The Aquatic Heteroptera (Hemiptera) of Marshes in the Florida Everglades

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The aquatic Heteroptera (Hemiptera) of marshes in the Florida Everglades

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Abstract

The Everglades is a large subtropical wetland that has been modified heavily by humans and now is undergoing restoration. Aquatic and semiaquatic Heteroptera (Hemiptera) in the infraorders Gerromorpha and Nepomorpha were collected in the Florida Everglades using standardized 1-m^2 throw-traps. Sampling efforts were conducted in marshes distributed from southern Everglades National Park, north throughout the Water Conservation Areas to Loxahatchee National Wildlife Refuge. In total, 12,833 individuals were identified representing 17 species in 13 genera and 8 families (Belostomatidae, Corixidae, Gerridae, Mesoveliidae, Naucoridae, Nepidae, Veliidae). The naucorid *Pelocoris femoratus* (Palisot de Beauvois) (Hemiptera: Naucoridae) was by far the most abundant species, whereas 2 other species, *Belostoma lutarium* (Stål) (Hemiptera: Belostomatidae) and *Neogerris hesione* Kirkaldy (Hemiptera: Gerridae), were widespread but less abundant. Two species, *Abedus immaculatus* (Say) (Hemiptera: Belostomatidae) and *Pelocoris balius* La Rivers (Hemiptera: Naucoridae) had localized distributions, whereas all other species were collected rarely. We discuss the abundance and distribution of species recorded, along with unique traits and the biology of the aquatic Heteroptera in the Everglades and implications for the restoration of the Everglades.

Key Words: aquatic insects; biodiversity; freshwater macroinvertebrates; Gerromorpha; Nepomorpha; water bugs

Resumen

Los Everglades es una tierra humeda subtropical que ha sido modificado en gran medida por los humanos y ahora está siendo restaurado. Se recolectaron Heteroptera (Hemiptera) acuáticos y semiacuáticos en los infraórdenes Gerromorpha y Nepomorpha en los Everglades de Florida utilizando trampas de tiro estandarizadas de 1-m^2. Se realizaron esfuerzos de muestreo en marismas distribuidas desde el sur del Parque Nacional Everglades, al norte y a lo largo de las Áreas de Conservación del Agua hasta el Refugio Nacional de Vida Silvestre Loxahatchee. En total, se identificaron 12,833 individuos que representan 17 especies en 13 géneros y 8 familias (Belostomatidae, Corixidae, Gerridae, Mesoveliidae, Naucoridae, Nepidae, Veliidae). El naucorido *Pelocoris femoratus* (Palisot de Beauvois) (Hemiptera: Naucoridae) fue con mucho la especie más abundante encontrada, mientras que otras 2 especies, *Belostoma lutarium* (Stål) (Hemiptera: Belostomatidae) y *Neogerris hesione* Kirkaldy (Hemiptera: Gerridae), tenian una distribución mas amplia pero menos abundante. Dos especies, *Abedus immaculatus* (Say) (Hemiptera: Belostomatidae) y *Pelocoris balius* La Rivers (Hemiptera: Naucoridae) tenian distribuciones localizadas, mientras que todas las demás especies se recolectaron raramente. Discutimos la abundancia y distribución de especies registradas, junto con los rasgos únicos y la biología de los Heteroptera acuáticos en los Everglades y las implicaciones para la restauración de los Everglades.

Palabras Clave: insectos acuáticos; biodiversidad; macroinvertebrados de agua dulce; Gerromorpha; Nepomorpha; chinches de agua

Located at the southern tip of the Florida Peninsula, the Everglades is a large subtropical wetland that has been modified heavily by humans. South of Lake Okeechobee, the greater Everglades ecosystem originally covered over 15,000 km^2, but channelization, drainage, and conversion to agricultural land has resulted in only 47% of the original ecosystem remaining as wetlands (Light & Dineen 1994; McVoy et al. 2011). A century of human alteration led to the decades-long effort to restore the Everglades that began in the 1990s (Sklar et al. 2005). The Everglades experiences a seasonal rainfall regime, receiving over 75% of annual rainfall between May and Oct (Gaiser et al. 2012). Variation in water depth and hydrological patterns are dominant drivers of the Everglades' ecology, while the karstic geology of the region makes the system naturally oligotrophic (McCormick et al. 2002). Although much of the Everglades does not dry each yr, a layer of organic flocculent material is at the bottom of the water column, such that when the water depth drops to 5 cm or lower, gilled aquatic organisms reliant on dissolved oxygen (fish and some macroinvertebrates) typically die (Trexler et al. 2005); hence, water depth can affect community structure without complete drying of habitats.

Invertebrates in the Everglades have received little attention relative to vertebrate species; Trexler and Loftus (2016) found only 20 papers focused on freshwater invertebrate ecology in the Everglades, whereas Batzer and Boix (2016) recognized the Everglades as among the global wetlands types with the lowest invertebrate richness, along with rock pools and alpine ponds, among others. Some taxa, particularly crayfishes and grass shrimp, are common, widespread, important primary consumers, and prey for vertebrates (Williams & Trexler 2006; Sargeant et al. 2011; Cocoves et al. 2021). Except for Chironomidae (King & Richardson 2002; Jacobsen 2008), insects largely have been overlooked aside from some theses, reports, and mentions in publi-

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cations addressing other aspects of Everglades ecology (e.g., Rader & Richardson 1992; Noe et al. 2003; Liston 2006); few publications, such as Rader (1994) and Trexler and Loftus (2016), have covered a wider taxonomic range of invertebrates. In particular, insects in the suborder Heteroptera (Hemiptera) are among the most abundant and widely distributed aquatic animals in the Everglades, but there have been no studies focused on this group in the system.

The aquatic Heteroptera are divided into 2 primary suborders, the semiaquatic surface-dwelling infraorder Gerromorpha and the fully aquatic Nepomorpha. Globally, these 2 infraorders consist of around 5,000 described species in 20 families (Polhemus & Polhemus 2007), whereas in Florida they are represented by at least 129 species in 14 families (Epler 2006; Epler & Denson 2017). Many of the species known from Florida are Nearctic species that are found only as far south as northern or central Florida and are absent from southern Florida. However, some of Florida's heteropterans are Neotropical species found at the northern edge of their range in the state, and others are more widely distributed throughout Florida, the coastal plain, or eastern North America. The diversity of aquatic Heteroptera in southern Florida and the Everglades is lower possibly relative to more northern parts of the state, which may be due in part to its geographic position at the southern end of the continent, the relatively young age of the Everglades (about 5,000 yr), and the prevalence of fish in the ecosystem (Means & Simberloff 1987; Trexler & Loftus 2016). At the same time, southern Florida may be more prone to colonization by both naturally arriving species from the Neotropics and those facilitated by humans through the many agricultural and pet trade products imported into the region (Polhemus & Rutter 1997; Simberloff et al. 1997).

Documentation of freshwater biodiversity is important for understanding freshwater systems in a changing world (Balian et al. 2008; Strayer & Dudgeon 2010). Critical to documentation are accurate identifications by taxonomic experts and verifiable records of taxa that were observed (including voucher specimens) – both are issues present throughout ecology (Grove 2003; Bortolus 2008). Aside from Epler's (2006) key to species in Florida, few studies report more than 1 or 2 aquatic Heteroptera taxa from the Everglades. Those that report multiple taxa contain potential errors in that they list species/genera/families not found in Florida or that are unlikely to be found in southern Florida, or possibly misidentify and aggregate taxa at levels that overlook some species (Rader & Richardson 1992; Rader 1994); these errors can propagate into other studies and summaries of taxa in the ecosystem (Trexler & Loftus 2016). Here, we review 4,471 samples of animals that were collected previously from marshes in the Everglades, with sampling occurring from southern Everglades National Park north through Loxahatchee National Wildlife Refuge. Marshes are the most spatially expansive freshwater habitat in the Everglades ecosystem and are conducive to standardized sampling. Therefore, our work serves as a faunistic study of this common habitat type, whereas other habitat types, such as solution holes, alligator ponds, larger ponds, canals, sawgrass ridges, creeks, and marsh/mangrove ecotone habitats are not included. We summarize the aquatic and semiaquatic Heteroptera that were collected, provide their abundances and distributions, and discuss notable traits of these species in the Everglades.

