Incus, ventral. (**I**) Manubrium, right, outer view. (**J**) Pseuduncus, outer view. (**K**) Epipharynx, ventral. a: alula; ap: adjoining platelets; bc: basal ramus chamber; dc: dorsal ramus chamber; dl: dorsal ramus lamella; fm: fimbriae manubrii; fp: fimbriae pseudunci; fr: fimbriae rami; mc: median manubrium chamber; ml: median ramus lamella; le: lamellar ramus extension; ph: pseuduncinal hook; pp: pseuduncinal plate; rr: ramus ridge; u: uncus; vl: ventral lamella. Scale bars: (**A**,**B**): 50 μm; (**C–E**): 20 μm; (**F–K**): 10 μm.

Amictic egg spherical, smooth.

Trophi (Figure 6F–K and Figure 7) typical *Synchaeta*, medium sclerified. Rami with ventral basal chamber (Figure 6H, Figure 7D: bc) and dorsal chamber (Figures 6H and 7D: dc) separated by strong ramus ridge (Figures 6J and 7D,E: rr); dorsal chambers with well-developed lamellar extension (Figures 6H and 7A,D: le); large rounded alulae (Figures 6H and 7D,I: a); median margin of basal chambers bearing median rami lamellae (Figures 6H and 7A,D: ml) showing obliquely rounded distal end; basal chambers with medium large latero-caudal spinula rami (Figure 7I: sr); ramus–ramus ligament (Figure 7D,E: rl) inserted slightly above mid-length of median rami lamellae; fimbriae ramorum (Figures 6H and 7J: fr) many separate sclerofibrillae. Epipharynx (Figures 6K and 7C,D: e) composed of two thorn-shaped elements connected distally by their tips in an inverted V-shaped way, and interconnected proximally by a rounded lamella with slightly reinforced free margin; body

of thorn-shaped elements hollow, showing large anterior opening; bases of thorn-shaped elements connected to ramus ridges (Figure 7D: e). Pseuduncus (Figures 6J and 7E), the ramus ("unci") teeth of Wilke et al. [86], composed of hook, sinus, plate, and adjoining platelet. Pseuduncinal hook (Figures 6J and 7E–G: ph) well developed, gutter-shaped dorsally with free sclerofibrillae emerging at its tip. Sinus between hook and plate with fimbriae pseudunci organised as close-set separate sclerofibrillae (Figures 6J and 7F,G: fp). Pseuduncinal plate (Figures 6J and 7D,E: pp) with comb of five (right) or six (left) lamellar slightly acute similar teeth, each comb terminating in a shallow rounded ventral tooth; teeth more or less gradually decreasing in length towards ventral; incisions between teeth medium without pronounced gap(s); adjoining platelet (Figures 6J and 7E,H,J: ap) more or less trapezoid with expanded base and an inner basal comb of sclerofibrillae; ramus ridge at base of pseuduncus with shallow small triangular projection medially. Uncus (Figures 6J and 7E,G: u) a single, weakly curved uncinus with slender acute tip; ventral at its base, often a short blunt sclerite (second vestigial uncinus?). Fulcrum thin, long, slightly longer than rami, in lateral view (Figures 6G and 7A) almost parallel-sided; distal end very weakly recurved ventrally, obliquely rounded, without dorsal distal indentation; composed of double layer of sclerofibrillae; ventral margin more or less strongly sclerified, proximal half of dorsal margin weakly sclerified. Manubria (Figure 6F,I and Figure 7B) long, *c.* 2/3 incus length, weakly curved near mid-length; median chamber (Figures 6F and 7B,K: mc) elongated, narrow, continuing as distal cauda; ventral chamber with large semi-circular lamella (Figures 6F and 7B: vl) extending from proximal end of median chamber till distal 1/4 of cauda, showing fairly pronounced more strongly sclerified concentric central area; perpendicular line of ventral lamella to median chamber at *c.* 2/6 from proximal end of the latter; opening of ventral chamber (Figure 7B,K: ov) at *c.* 1/3 from proximal manubrial end; dorsal chamber with medium large lamella (Figures 6F and 7B,K: dl); central part of dorsal lamella tongue-shaped flanked by very shallow proximal extension and less shallow distal tail, margin of top of lamella weakly oblique; perpendicular line of dorsal lamella at *c.* 1/5 from proximal manubrial end; opening of dorsal chamber (Figure 7B,K: od) at distal end of lamella; distal end of cauda weakly swollen, offset by weak torsion; fimbriae manubrii (Figures 6F and 7K: fm) composed of *c.* 40–45 tiny close-set scleropili; scleropili on shallow proximal extension longest, weakly increasing in length proximally; scleropili on the anterior margin of tongue-shaped part smallest, decreasing in length towards top of lamella.

