# Investigating Food Webs: State of Knowledge and Investigative Approaches

## Workshop Proceedings

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*Editors*

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# Executive Summary

Two half-day webinars, a 3-day in-person workshop, and follow-up discussions, reviewed food web fisheries and environmental management information needs and investigative approaches. Webinars consisted of 12 presentations from fisheries managers and food web investigators from across North America and Europe. Approximately, 85 people participated in the webinars, and 22 people attended the subsequent workshop. Great Lakes investigators and, to a lesser extent, fisheries managers, dominated the list of participants in both the seminars and workshop. The workshop facilitated the development of a conceptual model encapsulating fisheries management information needs and food web investigative approaches. Food web investigations are best suited to meet longer-term fisheries management information needs and require tools that can handle large data sets that are spatially and temporally extensive, multi-trophic and include associated physical and chemical descriptors. To be relevant and effective, investigative approaches need to link food web dynamics to drivers (e.g. nutrients, climate-change, invasive species), recognize the limits of management agency capacity to collect and analyze large data sets, and must also be able to deal with spatial, temporal, and process complexity. Simpler indicator methods show some promise, but more research is needed to link simpler metrics to food web-scale processes and dynamics. Twelve fisheries management relevant food web investigative initiatives were suggested in four categories. The categories were: 1) Applying and developing tools and approaches to quantify past and future Great Lakes food web structures, 2) Using modeled empirical and virtual food webs to better understand food web dynamics and the relationship among complex network metrics and simpler metrics, and 3) Applying and developing tools and approaches to incorporate movement and foraging behavior into food web analysis, and 4) Further review and summarization of food web analytical tools, applications and data needs.

## Introduction

A number of recent syntheses have listed knowledge gaps and hypotheses and made recommendations to advance management relevant Great Lake food web investigations (Ives et al., 2019, McMeans et al., 2016, IJC 2020). Science transfer efforts have introduced conceptual frameworks to fisheries managers that have increased utility and understanding of food web concepts and indicators (Stewart et al., 2018, Hinderer et al., 2021). Advances in food web investigative approaches continue to be developed. For example, a recent study demonstrated that linear inverse modeling (LIM) can exploit existing food web observational data, and account for uncertainty to better facilitate hypotheses evaluation (Stewart and Weidel, 2021). Another innovation is the use of spatially explicit end-to-end modelling approaches that integrate submodels for physical and biogeochemical processes, ecology, and human uses (Audzijonyte et al., 2019). However, it is not clear that Great Lakes food web investigators are fully exploiting available methods and data sets to meet priority fisheries management information needs. The objectives of the workshop were to review the current state of food web investigative methodologies, facilitate the transfer of technical knowledge, re-assess food web focused fisheries management information needs, and explore potential experimental designs and approaches.

## Workshop and Seminars

### *Seminars*

To promote the workshop and familiarize workshop participants with the current state of food web investigative methods, two webinars were developed and presented. Webinars consisted of 12 presentations from fisheries managers and food web investigators from across North America and Europe (Appendix A). Approximately, 85 people participated in the webinars, and 21 people attended the subsequent workshop (Appendix B). Great Lakes investigators and, to a lesser extent, fisheries managers, dominated the list of participants in both the seminars and workshop.

### *Approach to workshop*

To initiate the workshop participants responded anonymously to two questions; "What would you like to see come out of this workshop?" and 2) "What is the biggest challenge you see in applying food web science to fisheries management?" Responses were then coded to identify common themes among attendees. In response to question 1, most participants were interested in gaining a better understanding of the state of knowledge and data available for investigating food webs (8) or seeding ideas for future projects (7), with the remainder interested in learning more about how investigating food webs could be better tailored to management information needs (4). In response to question two, most attendees identified the biggest challenge as the underlying complexity of food webs (9), followed by the challenge of transferring results to managers or stakeholders (8), with the remainder citing data availability as the biggest challenge (2). A table of responses, with their assigned themes can be found in Appendix C.

To help focus discussions, a small technical steering committee (see Acknowledgements) developed a number of overlapping themes and associated questions (Appendix D). Final theme titles and summary descriptions of the themes were as follows:

Simpler Metrics - Development of simpler metrics of food web structure and function useful to fisheries and environmental managers (e.g. emergent properties, network analysis indices (Ulanowicz et al., 2009, Fath et al., 2019), GLFC Science Transfer Program food web metrics; trophic transfer efficiency, predator-prey ratio, staple isotopes).

Adaptive Architecture - Understanding drivers of adaptive capacity, including, but not limited to, exploring and expanding the ideas from McMeans et al., (2016).

Space - Importance of space (energy and nutrient flow among habitats, nearshore/offshore, depth gradients, water column, nearshore shunt and offshore nutrient depletion).

Phosphorus and Fish - Understanding characteristics of food webs that drive fish production including the role of phosphorus.

Improving Capacity - How do we increase the capacity to do the required monitoring and modelling work to support food web scale studies?

The first three themes were chosen by workshop participants for further exploration. The remaining two themes, while important, were considered to be part of a broader general conceptual model of longer-term management information needs and key elements to consider (Fig. 1). Food web-scale studies best inform longer-term (5 year or decadal) objectives such as, fish species restoration plans, predicting consequences of future invasive species establishment, Fish Community Objectives and associated strategies, habitat management plans, or Environmental Objectives. Food web-scale studies are less effective in informing annual management decisions like stocking numbers, or commercial catch quotas. Further, the challenges and opportunities to implementing food web investigations are related to careful consideration of "the data" (what types of data, how and when to collect it) and the tools (models, analyses, metrics, and communication). Other over-arching issues are to consider and better understand current and potential emerging drivers (e.g. phosphorus, invasive species), spatial and temporal scale and complexity, and the institutional capacity to collect, analyze and communication results of investigations (Fig. 1).

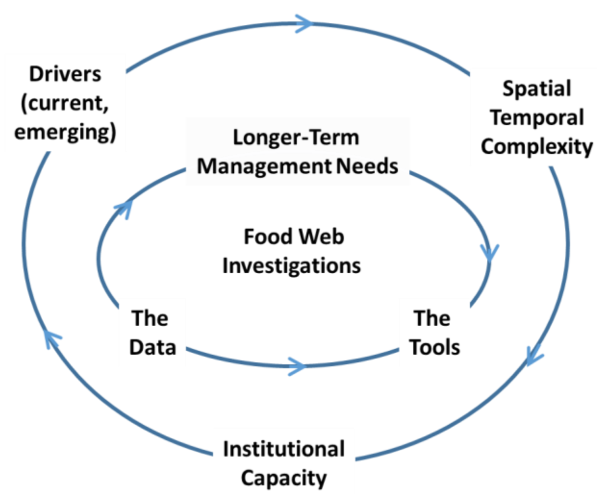

***Figure 1.*** *A general conceptual graphic of food web investigations in the context of longer-term management information needs and key elements to consider (see text for explanation).*

For each theme, breakout groups addressed specific questions customized to the themes as they related to management information needs, existing and potentially new approaches, hypotheses or investigative methods, and critical information gaps.