Materials and Methods

We reviewed samples of aquatic animals collected from freshwater marshes as part of 2 primary Everglades restoration projects: the Modified Water Deliveries to Everglades National Park project, and the Comprehensive Everglades Restoration Plan (South Florida Ecosystem Restoration Task Force 2020). All samples had been identified previously by technicians, but most identifications were made without specialized knowledge of species characteristics and, therefore, individuals were identified largely to higher levels (genus or family). All samples were collected with standard protocols using 1-m^2, 2-mm mesh throw-traps in marshes and sloughs with emergent vegetation types and densities conducive to the sampling method (Jordan et al. 1997; Turner & Trexler 1997). Throw-trap sampling can be biased toward larger individuals, and there may be some limits to the ability of technicians to efficiently collect the smallest of heteropterans, as was found with small fish (Gatto & Trexler 2019); however, we make note in the results and discussion of the taxonomic groups that we believe small size may limit the likelihood of their collection. Additionally, the semiaquatic Gerromorpha may escape collection from throw-traps and, therefore, may be somewhat under-represented relative to Nepomorpha. The samples were preserved initially with 10% formalin then transferred to 70% ethanol. As of 2021, these samples are stored in the museum room at Florida International University's Biscayne Bay Campus, North Miami, Florida, USA, and several are catalogued in, and on loan from, the South Florida Collections Management Center, Homestead, Florida, USA.

Sampling for Modified Water Deliveries began in 1996 and has continued through 2021 within 2 regions in Everglades National Park: Shark River Slough (6 sites) and Taylor Slough (3 sites), as well as in Water Conservation Area 3 (10 sites) (Fig. 1a). Samples from 3 of the 6 sites in Shark River Slough were collected by the National Park Service and are not included here. Starting in 2008, a fourth region was added: the eastern panhandle region of Everglades National Park and the area in the Southern Glades Wildlife and Environmental Area directly to its north, but south of the C-111 Canal (Panhandle; 4 sites). Each site consisted of either 3 (Panhandle, Shark River Slough, Water Conservation Area, 1 site in Taylor Slough) or 5 plots (2 northernmost sites in Taylor Slough), with either 7 (Panhandle, Shark River Slough, Taylor Slough) or 5 (Water Conservation Area) throw-trap samples collected within each plot. Samples were collected during 5 periods of each yr (Table 1). The water yr begins at the start of the wet season in May, with the first wet season samples collected during Jul, and sampling ending in Apr at the end of the dry season. For the Modified Water Deliveries project, we focused primarily on reviewing all samples collected during water yr 2017 (Jun 2016–Apr 2017; Table 1). Not all sites were accessible or contained water during the late dry season and, therefore, were not sampled, particularly in the Panhandle; we reviewed a total of 1,608 samples from water yr 2017. We also reviewed 547 samples collected immediately prior to water yr 2017 during Apr 2015 to Apr 2016, 855 samples after water yr 2017 during Jul 2017 to Feb 2018, and 138 samples ranging from 1997 to 2012. However, because these additional samples are not a comprehensive review of all sampling efforts during these time periods, we included these results only in taxonomic totals in Table 2, while focusing all other figures on water yr 2017. Additionally, 26 of the 138 earliest samples were collected from a site (11) at the western edge of Water Conservation Area 3A that has not been sampled since 2006.

Beginning in Nov 2017, sampling began within the Upper Taylor Slough region of Everglades National Park (Fig. 1a) as part of a subproject of the larger Modified Water Deliveries project. Sites were sampled every other mo when they were accessible and had adequate water depth, with 7 throw-trap samples collected per site at 6 sites, and 5 throw-trap samples collected per site at the 6 other sites due to limited accessibility. We reviewed all samples collected for the Upper Taylor Slough project from Nov 2017 through Nov 2019. Because of the different time period reviewed and sampling structure of this project, we present results of Upper Taylor Slough samples separately in Table 2 and exclude them from Modified Water Deliveries figures. In total, 523 throw-trap samples were reviewed for the Upper Taylor Slough project.

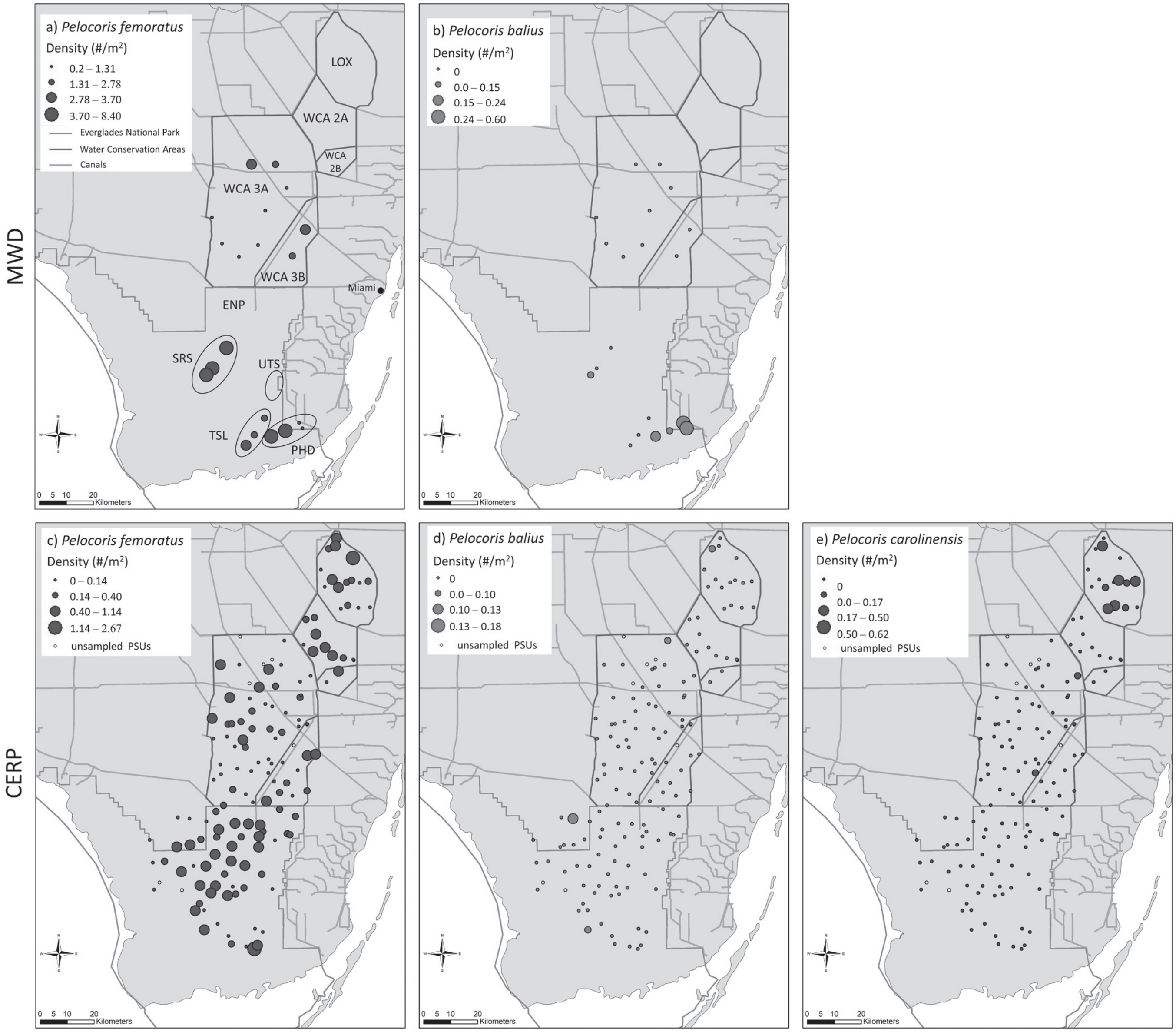

Fig. 1. Adult density (number of individuals per m²) maps of the 3 species of *Pelocoris* by project. The top row is Modified Water Delivery samples during water yr 2017, whereas the bottom row is Comprehensive Everglades Restoration Plan samples during 2016 and 2017. Each point represents 1 sample site (Modified Water Deliveries) or primary sampling unit (Comprehensive Everglades Restoration Plan). Regions are labeled in (a). No *P. carolinensis* were collected in Modified Water Deliveries samples. Regions: ENP = Everglades National Park; LOX = Loxahatchee National Wildlife Refuge; PHD = Everglades National Park panhandle; SRS = Shark River Slough; TSL = Taylor Slough; UTS = Upper Taylor Slough; WCA = Water Conservation Areas.

