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**A Conceptual Model for Seasonal Changes  
in Foodwebs in the Everglades:  
Implications for Mercury Bioaccumulation**

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## **A Conceptual Model for Seasonal Changes in Foodwebs in the Everglades: Implications for Mercury Bioaccumulation**

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### **EXECUTIVE SUMMARY**

Mercury concentrations in Everglades game fish have warranted the issuance of fish consumption advisories by the state of Florida. Investigations have revealed fluctuating patterns of mercury concentrations in animals at several steps in the Everglades food chain. This paper presents a conceptual model that links seasonal changes in Everglades water depth and ecology to mercury concentrations.

It is proposed that the Everglades oscillates between a dry season, detrital-based system and a wet season, algal-based system. In the dry season, low water depths decrease the range and populations of both fish and periphyton. However, invertebrates are able to survive in this environment by occupying small refugia and feeding on detritus. As water levels increase with the wet season, periphyton flourish and small fish migrate into previously dry areas. Initially, these small fish feed on abundant detritus but transition to feeding on periphyton and associated zooplankton. With deeper water, large bodied predators move into the marsh and feed on the abundant invertebrates. As the invertebrate populations are depleted, predators switch to feeding on small fish. However, the time frame for this change in feeding is limited by the onset of the dry season, which forces large predators out of the marsh. Such seasonal changes in the food web base and/or structure would have profound affects on mercury concentrations in biota and would be particularly apparent in small, omnivorous fish such as mosquitofish. If mosquitofish begin the wet season by feeding on detritus, but then transition to zooplankton, the change in trophic position would result in an increase in mercury concentration. In contrast, animals such as crayfish, which remain primarily detritivores, would display little change in mercury concentrations. A review of available stable isotope and mercury data shows patterns consistent with those predicted by the model.

Current plans for Everglades restoration include changes to hydroperiod which would likely affect mercury bioaccumulation at the community scale. Hence, monitoring of mercury concentrations at a variety of trophic levels across the landscape

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### **Abstract**

Research into mercury bioaccumulation in a portion of the Florida Everglades has revealed fluctuating patterns of mercury concentrations in biota at various trophic levels. It is theorized that the seasonal hydrologic cycle of the Everglades creates seasonal changes in food webs that affect mercury accumulation. Temporal changes in water depth allow for a change to the base of the food web from detritus to periphyton. Increased water depths allow small-bodied fish to emigrate into areas previously restricted to drought tolerant aquatic invertebrates. Additionally, large-bodied predators may also take advantage of increased water depths. Such changes in trophic base and structure result in changes in the mercury concentrations of the local biota. Data from published reports show changes in mercury concentrations in higher trophic level organisms that coincide with seasonal changes in water depth. Stable isotope data also provide support for seasonal changes in food web base. Current plans for Everglades restoration include changes to hydroperiod that would likely affect mercury bioaccumulation at the community scale. Increased monitoring of mercury concentrations at a variety of trophic levels across the landscape is suggested in order to provide early notification of landscape-scale increases of mercury and provide data for a mathematical model of mercury behavior in the Everglades ecosystem.

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# A CONCEPTUAL MODEL FOR SEASONAL CHANGES IN FOODWEBS IN THE EVERGLADES: IMPLICATIONS FOR MERCURY BIOACCUMULATION

## Introduction

The Florida Everglades is comprised of nearly a half million hectares of subtropical freshwater wetlands, dominated by sawgrass (*Cladium jamaicense*), wet prairies and open-water sloughs (Gunderson, 1994). In March 1989, a statewide survey revealed elevated levels of mercury in Everglades sport fish, including largemouth bass (*Micropterus salmoides*) and sunfish (*Lepomis* spp.) (Ware et al., 1990). Mercury concentrations in sport fish were sufficiently high to warrant issuing consumption advisories throughout the Everglades (Florida Department of Health and Rehabilitative Services, 1989). In addition to the potential human health risk, other species that depend on the aquatic food web are potentially at risk, including wading birds, panthers, otters and mink.

In response, an aggressive, multi-disciplinary research program was initiated to determine the sources, controlling factors and status of mercury in the Everglades. In 1995, the South Florida Water Management District (SFWMD) and the United States Geological Survey (USGS) initiated a process-level research program to study mercury in the Everglades. The Aquatic Cycling of Mercury in the Everglades (ACME) team also included representatives of the Florida Fish and Wildlife Conservation Commission, the University of Wisconsin, Academy of Natural Sciences, Department of Energy, and Tetra Tech, Inc. (Krabbenhoft et al., 1999). The United States Environmental Protection Agency (USEPA) and Florida International University initiated studies on large-scale spatial patterns of mercury. Additional studies on atmospheric sources and transport of mercury were initiated by Florida State University (Pollman et al., 1995) and by the University of Michigan under contract to the Florida Department of Environmental Protection (Dvonch et al., 1999).

One focus of Everglades mercury research has been the relationship between mercury and other environmental factors. Attempts to correlate surface water and pore water chemistry with mercury concentrations in biota have shown that any relationship is complex and varies with seasonal, temporal and spatial factors (Fink, 2001). Research by Krabbenhoft et al. (2001) suggests that at a landscape scale, the controlling factor for methylmercury (MeHg) bioaccumulation is the amount of methylmercury in sediment pools. However, at the habitat scale, other factors may become important. Stober et al., (2001) have suggested that organic carbon, sulfide, and spatial differences in food chains may be key to controlling mercury concentrations in mosquitofish. Similarly, Loftus et al., 1998, have suggested that hydroperiod, seasonal food availability, and fish growth rate may also be important controlling factors.

This report represents the first attempt to understand mercury concentrations in biota relative to seasonal changes in the Everglades food web. This is accomplished by presenting a conceptual model of Everglades ecology and food web dynamics supported by studies on the Everglades and other ecosystems. Mercury biogeochemical pathways are integrated into the conceptual model

and predictions of mercury species behavior are made. Stable isotope and other data supporting the model are presented.

## Area of Study

Before attempting to understand how the food web affects mercury accumulation in Everglades biota, it is first necessary to have a cursory understanding of the physical and ecological structure of the area. The remaining Everglades wetlands are compartmentalized into Everglades National Park (ENP) and the water conservation areas (WCAs). The focus of this paper is Water Conservation Area 2A (WCA-2A), a 450 km<sup>2</sup> portion of the Everglades located in southern Palm Beach County and northern Broward County. WCA-2A is a mosaic of freshwater marshes of emergent macrophytes and open water sloughs with occasional tree islands (SFWMD, 1992).

In the early 1960s, construction of levees to the north and south cut off historical overland flow in and out of the system, allowing the area to be used as a water storage body. The majority of surface water entering WCA-2A originates from or passes through the Everglades Agricultural Area and enters through the S-10 structures located along the L-39 canal, (Light and Dineen, 1994). From 1979 to 1998, the estimated annual rainfall contribution to the area was over 500 trillion liters (SFWMD, 1992). During the same period, the annual average water volume discharged from these structures was over 400 trillion liters (SFWMD, 1992). This inflow carries excess nutrients and micronutrients from fertilizer and soil amendments. Mean total phosphorus concentrations at the inflow structures from 1979 to 1991 ranged from 100 ug/L to 200 ug/L. However, since 1992, total phosphorus concentrations have steadily decreased to nearly 50 ug/L (Bechtel et al., 2000).

The surface water quality of the interior of WCA-2A has been monitored by 13 sites along three transects perpendicular to the flow, starting near the canals and ending in the middle of the WCA (McCormick et al., 1996) (Figure 1). Concentrations of most parameters decrease moving down the flowpath along the transect, possibly due to biotic uptake, sedimentation and dilution by rainfall. Moving away from the surface water inputs, water derived from rainfall dilutes the nutrients in surface waters. Chloride (a conservative tracer) decreases approximately 13% between F1 (up gradient) and U3 (down gradient) sites (Figure 1), which provides an estimate of the dilution of canal water moving down the transect into the marsh (McCormick and O'Dell, 1996).

Much of the phosphorus entering the conservation area is deposited with sediments immediately downstream of the inflow structures, creating a footprint of contamination. Using available data from several studies (DeBusk et al., 1994; Richardson et al., 1997; and Stober et al., 1998), a soil contour map of phosphorus concentrations in WCA-2A was generated (Figure 1, McCormick et al., 2000). In response to these nutrient inputs, an enrichment gradient has developed resulting in the northern portion of the WCA-2A marsh being dominated by near monospecific stands of cattail (*Typha domingensis*) (Rutchev and Vilchek, 1994). Approximately 7 km south of the S-10 structures, the marsh is considered relatively unimpacted by nutrients and is dominated by short hydroperiod marshes consisting of sawgrass and open-water sloughs of dense periphyton mats (Rutchev and Vilchek, 1994). Site U3 is a typical site within this area where long-term

