

Chapter 10

Invertebrates of the Florida Everglades

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Introduction

The Everglades is a large karstic wetland located at the southern tip of the Florida, USA, peninsula between the subtropical Western Atlantic and the Gulf of Mexico. Lying within the subtropics, between 25.3°N and 26.7°N, the Everglades experiences mild winters (the average temperature of all months exceeds 17.8 °C) because of the strong influence of the northerly flow of the Florida Current (Gulf Stream) to the east. However, winter temperatures in the interior Everglades are not moderated by the Florida Current and may experience occasional freezes with important effects on the biota, particularly those species derived from the tropics (Duever et al. 1994; Matich and Heithaus 2012; Boucek and Rehage 2014). The ecosystem experiences a seasonal rainfall regime, similar to other tropical/subtropical wetlands that drive annual hydrological cycles, with marked inter-annual variation in the magnitude of marsh drying (Duever et al. 1994). More than 75 % of the annual rainfall of 152 cm is delivered between May and October, the wet season in south Florida, with marked inter-annual variation in the annual deposition resulting from regional climatic drivers (Gaiser et al. 2012).

Peat dating has revealed that the ecosystem is relatively young (approximately 5000 years in its current wetland form). The karstic geology and surficial aquifer yield relatively hard water with high dissolved calcium carbonate (Gleason and Stone 1994), which binds phosphorus and renders the system naturally oligotrophic (McCormick et al. 2002).

The Everglades is recognized widely as a globally iconic ecosystem worthy of conservation, but that has been threatened by drainage, encroaching development, compartmentalization, and nutrient enrichment. It has been designated a World Heritage Site, an International Biosphere Reserve, a Wetland of International Importance, and a specially protected area under the Cartagena Treaty and is the focus of a major state and US Federal restoration effort (NRC 2006). Two observations about the Everglades illustrate the role that aquatic invertebrates play in

its ecology and conservation. The Everglades historically supported large colonies of nesting wading birds (>100,000 pairs/year, among the largest pelicaniform and ciconiiform aggregations recorded) that took advantage of the dry-season concentration of their prey, small fishes and crustaceans, to support their reproductive exuberance (Ogden 1994; Frederick and Ogden 2001; Ogden et al. 2005). How did an oligotrophic ecosystem support seasonally high abundances of apex predators? The Everglades stands out when compared to other aquatic ecosystems in the presence of massive accumulations of primary production in the form of periphyton mats while sustaining low density and biomass of aquatic consumers and, notably, herbivores (Turner et al. 1999; Trexler et al. 2015). Aquatic snails, commonly a key grazer in freshwater ecosystems, are present at extremely low densities and biomass when compared to other aquatic systems worldwide, though the regional species pool is not depauperate (Ruehl and Trexler 2011). Why does so much primary production accumulate in the presence of a robust aquatic-consumer community? In this chapter, we will explore the role of macroinvertebrates in the Everglades food web and use that information to answer these questions. The answers illuminate essential ecological processes that are at risk from water extraction and nutrient enrichment and which are focal goals for a massive restoration program aimed to conserve the unique character of the Everglades (Turner et al. 1999; Gaiser et al. 2012).

The Ecosystem and Its Habitats

Hydrology and Nutrients

The Everglades is the downstream portion of a watershed that extends south of Orlando, Florida to the marine habitats of Florida Bay and the Gulf of Mexico. It has an area of 28,205 km² and extends for 449 km north to south and 100 km east to west (Light and Dineen 1994). Prior to the onset of drainage in the late 1800s, the Greater Everglades habitat south of Lake Okeechobee covered an area of 15,000 km² (Gaiser et al. 2012), but this has been reduced to the Everglades Agricultural Area (EAA: 3059 km²), five water conservation areas (WCAs: 3554 km²), and Everglades National Park (ENP: 4363 km²) (Light and Dineen 1994; Fig. 10.1). Because the EAA has been drained for agricultural production, only 47 % (7917 km²) of the historical ecosystem remains as wetlands. Shallow freshwaters in the historical Everglades flowed south from the margins of Lake Okeechobee in a process called sheet flow, with wet-season current speeds believed to have been higher than the contemporary averages of 0.3–1.4 cm s⁻¹ (Larsen et al. 2011). Channelization and drainage have greatly diminished the broad, flowing water courses, accompanied by loss of topographic patterning called ridge and slough (Fig. 10.2; McVoy et al. 2011). Sloughs are, on average, 20 cm lower than adjacent sawgrass-dominated (*Cladium jamaicense*) ridges and

hold water longer in the dry season. Current velocities of at least 2 cm s^{-1} are typically cited as necessary to suspend and redistribute the flocculent organic layer of detritus that accumulates routinely from bladderwort, periphyton, and vascular plants that are characteristics of Everglades sloughs (Larsen et al. 2011). It has been proposed that water flows of this speed or higher are necessary to maintain the historical organization of the landscape (Larsen et al. 2011; but see Kaplan et al. 2012). The linear (anisotropic) patterning of the landscape parallel to water flow is critical in forming isolated pools of water during dry-season water recession that form early (December) on the system edges and appear progressively later (March–May) toward the center (deeper) areas of the ecosystem. This sequence is critical in providing high-quality foraging patches for wading birds raising chicks between January and May (Gawlik 2002).

Water-depth variation and hydrological patterns are primary drivers of the ecology of the Everglades in general and the lives of aquatic invertebrates in particular. Hydroperiod is defined as the number of days in a year that a site has a water depth exceeding 5 cm, a cutoff selected because of the ubiquitous loose layer of organic flocculent material (floc) that covers the bottom (Trexler et al. 2005). At 5 cm, a floc-filled space remains in the water column, causing fishes and some common macroinvertebrates to expire, presumably from anoxia. Much of the Everglades does not dry annually, but all of the system does dry for short periods of time in relatively dry years. Thus, hydroperiod may be a poor descriptor of hydrological impacts on aquatic ecology. Sites that dry for several days every 2 years (on average) are ecologically quite different from sites that dry for similar lengths of time, but only every 6 or 7 years, though the hydroperiod averaged over multiple years, say 10, would be similar. Everglades sites that dry annually are in a perpetual state of recovery from the event, while sites that dry less frequently may not be, depending on the time required to complete the successional process and the time passed since the most recent drought. Thus, Everglades wetlands are often better characterized by the number of days that have passed since a site last re-flooded (days since dry, DSD). This parameter is correlated with hydroperiod, but also captures time lags inherent in post-drought succession (Trexler et al. 2005). Because seasonal hydrological variation is a key driver of ecology in southern Florida, many workers characterize years by “water year” from the beginning of the wet season (typically considered to be May) to the end of the dry season (typically considered the following April). The transition from wet to dry season typically begins in November, and surface water at the edges of the ecosystem begins to diminish notably by December (“typically” is repeated several times here because marked inter-annual variation is an important element).

Everglades waters are generally described as oligotrophic with low level of total phosphorus (TP), the limiting element for plant growth. Median TP concentration in surface water throughout the Everglades ranges from 4 to 10 ppb, though much higher values routinely occur in some areas (McCormick et al. 2002). Drought conditions can lead to local elevations of about 10 ppb. High values are most common at the inflow points of water coming from the canal system, which receives runoff

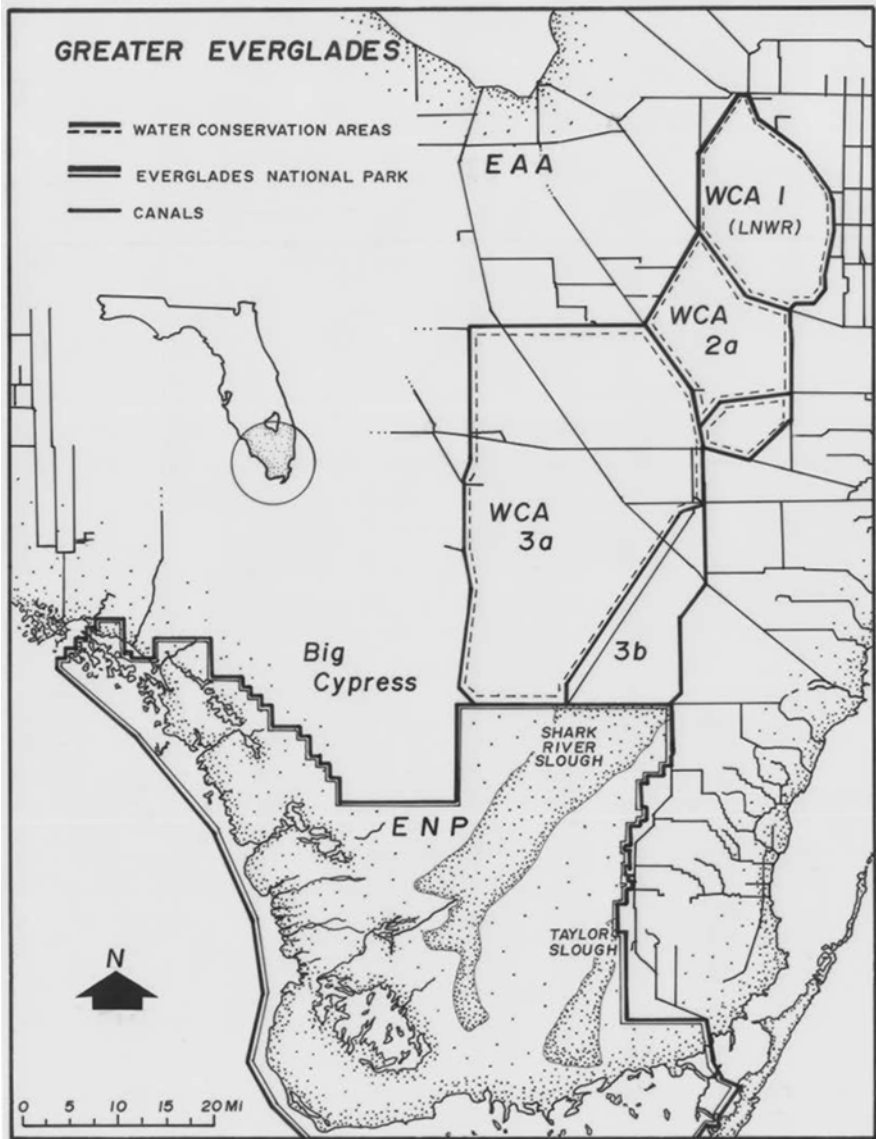


Fig. 10.1 The Greater Everglades ecosystem is located on the southern tip of the Florida peninsula, USA. Shark River Slough and Taylor Slough are bordered by short-hydroperiod marl prairie habitats and delineated on this map for clarity. Unlike other features on this map, they are not encircled by artificial barriers such as canals or levees. Water flows from Lake Okeechobee on the northern extremity of the map (see Florida inset) to the south through WCAs and by the canal system to ENP. *EAA* Everglades Agricultural Area, *WCA-1 (LNWR)* Water Conservation Area 1 (Loxahatchee National Wildlife Refuge), *ENP* Everglades National Park