Table 1. Modified Water Delivery water yr 2017 sampling periods, with start dates, end dates, number of sites sampled (sites), and number of throw-trap samples (throws) collected during each sampling period.

Sampling period	Start date	End date	Sites	Throws
1	27 Jun 2016	28 Jul 2016	20	388
2	3 Oct 2016	31 Oct 2016	20	377
3	28 Nov 2016	21 Dec 2016	20	387
4	30 Jan 2017	17 Feb 2017	18	272
5	3 Apr 2017	29 Apr 2017	13	184

Sampling for the Comprehensive Everglades Restoration Plan began in 2005 and continued through 2020, with 146 principal sampling units sampled once per yr during the wet season. Principal sampling units are located within 11 regions and distributed across the Everglades from southern Everglades National Park north through the Water Conservation Areas and Loxahatchee National Wildlife Refuge (Fig. 1b). Each yr, 3 throw-trap samples were collected from a randomly selected site within each principal sampling unit. We reviewed all Comprehensive Everglades Restoration Plan samples collected during water yr 2017 (collected 19 Sep 2016–22 Nov 2016) and 2018 (20 Sep 2017–24 Jan 2018). In total, 800 throw-trap samples were reviewed for the Comprehensive Everglades Restoration Plan project.

For all projects, we reviewed samples by counting and identifying all Heteroptera within each sample to the lowest feasible taxonomic level;

Table 2. List of the taxa of Heteroptera and their abundances by infraorder, family, genus/species, and life stage. Higher level taxa are sums of indented lower-level taxa and life stages.

Taxon	Author	Total	MWD*	UTS*	CERP*
Heteroptera		12,833	10,494	1,180	1,159
Gerromorpha		458	345	63	50
Gerridae		451	339	62	50
Limnogonus franciscanus	(Stål)	4	0	3	1
Neogerris hesione	(Kirkaldy)	445	338	59	48
Trepobates floridensis	Drake and Harris	2	1	0	1
Mesoveliidae		1	1	0	0
Mesovelia nymphs	Mulsant and Rey	1	1	0	0
Veliidae		6	5	1	0
Microvelia nymphs	Westwood	1	1	0	0
Platyvelia brachialis	(Stål)	5	4	1	0
Nepomorpha		12,375	10,149	1,117	1,109
Belostomatidae		1,442	1,079	281	82
Belostomatinae		1,437	1,074	281	82
Abedus immaculatus	(Say)	246	200	35	11
adults		232	200	23	9
nymphs		14	–	12	2
Belostoma lutarium	(Stål)	486	266	157	63
adults		331	266	35	30
nymphs		155	–	122	33
unidentified nymphs		705	608	89	8
Lethocerinae		5	5	0	0
Benacus griseus	(Say)	4	4	0	0
adults		1	1	0	0
nymphs		3	3	0	0
Lethocerus uhleri adults	(Montandon)	1	1	0	0
Corixidae		83	69	1	13
Trichocorixa minima	(Abbott)	83	69	1	13
Naucoridae		10,845	8,996	835	1,014
Pelocoris balius	La Rivers	416	399	1	16
adult females		110	106	1	3
adult males		107	103	0	4
nymphs		199	190	0	9
Pelocoris carolinensis	Torre-Bueno	39	0	0	39
adult females		17	0	0	17
adult males		22	0	0	22
Pelocoris femoratus	(Palisot de Beauvois)	9,985	8,597	834	554
adult females		3,493	2,939	306	248
adult males		4,168	3,579	283	306
nymphs		2,324	2,079	245	–
P. carolinensis; *P. femoratus*		405	–	–	405
unidentified adults		1	–	–	1
unidentified nymphs		404	–	–	404
Nepidae		5	5	0	0
Ranatra nymphs	Fabricius	2	2	0	0
Ranatra australis	Hungerford	1	1	0	0
Ranatra drakei	Hungerford	1	1	0	0
Ranatra nigra	Herrich-Schäffer	1	1	0	0

Total = cumulative abundance across all 3 projects
*MWD = Modified Water Delivery to Everglades National Park; UTS = Upper Taylor Slough; CERP = Comprehensive Everglades Restoration Plan

MRP was responsible for all identifications. Identifications were based primarily on Epler (2006) with additional sources consulted when necessary. Most taxa were identified to species, although *Mesovelia* Mulsant and Rey (Hemiptera: Mesoveliidae) and *Microvelia* Westwood (Hemiptera: Veliidae) were identified to genus because only 1 nymph from each of these genera was found in samples. For the subfamily Belostomatinae, initially we identified all adults to species and aggregated all nymphs at the subfamily level. However, after reviewing Modified Water Deliveries samples it became clear that there were only 2 species present and many of the larger nymphs could be separated, which we did for the Upper Taylor Slough and Comprehensive Everglades Restoration Plan samples. For instance, many *Belostoma lutarium* (Stål) (Hemiptera: Belostomatidae) nymphs were larger than adult *Abedus immaculatus* (Say) (Hemiptera: Belostomatidae). Small nymphs and others that were not clearly assignable to species remained identified at the subfamily level for Upper Taylor Slough and Comprehensive Everglades Restoration Plan.

Identification of 2 of the species of *Pelocoris* Stål (Hemiptera: Naucoridae), *Pelocoris carolinensis* Torre-Bueno (Hemiptera: Naucoridae), and *Pelocoris femoratus* (Palisot de Beavuois) (Hemiptera: Naucoridae), can be reliably accomplished only using adults, with key characteristics differing between males and females; nymphs of these 2 species are not clearly separable. We found that the presence of dark spots on the dorsal surface of the front femur of *Pelocoris balius* La Rivers (Hemiptera: Naucoridae) was consistent not only for adults, but also for nymphs and exuviae, all preserved with formalin and ethanol. Hence, we present results by species, life stage, and sex of adults. For the over 6,000 adult *Pelocoris* in Modified Water Deliveries samples and the nearly 600 adults in Upper Taylor Slough samples, none were *P*. *carolinensis*; therefore, we assume all nymphs from these projects lacking the aforementioned spots are *P*. *femoratus*. For Comprehensive Everglades Restoration Plan samples, we aggregated all *Pelocoris* nymphs that were not *P*. *balius* as either *P*. *carolinensis* or *P*. *femoratus*, along with 1 damaged adult. Exuviae of any taxa present in samples were excluded from our results because we cannot know if they were produced by individuals we collected, which could lead to double counting. Exuviae were rare and accounted for < 1% of all individuals collected within each taxon: Belostomatinae (*N* = 4 exuviae; 0.28% of total), *Neogerris hesione* Kirkaldy (Hemiptera: Gerridae) (*N* = 3; 0.67%), and *Pelocoris* spp. (*N* = 5; 0.05%). Three semiaquatic Heteroptera families, Gelastocoridae and Ochteridae (Nepomorpha), as well as Saldidae (Leptopodomorpha), were excluded because we did not find any and they are typically found adjacent to aquatic habitats rather than on the water surface, where the Gerromorpha typically occur (Epler 2006; Polhemus & Polhemus 2007).

Lastly, MRP reviewed the identifications of aquatic and semiaquatic Heteroptera specimens from Everglades National Park deposited at the South Florida Collections Management Center, Homestead, Florida, USA, and they are presented in the supporting information (Table S7) and incorporated into the discussion when pertinent.

Results

In total, 12,833 aquatic and semiaquatic Heteroptera individuals were found in samples, representing 17 taxa at their lowest identifiable taxonomic level (species/genus) within 7 families (Table 2). Six species were in 3 families of Gerromorpha and 11 species in 4 families of Nepomorpha. In the supplements, we provide additional tables of taxonomic abundances, densities (number of individuals per m^2), and relative abundances (number of individuals per total number of invertebrates) by region. We also provide maps of the 2 most abundant taxonomic groups (Belostomatinae and *Pelocoris*) in the supplements illustrating densities by principal sampling unit and yr for Comprehensive Everglades Restoration Plan samples, and proportions by region for Comprehensive Everglades Restoration Plan and Modified Water Deliveries samples. We discuss our results by family below.