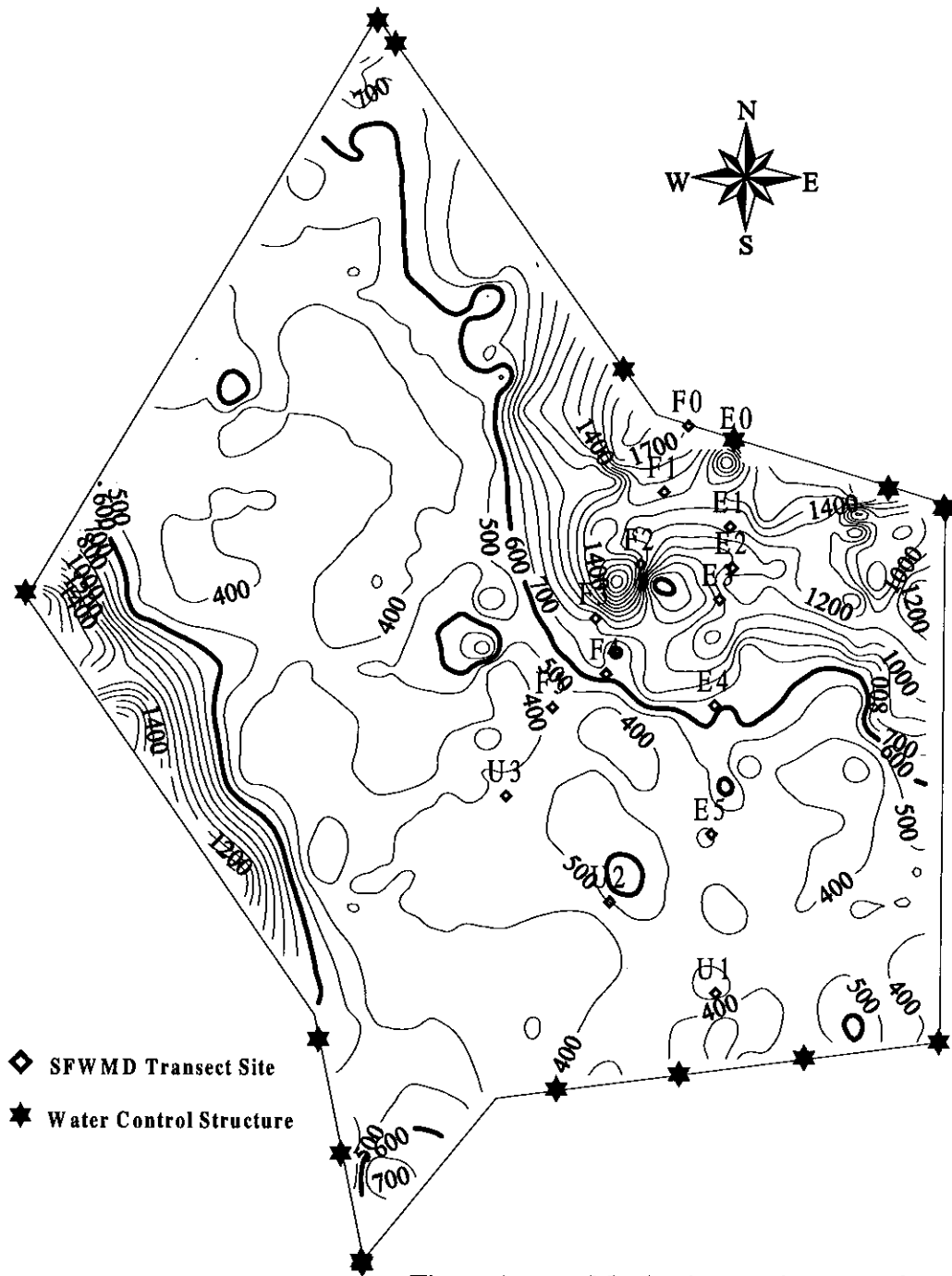


Figure 1. Monitoring sites and total phosphorus concentrations in sediments in WCA-2A.



data on water depths are available. Additional sites representative of unimpacted conditions include U1, U2, F5, and E5 (Figure 1). It is important to note here that while U3 may be considered unimpacted in WCA-2A, it may be considered impacted in comparison to other sites in the Everglades ecosystem. For a detailed review of the effects of these trends in water and soil quality, see McCormick et al. (2000).

A review of water depth data (Table 1) shows that in comparison to other unenriched sites, site U3 has the lowest average water depth of 50 cm and is less than 30 cm in depth for approximately 26% of the time. This suggests that U3 has a higher elevation than most other sites in WCA-2A and may be considered a shorter hydroperiod wetland in comparison to other unenriched sites in WCA-2A.

Table 1. Water depth data on unenriched sites in WCA-2A based on measurements from 1994 to 1999. Elevation data after Worth, 1983.

	F5	U3	U2	U1	E5
Approximate Elevation (meters above mean sea level)	3.47	3.38	3.32	3.11	3.35
Mean Water Depth (cm)	51	50	54	62	58
Percentage of Water Depth Measurements <less than 30 cm in depth	19%	26%	22%	15%	13%

## A CONCEPTUAL MODEL OF A DYNAMIC EVERGLADES FOOD WEB

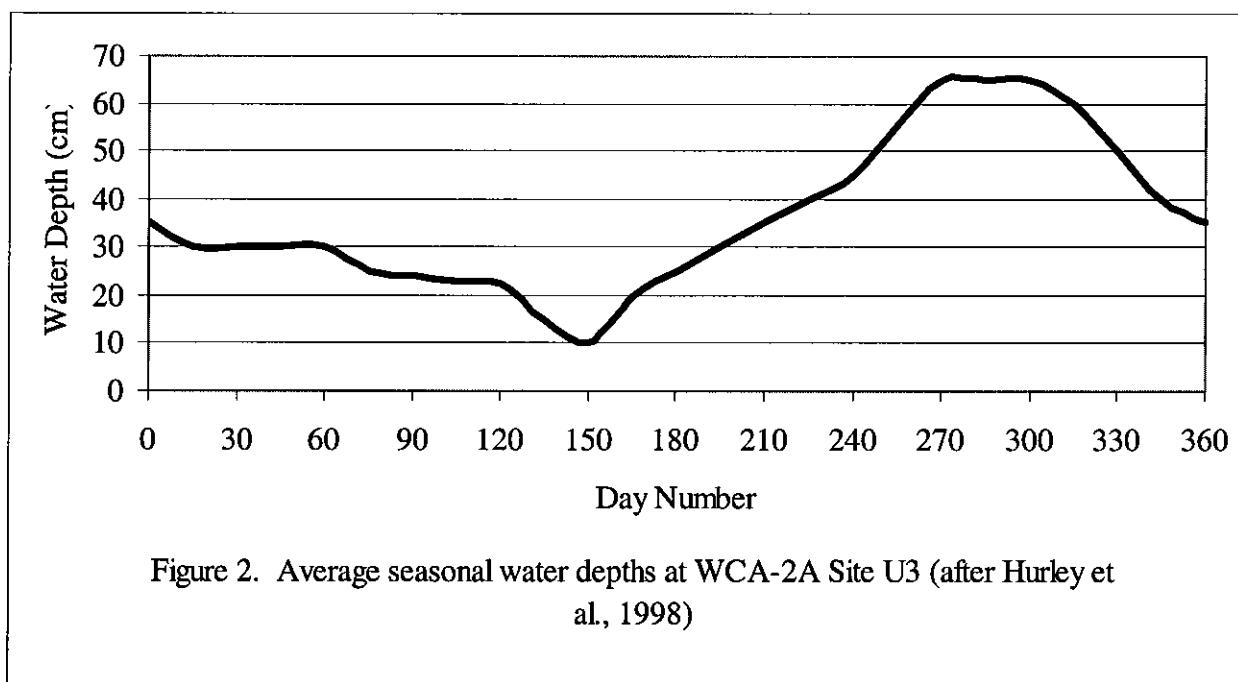
The following conceptual model was developed based on field observations and published ecological reports on the Everglades and similar ecosystems. Much of the mercury data and some of the isotope data used were available prior to or during the development of the model. Consequently some of the model concepts were made with full knowledge, or refined to match, the available data. This model is a first attempt to integrate environmental mercury data, isotopic data, and existing observations of the Everglades ecosystem. It is meant to provide a framework for discussion, further research and model development and refinement.

While the diversity of the Everglades biota is extensive (see Lodge, 1994 for species lists) this conceptual model will focus on a few key components of the ecosystem. For the purposes of this paper, the term “floc” will be used to represent the combination of accumulated organic debris (including macrophytic and algal components), and associated microbial and algal communities that exist in the top 5 cm of the sediment. Depending on biotic and abiotic factors, the floc may fluctuate between aerobic and anaerobic conditions. One portion of the floc, generally termed “periphyton”, is dominated by algal species. In the winter, the periphyton community is dominated by diatoms, particularly *Amphora lineolata*, *Mastoglia smithii* and *Synedra radians*. In contrast, cyanobacteria, particularly *Scytonema hofmanni* and *Chroococcus turgidus*, dominate the community in the summer (McCormick et al., 1998). A review of Everglades periphyton taxonomic composition and ecology can be found in Browder et al., 1994.

Representative macroinvertebrates include decapods such as crayfish (*Procambarus alleni*) and grass shrimp (*Palaeomonetes paludosus*), both of which are well adapted to low-water and drought conditions (Trexler and Jordan, 1999) and as omnivores can adapt to changes in resource availability (Hunt, 1952). Mosquitofish (*Gambusia holbrooki*) are also omnivorous which may give them an advantage over other small-bodied fishes such as herbivorous sailfin mollies (*Poecilia latipinna*) and carnivorous marsh killifish (*Fundulus confluentus*). Unlike decapods, populations of small-bodied fishes must seek refugia during low-water and drought periods or perish. The one exception to this is the marsh killifish, the eggs of which may survive even extended droughts (Lodge, 1994).

Important large-bodied fish include species of sunfish (*Lepomis spp.*) and largemouth bass (*Micropterus salmoides*). Like small-bodied fishes, these larger fishes must also seek refugia during low waters, but due to size must do so earlier and can only return when water is much deeper than those required by small-bodied fish. The one exception to this may be the Florida gar (*Lepisosteus platyrhincus*), which has a fusiform body shape and the ability to air-gulp, adaptations that may allow them to penetrate and survive in shallow, anoxic and macrophyte dominated areas.

These primary ecological model components are influenced by drastic variations in water depths (Figure 2) associated with seasonal rainfall patterns. These changes will be illustrated in 5 schematics of how the food web changes with season (Figures 3-7), starting with the end of the dry season. Generally, the dry season begins in November and lasts seven months, ending in May (Fennema et al., 1994). At this time, most surface water is confined to localized pools where remnant populations of aquatic organisms take refuge (Trexler and Jordan, 1999). These remnant populations include periphyton, small fish and macroinvertebrates. Also, large amounts of detritus from algae and macrophytes will be present in both the localized pools and exposed



areas. Under these conditions, while algal communities still exist, the algal biomass is likely insufficient to support higher trophic levels, therefore, omnivorous species such as mosquitofish, crayfish and grass shrimp that function as detritivores (Figure 3) will probably dominate. However, because both grass shrimp and crayfish are better adapted to low-water environments than mosquitofish, macroinvertebrate populations will likely dominate the refugia.

Rainfall dramatically increases in June, and re-flooding of marsh areas is rapid (Figure 3). In response to rain, crayfish and grass shrimp emerge from refugia and reproduce (Kushlan and Kushlan, 1979; Rhoads, 1980; Kushlan and Kushlan, 1980; Trexler and Jordan, 1999). Reflooding of the marsh also allows the surviving macroinvertebrates and small fish to feed directly on newly accessible and abundant detritus. At this stage of the hydrologic cycle, the algae are still not very abundant, but some species, particularly diatoms, may experience rapid growth.

