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Mercury contamination and its effects in the Everglades ecosystem

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Abstract. The Everglades is an ecosystem that is highly contaminated with mercury, in that concentrations in tissues of virtually all high trophic level fauna exceed or are in the range of human consumption criteria, and of negative biotic effects. In this review the possible sources of mercury, the abiotic and biotic mechanisms of methylation and bioaccumulation, and an analysis of potential effects of current contamination levels on community dynamics, are presented. Sources of mercury include both atmospheric and local deposition, though the proportions of each are not clear. Rates of methylation of mercury are high, geographically variable, and probably sensitive to several abiotic factors, especially the availability of sulfur. Most effects of mercury on biota are likely to be of a sublethal nature. Evidence of effects is prominent for piscivorous birds and mammals, and recent research suggests that population dynamics of fishes and invertebrates also could be affected through endocrine disruption, behavioral changes, and embryonic mortality. The potential for this contaminant to alter community composition and biotic processes seems high, through either bottom-up or top-down mechanisms. This review demonstrates an immediate need for further work on sublethal effects of mercury at virtually all trophic levels, especially at ecologically relevant doses, and under conditions that include multiple natural stresses.

1. Introduction

Contaminants of anthropogenic origin have traditionally been perceived as emanating from point-sources, such as factory and incinerator outfalls, urban centers, and toxic waste dumps. Increasingly, contaminants are being distributed worldwide through atmospheric deposition, oceanic currents, and other global processes. With these much more diffuse sources of contamination, the effects of contamination are acting not only at organismal and local levels, but at levels of biotic communities, ecosystems and regions. The assessment of effects and risk from diffuse sources of contamination therefore increasingly require studies at the level of communities and ecosystems, and will necessarily require an understanding of net effects in a variety of types of biomes.

The purpose of this paper is to present an overview of the currently understood effects of a single contaminant, mercury (Hg), in the Everglades, a shallow, seasonally fluctuating aquatic ecosystem. A focus on ecosystem effects of Hg has been relatively rare. The effects of several contaminants, including mercury, on the ecosys-

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tems of the Great Lakes has been well documented [99], resulting in a comprehensive view of both effects and management actions. However, there are vast differences in the cycling, bioavailability, and biomagnification of Hg between these different bioregions, and it is not obvious that criteria for protecton of biota in one ecosystem are necessarily applicable to another [92]. An in-depth analysis of the Everglades therefore may be a valuable contrast.

The Everglades is probably the first large shallow depression wetland in which Hg dynamics have been studied in breadth and detail, and is also an ecosystem towards which considerable ecological research has been directed [25]. As such, the Everglades may serve as a model for effects of Hg contamination in a class of similar wetlands in the tropics and subtropics of the world [83]. These wetlands may share similar hydrology, seasonal drying patterns, and aquatic animal community structure, and therefore may also show similar Hg cycling and bioaccumulation patterns. Examples include the Pantanal of Brazil, where large releases of Hg from gold mining occur [1], and the Usamacinta-Grijalva river delta in Mexico, where many of the ecological attributes are very similar to the pre-drainage Everglades [104].

The ecology and management of the Everglades has been studied in detail for several decades, with some records of resources or attributes reaching back for over a century [109,119,103,112]. These studies have provided important historical and ecological benchmarks, and a knowledge of biological organization and function upon which to build an understanding of the effects of contamination.

The Everglades is also an interesting example because the biota and ecosystem processes are known to be affected by numerous stressors other than Hg contamination, including altered hydrology, nutrient pollution, barriers to flow and animal movement, effects of introduced plants and animals, as well as effects from outside the ecosystem (summarized in chapters in 25). The Everglades is therefore similar to an increasing number of wetland ecosystems worldwide, that also face ecological degradation from numerous sources [1,31]. The fact that the effect of some of the stressors are known in the Everglades is of value in trying to tease apart the specific effects of Hg.

This review is intended to focus on the Everglades ecosystem, and a comprehensive review of Hg cycling and Hg effects in fish and wildlife is not an intentional part of this contribution. Clarkson [18] has provided an excellent overview of Hg contamination and effects, particularly in humans; reviews of effects of Hg on wildlife have been presented by Eisler [30], Heinz [64], Thompson [135], Wolfe et al. [156], and Wiener and Spry [153].

2. Hg – forms, sources and general toxicity

Hg is a naturally-occurring element that has no known biological function [18]. It has been used by humans for centuries for many medicinal and industrial purposes.

During the recent industrial era, the use of Hg in a variety of manufacturing processes and products has greatly increased compared to previous time periods, resulting in vastly increased releases of Hg to the environment [101]. By modeling Hg in the troposphere, Bergan et al. [8] have estimated that current anthropogenic Hg emissions are at least 30 % as large as natural emissions, and that the global deposition rate has increased by over 50 % since preindustrial times. If re-emission is taken into account, the deposition rate may have tripled, and in industrial parts of the world, deposition rate may have increased a factor of 2–10 during the last 200 yrs.

As a result of this increased deposition and an increasing awareness of Hg's effects, this contaminant has become a major issue in environmental health [18]. When deposited through wet and dry atmospheric processes, Hg is usually in an inorganic state, but may be transformed through biotic processes into an organic, methylated state, the most common form being CH_3Hg. There are important differences between organic and inorganic forms, both in their tendency to bioaccumulate, and in their toxicity. Inorganic Hg is only weakly absorbed in the gut (7–15 %), and much of ingested inorganic Hg is typically excreted from the mammalian body in a matter of hours. In contrast, over 98 % of methylmercury (MeHg) is absorbed by the gut of both birds and mammals [156], and though half-lives vary considerably with species, MeHg can be stored for considerable amounts of time. Inorganic Hg tends to be removed from the blood stream quickly and stored in liver and kidneys, while MeHg is lipophilic, and able to cross the blood-brain barrier. Both forms of Hg are known to produce neurological effects, including malcoordination, paralysis, and death at very high concentrations. Sensitive periods for both inorganic and organic forms of Hg for humans, rats, and birds are generally thought to be during the prenatal period, and MeHg contamination at this stage can result in severe developmental abnormalities in animals and humans [18]. In this review, use of the word "Hg" will refer to measurements of total Hg, and cases where the Hg species are unspecified, whereas mehylmercury will be refered to as MeHg. All measurements reported are on a wet weight basis, unless otherwise noted.

3. The Everglades Ecosystem

The Everglades is a unique waterscape including a variety of freshwater, estuarine and marine habitats, originally extending from north of Lake Okeechobee to the southern tip of the mainland Florida peninsula (originally 10500 km^2, 58, see Figure 1). The Everglades is an extremely flat basin, with very slight elevational drop (3 cm/km) and consequent sluggish water flow (0–1 cm/s) from north to south. Soils are of three main types: thick peats (generally in wetter areas), marl, or exposed limerock, with the whole of the basin underlain by eroded limestone. Rainfall is abundant (130 cm/yr, range 95–270 cm) and highly seasonal, with a distinct wet season beginning sharply in May and tapering off in October, and a dry season from November – April. Surface water levels fluctuate accordingly, with seasonal

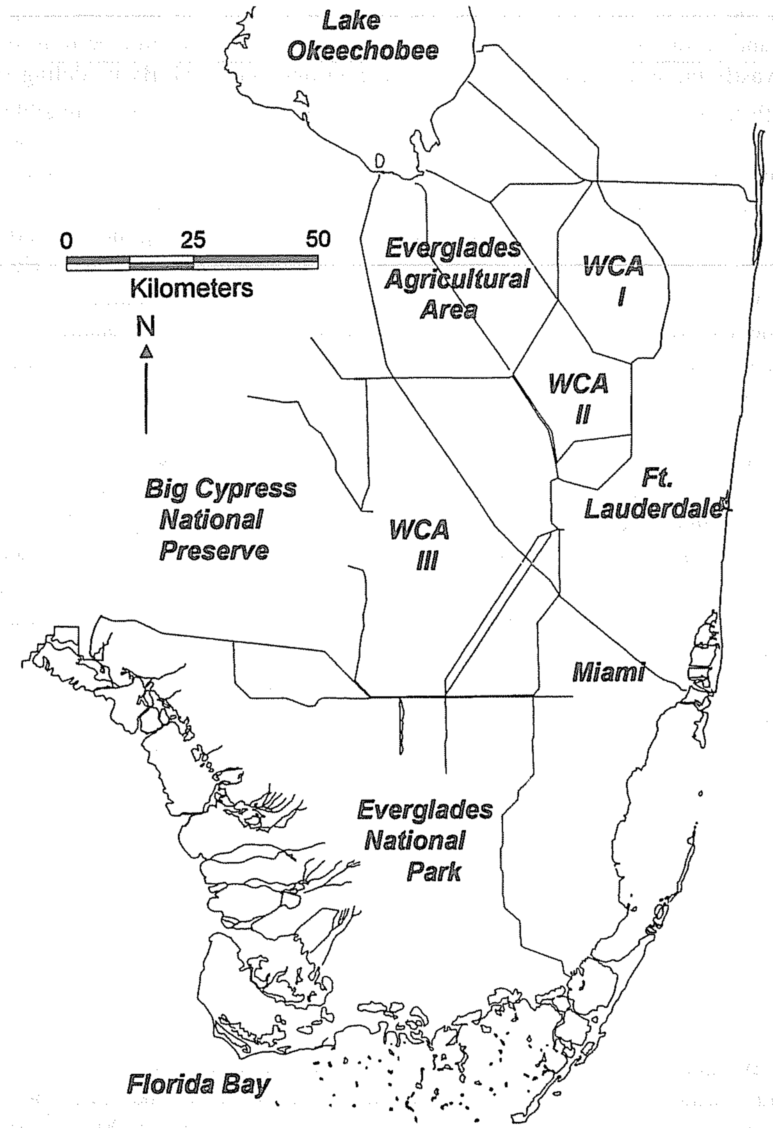

Fig. 1. Map of the Everglades, showing major urban areas, water conservation areas (WCA's), agricultural areas, and preserves.

highs in late summer and fall, and mimima in late spring; average depths of standing water range from less than 1 cm to over a meter in the deepest parts.

Within this seasonal context, however, there is extreme annual variability in weather, and both droughts and floods are common enough that an "average" year is difficult and often meaningless to describe. Everglades waters have historically been extremely clear and oligotrophic [58]. Vegetative associations in freshwater areas include vast areas of sawgrass punctuated by open-water and wet prairies of short emergents, higher elevation tree-islands, and cypress woodlands [58]. In estuarine and marine areas, mangroves are the predominant vegetation.

3.1. Human impacts on the ecosystem

Drainage efforts by humans began in the Everglades in the late 1800's and intensified greatly during the middle of the 19^{th} century, culminating in one of the largest water control projects in the world. By the late 1960's, over one third of the original area of the Everglades had been converted to agriculture or urban housing [58], the marsh had been compartmentalized by an extensive series of dikes and canals, and water flow patterns and hydrology had been radically changed as a result [119,91, 34]. In the freshwater sections of the Everglades, the main management tool has been the impoundment of water into vast shallow pools, called "Water Conservation Areas", where water is stored or released as needed for either urban and agricultural needs, or to counteract flooding in urban areas. This containment has resulted in a reduction in flow, or throughput of water, an increase in ponding effects (comparatively deep, stagnant water bodies), and long hydroperiods.