## Summary of breakout group theme discussions

### *Theme 1 – Adaptive Architecture*

Participants: (Nikki Saavedra, Elizabeth Whitmore-Stolar, Doran Mason, Kayden Nasworthy, Jim Watkins, Marten Koops, Tom Stewart, Roger Knight)

The overall conclusions of this group were that "*things change*!" meaning investigators are trying to capture non-equilibrium dynamics, but are often forced to assume that observed or modelled systems are in equilibrium. The structure and function of food webs exhibits adaptation through size structure and behavioral flexibility expressed as movement (size dependent) and diet diversity and flexibility (McMeans et al., 2016). Investigative needs include measuring diet diversity (e.g. stable isotopes, fatty-acid profiles, stomach analysis). Important considerations are how diets vary with habitat, season, and life-history stage and how that might confer adaptability. For example, Lake Ontario alewife diets and levels of consumption varies with life-history stage and bathymetric depth (Fig. 2).

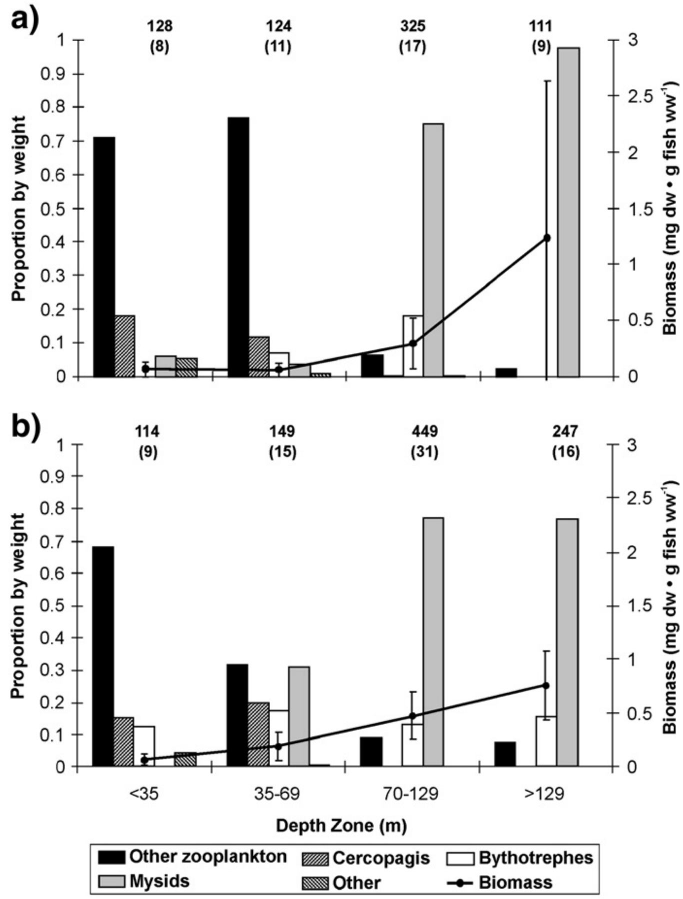


*Figure 2. Proportion of prey groups and mean total biomass of prey (±two standard errors) by bottom depth zone in the stomachs of adult alewife in 2004 (a) and 2005 (b). The zooplankton category includes small cladocerans, other large cladocerans, cyclopoid copepods and calanoid copepods. The number of fish examined and the number of sampling events (in brackets) are indicated above the bars. (From Stewart et al., 2009).*

Regarding investigative methods, GLATOS can be applied to understand size-dependent and species-specific movement. Food web models need to have spatial structures that capture important shifts in habitat and associated changed feeding behaviors. In lieu of complex models, simpler metrics (staple isotopes, habitat-stratified diet surveys) need to be developed and assessed. Food web investigations that account for flows among habitats, movements, and associated changes in feeding behavior will help better understand factors driving food web adaptability (*sensu* Ulanowicz et al., 2009). As movement can mean a shift in habitat use, it is important to know what these habitats are being used for.   Fisheries managers may be able to contribute to adaptive architecture by selecting desired species that can exploit different habitats and by making sure the habitat is suitable and maintained. The group concluded that a key principle of adaptive architecture is that generalists help to maintain the structure of food webs.  A key question (hypothesis) is "To what degree is food web adaptability in the Great Lakes attributable to generalists?"

### *Theme 2 – Space*

Participants:  (Alex Koeberle, Ed Roseman, Ed Rutherford, Kayden Nasworthy, Lars Rudstam, Nick Boucher, , Stephanie Figary, George Jackson, Roger Knight)

The take home messages from this group were:

- Space is important!
- Space and time have to be considered together
- Tools are improving (isotopes, GLATOS, otolith microchemistry, eDNA, physical models, lidar, acoustics)
- Investment in long-term monitoring is important
- Complexity depends on questions (not sufficient to think of any Great Lake as a bathtub)
- Connectivity has to be considered as a gradient
- Habitat is not just physical and must also be defined using biological data
- Need to better communicate why space is important

Space and time need to be considered together. Many spatial issues associated with food web flows are time-dependent, such as diurnal movements, seasonal changes to distribution associated with mixing and stratification, spawning migration, searching for food, avoiding predation, seeking optimal habitat or avoiding less desirable habitat as conditions change. Water movement and changes in physical structure will constrain ecological process (Fig. 2).

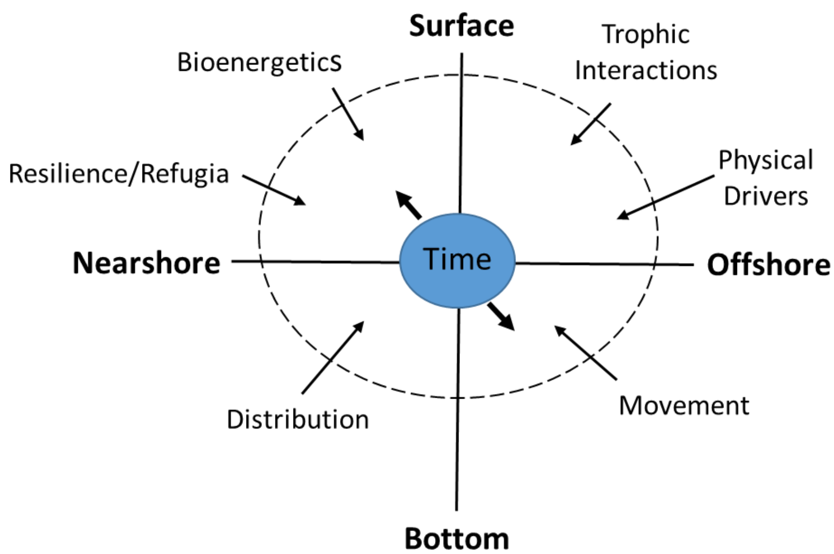


***Figure 2.*** *A conceptual model of Great Lakes spatial structure, influence, and dynamics.*

Commonly expressed spatial concepts in the Great Lakes are nearshore, offshore, embayments, tributaries, and connecting channels. Nearshore/offshore differences are of particular importance as many biological, ecological, and physical processes and conditions scale on depth (Fig. 3). Defining nearshore and offshore is problematic (less than 20-30 m depth?), and it is not clear whether there is utility in having a specific definition. Nuisance algae and water quality issues are mostly associated with the nearshore, related to dreissenind mussel shunting of nutrients and regional variation in sources of nutrients, which can create a mismatch between water quality management goals and fishery management goals. An important consideration is seasonal, annual, and regional variation in the extent and timing of the intersection of the thermocline with the lake bottom. Space may also provide refugia from predation and confer food web resiliency (e.g. Alewife in embayments).