Discussion

Naucoridae

Among all Modified Water Deliveries throw-trap samples collected during 1996 to 2019, the genus *Pelocoris* was the second most abundant (*N* = 86,430) invertebrate taxon and fifth most abundant animal taxon collected in Modified Water Deliveries throw-trap samples, accounting for 11.0% and 6.3% of individuals, respectively. In the samples we reviewed, *Pelocoris* accounted for 84.5% of all Heteroptera individuals, and *P*. *femoratus* adults in particular accounted for nearly 60% of all Heteroptera individuals. *Pelocoris femoratus* were distributed widely and were abundant across most of the Everglades in both Modified Water Deliveries (Fig. 1a) and Comprehensive Everglades Restoration Plan (Fig. 1c) samples; at the landscape scale, they had highest densities in Shark River Slough (6.6 individuals per m^2; Tables S2, S3) and occurred least often in southern and eastern Water Conservation Area 3A (1.5 per m^2). *Pelocoris balius* were most abundant (0.35 per m^2) in the Panhandle region (Fig. 1b), although they were found regularly at the southernmost Shark River Slough site, along with occasional occurrences throughout various parts of the Everglades, including Water Conservation Area 3A and Loxahatchee National Wildlife Refuge (Fig. 1b, d). *Pelocoris carolinensis* were restricted largely to Loxahatchee National Wildlife Refuge (Fig. 1e; 0.13 per m^2), with the exception of 2 individuals collected in Water Conservation Area 3A. Densities of *P*. *balius* in the Panhandle region, where they were most common, tended to be highest during the wet season (Fig. 2a, c, e), whereas densities of *P*. *femoratus* tended to be higher during the dry season in the Panhandle (Fig. 2b, d, f). However, several sites in the Panhandle region were not sampled in the late dry season, which might have skewed the observed patterns. Further, our intra-annual patterns should be interpreted cautiously because our data represent only a single water yr and there can be considerable inter-annual variation in populations, which often is tied to rainfall during the previous 12 mo (Ruetz et al. 2005; Banet & Trexler 2013). Densities of *P*. *femoratus* in other regions (Shark River Slough, Taylor Slough, Water Conservation Area 3) tended to be more consistent throughout the yr (Fig. 2b, d, f) and lacked strong seasonal differences among stages present in northern populations (McPherson et al. 1987).

Pelocoris balius was described originally as a distinct but relatively uncommon subspecies of *P*. *femoratus* unique to Florida (La Rivers 1970). Sites (2015) elevated *P*. *balius* to species; *P. balius* now also is known from Georgia (Epler 2006), and further study may reveal its presence in the coastal plain of other southeastern states. Within not only the same site but also the same throw-trap sample, *P*. *balius* often were found together with *P*. *femoratus*, and *P*. *carolinensis* with *P*. *femoratus*. However, all 3 species were not collected together at the same site, and we did not collect *P*. *carolinensis* and *P*. *balius* from the same site. This lack of site-specific co-occurrence may be a function of the limited number of sites (16 per yr) sampled once per yr for the Comprehensive Everglades Restoration Plan in Loxahatchee National Wildlife Refuge, where most *P*. *carolinensis* were found, rather than any true lack of co-occurrence on small scales. Regionally, all 3 species were found in Loxahatchee National Wildlife Refuge and Water Conservation Area 3A.

We found that *P*. *balius* had highest densities in the southernmost part of the Everglades in the Panhandle region (Fig. 1b); within Modified Water Deliveries samples, only at the 2 easternmost Panhandle sites just south of the C-111 Canal were *P*. *balius* more common than *P*. *femoratus*. These sites in the Panhandle region are the sites with the highest frequency of drying of all Modified Water Deliveries sites sampled, suggesting *P*. *balius* may be better adapted than *P*. *femoratus* to sites that are more prone to drying. We might expect such adaptation to be in the form of desiccation-resistant eggs capable of aestivation, or a greater dispersal ability; however, the ability of *Pelocoris* eggs to aestivate is unknown, and unlike most aquatic insects, naucorids rarely, if ever, fly (Polhemus 1979; Stout 1982). Restoration of historical hydrological conditions to the Panhandle region has been a recent focus of the restoration of the Everglades, and as efforts to restore water flow to this region continue, there may be a shift in the species composition resulting in fewer *P*. *balius* and more *P*. *femoratus*.

The previously documented southern extent of the range of *P*. *carolinensis* was in Highlands County (Epler 2006), but we now have

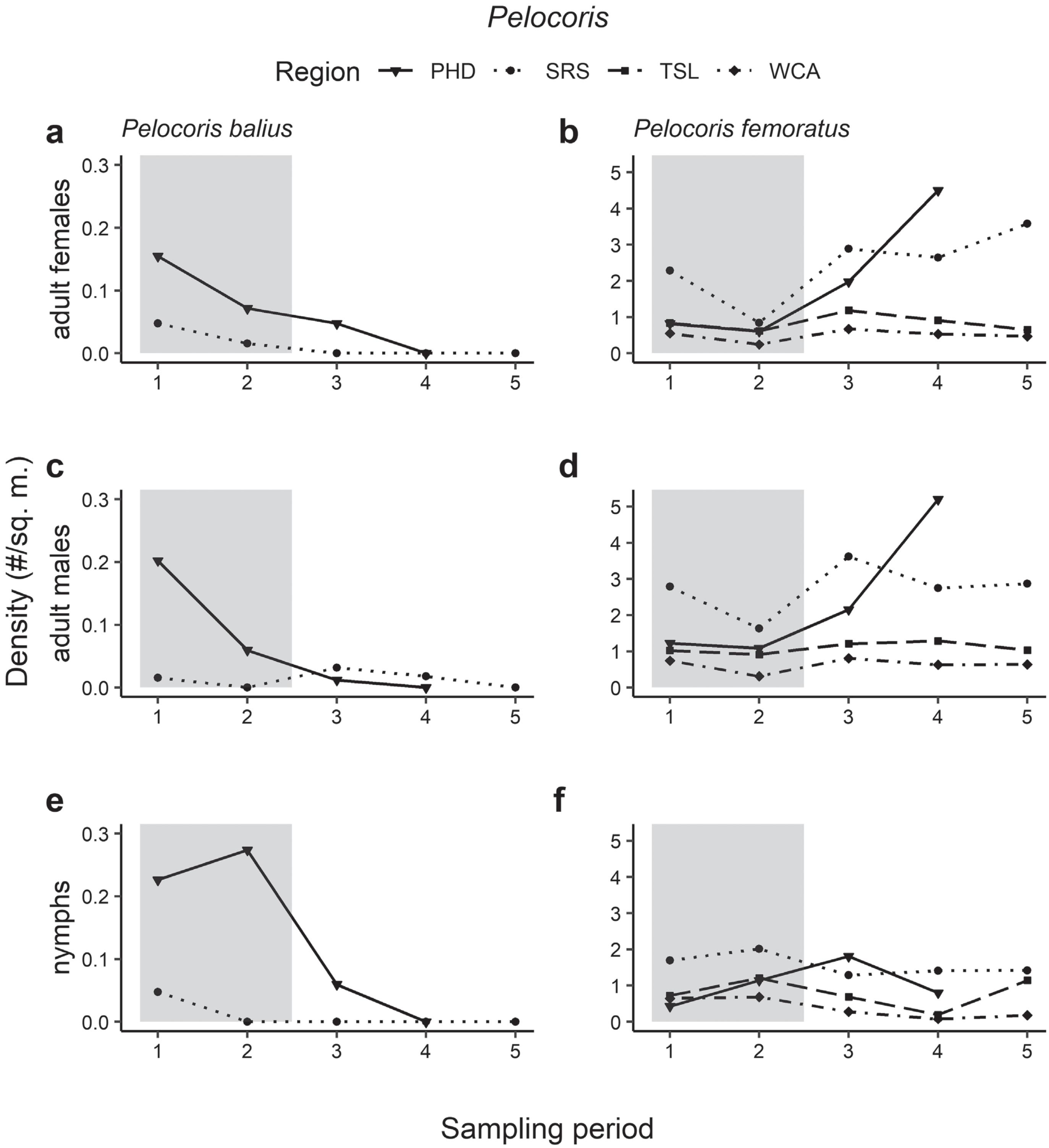

Fig. 2. Density (number of individuals per m²) of *Pelocoris balius* (left column) and *Pelocoris femoratus* (right column) by region in Modified Water Delivery samples by sampling period and life stage: (a, b) adult females; (c, d) adult males; (e, f) nymphs. Sampling periods represented encompass all of water yr 2017 from the start of the wet season (Jul 2016; period 1) to the end at the start of the dry (Apr 2017; period 5); see Table 1. Regions: PHD = Everglades National Park panhandle; SRS = Shark River Slough; TSL = Taylor Slough; WCA = Water Conservation Area 3. Shaded areas represent the wet season; unshaded areas are the dry season.