The effects of hydrological change on biota were dramatic in many cases, including reductions in numbers of wading bird nesting attempts by over 90 % and changes in timing of nesting by several months [103]. Similarly, reduced alligator nesting success has been documented as a result of unseasonal flooding of nests [90], and reductions in fish standing stocks [87,140]. By the late 1980's, it was also recognized that exotic fish and plant introductions had resulted in significant invasions, and sometimes in measurable change in community structure. Effects were also felt strongly in the estuarine and coastal zone, where chronically reduced freshwater flow is thought to have contributed to extremely high salinities, declining sport fisheries catches [137], declining commercial pink shrimp (*Penaeus duorarum*) catches [14], and decreased freshwater flows may have helped create the necessary conditions for a massive seagrass die-off in Florida Bay during the 1990's [160].

The Everglades has also been modified in large degree through nutrient additions, most significantly through inflows of nutrient laden water [24]. Historically an oligotrophic system, the sawgrass –dominated areas of the Everglades are quickly converted to areas of cattail as a result of even small increases in phosphorus concentration in the water. The affected areas, mostly in the northern extremes of the Everglades near water inflows (northern WCA 1, 2, and 3), tend to show higher primary and secondary productivity than pristine marsh, and have a more anoxic root zone and more poorly consolidated peat.

Thus it is clear that the Everglades is currently highly modified by humans, with massive, systematic changes in timing and quantity of water flows, introduced species, and nutrient inputs, resulting in concomitant effects on biota. Thus the biota of the Everglades are impacted by several sources of stress that are geographically widespread in the ecosystem.

3.2. Sources of non – Hg chemical contamination

The southern Florida region is an area of high pesticide use, with one quarter of all pesticide active ingredients being applied at a rate of over 218 kg/km^2 totalling over 15000 tonnes of pesticides and herbicides used per year [95]. South Florida also has the nation's highest per capita usage of municipal solid waste incineration, a potential source of PCB's, dioxins and furans. However, there is only equivocal evidence of contamination in biota from these sources, resulting in large part from a lack of recent surveys. Facemire et al. [33] presented evidence of contamination of Florida panthers (*Felis concolor coryi*) with a variety of pesticides and PCB's, and suggested that this contamination was affecting reproductive success of panthers. Although Ohlendorf et al. [106] found occasional high concentrations of organochlorine pesticides in adult wading birds from south Florida, Spalding and Forrester [121] found no high concentrations of organochlorines in a survey of 80 nestling and juvenile wading birds. Congenital deformities and low hatching success of wading birds have not been noted in south Florida despite intensive and long-term studies of reproductive success [47]. A recent survey of contaminants in canal water in south Florida showed detectable concentrations of ametryn, atrazine, bromacil, hexazinone, metolachlor, norflurazon, simazine, DDD, DDE, dieldrin, alpha-endosulfan, beta-endosulfan, endosulfan sulfate, ethion, ethoprop and three PCB compounds [95].

The southern Florida peninsula is generally considered to be poor in selenium, and high levels of selenium have not been reported for wildlife in the Everglades region. With the possible exception of ungulates [40], selenium deficiencies have not been noted in vertebrates. Nonetheless, selenium can act to ameliorate the effects of Hg contamination, and the paucity of selenium in the Everglades environment may have an effect on the severity of effects there [22]. In nestling and juvenile wading birds, Spalding and Forrester [121] found no extreme hepatic concentrations of lead, cadmium, zinc, or arsenic, with the exception of some high lead values in the vicinity of West Palm Beach.

Thus the only heavy metal in significantly elevated concentrations in Everglades vertebrates appears to be Hg (see below). Although many organochlorine pesticides are found in high concentrations in the more terrestrial Florida panther, there is no evidence that these substances are elevated in other predatory aquatic animals in south Florida. It is significant, however, to note that only a few of the more common compounds have been tested in the surveys that have been done [121], and that the most recent measurements of PCB's and dioxins are from the late 1970's [106]. One of the most obvious critiques about studies of mercury in the Everglades is that they have been done largely in the absence of knowledge about possible interactions with these contaminants.

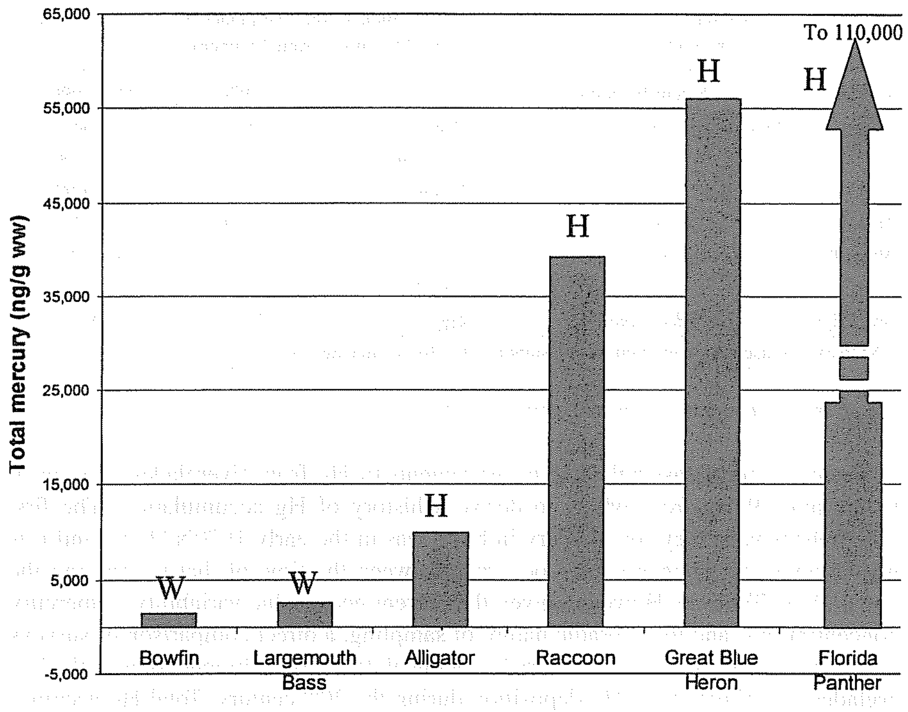

Fig. 2. Total mercury concentrations from livers of vertebrates from the upper trophic level in the Everglades. Sources: Raccoons: [110]; Great blue heron: [132]; Florida panther: [110]; Alligator: [69]; Fish: [146]. W = Whale animal sample, H = Hepatic tissue only.

4. Hg contamination in the Everglades

There is no ambiguity about Hg contamination of Everglades fauna. Although the nature, extent, and effects of contamination in biota are treated in detail in later sections, it is worth noting here that virtually all high trophic level vertebrates that have been examined from the Everglades show high concentrations of Hg. High levels have been reported for both freshwater and estuarine fishes [146,75,44], long-legged wading birds [132,9,117], Florida panthers [110,33], and raccoons [110], (see Figure 2).

The levels and consistency of the contamination in higher trophic level organisms has indicated that Hg is currently elevated in the Everglades food web. A central question of the Everglades mercury contamination problem has been that biota are generally contaminated despite mercury concentrations in water that are within federal and state criteria for contamination [92]. Everglades mercury contamination gained recognition in the late 1980's, and since that time at least $15 million has been spent on Hg research in the ecosystem.

Table 1.
Comparison of total mercury concentrations (ng/g ww) in biota of the Everglades in 1974, with those in the mid-late 1990's. Sources are listed by superscripted numerals.

Species	Scientific Name	Tissue	1974	Mid-1990's
Largemouth Bass	*Micropterus salmoides*	Whole	310[105]	210 – 620[85]
		axial muscle*		500 – 13,50[85]
		Whole		210 – 620[87]
Bluegill	*Lepomis macrochirus*	Whole	220 – 940[105]	479[87]
White Ibis	*Eudocimus albus*	liver		440 – 920[132]
		muscle	1795[105]	
Great Egret	*Ardea albus*	egg	300[105]	400[26]

* Note axial muscle measurements were standardized for a singe age class

4.1. History and sources of Hg contamination

There are embarrassingly few measurements of Hg from Everglades biota prior to the mid-1970s, from which to derive a history of Hg accumulation. The first comprehensive survey for mercury in biota was in the early 1970's [105], and it is not obvious that increases have occurred between the time of that survey and the late 1990's (Table 1). However, given the current geographic variability in mercury concentrations, and the sporadic nature of sampling, a direct comparison of surveys is difficult. Rood et al. [112] used radiochemical dating of sediment cores in the Everglades to estimate total Hg deposition during the 20^{th} century. Total Hg accumulation rates in the Everglades near the end of the century were estimated to have increased on average 4.9 times over rates measured in 1900. While there is the potential for considerable error in the use of sediment cores for paleoecological studies of Hg [54], the rates and timing of deposition estimated by Rood et al. [112] are similar to cores from deep lakes in Sweden and the northern U.S., suggesting a global atmospheric source of Hg.

The principal source of this historical accumulation of Hg is almost certainly from aerial deposition, as has been demonstrated through recent monitoring of an array of air sampling devices throughout Florida [84]. There is no general agreement, however, concerning the relative contribution of local and global sources of atmospherically-deposited Hg. Landing et al. [84] found that bulk deposition fluxes of all trace elements and ions was driven by air masses from outside of Florida, and a specific source for Hg was not identified. However, the sampling used in that study may not have been intensive enough to accurately measure the effect of local sources.

The south Florida area has the nation's highest per capita usage of municipal solid waste incineration, and the prevailing southeasterly wind direction typically carries aerosols from the urban east coast area directly over the Everglades. Using a grid of air sampling stations in the Everglades, Dvonch et al. [28] estimated that municipal waste incineration and oil combustion accounted for 71 ± 8 % of wet hg deposition. Although this estimated magnitude of local inputs to the Everglades Hg budget is not universally agreed upon, there seems to be growing evidence that local inputs are an important component.

4.2. Abiotic controls on Hg availability in the Everglades

Although the identification of sources of deposition are of obvious importance to management of Hg in the Everglades, the questions of within-ecosystem cycling and bioaccumulation are of equal or greater interest from biological and management points of view. Wetlands were perhaps first fully recognized for their unique ability to accumulate, concentrate, and cycle Hg by Zillioux et al. [161], and demonstrations of these abilities in northern temperate zones followed soon thereafter [126,127,67]. Shallow depression wetlands like the Everglades are likely to have Hg dynamics that are markedly different from lakes and streams that have been studied to date [120]. For example, although many studies have emphasized the importance of pH and water chemistry in predicting Hg concentrations in aquatic biota in northern lakes [153], Snodgrass et al. [120] found relatively little influence of water chemistry (sulfate levels and pH) on fish Hg in southeastern depression wetlands. Instead, maximum water depth and hydroperiod were the most important determinants of variation in standardized fish Hg samples, with both relationships being negative. Snodgrass et al. [120] suggested that leaching of Hg from sediments during drying and reflooding was a critical process in explaining Hg bioavailability, and emphasized that methylation of Hg was enhanced during repeated re-exposure of wetland soils. This effect has been previously recognized in numerous cases of flooding or reflooding of reservoirs, followed by pulses of Hg contamination in biota [11]. Thus shallowly flooded, hydrologically dynamic wetlands like the Everglades may generally have high potential for recycling and methylating Hg once it is deposited.

Within the Everglades, the dynamics of Hg and MeHg may be quite different. The major pool of total Hg is probably the sediment, and in an impounded area of the northern Everglades, less than 1 % of Hg was estimated to be stored in vegetation, water or fish [94]. The major pool of MeHg is also sediment, but other pools (fish and vegetation) are relatively more important than is the case with total Hg. In WCA 2 (see Figure 1), MeHg inflows exhibited a strong seasonal pattern, with highest levels entering the impoundment during July, and decreasing amounts during the dryer parts of the season [67]. Total Hg did not show this seasonal pattern.