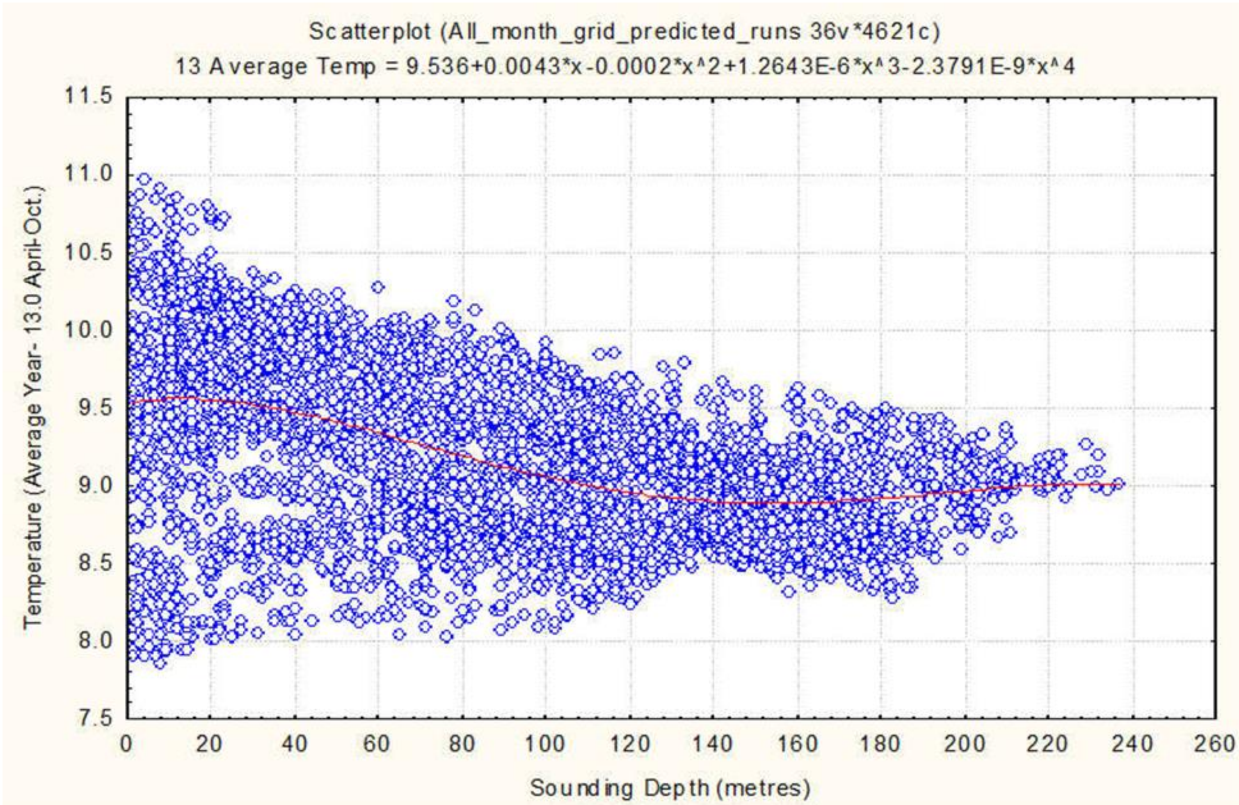


***Figure 3.*** *Empirical statistical model of average annual Lake Ontario temperature by sounding depth for 2 x 2 km grid scale with the mid-lake surface temperature of 13ºC (from Stewart et al., 2005).*

There is a mismatch between modeling and empirical measures (understanding) of space. What are the functional aspects of space? Can a community or species ecology be used to infer functional aspects of space? For example, integrating a salmonid bioenergetic models with an understanding of movement over time may suggest important spatial organization (Mason and Patrick, 1993). How are spawning and nursery habitat coupled and what are the physical dynamics (forcing) that influence where the habitats are and how that varies over time? Can physical models be applied to elucidate spatial structure? For example, can physical differences in east and west sectors of Oneida Lake be associated with ecological differences? There is a need to stratify food web models to capture spatial drivers. For example, depth stratification could encapsulate observed variation in dreissenid production, influence on phosphorus dynamics, and levels of round goby predation variability with bathymetric depth.

More consideration needs to be given on how to apply observations from GLATOS, sail drones, and remote sensing to better inform food web models. For example, influence of fish movement in three dimensions on species bioenergetics, understanding interactions between observed zooplankton and Mysid “layers” and fish movement and habitat use.

Food web models often treat habitats as separate boxes. However, in reality connections between habitats are a gradient. Understanding and considering these gradients in food web models is critical, because important interactions often occur somewhere along the gradient between habitats (i.e., between nearshore and offshore, benthic and pelagic zones, along the edge of harmful algal blooms). Mixed methods approaches that combine movement data, isotope analysis, and other methods can help to elucidate the gradient among habitat boxes.

Also, there is sometimes a mismatch between management units and spatial structure. A better understanding of spatial structure is relevant to fisheries management. For example, lake management units could be designed to be more ecologically relevant based on fishery catch, genetics, habitat type, stakeholder use and input. Also, fish stocking could exploit knowledge of spatial structure (e.g. offshore stocking to improve survival).

### *Theme 3 – Simpler Metrics*

Participants: Tony VanDeValk, Tom Brooking, Tomas Hook, Tim Johnson, Kimberly Fitzpatrick, Tom Evans, Tom Stewart, Roger Knight)

The key questions guiding this discussion were:

1. What characteristics of food webs do we think might be important to measures and understand?
2. Are there existing indices that may be useful and how could they be assessed?
3. Are there specific hypotheses that could be evaluated?
4. What are the critical information gaps?

The take home message from this group is that we need to develop and apply both simple and complex food web metrics that are fisheries management relevant, and to use empirical studies and simulation models to better understand their relationship to each other (Fig. 4).

