

**Fisheries Management Implications of Lower Trophic Level
Change: Proceedings of Workshop I**

**August 28-30, 2018
Cornell Biological Station, Bridgeport, NY**

Editors

Tom Stewart¹ and Julie Hinderer²

¹39 Elm Street
Kingston, Ontario, K7K 1M8

²Great Lakes Fishery Commission
2100 Commonwealth Blvd.
Suite 100
Ann Arbor, MI 48105

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Introduction to the workshop

An aquatic food web exchanges available biomass among organisms through consumption via a complex network of trophic (meaning “pertaining to nutrition, food, or nourishment”) interactions. The usage of the term “lower trophic levels” (LTLs) in fisheries management refers to nutrients (most notably phosphorus) and plants (algae, macrophytes) and small animals (zooplankton, mussels, bottom organisms), many of which are eaten by fish. Biological productivity and the overall amount of living and dead biomass changes in response to changes in nutrients. The species of plants and animals comprising a food web, their feeding and non-feeding interactions with each other, and the physical environment, determine how biological productivity and biomass are distributed. Food web changes can re-distribute biological productivity and biomass to undesirable species (e.g., nuisance algae or unwanted invasive organisms) or to desirable sports fish, commercial food fish, or valued native fish species. The linkages between LTLs and fish production are often indirect, nonlinear, and unclear, and leveraging them in a desired direction is generally outside the realm of fisheries management. Consequently, fisheries managers seek a better understanding of LTL changes that have occurred in the Great Lakes and how to account for them when addressing inter-jurisdictional fish community objectives, managing stocking and predator and prey balance, restoring native species, understanding production potential of fisheries, and communicating effectively with clients and partners. The Great Lakes Fishery Commission (GLFC) Science Transfer Board commissioned a workshop process with objectives to:

- Synthesize LTL data across the Great Lakes, focusing on trends post-1990
- Summarize case-histories and hypotheses relating LTL changes to fish community change
- Facilitate a discussion among fisheries managers and LTL technical experts to better understand and communicate potential influences of LTL changes on fish and fisheries

Discussions between fisheries managers and the project team identified four workshop themes to address these objectives:

1. Supporting data and literature syntheses
2. Comparative analysis of independent measures of trophic transfer efficiency (TTE)
3. Understanding the trophic consequences of reduced phosphorus and dreissenid mussel mediated increases in water clarity on Great Lakes fish communities and fisheries
4. Predicting commercial fisheries yield and fish biomass and production from measures of LTLs

A technical workshop was held August 28-30, 2017 at the Cornell Biological Station, Bridgeport, NY to explore fisheries management implications of LTL changes in the Great

Lakes, emphasizing technical synthesis and the development of conceptual models and approaches. A second workshop will further develop these concepts with fisheries managers. The final goal will be to develop conceptual models that can guide interpretation and communication of LTL changes and fisheries, that are scientifically sound, innovative, and understandable to an informed public.

The extended abstracts of the presentations and associated discussion notes are reported approximating the order of the workshop agenda listed in Appendix A. Presentations developed from the breakout group discussions were completed after the workshop based on input provided during breakout group discussions (Appendix B). The original description of the themes and associated rationale are provided in Appendix C, and a list of participants is given in Appendix D. Source of the Ecopath models and supplementary analysis is given in Appendix E. A list of key messages to convey to fisheries managers, suggested anonymously by workshop participants, is in Appendix F. Scientific names of fish species referred to in this report are listed in Appendix G.

Acknowledgements

The concept for this workshop was initially proposed by the GLFC Science Transfer Board and further developed by Tom Stewart in discussions with GLFC staff John Dettmers, Julie Hinderer and Andrew Muir. The final project team was composed of Tom Stewart, Andy Todd (Ontario Ministry of Natural Resources and Forestry), Brian Weidel (United States Geological Survey), David (Bo) Bunnell (United States Geological Survey), Lars Rudstam (Cornell Biological Station), and Julie Hinderer (GLFC). Logistic support and hospitality for the workshop were provide by Lars Rudstam and staff at the Cornell Biological Station with special effort by Joanne Getchonis. Funding for the project was provided by the Great Lakes Fishery Commission, grant number 2017_STE_77010.

Presentations

Fisheries managers' perspective of lower trophic level changes in Great Lakes fisheries

Roger L. Knight¹

¹Great Lakes Fishery Commission, 2100 Commonwealth Blvd., Suite 100, Ann Arbor, MI 48105

Abstract

Fisheries managers recognize the ecological importance of lower trophic level organisms (phytoplankton, zooplankton, and macroinvertebrates) to fish production in the Great Lakes but often cannot link changes in these organisms to fisheries in a manner that facilitates proactive decision-making and communication to stakeholders, who focus primarily on the current condition of fishable stocks and fishery performance (Fig. 1). Communication builds legitimacy, credibility, and trust, which allows managers to act with public support in the absence of perfect knowledge. Because status/trends in the lower trophic levels (LTL) may not be reflected in status/trends of fish populations or fisheries, fisheries managers have difficulty using LTL information in decisions about management policies, fishery regulations, stocking programs, stock assessment programs, and research priorities. Managers rely strongly on information about fishable stocks and fisheries performance to support those decisions. In some cases, status/trends of key prey fish populations (e.g., alewife) can drive decisions and may be an important nexus between LTL dynamics and fishery management.

Fig. 1. Trophic spectrum for proactive fishery management decisions



Generally, fisheries managers directly affect the ecosystem through “top-down” levers, e.g., regulating fishing mortality on fishable stocks. Land and water managers directly affect the ecosystem through “bottom-up” levers, e.g., regulating phosphorus (P) loads. Weather/climate, exotic species, and human actions are often unmanageable “wild card” factors that affect how energy is transferred into fish production, affecting spatial-temporal aspects of relevance to managers. For example, managers work at jurisdictional or lake-wide scales, but know that specific areas within lakes are important to fish production and to the availability of different management levers. LTL dynamics are important aspects of these areas and may respond differentially among areas to changes in wild card factors. Understanding the time lags between changes in nutrient loads (or the introduction of a new exotic species) and impacts on fish populations/fisheries is especially relevant to proactive management.

The interagency lake committees of the Great Lakes Fishery Commission offer guidance in their fish community and environmental objectives about LTL importance to fisheries management. Common principles among the five committees involve the linkage between fish production/fishery yield to lake productivity and how efficiently energy is moved across trophic levels. Common objectives recognize the importance of key fish species for having efficient food webs and functional habitats for both predator and prey species.

Specific examples of LTL relevance to fisheries management in the Great Lakes include:

- *Diporeia* declines – effects on native fish stocks and associated fisheries after the establishment of *Dreissena* spp. in the Great Lakes Basin,
- *Dreissena*/round gobies – separately and/or together affect fish production (negatively and positively), with an added aspect of enhancing contaminants transfer through the food chain and impacts on human fish consumption,
- Botulism *e* (*Clostridium botulinum*) – direct impacts on fish health and indirect effects on fishery effort (fewer fish and stigma from seeing moribund fish may reduce effort),
- Alewife – the importance of LTL in producing alewife and the top-down effects of alewife predation on LTL, are relevant to fishery management interests in native species restoration and salmon stocking program decisions,
- *Hexagenia* – lagged recovery in western Lake Erie from extirpation in 1950s (due to anoxia) to prominence in the 1990s, boosting fish production, but now at risk again given a recurrence of high P, cyanobacteria, and extensive anoxic zones, and
- Eutrophication/oligotrophication – varying responses in fish production and fishery yield of Percids in Lake Erie after *Dreissena* establishment.

In summary, the use of LTL information by fisheries managers in the Great Lakes could be improved by increasing their understanding of the linkages between LTL and fisheries for accommodation into fish community objectives (or implementation to achieve extant objectives) and proactive management of potential issues or opportunities with stakeholder support. Areas of exploration might include clarification of:

1. Ecological mechanisms that fundamentally link LTL to fish production (recruitment, growth, survival) in an era of established *Dreissena* populations
 - LTL influences on habitat requirements of key fishes across life stages (eggs, larvae, juvenile, adults)
 - Effects on fish behavior (biotic vs abiotic turbidity, movements, foraging activity)
 - Effects of dynamic trophic interactions (bottom-up, top-down, middle-out) due to eutrophication/oligotrophication
 - Effects of altered trophic interactions from exotic species
2. LTL effects on fisheries metrics
 - angler effort (travel distance to fish, expected catch)
 - catch per unit of effort (population age structure and abundance, spatial distribution/density, foraging behavior, by-catch)

3. General response times (or lags) for LTL effects on habitats, fish, and people (fisheries)
4. Variation in fish production and fisheries performance that can be attributed to manageable (nutrients, connectivity) vs. unmanageable (weather, lake levels, aquatic invasive species) aspects of LTL dynamics, to help managers understand
 - extreme recruitment events
 - unexpected levels of fishery catch per unit of effort
 - effects on stock assessment programs (e.g., sampling design, results)
 - how to leverage fish production and fisheries performance in a desired direction at relevant temporal-spatial scales

Discussion Notes

Q: What do fishery management agencies think about climate change?

A: Not all are on board with the concept, but no one can argue with data on intensity and frequency of spring storms. Focus on the evidence (water temperatures, storms) rather than linking to climate change.

Q: How does the public react to the concept of multiple stressors interacting? Is it better to talk about single stressors?

A: [One person's experience:] Tried not to throw in kitchen sink when meeting with stakeholders. We don't know.

Lake Constance - Upper Lake, a lake that has undergone intensive re-oligotrophication

R. Roesch¹

¹LAZBW, Fisheries Research Station, Argenweg 50/1, 88085 Langenargen, Germany

Abstract

Lake Constance is situated in Middle Europe between Germany, Switzerland and Austria. It is divided into the larger Upper Lake (ULC) and the smaller Lower Lake. In the following only ULC is considered. ULC is located at about 395 m above sea level, it has a surface area of 473 km², a maximum depth of 254 m and a drainage area of about 11.500 km². Water level is unregulated, it is lowest in late winter and highest in early summer with water level fluctuation reaching up to 3 m within a year. In general, ULC is a warm monomictic lake with total mixing occurring at the end of February, when homothermous conditions (4°C) are reached. In recent years due to climate change total mixing is not occurring every year. Average air temperature at ULC is increasing by 0.05 °C per year and water temperature in 0.5 m depth by 0.03 °C per year (www.KLIWA.de). Originally an oligotrophic perialpine lake, ULC has undergone eutrophication beginning in the 1950s and re-oligotrophication in recent years (Fig. 1). The P-concentration is now at the level before eutrophication (Güde et al. 1998, www.igkb.org).

The lake contains about 36 fish species (Eckmann & Rösch 1998). The commercially most important fish species are whitefish (*Coregonus lavaretus*) and perch (*Perca fluviatilis*) (Rösch 2014).

Commercial fisheries yield followed the trophic changes (Fig. 2). After low yield until the 1950s yield increased, and in 1956 for the first time commercial yield exceeded 1000 t. Up to 2005 in no year was yield below 800 t. Since about 1990 commercial yield is rapidly decreasing. In 2015 only 261 t fish were caught by commercial fishermen. This is the lowest yield since 1918. In 2016 commercial yield was only slightly higher. Whitefish yield was highest during periods of 10 to 30 µg/l TP concentration, whereas yield of perch and cyprinids was highest during the eutrophic phase of the lake.