4.3. Methylation

The process and rates of methylation in the Everglades are of primary concern for understanding contamination in the ecosystem, especially when considering the bioavailability and bioaccumulation of Hg in the food web. Methylation is known to be accomplished by sulfur-reducing bacteria, generally in sediments at or close to the soil-water interface [21,52]. MeHg production rates in the Everglades are substantial, with rates of 1–10 ng/g sediment/day [53]. MeHg concentrations in sediment (0.1–5 ng/g dry weight) varied from 0.2–2.0 % of total Hg. It is signficant that the sites of highest methylation potential matched geographically with MeHg concentrations in biota, since this suggests that production of MeHg drives local bioaccumulation. Similarly, local concentrations in biota can serve as an analog for production.

Methylation rates in the Everglades are maximal at the sediment surface, and were never observed in the water overlying cores [53]. Periphyton mats (extensive demersal mats of mixed algae) are also important sites for methylation [19], probably because the mats support an active microbial sulfur cylcle. Floating vegetation has also been found to be an important site of methylation in the Brazilian Pantanal [57]. Since periphyton is an important foodstuff for primary consumers in the Everglades [15], the link between production of MeHg and consumption at the base of the food web may be quite direct.

Of central interest to the study and management of Everglades Hg contamination is how methylation and bioavailability of Hg are affected by water quality, particularly water chemistry and nutrient inflows. In wetlands, MeHg production is probably maximal at intermediate levels of sulfur availability [52] – at high sulfur concentrations, MeHg production seems to be limited by the presence of sulfide, a byproduct of the bacterial metabolic cycle [53]. At low concentrations of sulfur, bacteria may be limited by sulfate availability. The Everglades currently receives much of its inflows from agricultural sources, and sulfur is frequently added to agricultural soils in south Florida in order to increase phosphorus availability in the heavily organic soils. It has been suggested that this source of sulfur has contributed to the Hg problem in the Everglades, though the range in which methylation is truly limited by sulfur has not been determined. Further, it is not clear whether sulfur was historically limiting to the methylation process in the Everglades.

The role of nutrients in the methylation process is also poorly understood. The Everglades was historically thought to be an extremely oligotrophic aquatic system, limited largely by the availability of phosphorus [24]. Inflows of phosphorus in the northern Everglades from upstream sources during this century have substantially changed the botanical community composition of the grassland communities [24], have increased the secondary productivity of affected areas [128], and established strong decreasing north-to-south gradients in phosphorus, sulfate and dissolved organic carbon (DOC) concentrations [129,53]. Along this gradient, Hg and MeHg concentrations increase, apparently in inverse proportion to nutrient and sulfate concentrations [129,67,53].

However, it is not obvious that any particular aspect of this eutrophication leads to decreased Hg or MeHg concentrations, and these apparent relationships may not be causally related. While eutrophy in lakes is frequently associated with decreased Hg concentrations in fish [125,85,153], trophic status was not related to Hg in standardized fish samples in an array of southeastern depression wetlands [120].

Vaithiyanathan et al. [141] found that rates of methylation and demethylation were both higher in eutrophic areas of WCA 2 than in areas less exposed to nutrient deposition. However this relationship did not seem to be due to the phosphorus gradient within WCA 2, since methylation/demethylation ratios did not correlate with soil phosphorus concentrations. Similarly, Marvin-Dipasquale and Oremland [89] found that demethylation rates in Everglades sediments (0.02–0.5 ng/gm dry sediment/d) were not affected by phosphate addition, and were inhibited slightly with nitrate addition, adding further evidence that nutrients may not be affecting methylation rates directly. At present then, it remains unclear whether exogenous nutrients are affecting methylation and therefore Hg availability in the Everglades. This question is of considerable importance, since abatement of nutrient imputs is a costly, but possible management option.

Hg concentrations in biota are often inversely proportional to dissolved organic carbon (DOC) concentrations in water [147], in part because certain Hg species are likely to sorb onto DOC particles and thus become unavailable [125,17]. Effects of DOC on Hg availability have been found for some Everglades DOC fractions [107, 16], and MeHg in Everglades canal waters apparently decreases with increasing DOC concentrations [129]. However, Stober et al. [129] found that total Hg concentrations in water and in mosquitofish (*Gambusia holbrooki*) in canals followed an opposite pattern, with concentrations highest in the northern areas that also had highest DOC and nutrient concentrations. Hurley et al. [67] found that total Hg concentrations in Everglades water samples were not related to DOC concentrations. Thus although DOC concentrations may affect total Hg and MeHg concentrations in water, the relative importance of DOC in affecting Hg concentrations in Everglades canals and marshlands is not clear. It has also been suggested that Hg levels may be lower in eutrophic areas of the Everglades because of "biodilution", or the increased density of large particles of organic material on which Hg may sorb. However, this hypothesis does not predict the strong geographic relationship between MeHg production and MeHg levels in biota that has been observed in both eutrophic and oligotrophic areas of the Everglades [53].

4.4. Summary of physical aspects of hg contamination

In summary, it seems generally agreed that the Everglades has received considerable increases in Hg deposition during the 20^{th} century, in a pattern that mimics worldwide increases in Hg deposition. This similarity, and recent measurements both suggest that the majority of deposition has been from aerial sources. However, there is also evidence that local sources may currently contribute substantial amounts to aerial deposition, and there is no general agreement on the history, or the proportional contributions of Hg from local sources. This is an important area for further research, since local sources can be regulated, whereas global sources cannot.

The Everglades shows high production rates of MeHg, and it is likely that sulfur plays an integral role in determining methylation rates. In this, the Everglades

Table 2
Mercury concentration in water, soil, and plants from the freshwater Everglades. Tissue samples are expressed on wet weight basis.

		Mercury concentration			
Species or Medium	Mercury measured*	Mean	s.d.	range of means	Source
Water	MeHg			0.03 – 0.49 ng/l	20
	THg			0.75 – 5.78 ng/l	88
	MeHg			0.39 – 0.41 ng/l	88
Sediment	THg			18 – 468 ng/g	88
	MeHg			0.81 – 6.39 ng/g	88
Periphyton	MeHg			0.03 – 0.44 ng/g	20
	THg			0.77 – 4.02 ng/g	20
Diatoms	THg	90.44 ng/g	49.58		88
Green Algae	THg	76.58 ng/g	66.32		88
Vascular plants	THg			13.08 – 57.85	88

* MeHg = Methylmercury, THg = Total mercury

seems to follow the pattern already defined for coastal salt marshes. The roles of nutrient pollution and DOC in methylation or bioavailability of Hg or MeHg are less obvious, but there are probably multiple abiotic controls on Hg methylation rates and the bioavailability of Hg. Despite the likely general importance of drying events to the cyclic reliberation of Hg from sediments, this aspect of Hg cycling has received little attention in the Everglades. This seems an important omission, since the Everglades is very shallow, hydrologically dynamic, and some or all of the marsh surface may dry during the majority of years. Further, hydrology is one of the parameters that can be manipulated. It is this propensity for rapid recycling of Hg in sediments through repeated wetting and drying that most thoroughly distinguishes bioavailability in the Everglades from that most lacustrine systems studied to date.

5. Patterns and extent of Hg contamination in biota

5.1. Hg in vegetation

Everglades emergent vegetation does not appear to be an important pool of Hg [94], though dry-deposited Hg is not washed off of foliage, and leaves may accumulate Hg as they age [56], (Table 2). No effects of Hg have been documented for plants in the Everglades. Hg in emergent vegetation is probably not an important factor in Hg dynamics in the food web, simply because there are relatively few grazers of the generally coarse living emergent wetland vegetation [58]. Any contributions of vegetation to Hg dynamics in the food web are therefore likely to result

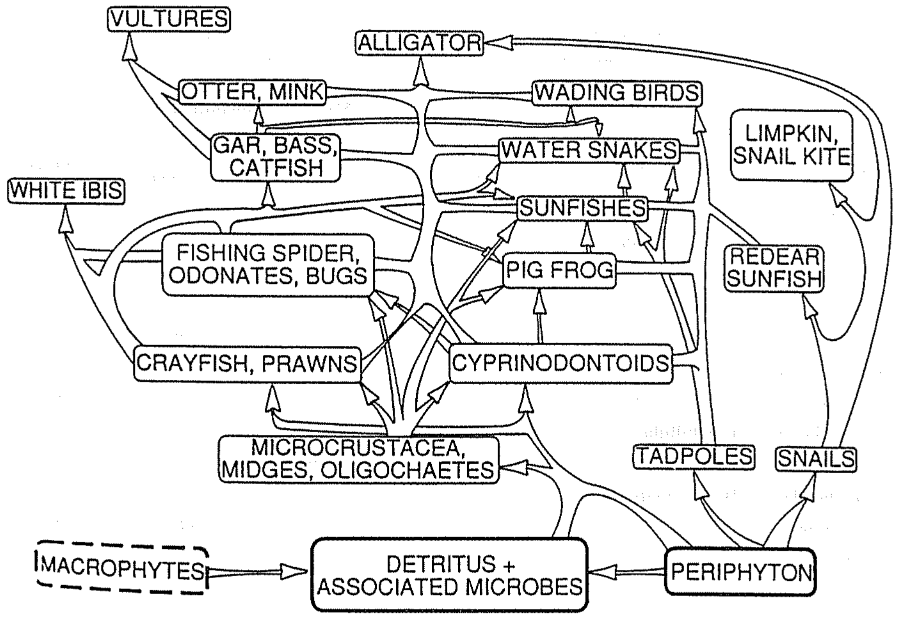

Fig. 3. Diagram of the aquatic food web that stems primarily from detritus and periphyton. After Gunderson and Loftus 1993.

from decomposition of detritus by detritivores, and it seems likely that these processes would be driven largely by abiotic soil and water chemistry dynamics.

5.2. Food web analysis of Hg bioaccumulation

A detailed analysis of animal food habits and Hg transfer through the Everglades food web [88] has shown a number of important features that help explain the bioaccumulation of Hg in the ecosystem, despite relatively low mercury concentrations in water. Most of the consumers eat either detritus or some component of periphyton mats (Figure 3). Although the ratio of MeHg to total Hg is low in sediments and periphyton [20,88,53] the transfer of MeHg as a result of consumers feeding in sediments may be fairly direct. The majority of animal biomass in the Everglades is composed of macroinvertebrates and fishes, and their standing stock therefore represents a large pool of Hg within the faunal component of the ecosystem [140].

In general, Hg concentrations increase with trophic level in the aquatic food web [88,128,20, see Tables 3–5, Figure 3], with contamination levels lowest among invertebrates and highest in vertebrate tertiary consumers. For example, total Hg in apple snails (*Pomacea paludosa*), is appropriately low for an algal grazer (mean of 0.056 mg/kg ww, 29), and concentrations in snails are not thought to constitute a risk either for the snails or for its predators, including the endangered Snail Kite (*Rostrhamus sociabilis*). Among other Everglades invertebrates, however, there is a

Table 3
Mercury concentrations in invertebrates from the freshwater Everglades.
All concentrations expressed as ng/g wet weight.