As the wet season continues and water levels rise through July (Figure 4), algal biomass in the floc and water column increases. With an increase in algal biomass, there is a potential for the local ecosystem to form a food web flowing directly from an algal source rather than through a detrital path. Studies of mosquitofish in Everglades National Park found the volume of algae in stomachs increases 2 to 6 times from January to July (Loftus et al., 1998). However, this study did not differentiate algal composition. Experiments by Browder (summarized in Browder et al., 1994) have found that the blue-green algae, which dominate short-hydroperiod wetland communities, to be a less than suitable food item, particularly in comparison to longer hydroperiod areas where algal mats are dominated by diatoms. Consequently, this increase in algae in the guts of mosquitofish may be indicative of selective feeding on diatoms or of accidental ingestion associated with increased predation on zooplankton and macroinvertebrates. The exact mix of diet is dictated by the seasonal lifecycles of the various species of zooplankton and macroinvertebrates responding to hydrology and plant senescence, as well as by competition from grazers (sailfin mollies) and carnivores. If there is a seasonal change in mosquitofish

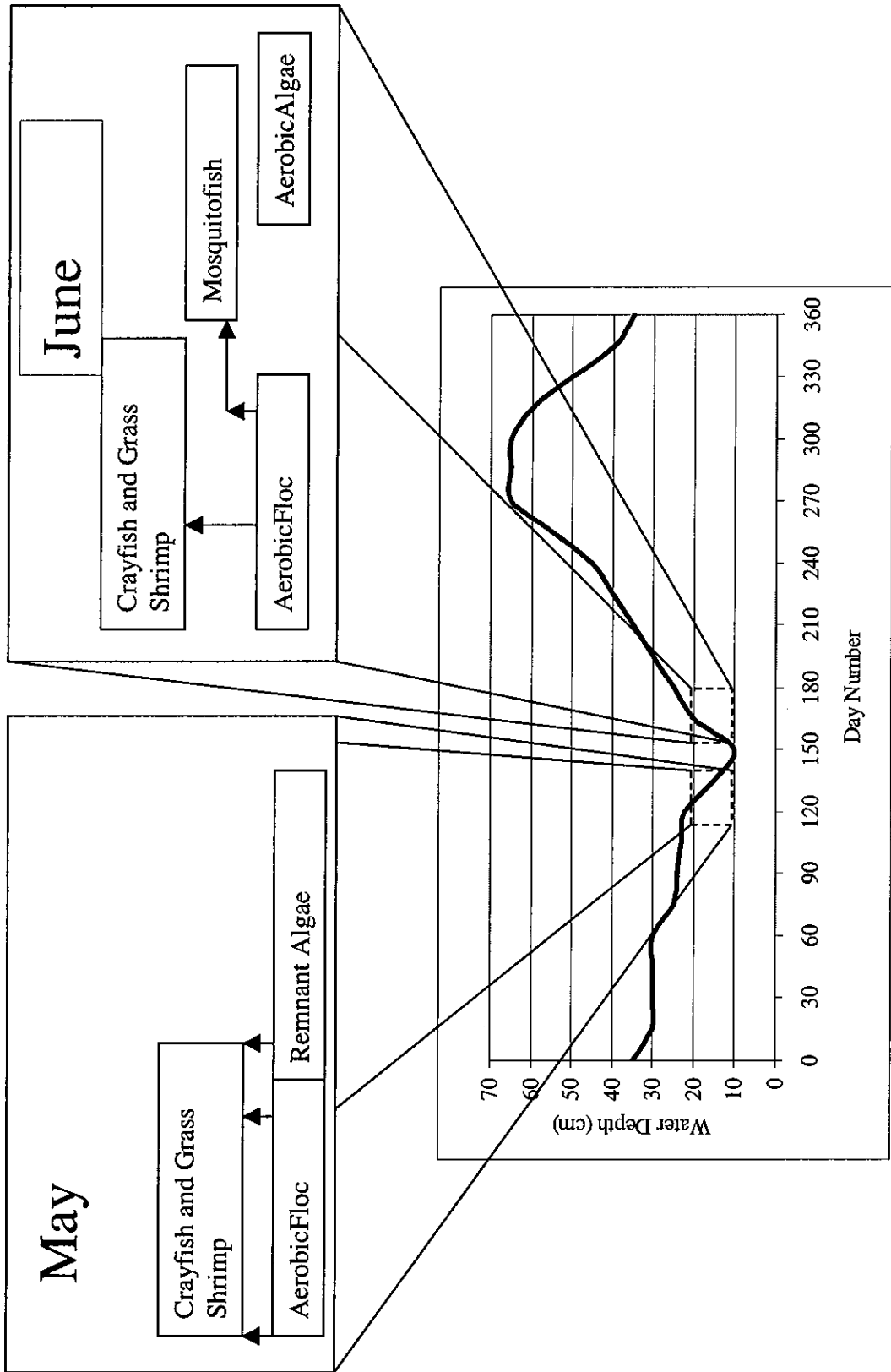


Figure 3. Everglades food web structure in May and June showing lack of fish in the environment.

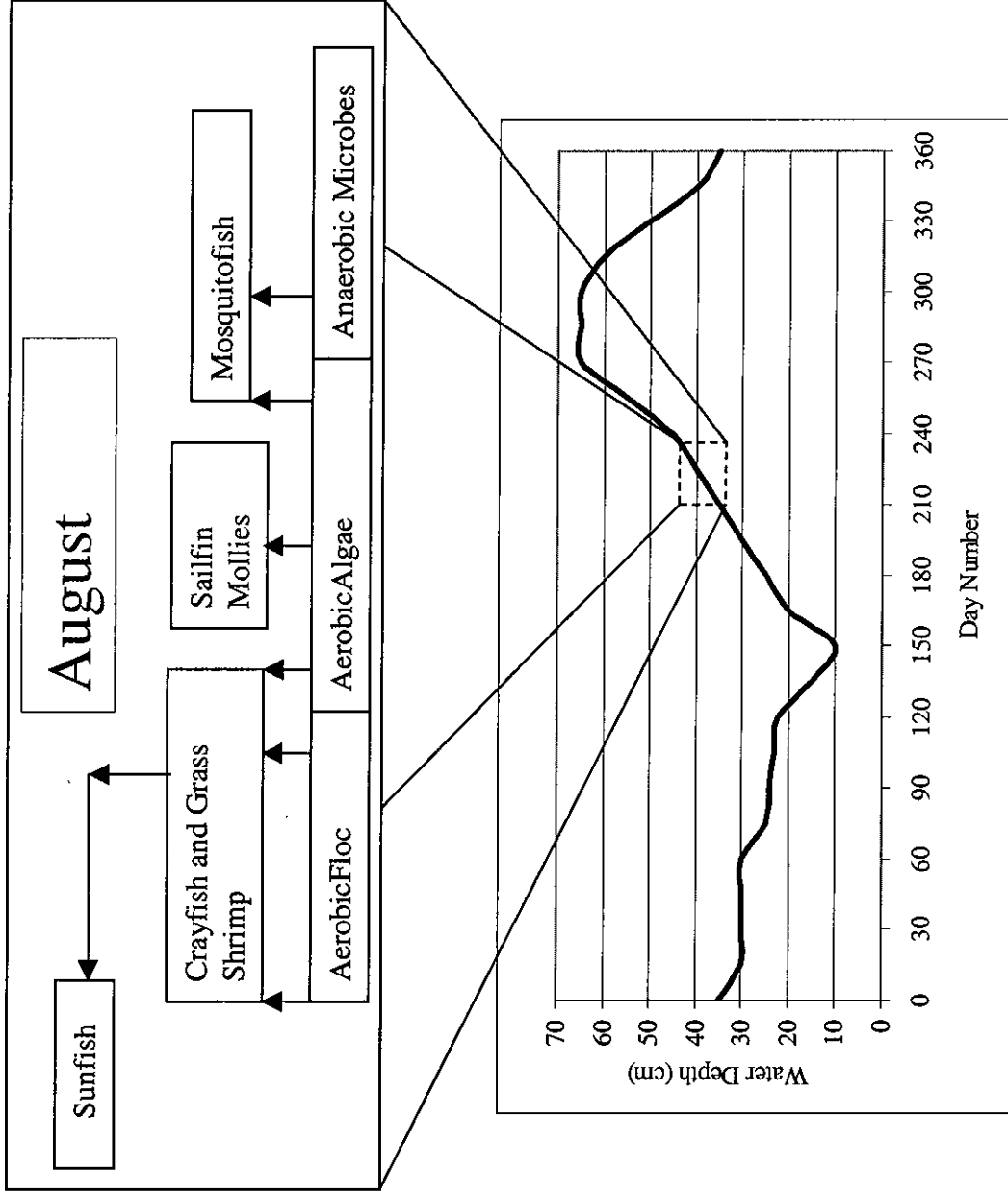


Figure 4. Everglades food web structure in August showing presence of small fish and influence of the algal community.

feeding behavior from detritus to diatoms and zooplankton, this could represent a shift of one to two trophic levels. Preliminary stable isotope data presented by Kendall et al. (2001) suggests seasonal and spatial differences in the base of the food web.

By August, water levels are sufficiently high to allow food webs based on the algal pathway and the detrital pathway to co-exist (Figure 4). Additionally, the detritus which is now covered by surface water and by extensive growths of periphytic algae and other microbial communities, will develop areas of anoxic and reducing conditions (-100 to -200 mV) (Koch-Rose et al., 1994). Such areas should be capable of supporting anaerobic communities, including sulfate-reducing bacteria (SRB). The detrital and algal pathways are likely to have distinct users. Crayfish are dependent primarily on detritus, while mosquitofish are dependent on select species of algae and zooplankton. Grass shrimp can probably digest both detritus and algae, although algae appears to be the primary food source (Hunt, 1952).

The increasing water depths will allow large-bodied predators such as sunfish and bass to move from deep-water refugia to areas of shorter hydroperiod (Trexler and Jordan, 1999). This migration may be mediated by various physical and chemical factors. For example, submergent macrophytes and periphyton may be sufficiently dense to prevent sunfish and bass from taking full advantage of prey. Additionally, some areas experience regular periods of anoxia (McCormick et al., 1997), which may deter aquatic predators.

The migration of large-bodied fish to shorter hydroperiod marshes may result in a significant change in the diets of these predators. In comparison to the deep-water refugia previously occupied by these predators, which can be assumed to be areas where the algal path food web never collapsed or at least was initiated earlier, the move into shallower areas represents a shift towards a more detrital-based food web. Since the macroinvertebrate populations of crayfish and grass shrimp developed slightly earlier in the season, invertebrate standing crops will be higher than small fish crops. Studies carried out in the unenriched areas of the Everglades have found macroinvertebrate standing crops to be two to six times higher than fish standing crops (Turner et al., 1999).

Feeding studies on Everglades fish have found that grass shrimp and crayfish are predominant in the diet of Everglades marsh predators (Loftus et al., 1998). Gut content analyses in Everglades National Park (ENP) have found that grass shrimp and crayfish make up more than 55% of the diet by volume of Warmouth (*Lepomis gulosus*), spotted sunfish (*Lepomis punctatus*), and largemouth bass (*Micropterus salmoides*) (Loftus et al., 1998). Additionally, macroinvertebrates including crayfish, grass shrimp, and snails as well as other species, are dominant in the diets of bluegill (*Lepomis macrochirus*) and redear (*Lepomis microlophus*). Macroinvertebrates also made up 40% by volume of the diet of Florida gar. These results are consistent with work carried out by Lange et al. (1998) at sites throughout the Everglades.