documented them as far south as Water Conservation Area 3A in Miami-Dade County, Florida, USA. Why *P. carolinensis* was not collected in Everglades National Park and most of the Water Conservation Areas but found in Loxahatchee National Wildlife Refuge remains a question. Habitat associations of naucorids, and Heteroptera in general, are understood poorly relative to other aquatic insect taxa, and studies that have assessed naucorid microhabitats have focused on stream taxa (Stout 1981; Sites & Willig 1991), not the predominantly lentic *Pelocoris*. Further study is needed to assess habitat-specific differences among all 3 species of *Pelocoris*.

Although Epler (2006) noted that there may be undescribed cryptic diversity among the *Pelocoris* in Florida, and Greer (1939) described morphological variation among the species, none of our individuals seemed to diverge from the typical characteristics used to describe Florida's 3 species or other species that may occur elsewhere (*Pelocoris biimpressus* Montandon [Hemiptera: Naucoridae] in Louisiana; *Pelocoris poeyi* Guérin-Méneville [Hemiptera: Naucoridae] in Cuba; Sites & Polhemus 1995; Naranjo et al. 2010).

Belostomatidae

In all Modified Water Deliveries throw-trap samples collected during 1996 to 2019 the subfamily Belostomatinae was the eleventh most abundant (*N* = 9,300) invertebrate taxon and eighteenth most abundant animal taxon collected in Modified Water Deliveries throw-trap samples, accounting for 1.2% and 0.7% of individuals, respectively. In the samples we reviewed, the Belostomatidae were the second most common family, accounting for 11.2% of heteropteran individuals collected (Table 2). Only 5 individuals of the larger-sized (adults can reach over 60 mm long) subfamily Lethocerinae were collected: 3 *Benacus griseus* (Say) (Hemiptera: Belostomatidae) nymphs, 1 *B. griseus* adult, and 1 *Lethocerus uhleri* (Montandon) (Hemiptera: Belostomatidae) adult. Within the subfamily Belostomatinae, *Belostoma lutarium* (Stål) (Hemiptera: Belostomatidae) (18–28 mm) were more abundant and present at more sites than *Abedus immaculatus* (Say) (Hemiptera: Belostomatidae) (about 13 mm). Similar to *P*. *balius*, in Modified Water Deliveries samples *A*. *immaculatus* had highest densities (0.26 per m^2) in the Panhandle region and at the southernmost site in southern Shark River Slough (Fig. 3a). However, unlike *P*. *balius*, *A*. *immaculatus* also was present in Upper Taylor Slough (Table 2), as well as the Comprehensive Everglades Restoration Plan samples taken between Shark River Slough and Taylor Slough (Fig. 3b), with 2 additional individuals collected from northern Water Conservation Area 3A. *Belostoma lutarium* were present in all Modified Water Deliveries regions and most Comprehensive Everglades Restoration Plan regions, but it had highest densities in Shark River Slough, the 2 eastern Panhandle sites, and northern Water Conservation Area 3A (Fig. 3c, d). Seasonally in Modified Water Deliveries samples, *A*. *immaculatus* adults tended to be more abundant during the wet and early dry season than the late dry season (Fig. 4a). *Belostoma lutarium* adults were most abundant during the early wet season in most regions but remained abundant in Shark River Slough yr-round (Fig. 4b). Nymphs also tended to be abundant during the early wet season (Fig. 4c), but these results are from combined data from both species and may confound species-specific patterns.

Abedus immaculatus is perhaps the most unique of Florida's belostomatids. It is smaller than any other belostomatid in the eastern US and is found throughout the state into Georgia and west to coastal Mississippi (Hussey & Herring 1950a, b; Wilson 1958). *Abedus immaculatus* is the only member of the subgenus *Microabedus* Hussey & Herring (Hemiptera: Belostomatidae); all other species of *Abedus* are much larger (27+ mm) and distributed from California, USA, to Panama (Menke 1979). Since their rediscovery in 1950, authors have noted the uniqueness and potentially problematic placement of *A*. *immaculatus* (Hussey & Herring 1950a; Menke 1979; Epler 2006). However, no work has been done to resolve its placement, including its absence from recent phylogenetic assessments of Nepomorpha (Ribeiro et al. 2018; Ye et al. 2020), and very little is known regarding its biology. *Abedus immaculatus* was found primarily within Everglades National Park when present (Fig. 3a, b), and was absent largely from many northern sites. In Modified Water Deliveries samples, the distribution of *A*. *immaculatus* was remarkably similar to that of *P*. *balius* (Fig. 1b), although *A*. *immaculatus* occurred in Upper Taylor Slough and some Comprehensive Everglades Restoration Plan sites that *P*. *balius* did not. Sites where *A*. *immaculatus* were present and had the highest densities tended to be those more prone to drying, and so like *P*. *balius* they could be better adapted to drying than are *B*. *lutarium*.

Corixoidea: Corixidae and Micronectidae

The remaining families and species within the infraorder Nepomorpha we recorded were relatively uncommon. The Corixoidea are unique among the Heteroptera we found in that, rather than being predators, they typically feed on plant and detrital matter (Hungerford 1948; Hädicke et al. 2017). *Trichocorixa minima* (Abbott) (Hemiptera: Corixidae) was the only species of the family Corixidae found, and specimens were collected from all Modified Water Deliveries regions except the Panhandle, although most individuals were in Water Conservation Areas 2 and 3. *Trichocorixa* is the only corixid genus documented south of Lake Okeechobee and all species are relatively small as adults (< 5 mm long) (Epler 2006).

Although corixids are uncommon in the Everglades, 2 species in the sister family Micronectidae are known to occur in southern Florida, but we did not record them here. Both *Micronecta ludibunda* Breddin and *Synaptonecta issa* (Distant) (both Hemiptera: Micronectidae) are non-native species likely introduced through the aquatic plant trade and appear to be expanding their range in Florida (Polhemus & Rutter 1997; Polhemus & Golia 2006; Epler & Denson 2017). Both species are very small (< 2.2 mm), and although we have not found them (they may have been missed by technicians) in Everglades marshes, they may be found in adjacent habitats if conditions are favorable. Indeed, an observation of *M*. *ludibunda* originally posted to iNaturalist along a canal on the eastern border of Everglades National Park is close to the Taylor Slough and Upper Taylor Slough regions and represents the first record of this species in Miami-Dade County, Florida, USA (GBIF.org 2021). Additionally, the South Florida Collections Management Center, Homestead, Florida, USA, has a series of 7 *M*. *ludibunda* (Table S7) collected during May to Jun 2000 at an unspecified location in Everglades National Park; these specimens were collected 1 yr prior to the earliest known records of the species in Florida (Polhemus & Golia 2006). Potential implications of the spread of these exotic insect species in the Everglades are unknown, as are effects of any aquatic Heteroptera as invasive species in freshwater systems. Nevertheless, these 2 additional species are among the numerous other non-native aquatic taxa already found in the Everglades (Kline et al. 2014; Schofield & Loftus 2015).