Species	Scientific name	Form measured*	Mercury concentration: Mean	s.d.	Range of means	Source
Molluscs						
Apple Snail	*Pomacea paludosa*	THg	19	8		88
Freshwater Clams	*Villosa sp.*	THg	19	3		88
Spiders	Arachnida	THg			136 – 148	
Aquatic insects						
Midge larvae	Chironominae	THg	38	14		88
Odonate larvae	Libelullidae	THg	92	76		88
Water beetles	Notonectinae	THg	96	34		88
Diving beetles	Belostomatinae	THg	127	51		88
Hemipterans		MeHg			3.0 – 61.8	20
Crustaceans						
Cladocera		THg	46	20		88
Ostracoda		THg	53	51		88
Copepoda		THg	63	32		88
Amphipods		MeHg			2.9 – 3.3	20
Shrimps	*Paleomenetes paludosus*	MeHg			0.6 – 50	20
Shrimps	*Paleomenetes paludosus*	THg	186	78		88
Crayfish	*Procambarus fallax*	THg	64	16		88
Crayfish	Unidentified	THg	50			104

* MeHg = Methylmercury, THg = Total mercury

wide range of Hg values, with some predaceous hemipteran beetles having total Hg concentrations on the same order as many omnivorous fishes [88,20, Table 3]. Many of the insects, crustaceans, and small fishes show wide ranging diets depending on available foods, and these animals can be characterized as generalist feeders. Spiders show relatively high levels of Hg among invertebrates (See Table 3) probably because they are predatory, and because they are often foraging on emergent aquatic insects, many of which may themselves be predatory as aquatic larvae (eg, dragonfly larvae). Spiders may be eaten by some of the smaller Everglades fishes, and some small bodied fishes are highly carnivorous, resulting in high bioaccumulation factors from water to some of the small fishes (10×10^2 to 10×10^4). Some of the smaller bodied omnivores in the Everglades are probably bioaccumulating at over one million times water concentrations [88,128].

Among Everglades fishes, the importance of trophic feeding seems paramount in determining Hg exposure, though Hg concentrations also increase with size of fish [88,44, Table 4]. Loftus et al. [88] also emphasized the importance of ontogenetic

Table 4
Total mercury concentrations in fishes from the freshwater Everglades. All concentrations expressed as ng/g wet weight basis.

Common name	Scientific name	Tissue	Mercury concentration			Source
			Mean	s.d.	Range of means	
Mosquitofish	*Gambusia holbrooki*	Whole	150			86
Mosquitofish	*Gambusia holbrooki*	Whole			247 – 321	88
Lake chubsucker	*Erimyzon sucetta*	Whole			119 – 210	88
Yellow bullhead	*Ameiurus natalis*	Whole			443 – 755	88
Golden Topminnow	*Fundulus chrysotus*	Whole			171 – 460	88
Pike killifish	*Belenesox belizanus*	Whole	595	147		88
Sailfin Molly	*Poecilia lattipinna*	Whole			105 – 157	88
Flagfish	*Jordanella floridae*	Whole	85	23		88
Warmouth	*Lepomis gulosus*	Whole			479 – 777	88
Warmouth	*Lepomis gulosus*	Whole			0.14 – 1.01	88
Bluegill	*Lepomis macrochirus*	Whole	478	383		88
Bluegill	*Lepomis macrochirus*	Whole			220 – 940	105
Spotted Sunfish	*Lepomis punctatus*	Whole			271 – 447	88
Spotted Sunfish	*Lepomis punctatus*	Whole			14 – 250	86
Mayan cichlid	*Cichlasoma uropthalmus*	Whole	393	122		88
Florida Gar	*Lepistosteus platyrhincus*	Whole	1,161	301		88
Florida Gar	*Lepistosteus platyrhincus*	Whole	1,270	551		86
Largemouth Bass	*Micropterus salmoides*	Whole	967	216		88
Largemouth Bass	*Micropterus salmoides*	axial muscle			500 – 1350	86
Largemouth Bass	*Micropterus salmoides*	Whole			21 – 62	86
Largemouth Bass	*Micropterus salmoides*	Whole	310			86
Bowfin	*Amia calva*	Whole	1,460	1,060		85

shifts in diet for explaining bioaccumulation and body burdens in fishes. For example, some fishes like the lake chubsucker (*Erimyzon sucetta*) are predatory when young, but switch to grazing when adult.

Among predatory fishes, bioaccumulation factors (BAF's) may be quite high, owing to complex aquatic food webs (Figure 3). BAF's from water to tissues in Florida gar (*Lepisosteus platyrhynchus*) and largemouth bass (*Micropterus salmoides*) are in the range of 7×10^6 to 10×10^{10}, and often have mean Hg concentrations in flesh that exceed the human consumption criterion for Florida [146,84,85].

5.3. Geographic distribution of Hg in fauna

Hg concentrations in Everglades biota have been used to describe geographic differences in Hg bioavailability within the ecosystem. The two most prominent biomarkers have been mosquitofish [128], and growing feathers from nestling wading birds

Table 5.
Total mercury concentrations in reptiles, amphibians, birds and mammals from the freshwater Everglades. Concentrations are expressed as ng/g, wet weight basis, unless otherwise noted.

			Mercury concentration			
Common name	Scientific name	Tissue	Mean	s.d.	Range of means	Source
Reptiles:						
Alligator	*Alligator mississippiensis*	liver	41,090*	5,900		69
Alligator	*Alligator mississippiensis*	egg	540			105
Amphibians:						
Frogs	Unidentified	whole	130	62		86
Leopard frog	*Rana sphenocephala*	whole	70			105
Birds:						
White Ibis	*Eudocimus albus*	liver	420		440 – 920	132
White Ibis	*Eudocimus albus*	muscle	1,795			105
White Ibis	*Eudocimus albus*	egg	68			105
Roseate Spoonbill	*Ajaia ajaja*	liver	550		160 – 5,380	132
Roseate Spoonbill	*Ajaia ajaja*	feathers	200			9
Tricolored Heron	*Egretta tricolor*	liver	720		120 – 4,960	132
Little Blue Heron	*Egretta caerulea*	liver	430		230 – 730	132
Great Blue Heron	*Ardea herodias*	liver	2,310		210 – 74,240	132
Great Blue Heron	*Ardea herodias*	feathers	3,500			9
Great White Heron	*Ardea herodias occidentalis*	feathers			4,700 – 8,200	9
Great White Heron	*Ardea herodias occidentalis*	liver			600 – 59,400	124
Great Egret (adult an	*Ardea albus*	liver	970		180 – 18,840	132
GE (nestling)	*Ardea albus*	blood			800 – 1,200	117**
GE (nestling)	*Ardea albus*	feathers			9,700 – 16,000	117**
GE (nestling)	*Ardea albus*	feathers	7,100			9
Great Egret	*Ardea albus*	egg	400			26
Great Egret	*Ardea albus*	egg	300			105
Anhinga	*Anhinga anhinga*	egg	620			26
Mammals:						
White-tailed deer	*Odocoileus virginiana*	liver			<100	110
Florida Panther	*Felix concolor coryi*	liver			50 – 110,000	110
Florida Panther	*Felix concolor coryi*	hair			280 – 130,000	134
Florida Panther	*Felix concolor coryi*	kidney			160 – 9,100	134
Raccoon	*Procyon lotor*	liver	24,000			110
Raccoon	*Procyon lotor*	liver	39,300			33
Raccoon	*Procyon lotor*	muscle	7,170			33
Raccoon	*Procyon lotor*	muscle	18,000			110
Humans	*Homo sapiens*	hair	3,620	3,000	1,280 – 15,570	39

* Concentration expressed on dry weight basis, ** Concentrations standardized for age of chick

[45,9,117]. The mosquitofish have been of tremendous utility as geographic markers of Hg contamination because they are nearly ubiquitous in the freshwater Everglades, and because they move relatively little during their short (< 4 months) lifetimes [88]. Feathers of wading bird nestlings are also of use in sampling larger geographic areas. During the time that young wading birds are confined to the nest, they are known to be fed from food sources found within the foraging range of parents (generally < 25 km, 6). Feathers are known to be an important excretion tissue, especially for growing birds [136,122], and if feathers are collected while still attached to the blood supply, they may be used to infer Hg concentrations in other tissues [122].

One of the most consistent findings about MeHg contamination in Everglades biota has been strong geographic variation. Nearly all studies have described increasing concentrations along a rough north-south gradient [53,20]. Stober et al. [128] described strong nonrandom distributions of Hg in mosquitofish sampled on a gridlike system, which showed that high concentrations were located in regions, rather than specifically along a single gradient. This variation probably is a direct result of differences in in situ methylation rates, since variation in methylation rates and in mosquitofish Hg concentrations vary together geographically [53,128]. Although the sampling distribution for wading bird feathers is on a much coarser scale than that of fish, the distribution of high and low values follows that of the mosquitofish with apparent fidelity. These "hotspots" of high mercury concentrations have been described in central-northern WCA 3, and northern Everglades National Park [128,88]. In addition, Beyer et al. [9] described an additional area of high Hg values in eastern Florida Bay, on the basis of feathers of nestling Great White Herons (*Ardea herodias occidentalis*). The estuarine regions of the Everglades also show contamination of sediments and gamefishes [75], though no areas of particularly high concentrations have been reported.

Hg in Everglades fauna has probably been most extensively documented in fishes. Perhaps the first recognition of Hg contamination arose from a statewide survey of Hg in largemouth bass [146], in which Hg concentrations from the Everglades routinely exceeded human consumption criteria (Table 4). Since that time, bass from the Everglades have consistently produced the highest concentrations in the state (Lange pers. comm., 32).

6. Effects of Hg contamination on biota

6.1. General

There is abundant evidence that the Everglades is an ecosystem heavily contaminated with Hg, and nearly all trophic levels of biota show readily measurable Hg concentrations in a pattern that implies a process of dietary bioaccumulation. The vast majority of research to date has, however, been focussed heavily on determining the source, species, fate, distribution and transport of Hg in the ecosystem. Considerably less work has been oriented towards understanding the effects of Hg on the species and communities of the Everglades, a problem that is reflective of the field of wildlife Hg contamination in general [156]. In fact, with the possible exception of birds and Florida panthers, an analysis of the possible and potential effects of Hg is limited to comparing known effects of similar levels of Hg on similar organisms in laboratory situations. In many cases, even these comparisons are lacking.

Although matching of Hg effects in different species and locations can quickly degrade into speculation, such an effort can serve two important purposes from the perspective of the Everglades example. First, in the context of uncertain information on effects, it is in most situations far more responsible to outline potential effects than to underestimate them simply because of poor quality information. Second, such an analysis may constructively reveal the location of critical gaps in our knowledge of responses of animal populations to Hg, and of promising areas of further research. It is hoped that this will allow a targeting of future research to correct these inadequacies. In the following analysis, I have considered those contaminant responses that are known to, or are likely to scale up to affect population dynamics and community structures of animals, since it is these levels of change that are most likely to cause ecosystem-wide effects.