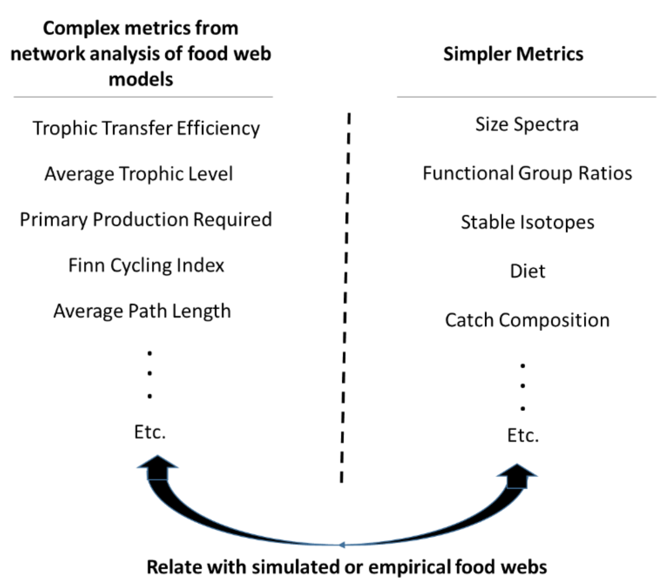


***Figure 4***. *Schematic of approach to linking complex and simpler metrics*

There are many ways to characterize the properties of food webs. Complex models can describe trophic interactions among species (e.g., Linear Inverse, Ecopath/Ecosim mass-balance models).

Application of network analysis to mass-balanced food web models can elucidate important fisheries management relevant metrics of food web structure and function (Fath et al., 2019). There is also an interest in developing and applying simpler metrics including stable isotopes, functional groups ratios, size spectra, and diversity indices (species, diet, functional group) and environmental DNA to capture important features of food web structure and function. Desirable properties of metrics are the ability to represent a variety of food webs, and low sensitivity to scale, or an ability to adjust for scale-dependence. Scale sensitivity is low for indices that are simple, integrative, annual, or have low spatial heterogeneity. Scale dependent indices are complex, seasonal, stratified, and have high spatial heterogeneity. Another issue is that Great Lakes ecosystem are dynamic, but metrics are generally representative of an assumed steady state or snapshot of a short-term state. Ideally, there needs to be an understanding of metrics from this perspective. Are metrics capable of effectively characterizing non-equilibrium states? Can a metric infer that there is stress on the system? Is variability around a metric an indicator of stress in the system? Metrics also need to be interpretable, rational, and relevant to stakeholders and fisheries managers. There is also a lack of understanding of the dynamics of metrics. How do they relate to each and what are desirable food web states? For example, is it more important to have efficient energy transfer (more fish production) or is a less efficient food web, with more redundant pathways, more important for stability and sustainability?

The group attempted to use some of the ideas above to evaluate a subset of metrics (Table 1) using the following criteria:

- The Tools (Inherent factors to the index)
    - Sensitivity to equilibrium (does the index represent change within the food web?)
    - Response to external and environmental stressors
    - Robustness to changes in scale (time, space, lumping splitting)
- The Data (what needs to be done to get the index)
    - Data needs
    - Ease of calculating index (from survey data to index)
- The Management Needs
    - Interpretability
    - Relevance to stakeholders (what do the indices tell us about fisheye sustainability and evaluation based on management objectives)

**Table 1.** Initial attempt at evaluating a subset of metrics. See text for explanation of evaluation criteria.

| | | | | The Tool (these aspects are current knowledge gaps in our understanding of indices) | | | The Data | | The Managment Needs | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Indices (simpler metrics)** | **Group** | **Does it require a foodweb model with connections between species to be calculated?** | **Description** | **Senstitivity to Equilibrium and/or stress (changes within the foodweb)** | **Response to stress (external influences on foodwebs)** | **Robustness to scale (space, time, resolution)** | **Ease of calculating (complexity fo indice)** | **Data needs** | **Interpretable** | **Relevance to stakeholderss (measure of fishery sustainability; management objectives)** |
| **TTE** | Network analyses | Yes | Trophic level 4+5 / Trophic level 3 | Yes | Yes | Can be adjusted | High (complex) | High | Easy | Yes |
| **PPR** | Network analyses | Yes | Primary Production channled to a species | Fails | Yes | Can be adjusted | Hard (needs pathways) | High | Easy | Yes |
| ***Average Path Length (APL) Finn (1976)** | Fath et al. 2019 (network indices) | Yes | How long something (e.g. carbon) stays in the system | Unknown | Unknown | Probably | Hard (needs pathways) | High | Hard | TBD |
| ***Finn Cycling Index (FCI) Finn (1980)** | Fath et al. 2019 (network indices) | Yes | The number of times something (e.g. carbon input) comes back to the same node in the foodweb (carbon captured in mussels that returns to mussels) | Unknown | Unknown | Probably | Hard (needs pathways) | High | Hard | TBD |
| ***Mean Trophic Level (MTL) Pauly et al (1998)** | Fath et al. 2019 (network indices) | Yes | trophic levels weighted by biomass | Unknown | Unknown | Probably | Hard (needs pathways) | High | Hard | Potentially |
| **Size spectra** | | No | Whole system particle size distribution | Unreliable | Unknown | Robust | Medium | Medium | Easy | Maybe, uncertain |
| **Functional group ratio** | | No | E.g. Predator/prey, cyclapoid/calanoids, % omnivores, bethic/pelagic | Unknown | Unknown | Sensitive to when, where; index dependent | Relatively easy | Medium | High | High |
| **Isotope-based indices** | Isotopes | No | Various | Yes, but challenging | Unknowwn | Sensitive to when, where, base values | Relatively easy | Low | Medium | Challenging to communicate |
| **Diet** | Species Diversity | No | Stomach analyses; fatty acid diversity; genetic | Yes, fairly sensative | Yes | Sensitive to when/where | Challenging and requires expertise (time intensive) | Low | High | Very high |
| **Catch composition** | Species Diversity | No | Richness, eveness (all of them); Includes different taxa "caught" using different methods (fish, algea, zooplankton, microbs ect) | Yes, fairly sensative but potentially confounded with environmental stressors | Yes | sensitive, to when/where | Easy | Low | High | Very high |
| **Detritivory Herbivory ratio (D:H) Ulanowicz and Kay (1991)** | Functional Group | Yes | Detitus flows/autotrophic flows | Yes | Unknown | Probably | Hard (needs pathways) | High | Easy | Potentially |

**Development of investigative approaches**

The final task assigned to workshop participants was to explore possible investigative approaches and possible projects, to facilitate the transfer of knowledge and address food web knowledge gaps and priority fisheries management information needs. The final set of ideas sorted into four categories; 1) Applying and developing tools and approaches to quantify past and future Great Lakes food web structures, 2) Using modeled empirical and virtual food webs to better understand food web dynamics and the relationship among complex network metrics and simpler metrics, 3) Applying and developing tools and approaches to incorporate movement and foraging behavior into food web analysis and, 4) Further review and summarization of food web analytical tools, applications and data needs. For each, the group developed a project idea that included rationale, possible methodological approaches, and stakeholder relevance. The approaches are outline below.

***CATEGORY: Applying and developing tools and approaches to quantify past and future Great Lakes food web structures***

Food web consequences of potential invasive species have been simulated using Ecopath/Ecosim (Zhang et al. 2016). This work needs to continue and be refined. Linear inverse modelling (LIM) can also be applied to simulate past and future food webs, and offers many advantages. LIM modelling frameworks explicating deal with uncertainty, include ancillary information (e.g. stable isotope, or size structure), have flexibility to model flows among habitats, and produces large ensembles of mass-balance solutions (consistent with specified levels of uncertainty). Solution ensembles can be examined in detail using multi-variate cluster analysis to derive clustered “families” of predicted food web structures and function (Marten Koops, Department of Fisheries and Oceans, pers. comm.). The multiple solutions can also be used to explore relationships among flow variables to better understand food web dynamics (Grami et al., 2011: van Oevelen et al., 2010).