Nepidae

Other than a single *Ranatra* Fabricius (Hemiptera: Nepidae) nymph collected in Taylor Slough, the only *Ranatra* we found were collected at a site on the western side of Water Conservation Area 3A that has not been sampled since 2006. Sampling at this site stopped in part because dense vegetation growth made the habitat difficult to sample and structurally different from other Modified Water Deliveries sites. In the few samples we reviewed from this site, we found 4 specimens of *Ranatra*: 1 nymph, and 1 adult each of the species *Ranatra australis* Hungerford, *Ranatra drakei* Hungerford, and *Ranatra nigra* Herrich-Schäffer (all Hemiptera: Nepidae). All 3 species are known from southern Florida (Sites & Polhemus 1994; Epler 2006), but clearly nepids are unlikely to be found in most of the Everglades marshes we sampled. Additionally, 3 specimens of *Ranatra buenoi* Hungerford (Hemiptera: Nepidae) from Everglades National Park are in the South Florida Collections Management Center, Homestead, Florida, USA.

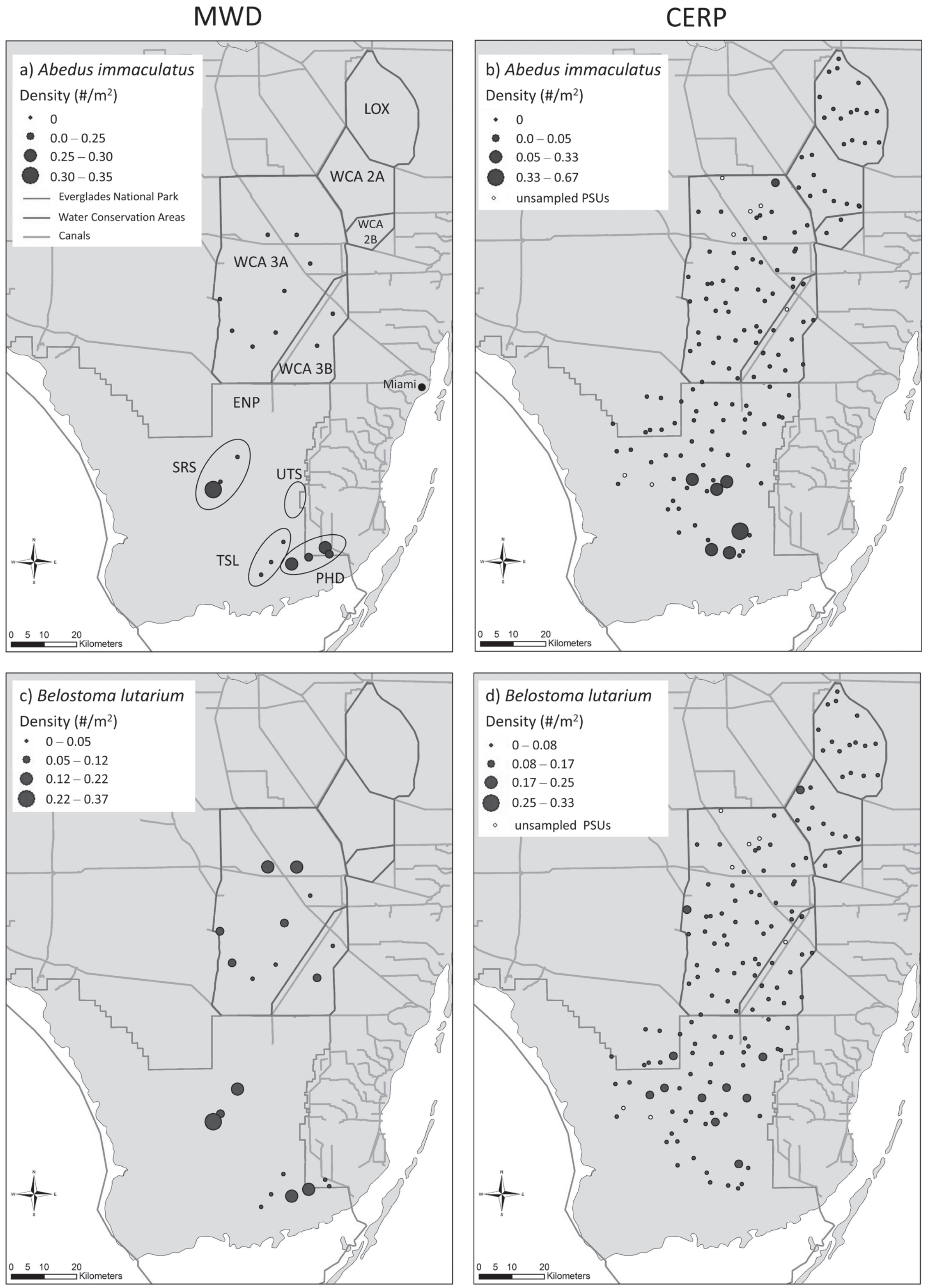

Fig. 3. Adult density (number of individuals per m^2) maps of the 2 species of Belostomatinae, (a, b) *Abedus immaculatus* and (c, d) *Belostoma lutarium*, from Modified Water Delivery (left column) during water yr 2017 and Comprehensive Everglades Restoration Plan samples (right column) during 2016 and 2017. Each point represents 1 sample site (Modified Water Deliveries) or primary sampling unit (Comprehensive Everglades Restoration Plan). Regions are labeled in (a). Regions: ENP = Everglades National Park; LOX = Loxahatchee National Wildlife Refuge; PHD = Everglades National Park panhandle; SRS = Shark River Slough; TSL = Taylor Slough; UTS = Upper Taylor Slough; WCA = Water Conservation Areas.

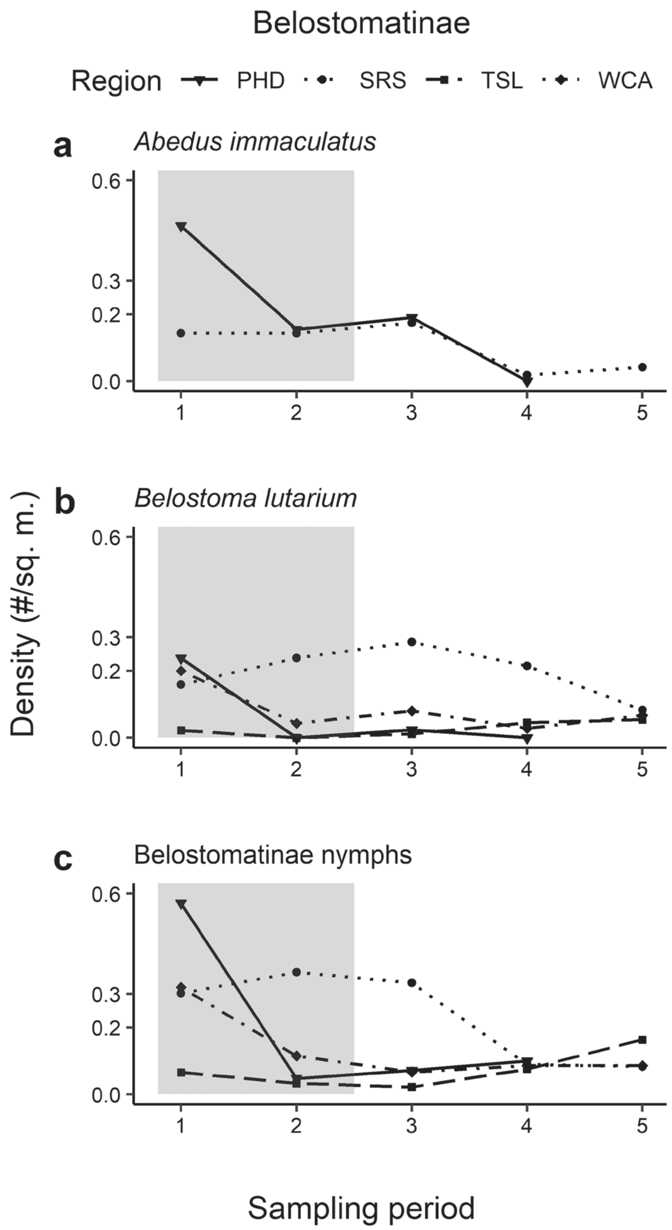

Fig. 4. Density (number of individuals per m^2) of species of Belostomatinae by region in Modified Water Deliveries samples by sampling period: (a) *Abedus immaculatus*, (b) *Belostoma lutarium*, (c) combined nymphs of both species. Sampling periods represented encompass all of water yr 2017 from the start of the wet season (Jul 2016; period 1) to the end at the start of the dry season (Apr 2017; period 5); see Table 1. Regions: PHD = Everglades National Park panhandle; SRS = Shark River Slough; TSL = Taylor Slough; WCA = Water Conservation Area 3. Shaded areas represent the wet season; unshaded areas are the dry season.