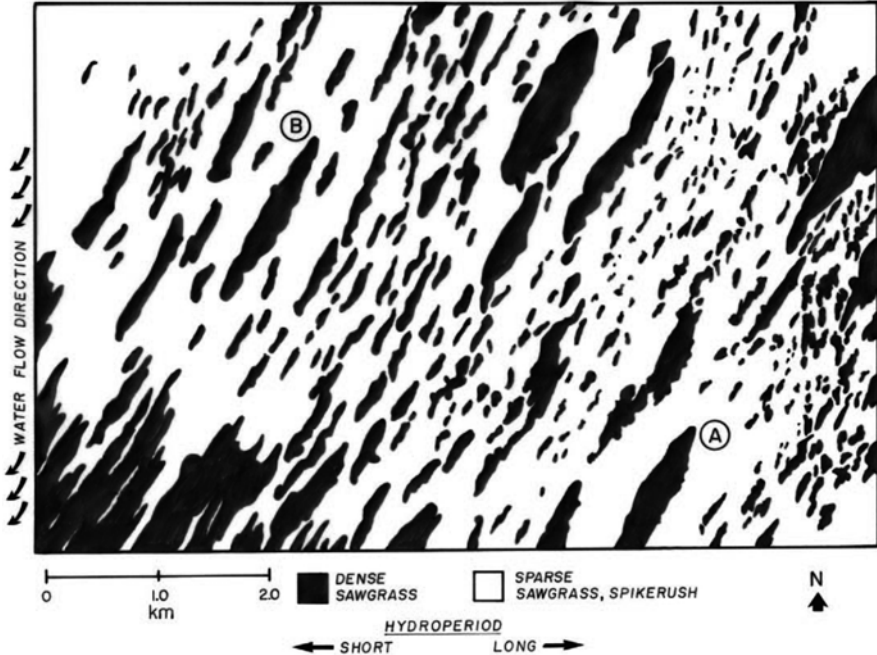


Fig. 10.2 A slice of ridge-and-slough relief from the Shark River Slough, ENP, illustrates landscape characteristic of the Everglades. The long axis of this slice (compass direction N) is approximately 10° to the west or perpendicular to the direction of water flow and captures a short- to long-hydroperiod gradient (west to east). Sawgrass-dominated ridges are modestly higher in elevation than the surrounding sparse sawgrass and spikerush-dominated (*Eleocharis* spp.) sloughs. Point A is located at $25^\circ 38' 0.79''\text{N}$, $80^\circ 41' 40.55''\text{W}$ and point B is located at $25^\circ 39' 30.87''\text{N}$, $80^\circ 43' 42.18''\text{W}$

from agricultural areas. Water-column TP often drops sharply with distance from a canal. Rapid uptake and accumulation of allochthonous TP by bacteria and algae lead to loading that can result in eutrophic conditions (McCormick and O'Dell 1996; Gaiser et al. 2005). The water is also hard, with high levels of calcium carbonate because of the limestone foundation of the Florida peninsula. Phosphorus binds with calcium carbonate, making it biologically unavailable and rendering the ecosystem naturally oligotrophic. The concentration of TP may increase by natural and anthropogenic mechanisms. Natural mechanisms such as accumulation of animal waste beneath wading-bird rookeries or in alligator ponds lead to local patches of enriched conditions, while agricultural runoff has eutrophied large expanses of the ecosystem, notably in northern WCA 2A and much of the perimeter of WCA 1 (LNWR) (Fig. 10.1). Everglades periphyton mats are unusual because in the presence of excess P, the factor limiting their growth at low to moderate concentrations,

they disassociate (McCormick and O'Dell 1996; Gaiser et al. 2005). Thus, eutrophied areas of the Everglades generally lack periphyton mats characteristic of areas unaffected by nutrient enrichment.

Habitats

Gunderson and Loftus (1993) identified four habitats in the Everglades ordered by hydroperiod and depth: ponds, sloughs, graminoid wetlands, and forested wetlands (Table 10.1). Canals are an additional habitat added over the past 100 years, with important implications for aquatic animal life (Loftus and Kushlan 1987; Rehage and Trexler 2006; Harvey et al. 2010). Only canals can be considered permanently flooded habitats in this ecosystem because the limestone basement rock limits the depth of alligator-maintained ponds and sloughs to be shallower than the minimum hydrological stage experienced on a decadal scale in all but the most impounded region (southeast WCA 3A; Fig. 10.1). These habitats may be ranked by the diversity of structure in the water column. Canals and ponds typically include areas of open water lacking vegetation; sloughs may have areas of relatively open water, but generally have stems of emergent plants, some submerged aquatic vegetation (SAV), and some periphyton mats; while graminoid wetlands typically have extensive emergent plants, SAV, and luxuriant mats of periphyton.

Most of the ecological studies of Everglades invertebrates have been conducted in slough and wet prairie habitats, with a small amount of work on sawgrass-dominated ridges. There is vertical structure in these habitats that creates a variety of microhabitats for distinct invertebrate communities (Fig. 10.3). Algal production in the Everglades is quite high and may be present as benthic, epipelagic, and epipelagic mats covering all surfaces (Gottlieb et al. 2015). Those mats may be quite thick (up to 8 cm) and structured within. The external layers are largely dead algal material, with cyanobacteria dominating the inner living areas. Diatoms, desmids, and green algae, along with heterotrophic bacteria and fungi, make up the interior structure of these mats (Donar et al. 2004). Cyanobacteria that secrete a mucilaginous matrix of extracellular polymeric substances (Thomas et al. 2006; Stewart et al. 2013) are responsible for holding together the mats to form coherent habitats for periphyton infauna. Extracellular polymeric substance is high in protein and polysaccharides (Stewart et al. 2013) and may be a relatively rich food source for heterotrophs. This creates a complex habitat structure, particularly when combined with the diversity of emergent and submerged vascular plants present in much of the ecosystem.

The formation of complex periphyton mats is common in shallow systems where microbes grow attached to substrates because of access to nutrients. It is believed that the more closely related the algal cells are to heterotrophic bacterial ones, the better access they have to enzymes that break organic-bound nutrients,

Table 10.1 Freshwater wetland habitats of the Everglades (modified from Gunderson and Loftus 1993)

A. Canals
B. Ponds—open water lacking substantial submerged aquatic vegetation, e.g., Illinois pondweed (<i>Potamogeton illinoensis</i>)
C. Sloughs—deeper area with slow moving water, e.g., white water lily (<i>Nymphaea</i>), spatterdock (<i>Nuphar</i>)
D. Graminoid wetlands
1. Sawgrass (<i>Cladium</i>) marshes; abundant periphyton mats, epiphyton, benthic periphyton
(a) Tall stature
(b) Intermediate stature
2. Wet prairies (peat); abundant periphyton mats, epiphyton, benthic periphyton
(a) <i>Eleocharis</i> spp. marshes
(b) <i>Rhynchospora tracyi</i> flats
3. Wet prairies (marl); sparse emergent sawgrass, thick benthic periphyton
E. Forested wetlands
1. Bayhead swamp forest (tree island)
2. Pond apple (<i>Annona</i>) forests
3. Willow (<i>Salix</i>) heads
4. Cypress (<i>Taxodium</i>) forests

resulting in increased efficiency of exchange. This requires the microbes to cope with plant allelopathic chemicals and sometimes a reduced light environment (Wetzel 1983). Thus, phytoplankton are relatively uncommon in wetlands unconnected to lakes (Goldsborough and Robinson 1996), so it may not be surprising that waters in the Everglades have high clarity and virtually no phytoplankton. This is partly a result of frequent drying—phytoplanktonic species rarely have adaptations found in benthic species to survive desiccation, so they have trouble establishing in benthic environments (Evelyn Gaiser, personal comm). Most wetland phytoplankton are thought to be benthic species that have become suspended by wind (Goldsborough and Robinson 1996). Periphyton coverage in the Everglades varies seasonally. Floating-mat cover and biomass are lowest in February through April but increase by as much as 30 % and 110 %, respectively, by October (Liston and Trexler 2005). The mats are a critical habitat feature that distinguishes the ecology of the Everglades from other large wetlands in North America (Turner et al. 1999), rendering them more similar to other karstic wetlands throughout the Caribbean (La Héé and Gaiser 2012).