The feeding preferences of predators may have an effect on the ratio of prey in the ecosystem. Estimates of mosquitofish reproduction rates suggest that a new generation is spawned every 30 days (Maglio and Rosen, 1969). In contrast, crayfish breed only once or twice a year (Payne, 1978). As predators feed on crayfish and grass shrimp, the population of these species decreases faster than reproduction can replace them. However, at the same time, the population of mosquitofish is increasing. Consequently, the ratio of these macroinvertebrates to small fish decreases. The longer water levels stay stable, the more crayfish densities decrease and small

fish densities increase. Consequently, by October it is possible that small fish densities will equal or surpass the densities of crayfish, and predators may switch from feeding primarily on macroinvertebrates to small fish (Figure 5). Thus, in unenriched areas a long, stable hydroperiod drives a shift from omnivorous macroinvertebrates and small fish to large-bodied carnivorous fish (Kushlan, 1976). This would also represent a shift away from detrital pathways.

Through November and into December, rain decreases, and water levels begin to drop. This decrease in water depth forces larger fish out of the marsh and into deeper water habitats (Figure 6). As water levels continue to drop, algae, submerged macrophytes, small fish and macroinvertebrates will be concentrated in local refugia. Unlike large fish, small fish and macroinvertebrates do not move across the landscape to deep-water refugia. For example, the seasonally increased fish density in long hydroperiod marshes during the dry season is derived from closely adjacent marshes but not from marshes outside the local landscape (Turner et al., 1999). Trexler et al. (1999) have hypothesized that the decreases in water level are too slow, and the topography too variable to allow small fish to migrate *en masse* in the Everglades.

Eventually, perhaps by March (Figure 7), decreasing water levels may drop to such a level that portions of the floc and submerged aquatic vegetation mats will begin to dry out. This may result in a shift in dominance back to a detrital-based food web. It is important to remember that this detritus has both macrophyte and periphyton components. Consequently, feeding studies may show evidence of algae in the gut of detritivores. At the same time, large numbers of small fish appear to be removed from the system. Studies of genetic structure in mosquitofish have suggested that the local populations are nearly eliminated during dry down (Trexler and Jordan, 1999). This removal may be through fish kills associated with dry out and low dissolved oxygen, or by predation from wading birds (Trexler and Jordan, 1999). Jordan (1996) suggests that crayfish and dragonfly naiads may be significant predators on mosquitofish (Figure 7). In contrast to these season end fish kills, the local populations of grass shrimp and crayfish survive drought (Trexler and Jordan, 1999) and are once again positioned to dominate the ecosystem at the beginning of the next wet season.

The annual cycle of succession presented here is strongly linked to fluctuating water depths. Any perturbation of the system that shortens or extends the period of drought or inundation will have a significant effect on the trophic structure. For example, if there is an extended wet season, populations of invertebrates and prey fish could be decimated by predators, which have not retreated to deep water refugia. In contrast, an extended dry season could result in a severe dry down, which could kill even invertebrates, thus reducing post-rain spawning populations. Consequently, the Everglades ecosystem sits in a delicate balance between extreme hydrological conditions.

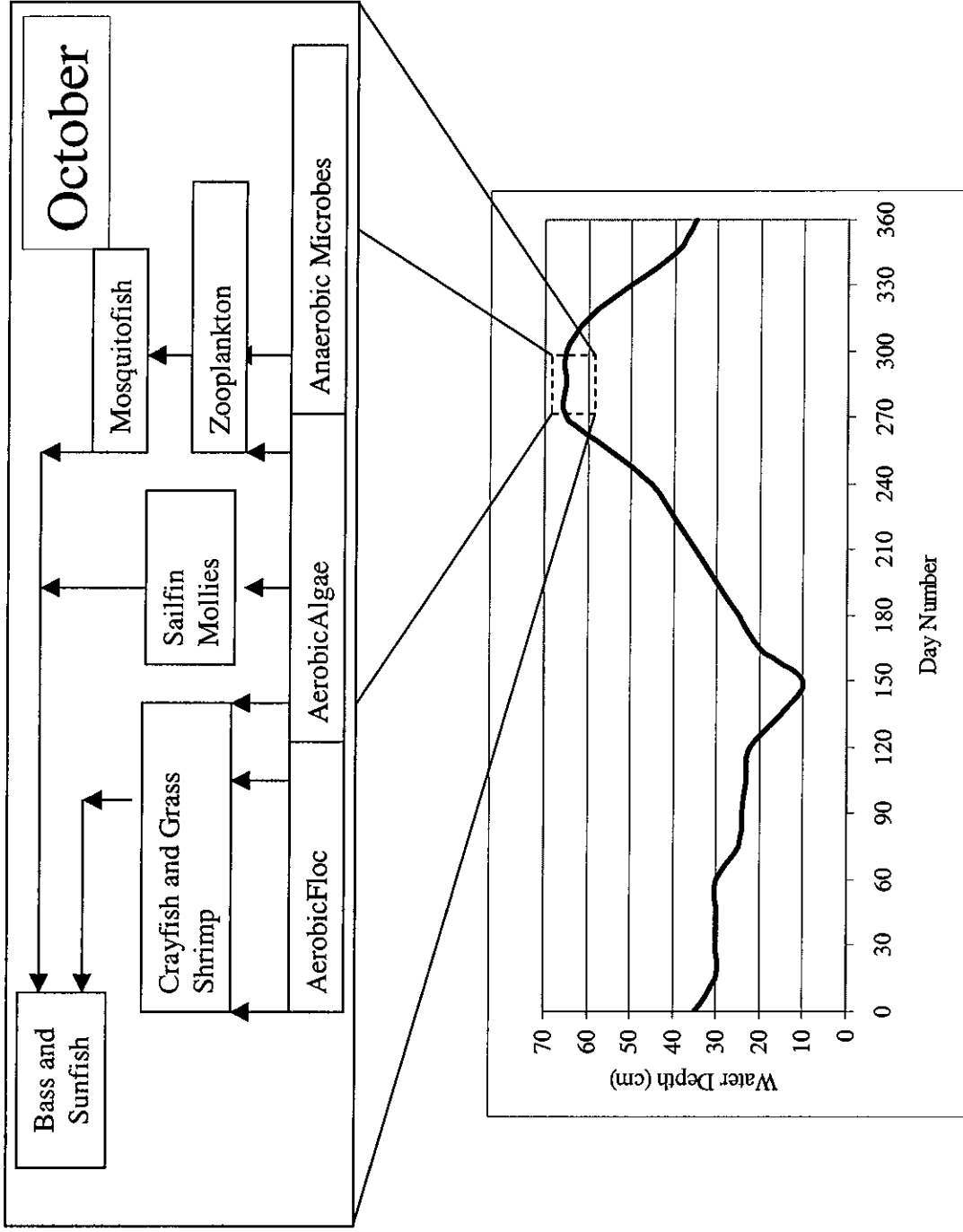


Figure 5. Everglades food web structure in October showing extensive algal paths and higher trophic levels.



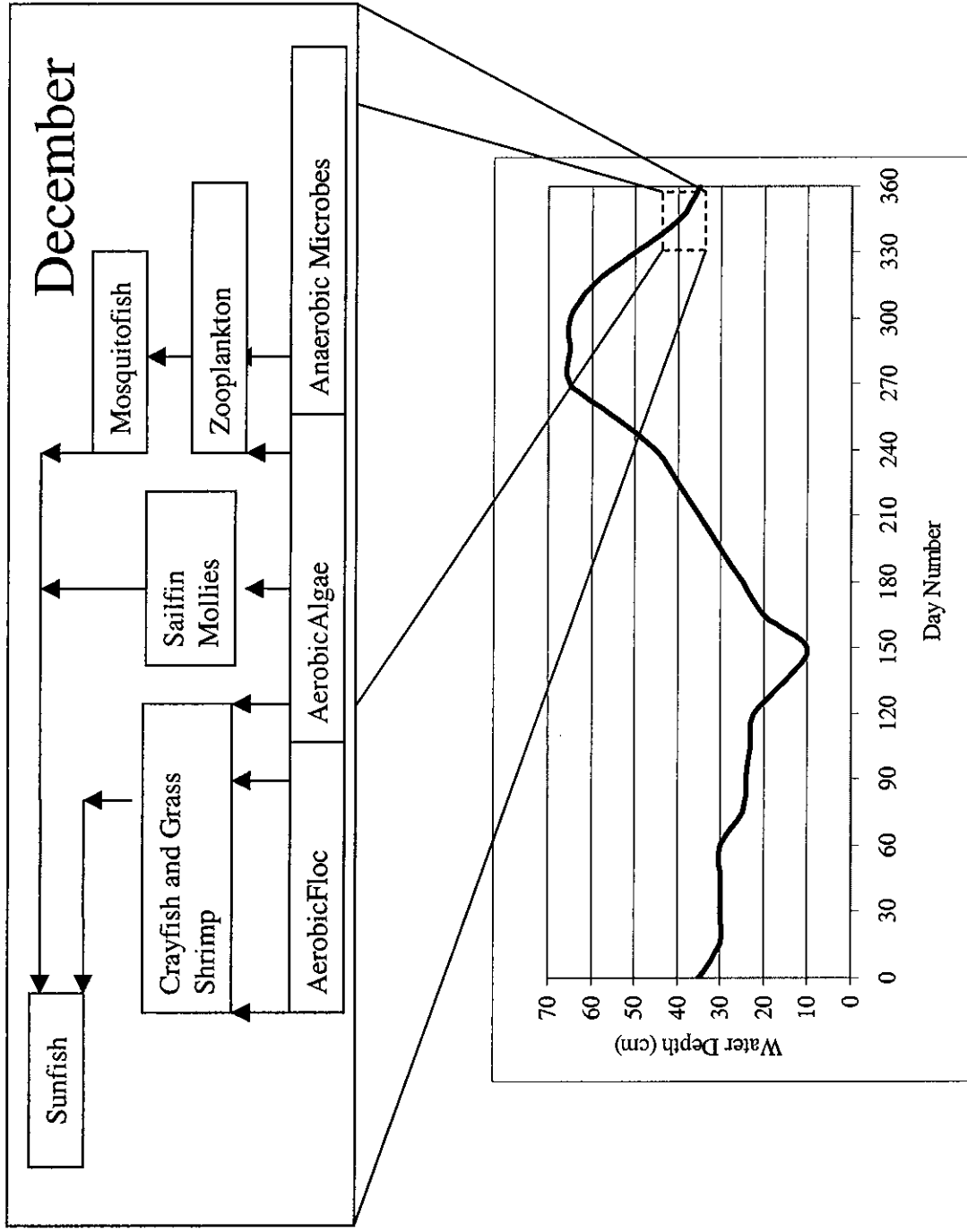


Figure 6. Everglades food web structure in December showing loss of components in response to onset of dry season..