The recent yield is far below the yield expected with the actual trophic status of the lake. The main reason is the invasion of nonnative invasive stickleback (*Gasterosteus aculeatus*) into the pelagic zone in 2013. In 2014 stickleback consisted of more than 80% of the pelagic fish community in numbers and more than 20% in biomass (Alexander 2016). This situation persists until now (autumn 2017). Stickleback are considered as direct competitors for food (zooplankton) to coregonids as well as effective predators on fish larvae: on newly hatched whitefish larvae in early spring after hatching, and on perch, pike (*Esox lucius*), and cyprinid larvae in spring on the shore. In parallel to the decreasing fisheries yield year class strength of pelagic whitefish seems to decline (Roesch et al., submitted). Yield of perch, burbot (*Lota lota*), migrating brown trout (*Salmo trutta*) as well as Arctic char (*Salvelinus alpinus*) decreased drastically in recent years, too. For perch and burbot the reason may be larval predation, but for Arctic char the direct connection with stickleback population remains speculative. The only species apparently profiting from stickleback are pike and European catfish (*Silurus glanis*). Both species use stickleback for food, and in 2016 yield of both species was the highest since the beginning of fisheries statistics in 1910

(www.ibkf.org). However, actually (2017) preliminary data suggest that pike yield is much lower than in 2016, indicating lower recruitment.

Before eutrophication yield consisted of about 75% whitefish (Fig. 3). During the eutrophic phase proportion of whitefish yield to total yield decreased to 30-50%. During this phase perch comprised up to 50% of the commercial yield. With re-oligotrophication the situation reversed and the proportion of whitefish in the total yield increased to about 75% again. However, in recent years (with stickleback) whitefish yield comprises only about 60% of total yield, i.e., a much lower percentage than before stickleback.

The number of licenses for commercial fishermen decreased from 180 at the end of 1970s to 100 in 2016, mainly due to decreasing fisheries yield which is a disastrous economic situation for the commercial fishermen.

In conclusion, it is assumed, that the situation will persist, as long as the stickleback population remains at this high level. Actually, the stickleback population does not show any signs of decreasing.

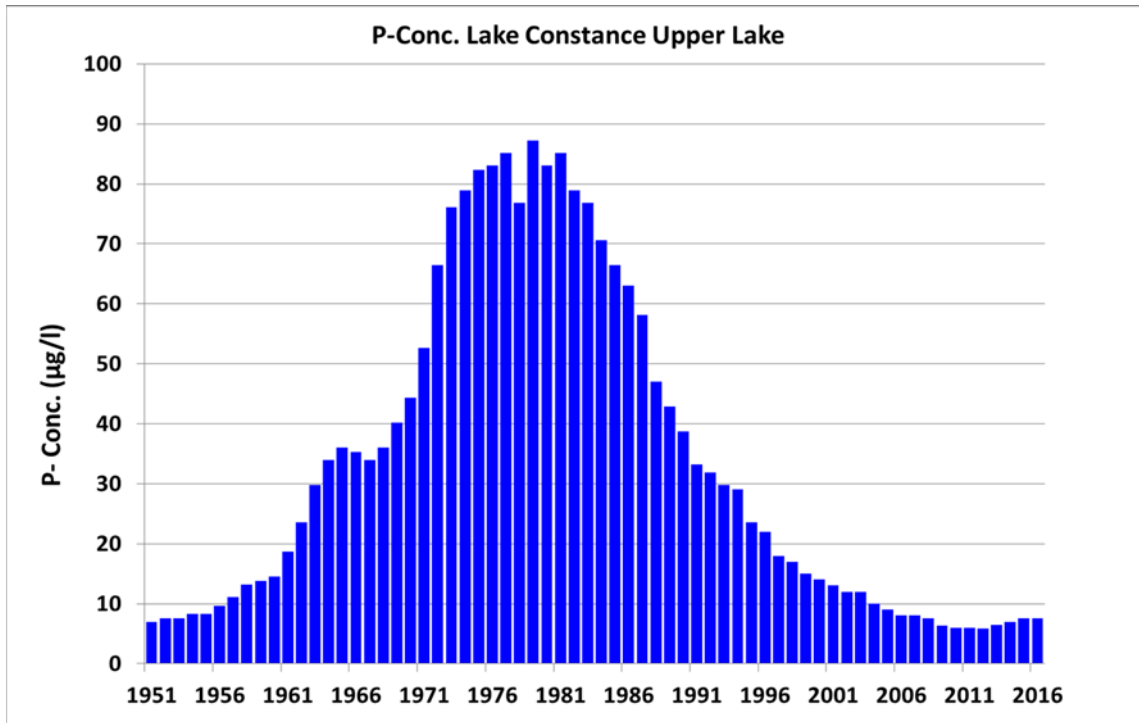


Figure 1. Volume weighted annual mean of Total-Phosphorus (mg/m^3) 1950-2016 in ULC (www.IGKB.org).

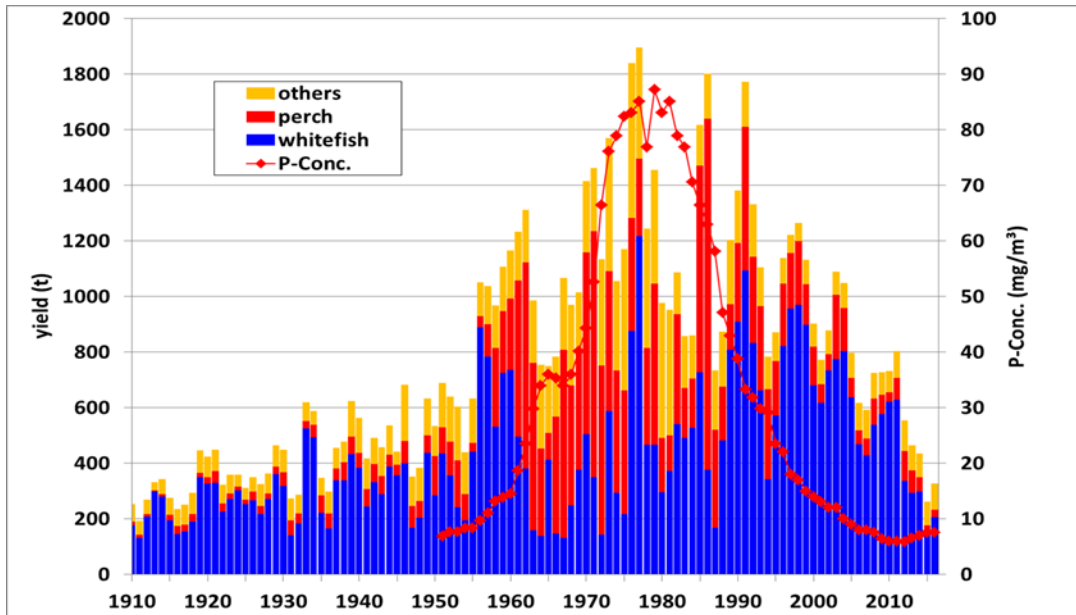


Figure 2. Commercial fisheries yield (t) in ULC 1910-2016: whitefish, perch, others (others: all species except whitefish and perch).

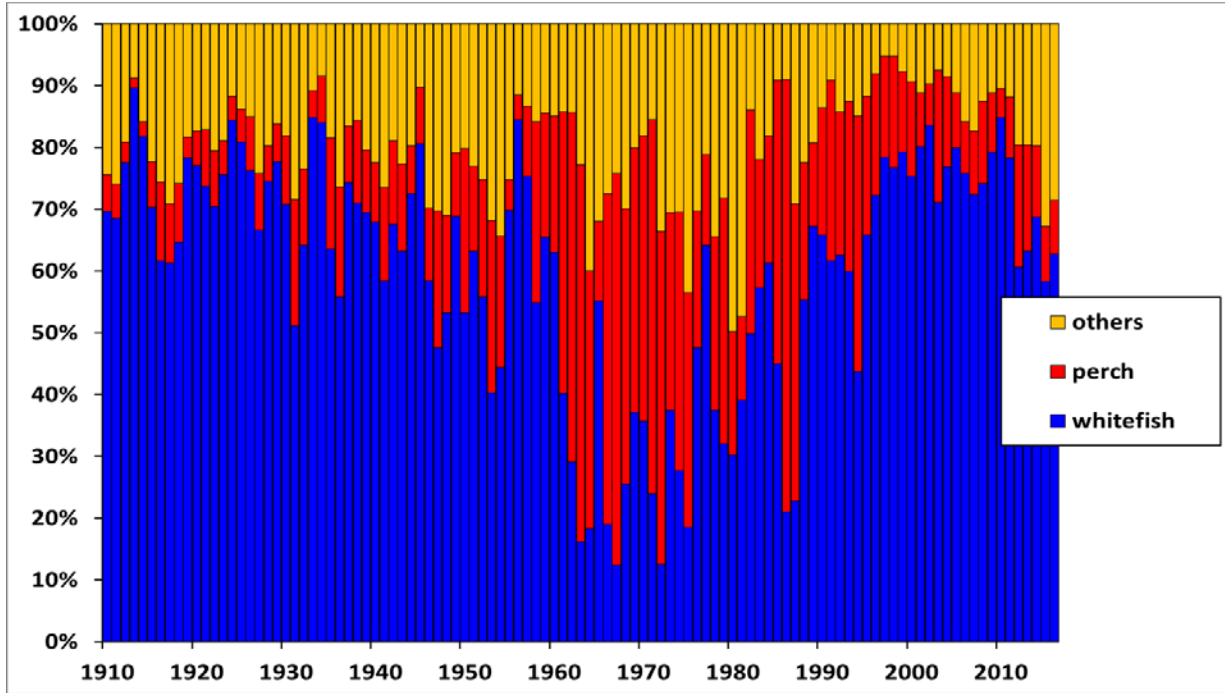


Figure 3. Relative composition (%) of commercial fisheries yield in ULC of whitefish, perch and others.

References

- Alexander T. J., Vonlanthen P., Périat G., Raymond, J.C., Degiorgi, F., Seehausen O. 2016. Artenvielfalt und Zusammensetzung der Fischpopulation im Bodensee. Projeť Lac, Eawag. Kastanienbaum
- Eckmann, R. & Roesch, R. 1998. Lake Constance fish and fisheries. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 53: 285–301
- Eckmann, R., Gerster, S. & Kraemer, A. 2006. Yields of European perch from Upper Lake Constance from 1910 to present. Fish. Manage. Ecol., 13: 381–390
- Güde, H., Rossknecht, H. & Wagner, G. 1998. Anthropogenic impacts on the trophic state of Lake Constance during the 20th century. Arch. Hydrobiol. Spec. Issues Advanc. Limnol., 53: 85–108.
- Roesch, R. 2014. Lake Constance fish and fisheries. In: Welcomme, R. L., Valbo-Jorgensen, J. & Ashley Halls, A. S. Inland fisheries evolution and management. Case studies from four continents. FAO Fisheries and Aquaculture TECHNICAL PAPER 579: 21-32.
- Roesch, R., Baer, J. & Brinker, A. (2017). Impact of the invasive three-spined stickleback (*Gasterosteus aculeatus*) on relative abundance and growth of native pelagic whitefish (*Coregonus wartmanni*) in Upper Lake Constance. Hydrobiologia (2017). <https://doi.org/10.1007/s10750-017-3479-6>.

Discussion Notes

Q: Are there any data back in 1970s, 1950s before eutrophication to know the gonado-somatic index (GSI)?

A: Not for GSI unfortunately. A few data from the 1930s about whitefish condition (length-weight relationship), which is even lower now than it was.

Q: Are the whitefish planktivores?

A: Yes, partly benthivores as well nearshore feeders.

Q: Are there different forms of whitefish?

