Bioenergetics as a Unifying Concept in Environmental Restoration Planning

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Abstract

All other things being equal, including niche width, in intra-or inter-species competition, an organism that is capable of more efficient access to, availability of or use of the matter and energy at its theoretical disposal in its niche will have more matter and energy for predation, predator avoidance, growth, and reproduction, be more reproductively successful, and eventually outcompete and displace those less capable from the niche. One can infer from this that an ecosystem that is composed of such bioenergetically efficient niches is maximizing the capture, storage, and use of solar energy to convert less to more complex forms of matter and energy at each successive trophic level with the least entropy production. In addition to its general diagnostic value, the concepts, principles, and practices of mass and energy balances in the form of bioenergetics accounting has practical applications in testing hypotheses regarding food web statics and dynamics, the management of resource utilization for maximum sustainable yield, and for quantifying bioaccumulation/biomagnifications in aquatic and terrestrial ecosystems for ecotoxicological risk assessment (ERA). One practical application of bioenergetics to ERA involved testing the claim by third parties that attaining the proposed total phosphorus (TP) water quality standard of 10 ppb would result in such an ecotoxicologically significant increase in methylmercury concentrations in the aquatic food web due to a loss of phosphorus-mediated biodilution that it would threaten the reproductive success of fish-eating wading birds, including the endangered wood stork (*Mycteria americana*) and protected migratory birds such as the great blue heron (*Ardea herodias*) feeding in areas now at much higher TP concentrations. The empirical models used by the third parties to infer these unacceptable risks were unconstrained by mass or energy balance requirements. To remedy this deficiency, I developed a spreadsheet model of a wetlands unit world, where the coverages, densities, primary productivities, and refractory and decomposable fractions of algae and macrophyte species were dictated solely by the TP concentration in the water column. The equation for each was derived as empirical relationships from published studies conducted by others. The food chains included both autotrophic and saprotrophic pathways. To fully initialize the model, assumptions were made about foraging preferences and the fraction of carbon routed to the detrital pathway at each trophic level. The trophic transfer efficiencies of carbon and methylmercury were obtained from the literature for representative Everglades species, but where such data were unavailable, to the most similar species for which data were available. The carbon transfer model was calibrated to reproduce the observed aquatic plant and animal species densities reported by Trexler and co-workers at a representative unimpacted site in Water Conservation Area 2A. The methylmercury transfer model was calibrated with data collected at the same site by or for SFWMD. The results of the calibrated model indicated a 2.5 to 3.5-fold increase in methylmercury exposure at U3 when TP concentrations decreased from 70 ppb to 10 ppb., not the 15-fold increase predicted by the empirical model. The next step is to reinitialize the model with the most recent Everglades data and compare the results of and conclusions from the original and revised models.

Need

- The ability to make accurate and reliable quantitative cause-effect predictions is critical for well-informed restoration decision-making …
- … especially where the consequences of inaccurate or unreliable predictions are socially, economically, or environmentally disastrous and irreversible …
- … or reversible only over a period of time > planning horizon, i.e., outside of the adaptive management domain.

Need

- Empirical models have limited quantitative predictive value that diminishes in accuracy & reliability as one extrapolates further outside their conceptual, spatial or temporal data domains.
- This problem is exacerbated where the empirical models are unconstrained by limits imposed on the real world by the laws of physics, chemistry and biology.
- The most fundamental of these constraints requires mass and energy balances.

Need

- Mechanistic ecological models play an important role in restoration planning:
  - System conceptualization, problem definition, & hypothesis formulation
  - Development & interpretation of stress diagnostics at the specie, community & ecosystem scales
  - Organizing, analyzing, integrating & synthesizing results for hypothesis testing
  - Development of critical habitat quantity, quality & connectivity criteria for trust species

Need

- Mechanistic ecological models applications (continued):
  - Development of min/max flows & levels regulation schedules for fresh/estuarine/salt waters & wetlands
  - Quantitative predictions of changes in ecosystem internal state over time in response to changes in external forcing functions for evaluating restoration alternatives
  - Uncertainty and sensitivity analysis to guide allocation of monitoring, research, and modeling resources

Stoichiometrics

- Each organism has the biological equivalent of an empirical formula or stoichiometry representing the optimum ratio of the elements required for healthy life functions.
- Its stoichiometry is a function of genotype, phenotype, sex, age, and environmental conditions.
- The optimum N to P or Redfield ratio is an example of plant stoichiomtetry, albeit limited to 2 elements.
- A community or ecosystem has a stochiometry that is the biomass-weighted average of empirical formulas of the organisms of which it is comprised.