There is a size-structured separation of macroinvertebrate distribution in a typical slough habitat of the Everglades. Smaller invertebrates use the periphyton and benthic floc as a refuge from larger predatory invertebrates and fishes (Dorn et al. 2006; Chick et al. 2008; Trexler et al. 2015), while larger ones graze surfaces or patrol the outside of periphyton capturing prey that venture out. In the laboratory, physical disruption of the mat structure leads to increased consumption of edible

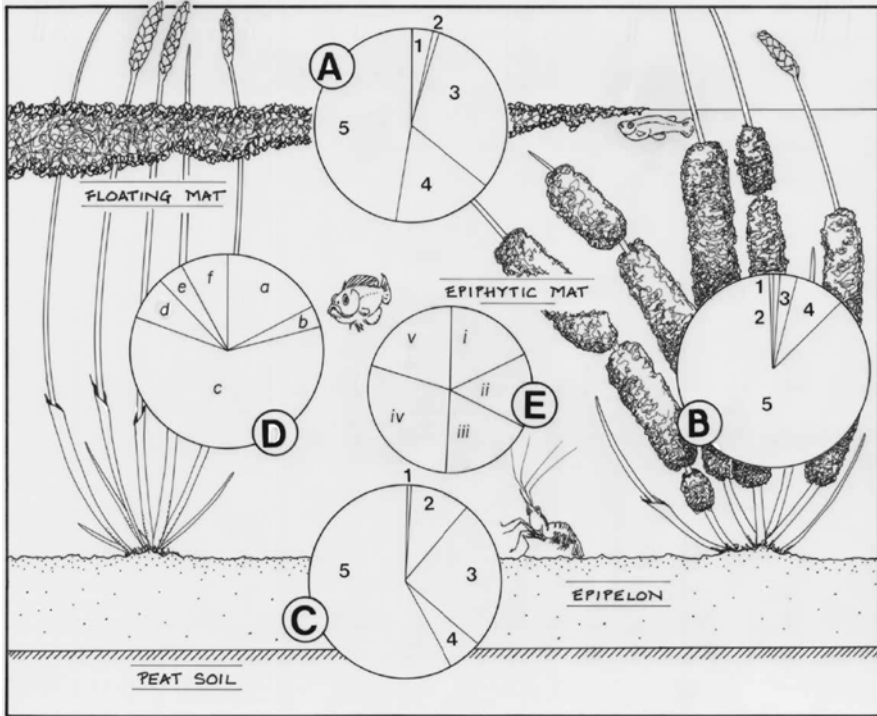


Fig. 10.3 Cross-section of slough habitat illustrating four microhabitats: (A) floating mat, (B) epiphytic mat encircling emergent plant stem, (C) epipelon (benthic organic floc), (D) water-column large macroinvertebrates, and (E) water-column zooplankton. Pie charts indicate the relative abundance of taxa in each habitat: (1) aquatic bladder snails, (2) cladocerans + copepods, (3) amphipods, (4) biting midge (ceratopogonid) larvae, (5) midge (chironomid) larvae; (a) dragonfly naiads, (b) diving beetle larvae, (c) riverine grass shrimp, (d) creeping water bugs, (e) ramshorn snails, (f) crayfish, (i) flatworms, (ii) cladocerans, (iii) copepods, (iv) ostracods, and (v) others

algae and invertebrates that live inside (Geddes and Trexler 2003; Trexler et al. 2015). Floating-mat invertebrates are dominated numerically by bladder snails (physids), amphipods, and biting midges (ceratopogonids) (Fig. 10.3; see Appendix for taxa names). Epiphytic algal mats are dominated numerically by bladder snails, while benthic-floc communities are dominated by midge (chironomid) larvae and amphipods (Fig. 10.3); the density of invertebrates in the mats is substantially higher than in the floc (see next section). The water column is home to larger invertebrates, numerically dominated by riverine grass shrimp (*Palaemonetes paludosus*) and dragonfly naiads (Fig. 10.3); crayfishes (*Procambarus* spp.) are also abundant and dominate invertebrate biomass (not shown) because of the large size of adults. Zooplankton are relatively uncommon in the Everglades water column, particularly during daylight hours (see next section). Zooplankton emerging from the benthos at night are composed equitably of ostracods, copepods, flatworms, and cladocerans (Loftus et al. 1990) (Fig. 10.3).

In the dry season, as the water table drops, water first drains from sawgrass-dominated ridges to the adjacent sloughs. This small topographic heterogeneity has important consequences at the sub-kilometer scale. For example, the recurrent draining leads to a narrow band of nutrient-enriched habitat at the ridge-slough margin that is typically home to elevated abundances of aquatic animals such as riverine grass shrimp. Also, several studies have found that ridges, with dense sawgrass, support elevated densities of crayfish (*P. fallax*) compared to the adjacent sloughs when water level is high enough to flood both habitats (Jelks et al. 1992; Hendrix 2000; Hagerthey et al. 2014). In the dry season, when water drops to expose the surface of ridges, *P. fallax* move to adjacent sloughs where their densities may increase dramatically (Jordan 1996; Cook et al. 2014). In an experimental study, crayfish (*P. fallax*) left ridges as depths dropped below 20 cm, leading to a pulsed increase in their density in recipient sloughs (Cook et al. 2014). The short-hydroperiod dominant species, *P. alleni*, have also been shown to disperse upon reflooding of marshes, but to burrow as water recedes (Acosta and Perry 2001). Habitat shifts and dispersal demonstrated for these crayfish have potential impacts on food availability and habitat use by foraging predators, including wading birds.

Sampling Invertebrates in Everglades Wetlands

Our understanding of aquatic macroinvertebrates is influenced in large part by the methods used to sample them and taxonomic resolution employed to group animals. The standard definition of macroinvertebrates is fauna retained on a 500 μ sieve (Hauer and Resh 2007); those passing through but retained on a 40 μ sieve are meiofauna (Palmer et al. 2007). However, aquatic ecologists commonly term all life stages of aquatic invertebrates with macro-sized adults as macroinvertebrates. In our review, we identified no published Everglades studies that used the term meiofauna.

Most published research on the Everglades invertebrates is either systematic or ecological, conducted on the assemblage of invertebrates obtained by selected sampling devices. The researchers often failed to identify to species those taxa difficult to distinguish. Ecologists often argue that complete taxonomic resolution is unnecessary to document patterns of community structure and invertebrate production relevant to understanding ecological processes. However, King and Richardson (2002, 2008a) provided a compelling case of the benefit of high-resolution taxonomic identification of chironomid larvae for use in biomonitoring in the Everglades. Larvae of the Chironomidae are notoriously difficult to identify to species, requiring mounting of individual specimens and specialized taxonomic knowledge. Because those larvae may be quite abundant, King and Richardson (2002) recommended using a fixed-count method to produce data on relative abundance of species. They demonstrate that some species of midge larvae in the Everglades display habitat specialization that makes them excellent indicators of

nutrient enrichment. Jacobsen (2008) developed a key to pupal exuviae of Everglades midges in an effort to simplify taxonomic identification and potentially speed sample processing.

The highly variable and often dense submerged and emergent vegetation of the Everglades creates a challenge for sampling and renders of little use some methods commonly used in other ecosystems. Turner and Trexler (1997) compared eight invertebrate samplers in vegetated habitats by employing them side by side in the Everglades and found that they differed in the number of individuals captured, the number of species captured, and the equitability of species abundances. The methods evaluated were an inverted-funnel trap, a D-frame sweep net, a 1-m² throw trap, a stovepipe sampler, a Hester-Dendy artificial substrate, a minnow trap, a benthic corer, and a plankton net. Turner and Trexler (1997) recommended that complementary methods be used to gain a complete representation of the invertebrate assemblage, for example, the funnel trap to capture plankton emerging from the benthos, the D-frame sweep net to capture mat-associated fauna, and the 1-m² throw trap to capture larger species such as crayfish and grass shrimp. Though commonly used for bioindicator analysis in other parts of Florida, Turner and Trexler (1997) discouraged the use of Hester-Dendy artificial substrates in the Everglades, because they yielded small collections of animals, they produced a distinctive, non-typical assemblage of animals, and the hard surface had no analogy to indigenous habitats of the region. King and Richardson (2002) recommended the use of a D-frame sweep net deployed in a method similar to Turner and Trexler (1997) and following State of Florida and US Environmental Protection Agency guidelines. The sweeps include brushing across the top of the substrate, followed by sweeping up to the surface with the goal of producing a representative sample of all microhabitats. Liston and Trexler (2005) pointed out that in many areas of the Everglades, this method is problematic because the extensive periphyton mats impede a smooth sweep and may overfill the net bag. The strong integrity of the mats precludes pulling up the net without dragging additional mat from the surrounding area, leading to an overrepresentation of that habitat and possible escape by large mobile macroinvertebrates. Liston and Trexler (2005) recommended sampling periphyton infauna by taking cores (6-cm diameter), which they sorted under magnification to enumerate infauna retained on a 250-mm mesh sieve and with a maximum dimension of 1 mm. This excluded small midge larvae that could be characterized as meiofauna. The authors suggested reporting data as density (number or mass/area sampled) and "crowding" (number or mass/g periphyton). Crowding accounts for the patchy nature of periphyton mats, even when sampled at the small scale of their cores, and represents the encounter rate of animals enumerated within the sample. Later work using this method counted all midges retained on the 205 μ m mesh (Sargeant et al. 2011), which increased the number of animals counted, but did not change the spatial or temporal patterns revealed (unpublished data). Dense vegetation typical of areas receiving continuous nutrient enrichment cannot be properly sampled by throw traps because the trap neither settles quickly nor seals effectively on

the marsh substrate (Jordan et al. 1997; Turner et al. 1999). Hagerthey et al. (2014) used a portable bottomless lift net to overcome this problem.