**Project 1:**

**Title: Quantifying Great Lakes pre-colonization food web structures**

**Rationale:** Methodology has progressed enabling realistic quantification of pre-colonization Great Lake’s food webs while accounting for potentially large levels of empirical and structural uncertainty. Understanding how material and energy may have flowed among habitats (e.g. forested landscapes, nearshore-offshore, pelagic and benthic) and among species-groups, including humans, in presumably sustainable equilibrium states would have many benefits. Food web-scale descriptions of endemic systems would result in objective hypotheses regarding how endemic ecosystems likely functioned.

**Methods:** Use multiple methods (Traditional Ecological Knowledge, sediment cores, less perturbed post-glacial lakes, historical records, middens, etc. ….) to construct probable pre-colonization food web structures (biomass, production, feeding relationships, allocthonous inputs/output, harvests) consistent with available data and associated levels of uncertainty. Apply linear inverse modelling to derive large ensembles of possible balanced representations of the food web structures. Use cluster analysis of outputs to derive 3-4 subsets, or “families” of likely food webs representative of pre-colonization conditions. Calculate selected network and simpler metrics from endemic food web descriptions and compare them to similar metrics from contemporary Great Lakes' food web descriptors.

**Stakeholder Relevance:** The data synthesis required would result in engagement, and improved understanding among multi-disciplined investigators, Indigenous communities, and other stakeholders. Descriptive food-web metrics will result in hypothesized quantitative descriptions of "pristine" conditions, which could be applied to setting management goals for the functioning of food webs. A better understanding of the functional role of native species will provide further rationale for restoration programs.

**Project 2:**

**Title: Determining the food web consequences of native fish species restoration**

**Rationale:** Methodology has progressed enabling realistic quantification of Great Lake's food webs, while accounting for potentially large levels of empirical and structural uncertainty. There are numerous programs to restore native species such as, lake trout, deep-water coregonines, and Atlantic salmon in the Great Lakes (Stapanian, 2007). Predicting food web consequences of the re-establishment of a native species, or suites of multiple native species (e.g. lake trout, deep-water cisco, and Atlantic salmon in Lake Ontario) would help develop hypotheses regarding the bioenergetic potential and multi-trophic food consequences of native species restoration.

**Methods:** Apply linear inverse modelling to derive large ensembles of possible balanced representations of the food web structures that include a range of native species production outcomes. Diet compositions of native species would be based on known diet topologies from other systems, and constraints imposed by multi-species bioenergetics and the requirements of mass-balance. Use cluster analysis of outputs to derive 3-4 subsets, or "families" of likely food webs describing different pathways to trophic balance including restored native fish species the associated food web conditions.

**Stakeholder Relevance:** The results would inform fisheries managers of the limitations and potential for native fish restoration in the studied systems. Alternative "families" of food web structures may assist stakeholder discussions of what the range of possible endpoints are for trophically-sustainable populations of native species, associated trade-offs, and potential impediments. This could lead to the review of the possible scale or extent of restoration, what other ecological conditions (e.g., habitat, stocking, productivity, or fisheries) are required to achieve restoration goals. This may result in review of restoration goals, including focusing on perhaps smaller regional goals. It may also provide direction on the extent of habitat remediation, or other necessary conditions, required to meet restoration goals.

***CATEGORY: Using modeled empirical and virtual food webs to better understand food web dynamics and the relationship among complex network metrics and simpler metrics.***

Great Lake's food web descriptions and associated models are complex representations of vital processes and interactions. They provide holistic descriptions and potential understanding of ecosystem-scale process relevant to water quality management, species and habitat restoration, and fisheries development and sustainability. Food web descriptions require characterizing the bioenergetics of species-groups across trophic levels and an understanding of the behaviour, habitat use, population dynamics, and feeding interactions among species-groups. Turnover rates, biomass, production, size, and mobility of species-groups span several orders of magnitude.

Observational data required to populate the models is immense. Developing and analyzing the models takes specialized expertise and a considerable amount of time. Network analysis of mass-balanced food web models has resulted in some stakeholder relevant metrics such as trophic transfer efficiency (TTE) and primary production required (PPR). Understanding of the response of these metrics to change is emerging but limited. Other network analysis-based metrics are available, but their dynamics and stakeholder relevance are not well understood. The large data and analytical requirements to describe food webs has behooved investigators to consider other metrics or tracers of food web processes that might be simpler, and require less data and time to produce. Examples include stable isotopes, size-spectra, functional group ratios, diet descriptions, and species diversity as measured by species-group catch compositions. The investigative approaches described below focus on understanding how food webs respond to change, what network metrics best capture the dynamics, considers the relationship among simpler metrics and network metrics, and how both complex and simpler metrics could be applied to set longer-term management goals.

**Project 3**

**Title: Using simulation or synthesis of existing models and observational data to develop and validate simpler metrics describing the structure and function of Great Lake food webs.**

**Rationale:** Network analysis of mass-balanced food web models requires large data sets, specialized modelling expertise, and considerable time to collect, analyze, and synthesize the data. Simpler metrics (e.g., stable isotopes, functional-group ratios, diet diversity indices, diet size-structures, species-group diversity indices, detrivory to herbivory ratios, size spectra, predator/prey ratios) which are less data and analytically intensive, may also capture elements of food web structure and function. However, uncertainty remains concerning how simpler metrics relate to more complex metrics describing functional and structural features of food webs.

**Method A:** Linear inverse modelling (LIM) is a modelling platform that could facilitate these simulations and calculation of both simple and complex metrics. Observational data exists to derive realistic representations of each Great Lake or to describe changed Great Lake food webs over time. Models can be designed to simultaneously generate simpler metrics (e.g. species-group stable isotope values, functional-group ratios, diet diversity indices, diet size-structures, species-group diversity indices, detrivory to herbivory ratios, size spectra, predator/prey ratios) that are internally consistent with mass-balanced food web structures. LIM allows for simultaneous mass balancing of consumptive and stable isotopic fractionation flows (van Oevelen et al., 2006). Functional group production ratios and size-based diet metrics can be calculated from LIM outputs (Stewart and Weidel, 2021). Taxa-specific mean body size or randomly selected values from observed taxa-specific body size distributions applied to LIM outputs could generate biomass size spectra.

**Method B:** A synthesis of selected network analysis metrics from existing Ecopath mass-balance models and calculation of simpler metrics from independent observational data can be used to explore relationships among complex and simple metrics of food web structure and function. For example, much of the original data used to calculate Ecopath mass-models could be used to derive independent estimates of simpler food web metrics. In addition, many of the modelled systems have measures of biomass size spectra (Yurista et al., 2014) or species-group isotopes

(Turschak et al., 2014), or independent measures of predator/prey ratios from bioenergetics models (Murry et al., 2010).