Need

- Unfortunately, not all mechanistic ecological models that were, are, or will be used for any of the above include bioenergetics and stoichiometrics accounting & constraints.
- This increases the probability of an apparently calibrated and validated mechanistic ecological model generating inaccurate and unreliable predictions with unacceptable, irreversible adverse consequences for ecosystem restoration & protection planning & decision-making.

Objectives

- To define, illustrate the general utility of, and apply the principle of bioenergetics and stochiometrics to mechanistic ecological models intended to support well-informed ecosystem restoration and protection planning and decision-making
- To reduce to acceptable levels the probabilities of committing Type I & II errors with unacceptable, irreversible adverse consequences of misinformed planning and decisionmaking

Ecosystems

- Definition: Eugene Odum's Fundamentals of Ecology (5th ed.):

  "Any unit that includes all of the organisms (i.e., the 'community') in a given area interacting with the physical environment so that a flow of energy leads to clearly defined trophic structure, biotic diversity, and material cycles (i.e., exchange of materials between living and nonliving parts) within the system is an ecosystem."

Bioenergetics

- To sustain its health throughout its life cycle, a biological organism must acquire the matter in the form of nutrients and energy in the form of calories required for basal metabolism, survival activity, growth and reproduction within the normal ranges dictated by its genotype, phenotype, sex, age and environmental conditions.
- One can measure the quantity and quality of nutrients and calories in biologically usable form required by an organism or population of organisms for each of these life processes.

Bioenergetics

- One can measure the transfer and conversion efficiencies of matter and energy in biological form between the energy source (e.g., sunlight) and primary producers (e.g., plants), between primary producers and primary consumers, and between predator and prey at each trophic level.
- One can measure or infer the effect of the bioenergetic budget of a population of organisms on population spatial coverages, densities, turnover rates, death rates, consumption by detritivores and decomposition rates by aerobic and anaerobic microbiota.

Bioenergetics

- All other things being equal, the closer the empirical formula of the forage or prey is to the empirical formula of the grazer or predator organism, the more efficiently the forage or prey is assimilated by the grazer or predator and the more efficiently it is converted for use in basal metabolism, activity, growth, and reproduction.
- By that logic, cannibalism is bioenergetically favored but behaviorally discouraged to ensure reproductive success. However, where the carrying capacity of the environment is exceeded, cannibalism will occur.

Bioenergetics

- In general, assimilation and utilization efficiencies increase with trophic level.
- All or things being equal, a population exhibiting a bioenergetic deficit, break-even, or surplus will shrink, reach steady state, or expand in its niche.
- Absent more specific information, the standing crop biomass at trophic level T+1 is ~10% of that at trophic level T, the so-called 10% rule in applied bioenergetics.

Carrying Capacity

- There is an optimum relationship that maximizes reproductive success by maximizing bioenergetic efficiency among the following:
  - hydrology
  - primary production
  - habitat types, coverages and densities
  - prey availability
  - refugia
- The ecosystem carrying capacity for each species is dictated by that relationship,
- … e.g., fish stocking rates & sustainable catches

Stress Diagnostics

- Measures of Stress at the Organism, Community or Ecosystem Level of Biological Organization

  -- Deviations from optimum stoichiometry

  -- A reduction in assimilation or utilization efficiencies of otherwise bioavailable nutrients or calories

  -- A reduction in the ratio of actual relative to theoretical carrying capacity

Ecotoxicology

- Some toxicants, such as H_2S, interfere with metabolic efficiency by uncoupling the e- transport chain.
- A toxic metal like inorganic mercury, $Hg(II)^{2+,}$ is absorbed across the gut with an efficiency ~2%-5% and is rapidly excreted, while carbon is assimilated with an efficiency of 10-50%, supporting a growth rate of 2% to 25%, depending on organism genotype, phenotype, sex, age, and environmental conditions, so Hg(II) is growth diluted and does not bioaccumulate at the organism level or biomagnify up the aquatic or terrestrial food chains.