There has been limited study of zooplankton in the Everglades. Turner and Trexler (1997) used a conical plankton net to take water-column samples of plankton, but found a number of benthic taxa in the collections. They concluded that the vegetation in the water column made this method ineffective, leading to few animals collected and high inter-sample variation. The Everglades water column is generally very clear, further suggesting that few plankton are present there, at least during the day. Loftus et al. (1990) placed Brakke's (1976) modified Whiteside-Williams (1975) pattern samplers (multiple-funnel trap) on the substrate surface to capture zooplankton as they emerged at night to swim into the water column. To enable more rapid processing of Everglades carbonate-sediment samples, Daraghy et al. (1988) developed a rapid acid-wash method to dissolve carbonate and expose the invertebrates. Bruno et al. (2003) and Bruno and Perry (2004, 2005) studied groundwater copepods with a water suction pump to sample ground water by filtering water drawn from wells reaching into the limestone bedrock with a 40- μ m mesh net.

Invertebrate Diversity, Habitat, and Control of Dynamics

Biodiversity

Knowledge of invertebrate communities in the Everglades has greatly increased since it was first reviewed by Rader and Richardson (1992), Gunderson and Loftus (1993), and Rader (1999). Rader (1999) reported that only seven studies were available that described invertebrate communities, and few of those were in the peer-reviewed literature. In a spring 2015 literature search, we found only 20 papers focusing on the ecology of invertebrates in freshwater habitats of the Everglades. Additional papers tangentially provided information on invertebrates as prey of wading birds and snail kites and fish, or as contributing to biogeochemical cycles, particularly of mercury. A small number of book chapters, unpublished theses and dissertations, and technical reports provide yet more information. Little work has focused explicitly on diversity or natural history of aquatic invertebrates living in the Everglades, particularly the diverse aquatic insects. The exception is exemplary work on midge larvae (family Chironomidae) for use as bioindicators (King and Richardson 2002, 2003). The diversity of copepods has also been given careful treatment, described below. Crayfishes and apple snails have received special attention by one or more researchers because of their importance as prey of apex predators (both) and because of the addition of potentially invasive species (snails).

Surveys of Everglades macroinvertebrate biodiversity are limited, but King and Richardson (2002) reported a total of 93 families, 181 genera, and 252 spe-

cies from their work along a marked gradient of nutrient enrichment in the northern Everglades (WCA 2A). Coleopterans, dipterans, gastropods, odonates, and oligochaetes were the most diverse of the major taxonomic groups. Chironomidae was the most diverse family, represented by 30 and 51 genera and species, respectively. Jacobsen (unpublished technical report) collected approximately 160 species of midges (families Chironomidae and Ceratopogonidae) and 25 species in other dipteran families from ENP. He concluded that his work raised the estimated species richness of the Everglades macroinvertebrate community from 200–250 (Rader 1994, 1999) to over 400 species (summarized in Appendix). Certain groups, particularly the turbellarians and oligochaetes, have been undersampled and understudied and will require a great deal of systematic and ecological work in the future.

Since Rader's (1999) review, Hendrix and Loftus (2000) documented the presence of two species of epigeal crayfish in the Everglades and Big Cypress, rather than the one reported in all prior work: Everglades crayfish *P. alleni* (reported by Rader) and slough crayfish *P. fallax*. Hendrix (2003) noted that *P. fallax* ranges throughout Florida, motivating him to reanalyze historical samples from the Shark River Slough. The ecology of these two species is complementary, with *P. fallax* dominating sites that dry infrequently (at least two consecutive years without drying), while *P. alleni* dominate habitats that dry more frequently (Hendrix and Loftus 2000; Dorn and Trexler 2007). Ecological studies carried out without separating the two species tend to find small effects of changing hydrology on crayfish biomass, which overlooks marked species turnover dynamics with possible management implications (Fig. 10.4). VanArman (2011) reviewed the prey and predators of the Everglades crayfishes in the food web.

Bruno and Perry (2004) and Bruno et al. (2001, 2005) surveyed zooplankton, particularly copepods, inhabiting surface and groundwaters of Everglades National Park. From surface waters they recorded a total of 65 taxa of free-living copepods: 9 calanoids, 41 cyclopoids, and 15 harpacticoids (Appendix). Of these, four were newly recorded to the area. They also found 22 species of copepods pumped from groundwater wells, mainly surface-water species.

Cladoceran collections from Everglades National Park were made by Conrow and Loftus during a study described in Loftus et al. (1990), but the data were never published. Identification of specimens was confirmed by David Frey of Indiana University. The samples revealed a diverse fauna of lentic-water Cladocera. A total of 24 genera and at least 42 species were identified in the collections, and chydorids were the most diverse family with 11 genera and 24 species.

The Everglades is home to a diverse anisopteran fauna (Appendix). Urgelles (2010) identified 16 species of dragonfly naiads from Everglades wetlands with hydroperiods of at least 225 days.

In summary, macroinvertebrate biodiversity is not well characterized from the Everglades, particularly in highly diverse groups like the midges, but knowledge has been increasing since the mid-1990s. There is little comparative analy-

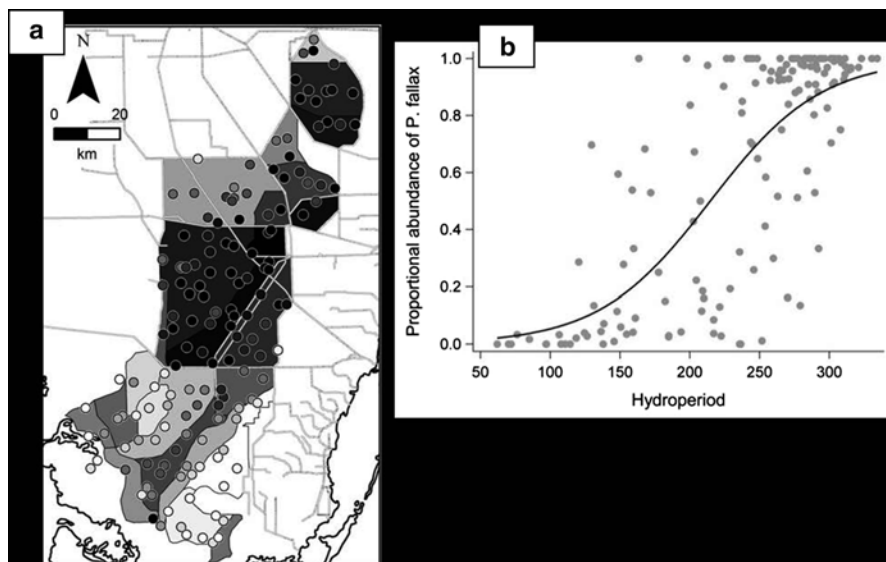


Fig. 10.4 (a) Spatial distribution of *Procamburus alleni* and *P. fallax* across the Greater Everglades ecosystem. Circles are shaded by the mean proportion of *P. fallax* at a site (i.e., black = 100 % *P. fallax* and 0 % *P. alleni*; white = 0 % *P. fallax* and 100 % *P. alleni*). Landscape sampling units are shaded according to hydroperiod, with longer-hydroperiod sites being darker and short-hydroperiod sites being lighter. Data collected annually in October through December, 2005–2012 by throw trap with three samples from each of 145 sampling locations. (b) Average proportional abundance of *P. fallax* by hydroperiod of sites plotted in (a). Response curve was estimated by logistic regression

sis on invertebrate species richness in the Everglades, undoubtedly because identification of specimens in many groups of aquatic invertebrates requires specialized skills that are not widely supported by academic or management organizations. If amphibians and freshwater fish, aquatic taxa better known than invertebrates, are considered, south Florida is species poor (Loftus and Kushlan 1987; Means and Simberloff 1987; Trexler 1995). This has been attributed to a peninsula effect resulting from limited dispersal for obligate freshwater species, the zoogeographical derivation of the aquatic fauna, and the relative youth and lack of diversity of southern Florida aquatic habitats. The karstic wetland yields water chemistry that is hard and alkaline (e.g., the region lacks softwater/blackwater habitats); taxa that require acidic and/or lotic waters may be excluded. Unlike native fishes and amphibians, almost entirely derived from temperate North America, Everglades copepods, cladocerans, and midges have both temperate and tropical affinities. For most invertebrate groups, there has not been a similar state-wide systematic survey of biodiversity to permit a biogeographic analysis. More work is needed!

Periphyton Infauna: Mats, Epiphyton, and Benthos

Floating and epiphytic periphyton mats, and benthic floc, are home to the bulk of small macroinvertebrates, midge larvae, amphipods, and similar-sized taxa that make up a major part of the diets of secondary consumers of the Everglades (Fig. 10.3). Crowding of the most common taxa increased 33–153 % from early to late wet season, and community differences between the two habitat types became more pronounced (Liston and Trexler 2005). Liston (2006) observed that differences in community structure between floating-mat periphyton and epipelon (benthic-floc) microhabitats were greater than any variation attributable to gradients of hydroperiod, P availability, or other spatial factors at the ten sites she sampled from SRS and WCA3A. These studies revealed that floating mats held the highest crowding and density of infauna, followed by epiphyton, with substantially less in epipelon (mat held 6.7 times higher crowding than floc). There were also 1.6 times more taxa per sample in floating-mat samples than in floc, though when the cumulative number of specimens examined was accounted for, the asymptotic species richness was only 17 % higher in mat than floc (35 versus 30).

The drivers of infaunal dynamics appear to differ between floating-mat and epipelon habitats at the same site. Multivariate analyses indicated community structure of epipelon infauna was driven by hydroperiod, although crowding of individual taxa showed no consistent responses to hydroperiod or TP availability (Liston 2006). In contrast, community structure of periphyton mat infauna was driven by the interaction of TP availability and hydroperiod, while densities of mat infauna (no. m⁻²) were most influenced by hydroperiod (positive correlations). Liston (2006) noted that crowding of mat infauna doubled with P availability in short-hydroperiod marshes, but was constant across the TP gradient in long-hydroperiod marshes. She hypothesized that community structure and density were not different among long-hydroperiod, constantly inundated sites because of the high density of small fish found at these sites. She hypothesized that increased abundance of floating-periphyton mat infauna with P availability at short-hydroperiod sites may result from a release from predation by small fish (Fig. 10.5).