6.2. Hg Effects on plants

It seems unlikely that the levels of Hg in plants in the Everglades are in most locations high enough to result in acute or even measurable effects on plant growth, survival, or community structure (Table 2). It is possible, however, that Hg could be high enough at specific sites to cause measurable effects in plants, due to bioaccumulation patterns. For example, Klekowski et al. [77] discovered an association between high Hg concentrations in sediment at specific sites in a Trinidadian mangrove swamp, and elevated mutation rates in the leaves of mangroves (*Rhizophora mangle*). Sediments with high Hg concentrations were found only underneath roosts of Scarlet Ibises (*Eudocimus ruber*), which aggregate seasonally in the swamp, and may acquire Hg loads in their tissues by spending part of their year in Hg-contaminated sites on the South American mainland. Hg may accumulate under the roosts either through feces, or shed feathers. Since Everglades wading birds, which also carry high body burdens of Hg, create areas of concentrated fecal deposits in Everglades wading bird colonies [46] and do shed feathers in roosts prior to and following breeding, it seems quite possible that the same phenomenon could be occurring at wading bird roosts and colonies in the Everglades. No research has been directed to date towards measuring effects of Hg on plant life in the Everglades.

6.3. Hg effects on invertebrates

The potential for effects of Hg on Everglades invertebrate populations are generally difficult to evaluate, simply because there has been relatively little work devoted to the subject, and because there is such a large range of tissue concentrations, depending on species and location. There are also large differences among invertebrates in the proportion of total Hg that is organic, making it difficult to readily apply the results of lab studies that have used only a single form of Hg for dosing. Most lab studies of Hg's effects on invertebrates have incorporated Hg into the water as a dosing method, rather than putting Hg into the diet. This further exacerbates the problem of transposing exposure levels in lab and field conditions. When evaluating ecosystem effects, invertebrates are not usually considered as a candidate for effects, simply because they do not usually accumulate high concentrations; attention is instead focussed on tertiary consumers [64,156]. While this tradition is supported by a knowledge of effects at the top end of the food web, it is also somewhat surprising, since sublethal behavioral and tissue-level effects in invertebrates and fishes have been frequently suggested as bioindicators of contaminants, including heavy metals [2,4,27,131].

There is frustratingly little information on the potential effects of Hg on invertebrates at low, chronic doses, and given the potential for a wide range of sensitivities among organisms to Hg, it is not clear that invertebrate populations are free from effects. It is especially important to consider possible effects of Hg on macroinvertebrates in the Everglades, since snails, insects, shrimps, and crayfishes in varying degrees may accumulate considerable Hg body burdens, and since these animals form the foodstuffs of vertebrates. Any population effects at the level of the food source has the potential for bottom-up interactions.

Naimo [97] reviewed the effect of heavy metals on fresh-water mussels, and concluded that sublethal effects can be manifested at levels of less than half the lethal concentrations. Naimo also suggested that the widespread decline of species diversity in North America may be partly related to low level, chronic exposure to heavy metals. Mussels native to the Everglades (*Elliptio buckleyi*) exposed in the lab to MeHg in water (5.0 and 10.0 ng/l) showed no bioaccumulation or effects of Hg exposure, but mussels exposed to diets of algae raised in contaminated water (10 ng/l) showed signficant bioaccumulation. Animals in this latter group were found to have decreased circulating estradiol concentrations [76]. Mussels collected from sites contaminated with mercury and pesticides in the Everglades showed decreased body condition indices, decreased mantle glycogen, reduced testosterone in males and reduced estrogen in females, and reduced likelihood of breeding by comparison with cleaner sites [113]. These studies suggest that in the south Florida environment, ambient mercury exposure levels in mussels are likely to decrease reproductive potential and may act as an endocrine disrupter.

Because of their demersal feeding habits, crayfishes are known to be exposed to heavy metals in sediments, and in so doing also accumulate histological damage to the hepatopancreas [3]. These exposure and histological damage characteristics are reliable enough to cause crayfishes to be recommended as biomarkers for heavy metals in aquatic systems [143,12]. Using radiolabeled MeHg incorporated into food, Headon et al. [60] measured MeHg assimilation efficiencies in crayfish at over 96 %, and estimated the biological half-life in crayfish at 1000–2000 days, or nearly the entire lifetime of individual animals [60]. This finding is somewhat in contrast to earlier studies of Hg retention [158] which suggested relatively little uptake of MeHg from food, followed by rapid (20 d) depuration from the hepatopancreas. These results suggest that uptake and retention may be variable, but that the potential exists for crayfishes to be efficient bioaccumulators of MeHg, and that short-term exposures may have lasting effects.

Experimental exposure of *Procambarus clarkii* to high, but sublethal concentrations of inorganic Hg in water (0.25 mg/l) led to decreases in protein, lipid and caloric concentrations in gills and hepatopancreas, and glycogen concentration in muscle [138]. Following starvation, crayfishes exposed in this fashion also showed an inhibited ability to replenish energetic reserves in the hepatopancreas [139]. These reserves are typically most often used during critical biological events such as molting and reproduction. Exposure to high but sublethal concentrations of Hg in water (0.1 mg/l) has also been linked with increasing heart rate and arhythmicity in crayfishes [131], and altered limb regeneration and molt cycles in crustaceans [148]. Although these effects are documented for water concentrations that are at least an order of magnitude higher than the concentrations found in the Everglades (Table 2), it is not clear whether the effects may also be found at lower concentrations in water, or that similar effects might be induced through ambient dietary consumption of Hg in the Everglades. It is difficult to compare exposure rates from Hg dosed in water vs. diet, since resulting concentrations in body tissues were not given in these water-exposure studies.

Sublethal exposure to Hg may have an effect on reproductive potential of crayfishes. Reddy et al. [108] found that both cadmium and inorganic Hg inhibited *in vivo* ovarian maturation in *Procambarus clarkii*, probably by directly inhibiting protein synthesis in the ovaries. However, it is difficult to translate the levels of Hg applied *in vivo* to circulating levels in Everglades crayfishes. Metals, including cadmium and inorganic Hg have been implicated generally in interruptions of crustacean endocrinology [36].

Grass shrimp (*Paleomenetes pugio*) reared in a site with high Hg concentrations and exposed to 0.01 mg/l MeHg were more likely to be captured by fish predators than were controls from the same site [79].

Thus there is evidence that inorganic and organic Hg are readily bioaccumulated by large crustaceans generally and in the Everglades specifically (Table 3), and that the half-lives of Hg in these organisms may include the lifetime of the animal. It is not clear what the sublethal effects of accumulated Hg actually are for large crustaceans experiencing dietary exposure levels in the Everglades, but there is clearly the potential for this contaminant to affect reproduction, energy mobilization and storage, and survival. Crustaceans are abundant organisms in the Everglades food web [88,71], and are often an important foodstuff for large fish, mammals, and wading birds [82,98]. Depending entirely on the frequency and intensity of effects under field conditions, Hg could either be having little effect on invertebrate communities, or could be strongly affecting the entire food web. Given that shrimp, crayfishes, and predatory aquatic insects show Hg concentrations in the range of many of the fishes, it seems prudent in the future to aim research at understanding potential effects of Hg exposure on reproduction of key invertebrates, like crayfishes, shrimps and insects.

6.4. *Effects of Hg on fishes*

In contrast to the invertebrates, the effects of Hg on fishes have been studied more extensively [see 153]. Fish may absorb Hg from water through gills, but the vast majority of Hg accumulation in fishes is from diet, probably contributing > 90 % of MeHg accumulated [125,59]. Nearly all of the Hg in axial muscle of fishes is MeHg [10], though inorganic Hg is more often found in liver and kidney. Fishes do not appear to have a mechanism for demethylating Hg, nor are they able to detoxify MeHg via binding with metalothioneins, either as adults [153] or juveniles [151].

The primary toxic action of MeHg in fishes is through degeneration of the central nervous system, leading to malcoordination, inability to feed, diminished responsiveness, and eventually, abnormal movements, brain lesions and death [153]. There have been no observations of direct toxicity in Everglades fishes, though studies to date have not been of a type likely to have detected any of the less extreme behavioral manifestations. Although the direct toxicity of Hg has been well studied in fishes there has been relatively little work on the level of Hg contamination that results in sublethal impairment of behavior. This is a critical gap, since changes in behavior may well result in changes in survival, feeding, growth, and population dynamics. It is also likely that sublethal effects are likely to occur at chronic exposure levels that are far lower and more often ecologically relevant than those that cause direct toxicity.

Growth, development and survival of fish eggs and embryos are far more sensitive to MeHg than are any functions in adult forms, and effects may be seen at less than 1% of water concentrations that are directly toxic to adults [153]. Most of the MeHg exposure for eggs and embryos is derived from maternal sources [61], and this source probably poses greater risks than waterborne Hg. Thus Hg exposure for eggs and juveniles reflects maternal exposure [61,150]. Whitney [152] found reduced hatching success and survival of walleye embryos having a range of 0.015 to 0.058 ug/g total Hg, as compared with eggs having 0.002–0.013 ug/g. The concentrations of Hg in eggs of Everglades fishes have not been measured, but given the concentrations in maternal tissues, fish eggs from the Everglades could be within this range of values.

Early embryonic and juvenile exposure to Hg may also affect development and behavior ("behavioral teratology", 150,149). At dietary MeHg levels similar to those experienced by adult predatory fishes in the Everglades (0.1–1.0 ug/g in food, see Table 4), Friedmann et al. [49] found that MeHg impaired growth of juvenile male walleye (*Stizostedion vitreum*), resulting in reduced mass and length. This reduction in growth may be related to a more common finding of reduced feeding activity in Hg-dosed fishes [153]. Fjeld et al. [37] found that embryonic exposure of grayling (*Thymallus thymallus*) resulting in yolk-fry concentrations of 0.27 ug/g and greater led to reduced foraging efficiency in adult fish of 3 yr age. In competitive foraging experiments, these animals caught 2–6 times less prey than did control fishes, and reduced survival was suggested as the probable consequence of these effects in the wild. Similar effects on mummichogs (*Fundulus heteroclitus*) have been found at somewhat higher embryonic exposure (5–10 ug MeHg/l, 149), and in wild populations of mummichogs at contaminated sites [118]. Sublethal MeHg intoxication may result in reduced movement behavior, possibly as a result of an inhibitory effect of Hg on serotonin excretion [118].

Behavioral alterations through Hg exposure may also affect the likelihood of predation. Kania and O'hara [74] found that adult mosquitofish exposed to 0.01 mg inorganic Hg/l (resulting in whole-body concentrations of 0.67 mg/kg, similar to the high end of the range for Everglades mosquitofish; Table 4) showed an impaired ability to avoid predation by largemouth bass. Similar effects have been found at higher mercury exposure levels with populations of mummichogs exposed as embryos to MeHg [118,159]; the increased exposure to predators was a result of MeHg-induced hyperactivity. The notion that Hg contamination can result in selective predation on Hg-contaminated fish and shimp suggests a mechanism by which biomagnification of Hg can be enhanced. This effect has not been modeled.

Sublethal exposure in fishes may also lead to reproductive impairment. Friedmann et al. [49] found that dietary MeHg (described above) led to reduced testicular growth in male walleye, and reduced plasma cortisol levels in both sexes, indicating that reproductive potential, endocrine function, and health may be reduced in a wild situation. There is also evidence that endocrine function is affected in adult fishes. Arnold [5] implanted adult Nile tilapia (*Oreochromis niloticus*) with pellets that released methylmercury slowly into the abdominal cavity over a period of 9 months, resulting in final concentrations in muscle of 7.0 mg/kg and 3.2 mg/kg (high dose, females and males, respectively), 0.8 and 0.6 mg/kg (low dose) and 0.3 and 0.3 mg/kg (controls). Within sexes, significant differences were found between controls and low dose groups in estrogen concentration (females), testosterone (males) and estrogen-testosterone ratios (both sexes). Adult males produced less testosterone, and adult females produced less estrogen than controls, at levels of mercury contamination that are within the range of concentrations known from wild-caught fish in both the Everglades and the Okefenokee swamp [5]. Gross et al. [55] have also found effects of mercury on the endocrine system of largemouth bass. Adult fish were dosed in captivity with methylmercury to resulting tissue concentrations of 2.5–3.0 mg/kg. By comparison with control fish, dosed male fish had significant decreases in plasma 11-ketotestosterone, whereas dosed females showed decreases in plasma estradiol and vitellogenin. No differences were seen in gonadal histology of dosed fish of either sex in this short-term study, however, and the reproductive consequences of these hormonal changes are unknown. Over 25 % of adult bass in south Florida have greater body burdens than the dosed fish. There has also been some evidence of abnormal sex ratios in adult largemouth bass in areas of the Everglades with high mercury concentrations (T.S. Gross, pers. comm.), though there has been no evidence other than association to link mercury exposure with sex ratio abnormalities.