Measurements: Total length up to 256 μm, foot (N = 5, extended): 44–60 μm, toe (N = 13): 6–9 μm; trophi (N = 10) length: 80.0–87.4 μm (mean 84.2 μm), ramus (inclusive pseuduncus) 34.4–48.3 μm (mean 39.2 μm), fulcrum 42.9–51.7 μm (mean 48.0 μm), pseuduncus (w × h) 19.6–23.4 × 12.4–14.7 μm (mean 21.1 × 13.4 μm), uncus 4.4–5.5 μm (mean 5.0 μm), manubrium 53.9–62.9 μm (mean 56.7 μm), epipharynx (w × h) 10.7–7.8 × 23.0–20.8 μm. Amictic egg (N = 5): 67–82 × 67–78 μm (mean 70 × 75 μm).

Distribution and ecology: *Synchaeta grossa* sp. nov. was present in samples from New Jersey, Maine, and Massachusetts. It was found exclusively in samples collected from marshes. Samples were collected in March, June, and September at salinities ranging from 10‰ to 34‰. Examination of the gut content showed that the species feeds on small cocciform Cyanobacteria and fungal spore-rich detritus.

Comments: There is a lot of disagreement on the number of valid species in *Synchaeta*, which varies from 34 [86], over 37 with 9 more *species inquirendae* and insufficiently described ones [87], to 41 and 10 *species inquirendae* [53]. These numbers have to be questioned, as diagnosis and identification rely traditionally on external morphological characters, of which many appear variable or at least difficult to ascertain. Due to this issue, it appears impossible to determine the next related species to *S. grossa* sp. nov. Most of the information on the delicate trophi of the *Synchaeta* species is based on light microscopy and, as such, is incomplete or unreliable and highly useless for strict species discrimination. The very few published SEM studies of the trophi and own unpublished data do not allow for a thorough comparison with the new *Synchaeta*.

Figure 7. *Synchaeta grossa* sp. nov., SEM photographs of trophi. (**A**) Incus, ventral. (**B**) Left manubrium, outer view. (**C**) Epipharynx. (**D**) Detail incus, ventral. (**E**) Pseudunci, ventral. (**F**) Detail right pseuduncus, inner view. (**G**) Detail left pseuduncus, outer view. (**H**) Adjoining platelet of pseuduncus plate, inner view. (**I**) Left alula and spinula rami, outer view. (**J**) Fimbriae ramorum, dorsal. (**K**) Fimbriae manubrii, outer view, right. a: alula; ap: adjoining platelet; bc: basal chamber; dc: dorsal chamber; dl: dorsal lamella; e: epipharynx; fm: fimbriae manubrii; fp: fimbriae pseudunci; fr: fimbriae rami; mc: median chamber; ml: median ramus lamella; le: lamellar ramus extension; od: opening dorsal chamber; ov: opening ventral chamber; ph: pseuduncinal hook; pp: pseuduncinal plate; rl: ramus-ramus ligament; rr: ramus ridge; sr: spinula rami; u: uncus; vl: ventral lamella. Scale bars: (**A**,**B**,**D**,**E**): 10 μm; (**C**,**F**,**G**,**I–K**): 5 μm, (**H**): 2.5 μm.