A: Yes, 3 types... pelagic spawning, nearshore spawning and benthic spawning

Stickleback are an invasive species, were nearshore for a while, then exploded in pelagic zone around 2013. Direct competition for zooplankton between stickleback and whitefish. Stickleback are also able to prey on larval fish (including whitefish larvae). This caused declines in weight-at-age in whitefish. Declines in CPUE. High densities of stickleback on shoreline during whitefish spawning. Whitefish net-pen aquaculture is being proposed.

Q: Were there trends in whitefish condition before sticklebacks?

A: Yes, it was already changing with oligotrophication, stickleback just aggravated.

Q: Why did stickleback explode after being in the lake for so long?

A: We have absolutely no idea about the reason. Started showing up as bycatch in pelagic gill nets from 13 on.

Q: Do you stock whitefish?

A: Yes. We have started marking eggs using Alizarin red S in winter 2016 to evaluate proportion of fish from stocking. No data yet.

Q: Stickleback are similar to white perch in Lake Erie – didn't really take off until mid-1980s. There was a series of warm winters, and these are cold-sensitive fish, so we think this allowed populations to overwinter well, and there was a reduction in walleye biomass at the time. Are stickleback cold sensitive? Any missing predators?

A: Stickleback is not cold sensitive. To our knowledge this is the first oligotrophic "large" lake where this has happened.

Q: P concentration shows a rapid increase and then almost symmetrical decrease. In some cases this matches up well with biota, other cases not at all. There seems to be hysteresis in how different biota are responding.

A: For zooplankton we only have counts, not production.

Q: Who has final decision-making authority between fishermen and the environmental community?

A: It's a political decision, there are commissions/groups of experts and then politicians that decide. It's is not just based on science.

C: The decline in fisheries yield is a lower magnitude than decline in P concentration – not a direct relationship.

C: It would be nice to look at relationship between numbers of zooplankton and fish biomass.

Q: Do you have water clarity data? Did it do what would be expected with eutrophication?

A: Don't have the data here, Secchi depth was 10-15 m in 1950s, and it's back to that now. There is submerged vegetation up to 20m; this totally disappeared during eutrophic period

C: The response to zooplankton is similar to Bay of Quinte, one perspective is that zooplankton are influenced by both bottom-up and top-down effects, another perspective is that zooplankton tend to do their own thing.

C: The lake has had zebra mussels since ~1965 and quagga mussels just recently arrived.

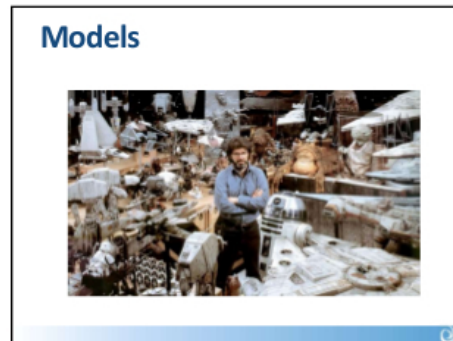
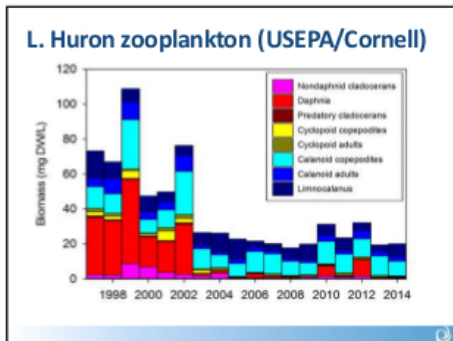
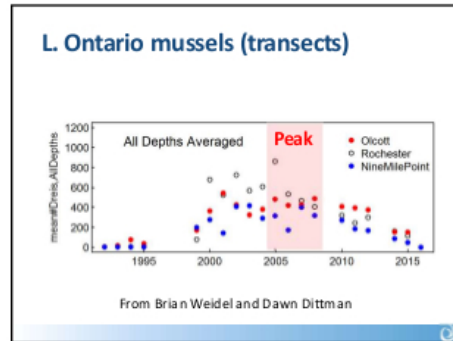
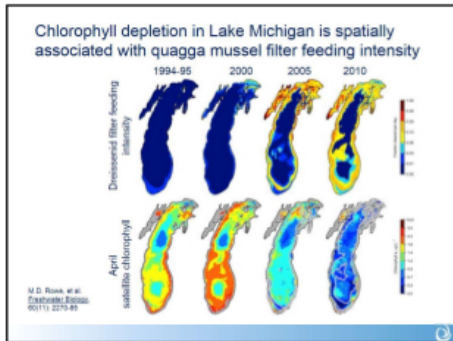
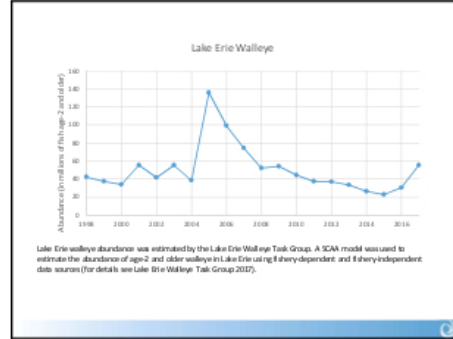
Q: The decline in number of commercial fishermen happened at the same time as the decline in yield, but decline in effort shouldn't really effect yield, correct?

A: Yes, for whitefish. > 95 % of whitefish are fished out when reach legal size.

Update on IJC assessment of declining offshore productivity in the Great Lakes

John Bratton¹, Doug Bradley¹, Jen Daley¹, and Nate Jacobson¹

¹LimnoTech, Ann Arbor, Michigan



Discussion Notes

Q: Dreissenids have peaked in Lake Ontario and are declining?

A: Yes, according to Weidel data.

Q: Any possibility that there are so many dead dreissenid shells on the bottom that ehippia/resting eggs can't survive? Could this be causing a bottleneck?

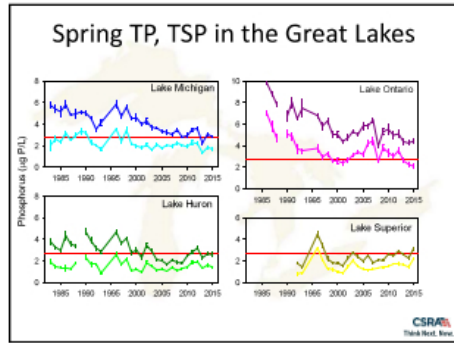
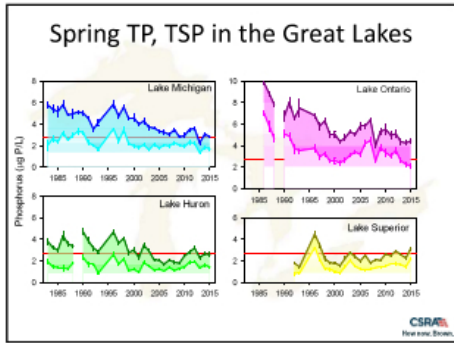
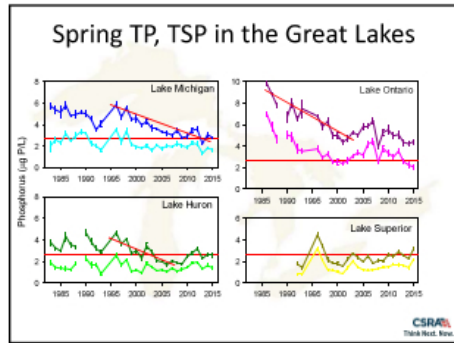
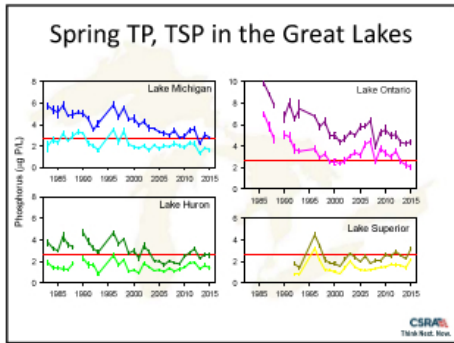
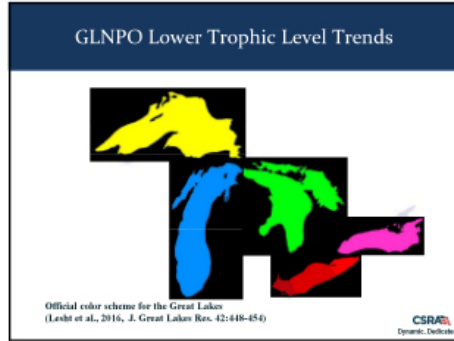
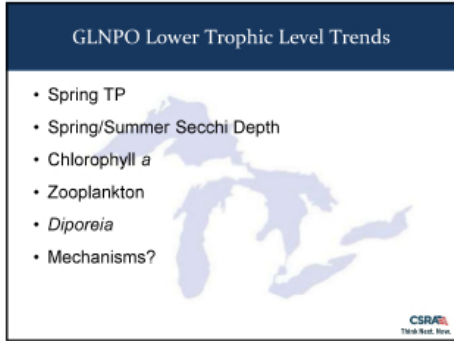
A: You've definitely changed grain size of deep sediment, have changed shallow sediment chemistry with pseudofeces, and there's more organic matter. This is a good point, it's a fundamentally different lakebed physically and chemically. We tend to focus on filter feeding aspect but there are other aspects. Lake Huron's biggest decline is in cladocerans – but this pre-dated dreissenid impacts. There is also new material being put on top of the lake bottom.

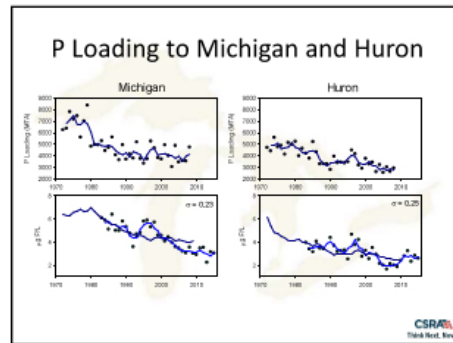
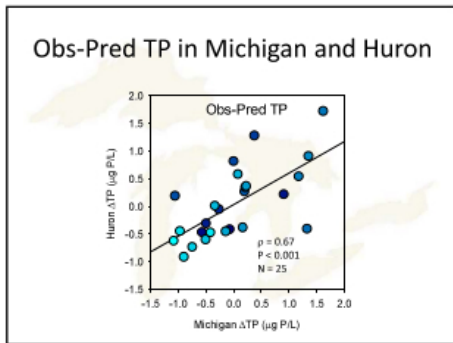
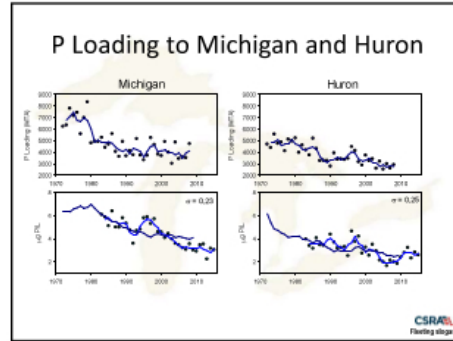
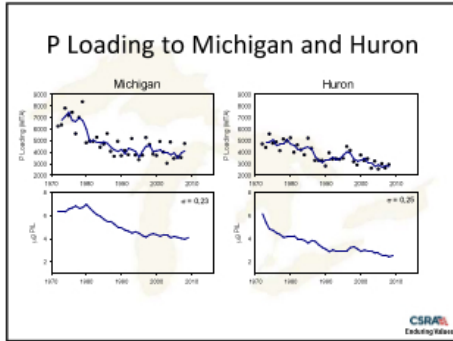
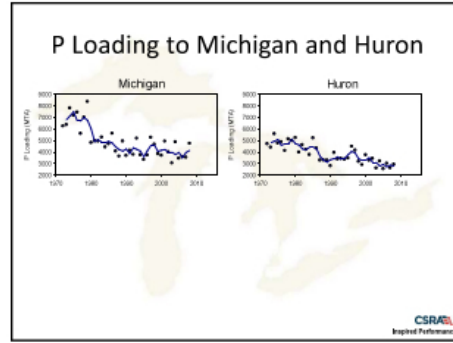
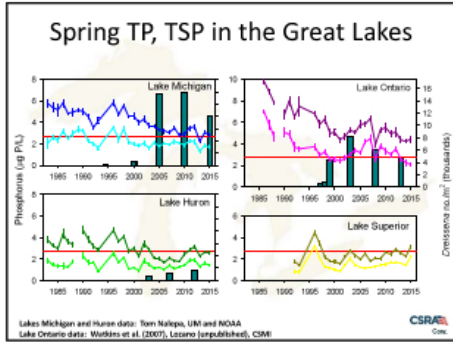
Great Lakes lower trophic level indicator trends