Depending on the models chosen, study design, and focus, several hypotheses that propose relationships between complex metrics and simpler metrics could be evaluated. Examples, of possible questions or hypotheses to explore using either method are:

- Is there a relationship between networks estimates of TTE and size-spectra derived estimates of TTE?
- How do stable isotope calculation assumptions influence stable isotope metric values?
- How are functional group ratios related to network analysis measures of food web structure and function?

**Stakeholder Relevance:** Simpler metrics are easier, less costly and less data and analytically intensive to calculate than complex metrics. These projects would determine the likely relationship between complex and simple food web metrics in Great Lakes food webs, making it easier to develop simple metric-based, longer-term, food web-scale management objectives and monitoring programs. Empirical comparisons of food web indices derived from simpler metrics will allow for comparison of food web structure across less intensively studied systems, increasing knowledge of food web dynamics and management applications.

***CATEGORY: Applying and developing tools and approaches to incorporate movement and foraging behavior into food web analysis***

**OVERVIEW:** The structure and function of food webs exhibits adaptive capacity through size structure and behavioral flexibility expressed as movement (size dependent) and diet diversity and flexibility (McMeans et al., 2019). Great Lakes exhibit a large degree of spatial heterogeneity in environmental conditions and process, along with patchy distributions of predator and prey. A spatiotemporal approach to food web assessments and modelling will lead to a better understanding of food web structure and function (Mason and Patrick, 1993).

**ProjectS**: Although the influence of movement and foraging behavior was recognized as an important area of investigation, no new projects were proposed. However, there is some ongoing relevant research. An important question is how prey preference will vary as abundance of food web species-groups change over time and space. It is also important to describe food webs of connecting waters, both resident and transitory and their relationships to nearshore and offshore food webs in the Great Lakes. Some connecting waters may be "islands" of warmwater/coolwater food webs situated between coldwater lakes (e.g. St. Mary’s River). The magnitude of energy transfer from open-water migratory fishes into connecting waters through egg deposition or spawning mortality is unknown. Do connecting waters provide a production subsidy to nearshore and offshore food webs? How do connecting waters and movement of fish influence contaminant concentrations? Ongoing work at the Cornell University Biological Station is using acoustics and laser optical plankton counters to identify the distribution of predator and prey and the potential bioenergetics consequences of the observed structure (Lars Rudstam, Cornell University, pers. comm.). In addition, a summit is planned to look more closely at the importance of connecting waters to Great Lakes ecology (Ed Roseman, U. S. Geological Survey, pers. comm.) Some of the modelling projects described above could include spatial structure and quantification of flows among spaces through movement (nearshore/offshore, tributary/lake).

***CATEGORY: Further review and summarization of food web analytical tools, applications and data needs***.

**OVERVIEW**: In the Great Lakes, interest and investigations into food webs has increased substantially in the last two decades (Ives et al., 2019). Food web network analysis metrics such as trophic transfer efficiency (TTE) and primary production required (PPR) are being applied to develop food web fact sheets describing food process relevant to managers and stakeholders (http://www.glfc.org/pubs/pdfs/research/A_Changing_Lake_Huron.pdf, accessed January, 2023). Research continues to develop simpler metrics and tracers of food web processes (e.g. stable isotopes, fatty acid profiles; Patterson et al., 2014; Chouvelon et al., 2015). The GLATOS telemetry network (https://glatos.glos.us/, accessed January, 2023) has increased knowledge of fish movements hypothesized to increase food web adaptive capacity (McMeans et al., 2016). Workshop discussions revealed that it would be useful to "take the lid off" food web modelling and analytical methods and applications, to better disseminate knowledge and help identify approaches that are most relevant to managers and stakeholders.

**Project 1:** A review of food web investigative and analytical approaches, data needs, and management and stakeholder relevance.

**Rationale:** Food web modelling, analytical methods and applications have continued to develop (Appendix A, Fath et al., 2019). There is a need to summarize, and critically review food web analytical tools, applications, and data needs. A review would be a summary of available investigative approaches, provide examples of applications, and discuss advantages and disadvantages of different approaches. The review will encourage refinement and applications identify potential limitations or impediments to applications, suggest priority data needs or metrics, and increase the opportunities for collaboration. The review would seek to identify investigative approaches and associated metrics that would be most relevant to longer-term management planning and stakeholder communication.

**Methods:** Literature review.

**Stakeholder Relevance:** The review would provide a reference for both investigators and fisheries managers to better understand the meaning of different food web metrics and their potential management appliciations.

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## References


Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I., Fulton, E., 2019. Atlantis_ A spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. Methods Ecol. Evol. 10: 1814–1819.

Chouvelon, T., Schaal, G., Grall, J., Pernet, F., Perdriau, M., A-Pernet, E.J., Le Bris, H., 2015. Isotope and fatty acid trends along continental shelf depth gradients: Inshore versus offshore hydrological influences on benthic trophic functioning. Prog. Oceanogr. 138, 158–175. doi:10.1016/j.pocean.2015.07.013

Fath, B.D., Asmus, H., Asmus, R., Baird, D., Borrett, S.R., de Jonge, V.N., Ludovisi, A., Niquil, N., Scharler, U.M., Schückel, U., Wolff, M., 2019. Ecological network analysis metrics: The need for an entire ecosystem approach in management and policy. Ocean Coast. Manag. 174, 1–14. doi:10.1016/j.ocecoaman.2019.03.007

Grami, B., Rasconi, S., Niquil, N., Jobard, M., Saint-Béat, B., Sime-Ngando, T., 2011. Functional effects of parasites on food web properties during the spring diatom bloom in Lake Pavin: A linear inverse modeling analysis. PLoS One 6. doi:10.1371/journal.pone.0023273

Hinderer, J.L.M., Blevins,  Z, Cooke,  S J, Dunlop,  E, Robinson, K F, Stang,  D L, Stewart, T J, Tyson, J T, Welsh, A B, Young, N, Muir, A M, Muir, A.M., Org, A., 2021. Insights from a novel, user-driven science transfer program for resource management. Socio-Ecological Pract. Res. 3, 337–362. doi:10.1007/s42532-021-00093-4

International Joint Commission Canada and United States, 2020. Understanding Declining Productivity in the Offshore Regions of the Great Lakes. A report submitted to the International Joint Commission by the Great Lakes Science Advisory Board, Science Priority Committee Declining Offshore Productivity Work Group June 29, 2020, 59 pgs.

Ives, J.T., McMeans, B.C., McCann, K.S., Fisk, A.T., Johnson, T.B., Bunnell, D.B., Frank, K.T., Muir, A.M., 2019. Food-web structure and ecosystem function in the Laurentian Great Lakes—Toward a conceptual model. Freshw. Biol. 64, 1–23. doi:10.1111/fwb.13203

Mason, D.M., Patrick, E.V., 1993. A model for the space–time dependence of feeding for pelagic fish populations. Trans. Am. Fish. Soc. 122, 884–901. doi:10.1577/1548-8659(1993)122<0884:amftst>

McMeans, B.C., McCann, K., Tunney, T.D., Fisk, A.T., Muir, A.M., Lester, N., Shuter, B., Rooney, N., 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. Ecol. Monogr. 86, 4–19.