The most characteristic features of the *S. grossa* sp. nov. concern the medium-sized typical foot with its large pedal glands provided with large reservoirs, and the small ventral round opening

at its distal end some distance anterior to the bases of toes. Such a small opening has never been reported in *Synchaeta* and is reminiscent of a sensory pit, to date only demonstrated in Lepadellidae and Cotylegaleatidae [88]. However, in the latter families this pit is always located on the dorsal side of the foot. Alternatively, this ventral structure could be a modified and proximally displaced caudal antenna. In *Synchaeta baltica* Ehrenberg, 1834, *S. grimpei* Remane, 1929, *S. tavina* Althaus, 1957, and *S. triophthalma* Lauterborn, 1894, Peters [89] observed the caudal antenna to be situated ventrally, near or between the bases of the toes, contrasting with the other monogononts, which always show a dorsal caudal antenna [90].

3.2. Species Composition

In total, we identified 44 taxa across the 27 sites studied (Table 2): two of those were identifiable bdelloids (*Philodina citrina* Ehrenberg, 1830 and *Rotaria rotatoria* (Pallas, 1766)) and 41 belonged to the monogononts. A few specimens identified as bdelloids were too contracted after fixation to allow an accurate diagnostic analysis and are classified as "Bdelloidea indet." in Table 2 and Supplementary Table S1. The monogonont species were distributed over 21 genera and 14 families; 33 of them could be identified to species level, four monogonont species did not match any of the species already described and represented new species for science. Two of these new species were collected in good condition and sufficient numbers, allowing for their description presented above.

Table 2. Rotifer taxa collected at the different sampling sites [1]. Numbers refer to the sampling sites (Table 1).

BDELLOIDEA
Bdelloidea indet.: 131, 142, 144, 145, 146, 147
Philodinidae
* *Philodina citrina* Ehrenberg, 1830: 126
* *Rotaria rotatoria* (Pallas, 1766): 126, 132
MONOGONONTA
Brachionidae
Keratella americana Carlin, 1943: 125
Notholca marina Focke, 1961: 126, 145, 146
* *Plationus patulus* (Müller, 1786): 142
Dicranophoridae
Encentrum algente Harring, 1921: 141
* *E. graingeri* Chengalath, 1985: 145
E. marinum (Dujardin, 1841): 100, 101, 104, 121
* *E. melonei* sp. nov.: 121, 124, 125, 139
E. rousseleti (Lie-Pettersen, 1905): 125, 144
E. villosum Harring and Myers, 1928: 101, 121, 125
* *E.* cf. *villosum* Harring and Myers, 1928: 142
Gastropodidae
* *Gastropus hyptopus* (Ehrenberg, 1838): 142
Lecanidae
Lecane closterocerca (Schmarda, 1859): 126

Table 2. *Cont.*

L. grandis (Murray, 1913): 130, 131
L. hastata (Murray, 1913): 131
L. luna (Müller, 1776): 126
L. punctata (Murray, 1913): 132
* *L. quadridentata* (Ehrenberg, 1830): 126
Lepadellidae
Colurella adriatica Ehrenberg, 1831: 104, 118, 119, 120, 125, 126, 141
C. colurus (Ehrenberg, 1830): 104, 118, 125, 132
C. colurus compressa Lucks, 1912: 126, 132
C. dicentra (Gosse, 1887): 100, 104, 120, 121, 124, 125, 126, 141, 147
C. obtusa (Gosse, 1886): 125, 126
* *C. uncinata* (Müller, 1773): 139
* *C. unicauda* Eriksen, 1968: 120, 122, 123
* *Lepadella patella persimilis* De Ridder, 1961: 126
Lindiidae
Lindia tecusa Harring and Myers, 1922: 141, 144, 145
Mytilinidae
* *Lophocharis oxysternon* (Gosse, 1851): 126
* *Mytilina brevispina* (Ehrenberg, 1830): 126
Notommatidae
* *Cephalodella* sp. [undescribed species]: 131, 132
* *Monommata* sp.: 142
Pleurotrocha atlantica Myers, 1936: 131
Proalidae
Proales halophila Remane, 1929: 104
P. reinhardti (Ehrenberg, 1834): 104, 118, 119, 124, 125, 139, 144
P. similis Beauchamp, 1907: 121, 131
Synchaetidae
* *Synchaeta grossa* sp. nov.: 100, 102, 103, 104, 121, 125, 140, 143
Testudinellidae
Testudinella clypeata (Müller, 1786): 102, 103, 118, 120, 121, 122, 123, 124, 125, 143, 146, 148
Trichocercidae
* *Trichocerca brachyura* (Gosse, 1851): 126, 142
* *T. longiseta* (Schrank, 1802): 142
* *T. tigris* (Müller, 1786): 142
* *Trichocerca* sp. [undescribed species]: 126, 142
Trochosphaeridae
Filinia sp.: 142