Ecotoxicology

- Conversely, methylmercury (CH_3Hg) is readily absorbed across the gut with an efficiency of 35%-85% and is only slowly excreted, so it is not rapidly growth-diluted and is readily bioaccumulated and biomagnified.
- Hg(II) and CH_3Hg algae bioconcentration factors are typically 3,000-30,000 times the concentration in water.
- CH_3Hg biomagnification factors at each subsequent trophic level are in the range of 2-10, with 3-7 being more typical.

Ecotoxicology

- If the algae growth rate increases relative to the CH_3Hg production rate due to eutrophication, this biodilutes the CH_3Hg at the base of the food chain and each successive trophic level.
- CH_3Hg biodilution has been documented in lakes (D'Itri, 1976; Hakanson, 1980) and lake-like mesocosms (Pickhardt et al. 2003), but not in wetlands, where rooted macrophytes, not algae, predominate (Fink and Rawlik; 2000; Fink, 2004).

Ecotoxicology

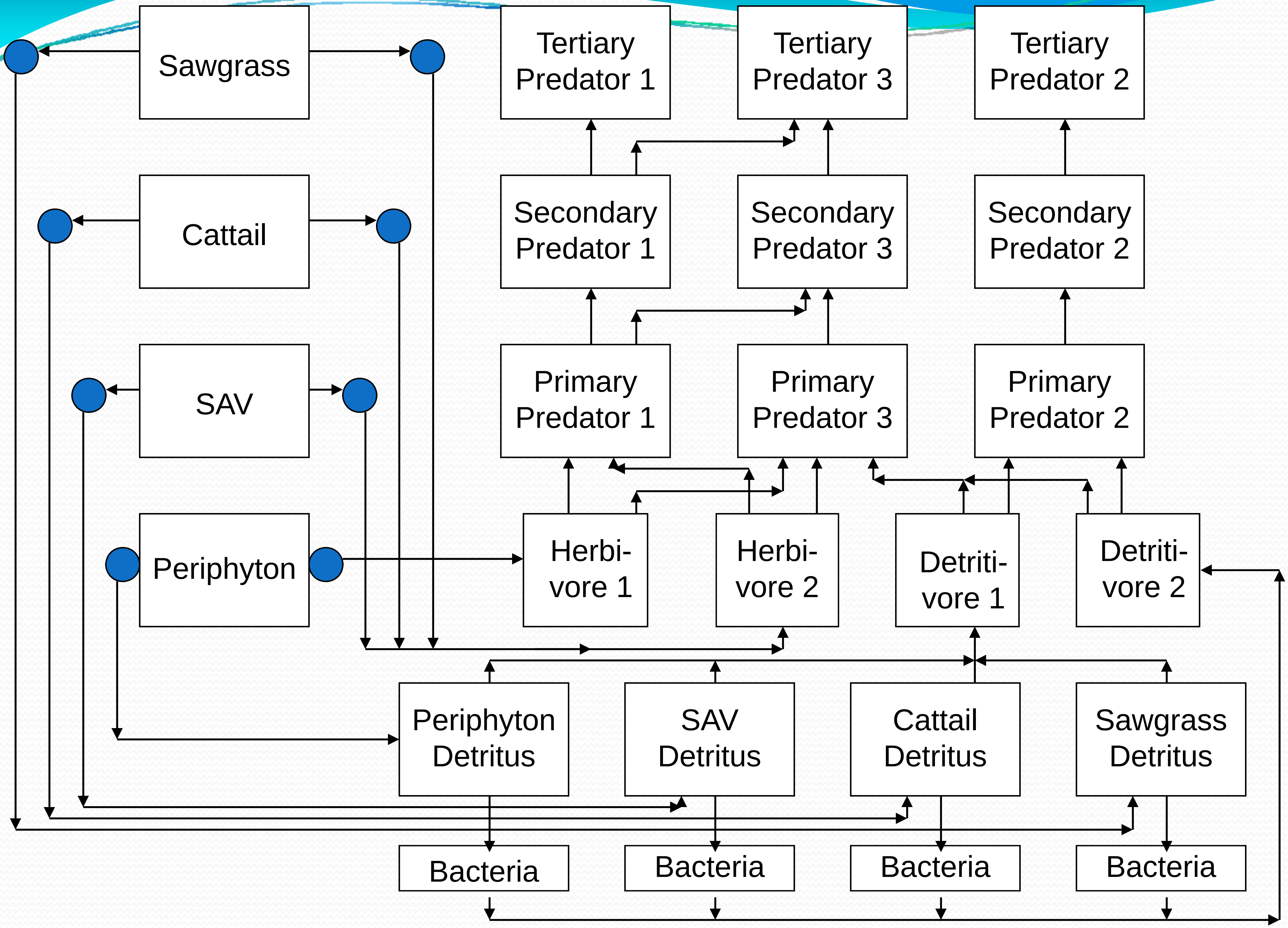
- Nevertheless, the Sugar Cane Growers Cooperative, via Exponent, Inc., invoked a loss of biodilution of CH_3Hg due to a reduction in eutrophication as a likely unintended consequence of reducing TP concentrations from 100-70 ppb to 10 ppb.
- The model predicted greatly increased CH_3Hg concentrations at each successive trophic level with the shift from eutrophic to oligotrophic conditions.