Murry, B.A., Connerton, M.J., O'Gorman, R., Stewart, D.J., Ringler, N.H., 2010. Lakewide estimates of alewife biomass and Chinook salmon abundance and consumption in Lake Ontario, 1989–2005: implications for prey fish sustainability. Trans. Am. Fish. Soc. 139, 223–240. doi:10.1577/T08-216.1

Paterson, G., Rush, S.A., Arts, M.T., Drouillard, K.G., Haffner, G.D., Johnson, T.B., Lantry, B.F., Hebert, C.E., Mcgoldrick, D.J., Backus, S.M., Fisk, A.T., 2014. Ecological tracers reveal resource convergence among prey fish species in a large lake ecosystem. Freshw. Biol. 59, 2150–2161.

Stewart, T. J., Weidel, B.C., 2021. Advancing Great Lakes Empirical Food Web Modeling. Great Lakes Fishery Commission, Technical Assistance for Fishery Research Completion Report, 2021_STE_460020.

Stewart, T. J.; Sprules, W. G.; Shuter, B. J. (2005, June 19-24), Biological significance of spatial and temporal variability in Lake Ontario thermal structure.[Paper presentation]. ASLO 2005, Santiago de Compostella, Spain.

Stewart, T.J., Sprules, W.G., O'Gorman, R., 2009. Shifts in the diet of Lake Ontario alewife in response to ecosystem change. J. Great Lakes Res. 35, 241–249. doi:10.1016/j.jglr.2008.12.010

Stewart, T.J., Todd, A., Weidel, B.C., Rudstam, L.G., Bunnell, D., Hinderer, J., 2018. Changes in nutrient status and energy flow through lower trophic levels: Implications for Great Lakes fishery managers. Great Lakes Fishery Commission. Science Transfer Program Completion Report.

Turschak, B.A., Bootsma, H.A., 2015. Lake Michigan trophic structure as revealed by stable C and N isotopes. J. Great Lakes Res. 41. doi:10.1016/j.jglr.2015.04.004

Ulanowicz, R.E., 2009. Increasing entropy: Heat death or perpetual harmonies? Int. J. Des. Nat. Ecodynamics 4, 83–96. doi:10.2495/DNE-V4-N2-83-96

Van Oevelen, D., Soetaert, K., Middelburg, J.J., Herman, P.M.J., Moodley, L., Hamels, I., Moens, T., Heip, C.H.R., 2006. Carbon flows through a benthic food web: Integrating biomass, isotope and tracer data. J. Mar. Res. 64, 1–30.

Van Oevelen, D., van den Meersche, K., Meysman, F.J.R., Soetaert, K., Middelburg, J.J., Vézina, A.F., 2010. Quantifying food web flows using linear inverse models. Ecosystems 13, 32–45. doi:10.1007/s10021-009-9297-6

Yurista, P.M., Yule, D.L., Balge, M., VanAlstine, J.D., Thompson, J.A., Gamble, A.E., Hrabik, T.R., Kelly, J.R., Stockwell, J.D., Vinson, M.R., Ramcharan, C., 2014. A new look at the Lake Superior biomass size spectrum. Can. J. Fish. Aquat. Sci. 71, 1324–1333. doi:10.1139/cjfas-2013-0596

Zhang, H., Rutherford, E.S., Mason, D.M., Breck, J.T., Wittmann, M.E., Cooke, R.M., Lodge, D.M., Rothlisberger, J.D., Zhu, X., Johnson, T.B., 2016. Forecasting the Impacts of Silver and Bighead Carp on the Lake Erie Food Web. Trans. Am. Fish. Soc. 145, 136–162. doi:10.1080/00028487.2015.1069211

## Appendix A: Virtual Seminars Schedule and Presentations

(submitted as a separate pdf document)

## Appendix B: List of Workshop Participants

**Table 1.** List of workshop attendees and their affiliation.

| Name | Affiliation |
|---|---|
| Tony VandeValk | Cornell University |
| Alex Koeberle | Cornell University |
| Nikki Saavedra | Cornell University |
| Thomas Brooking | Cornell University |
| Elizabeth Whitmore-Stolar | Cornell University |
| Roger Knight | Great Lakes Fishery Commission |
| Ed Roseman | US Geological Survey - Great Lakes Science Center |
| Tomas Hook | Purdue University |
| Ed Rutherford | National Oceanic and Atmospheric Administration - Great Lakes Environmental Research Laboratory |
| Doran Mason | National Oceanic and Atmospheric Administration - Great Lakes Environmental Research Laboratory |
| Tim Johnson | Ontario Ministry of Natural Resources and Forestry (Emeritus) |
| Tom Stewart | Ontario Ministry of Natural Resources and Forestry |
| Geo Jackson | Queens University |
| Jim Watkins | Cornell University |
| Lars Rudstam | Cornell University |
| Nick Boucher | Great Lakes Fishery Commission |
| Sarah Lawhun | Cornell University |
| Kayden Nasworthy | Cornell University |
| Steph Figary | Cornell University |
| Kimberly Fitzpatrick | Cornell University |
| Marten Koops | Department of Fisheries and Oceans Canada |

## Appendix C: Participants perspectives and expectations for the workshop

**Table 1.** Anonymous responses to the pre-workshop question, "What would you like to see come out of this workshop" and each response's assigned theme.

| **Question 1: What would you like to see come out of this workshop?** | **Theme** |
|---|---|
| Interesting discussions about interesting ideas, possibly leading to learning something new about Great Lakes food webs. | Idea seeding |
| Ideas for future projects | Idea seeding |
| A better understanding of the data that's most valuable and most easily collectable to describe food webs and their effects | Gaining understanding |
| Identify management relevant needs from scientists | Management relevance |
| Learn and give input to the connection between research and management | Management relevance |
| I would like to learn more about the food web in general but specifically the lower food web and be able to communicate what we've learned to others | Gaining understanding |
| A better understanding of current knowledge gaps in food webs of the lakes--specifically lower trophic levels | Gaining understanding |
| Better understanding of future directions of food web modeling specifically in the Great Lakes | Gaining understanding |
| To learn more about food web dynamics to learn about new techniques for studying food webs | Gaining understanding |
| Understanding of tools (i.e. quantitative models etc.) available from Great Lakes setting that I can apply to my own work 2) networking and get to know experts from the field who also could provide knowledge to my research. | Idea seeding |
| Insights into different perspectives to understand and quantify food web structural relationships. Energy flow, trophic transfer, etc | Idea seeding |
| Research directions to tackle complexities | Idea seeding |
| I hope to discuss food web issues and study approaches related to the Great Lakes (i.e. brainstorm) I hope this workshop moves towards some sort of goal (proposals, papers, etc.) | Idea seeding |
| New ideas/collaborations for using data and samples | Idea seeding |
| Some new ideas of how to apply results and synthesis of food web dynamics to fish managers' needs | Management relevance |

| | |
|---|---|
| How do resource managers view foodweb/ecosystem models and how can they use these in an ecosystem management approach | Management relevance |
| I would like to gain a better understanding of food web modeling and the components used in modeling | Gaining understanding |
| I'd like to get a better understanding of what kinds of knowledge there is in the scientific community currently on food web modeling/what the most modern approaches are and how these could be applied to zooplankton research | Gaining understanding |
| A way to move forward comparing different food web analysis methods | Gaining understanding |