* new for the thalassic fauna of the U.S.A; [1] Nomenclature according to the proposal of Segers et al. [52] and Jersabek et al. [53].

A total of 32 taxa were recorded from the brackish environment, whereas 23 were recorded from the marine sites. Species richness for each sample (α-diversity) ranged from 1 to 15 (mean 5.1) for the brackish environment, and from 1 to 11 (mean 3.7) for the marine habitat. Most of the samples (59%) had between two and four species. The site with the highest richness (15 species) was the brackish backshore pool from California (site 126; S = 4‰). The sites with the lowest richness (one species) were in the brackish marsh from Maine (site 140; S = 20‰) and two additional marine sites (S = 30‰) from New York (site 130; pond) and Connecticut (site 148; pond). None of the taxa were recorded in all samples, and the majority of them were only found once (21 taxa) or twice (eight taxa).

Bdelloids were found at eight sites: once in a truly marine habitat (New York, site 131; coast, S = 32‰) and seven times in brackish habitats with salinities ranging from 2‰ to 10‰. As mentioned above, their diversity was low and the only two identifiable species, *Philodina citrina* and *Rotaria rotatoria*, were found in the brackish environment (S = 4–8‰).

Monogononts (41 taxa) were found at all 27 sites and occurred in the whole range of salinities measured during this study (S = 2–40‰). The most common species across samples was *Testudinella clypeata* (Müller, 1786), which was found at 12 sites, both brackish and marine (salinity ranging between 6‰ and 34‰), across three states (New Jersey, New Hampshire, Connecticut), and different habitats, such as coastal beaches, channels, lagoons, ponds, and marshes (Table 1 and Supplementary Table S1). The other most frequently occurring species were *Colurella dicentra* (Gosse, 1887) (nine sites), *C. adriatica* Ehrenberg, 1831 (seven sites), and *Proales reinhardti* (Ehrenberg, 1834) (seven sites). The most speciose genera were *Encentrum* and *Colurella*, both containing seven species, followed by *Lecane*, with six species. The most frequently encountered genus was *Colurella*, occurring at 15 sites.

Most of the taxa identified to species level were common cosmopolites or showed a widespread distribution. A few have a more restricted range: *Encentrum rousseleti* is known from the Holarctic and Neotropical region; *E. villosum* Harring and Myers, 1928, *Lindia tecusa* Harring and Myers, 1922, *Notholca marina* Focke, 1961, and *Pleurotrocha atlantica* Myers, 1936 have only been reported from the Holarctic, and the finding of *Colurella unicauda* Eriksen, 1968, hitherto only known from the Palearctic, is a new record for the Nearctic region. The new species, *Encentrum melonei* sp. nov. and *Synchaeta grossa* sp. nov., have at least a Cold Temperate Northwest Atlantic distribution.