Ecotoxicology

- This was then predicted to threaten CH_3Hg toxicity to fish-eating trust species such as the wood stork and the great blue heron.
- To prevent this alleged catastrophe, the Coop argued before the Environmental Resources Commission that the TP standard should be raised to 16 ppb, it should only apply at the edge of a mixing zone, or the implementation of the 10 ppb TP WQS should be delayed until the inorganic mercury deposition rate to the Everglades was reduced to acceptable levels.

Ecotoxicology

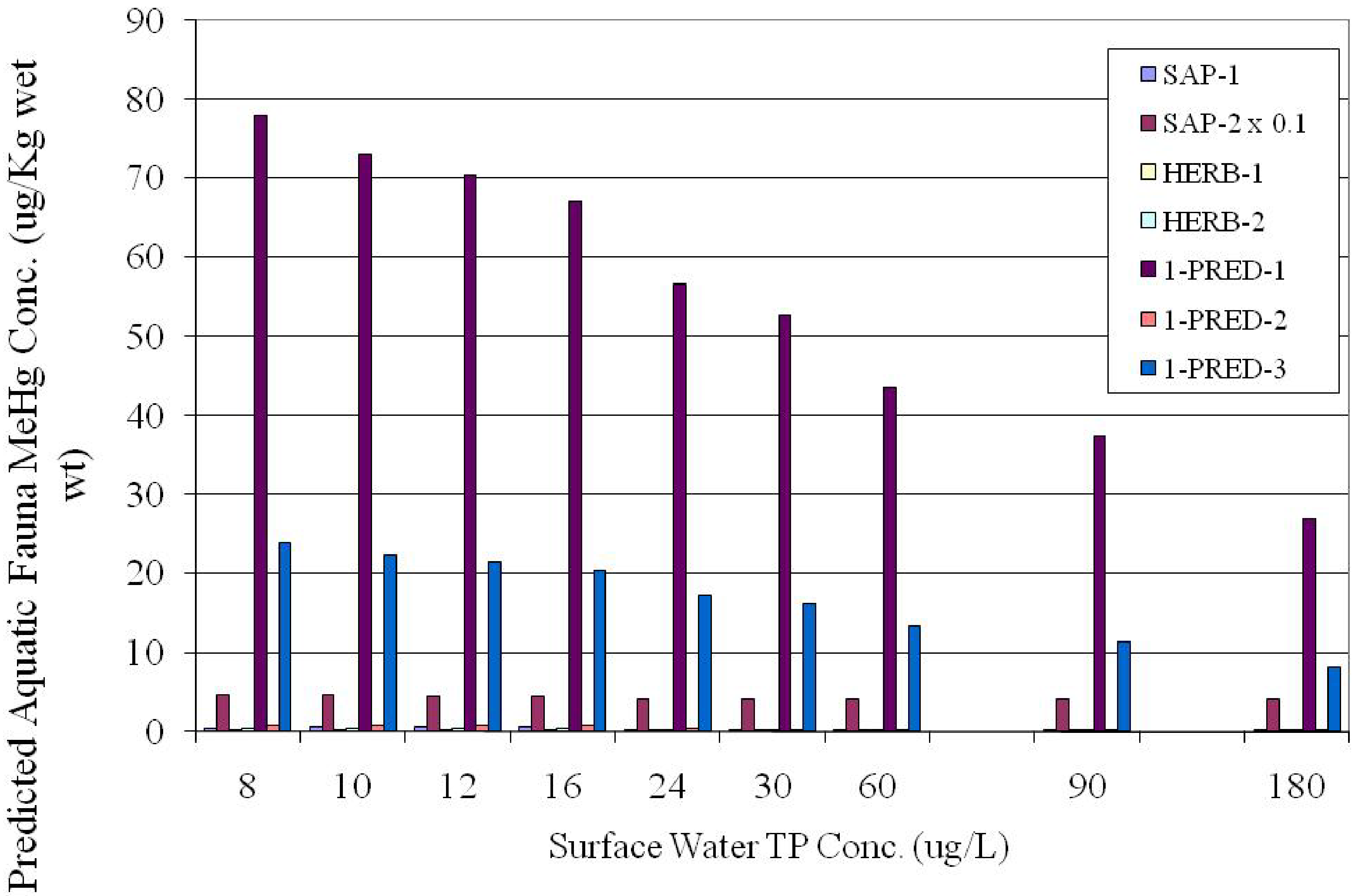
- The empirical model Exponent used to predict a CH_3Hg catastrophe did not include:
  -- mechanistically based biodilution processes
  -- bioenergetics constraints
- Inconsistent to simultaneously reduce biodilution without concomitant decrease in carrying capacity and contact freq. of exposed species.
- To test hypothesis, author constructed a steady-state wetlands carbon transfer model with TP-mediated coverages and densities and 1^0 prod. and decomp. rates and CH_3Hg bioaccumulation.


Sawgrass
Tertiary Predator 1
Tertiary Predator 3
Tertiary Predator 2
Cattail
Secondary Predator 1
Secondary Predator 3
Secondary Predator 2
SAV
Primary Predator 1
Primary Predator 3
Primary Predator 2
Periphyton
Herbi-vore 1
Herbi-vore 2
Detriti-vore 1
Detriti-vore 2
Periphyton Detritus
SAV Detritus
Cattail Detritus
Sawgrass Detritus
Bacteria
Bacteria
Bacteria
Bacteria