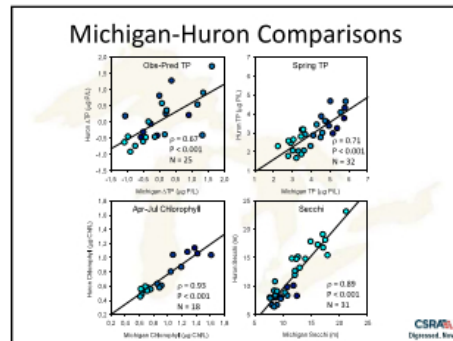
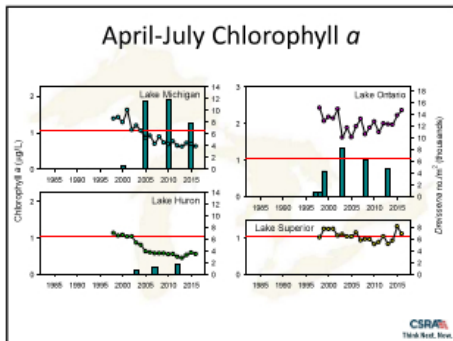
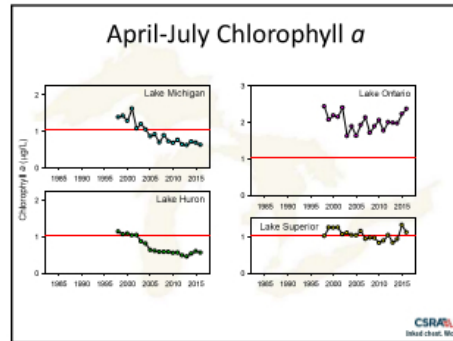
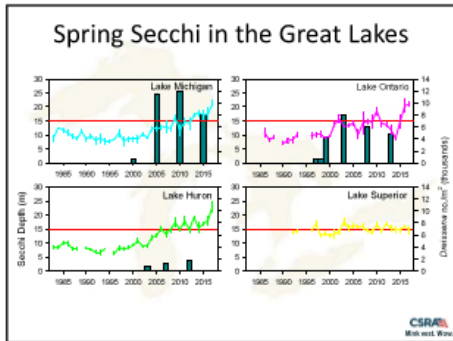
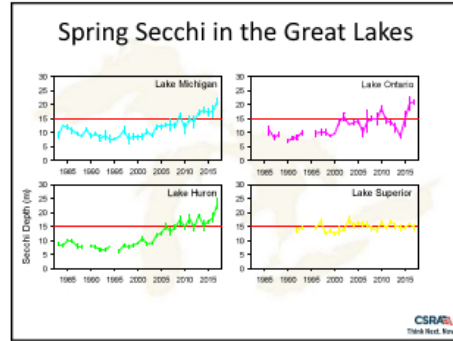
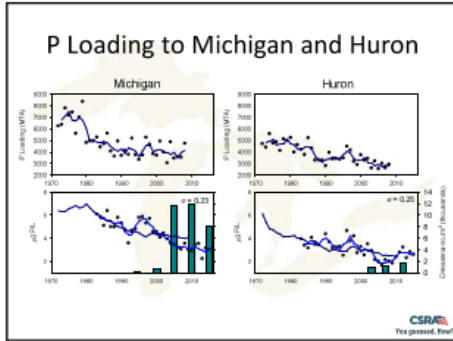
Rick Barbiero¹ and Elizabeth Hinchey²

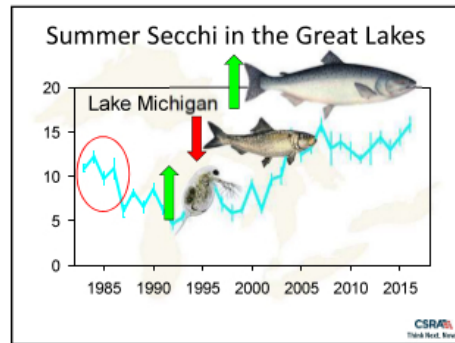
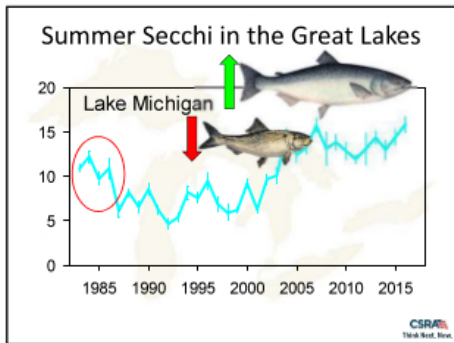
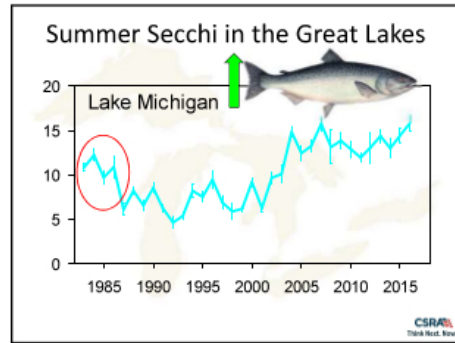
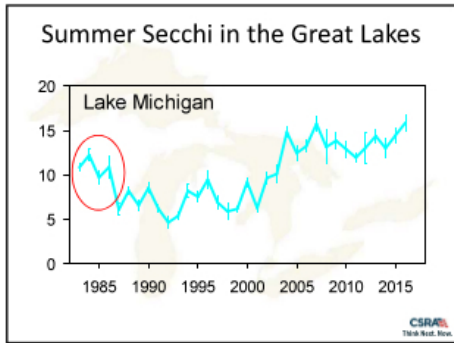
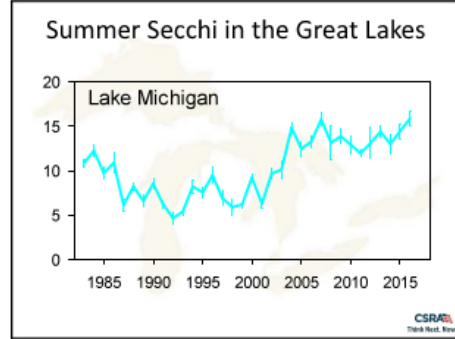
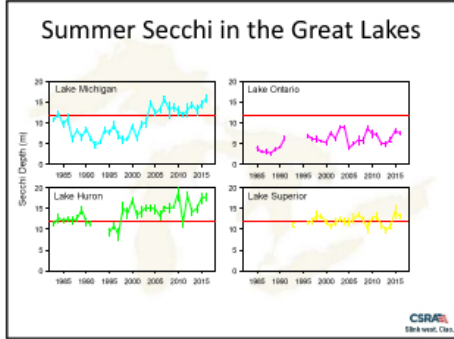
¹DynCorp Environmental, Alexandria, Virginia, USA

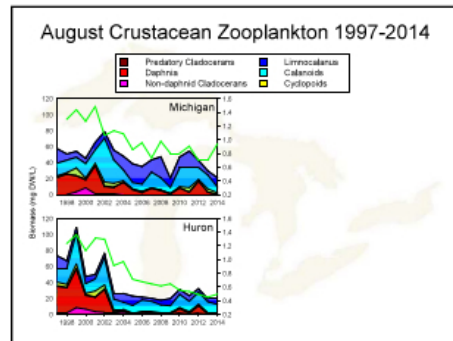
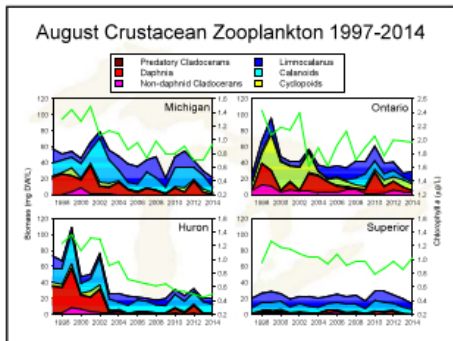
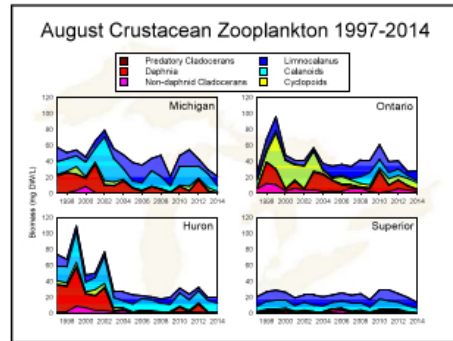
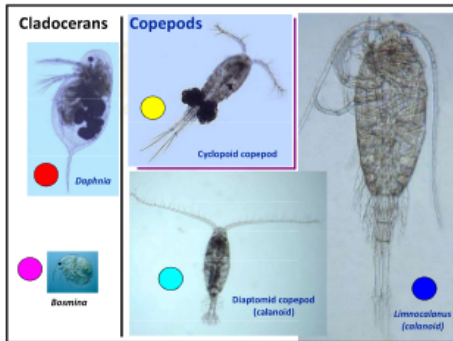
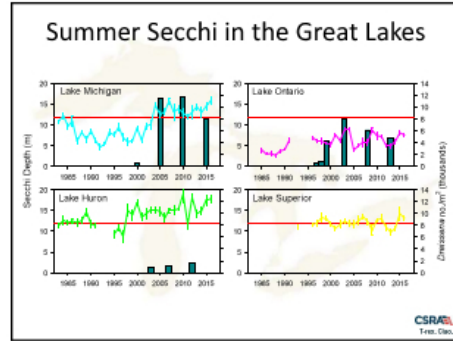
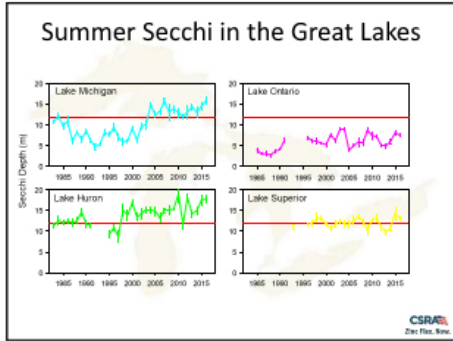
² U.S. Environmental Protection Agency, Great Lakes National Program Office, 77 West Jackson Blvd., Chicago, IL