3.3. Community Ecology

The results of the PERMANOVA analyses showed significant differences in the whole community structures across different salinity values ($p = 0.041$) and ecosystems ($p = 0.003$), as well as in the interaction of the two variables ($p = 0.027$). Nevertheless, the type of ecosystem was a significant predictor of salinity ($p = 0.042$; Figure 8). The highest richness was found in the polyhaline waters (28 species; 12 samples), followed by oligohaline (22 species; 4 samples), euhaline (20 species; 8 samples), and mesohaline (11 species; 4 samples). Circumscribed ponds were the ecosystems with the highest richness (28 species; 7 samples), followed by marshes (18 species; 12 samples), and coasts and environments connected to the ocean (11 species; 8 samples).

Using ordination techniques that combined taxon richness and community composition, we found that rotifer community structures from different salinities or ecosystems partially overlapped (Figure 9); however, all the rotifer communities were significantly different across ecosystems (coast versus marsh, $p = 0.021$; coast versus pond, $p = 0.037$; marsh versus pond, $p = 0.037$). Moreover, oligohaline communities, present in salinities lower than 5‰, were found to be the most dissimilar to other communities collected at higher salinity. In detail, oligohaline communities were found to be significantly different than both euhaline ($p = 0.015$) and polyhaline communities ($p = 0.015$).
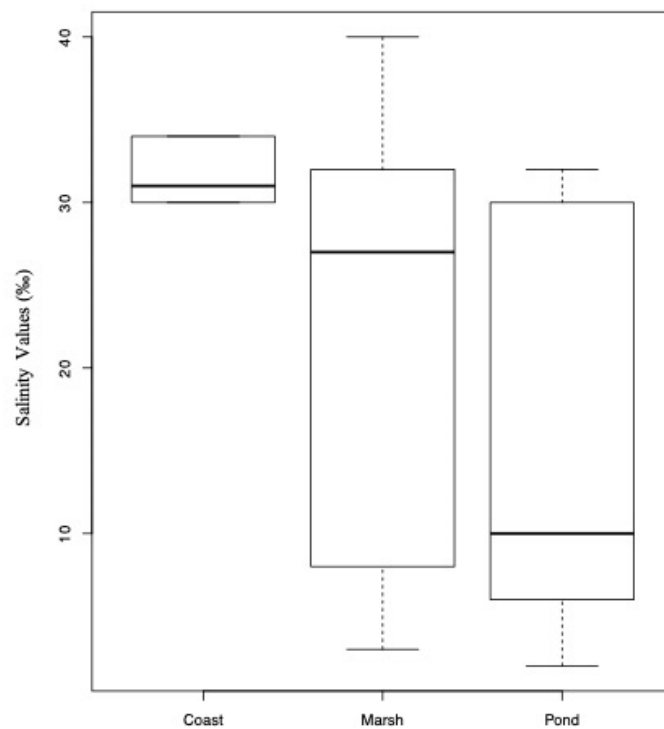
Figure 8. Boxplot showing salinity ranges for each ecosystem. The type of ecosystem was a significant predictor of salinity (*p* = 0.042).
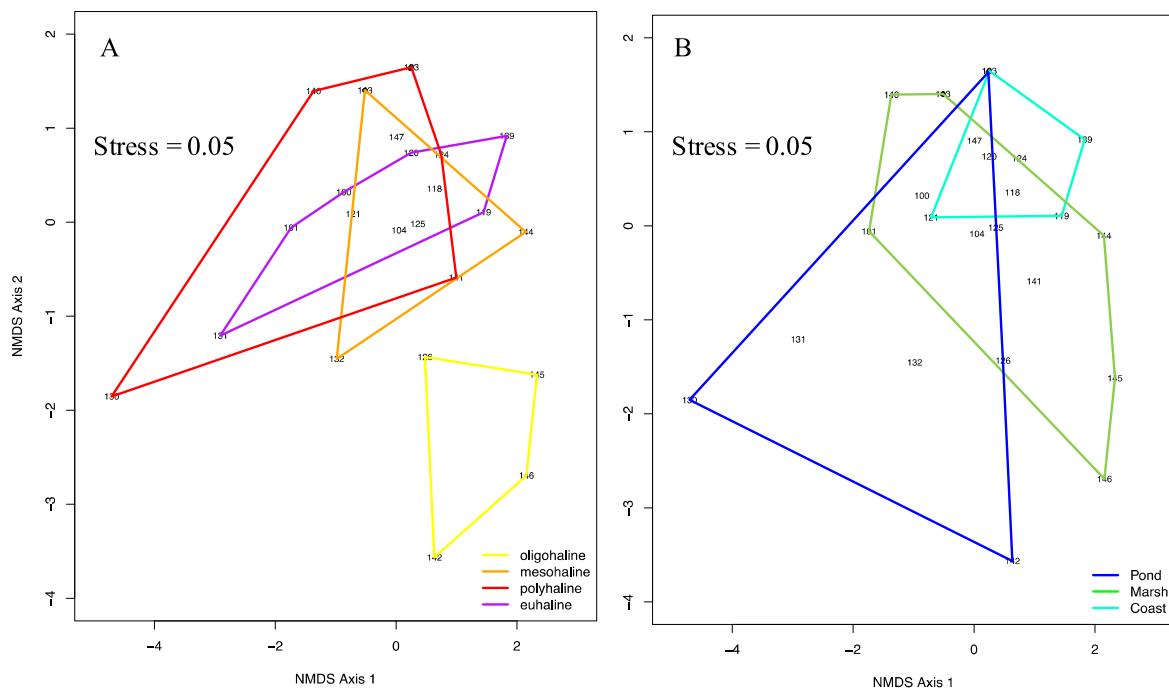
Figure 9. Two-dimensional nonmetric MDS ordination of rotifer community data from 27 sites sampled in the present study. Sites are grouped by salinities according to the Venice System (**A**) and ecosystems (**B**).