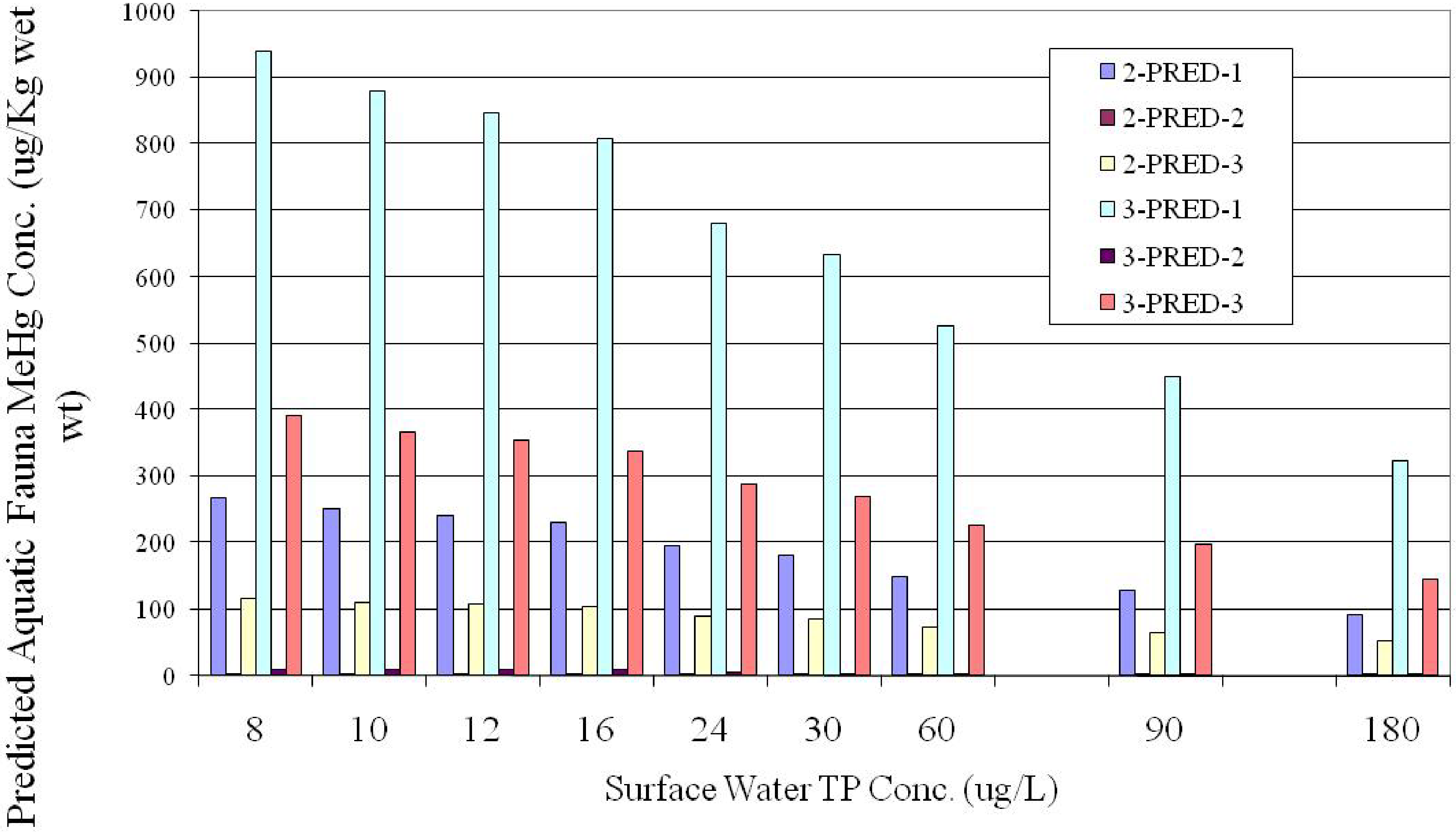
Steady-State Model Parameterization

- Plant coverages, densities, and primary production, turnover, and decomposition rates vs. water [TP] via regression equations derived from Swift and Nicholas (1987), Davis (1989 and 1991), and Richardson et al. (1995)
- Calibrated with plant and fish coverages and densities values from nominally unimpacted Everglades site WCA-2A-U3 from McCormick et al. (1999) and Turner et al. (1999)
- Bioenergetics-based MeHg bioaccumulation modeling based on Norstrom et al. (1976)

Steady-State Modeling of MeHg Bioaccumulation as Function of Water TP Concentration



Steady-State Modeling of MeHg Bioaccumulation as Function of Water TP Concentration