These studies imply strongly that mercury at ambient levels in the Everglades may act to disrupt endocrine function, and possibly affect breeding potential in large, piscivorous fishes. For smaller fishes, there may be embryonic effects, as well as changes in behavior that lead to increased mortality by predation. The potential for effects on reproduction are of particular interest, both because of the relatively low concentrations of mercury apparently required for effects, and because small changes in the productivity and densities of small fishes in a low-productivity, oligotrophic system like the Everglades could affect community structure, especially of piscivorous fishes and birds.

Hg contamination may also affect fish populations by affecting selection of life history characteristics and genetic structure. Weis and Weis [150] have demonstrated that populations of mummichogs exposed chronically to high levels of MeHg develop, through selection, a tolerance to the effects of embryonic MeHg exposure (developmental abnormalities, low hatching success, reproductive effects, and cytogenetic effects). However, this development of resistance to embryonic MeHg effects was associated with an increased susceptibility of juveniles to inorganic Hg, and adults displayed, slower growth, weakness, lowered fecundity, and reduced longevity. Thus although populations of animals stressed by MeHg may, through selection, develop a tolerance to some of the effects of that stress, the tolerance may result in tradeoffs in life history parameters that may ultimately decrease productivity. Mulvey et al. [96] and Tatara et al. [133] have found that similarly high Hg exposure in mosquitofish leads to changes in the allele frequencies of populations at a single locus (*Gpi-2*). During the first several months of their experiment, Hg exposure resulted in reduced population size, male-biased sex ratio, differential mortality of small individuals, and selection for reduced female fecundity. After 2 years, these differences had disappeared, but evidence of biased selection based on genotype at the *Gpi-2* locus remained. Exposure rates in water were very much higher than those measured in the Everglades, and it is difficult to translate water exposure to dietary exposure levels.

In summary, there seems reasonable evidence to conclude that many species of fishes in the Everglades are exposed to dietary mercury concentrations that may result in effects on behavior, reproduction, exposure to predation and possibly, altered population structure. The extent to which these potential effects actually apply in the Everglades, however, has not yet been demonstrated.

6.5. *Effects on reptiles and amphibians*

Of this group, alligators seem most obviously at risk. Although alligators are cold blooded, in the Everglades they are exposed to high temperatures for much of the year, occupy a high position in the food chain, have long lifespans and, for much of their life histories, a piscivorous diet [72]. Hg concentrations from Everglades alligators have been repeatedly identified as being the highest in the southeastern United States, with mean hepatic mercury concentrations in excess of 10 mg/kg (Table 5, 62, 69). Heaton-Jones et al. [62] found that muscle concentrations of total Hg in alligators in the Everglades often exceeded state (0.5–1.5 mg/kg) and federal (1.0 mg/kg) guidelines for human consumption. Although no signs of toxicosis (hepatic, neurologic, or renal degeneration) have been detected in alligators to date, there also have been few studies of sublethal effects of free-ranging animals.

Very little is known about the effects of Hg on other reptiles and amphibians. Hg concentrations in frogs have not been found to exceed human health standards to date, though surveys have not been comprehensive. Ide et al. [68] reported that 50 ng/l Hg applied to eggs of the anuran *Xenopus laevis* reduced survival to 0 % by 7 d post-treatment. This level of Hg contamination is probably at minimum 5 times higher than Everglades water contamination levels and therefore poorly applicable to Everglades frogs. However, the effect was concomitantly strong, and the possibility exists that at lower concentrations Hg can have substantial effects on embryonic survival.

Snakes may be more resistant. Garter snakes (*Thamnophis sirtalis*) tested by Wolfe et al. [156] showed no health or reproductive effects even with concentrations of up to 200 mg/kg food. However, no other studies have been done to date on this group of animals, and it is difficult to conclude much about their sensitivity from a single study.

The alligator is considered a keystone species in the Everglades because of its abundance, trophic level and ability to dig holes and ponds that function as dry-season refugia for other aquatic animals [90]. While there have been no obvious effects of mercury reported in amphibians and reptiles in the Everglades, there also has been very little effort directed at looking for effects. The ecologic role of amphibians in the Everglades, and of mercury effects at current exposure levels, is virtually undocumented.

6.6. Effects of Hg on birds

The effects of high exposure rates of MeHg on birds have been relatively well researched, and comprehensive reviews of specific studies have been authored by Scheuhammer [114], Heinz [64], Thompson [135], and Wolfe et al. [156]. MeHg is known to affect the central nervous system in adults and young, and is able to penetrate the blood-brain barrier, resulting in brain lesions and central nervous system effects. In birds, acute MeHg poisoning is indicated by reduced food intake leading to weight loss, progressive weakness, malcoordination, inability to fly or walk, and in severe cases, liver and kidney disease, and brain lesions.

MeHg is a potent embryo toxicant in birds, and relatively low concentrations in the egg can sometimes result in embryonic death, and eggshell thinning [35,130, 65]. Exposure of embryos to Hg through contamination of adults can also lead to abnormal chick behavior, such as reduced responsiveness to maternal calls and hypersensitivity to frightening stimulus in ducklings [63,65], as well as brain lesions and death. Similarly, in wild common loons (*Gavia immer*), percent of time spent chick brooding was negatively correlated with blood Hg levels [100], though it was unclear whether the behavior of adults, chicks, or both was affected. Unfortunately, it has been difficult for logistical reasons to extend these studies of chick behavior to include measurements of survival in the wild.

MeHg exposure may also affect behavior and fecundity of adult birds. Adult mallards (*Anas platyrhynchos*) fed 0.5 mg/kg in their diet (dry weight) showed a higher percentage of eggs laid outside nestboxes, decreased clutch size and productivity of nestlings [65]. This level of maternal exposure is roughly equivalent to 0.06 mg/kg body mass/d (Heinz pers. comm), and is similar to the level of exposure of adult-sized great egrets (*Ardea albus*) in the Everglades (0.8 mg/kg/d, 44).

Links between Hg exposure and reproductive success of fisheating birds have been difficult to establish in the wild, in part because of the logistical difficulty of isolating the effect of Hg from the myriad variables that may affect reproduction. For example, there appears to be a link between Hg exposure and reproduction in common loons [7,93], but this finding is confounded by a close negative relationship between lake productivity and Hg concentrations in fish.

There is some evidence that MeHg affects survival of young and adult birds. Van der Molen et al. [142] suggested that during a period of severe winter weather in Holland, Hg contamination predisposed grey herons (*Ardea cinerea*) to mortality, though the evidence was associative rather than experimental. Similarly, elevated Hg values have been found in tissues of emaciated loons [115,23], but it is difficult to tell if this result was an effect of Hg – induced impairment, or whether the process of tissue wasting simply resulted in higher hg concentrations [135].

The ability to directly apply the results of these studies to piscivorous birds in the Everglades is severely constrained by large differences in methodologies, Hg dose rates, Hg species involved, and by inherent species-specific differences in sensitivity [51,135]. However, of all the groups of biota affected by exposure to Hg in the Everglades, birds are virtually the only one in which sublethal effects have been investigated within the Everglades ecological context.

Of all biota in the Everglades, piscivorous wading birds are thought to be at greatest risk of Hg contamination, based on their exposure levels, and the risk inferred from the duck studies cited above [72]. Sepulveda et al. [117] showed that Hg concentrations in nestling Everglades wading birds were higher than for nestlings of any fisheating bird so far measured in the world. Hepatic Hg concentrations in the larger, more piscivorous wading birds (great blue herons *Ardea herodias*, great egrets) have frequently exceeded the thresholds of 20–30 mg/kg suggested by Thompson [135] and Heinz [64] for acute effects of MeHg poisoning (Table 5). Hepatic Hg concentrations in most birds examined from the Everglades exceed the 5 mg/kg suggested by Wolfe et al. [156] and Spalding et al. [124] for sublethal effects in waterbirds [121,117]. Feathers of Everglades wading birds often exceed the 20 mg/kg suggested by Scheuhammer [114] to reflect a diet that results in substantial risk to wetland birds [9], and feather concentrations in the Everglades frequently fall in the range of values (5–40 mg/kg) associated with impaired reproduction in fisheating birds. The dietary concentrations measured (mean of 0.41 mg/kg, 44) correspond to the range in which Barr [7] found reproductive impairment in common loons. Thus there seems little question that the birds in the Everglades are exposed to high concentrations of Hg through their diet, in the range of Hg exposure in which other species in other locations have shown reduced reproduction or survival.

Several authors have reported that the most obvious and sensitive endpoint of Hg contamination in birds is embryonic mortality [65,114], and egg concentrations as low as 3 mg/kg total Hg have been suggested as thresholds for adverse effects [156]. However, in some studies, even very high concentrations of Hg in eggs have not been associated with reproductive or developmental abnormalities. Vermeer et al. [144], for instance, found no reduction in hatching success of herring gull (*Larus argentatus*) eggs at concentrations of 2.3–15.8 mg/kg. Similar lack of hatching impairment has been found in other studies where eggs had high or very high concentrations [50,78,66]. Thus there may be wide species-specific differences in the susceptibility of embryos to mortality and deformities as a result of Hg burden.

Eggs of piscivorous birds in the Everglades have not shown particularly high concentrations of Hg (range of means 0.06–0.60 mg/kg total Hg; 105, 26, see Table 5). Although the apparently low Hg levels in eggs are based on a small sample of species (anhingas *Anhinga anhinga*, wood storks *Mycteria americana* and great egrets), these species sampled are known to feed exclusively on large fishes and thus represent high end of the range of exposure. There have been no indications of poor hatchability among Everglades wading birds (mean of 91–95 % depending on species, 41). However, the measurement of hatchability has in many years been confounded by frequent abandonment of nests by wading birds [43]; those nests abandoned are not included in measurements of hatchability. If nests with infertile eggs are abandoned more often than chance, this may have introduced a bias which results in an artificially high estimation of hatching success. In a study of wood stork eggs with geometric mean concentrations of 0.22 mg/kg total mercury, Fleming et al. [38] found no indication that either hatchability or fledging success were affected.

Similarly, there has been little evidence of embryonic deformities in the Everglades population. Of 2160 nestlings examined, Spalding and Forrester [121] found only 0.46 % with any kind of deformities. The weight of evidence (low egg Hg burdens, high hatching success, low rates of teratogenesis) therefore seems to indicate that Hg exposure in eggs in Everglades birds is probably not high enough to be affecting embryonic processes acutely. However, the ability to detect effects of Hg on embryos has been limited to an imperfect measurement of hatching success, and a lack of gross developmental abnormalities. Further research should concentrate on the histological, behavioral, or immunological effects of embryonic Hg exposure.