Results from linear regression analyses showed that, in our study, sample size (number of samples collected from each ecosystem or salinity) was not correlated with biodiversity, estimated as both species richness and species composition (*p* > 0.1).

3.4. Thalassic Rotifer Taxa from the U.S.

The checklist and distribution of rotifer taxa reported to date from the United States are presented in alphabetical order in Supplementary Text S1 and organized per family in Supplementary Table S1. Our search of more than a century of literature [3,18–41,59–79] for thalassic rotifers of the U.S. revealed 105 taxa, among which were 87 species-level taxa. The 44 taxa recorded in the present study and two additional unpublished records add 24 new taxa to this list, of which 19 are fully identified species (inclusive of the two described new species). This brings the total richness of thalassic rotifer taxa reported for the U.S. to at least 124, of which 106 are species-level taxa. Seisonacea is represented by a single species, *Paraseison kisfaludyi* Leasi, Rouse, Sørensen 2011; only two Bdelloidea, *Philodina citrina* and *Rotaria rotatoria*, belonging to the family Philodinidae, were identified to species level. The Monogononta form the most represented group, including 103 (98%) species-level taxa, distributed over 17 families and 30 genera; another two taxa were reported at the genus level solely (*Asplanchna*, *Monommata*). The most speciose families are Brachionidae (18 species, 5 genera), followed by Synchaetidae (15 species, 3 genera), Dicranophoridae (14 species, 3 genera), Lecanidae (10 species, 1 genus), and Lepadellidae (9 species, 2 genera).