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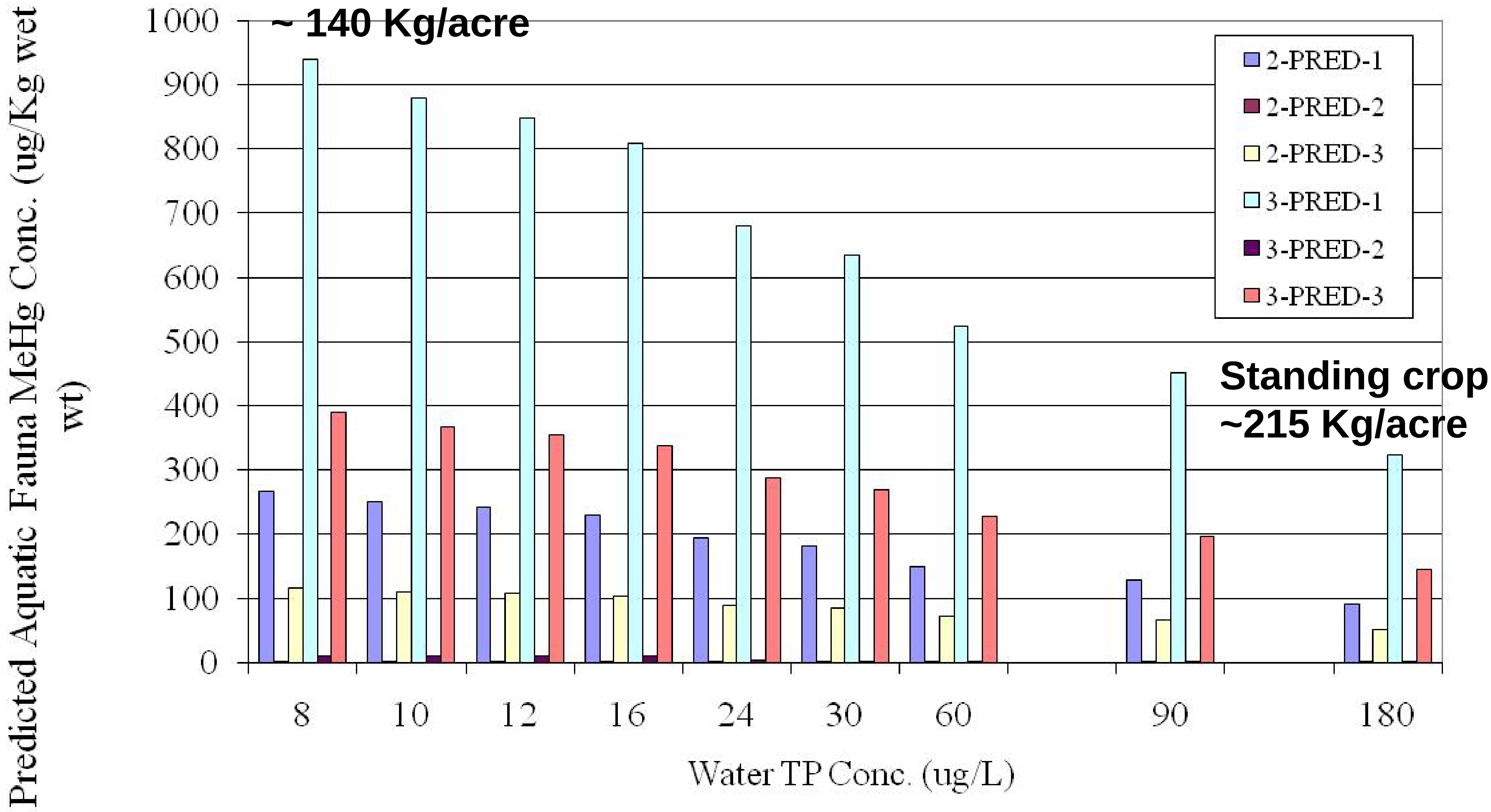

Standing crop ~ 140 Kg/acre

Standing crop ~215 Kg/acre

Conclusions

- Bioenergetics and stochiometrics are critical constraints on reproductive success at every level of biological organization
- If the hydrology is optimal but the bioenergetics or stochiometrics is suboptimal, reproductive success will be suboptimal
- Bioenergetic and stoichiometric accounting are essential for translating conceptual ecological models into their quantitative equivalents in a rigorous way

Recommendations

- Use deviations from optimal stoichiometrics and bioeneregtics as diagnostics of ecostress
- Test all population, bioaccumulation, and ecotoxicology models for stoichiometric and bioenergetic self-consistency
- Functionally representative species at each trophic level should be assayed for the following to guide resource management decisionmaking :
  - stoichiometry
  - organic carbon content, assimilation efficiencies, and utilization efficiencies
  - calorie content, assimilation efficiencies, and utilization efficiencies