Several studies support the hypothesis that the dynamics of periphyton infauna are closely tied to the fate of the periphyton mat they inhabit. A meta-community analysis demonstrated that crowding and composition of periphyton infauna are better described as being controlled by “species sorting” than “mass effects,” compared to larger invertebrates like crayfish, grass shrimp, dragonfly naiads and creeping water bugs (Naucoridae, *Pelocoris femoratus*), and small fishes (Sokol et al. 2014). The “species sorting” model suggests that dispersal limits local species composition and community-level responses to local environmental conditions, compared to the “mass effects” model that posits species are so mobile that those best matched to the local environment colonize rapidly and saturate the local community (similar to the Baas-Becking hypothesis that

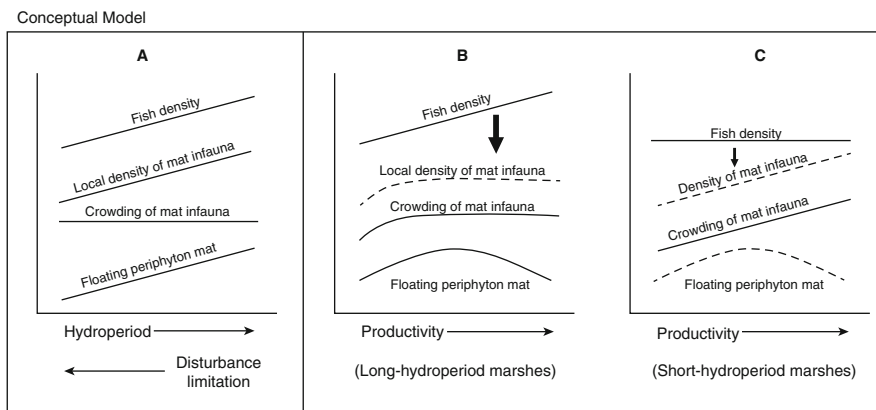


Fig. 10.5 Conceptual model of hypothesized interactive effect of hydroperiod and nutrient addition on the density of periphyton infauna. (a) Fish density, periphyton map cover, and infauna density increase with increasing hydroperiod, but infauna crowding is constant because of density-dependent feedback within the mat. (b) Fish density increases with increasing primary productivity (TP) at long-hydroperiod sites, but periphyton cover peaks at an intermediate level. Infauna density is flat with decreasing productivity because of the loss of mat cover but stimulation from better quality of food, though at lower abundance; crowding is unaffected because increased food quality is compensated by increased predation. (c) Fish density is limited by drying disturbance and does not increase with increasing TP at short-hydroperiod sites. This frees infauna from top-down control to increase crowding in the presence of better quality food, which increases their density in spite of loss of periphyton mat coverage (Redrawn from Liston (2006))

“everything is everywhere, but the environment selects”). Periphyton infaunal communities were modeled best by inclusion of both spatial proximity and local environmental measures, while larger mobile invertebrates were best modeled using just local environmental measures; spatial proximity had the least contribution to explaining landscape patterns of fish community metrics. This result suggests that large invertebrates and fishes are better able to sort themselves in the environment in response to their food availability, physical factors, and predators than are periphyton infauna. Because these large invertebrates and fishes are predators of infaunal invertebrates, the hypothesis of top-down, density-dependent regulation of infaunal invertebrates (Fig. 10.5; Liston 2006) seems reasonable.

Sargeant et al. (2011) used a structural equation modeling (SEM) approach to evaluate competing hypotheses of all bottom-up and mixed bottom-up and top-down control of periphyton mat infauna at 28 sites from Shark River Slough, WCA 3A, WCA 2A, and WCA 1 (LNWR). The best model included both bottom-up and top-down effects among trophic groups and supported top-down control of infauna by omnivores and predators that cascaded to periphyton biomass. The second-best model included bottom-up paths only. Total effects (estimated as the product of all direct and indirect effects) of days-since-dry were negative for all

three consumer groups in the study, even when both preferred models suggested positive direct effects for some groups. Total effects of periphyton TP were positive for consumers and generally larger than those of hydrological disturbance and were mediated by paths indicating changes in periphyton community composition and edibility. Finally, Abbey-Lee et al. (2013) used SEM to evaluate models explaining the isotopic niche of Eastern Mosquitofish (*Gambusia holbrooki*), the most abundant intermediate consumer of the Everglades, that has been demonstrated to consume midge larvae, amphipods, cladocerans, and other small macro-invertebrates (Loftus 2000; Taylor et al. 2001; Chick et al. 2008). They reported stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) from samples of at least 17 individual Eastern Mosquitofish collected in the wet season of 2005 from each of the 21 sites located in the Shark River Slough, WCA 3A, WCA 3B, WCA 2A, and WCA 1 (Loxahatchee National Wildlife Refuge). The data indicated that the mosquitofish isotopic niche decreased with increasing density of most types of periphyton infauna (direct effects) and increased as the density of conspecifics and potential competitors increased (indirect effects through periphyton infauna and periphyton edibility). These diet changes are *consistent* with food limitation of Eastern Mosquitofish (the local population became more specialized as food became more available and less specialized as intra- and interspecific competition increased), which could yield a density-dependent, top-down effect on the infauna they consume.

Experimental studies have also indicated the potential of predators to limit the abundance of periphyton infaunal invertebrates. Working in long-hydroperiod marshes of the Shark River Slough, Dorn et al. (2006) compared periphyton, invertebrates, and fish in 1-m³ cages with 2.54-cm mesh on one side (exclosure cages) to similar cages with a side lacking mesh (control cages) to evaluate the effects of excluding large predators, mostly fishes. After 2 weeks, the exclosure cages held higher densities of intermediate consumers, particularly grass shrimp, than the control cages, suggesting that greater predation risk in the controls caused avoidance. More importantly, small primary consumers (mostly small snails, amphipods, and midges) living in floating periphyton and the flocculent benthos were less abundant in the exclosures, indicative of a trophic cascade. In a similar experiment also conducted in the Shark River Slough, Chick et al. (2008) noted a similar effect of exclosure cages on intermediate consumers, with increased density of dragonflies, crayfish, and grass shrimp inside. Periphyton infauna were not sampled, but inverted-funnel traps were placed in each cage on the last day of the experiment to document zooplankton emergence. Also, similar to the Dorn et al. (2006) study, the treatments had no effect on algal composition or biomass of native periphyton mats placed in the cages, but exclosure cages had less epiphytic algae growing on plastic strips placed in the cages at the start of the study. There were minimal treatment effects on the zooplankton in the presence of elevated density of intermediate consumers, however. Thus, cascading effects on zooplankton and floating-periphyton mats (algal composition and biomass) were small, which Chick et al. (2008) interpreted as support for the hypothesis that periphyton serves as a refuge for infauna. Finally, Liston et al. (2008) observed a

dose-dependent increase in periphyton and benthic infauna at low and intermediate TP addition to field mesocosms. Total macroinvertebrate density in periphyton mats increased with intermediate P loads, driven primarily by chironomids and nematodes. However, infaunal crowding in benthic floc decreased with enrichment, driven primarily by loss of chironomids and ceratopogonids (*Dasyhelea*). Thus, macroinvertebrate density increased with TP enrichment until the periphyton mats were lost, after which density decreased markedly. Apparently, mat infauna failed to move into benthic substrates in response to mat loss. These results were noted at nutrient levels too low to yield anoxia and appeared to be linked to the loss of habitat and predation by intermediate consumers present in the mesocosms when the mat-refuge effect was lost.

The recent colonization of the Everglades by a variety of nonnative fishes has been well documented, and their effects have begun to be studied (Kline et al. 2014). Several studies conducted in Everglades field cages and in mesocosms have shown that introduced predatory fishes, particularly the cichlids African Jewelfish (*Hemichromis letourneuxi*) and Mayan Cichlid (*Cichlasoma urophthalmus*), have the potential to affect densities and biomass of aquatic snails and riverine grass shrimp (Porter-Whitaker et al. 2012; Schofield et al. 2013).

Habitat and Size-Structured Predation

Invertebrates in the Everglades live within a dynamic food web affected by the mortality and stress associated with periodic drought. Invertebrates are critical links between primary producers and those apex predators of great ecological, conservation, and economic importance. Furthermore, invertebrates are a key link between the effects of anthropogenic nutrient enrichment and vertebrate species because there are few strictly herbivorous aquatic vertebrates in the Everglades. For example, only two species of the 33 common fish species are primarily herbivorous (Loftus and Kushlan 1987; Loftus 2000), while the vast majority of fishes include invertebrates in their diet. Microbial metabolism of periphyton detritus is an important route for energy flow in this ecosystem (Williams and Trexler 2006; Belicka et al. 2012); mat infaunal consumption of edible algae taxa, extracellular polymeric substances, and heterotrophic bacteria is likely to be a critical link to higher consumers. Many Everglades aquatic invertebrates are predators of other invertebrates (Loftus 2000). Thus, all past reviews of the ecology of invertebrates in the Everglades have speculated about the importance of predation in controlling their dynamics (Rader 1999; King and Richardson 2008b; Trexler et al. 2015). Liston (2006), Sokol et al. (2014), and Trexler et al. (2015) have separated discussion of the controls of invertebrate communities by habitats and size, between (1) taxa that live as periphyton infauna (midge larvae, amphipods, etc.) and may experience a refuge from larger predators and (2) mostly larger invertebrate taxa that cling to the outside of the mats or inhabit the benthos, scavenging for small vulnerable vertebrates and unfortunate infaunal taxa exposed from their refuges.