3.5. Distribution of U.S. Thalassic Rotifers

It follows from Supplementary Table S1 that our knowledge on the distribution of U.S. thalassic rotifers is very incomplete and limited to only a few relatively small areas. Therefore, in the tabulation of the data, we used the system by Fautin et al. [15], which broadly recognizes six geographically-based sections (Northeast U.S. Continental Shelf Large Marine Ecosystem (LME), Southeast U.S. Continental Shelf LME, Gulf of Mexico, Insular-Pacific Hawaii LME, California Current LME, and High Arctic), instead of Spalding et al. [91], who proposed a detailed marine biogeography system including Realms, Provinces, and Ecoregions. Most of the research and occasional records on thalassic rotifers are focused in the Northeast U.S. (93 taxa), followed by the Gulf of Mexico (43 taxa), California Current (26 taxa), Southeast U.S. Continental Shelf (3 taxa), Insular-Pacific Hawaii (6 taxa), and High Arctic (9 taxa). Although the majority (about 90%) of the species are believed to be cosmopolitan or widely distributed, none of them are reported from all the U.S. marine biogeographical sections. Eleven species are, to date, only known from their type locality or from a limited number of U.S. locations: *Cephalodella epitedia* Myers, 1924 (New Jersey), *C. mineri* Myers, 1924 (New Jersey), *Encentrum eristes* Harring and Myers, 1928 (Maine), *E. lacidum* Harring and Myers, 1928 (New Jersey, Maine), *E. melonei* sp. nov. (New Jersey, Maine), *E. salsum* Myers, 1936 (New Jersey), *Ptygura agassizi* Edmondson, 1948 (Massachusetts), *Synchaeta grossa* sp. nov. (New Jersey, Maine, Massachusetts), *S. johanseni* Harring, 1921 (New Jersey, Maine), *Testudinella dentata* Myers, 1934 (New Jersey, Maine), and *Paraseison kisfaludyi* (California). The only species characteristic for a well-defined section or ecoregion, namely the High Arctic, are *Synchaeta hyperborea* Smirnov, 1932 and *S. tamara* Smirnov, 1932 found in Alaska (Bering and Beaufort Seas), and known as typical inhabitants of marine plankton from the Arctic Ocean and Arctic seas, and brine channels of Arctic sea ice [92].

To date, 355 species are known to occur in thalassic environments world-wide, thus, at least about one-third (106 species) of the known global thalassic rotifer diversity is present in U.S. waters. The finding of *Trichocerca tigris* (Müller, 1786) in oligohaline water, hitherto only known from freshwater, is an extension of it to the saline habitat [6].

4. Discussion

The biodiversity of freshwater rotifers is regularly explored: new species are described continuously and environmental interactions are profoundly tested (e.g., [1–3,93,94]). In contrast, taxonomic and ecological investigations targeting thalassic rotifers are sporadic (but see [9–11,43,92,95–97]). This study allowed us to improve our knowledge of the biodiversity of

thalassic rotifers in the United States and revealed new correlations between rotifer communities and their environments.

Overall, 106 thalassic rotifer species-level taxa are reported for the United States, representing 30% of the total number of thalassic rotifer species recognized worldwide. Most of the recorded species are common cosmopolites. A total of 11 species so far are exclusively known for the United States, however, too little information is available to speculate about possible endemisms. The results of our investigation and the data from the checklist show (1) a low thalassic species richness compared to the known freshwater species world-wide (ca. 1830 species, among bdelloids and monogononts), and (2) an obvious predominance of monogonont species (95–98%) with regard to bdelloids (2–5%). This concurs with the general observations that the thalassic rotifer fauna is rather poor and that bdelloids are highly underrepresented in thalassic environments [2,4,6,7,11]. For example, the work performed by Myers [24] focused on the rotifer diversity from the small Mount Desert Island (280 km^2) situated on the coast of Maine. He reported 435 freshwater species (and many more were added in subsequent papers) and only 14 marine ones. Almost a century later, only a total of 22 thalassic rotifer taxa are known for the entire State of Maine (Supplementary Table S1). No doubt, besides a real difference in the rotifer diversity between the freshwater and marine environment, these numbers may also be biased by unequal sampling efforts. Regarding the bdelloid/monogonont ratio, in a review of rotifer diversity from saltwater environments, Fontaneto et al. [6] reported the presence of 443 species, and an overall ratio of bdelloid to monogonont species of 1:3 in freshwater habitats and 1:83 in thalassic ones. This ratio is 1:53 for the U.S. thalassic rotifers identified to species level.