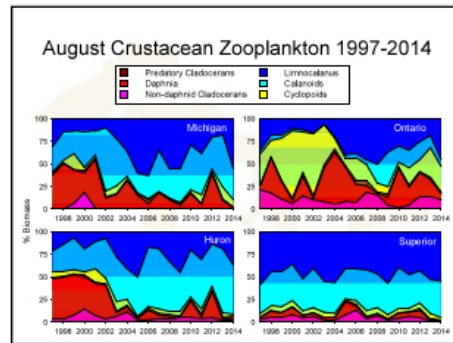
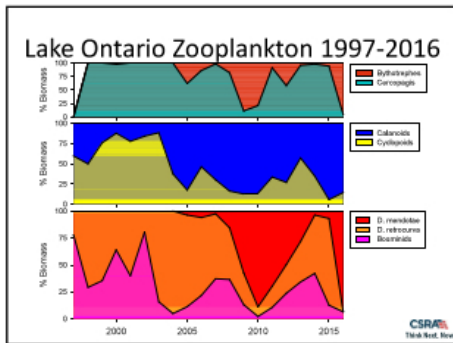
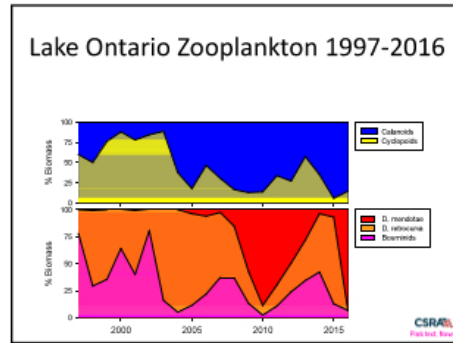
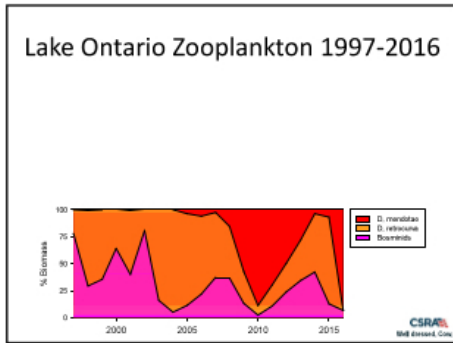
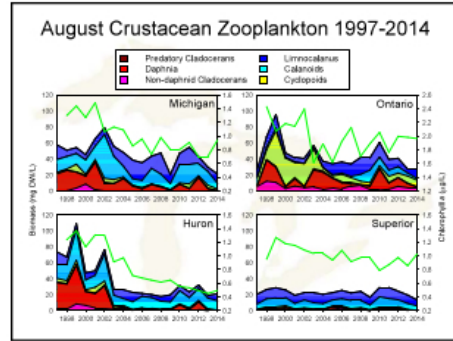
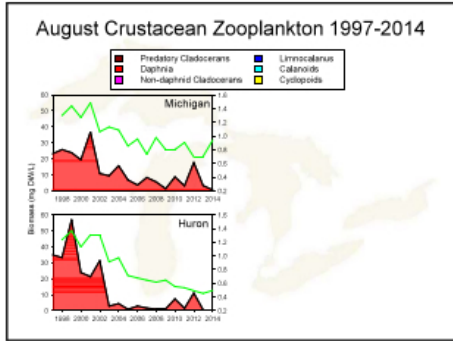


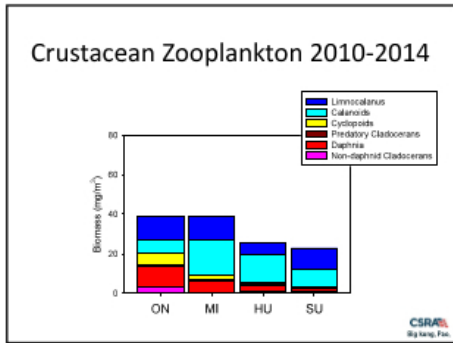
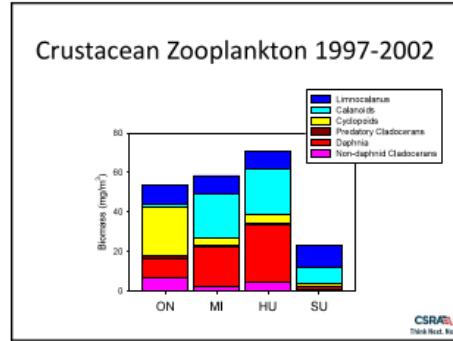
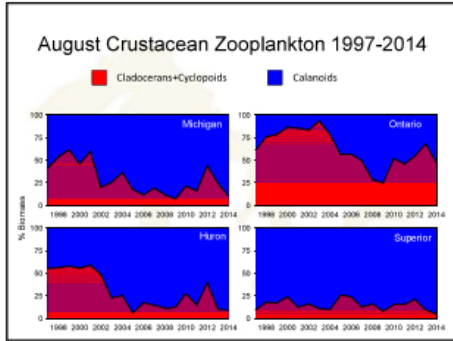






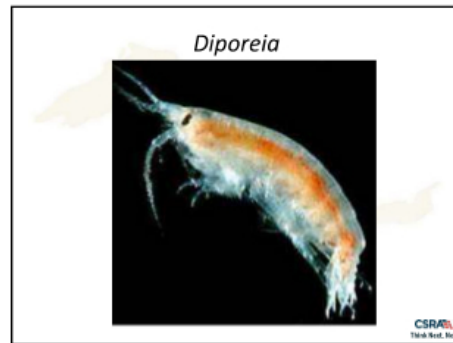
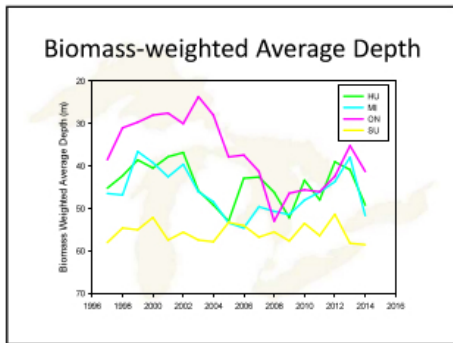


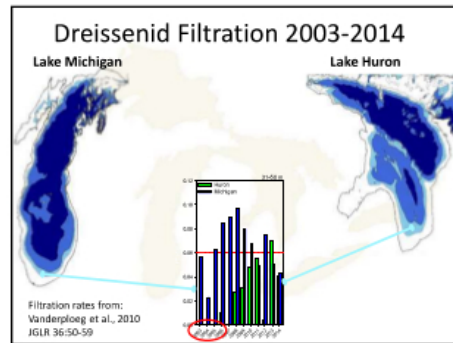
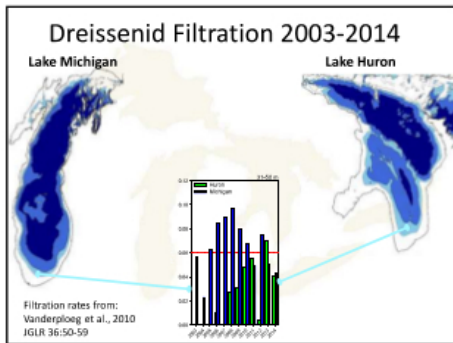
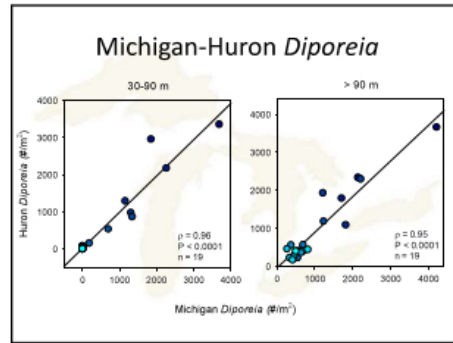
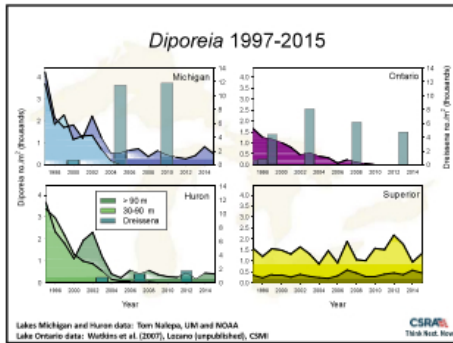
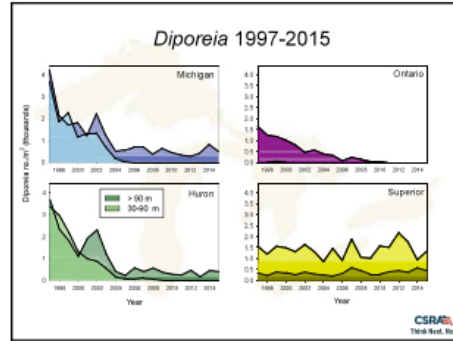
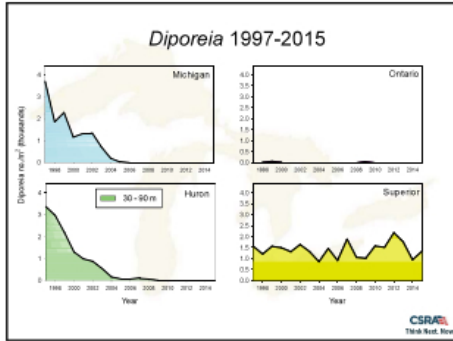


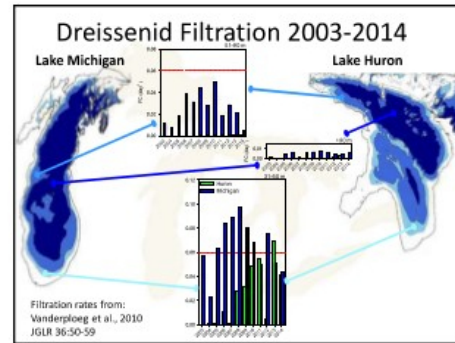
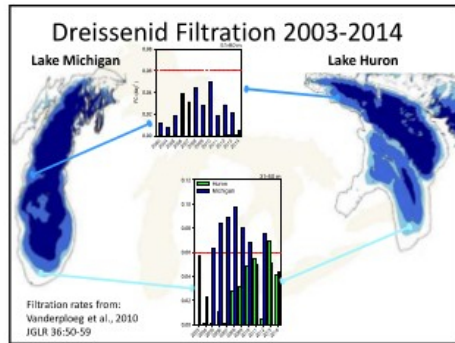


Biomass-weighted Average Depth

Species	Day dist	Depth
<i>Cercopagis pengoi</i>	E	5
<i>Epischura lacustris</i>	E	5
<i>Bythotrephes longimanus</i>	E-M	18
<i>Daphnia retrocurva</i>	E-M	18
<i>Leptodaptomus minutus</i>	E-M	18
<i>Diacyclops thomasi</i>	M	20
<i>Epischura lacustris</i>	M	20
<i>Leptodaptomus eschlandi</i>	M	20
<i>Bosmina longirostris</i>	M-UH	30
<i>Daphnia mendotae</i>	UH	40
<i>Leptodaptomus sicilis</i>	H	60
<i>Limnocalanus macrurus</i>	H	60







Discussion Notes

Q: Are there effects of *Bythotrephes*?

A: We haven't seen a trend, haven't found correlation in this part of data series.

C: Lake Ontario cladocerans - about the same but there has been a shift to larger-bodied cladocerans (*D. mendotae*), around 2005. Also shift to more calanoids, fewer cyclopoids. Now governed more by invertebrate than vertebrate planktivory.

C: *Bythotrephes* always causes shifts away from *D. retrocurva* to *mendotae*.

C: There have been changes in depth where zooplankton biomass is distributed – got deeper in mid-2000s and then shallower again after 2010 (in all lakes except Erie).

C: Total P loading declined early in dataset and might have stabilized. Seems there is a clear nutrient input, as declines lead to reduction in plankton and *Diporeia*. The difference in Lake Superior is that maybe Michigan and Huron crossed some loading threshold, that combined with added stress of dreissenids might have caused collapse.