Dorn and Trexler (2007), Dorn (2008), and Gaiser et al. (2012) pointed out that abundance patterns of some Everglades invertebrates, notably apple snails (Darby et al. 2008), ramshorn snails (Ruehl 2010), and crayfish (Acosta and Perry 2002; Dorn and Trexler 2007), cannot be predicted solely by the time passed since a local site has dried, probably because of their ability to survive mild drying events by burrowing into the sediments and/or rapidly recolonize after droughts. In contrast, riverine grass shrimp, dragonfly naiads, and creeping water bugs are abundant throughout the Everglades, but appear to suffer high mortality during drought events. Using observational data from high-nutrient wetlands, Dorn (2008) suggested that the biomass of crayfish and large predaceous insects could be enhanced indirectly by drying that temporarily eliminated their fish predators (see also Kushlan 1976). Experimental work in low-nutrient constructed wetlands (similar to the Florida Everglades) supported the prediction that crayfish are sensitive to predatory fish (Kellogg and Dorn 2012), but experiments investigating the interactive effects of predators along with other changes associated with drying are lacking. Knorp and Dorn (2014) found that predatory sunfish (Warmouth, *Lepomis gulosus*; Bluespotted Sunfish, *Enneacanthus gloriosus*; and Dollar Sunfish, *Lepomis marginatus*) decreased the density of *P. fallax* but not dragonfly naiads in experimental wetlands. *Procambarus fallax* benefited by simulated marsh drying because it eliminated sunfishes; dragonfly naiad density also decreased. Juveniles of these sunfishes consume macroinvertebrates, particularly odonates, midge larvae, and amphipods. Depending on the season, warmouths display some separation of diet from the other two species, consuming more crayfish and fish as they grow (Loftus 2000; Bransky and Dorn 2013). Gape-size-matched diet overlap of Warmouth with the other two sunfishes was greatest during the wet season, when prey abundance was the greatest. In an 8-year experimental study at the landscape scale (500 km² of the Everglades), crayfish densities were positively correlated with the severity of drying (up to 99 days dry) during the preceding dry season (Dorn and Cook 2015). This contrasts with drying effects on small-bodied fishes in the same wetlands, whose densities were seasonally depressed by drying disturbance.

Fire

Fire is an important component of the ecology of the Everglades, both historically and in the present (Ogden et al. 2005). Lightning is responsible for starting fires, primarily in the spring and summer months when water depths may be low or even below ground surface. Many Everglades fires spread in emergent plant stems over shallow standing water, but severe fires on desiccated marshes that consume the peat substrate also occur. Drainage of the Everglades increased the frequency of these peat-consuming fires during the twentieth century, with important effects on the topography, hydro patterns, and biogeochemistry in the aftermath (Gunderson and Snyder 1994; Lockwood et al. 2003; McVoy et al. 2011). There have been few studies of the effects of fire on aquatic invertebrates (or aquatic animals in general)

in the Everglades, though relevant impacts have been documented in other ecosystems (e.g., Gresswell 1999; Beganyi and Batzer 2011). A 2015 literature search with key words “Everglades” and “fire” returned 128 papers, but only one of those papers reports studies of the effects of fire on aquatic macroinvertebrates (Venne and Frederick 2013).

The most immediate impacts of fire on aquatic invertebrates are to remove plant cover, increase light penetration into the water column, decrease stem density and habitat structure in the water column, and release nutrients to stimulate primary production (Venne 2012; Venne and Frederick 2013). Some wading birds, notably white ibis (*Eudocimus albus*), are known to include a high frequency of crayfish in their diets and have been observed to forage in and adjacent to wetland areas burning or recently burned (Epanchin et al. 2002). Focusing on wading bird prey, Venne and Frederick (2013) sampled in burned and unburned Everglades sites after controlled burns, but noted few fire-killed prey (minimum water depth in the burned areas was 10 cm). They also found no difference in the density of fishes or macroinvertebrates (grass shrimp, crayfish, belostomatids, dysticids, leeches, odonates, oligochaetes, and creeping water bugs) between burned and adjacent unburned habitats. When they manipulated fire experimentally in plots with shading and vegetation-removal treatments, they also found no treatment effects on macroinvertebrates (Venne 2012). The fire caused a short-lived pulse in nutrients (P) in the water column that was rapidly taken up by bacteria and periphyton in the area, such that it could not be distinguished from unburned control areas within a matter of days.

Conservation and Management Issues for Everglades Invertebrates

Beginning with efforts to regulate hydrology in the Everglades in the twentieth century, phosphorus-laden runoff from agricultural areas has been added to the ecosystem through a network of canals carrying water from Lake Okeechobee and the EAA (Davis 1994; Noe et al. 2001). This has led to eutrophication in several areas (notably northern WCA 2A, southern WCA 1 (LNWR), northern WCA 3A), accompanied by loss of native flora and expansion of cattail (*Typha domingensis*) monocultures (Davis 1994). Cattail invasion is facilitated by drought and fire, which occur more commonly in the modern Everglades that has been reduced in size and suffers from a lowered water table (Newman et al. 1998). Addition of phosphorus leads to the loss of periphyton cover and increase in abundance of nutrient-tolerant macroinvertebrates (Rader and Richardson 1992; King and Richardson 2003, 2008a), changing the ecological character of the ecosystem from one typical of oligotrophic wetlands in the Caribbean basin (Turner et al. 1999). The dense cattails hamper foraging by wading birds (Crozier and Gawlik 2002) and generally diminish the ecological integrity of the affected areas (Sklar et al. 2005). Ecological

damage resulting from nutrient enrichment has led to lawsuits and massive investments in public works to remove phosphorus from waters destined for the Everglades. Solving environmental problems resulting from water extraction and nutrient enrichment is the primary goal of a major US Federal and State of Florida partnership to restore the Everglades initiated in 2000 and called the Comprehensive Everglades Restoration Plan (CERP; Sklar et al. 2005; NRC 2006).

In this section, we will focus on four areas of environmental challenges for Everglades restoration and management that are relevant to aquatic invertebrates: phosphorus enrichment, nonnative species invasions, xenobiotics, and trophic dynamics.

Phosphorous Enrichment: The Subsidy-Stress Hypothesis

Anthropogenic nutrient runoff pushes Everglades aquatic communities into a resource state that is enriched beyond what is believed to have been historically present and is absent from areas not receiving enrichment today (Turner et al. 1999). King and Richardson (2007, 2008a) used sweep-net sampling to document a unimodal pattern of invertebrate biomass along a spatial (distance from a canal) and phosphorus (TP in sediment) gradient in an area of the Everglades experiencing extreme P enrichment over a multi-decadal timescale (Fig. 10.1, northern WCA 2A). They interpreted these results in light of the subsidy-stress model first proposed by Odum et al. (1979; Fig. 10.6). In this study, 8 of 12 major taxonomic groups (Amphipoda, Decapoda, Diptera, Ephemeroptera, Gastropoda, Hirudinea, Odonata, Oligochaeta) displayed a unimodal response, three (Coleoptera, Hemiptera, Isopoda) increased monotonically, and one (Trichoptera) decreased monotonically in response to TP. As is typical in the Everglades, periphyton cover was absent at high levels of TP enrichment, and the loss of periphyton is correlated with low invertebrate biomass. The unimodal pattern changed seasonally, however, and was absent early in the wet season following marsh flooding when periphyton is infrequent in all marshes (TP enriched and oligotrophic) because of winter senescence. The authors suggested that nutrient enrichment created an interaction between increased quality and decreased quantity of periphyton, leading to the subsidy-stress patterns observed. An experimental TP-addition study conducted in WCA 2A supported the hypothesis that macroinvertebrates in the Everglades are resource limited (King and Richardson 2008b), supporting the subsidy part of the subsidy-stress hypothesis. McCormick et al. (2004) also observed a decline in abundance and change in species richness to favor nutrient-tolerant taxa at nutrient-enriched sites in WCA 2A. Liston et al. (2008) reported complementary observations in a mesocosm study from the southern Everglades (Taylor Slough); invertebrate density increased with low and intermediate addition of TP, but dropped markedly when experimental nutrient enrichment led to loss of the periphyton mat. It appeared that the loss of periphyton habitat caused the infauna to be vulnerable to predators, leading to their consumption or emigration.

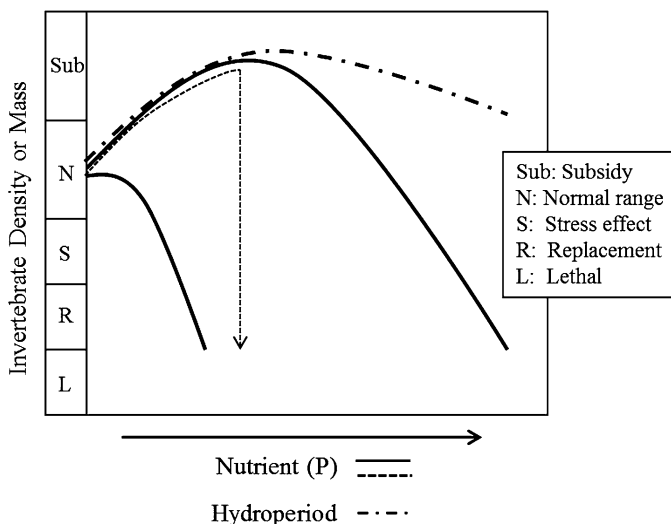


Fig. 10.6 Conceptual diagram of subsidy-stress model redrawn and expanded from King and Richardson (2008a). Two possible patterns are illustrated for TP enrichment, a unimodal subsidy-stress pattern as drawn in King and Richardson (2008a, *solid line*) and an alternative suggested by Liston et al. (2008, *dashed line*). The Liston et al. (2008) relationship illustrates loss of the periphyton mat at a threshold TP concentration with consumption or emigration of all mat inhabitants. A second relationship is illustrated for hydroperiod effects on macroinvertebrates. In this case a subsidy is produced by lengthening hydroperiod until it becomes long enough to permit invasion by carnivorous fishes that crop invertebrate production outside of refuge habitats such as periphyton mats. Note that Everglades marshes not receiving anthropogenic nutrient enrichment seldom pass the inflection point of maximum subsidy because natural processes do not lead to marked elevation in cycling P. Exceptions exist in dry-season alligator ponds and under bird rookeries

Hagerthey et al. (2014) experimentally removed dense cattail and sawgrass from areas experiencing nutrient enrichment to evaluate methods for managing these habitats to regain wading-bird foraging opportunities lost because of the dense habitat cover (Crozier and Gawlik 2002). They found similar species composition in cleared areas and background unenriched sites, but higher density and biomass of macroinvertebrates in the enriched sites, notably crayfish and grass shrimp. Enriched sites with intact vegetation had fewer fishes but more crayfish than cleared areas. Vegetation was so dense in the enriched area that fishes were excluded for lack of space.