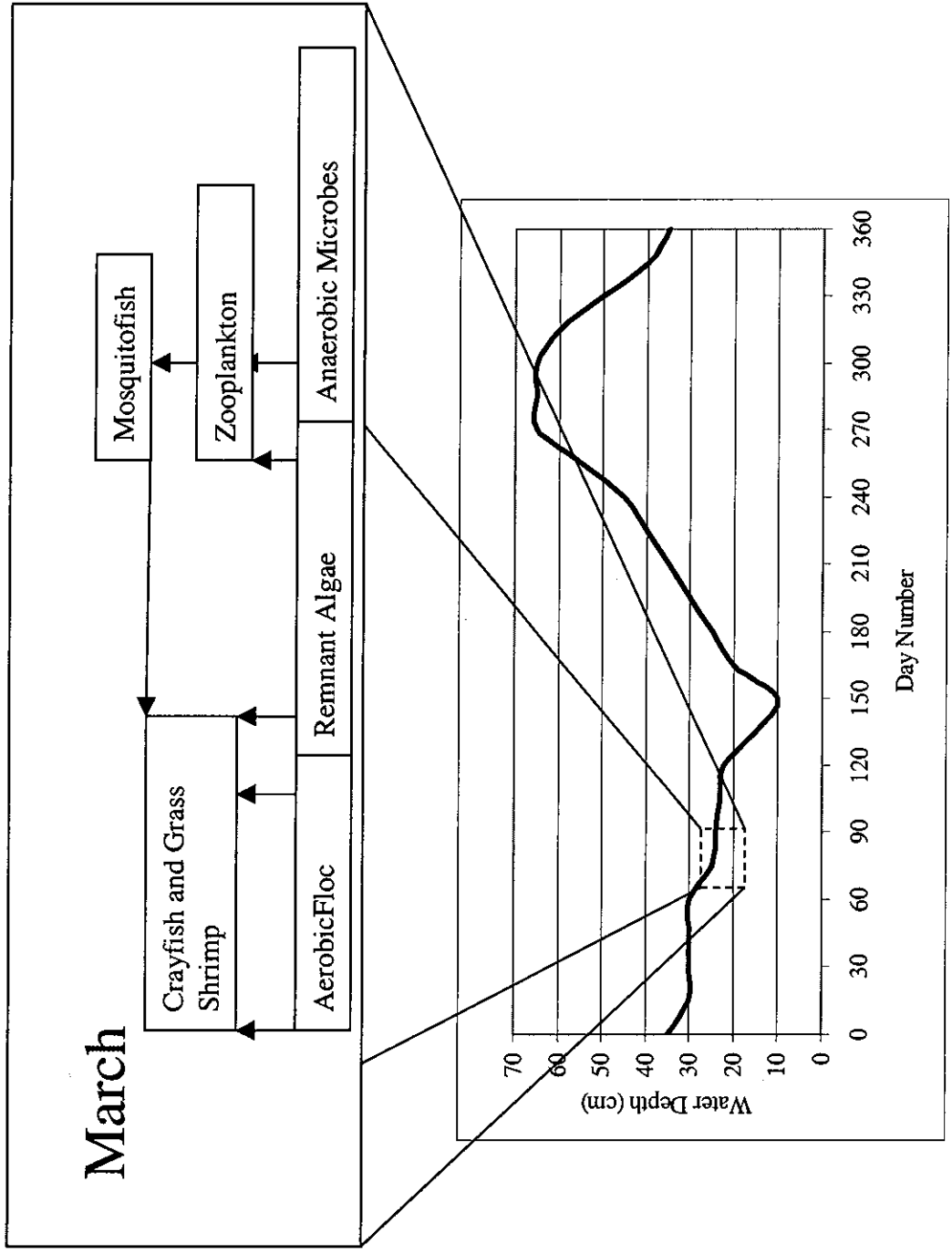


Figure 7. Everglades food web structure in March showing loss of upper trophic levels.

## INTEGRATING MERCURY INTO THE CONCEPTUAL MODEL

Generally, studies that attempt to integrate mercury into the aquatic chemical cycle have focused on the abiotic and biotic processes that introduce, remove, transform and store mercury species in the surface water and sediment compartments in lakes (Morel et al., 1998; Zillioux et al., 1993). Even biomagnification studies that recognize the importance of biota in the cycling of mercury typically present a review of the bioaccumulation of inorganic mercury and methylmercury into generalized unicellular microorganisms and their predators, as illustrated by Figure 8.

Research on biomagnification of mercury in freshwater, aquatic food chains has, for the most part, focused on temperate lake systems rather than wetlands. The few papers that have focused on wetlands have suggested that the drying and reflooding cycle is a primary factor in controlling mercury bioavailability (Snodgrass et al., 2000; Zillioux et al., 1993). As with other wetlands, the hydroperiod of the Everglades is theorized to be a primary factor in the bioaccumulation of mercury in biota through the release of mercury from sediments (Snodgrass et al., 2000). Hence, the changes in Everglades trophic structure brought about by increased water depths should also result in changes in mercury bioaccumulation. Using the conceptual model presented previously, it is possible to make predictions about the behavior of mercury in the Everglades ecosystem.

During the course of the dry season, inorganic mercury continues to enter the Everglades as a component of dryfall. While portions of this mercury may be lost back to the atmosphere through abiotic processes (Tsiros and Ambrose, 1999), some accumulates in the water column and moist peats of the Everglades. Additionally, chemical processes and photo-oxidation may release mercury bound to particles in the surface sediments (Carpi and Lindberg, 1997). Finally, mercury in deeper sediments may be re-exposed to the food web because of bioturbation, fire, and sediment cracking (Snodgrass et al., 2000). Consequently, towards the end of May, large quantities of mercury may be readily available to the ecosystem. These sources, combined with the high levels of mercury already present in rainfall, should provide a seasonal flush of mercury to the system immediately following spring rains.

Following the first rains, mercury and any existing methylmercury are transferred to crayfish and grass shrimp through ingestion. Increasing water levels allow small fish to colonize and take advantage of local food sources. At this point, the algal component of the floc is relatively undeveloped, and grazing will be primarily on detritus and associated microbial communities (Figure 3). Initial mercury concentrations in small fish will be dependent on environmental conditions in the source refugia, but these populations will respond to local mercury and methylmercury concentrations, and *de novo* methylation rates in the detritus.

As water levels continue to increase, algae flourishes and an algal path food web eventually establishes (Figure 4). However, early algal communities and the floc will be primarily aerobic (Browder et al., 1982) and thus the anaerobic SRB that drive methylmercury production are limited by available habitat. This means that even if large quantities of inorganic mercury are available, it will not be methylated. Consequently, while total mercury concentrations in mosquitofish might continue to rise, methylmercury concentrations might actually be low. In time, the anaerobic areas will increase and provide increased habitat for SRB.

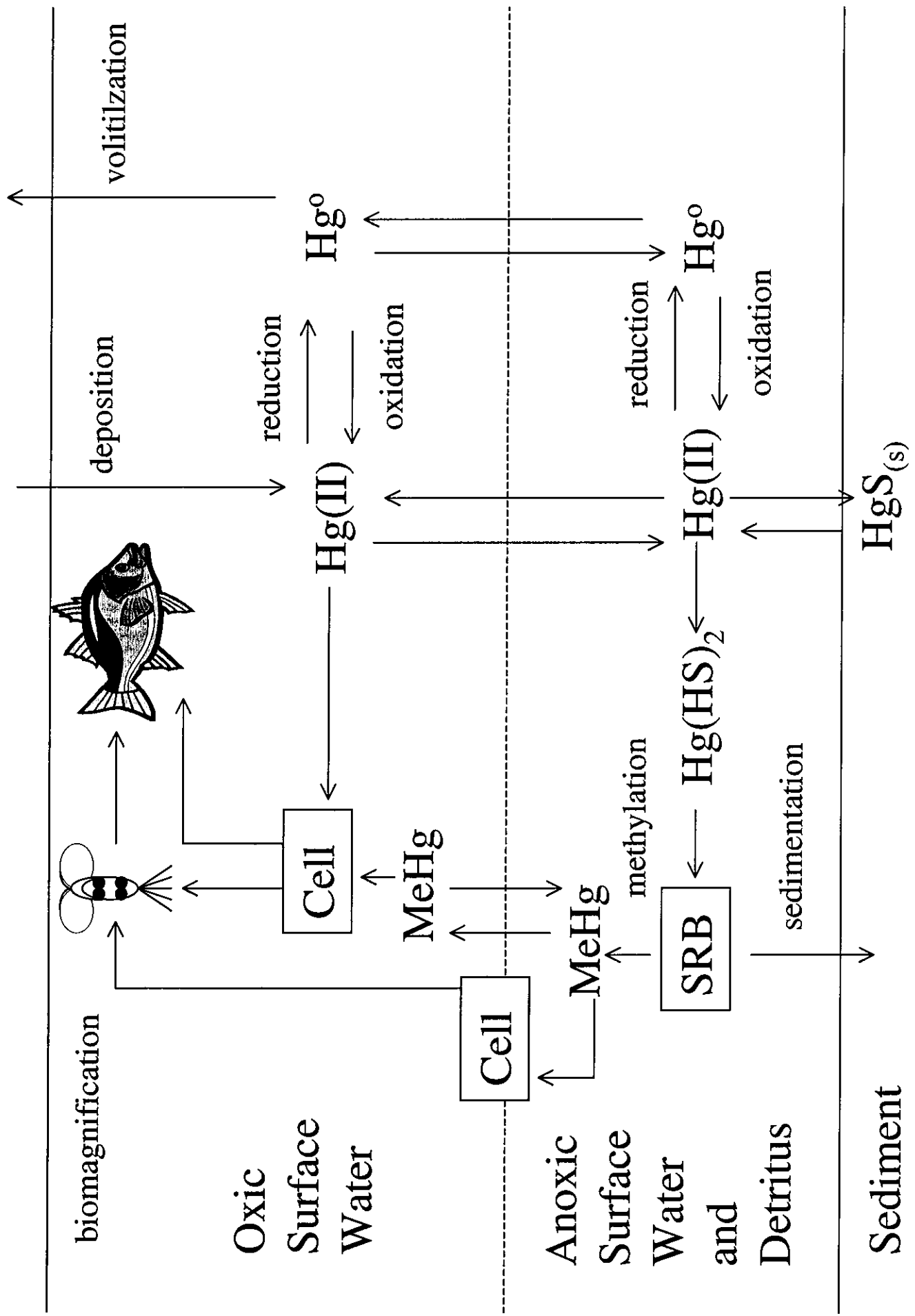


Figure 8. The aquatic mercury cycle (after Morel et al., 1998)

The methylation of mercury in the floc is influenced by a variety of biogeochemical factors, including sulfate, sulfide (Benoit et al, 1999), calcium, dissolved organic matter (Ravichandran et al., 1999), and other water column parameters (Zillioux, et al., 1993). Given the natural and anthropogenic variability of these parameters, it is likely that *de novo* mercury methylation will also vary. Additionally, some of these variables may have non-linear, synergistic or opposing effects on mercury methylation rates. Consequently, the methylation rate may not be linear in nature and may vary over time as conditions fluctuate. Additionally, demethylation also occurs in these habitats. However, measurements have shown that demethylation rates are homogeneously low throughout the Everglades, and thus can be ignored (Marvin-DiPasquale, 2001).