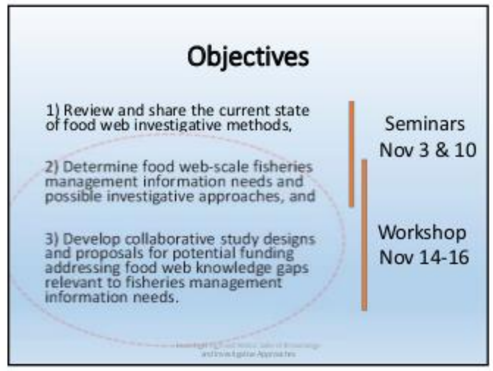
**Table 2.** Responses to the question, "What is the biggest challenge you see in applying food web science to fisheries management?" and each response's assigned theme.

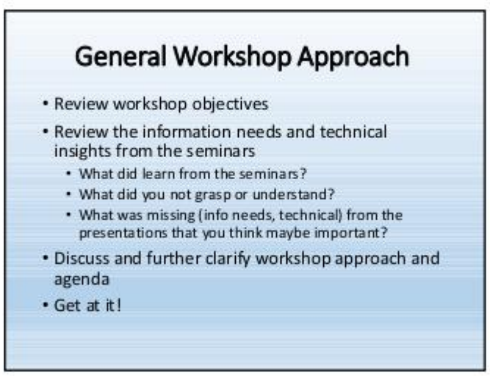
| **Question 2: What is the biggest challenge you see in applying food web science to fisheries management?** | **Theme** |
|---|---|
| Data that allows us to distinguish among critical concepts about how the Great Lakes food webs will respond to future and current pressures | Data availability |
| Developing information that is understandable/actionable to managers | Transfer of Results |
| The complexity of food webs makes me question their applicability to understanding fisheries | Complexity |
| 1) matching spatial and temporal needs of managers 2) keeping things simple/understandable for lay people | Transfer of Results |
| Communication of field results and how to interpret highly variable results--uncertainty | Transfer of Results |
| I think the biggest problem for using food web science to inform fish management is convincing the public food webs are important/the two are related to one another. | Transfer of Results |
| Thinking less of "who eats what" and moreso thinking about how energy moves through the system | Complexity |
| 1) Translating complex structures and results into something that can be understood and actively used. 2) Need for large datasets; food web models tend to require more and more higher resolution data than currently available from regular monitoring programs | Complexity |
| Connecting changes in food web structure to changes in the fish population. Convincing people that changes in small animal population influences fish. | Transfer of Results |
| Limitation of data availabilty, knowledge (species, ecology) gaps due to incomplete surveys to build robust models. | Data availability |

| | |
|---|---|
| Scale--taxonomy, space, time--these are complex and dynamic systems so what is the correct balance of detail without being overly (unnecessarily) complex. | Complexity |
| Time and spatial disparity of different levels of food webs. | Complexity |
| Challenges include integration from field work to models to fishery decisions | Transfer of Results |
| Prediction and understanding long-term projections with high uncertainty | Complexity |
| Difference in time space scaling of information generated from f.w. studies and what is needed by fisheries managers | Transfer of Results |
| communication, needs and confidence building in models | Transfer of Results |
| Greatest challenge might be understanding how lower trophic nutrients affect large predators. | Complexity |
| Making sure all parts of aquatic food webs are weighted correctly and incorporated (benthos, zooplankton, primary producers, etc.) | Complexity |
| Complexities in food webs and lack of appreciation for spatial patterns. | Complexity |

## Appendix D: Initially proposed workshop themes and questions




## Approach and agenda

- Develop 3-4 themes for consideration - **today**
  - likely to be overlap but that is OK
  - establish sub-groups to explore selected themes

- Under each theme
  - **Tuesday**
    - What are the fisheries or environmental management information needs
    - What science do we have now, or could be further developed, to meet those needs?
    - Are there critical knowledge gaps that need to be addressed before moving forward, and how could they be addressed?
    - Start reporting out to the group
  - **Wednesday**
    - Finish reporting out
    - Select priority investigative approaches to address specific management information needs or critical information gaps
    - Scope-out actual study designs, collaborations, proposals, and potential sources of funding

## Theme – Adaptive Architecture

Understanding drivers of adaptive capacity. Includes, but not limited to, exploring and expanding the ideas from McMeans et al. (2016)

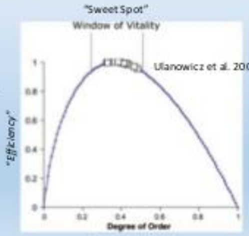
- **What adaptive responses are most relevant to fisheries managers and what are the features of food webs that drive that drive adaptive responses?**
- What are some of the leading hypotheses? Are there others?
- Are there specific hypotheses that could be evaluated
- What are the critical information gaps?

**McMeans et al. 2016**

## Theme – Simpler Metrics

Development of simpler metrics of food web structure and function **<u>useful to fisheries and environmental managers</u>** ( emergent properties, network analysis indices, TTE, PPR, isotopes)

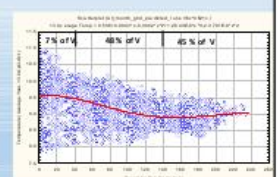
- **What characteristics of food webs do we think might be important to measure and understand?**
- Are there existing indices that may be useful and how could they be assessed?
- Are there specific hypotheses that could be evaluated?
- What are the critical information gaps?




## Theme – Space (the final frontier!)

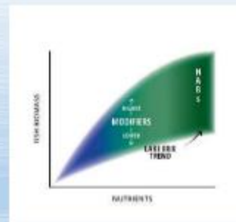
Importance of space (energy and nutrient flow among habitats, nearshore/offshore, depth gradients, water column, nearshore shunt and offshore nutrient depletion)

- **What are the most important and management relevant spatial features of food webs to understand?**
- What are some of the leading hypotheses? Are there others?
- Are there specific hypotheses that could be evaluated
- What are the critical information gaps?



## Theme – Phosphorus and Fish

- **What is the issue? How do we "bridge the gap" between a water quality mind-set and a fisheries managers mind-set?**
- What scientific information could help with this issue?
- What are the process or communication gaps?
- Are there specific hypotheses that could be evaluated
- What are the critical information gaps?




## Theme – Improving Capacity

*"keeping a consistent modeling workforce is really a problem"*
*"Is there a need for discussion about collection of food web samples and data?"* (emails from Yu-Chun Kao & Ed Roseman et al.)

- **How do we increase the capacity to do the required monitoring and modelling work to support food web scale studies?**

Image Credit - http://whywesuffer.com