The King and Richardson (2007, 2008a) subsidy-stress model for macroinvertebrates is supported for nutrient enrichment as a stressor in the Everglades. The effect of TP enrichment initially subsidizes algal production and changes periphyton species composition to include a higher frequency of edible taxa (green algae and diatoms). This increase in edibility stimulates invertebrate productivity (Sargeant et al. 2011; Trexler et al. 2015). Several studies suggest that this increased productivity is in excess of consumption, and algal mass and macroinvertebrate mass/density all increase with low to intermediate enrichment (King and Richardson 2008b; Liston

et al. 2008; Trexler et al. 2015). A few studies provided contrary results, suggesting no response by macroinvertebrates depending on the substrate sampled (Turner et al. 1999; Liston 2006; Liston et al. 2008). Ruehl and Trexler (2015) used a reciprocal transplant of periphyton from enriched and unenriched sites to demonstrate that ramshorn snails (*Planorbella duryi*) do not increase growth rate in areas with high predator density near a canal even when fed nutrient-enriched periphyton. The snails also laid fewer eggs when held in the high-predator area, regardless of the periphyton type provided. In mesocosm experiments, the same snail species increased shell thickness, a predator defense, and decreased growth rate in the presence of crayfish predators feeding on conspecifics (Ruehl and Trexler 2013). Thus, life history trade-offs may slow invertebrate-production responses to nutrient enrichment if predators are also benefited.

We may expect alternative shapes to the subsidy-stress pattern than proposed by King and Richardson (2007, 2008a) depending on the organisms analyzed. Once TP loads became high, periphyton structural coherence was lost and the mats dissociated, exposing the infauna to consumption (Fig. 10.6). This could lead to a shift in production from infaunal taxa to consumers with other predator defenses. Thus, community-wide biomass may not display the threshold decline predicted for mat infauna when the mat disassociates. Hydroperiod and marsh drying is a second important driver in the Everglades. Drying events may lead to high mortality for species lacking adaptations to survive (Gaiser et al. 2012). However, the Everglades is home to several species that can survive moderate-length droughts and may be as abundant or even more abundant following droughts. Dorn and Cook (2015) illustrate that *P. fallax* benefits from drought because of predation release. This suggests a more shallow response to subsidy stress (Fig. 10.6) or a redefinition of stress. However, because drought is very stressful for many taxa, it would be appropriate to be plotted on the *x*-axis of Fig. 10.6 for a community-wide analysis (see Trexler et al. 2005, Fig. 10.6, for an example with fishes). In this case, species turnover and replacement may buffer the community-wide response to the stressor.

Nonnative Species

The Everglades has been invaded by many plant and vertebrate animal species but few aquatic invertebrates. Several nonnative species of mollusks occur in the ecosystem, though only nonnative apple snails have raised conservation concerns. Canals are implicated in playing a role in the survival and dispersal of nonnative invertebrates in the Everglades system (Harvey et al. 2010). Two species of apple snails (Ampullariidae, *Pomacea* spp.) have been introduced to south Florida and now are found in the Everglades or nearby waters. Rawlings et al. (2007) determined that *Pomacea haustrum* were observed in the 1970s in Palm Beach County, Florida but have not spread appreciably in 30 years; however, a disjunct population was identified from the Big Cypress Swamp in the 1990s (Loftus, unpublished data *vide* T. Collins). In contrast, *P. insularum/maculata* was established in

Texas in the late 1980s and spread to Florida by the mid- to late 1990s, where it has continued to expand its range (note that Hayes et al. (2012) recently proposed to group several species of *Pomacea*, including *P. insularum*, under the name *P. maculata*, currently the name that should be used for that introduced species). There is concern about the spread of *P. maculata* into the Everglades and its potential to affect adversely native *P. paludosa* or affect vascular plant density, benthic habitat structure, or water clarity as documented in other systems (Horgan et al. 2014). However, in at least one Florida lake, the highly productive *P. maculata* may provide a valuable food source for the endangered Snail Kite (*Rostrhamus sociabilis*; Cattau et al. 2010). Other nonnative gastropods commonly collected are *Marisa cornuarietis* and *Melanoides tuberculata* (described in Thompson 2004). The bivalve *Corbicula fluminea* is found in canals of south Florida, but not in interior Everglades wetlands.

Mercury, Copper, and Zinc Contamination

There are several xenobiotics that show elevated levels in parts of the Everglades with potential impacts on aquatic invertebrates or on predators that consume them. Copper, in particular, is known to be elevated in three areas that receive runoff from agricultural lands, and herbicide used on those lands is the likely source (Rand and Schuler 2009). Apple snails are sensitive to heavy metals, particularly copper and zinc (Hoang et al. 2009; Hoang and Tong 2015). Though it appears that *P. paludosa* can detoxify stored copper to some extent, it is also clear that exposure increases their mortality rates in experimental settings (Hoang and Rand 2009).

Mercury has been studied extensively in Everglades fishes (Stober et al. 2001), and some data have been gathered for aquatic invertebrates (Cleckner et al. 1998; Loftus 2000). Tissue mercury concentrations in the animals surveyed were well predicted by trophic position estimated by analysis of stable isotopes (Loftus 2000). Thus, all snails tested yielded relatively low tissue concentrations, while fishing spiders, riverine grass shrimp, and some dragonfly naiads had relatively high levels similar to some carnivorous fishes such as *Gambusia holbrooki*.

Trophic Dynamics and Species of Special Concern

The Everglades is home to a number of bird species with protected status that consume macroinvertebrates as their prey. Food limitation appears to be a major driver for the decline of these birds from historical levels; therefore, production of their invertebrate prey is of concern for their management, conservation, and restoration. Snail Kites are specialists on apple snails, and their nest initiation rate is correlated with the availability of these snails as prey (Cattau et al. 2014). Monitoring of Snail

Kite prey and analysis of their habitat requirements are important facets of managing this federally endangered species (Martin et al. 2007). Crayfishes are important diet items of White Ibis and possibly Wood Storks (*Mycteria americana*) (Frederick et al. 2009). Monitoring programs to measure the success of Everglades management and restoration incorporate assessments of crayfish as prey for wading birds (Frederick et al. 2009; Trexler and Goss 2009). Alligators (*Alligator mississippiensis*) are another hallmark charismatic species monitored as an indicator for restoration (Mazzotti et al. 2009). Crayfish, apple snails, and grass shrimp are probably minor components in their diet, but are taken at times. However, aquatic invertebrates sustain the vertebrate prey of alligators and so are also an important part of the food web that supports their health in the environment.

In Everglades management, invertebrates are rarely used as an indicator of general ecosystem health. King and Richardson (2002) discussed the issues required for an invertebrate monitoring program and suggested using midges and other small macroinvertebrates as indicators of nutrient enrichment. However, periphyton was developed to fill this role early in the restoration process, and there has been little interest in funding a second system based on macroinvertebrates.

Conclusions

Aquatic invertebrates are essential elements of the Everglades ecosystem, providing critical links in the food web that sustain animals of great interest to the public. They also contribute to ecosystem function through detrital processing and energy flow. Despite these fundamental roles, their systematics, distribution, and ecology remain poorly understood and documented. More work on biodiversity and ecological processes is needed to understand their roles in the Everglades. Several key taxa are already identified as important contributors to the successful restoration of the Everglades, defined in part as recovering the historical abundance of wading birds and herpetofauna. The glass is certainly half full for aquatic ecology of invertebrates in this internationally important ecosystem. With continued investment in restoration of the Everglades, however, the future for the study of invertebrates there is bright and certain to be rewarding.