MeHg concentrations in biota may also be affected by shifts in the food web. In detrital-based food webs, crayfish, grass shrimp, and small fish feed directly on detritus or organisms in the detritus (e.g., microbes) that have low mercury concentrations, and this represents only a few trophic levels. However, by October, omnivorous mosquitofish switch to feeding on zooplankton and macroinvertebrates, resulting in two changes to the food web. The first change is to the pathway for energy, nutrients and contaminants, including mercury (i.e., the foodweb base and structure). Secondly, as the species takes advantage of these new pathways, additional trophic levels are created in the food web (i.e., the number of links in the foodweb). These additional links and the change in food web base represent a process that may allow for higher bioaccumulation of mercury in mosquitofish.

Similar processes probably occur in grass shrimp and sailfin mollies. However, because these species feed directly on algae, their mercury concentrations are derived more strongly from methylation rates. Consequently, mercury concentrations in grass shrimp and sailfin mollies should be lower than in omnivorous mosquitofish. Although marsh killifish are carnivores, and consequently should have higher mercury concentrations than mosquitofish, studies in ENP found that the marsh killifish feed mostly on zooplankton and macroinvertebrates from the detritus (Loftus et al., 1998), which may keep mercury concentrations low.

As large bodied predators migrate into the shorter hydroperiod marshes, they begin feeding on crayfish and grass shrimp. Since crayfish and grass shrimp are either part of the detrital pathway or feed directly on algae, there is less opportunity for biomagnification of mercury than in the algal pathway. The longer water levels stay elevated, the more likely predators will switch to a longer food web based on an algal pathway, thus increasing mercury levels. However, under normal hydrologic cycles, water levels are unstable, and the residence time of these animals in the marsh habitat can be assumed to be short, likely less than three months (Trexler and Jordan, 1999). While studies of marsh feeding rates are limited, this time period is probably insufficient for large fish to deplete the local macroinvertebrate populations. Thus a switch to a diet of small fish with higher mercury concentrations is unlikely. Even if such a switch occurs and mercury concentrations begin to rise, they will still lag behind concentrations in areas with deeper waters. Consequently, seasonal communities of predators in short hydroperiod wetlands may have lower mercury concentrations than communities in longer hydroperiod wetlands.

This does not mean that mercury concentrations in all large fish will be low. Mercury concentrations in large fish are likely the integrated result of environmental conditions in deep water refugia (long hydroperiod marshes, canals, airboat trails) where the animals reside for six to nine months, individual feeding behaviors, concentrations of mercury in prey, and individual

uptake and depuration. Given these variables, wide ranges of mercury concentrations in large fish within the same area may manifest.

As water levels drop in November and December, large fish will migrate to deeper water habitats, while small fish will become concentrated and hence available to predators such as wading birds. Both the migration of large fish and the loss of small fish result in a reduction of mercury, particularly methylmercury, in the local system. Additionally, lower water levels allow more light to penetrate and may also lower methylmercury concentrations through photodemethylation. Finally, the lower water levels leave portions of the periphyton mat to dry and decompose. This will initiate a shift to a detrital pathway but also will disrupt the anaerobic community inside the mat and the sediment layer. Consequently, overall methylation rates drop. This process also has an affect on the total mercury available to the system. The drying and decomposition of periphyton and macrophytes generates peat. The formation of new peat, although a very slow process, removes some mercury from the system. The net result of these biotic and abiotic processes is that both total mercury and methylmercury concentrations in the remaining fish and macroinvertebrates should drop.

## **SUPPORTING MERCURY EVIDENCE**

The conceptual model presented for the behavior of mercury in the Everglades is complex. While it describes ecosystem responses to changes in hydrology and food web base, there are dozens of other factors and perturbations, the effects of which will have to be measured. Validation and integration of other factors in the model will take the combined efforts of a variety of disciplines and repeated seasonal studies to isolate the factors that are key to making sufficiently accurate predictions. Much of this research is already underway, and preliminary Hg and stable isotope data provide some support of the model presented here.

### **Seasonal Patterns of Mercury in Macroinvertebrates and Mosquitofish**

The model predicts that mercury concentrations in macroinvertebrates and mosquitofish will rise in response to rain in the spring, and continue to rise as the algal based food web develops and methylation rates in periphyton increase. Hence, mercury concentrations will be lower in the winter than in the summer. Table 2 shows that concentrations of MeHg in grass shrimp, hemipterans, amphipods, and mosquitofish in WCA-2A are consistent with this prediction. Cleckner et al. (1998) attributed the lower winter Hg values in mosquitofish to seasonal differences in feeding. Some percentage of these increases may be attributable to winter-summer changes in temperature. Increases in metabolic activity associated with an increase of 10° C have been found to increase mercury bioaccumulation in mosquitofish up to five times (Boudou et al., 1979). However, such metabolic increases should be seen at all sites and, while some variation may occur, across all species. The data presented in table 2 show that while mercury concentrations increase for all species from winter to summer, the increases are not of the same magnitude for different species at similar trophic levels or even for the same species at different sites. Consequently, while temperature changes may be a factor in seasonal mercury increases, other factors must be influencing the processes involved. Additionally, it must be noted that the gut contents of these samples were not systematically voided, which may contribute some error to these measurements.

Table 2. Seasonal patterns in mercury concentrations (ng/g) in WCA-2A macroinvertebrates and mosquitofish.

Species (site)	Winter/Spring	Summer/Fall	Source
Grass shrimp (U3)	5-6	15-20	Cleckner et al., 1998
Hemipterans (F1)	2	4-5	Cleckner et al., 1998
Amphipods (U3)	2-3	3-4	Cleckner et al., 1998
Mosquitofish (U3)	6	35-40	Cleckner et al., 1998
Mosquitofish (F1)	1-2	2-3	Cleckner et al., 1998
Grass shrimp (F4)	10-15	30-40	SFWMD, unpublished
Grass shrimp (F1/E1)	4-8	9-40	SFWMD, unpublished

Beginning in September 1997, mercury concentrations in mosquitofish have been monitored at sites in WCA-2A, including unenriched sites F5 and U3 (Fink, 2001) (Figure 9). As predicted by the model, mercury concentrations in mosquitofish appear to be low in the winter and increase through the spring and summer. The failure of a peak to appear in summer 1998 may be an artifact of the frequency of sampling or the existence of an El Niño event that increased rainfall to the area. The similar patterns but different magnitudes of mercury concentrations at the two sites may be indicative of differences in mercury inputs, de novo methylation rates or hydroperiod (Table 1).

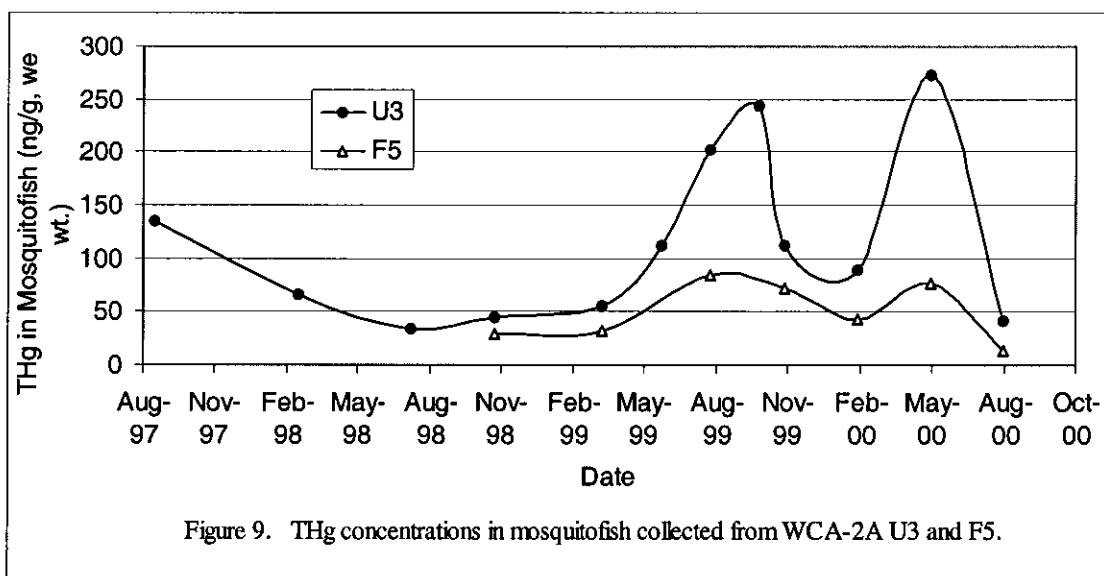


Figure 9. THg concentrations in mosquitofish collected from WCA-2A U3 and F5.

## Relative Mercury Concentrations for Mosquitofish and Macroinvertebrates

The model predicts that in May and June, mosquitofish will have mercury concentrations similar to grass shrimp, but both of these will be higher than in other invertebrates. In August through October, mercury concentrations in mosquitofish and macroinvertebrates will increase, but because mosquitofish may assume higher trophic positions, mercury concentrations in these fish will be higher than in macroinvertebrates. In March 1996, mosquitofish and grass shrimp at U3 had very similar Hg concentrations (Table 2). However, in the summer, Hg concentrations in mosquitofish were more than double the concentrations in grass shrimp. As predicted, amphipods had relatively low mercury concentrations in comparison to mosquitofish. However, hemipterans had higher Hg concentrations than mosquitofish (Table 2). Hemipterans are predatory insects, and thus may occupy trophic positions higher than mosquitofish.

Mercury concentration data collected in ENP (Loftus et al., 1999) also show the relative concentration trends predicted by the conceptual model (Table 3). Crayfish and chironomids, primarily detritivores, have the lowest mercury concentrations, while grass shrimp and sailfin mollies, primarily herbivores, have higher concentrations. Mosquitofish, which assume a position as predators, have higher mercury concentrations. The slightly higher mercury concentrations in grass shrimp, as compared to sailfin mollies (and also crayfish versus chironomids), may be indicative of their omnivorous ability to take advantage of animal tissue when it becomes available.