Notonectidae

Notonectids were absent completely from the samples we reviewed. We mention them here because 1 species is possibly endemic to southern Florida, *Buenoa marki* Reichart (Hemiptera: Notonectidae). This species is known only from the solution holes of the Pinelands area of Everglades National Park and ponds in a cypress hammock in southern Collier County, Florida, USA (Reichart 1971; Polhemus 1997). Since species of *Buenoa* are uniquely adapted to low oxygen conditions (Miller 1964) and typically inhabit ponds, often those with few or small fish (Schilling et al. 2009), their absence from Everglades marshes is not surprising. Little is known about this unique, small species (5.0–5.7 mm).

Gerridae

Insects in the semiaquatic infraorder Gerromorpha overall were much less common than the aquatic Nepomorpha, accounting for only 3.6% of all individuals we reviewed (Table 2). A single gerrid species, *Neogerris hesione* Kirkaldy (Hemiptera: Gerridae), accounted for 97.2% of all Gerromorpha collected. *Neogerris hesione* was found across the Everglades in Comprehensive Everglades Restoration Plan samples and was relatively common (densities 0.14–0.34 individuals per m^2; Table S2) in most Modified Water Deliveries regions, with the exception of Water Conservation Area 3A (overall density 0.05 per m^2), where it tended to be abundant only at the western sites (Fig. 5 a, b). In Modified Water Deliveries samples, *N. hesione* tended to have highest densities from Oct to Feb (Fig. 5c; periods 2–4). *Neogerris hesione* also is one of the most common gerrid species in Florida, typically found in a variety of lentic habitats from ponds and lakes to marshes, ditches, and canals (Epler 2006).

Aside from *N. hesione*, the only other species in the subfamily Gerrinae we found was *Limnogonus franciscanus* (Stål) (Hemiptera: Gerridae). Three of the 4 *L. franciscanus* individuals were collected in Upper Taylor Slough (2 females, 1 male), whereas the fourth (female) was from west of Shark River Slough. *Limnogonus* Stål is a largely tropical genus that reaches its northern range limit in Florida (Andersen 1995; Damgaard et al. 2014; Ye et al. 2017). *Limnogonus franciscanus* previously was thought to be the only species of *Limnogonus* in Florida (Epler 2006), but recent observations have documented the presence of *Limnogonus recens* Drake and Harris (Hemiptera: Gerridae) throughout the region (MRP, unpublished data).

The third and final gerrid species we found was *Trepobates floridensis* Drake and Harris (Hemiptera: Gerridae) (Trepobatinae), which is found statewide, north into Georgia, and west to coastal Mississippi. The 2 individuals we found were located at sites in the eastern part of Everglades National Park, one 2.7 km south of the C-111 Canal (Panhandle region) and 1 in the northeastern part of the park, 5.8 km northeast of the Chekika entrance station. *Trepobates* typically occurs in more open water habitats such as ponds and calm streams rather than in marshes (Kittle 1977; Epler 2006). One of the individuals we found was relatively close to a canal, which may be a favored habitat of this species, but *T. floridensis* are also small and may easily be missed or escape throw-traps. Both of the individuals we found were females and lighter in coloration (Figs. 6, S5, S6), somewhat similar to Kittle's (1977) illustration of an individual from Paurotis Pond in Everglades National Park, rather than the typical dark form observed in much of the state (Drake & Harris 1928). One of the individuals was considerably lighter than any of Kittle's (1977) illustrations (Fig. 6b, d), and both individuals had small mesopleural spots (Fig. S6). Although Kittle (1977) included "only rarely with a mesopleural spot" in his key to females, he stated these spots were absent in his species redescription. Both of our individuals possessed all other described characteristics of *T. floridensis*, including their small size (< 3.3 mm), and lacked the combination of characteristics of all 11 other described species of *Trepobates* (Kittle 1977, 1982, 1991). Hence, identification with keys that include the mesopleural spot as a defining characteristic (Epler 2006) may lead to misidentification of some *T. floridensis* as *Trepobates inermis* Esaki (Hemiptera: Gerridae). However, *T. inermis* can be distinguished by the shorter second antennal segment and typically larger size (3.2–4.3 mm); additionally, *T. inermis* specimens have been observed only as far south as northern Florida (Kittle 1977; Epler 2006). Color patterns of *Trepobates* can be highly variable within species (Kittle 1977).

Veliidae

Veliidae were rare in the samples from Everglades marshes. Only 5 *Platyvelia brachialis* (Stål) (Hemiptera: Veliidae) were found along with a single *Microvelia* nymph. Without adults, *Microvelia* species are not

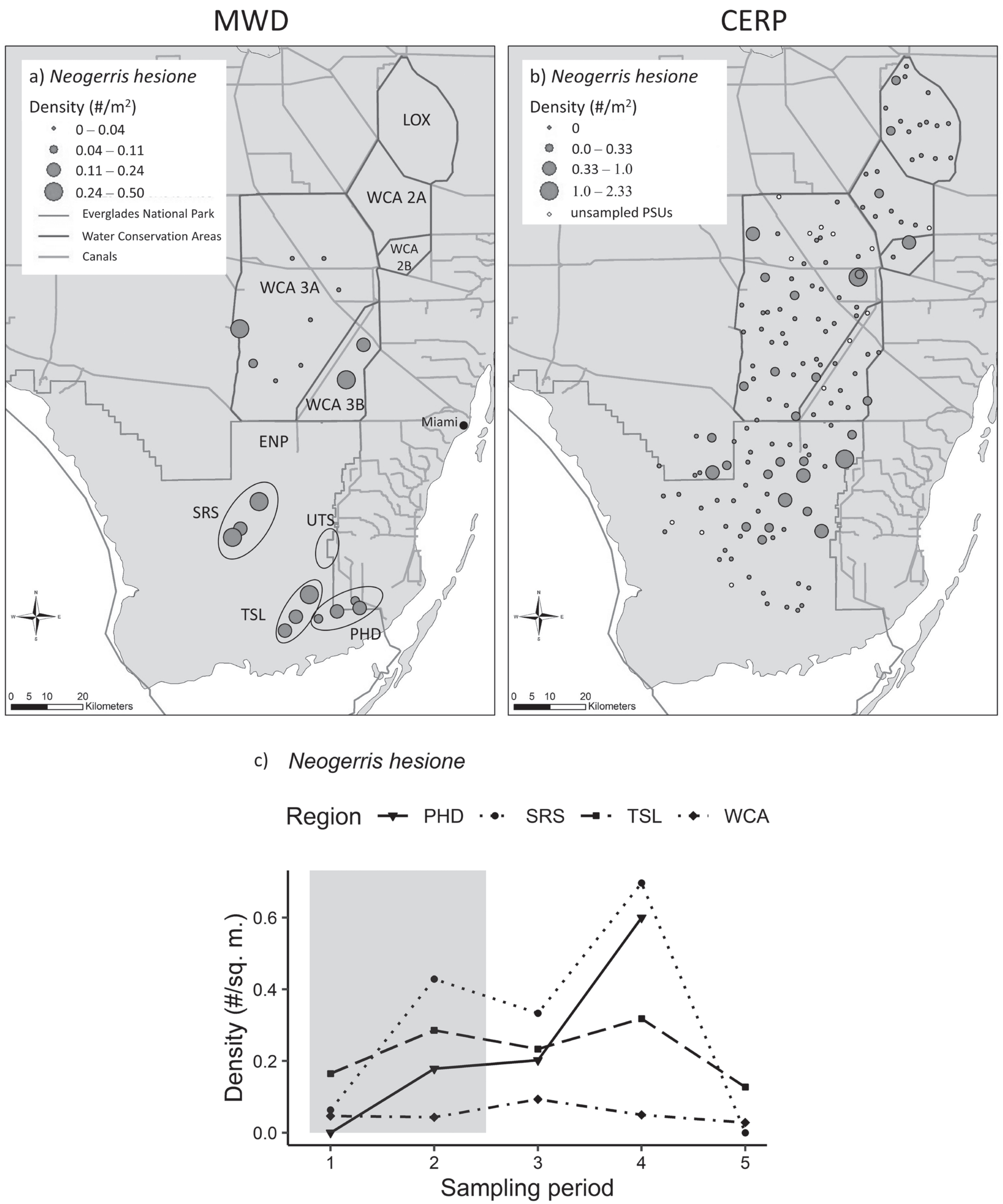

Fig. 5. Density maps (number of individuals per m²) of *Negerris hesione* in (a) Modified Water Delivery during water yr 2017 and (b) Comprehensive Everglades Restoration Plan samples during 2016 and 2017; (c) density (number of individuals per m²) of *N. hesione* by region in Modified Water Deliveries samples by sampling period. Sampling periods represented encompass all of water yr 2017 from the start of the wet season (Jul 2016; period 1) to the end at the start of the dry (Apr 2017; period 5); see Table 1. Regions: LOX = Loxahatchee National Wildlife Refuge; PHD = Everglades National Park panhandle; SRS = Shark River Slough; TSL = Taylor Slough; WCA = Water Conservation Areas. Shaded area represents the wet season; unshaded area is the dry season.