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Appendix

Aquatic invertebrate taxa recorded from across the Everglades. Data from Conrow and Loftus (unpublished), Rader (1994), Jacobsen (2008), Jacobsen and Perry (2000), Urgelles (2010), Trexler (unpublished), Bruno (unpublished), and Turner and Taylor (1998)

Higher taxa	Family	Genus
Porifera	Spongillidae	<i>Spongilla</i>
Cnidaria		
Trachylina	Hydridae	<i>Hydra</i>
Rotifera		>50 spp.
Platyhelminthes		<i>Planaria</i>
Nemertea		<i>Prostoma</i>
Gastrotricha		
Nematoda		
Mollusca		
Gastropoda	Ampullariidae	<i>Marisa</i>
		<i>Pomacea</i>
	Hydrobiidae	<i>Aphaostracon</i>
		<i>Littoridinops</i>
		<i>Lyogyrus</i>
	Lymnaeidae	<i>Fossaria</i>
		<i>Lymnaea</i>
		<i>Pseudosuccinea</i>
	Physidae	<i>Haitia</i>
		<i>Physella</i>
	Planorbidae/Ancylidae	<i>Biomphalaria</i>
		<i>Drepanotrema</i>
		<i>Ferrissia</i>
		<i>Gyraulus</i>
<i>Laevapex</i>		
<i>Helisoma</i>		
<i>Micromenetus</i>		
<i>Planorbella</i>		
<i>Planorbula</i>		
Thiaridae	<i>Melanoides</i>	
Bivalvia	Sphaeriidae	
	Unionidae	<i>Elliptio</i>
		<i>Uniomereus</i>
		<i>Villosa</i>
Annelida		
Polychaeta	Nereidae	<i>Namanereis</i>

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Higher taxa	Family	Genus
Oligochaeta	Lumbriculidae	<i>Eclipidrilus</i>
	Tubificidae	<i>Allonais</i>
		<i>Bratislavia</i>
		<i>Dero</i>
		<i>Pristina</i>
<i>Stylaria</i>		
Hirudinea	Erpobdellidae	<i>Mooreobdella</i>
	Glossiphoniidae	<i>Helobdella</i>
Bryozoa	Plumatellidae	<i>Pumatella</i>
Acarina		
Crustacea		
Branchiopoda	Bosminidae	<i>Bosmina</i>
		<i>Streblocerus</i>
	Chydoridae	<i>Alona</i>
		<i>Alonella</i>
		<i>Camptocercus</i>
		<i>Chydorus</i>
		<i>Dunhevedia</i>
		<i>Ephemeroporus</i>
		<i>Kurzia</i>
		<i>Leydigia</i>
		<i>Pleuroxus</i>
		<i>Pseudochydorus</i>
		<i>Euryalona</i>
	Daphnidae	<i>Ceriodaphnia</i>
	Macrothricidae	<i>Scapholeberis</i>
		<i>Simocephalus</i>
		<i>Guernella</i>
		<i>Grimaldina</i>
		<i>Ilyocryptus</i>
		<i>Macrothrix</i>
	Moinidae	<i>Moinodaphnia</i>
	Sididae	<i>Diaphanosoma</i>
		<i>Latanopsis</i>
<i>Pseudosida</i>		
Ostracoda	Cypridae	<i>Physocypria</i>
		<i>Scottia</i>

Higher taxa	Family	Genus
Copepoda	Argulidae	<i>Argulus</i>
	Centropagidae	<i>Osphranticum</i>
	Cletodidae	<i>Cletocamptus</i>
	Cyclopidae	<i>Acanthocyclops</i>
		<i>Diacyclops</i>
		<i>Ectocyclops</i>
		<i>Eucyclops</i>
		<i>Homocyclops</i>
		<i>Macrocyclops</i>
		<i>Mesocyclops</i>
		<i>Microcyclops</i>
		<i>Paracyclops</i>
		<i>Thermocyclops</i>
<i>Tropocyclops</i>		
Cletodidae	<i>Cletocamptus</i>	
Lernaeidae	<i>Lernaea</i>	
Canthocamptidae	<i>Canthocamptus</i>	
Laophontidae	<i>Onychocamptus</i>	
Phyllognathopodidae	<i>Phyllognathopus</i>	
Amphipoda	Crangonyctidae	<i>Crangonyx</i>
	Dogielinotidae	<i>Hyaella</i>
Decapoda	Cambaridae	<i>Procambarus</i>
	Mysidae	<i>Taphromysis</i>
	Palaemonidae	<i>Palaemonetes</i>
Isopoda	Asellidae	<i>Caecidotea</i>
Insecta	Sphaeromatidae	<i>Sphaeroma</i>
Collembola	Entomobryidae	<i>Entomobrya</i>
	Isotomidae	<i>Isotomurus</i>
	Poduridae	
	Sminthuridae	
Ephemeroptera	Baetidae	<i>Callibaetis</i>
	Caenidae	<i>Caenis</i>
Odonata	Aeshnidae	<i>Anax</i>
		<i>Coryphaeschna</i>
		<i>Nasiaeschna</i>
	Coenagrionidae	<i>Enallagma</i>
		<i>Ischnura</i>
		<i>Telebasis</i>
	Gomphidae	<i>Aphylla</i>
		<i>Arigomphus</i>
	Corduliidae	<i>Epithea</i>
<i>Epicordulia</i>		

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Higher taxa	Family	Genus
	Libellulidae	<i>Brachymesia</i>
		<i>Celithemis</i>
		<i>Erythemis</i>
		<i>Erythrodiplax</i>
		<i>Idiataphe</i>
		<i>Libellula</i>
		<i>Macrodiplax</i>
		<i>Pachydiplax</i>
		<i>Pantala</i>
		<i>Perithemis</i>
		<i>Tramea</i>
Hemiptera	Belostomatidae	<i>Belostoma</i>
		<i>Lethocerus</i>
	Corixidae	<i>Palmacorixa</i>
		<i>Trichocorixa</i>
	Gerridae	<i>Gerris</i>
	Hebridae	<i>Neogerris</i>
	Hydrometridae	<i>Merragata</i>
		<i>Hydrometra</i>
	Macroveliidae	<i>Oravelia</i>
	Mesoveliidae	<i>Mesovelia</i>
	Naucoridae	<i>Pelocoris</i>
	Nepidae	<i>Ranatra</i>
	Notonectidae	<i>Buenoa</i>
Veliidae		
Coleoptera	Chrysomelidae	<i>Donacia</i>
	Dryopidae	<i>Pelonomus</i>
	Dytiscidae	<i>Agabetus</i>
		<i>Bidessonotus</i>
		<i>Celina</i>
		<i>Cybister</i>
		<i>Desmopachria</i>
		<i>Hydroporus/</i>
		<i>Neoporus</i>
		<i>Hydrovatus</i>
		<i>Ilybius</i>
	<i>Laccophilus</i>	
	Gyrinidae	<i>Gyrinus</i>
Haliplidae	<i>Haliplus</i>	
	<i>Peltodytes</i>	

Higher taxa	Family	Genus	
	Hydrophilidae	<i>Berosus</i>	
		<i>Chaetarythria</i>	
		<i>Crenitulus</i>	
		<i>Derallus</i>	
		<i>Enochrus</i>	
		<i>Helobata</i>	
		<i>Hydrobiomorpha</i>	
		<i>Hydrochus</i>	
		<i>Paracymus</i>	
		<i>Tropisternus</i>	
	Helophoridae	<i>Helophorus</i>	
	Noteridae	<i>Hydrocanthus</i>	
		<i>Suphis</i>	
		<i>Suphisellus</i>	
	Psephenidae		
	Scirtidae	<i>Prionocyphon</i>	
Trichoptera	Hydroptilidae	<i>Leucotrichia</i>	
		<i>Oxyethira</i>	
	Leptoceridae	<i>Leptocerus</i>	
	Philopotamidae	<i>Nectopsyche</i>	
<i>Oecitis</i>			
Lepidoptera	Noctuidae	<i>Simyra</i>	
	Crambidae	<i>Acentria</i>	
		<i>Paraponyx</i>	
Diptera	Ceratopogonidae	<i>Bezzia/Palpomya</i>	
		<i>Culicoides</i>	
		<i>Dasyhelea</i>	
			<i>Forcipomyia</i>
	Chironomidae	<i>Ablabesmyia</i>	
		<i>Apedilum</i>	
		<i>Asheum</i>	
		<i>Beardius</i>	
		<i>Cantopelopia</i>	
		<i>Chironomus</i>	
		<i>Cladopelma</i>	
		<i>Cladotanytarsus</i>	
		<i>Clinotanypus</i>	
		<i>Coelotanypus</i>	
		<i>Corynoneura</i>	
<i>Cricotopus</i>			
<i>Cryptochironomus</i>			
<i>Cryptotendipes</i>			

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Higher taxa	Family	Genus
		<i>Denopelopia</i>
		<i>Dicrotendipes</i>
		<i>Djalmabatista</i>
		<i>Einfeldia</i>
		<i>Endochironomus</i>
		<i>Endotribelos</i>
		<i>Fittkauimyia</i>
		<i>Glyptotendipes</i>
		<i>Goeldichironomus</i>
		<i>Guttipelopia</i>
		<i>Kiefferulus</i>
		<i>Labrundinia</i>
		<i>Larsia</i>
		<i>Limnophyes</i>
		<i>Manoa</i>
		<i>Microchironomus</i>
		<i>Monopelopia</i>
		<i>Nanocladius</i>
		<i>Natarsia</i>
		<i>Nilothauma</i>
		<i>Nimbocera</i>
		<i>Parachironomus</i>
		<i>Parakiefferiella</i>
		<i>Paralauterborniella</i>
		<i>Paramerina</i>
		<i>Paratanytarsus</i>
		<i>Paratendipes</i>
		<i>Phytotelmatocladius</i>
		<i>Polypedilum</i>
		<i>Procladius</i>
		<i>Psectrocladius</i>
		<i>Pseudochironomus</i>
		<i>Pseudosmittia</i>
		<i>Stenochironomus</i>
		<i>Tanypus</i>
		<i>Tanytarsus</i>
		<i>Thienemanniella</i>
		<i>Tribelos</i>
		<i>Xenochironomus</i>
		<i>Zavreliella</i>
	Culicidae	<i>Aedes</i>
	Dolichopodidae	
	Ephydriidae	<i>Ephydra</i>
	Psychodidae	<i>Pericoma</i>

Higher taxa	Family	Genus
	Stratiomyidae	<i>Odontomyia</i>
	Tabanidae	<i>Tabanus</i>
	Tipulidae/Limoniidae	<i>Elliptera</i>
		<i>Limonia</i>
		<i>Polymera</i>
		<i>Tipula</i>

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