Table 3. Mercury concentrations in biota from Everglades National Park (Loftus et al., 1998)

Species	Feeding Behavior	THg (ng/g, wet weight)
Chironomids	detrital omnivores	38
Hyalella	filter feeders	45
Crayfish	detrital omnivores	65
Grass shrimp	periphyton-based omnivores	186
Sailfin Molly	herbivores	105-158
Least killifish	bottom feeding carnivores	258
Mosquitofish	omnivores	250-320



## **SUPPORTING CARBON AND NITROGEN STABLE ISOTOPE EVIDENCE**

The traditional method of food web investigation focused on the determination of gut contents, and is still a valuable tool used today. More recently, carbon and nitrogen stable isotope analyses of plants and animals have been used to establish relative trophic (i.e., consumer-diet) relations among various organisms (Fry and Sherr, 1984; Peterson and Fry, 1987). This method is based on the observation that selective metabolism of the lighter isotopes during food assimilation and waste excretion causes animals to become isotopically enriched in  $^{13}\text{C}$  and  $^{15}\text{N}$  relative to their diets. Thus, at each ascending trophic level there is a 1-3‰ (permil) increase in  $\delta^{15}\text{N}$  and 0-1‰ increase in  $\delta^{13}\text{C}$ .

Based on their analysis of several thousand aquatic samples for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the Everglades, Kendall et al. (in review, in prep) concluded that sites with longer hydroperiods usually had predominantly algal-based food webs, whereas food webs in shorter hydroperiod sites usually had significant contributions from macrophyte debris. Furthermore, depending on hydroperiod, some sites appeared to show a seasonal shift in food web base (Kendall et al., in review). Hence, the stable isotope data support the main tenet of the conceptual model developed in this paper: that there is seasonality in food webs. Available stable isotope data from U3 can be used to test specific hypotheses about changes in animal diets in the conceptual model (Figure 10).

Because of large variations in the  $\delta^{13}\text{C}$  of aquatic plants in the Everglades,  $\delta^{15}\text{N}$  values were found to be much more useful in identifying differences in trophic levels than  $\delta^{13}\text{C}$  values. On the other hand, because macrophytes almost always had significantly higher  $\delta^{13}\text{C}$  values than periphyton, seasonal differences in the  $\delta^{13}\text{C}$  values of animals could be used to determine whether the dominant base of the food web was algal or detrital (combined macrophyte and algal) (Kendall et al., in prep.).

### **Seasonal Patterns of Stable Isotopes in Macroinvertebrates and Mosquitofish**

According to this model, in March mosquitofish feed on zooplankton in an algal-based food web, whereas at the beginning of the wet season in July, the food web is mainly detritus-based with no available zooplankton. Therefore, the conceptual model predicts that mosquitofish  $\delta^{15}\text{N}$  in March should be higher than in July. Indeed, a decrease in the  $\delta^{15}\text{N}$  values for mosquitofish of about 3.5‰ between March and July at Site U3 is consistent with a seasonal shift in trophic level.

The model also predicts that crayfish  $\delta^{15}\text{N}$  should be higher than for mosquitofish at the end of the dry season, because crayfish may be significant predators on mosquitofish during the small fish die-outs of the dry season. Bulk crayfish  $\delta^{15}\text{N}$  values are about 4‰ lower than those of mosquitofish during the dry months of December 96 and June 98. Assuming that the  $\delta^{15}\text{N}$  of bulk crayfish (flesh plus carapace) is no more than 1-2‰ lower than the  $\delta^{15}\text{N}$  of crayfish flesh (Kendall et al., in prep.), the isotope data suggest that mosquitofish is not a dominant source of food for crayfish during these times.

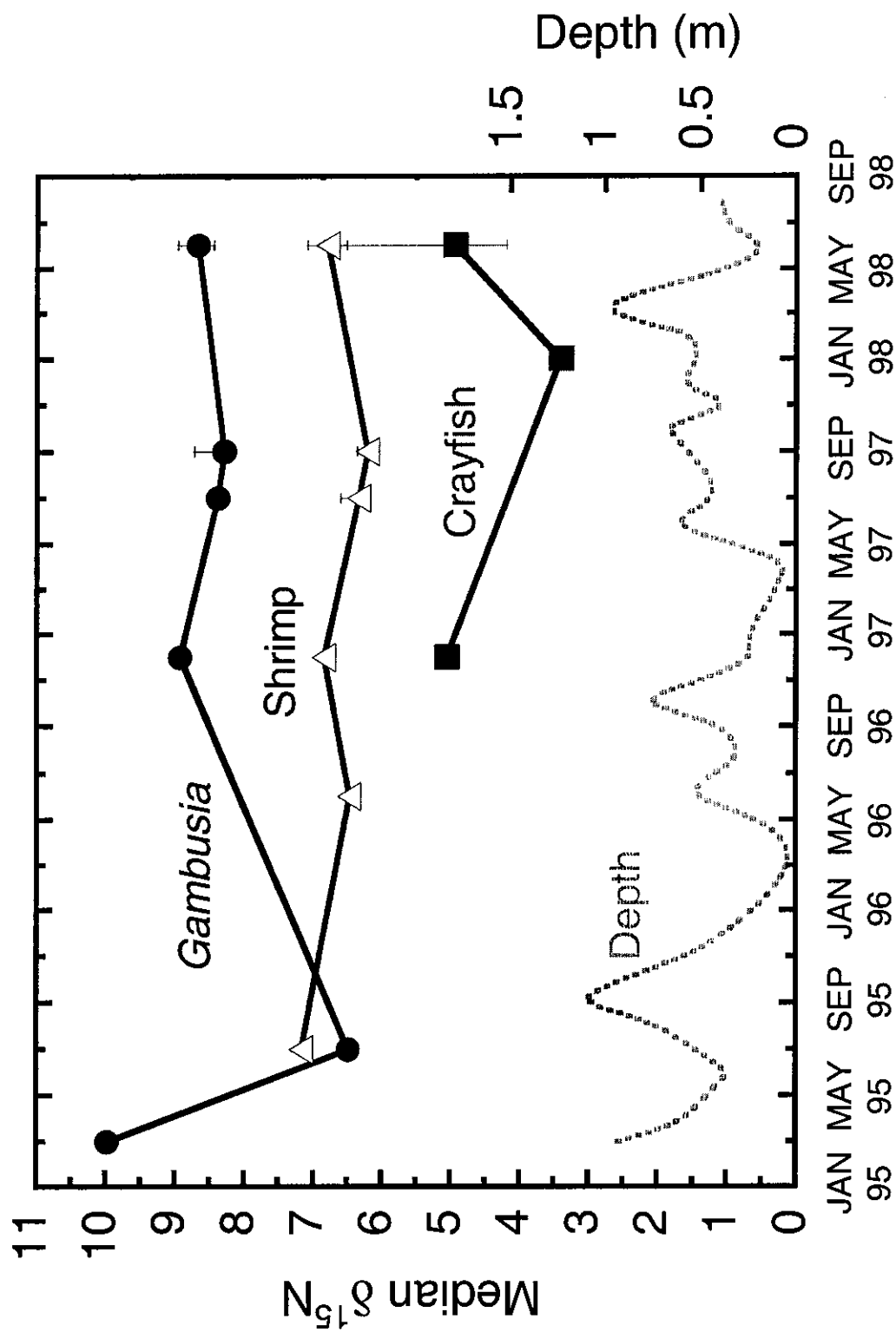


Figure 10. Median  $\delta^{15}\text{N}$  values for select species suggesting changes in animal diets.

The model predicts that sunfish collected later in the wet season should have higher  $\delta^{15}\text{N}$  than those collected earlier, because the longer conditions are wet, the more time there is to develop an algal-based food web with more trophic levels. This is consistent with the available isotope data. Both Spotted sunfish and Redear sunfish  $\delta^{15}\text{N}$  values increase 0.7‰ and 1.0‰, respectively, between the fifth (September 1997) and ninth months (June 1998) of the wet season (depths >0.4 m throughout).

Seasonal shifts in the  $\delta^{15}\text{N}$  of algae and other plants at the base of the food web make it difficult to determine whether temporal changes in the  $\delta^{15}\text{N}$  of animals are due to seasonal differences in trophic level or environmental conditions (Kendall et al., in review). One solution is to report the  $\delta^{15}\text{N}$  values of fish relative to some organism at a different (usually lower) trophic level (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999). If this “normalization” is done, the model predicts that  $\delta^{15}\text{N}$  differences among mosquitofish, shrimp, and crayfish should vary with season due to changes in food sources. During the dry season, the three animals should eat primarily detritus and thus show similar  $\delta^{15}\text{N}$  values. However, as the wet season progresses and an algal-based food web develops with more trophic levels, mosquitofish should switch to a more carnivorous diet with corresponding increases in  $\delta^{15}\text{N}$ . Shrimp may also eat at higher trophic levels as water levels increase, whereas crayfish should generally continue to eat only detritus throughout. As shown in Figure 10,  $\delta^{15}\text{N}$  differences among crayfish, shrimp, and mosquitofish are essentially constant across seasons (except for a mosquitofish versus shrimp reversal during July 95), indicating no seasonal shifts in relative trophic level. This finding casts doubt on whether the seasonal differences in  $\delta^{15}\text{N}$  seen for mosquitofish and sunfish (described earlier) are caused by trophic differences or environmental differences.

The model predicts seasonal differences in the dominant base of the food web for many animals. An increase in the contribution of algal-derived carbon to food webs as the water levels increase should cause a decrease in the  $\delta^{13}\text{C}$  of animals. There is an apparent inverse correlation of the shrimp-mosquitofish  $\delta^{13}\text{C}$  difference with water depth, and a positive correlation with the number of months of inundation since the start of the wet season. Therefore, there does seem to be a seasonal influence on the dominant base of the food web, although the specific processes are unknown at this time.

### Relative Stable Isotope Values for Mosquitofish and Macroinvertebrates

The model predicts that, in general, mosquitofish eat at a higher trophic level than shrimp, and that shrimp eat at a higher trophic level than crayfish because mosquitofish are omnivores, shrimp are primarily herbivores (but can eat at higher trophic positions), and crayfish are detritivores. If these relative trophic positions are accurate, then we would expect that  $\delta^{15}\text{N}_{\text{mosquitofish}} > \delta^{15}\text{N}_{\text{shrimp}} > \delta^{15}\text{N}_{\text{crayfish}}$ . The available  $\delta^{15}\text{N}$  data for U3 (Figure 10) generally confirm these species-specific differences in trophic levels. For example,  $\delta^{15}\text{N}_{\text{mosquitofish}}$  is ~4‰ higher than  $\delta^{15}\text{N}_{\text{crayfish}}$  in December 1996 and June 1998. Also,  $\delta^{15}\text{N}_{\text{mosquitofish}}$  is ~2‰ higher than  $\delta^{15}\text{N}_{\text{shrimp}}$  in December 1996, July 1997, September 1997, and June 1998. However,  $\delta^{15}\text{N}_{\text{mosquitofish}}$  is ~0.7‰ lower than  $\delta^{15}\text{N}_{\text{shrimp}}$  in July 1995. It is important to keep in mind that these shrimp and crayfish  $\delta^{15}\text{N}$  values are for the whole “bulk”

organism (i.e., not corrected for the  $\delta^{15}\text{N}$  of the carapace, which should increase  $\delta^{15}\text{N}$  of tissue by 1-2‰).