C: There are problems with timing with this hypothesis. How is stress being applied by dreissenids to zooplankton? What is the mechanism?

Q: Is there some threshold/tipping point below which you can't recover from?

A: Certainly looks like *Diporeia* hit a tipping point ~2003 in Michigan and Huron, particularly Huron.

C: Huron is less productive to begin with so may be “more sensitive” because of this.

Q: There is actual communication of water between Michigan and Huron, and some loading Huron is receiving from Michigan. Is that something to consider?

A: It is just a couple drops really when you look at residence time. My guess is that there would be no impact.

C: There has been a shift in size structure of phytoplankton, such that it is now dominated by picophytoplankton. Not as useful for most of food web, only *Daphnia* in late summer can use. Has to pass through microbial food web before it is available to zooplankton. Combined with chlorophyll trends, loss of spring bloom, and shift in size structure, is chlorophyll functionally not being transferred as efficiently up the food web?

Q: How does depth of epilimnion (increased clarity) affect availability of phytoplankton to filtering? What about senescence and settling; material getting locked in pseudofeces doesn't get resuspended. Might be possible that dreissenids would have impact on deep lake without filtering at surface.

A: If there's a density-influenced vertical structure it could affect filtration, and yes turning phytoplankton into something that is unavailable is a reasonable hypothesis.

Q: Is the deep chlorophyll layer (DCL) more vulnerable where it is now?

A: It will only form in a place with density structure though, so it's blocked.

C: DCL forms when phytoplankton have enough light for photosynthesis and there is enough nutrients. Tend to be at the bottom of the euphotic zone in GL – does not necessarily form at

Presentations

density gradients. Also affected by photoacclimation and biomass peaks higher than chlorophyll peak in upper lakes

Trends in benthification of the Canadian nearshore

Todd Howell¹

¹Environmental Monitoring and Reporting Branch, Ontario Ministry of the Environment and Climate Change, 125 Resources Road, Toronto, Ontario. M9P 3V6

Abstract

The colonization of the Great Lakes by the filter-feeding mussel *Dreissena* has altered the ecology of nearshore areas as evidenced by obvious changes to the lakebed. These changes have included: increased autotrophic and heterotrophic biomass on the lakebed and presumably increased benthic primary and secondary productivity; increased amounts of organic material and macro-nutrients on the lakebed; and, increased physical-structural complexity of the lakebed. A process termed benthification is used to describe the cascade of biological and physical effects correlated with the *Dreissena* invasion that increasingly focus biological activity and materials to the lakebed. The contrasting physical settings and ecologies among the sub-basins of the Great Lakes modify the effects of the *Dreissena* on nearshore ecology. Changes linked to benthification are seemingly interactive with a range of features including trophic state of the basin, prevailing photic depth, prevailing substrate type, and features of lake circulation in the nearshore.

A review of water quality and benthic algae data collected in the Ontario Ministry of the Environment and Climate Change's nearshore monitoring program suggests that changes suggestive of benthification vary widely from region to region on the Canadian shores of the Great Lakes. Two data sources have been used to inform this analysis. Periodic monitoring of water quality and benthic invertebrate assemblages at a network nearshore index and reference stations (Fig. 1) provide insight on the distribution of *Dreissena* and changes in water quality correlated with the invasion. Diver-based quantitative surveys of benthic biota have been conducted around the Great Lakes in recent years and provide insight on benthic ecology (Fig. 2).

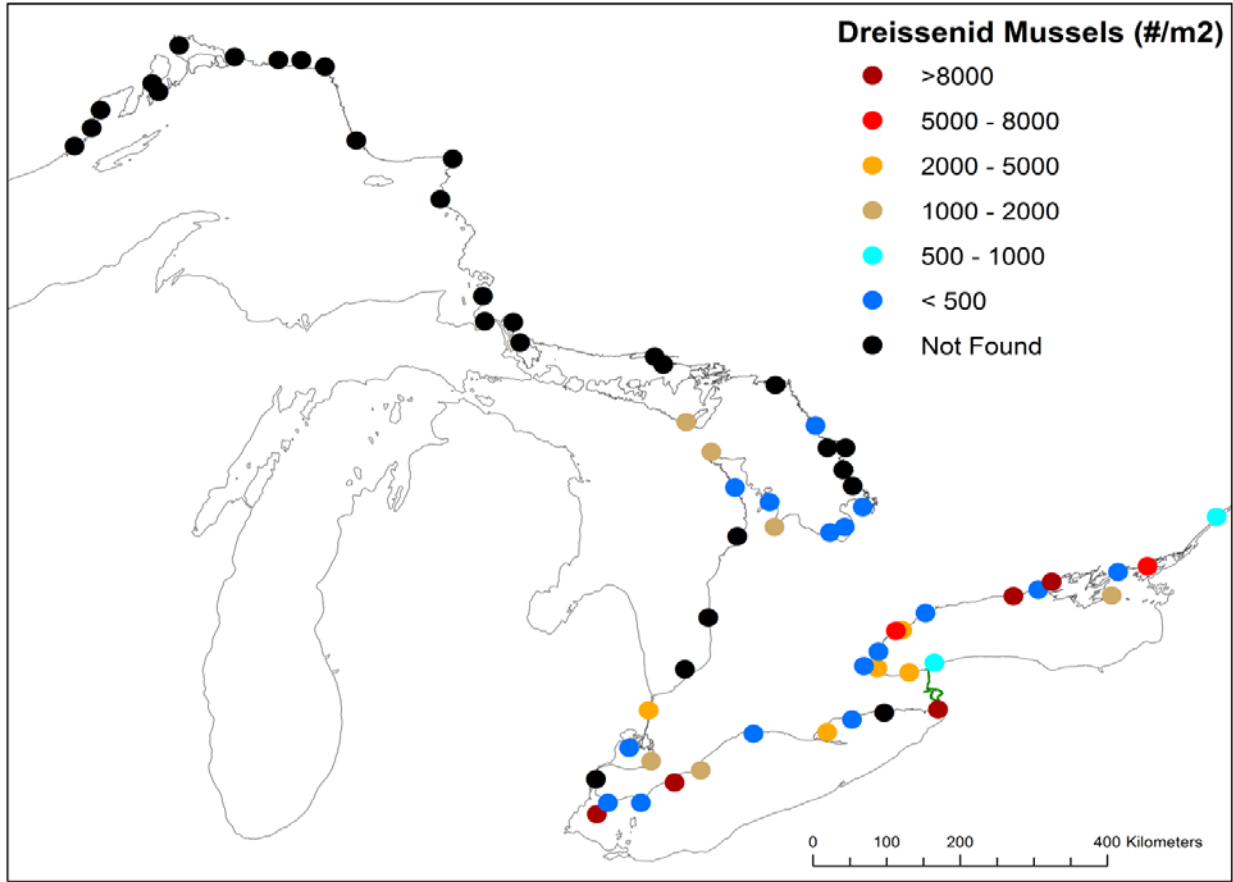


Figure 1. Abundance of *Dreissena* at MOECC nearshore index and reference station averaged over the two most recent years of survey (ranging from 200x to 2015; n=10 in most cases). Samples were collected using a 9-inch Ponar and sieved with 600 μ m mesh.

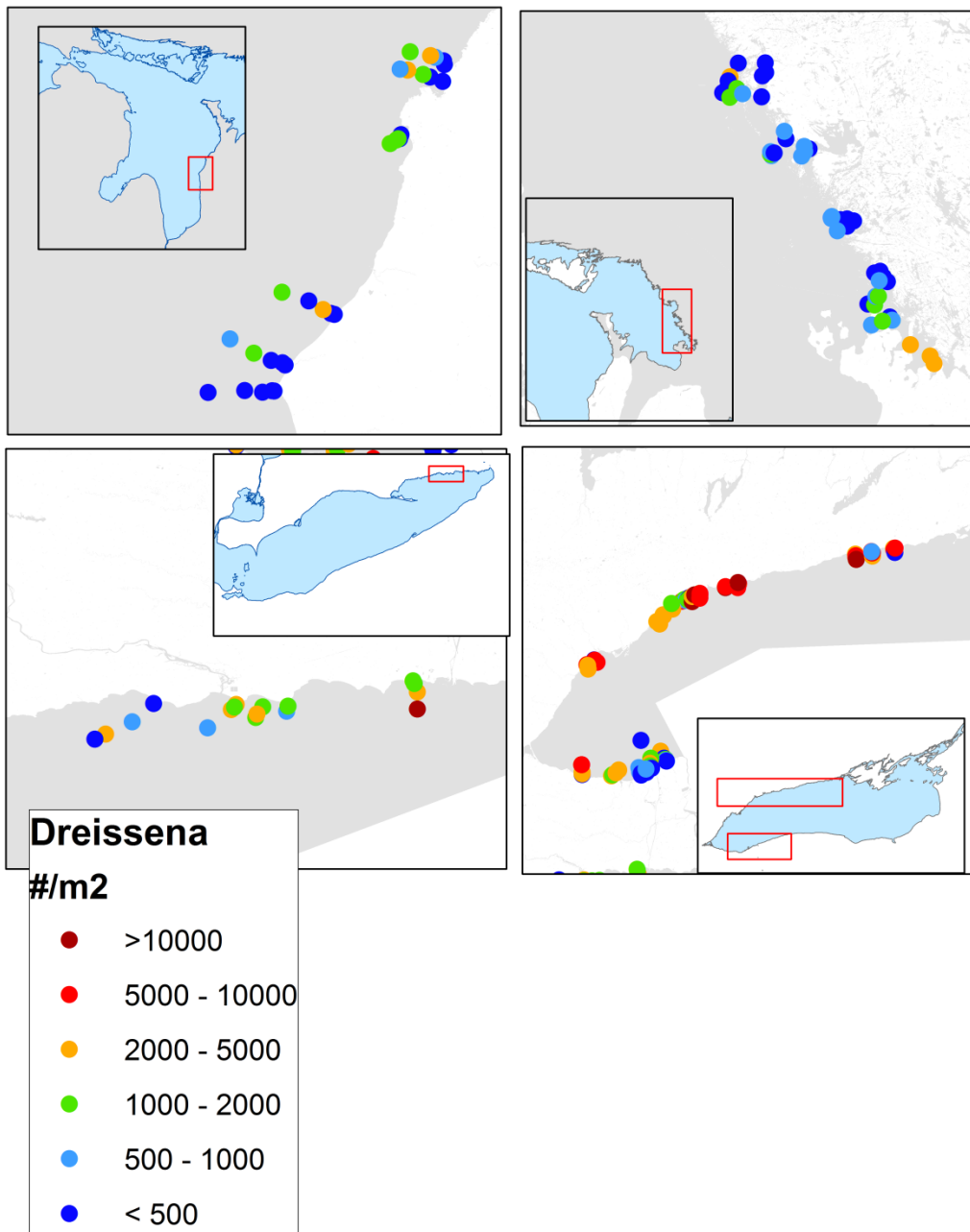


Figure 2. Abundance of *Dreissena* on hard substrate at nearshore study areas surveyed from 2008 to 2014. Samples were collected by divers from randomly placed 0.15 m² quadrats at depths of 1 to 20 m.

Benthification is obvious in Lake Ontario where there is a widespread high density of mussels (Fig. 2). The green algae *Cladophora* proliferates on the lakebed at shallow depths (Fig. 3) facilitated by a moderate to deep photic zone (Fig. 4) and abundant hard substrate at shallow depths. There is copious periphyton and organic debris on the lakebed. Water column productivity appears low and possibly trending downward.