In the present research, we found 44 taxa, among which 17 identified at the species level are first records for the U.S. thalassic rotifer fauna, including two species new to science (*Encentrum melonei* sp. nov., *Synchaeta grossa* sp. nov.). Two other species new to science were only identified to genus level (*Cephalodella*, *Trichocerca*). A half century ago, Björklund [28] described a new species of monogonont rotifer, *Notholca liepetterseni* Bjorklund, 1972 from the Hudson River mouth (New York). Since then, no new marine rotifer species have been discovered and described for the U.S. until today. Exceptionally, a few years ago a new species of Seisonacea was described for California [38]. However, Seisonacea is an aberrant group of marine rotifers that live as epizoonts on the crustacean genus *Nebalia*. Hitherto, only four species are known and their discovery is likely due to coincidental circumstances rather than actual sampling efforts focused on this group. The discovery of four monogonont species new to science, two of which are described herein, encourages further investigations on the U.S. marine rotifers. Reporting the presence of additional rotifer species in the U.S. may not be surprising, especially considering the limited number of investigations on thalassic environments. The highest richness (93 taxa, 83 species) is reported for the Northeast Continental Shelf. No doubt this highest richness is a clear case created by bias in sampling intensity, known as the "rotiferologist effect" [12]: indeed, the majority of investigations, as well as the present ones, have been focused on this region. Notwithstanding this rotiferologist effect, the finding of additional 15 taxa and 11 species never reported for the Northeast Continental Shelf reveals that the biodiversity of thalassic rotifers is largely overlooked and underestimated. In particular, the environmental heterogeneity of the Northwest Atlantic coast, characterized by a variety of ecological niches, may play a fundamental role in the diversification of small species. A highly debated and still open issue in ecology is whether the patterns of distribution of biodiversity are caused by spatially limited dispersal or by niche-related factors [98]. Carugati et al. [99] showed that the assemblage structure of meiofauna is mainly shaped by dispersal limitation and habitat features. Older studies rarely indicated the habitat and its features, and it is often even difficult to track down the precise sampling location.

The present study shows that both the salinity and the type of ecosystem, as defined herein, significantly drives species assemblage. The oligohaline environment contained mainly species known to live in freshwater and a few euryhaline species, whereas the euhaline environment was dominated by euhaline and euryhaline species. Previous studies based on DNA taxonomy suggested that rotifer species respond differently to salinity. Some taxa seem ecologically specialized to narrow salinity

ranges (e.g., *Brachionus plicatilis* Müller, 1786: [100]), while other species occurring at different salinities are likely ecologically tolerant (e.g., *Testudinella clypeata*: [43]). The response of an organism to an environmental condition mainly depends on its eco/evolutionary origin (e.g., [101–104]). However, the evolutionary origins of most small organisms are still unknown and should be clarified by further phylogenetic studies. Not surprisingly, the type of ecosystem resulted significantly correlated with the salinity values; inevitably, rotifer species were differently distributed also across all the three ecosystems, besides salinities. This suggests that each ecosystem hosts a peculiar rotifer community and certain environments, such as salt marshes, may represent a hotspot of biodiversity also for microscopic species [105,106]. A comprehensive understanding of such unstable environments is critical, given their unique dynamics and susceptibility to anthropogenic stressors [106].

The United States is affected by numerous anthropogenic activities occurring in salt waters, such as oil drilling, fisheries, and tourism. As such, the territory is significantly impacted, and delicate and valuable ecosystems, such as salt marshes and beaches, could be quickly and irremediably endangered. Because small species respond quickly to environmental changes due to their rapid life cycle, they can be used also to determine the impact of habitat loss and modification due to human activities. Moreover, salinization plays a fundamental role under a climate change scenario and investigating the biodiversity of small species will provide fundamental information for long-term ecosystem biomonitoring programs [107]. As suggested by Zeppilli et al. [108], this work supports the value of investigating the biodiversity of small invertebrates as ideal models to evaluate and understand the either short- or long-term effects of human activities on the surrounding environments.

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