It seems somewhat more likely that Hg would have effects on nestlings and fledgling birds through dietary exposure posthatching. This conclusion arises from the apparent lack of effects on embryos, high concentrations measured in the diet of nestlings, and a growing body of evidence that the postfledging period is one of particular sensitivity to Hg. By measuring food consumption, species composition of food, and species-specific concentrations in prey over a period of four years, Frederick et al. [44] estimated that great egret nestlings in the Everglades consume an average of 0.41 mg MeHg/kg diet (annual range 0.37–0.47 mg/kg diet). During the period of maximum growth (nestling through independence), young great egrets consumed approximately 4.3 mg MeHg, or about 4.3 mg/kg body mass (fledged young weigh approximately 1 kg).

The consequences of this level of dietary intake of Hg have been examined in several field and lab studies. Williams [154] estimated the effect of Hg on appetite by measuring food intake in wild nestlings at colonies with different exposure to mercury. Hg in growing feathers was significantly and negatively correlated with food consumption. Using an experimental approach, wild nestlings were dosed orally once every 3 d with gelatin capsules in order to establish a group receiving 1.76 mg MeHg/kg food, and a group receiving the 0.41 mg MeHg/kg food typical of an unsupplemented Everglades diet. The higher level of dietary Hg resulted in a significant reduction in food intake, though the average absolute amount of reduction was small (< 6 gm food/d) and the disparity in food consumption between the two groups did not result in measurable growth differences. The survival of these groups of birds was followed during the 6 months postfledging using radio telemetry [116]. The vast majority of mortalities occurred during the first three months, and there were no significant differences in mortality between dose groups. However, the dose groups were likely to have been confounded, since subsequent research (below) with captive birds demonstrated that between the end of Hg dosing at 28 d of age, and fledging (> 60 d of age), the Hg-dosed birds would almost certainly have depurated much of the extra Hg they had been given, through feather growth. Due to the increased mobility of older chicks, it was impossible to catch and dose wild nestlings past 28 d of age. Thus it remains unclear whether Hg has an effect on juvenile survival.

Spalding et al. [124] provided evidence that Hg levels in the Everglades may predispose juvenile great white herons (*Ardea herodias occidentalis*) to disease. This subspecies of the great blue heron is restricted to nesting in Florida Bay, and juveniles regularly emigrate through the Everglades from natal areas during the postfledging period. Spalding et al. [124] followed the fates of postfledging birds as they emigrated and became exposed to MeHg in variable degrees in the Everglades. A strong association was found between total hepatic Hg concentrations of birds found dead, and tendency to die of chronic diseases, with a suggested threshold for disease susceptibility of 5 mg/kg total hepatic Hg.

The effects of exposure of nestling great egrets to Everglades dietary levels of MeHg have also been measured during a controlled captive rearing experiment

[122,123]. MeHg was administered orally in a blind fashion to groups of birds at doses of 0, 0.5 and 5.0 mg MeHg/kg food, with the 0.5 mg/kg food group the most similar to the 0.41 mg/kg dietary exposure estimated for wild birds [44]. By comparison with controls, low-dose (0.5 mg/kg diet) birds ate significantly less, had lower fledging masses, dingier feathers [122], altered liver and muscle enzyme profiles [45], tended to seek lower-energy behaviors (lethargy), and showed a decreased willingness to hunt live prey [13]. There was also histological evidence of physiological and immunological responses, including lower packed-cell volumes, increased lymphocytic cuffing in a skin test, increased bone marrow cellularity, decreased bursal wall thickness, decreased thymic lobule size, and increased perivascular edema in lungs in the low-dose birds compared to the control birds [123]. Although none of the low-dose birds died during the experiment, and all showed good fat reserves by the end of the experiment (14 weeks), the laboratory situation provided for *ad libitum* food, few opportunities for physiological stress, and few or no disease challenges. The low packed-cell volume and immunological effects (as well as the earlier work by 124) together suggested that young Everglades birds would be more susceptible to disease than birds receiving no Hg, while the low fledging weight, reduced appetite, lethargy and decreased willingness to capture live prey suggested that birds on an Everglades diet would be less likely to survive.

The timing of these effects in the captive birds further suggested that young birds were largely protected from the effects of Hg. With the exception of low packed-cell volume, the effects on low-dose birds were not evident until week 9. Similarly, despite massively higher Hg intake rates, birds in the high dose group did not show significant differences from the control or the low-dose group until 10–12 wk of age, at which time they began to develop weakness, malcoordination, and severe ataxia, and eventually all had to be euthanized. The sudden onset of effects due to Hg in both dose groups were accompanied by the normal cessation of feather growth, and rapid increases in blood Hg concentrations. Growing feathers are a major excretion route for birds, and the most plausible explanation for the timing of effects was that young birds were protected from the effects of MeHg as long as feathers were growing. Once feather growth largely stopped, the birds were exposed to increasing physiologic concentrations of Hg, and so developed symptoms of sublethal or lethal Hg toxicosis [122].

Taken together, the field and lab studies of great egrets suggest a sensitive period for MeHg effects shortly following fledging. At that time, physiological levels of Hg are suddenly elevated due to the cessation of feather growth. At levels of dietary consumption typical of nestlings in the Everglades, this results in decreases in appetite, lethargy, weakness, decreased mass gain, and various physiological and organ changes that may contribute do an increased susceptibility to disease. All of these changes are occurring at or near the time of fledging, when young birds are normally facing the multiple stresses of learning to forage alone, enduring exposure to diseases and predation, and emmigrating from natal habitats, resulting in a period of the highest potential mortality of their lifetimes [73,116]. Finally, the lab studies were done under conditions that eliminated most of the normal stressors, and it is likely that many of the effects would occur at lower thresholds in the wild [123]. For these reasons, it is strongly suspected that exposure of nestlings to Everglades diets is likely to result in increased juvenile mortality. This biotic scenario is generated largely as a function of the dynamics of feather growth in altricial or semi-altricial nestling birds, and it is likely that similar timing of effects may occur in young of most fish-eating birds.

The impact of this potenial mortality at the population level is unknown, because the increase in mortality induced by MeHg exposure in the Everglades has not been measured in the presence of normal stressors. However, population modeling has suggested that demographic change in populations of great egrets would be sensitive to small changes in juvenile survival (Frederick unpublished). The great egret shares many life history characteristics with most of the wading birds, and feeds at a trophic level quite similar to the great blue heron and the endangered wood stork. Great egrets probably represent the upper end of the exposure continuum for fisheating birds in the Everglades. Although it is widely assumed that risk increases with exposure in fish-eating birds, this assumption has never been tested and could be compromised by species-specific differences in sensitivity [156]. Thus potential effects in birds at lower trophic levels should not be ruled out.

Wading birds have provided the most complete evidence to date that current MeHg exposure levels are harmful to individual birds, and may well result in effects felt at the population level. However, with the exception of appetite, and predisposition to disease, these effects have not been measured under field conditions. Spalding et al. [123] presented a range of effects observed in Everglades wading birds in field and lab situations at a range of tissue Hg levels, and suggested that sublethal effects (such as loss of appetite, reduced packed-cell volume, health effects) are likely to be manifested in the field at lower concentrations than in the lab. Hg exposure criteria derived from lab studies should therefore include a large safety factor.

One of the areas of avian effects that has not been investigated in the Everglades is the potential for Hg to affect reproduction of adult birds. Although there is no evidence of poor hatching success, the abandonment rates of Everglades wading birds are high, and nesting success concomitantly low, by comparison with similar measures in other locations [43,41]. Although this difference might be explained purely on the basis of rapid changes in the availability of food [47], Hg could be acting as a stressor that lowers the threshold for nest abandonment. One of the most consistently noted sublethal effects of Hg in birds is a decrease in appetite [114,156,135,64, 122]. This lack of appetite might cause birds to abandon nesting during even brief interruptions in food supply, or might also act to prevent birds from eating enough to even come into reproductive condition. While these scenarios are obviously speculative, they serve to point out a need to better define the role of Hg contamination in the reproduction of fisheating birds.

6.7. Effects of Hg on mammals

The effects of MeHg in mammals have been the subject of several recent reviews [18,156,135]. As with birds, high concentrations of MeHg in mammals results in neurotoxic effects, such as neuronal necrosis and demyelenation, resulting in ataxia, anorexia, disorientation and death. As a result of bioaccumulation factors and high metabolic rate, carnivorous mammals are those most likely to be at risk, and those in aquatic systems that eat fish are probably at elevated risk because of high bioaccumulation factors. In the Everglades, the primarily fish diet of river otters (*Lutra canadensis*) and Everglades mink (*Mustela vison*) puts them in a high risk category among mammals [72]. If these two mammals are eating at trophic levels similar to or higher than wading birds, they are probably experiencing diets in excess of 0.5 mg/kg food ww. O'Connor and Neilson [102] found that river otters fed rations with 2 mg/kg MeHg ww developed classic signs of Hg toxicosis; a NOAEL was not established. The captive dosing experiments of Wobeser et al. [155] and Wren [157] suggest that diets containing 1.0 mg/kg ww represent a LOAEL for mink. In the absence of more precise information about the diet of otters and mink in the Everglades, there seems to be the potential for overlap between Everglades diets (> 0.5 mg/kg, based on concentrations in large fish) and the LOAEL diet (1.0 mg/kg). Raccoons (*Procyon lotor*) may also feed at high trophic levels in the aquatic food web, and hepatic mercury concentrations from several locations in the Everglades have ranged between 7000 and nearly 40000 ng/g ww [110, Table 5].

The Florida panther (*Felis concolor coryi*) has been identified as another mammal at high risk of MeHg accumulation in the Everglades [110,72,33]. The Florida panther is a highly endangered subspecies which has extremely low breeding potential, due to exceptionally low genetic diversity and population size [111]. Panthers may eat a widely varied diet, and some individuals rely on small prey, including raccoons. This diet would suggest a high bioaccumulation factor, since raccoons subsist at a mid- to upper level in the aquatic food web. The geographic pattern of mercury contamination in panthers is similar to that in raccoons. Roelke et al. [110] assigned Hg toxicosis as the cause of death in at least one panther that died convulsively, and was later found with 110 mg/kg total hg measured in the liver. Roelke et al. also showed a relationship between Florida panther litter size and maternal blood Hg concentrations, and suggested that 0.5 mg/kg liver was a threshold concentration for litter size effects. However, there may also be other contaminant stressors in the panther diet [33].

Hg may also have effects on the endocrine system of mammals. Facemire et al. [33] showed that levels of male and female panther reproductive hormones were nearly indistinguishable, and suggested that males had become feminized as a result of pre or post-natal exposure to endocrine disrupting contaminants, including Hg. In rats, Friedmann et al. [48] showed that rats exposed to 0.08 mg MeHg/kg mass (a low mercury diet by comparison with Everglades panthers and raccoons) showed a 44 % reduction in intratesticular testosterone levels and a 17 % reduction in numbers of sperm produced. This work suggests that MeHg may have direct effects on male sexual hormone expression and male fertility, and may do so at levels that many mammals in the Everglades currently experience.