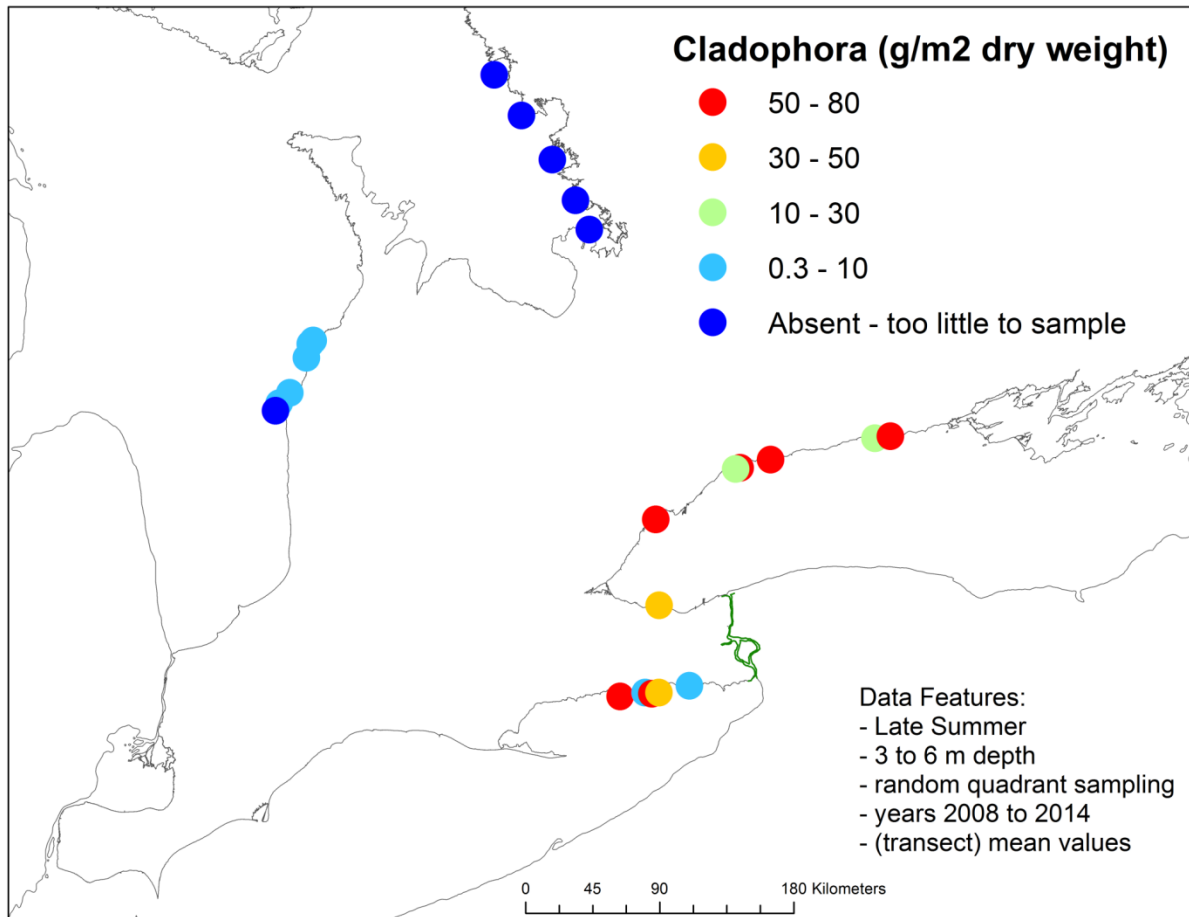


Figure 3. Biomass of *Cladophora* on hard substrate in late summer averaged over sites from 3 to 6 m depth among study areas and study periods for areas with multiple years of study. Samples were collected by divers from randomly placed 0.15 m² quadrants. Surveys were conducted from 2008 to 2015.

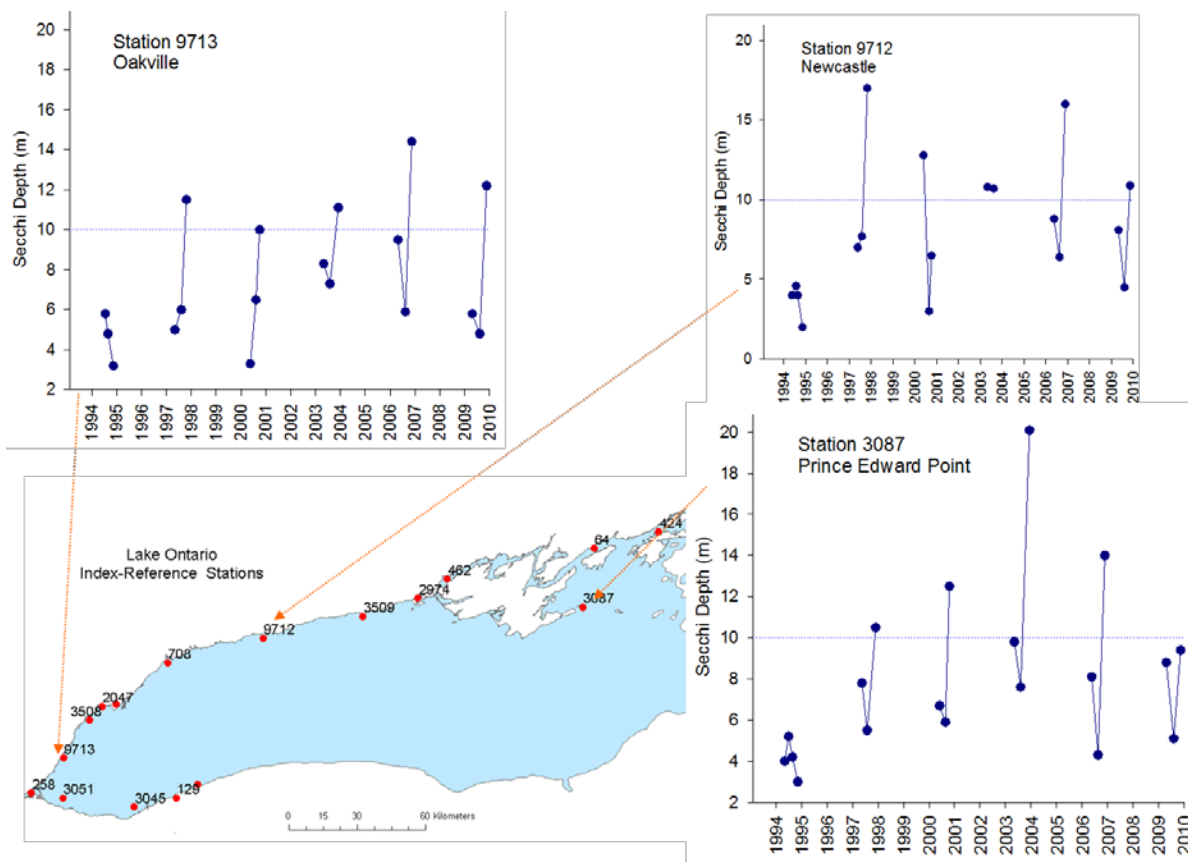


Figure 4. Secchi depth from 1994 to 2010 at three sites selected to represent ambient nearshore conditions from the suite of MOECC nearshore index and reference station in Lake Ontario.

Eastern Lake Huron and eastern Georgian Bay contrast with the lower lakes with more limited evidence of benthification in the nearshore. *Dreissena* is widely distributed but generally not highly abundant (Figure 2). *Cladophora* is not abundant (Fig. 3) with the exception of near localized nutrient sources at the shoreline. Unexpectedly, diatom-dominated periphyton appears to proliferate at mid to deeper depths in eastern Lake Huron possibly benefiting from a deep photic zone despite ultra-low phosphorus concentrations that appear to be trending downward.

Lake Erie poses a challenge in assessing nearshore benthification because of the varying ecologies among lake basins and the generally heterogeneous conditions in the nearshore. Benthification is most obvious in the less nutrient-rich eastern basin where there is abundant hard substrate; lakebed conditions resemble Lake Ontario but seemingly with a more heterogeneous and less pervasive distribution of *Dreissena*. As in Lake Ontario, *Cladophora* proliferates on the lakebed at shallow depths (Fig. 3).

Diver-based surveys of the lakebed have not been conducted in the central and western basins by MOECC because of the limited potential for proliferation of *Cladophora*, which has been the primary focus of this monitoring approach. A prevalence of soft substrate and low water clarity limit habitat for *Cladophora* growth. High densities of *Dreissena* are periodically detected over the soft lakebed in sampling by Ponar dredge (Fig. 1); however, the heterogeneous distribution of mussels makes it difficult to infer a general condition on the lakebed using these data. It is obvious

that the nature of benthification on a soft lakebed under a productive and low transparency water column will contrast from areas where the scope for benthic autotrophic production is qualitatively higher; however, this contrast is not well defined.

Monitoring at north shore Lake Superior index and reference stations has provided little indication of a *Dreissena* presence; however, detailed information on nearshore lakebed conditions are limited.

Discussion Notes

C: Benthification most obvious and extreme in Lake Ontario.

Q: Is the low number of mussels due to a calcium availability issue in Lake Superior and Georgian Bay?

A: Yes, offshore waters constantly moving into the nearshore, machinery to interact with offshore.

C: Benthification story doesn't really have a *Cladophora* component in Lake Huron – different from Erie, Ontario, and Michigan. Nearshore lake bed can interact with lake in ways that we don't fully understand. For instance in east Lake Huron – increased turf algae (periphyton). Could goby predation of grazers be a driver? Don't find amphipods, gastropods anymore. Lake Erie is somewhat baffling – features of benthification hard to assess. Less physical interaction with offshore than in Lake ON.

Q: What makes Erie different from Ontario?

A: Less suitable substrate for large mussels, water clarity more variable and often not as high, drop-off into deeper water is much broader, so light is attenuated more keeping them at one strata? We don't know but it's there. It's not as wide and intense as it used to be.

Q: Lake Huron has less nearshore development. Can anyone comment on Lake Michigan nearshore conditions?

A: Very gradual slope, internal waves on thermocline that bring in cold water from offshore. It's more like eastern basin Erie than like Ontario, but I think depth sets it more than how gradual that depth is. Get really variable water clarity and sharp changes in temperature. Pump at lakebed associated with seiching.

C: Lake Ontario basically ideal for pumping P into *Cladophora* beds – orientation, substrate, more upwelling, excreting P at rate taking it in. Imagine they are really sucking up P and pumping out as SRP right away in early season. Just finished study looking at stoichiometry, feeding rate impacted by zebra mussels.

C: It's also about discharges from shoreline – could be retarding movement offshore.

Q: Is anyone doing mass balance to understand where P is ending up? Have we looked at what's locked in biota, what's being removed in biota?

Presentations

A: Too big a study, encompasses multiple ranges in expertise and agencies and haven't been able to make it happen. Baby steps with CSMI next year, but not enough. Need whole system accounting.

C: Bay of Quinte P budget work – loading, concentrations, sediments.

C: No updated loading data in Michigan and Huron since 2008.

C: Have seen uptick in primary productivity/chlorophyll in Georgian Bay, especially the North Channel, in the last few years.