### Correlation of Fish Lengths and $\delta^{15}\text{N}$ Values

It is well known that as organisms grow larger, their mouths also get larger; hence, it is reasonable to assume that their trophic level would increase as they get larger. Based on this reasoning, one would expect that there would be a correlation between fish length (i. e., age) and  $\delta^{15}\text{N}$  value (i.e., trophic level), especially for small fish less than one year in age. Gut contents data showed that dietary shifts to larger prey were apparent as predators increased in size (Loftus et al., 1998). However, an examination of the  $\delta^{15}\text{N}$  values of 5-10 mosquitofish collected by the EPA REMAP program at each of ~70 Everglades marsh sites sampled in September 1996 showed no correlation of  $\delta^{15}\text{N}$  and length (Kendall et al., in prep.). This lack of correlation might be because the mosquitofish populations sampled during September 1996 showed little range in length, however, preliminary evaluation of the  $\delta^{15}\text{N}$  values of mosquitofish collected in May and September 1999 at REMAP sites also showed no evidence of a correlation. There was also no evidence of any length- $\delta^{15}\text{N}$  correlation for sets of sunfish, gar, warmouth, and largemouth bass collected at or near U3 in 1996-97 by the FFWCC (Kendall et al., in prep.). One explanation for the lack of the expected correlations of length and  $\delta^{15}\text{N}$  for fish is the high degree of seasonal and spatial differences in  $\delta^{15}\text{N}$  at the base of the food web. This variability in  $\delta^{15}\text{N}$  is apparently much larger than seasonal differences in trophic position.

## DISCUSSION

The conceptual model for basing the Everglades food web at least partially on detritus is not unprecedented. In wetlands, most of the photosynthetically active radiation is intercepted by emergent vegetation before reaching the water. Furthermore, the highly colored waters of wetlands reduce light penetration, effectively reducing phytoplankton growth. Consequently, the main energy source to the water column of wetlands is litter falling from the canopy (Sato et al., 1982). Additionally, there is a body of literature showing that macrophytes that were incapable of supporting grazers while alive were capable of supporting a food chain as detritus (Dickinson and Pugh, 1974). This transformation is accomplished through mechanical and microbial action that disintegrates plant fragments and, more importantly, increases the proportion of proteins with decreasing particle size (Odum and de la Cruz, 1967; Heald, 1971). Consequently, in ecosystems where live plant matter is of poor quality, detritivores have a clear advantage over grazers.

Crayfish and grass shrimp are well suited to take advantage of the detrital pathway. The ability of crayfish and grass shrimp to act as detritivores, survive drought, and reproduce early in the wet season makes them better suited than small fish to exploit marshes which regularly experience drydown. Species capable of surviving and reproducing within a particular routine of disturbance gain a competitive advantage over those species that cannot (Reiners, 1983). In the Everglades, the competitive advantages of crayfish and grass shrimp result in these species probably becoming an early and important portion of the diet of large predators.

Unlike crayfish and grass shrimp, mosquitofish cannot survive the routine drydowns and thus must colonize areas as they become more habitable. The food sources available to these colonizers are limited because the algal community does not establish itself until the rainy season has created sufficient habitat. Once established, the algal community may become the base for an autotrophic food web. However, many organisms can take advantage of only portions of the periphyton (e.g., diatoms), because other components such as blue-green algae are unpalatable. Therefore, to take full advantage of available resources, mosquitofish will assume positions as carnivores in the autotrophic food web. The shift from detritivores to autotrophic-based carnivores has several effects: (1) an increase in total mercury exposure in biota associated with biomagnification through the food web; and (2) an increase in the percentage of methylmercury associated with bioconcentration through the food web. These factors combine to increase the concentrations of both total mercury and methylmercury in the mosquitofish population.

The conceptual model predicts seasonal changes in both (1) the base of the food web (algal vs detrital) and (2) the trophic levels of organisms. While the available Hg data provide support for seasonal changes in trophic levels for some organisms, the available  $\delta^{15}\text{N}$  data show little evidence for seasonal changes in trophic levels. However, as discussed previously, the  $\delta^{13}\text{C}$  differences between mosquitofish and grass shrimp at U3 show some evidence for seasonality in the base of the food web. A companion study of spatial differences in the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of mosquitofish and periphyton at sites sampled by the EPA REMAP program in 1996 (Kendall et al., in prep, in review) also showed little evidence of spatial differences in trophic position ( $\delta^{15}\text{N}$ ) for mosquitofish in the Everglades but significant spatial differences in the apparent base of the food webs ( $\delta^{13}\text{C}$ ) leading to mosquitofish. Hence, there is ample evidence for differences, both temporal and spatial, in food webs across the Everglades. However, it is not yet clear how much of these differences in food webs are caused by seasonal shifts in food web base versus actual differences in trophic position.

Landscape scale research in the Everglades found that trophic position did not explain mercury concentration in mosquitofish (Stober et al., 2001). These results have led to the conclusion that while mosquitofish diet and Everglades food webs show seasonal and spatial variability, the effect on mosquitofish mercury concentrations is small compared to other factors (Stober et al., 2001). However, the data set used for this analysis was derived from samples collected over the entire Everglades with only three sampling events in three years. Additionally, the landscape scale data cannot take into account local variations in mercury deposition, methylation and hydroperiod. Consequently, the seasonal changes in feeding and mercury discussed here, that appear to occur on the order of weeks to months, and vary in timing and magnitude between sites, are unlikely to be detected at such a scale.

## Parallels to Other Systems

As described in the conceptual model, the dry season effectively eliminates both algae (the base of the autotrophic food web) and populations of small fish. In contrast, macroinvertebrates, particularly crayfish and grass shrimp, are capable of surviving and taking advantage of the vast amounts of macrophyte detritus. This advantage lasts through the dry season and into the early wet season when the ecosystem changes in response to deeper waters. Kushlan (1976) recognized such a shift in Everglades National Park where longer hydroperiods resulted in a

change from highly diverse detritus-based omnivore communities to predator-driven systems with decreased abundance of forage fishes.

Similar shifts from detrital to algal based food webs have been noted elsewhere; wetlands, in particular, seem prone to such switching. For example, in the Tasek Bera Swamp of Malaysia, the base of the food web routinely switches from autotrophic to detrital in response to monsoons which damage and wash away submergent vegetation (Mizuno et al., 1982). African swamps which experience periodic drought and associated decreases in water depth also shift between autotrophic and detrital based food webs (Denny, 1985).

Similar seasonal changes in mercury concentrations have been observed in other wetlands that have drastic hydroperiod changes. In the Tapajos River of the Amazon, total and methylmercury concentrations in zooplankton were observed to double and triple, respectively from the dry season to the wet season (Roulet et al., 2000). In contrast, piranha and catfish collected from the Brazilian Pantanal showed a 50% reduction in mercury concentrations during the wet season in comparison to the dry season (Hylander et al., 2000). This reversal of peaks from the rainy season to the dry season may have to do with differences in soil mercury concentrations, different soil types, or increased dilution of mercury inputs from upstream gold mining areas (Hylander et al., 2000).

## CONCLUSIONS

This paper presents a conceptual model of the Everglades food web that is dynamic and responsive to seasonal changes in hydroperiod. Seasonal changes likely play an important role in determining the sources of food in the Everglades, as well as the complexity and structure of the food web. The patterns of mercury concentrations in small fish and grass shrimp in unenriched areas are likely the result of the combination of several factors. Sediment mercury concentrations and *de novo* methylation rates may be the primary mediating factor determining the amount of methylmercury in the system, but the degree of transition from detrital food webs to autotrophic food webs is likely to control the bioaccumulation and biomagnification of all mercury species. The seasonal shift in feeding behaviors by mosquitofish affects mercury concentrations by changing the number of trophic levels serving to bioconcentrate methylmercury in mosquitofish prey and exposing them to the anaerobic microbial community, a source of methylmercury.

In contrast, crayfish likely do not shift to an autotrophic food web and thus may not be subject to food chain biomagnification of mercury to the extent that mosquitofish are. Consequently, only local mercury concentrations and *de novo* methylation rates may be the driving forces for concentrations in crayfish. Similarly, grass shrimp also feed close to the base of the food web, but unlike crayfish, may take advantage of non-detrital food sources as indicated by seasonal changes in mercury concentration.

Mercury concentrations in sportfish, such as sunfish and largemouth bass, are likely mediated by conditions in deepwater refugia where bioaccumulation through the food web is elevated in comparison to short hydroperiod marshes. However, large-bodied predators often may move from deep waters to short hydroperiod marshes, and may show corresponding short-term decreases in mercury concentration. Thus, the model of short hydroperiod marshes presented

here helps to explain behavior of Hg dynamics when these areas are available to larger fish (i.e. higher water levels).

Current plans to restore the Everglades call for drastic changes to its hydrologic regime. Aspects of restoration, like hydroperiod restoration and increased flows, could have varied effects on bioaccumulation. Because these are complex processes, existing models may not be adequate to predict scenarios outside of the existing set of conditions. Seasonal monitoring of mercury concentrations at representative sites, at multiple levels in the food web, may be necessary to provide sufficient data to assess the current status of the ecosystem. Sentinel species should be selected that are important to higher trophic levels, relatively abundant, responsive to mercury concentrations and capable of maintaining a stable position in the food web. Crayfish, which appear to function as detritivores in the Everglades, sailfin mollies, which are strictly herbivores, and grass shrimp, which are important to the diet of sunfish, seem to meet these criteria. Mosquitofish, while ubiquitous, are omnivores and the contribution of these animals to the upper trophic levels is unclear. Consequently, the usefulness of mosquitofish as a sentinel species is limited.

Despite the fact that the available Hg and stable isotope data appear to fit the conceptual model, the interactions between the various factors are complex enough to warrant the development of a habitat-scale mercury cycling model that takes into account the shift from detrital to algal based food webs. This model could then be linked to an Everglades landscape-scale model and used to predict mercury concentrations in response to restoration scenarios. Such a model is currently in development.

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