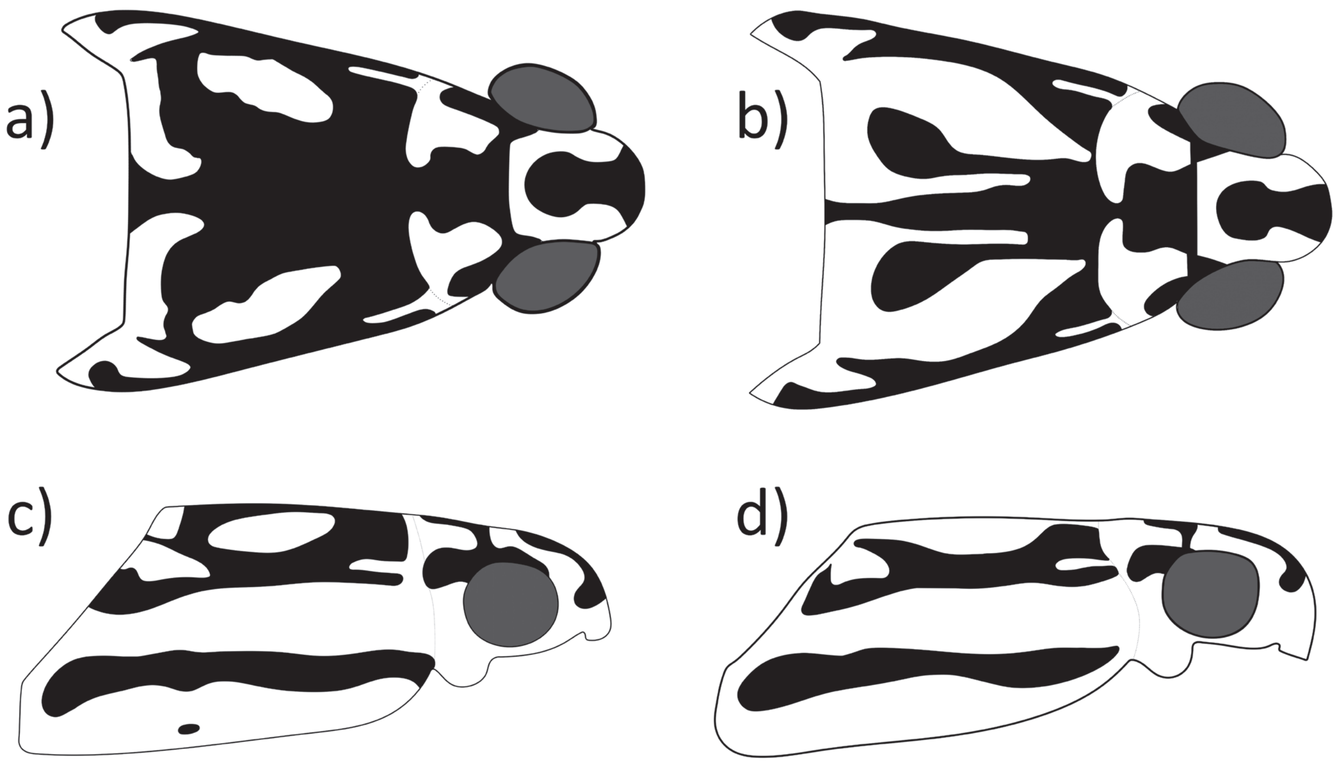

Fig. 6. Illustrations of the color patterns on the head and thorax of the 2 adult female individuals of *Trepobates floridensis* found in Everglades marsh samples. (a, b) are dorsal illustrations and (c, d) are lateral illustrations; (a, c) are of the individual from the Panhandle region on 5 Jul 2017; (b, d) are of the individual from northeastern Everglades National Park on 19 Sep 2016. Corresponding photographs are in the supplements (Figs. S5, S6).

identifiable reliably, and multiple species occur in southern Florida (Epler 2006). Species of *Microvelia* are the smallest veliids (most < 3 mm) and, therefore, may largely be overlooked in throw-trap samples. Based on our observations, *Microvelia* appears to be less common in open marshes like those we sampled than in other lentic habitats such as ponds, solution holes, canals, or even marsh edges. *Platyvelia brachialis* and 1 unsampled species that may be found in the Everglades, *Steinovelia stagnalis* (Burmeister) (Hemiptera: Veliidae), typically are found in dense emergent vegetation, perhaps denser vegetation than at sites we sampled (McPherson & Taylor 2006; Moreira et al. 2020; Rodrigues et al. 2021). The sizes of *P. brachialis* (4–6 mm) and *S. stagnalis* (4–5 mm) are larger than *Microvelia*, but still small compared to most taxa we found (Polhemus & Polhemus 1993). Two other Veliidae genera, *Husseyella* Herring and *Rhagovelia* Mayr occur in southern Florida, but neither are represented by freshwater species in this region.

Mesoveliidae

Only a single *Mesovelia* nymph was found in the samples we reviewed. Without a mature individual we are unable to identify the species; both *Mesovelia amoena* Uhler and *Mesovelia mulsanti* White (both Hemiptera: Mesoveliidae) have been observed in freshwater habitats in southern Florida (Epler 2006; MRP personal observation). *Mesovelia* is another genus that is likely under-sampled due to their small size (1.8–4.0 mm) and their ability to escape throw-traps.

Other Gerromorpha families

We have observed 2 other Gerromorpha families, Hebridae and Hydrometridae, in the Everglades, although not necessarily at the sites reviewed here. Therefore, these families may be present only in regions with slightly different habitats or are missed by standardized throw-trap sampling within marshes. Hebridae are very small (< 2 mm) and may be overlooked, while *Hydrometra* Latreille is longer (8–15 mm) but very thin and may not appear as an insect to technicians; both taxa may escape throw-traps easily.

In conclusion, we found that the aquatic and semiaquatic Heteroptera in the marshes of the Everglades are dominated by 1 species, *P. femoratus*, while 2 other species, *B. lutarium* and *N. hesione*, are distributed widely and are more abundant than other taxa. Two additional species, *A. immaculatus* and *P. balius*, had higher densities in regions more prone to drying. All other species rarely were collected, and overall species richness was low, because we only documented 17 taxa at the lowest identifiable level. Nevertheless, the Everglades contains aquatic species of Heteroptera not found in most of North America (*A. immaculatus*, *P. balius*), unique forms of species (lighter *T. floridensis*), and Neotropical species (*L. franciscanus*) not found in northern Florida or most of the US. Most of these aquatic Heteroptera of the Everglades also serve as prey and low-level predators in an ecosystem better known for its wading birds and alligators. Although their role as predators in the ecosystem is not well understood, aquatic heteropterans occupy unique niches relative to other invertebrate and vertebrate predators, as well as among Heteroptera families (Merritt et al. 1996; Rudolf 2020). Their prevalence and typically small sizes, microhabitats used, and behavior suggest that some heteropteran taxa, particularly *Pelocoris* and belostomatids, may act as functionally unique and important predators on other invertebrates, anurans, and early life stages of smaller species of fishes in the Everglades ecosystem.

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