Humans are another prominent fisheater in the Everglades that may be exposed to high levels of MeHg. Since the early 1990's the concentrations of Hg in sportfish of the Everglades have been known to exceed state human health advisories (0.5 mg/kg ww in fillets, 146, 85]. Fleming et al. [39] collected over 350 hair samples from fishermen in the Everglades. Of these, only 36 % had Hg concentrations that were above detection levels, with a mean of 3.62 mg/kg, and most fishers in the Everglades reported relatively low consumption levels of fish. The populations most at risk were Blacks and men. Although rare individuals may be at risk of MeHg poisoning as a result of consuming large amounts of fish from the Everglades, current consumption habits of humans apparently do not result in a widespread problem.

7. Potential for Hg contamination to affect faunal structure and ecological function in the Everglades.

In an evaluation of ecosystem effects of Hg, it is important to first identify what kinds of changes could actually affect the ecosystem. These would include perturbations to the essential physical or biotic structure and characteristic functions of the ecosystem. Although mercury contamination is widespread throughout the ecosystem, it seems unlikely that the physical structure would be affected by mercury contamination, and even the vegetative structure is unlikely to be significantly stressed by mercury accumulation, except in areas of particularly high sediment mercury concentrations. However, given that many of the critical functions of the ecosystem are carried out by animals [46,90] the biotic structure and function of the ecosystem might well be affected by significant changes in population sizes, or in community composition of animal species.

7.1. Uncertainties in assessment

The taxa-specific analyses presented above indicates that with the possible exceptions of fish-eating birds and humans, the effect of Hg is difficult to estimate with certainty for any group of Everglades animals. For invertebrates, fishes, reptiles, and many of the birds, the range of possible effects extends from no measurable population effects, to changes in reproduction, survival, and possibly, population structure. This very large uncertainty is not due to a paucity of information about contamination levels – these are generally well documented. Instead, there is a profound paucity of information linking specific tissue concentrations with effects on individuals or populations. This stems from several sources. First, the proportion of studies examining effects, rather than distribution or cycling of Hg, is small (Figure 4). Second, there has been a lack of interest in the effects of Hg on particular an-

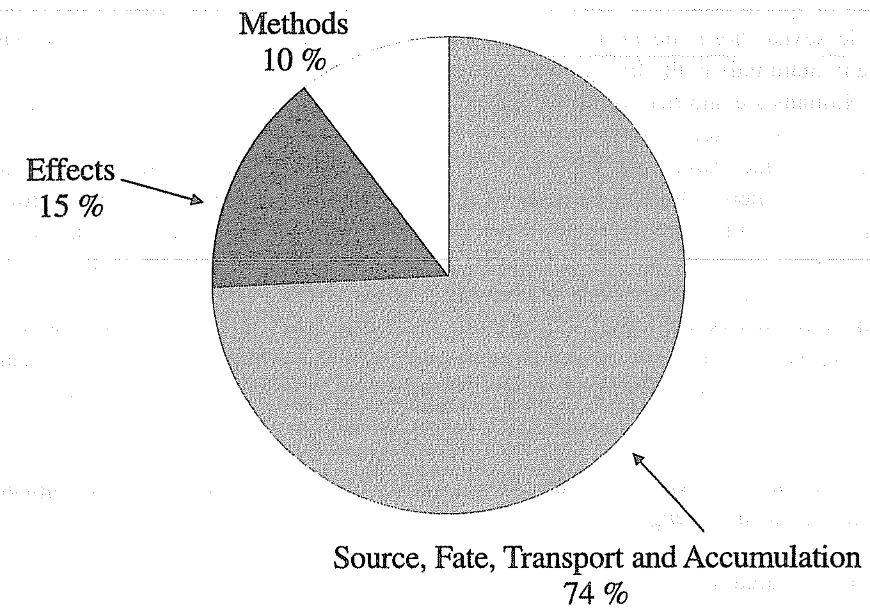

Fig. 4. Pie-chart showing proportional representation of types of published studies of mercury in the Everglades ecosystem.

imal groups (invertebrates, reptiles, amphibians), and a lack of studies that have assayed for effects at Hg concentrations that are in the same range as the Everglades (fish, birds). These problems have been previously identified as challenges for the field of wildlife Hg toxicosis [153,156]. However, there must also be a recognition that at most contamination levels found in the Everglades, the primary mode of action of Hg poisoning will be to weaken animals, rather than kill them outright. Thus a host of other stressors are brought into play, making the specific effect of Hg very difficult to recognize or isolate [64]. This does not indicate that Hg is unimportant as a stressor – merely that its signature is often cryptic.

7.2. Effects of Hg on populations and communities

Perhaps the most direct statements can be made concerning the effects of Hg on fisheating birds. Occasionally, adult wading birds may die directly from Hg toxicosis (see examples in 123], but it is likely that most effects of Hg on adults are sublethal. To date, there is little evidence that Hg is affecting embryogenesis or survival of nestlings, though this conclusion needs to be better tested in the future by controlled experimentation. Laboratory studies have clearly identified a period of high sensitivity to Hg during the first few months following fledging, and have indicated several effects that suggest a mechanism for decreased survival during this period. However, there are no measurements of Hg-induced reductions in survival in the field. The potential net effect of reduced survival of juveniles on population structure depends strongly on the degree of change in survival, but modeling has suggested that small changes could make the difference between a declining or growing population. Thus there exists a reasonable train of evidence to suggest that wading bird populations are being affected by current levels of Hg exposure. This population change would likely have effects on other parts of the ecosystem, since wading birds have been shown to have effects on prey animal populations [81,42], and on nutrient redistribution within the ecosystem [46].

The Florida panther is the only mammal for which there is good evidence of direct Hg toxicosis, and the case for reproductive problems also seems well documented. Nonetheless, this subspecies is so beset by the genetic limitations of small population size, and multiple contaminants, that it is difficult to attribute any one response to any one source. Since the population size of this highly endangered species is currently vestigial, it is difficult to see how the loss of the species is likely to have a large effect on current ecosystem structure or processes. However, if Hg contamination also stands to retard the prospects for the recovery of healthy populations of panthers, and if a healthy population of large mammalian predators is likely to have an effect on herbivores, then Hg contamination can be seen as having an effect on some future ecosystem.

It is somewhat more plausible that Hg contamination has resulted in ecosystem-level change by affecting reproduction and survival in populations of raccoons and otters. These species are much more numerous and widespread by comparison with panthers, and may have important top-down effects on the aquatic ecosystems that they exploit. However, outside of laboratory studies there are few concrete results upon which to examine this possibility.

The possible effects of MeHg on fishes in the Evergaldes are somewhat ambiguous. Fishes with even the highest concentrations in the Everglades are only barely within the range normally associated with increased mortality or reproductive effects [153]. However, the recent work by Arnold [5] suggests that low body burdens of Hg may result in changes in endocrine expression, resulting in sex-ratio changes and consequent effects on reproduction. There is the possibility that predatory fishes exert a significant amount of "top-down" control upon aquatic communities in the Everglades [80]. If predatory fish population dynamics are altered by Hg contamination, it is also possible for top-down effects to be felt throughout aquati the ecosystem.

It remains to be seen whether there are any measurable effects of Hg on populations of smaller, less predatory fishes. Hg contamination in mosquitofish is within the range that has been shown to affect susceptibility of mosquitofish to predation. There is considerable evidence that populations of wading birds and predatory fishes are controlled in large degree by fluctuations in standing stocks and availabilities of small fishes and macroinvertebrates [145,87,47,70]. Thus any significant perturbations to populations of these "forage" species that occurred as a result of Hg contamination would be expected to result in "bottom-up" effects on other components of the ecosystem. This possibility has led to the suggestion that it is the population sizes and dynamics of small fishes that should be targeted for conservation in the Everglades [140].

The possibility of Hg-induced changes to populations of invertebrates and small fishes has to date received almost no attention in the Everglades ecosystem. Hg-induced effects upon populations at this trophic level have largely been ignored, since there is little evidence of lethal effects for animals with such low bioaccumulation factors. However, this reasoning seems circular, since there have also been vanishingly few attempts to look for sublethal effects at these levels. The possibility of Hg acting on the reproductive or endocrine systems of invertebrates is not without evidence, and is bolstered by studies showing such effects on molluscs and fishes. The complete lack of research on Hg effects in invertebrates and small fishes seems to be an important gap, given the potential for bottom-up effects in the aquatic food web [88].

7.3. Mercury and Everglades restoration

A large and expensive Everglades restoration plan is currently aimed largely at re-plumbing the ecosystem to allow more natural flows of fresh water, and in so doing to restore more natural variability and ecosystem functions. While Hg contamination is a fully acknowledged phenomenon within this framework, the potential effects of contamination are not considered to be capable of thwarting the recovery of animal populations. As revealed in this review, however, the potential for population effects of mercury are real, and could well remain after the expensive hydrological restoration is completed. There is a recognition at the state level that current EPA mercury water criteria (12 ng/l) are currently being met, yet are not apparently resulting in protection of much of the wildlife in the Everglades [92]. Within state legislation designed to protect the Everglades ("Everglades Forever Act"), however, there is a mandate for the development of Hg criteria for the protection of wildlife.

7.4. Research priorities

Some research priorities can be identified from this review that may aid in the establishment of criteria that are protective of wetland wildlife. First, although there is good evidence for increasing mercury accumulation in sediments of the Everglades during the 20^{th} century, there is only weak evidence for increasing concentrations in biota through time, due largely to a lack of studies. Establishment of mercury concentrations in biota at the turn of the last century (1900), for example, would help significantly in understanding the relative importance of current concentrations, and could help in defining safe levels for much of the biota. This could be done in large part through analysis of samples from existing museum specimens [136].

Second, this review has demonstrated the difficulty of assessing the net effect of current Hg contamination, without better information that matches contamination levels with known effects, especially in the context of multiple natural stresses. There seems to be ample reason to do this work on organisms that exist at several different trophic levels, since sensitivities may vary, and since bottom-up effects on upper trophic levels could result from relatively small changes in reproductive rates in invertebrates and fishes.

The utility of such work will rely heavily on experimentation that includes a range of Hg values, and uses dietary intake pathways that are pertinent to the Everglades. Some combination of lab and field studies will be integral to the process of identifying relevant Hg criteria. This is because field studies are usually poor at isolating the effect of Hg from the multiple stresses of wild animals. Similarly, lab studies are often of only weak utility because they do not measure effects in a setting that includes the multiple stresses that allow full expression of a contaminant, and usually do not include population changes as an endpoint.

Third, the endpoints examined in new studies should be specifically oriented at detecting sublethal endpoints. It seems likely that mercury may affect populations and ecosystem dynamics by causing changes in survival rates and reproduction. Thus studies must focus on fecundity, survival, health and predation risk as possible endpoints. The possibility that mercury can affect functioning and development of endocrine systems at low exposure levels must also be taken seriously.

New approaches will almost certainly be necessary, including the use of mesocosms, long-term studies of marked individuals, and field dosing trials in "clean" environments. It has not yet been established whether the Everglades ecosystem is impacted by contaminants other than mercury – future work must either demonstrate a lack of other contaminants, or focus on possible interactions between contaminants.

The Everglades Hg situation is somewhat novel in the context of similar studies of Hg in northern lakes and boreal wetlands, in terms of Hg dynamics, the structure of the food web, and in the extent of bioaccumulation in and contamination of the biota. Although there are strong hints that Hg is having effects on the structure and function of the ecosystem, the Everglades reflects in microcosm the central problem of current wildlife Hg toxicology – that there is far too little research linking effects with ecologically relevant concentrations and contexts. Since atmospheric deposition of Hg is not showing any signs of abatement, it seems likely that this need for ecologically relevant toxicological research will only grow.

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