Fisheries management implications of lower trophic level change: Paradigms and case histories

Tom J. Stewart¹ and Lars Rudstam²

¹39 Elm Street, Kingston, Ontario, K7K 1M8

²Cornell Biological Station, Shackelton, NY

Abstract

Several hypotheses relating lower trophic level changes to fish community and fisheries changes in marine and freshwater systems were examined. Case studies, mesocosm experiments and simulation models suggest that both top-down (Fig. 1) and bottom-up controls (Fig. 2) influence fish populations (McQueen et al., 1989,1986; Bunnell et al., 2014; Cury et al., 2014; Deines et al., 2014; Kao et al., 2016). In the Great Lakes, bottom-up influences are likely dominant during the past two decades (Bunnell et al., 2014) but importantly, bottom-up and top-down regulations can interact in complex ways (Kao et al., 2016). Wasp-waist control, whereby a prey fish predominantly controls energy flow, has been observed in marine up-welling systems (Fig. 3; Cury et al., 2014). The substantial influence of alewife on zooplankton community structure and abundance, and the potential for alewife biomass to also limit top-predator production in Lakes Michigan and Ontario, may be another example of wasp-waist control. It is less helpful to debate the type of control (bottom-up vs. top-down) dominating but more important to understand what determines the relative importance of controlling influences under different environmental conditions and community structures (Matson and Hunter, 1992). For example, it was hypothesized that top-down control may have a stronger influence in oligotrophic systems compared to eutrophic systems because of stronger predator-prey linkages (McQueen et al., 1989). A Lake Huron simulation model suggests reduced nutrients can amplify both bottom-up and top-down influences on alewife (Kao et al., 2016). Declines in nutrient loading resulting in increased water clarity (enhanced by dreissenid filtering in the Great Lakes) can be described as oligotrophication. Abrupt changes in fish community composition and other ecosystem state metrics in Bay of Quinte, Lake Ontario (Nicholls et al., 2010) associated with oligotrophication have been referred to as a regime shifts. However, a recent literature review of regime shifts suggests confusion and misuse of the term, which by definition must be non-reversible (Capon et al., 2015) or at least quasi-stable (Carpenter 2003). An alternative explanation for the same set of observations in the Bay of Quinte and additionally Lake Erie, Ontario and Oneida Lake, New York, has been described as benthification related to dreissenid mussels (Fig 4; Mayer et al., 2014). In these cases, increased light penetration induced by reduction in nutrients and dreissenid filtering causes a shift from turbid-phytoplankton dominated system to a clear-macrophyte dominated system with associated shifts in fish community structure (e.g., Hoyle et al., 2012). These changes may be reversible and may not fit the strict definition of a regime shift (Capon et al., 2015). Abrupt changes in Lake Huron offshore food web have also been referred to as a

regime shift (He et al., 2015). Declines in zooplankton grazers and alewife were quickly followed by shifts in predator fish communities (Barbiero et al., 2009, 2011; Kao et al., 2016). Regardless of terminology, fish community shifts associated with oligotrophication are well documented and an important fisheries management issue in the Great Lakes. Although changes in fish species abundances and community shifts matter to fish managers, biomass size spectra studies show persistent distributions of biomass across size-classes independent of species composition across many different ecosystem states (Sprules, 2008; Yurista et al., 2014; Sprules and Barth, 2016). The relatively invariant biomass size-spectra (Fig. 5), and its apparent insensitivity to species composition and ecosystem change suggest that Great Lakes pelagic food web structure and rates of energy transfer maybe constrained by physiological processes scaled to body size. Another important case history and perspective is that of Lake Erie in the late 1960s. At that time, Lake Erie was declared dead due to industrial pollution and sewage outflows, resulting in closed beaches, algal blooms and dead fish washing up on shore causing public outcry (<https://clevelandhistorical.org>, accessed August, 2017). This was undoubtedly an undesirable ecosystem state, but as reported in Applegate and van Meter (1970), Lake Erie's biological capacity to produce fish was at a record high. However, eutrophication and likely overfishing of desired species (Leach and Nepszy 1976), altered food web structure and diverted biological productivity into low-valued species reducing economic benefits. A corollary to this, is that improving water quality and aesthetics associated with oligotrophication may be broadly supported by the public but result in fish communities and fisheries that might be less valued by stakeholders due to reduced yields or changed fish species dominance (Dettmers et al., 2012).

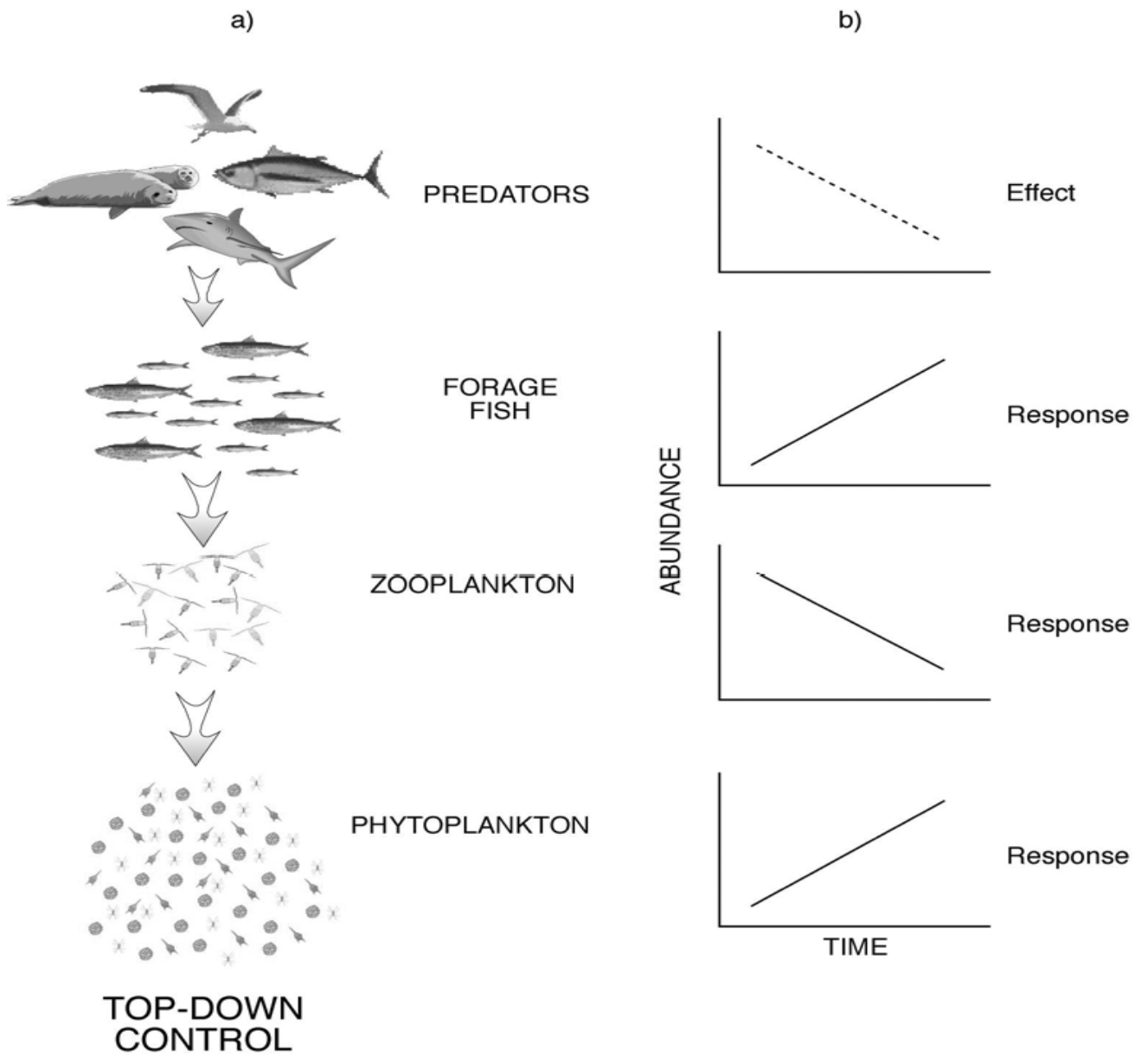


Figure 1. Illustration of top-down control (from Cury et al., 2014).

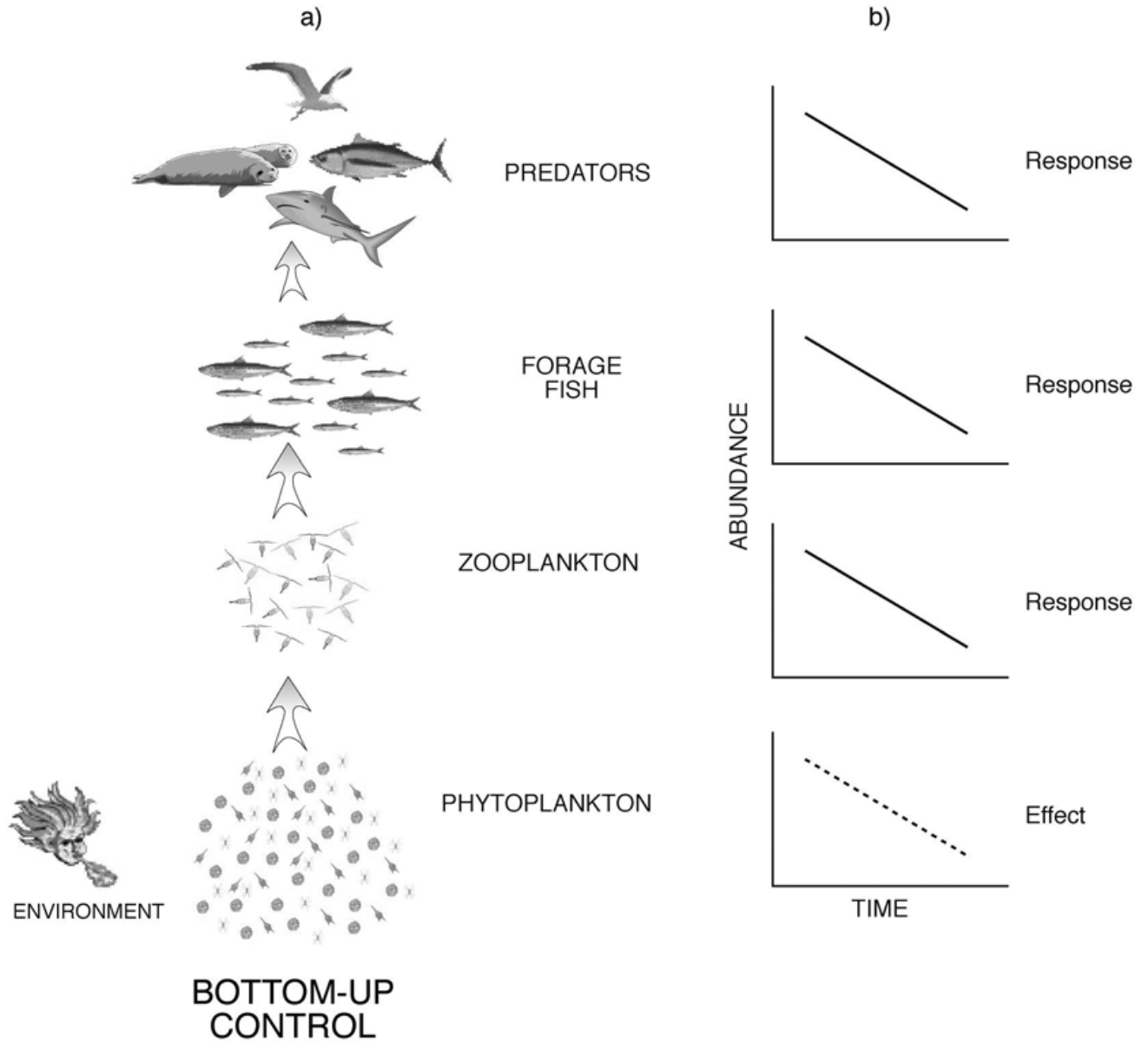


Figure 2. Illustration of bottom-up control (from Cury et al., 2014).

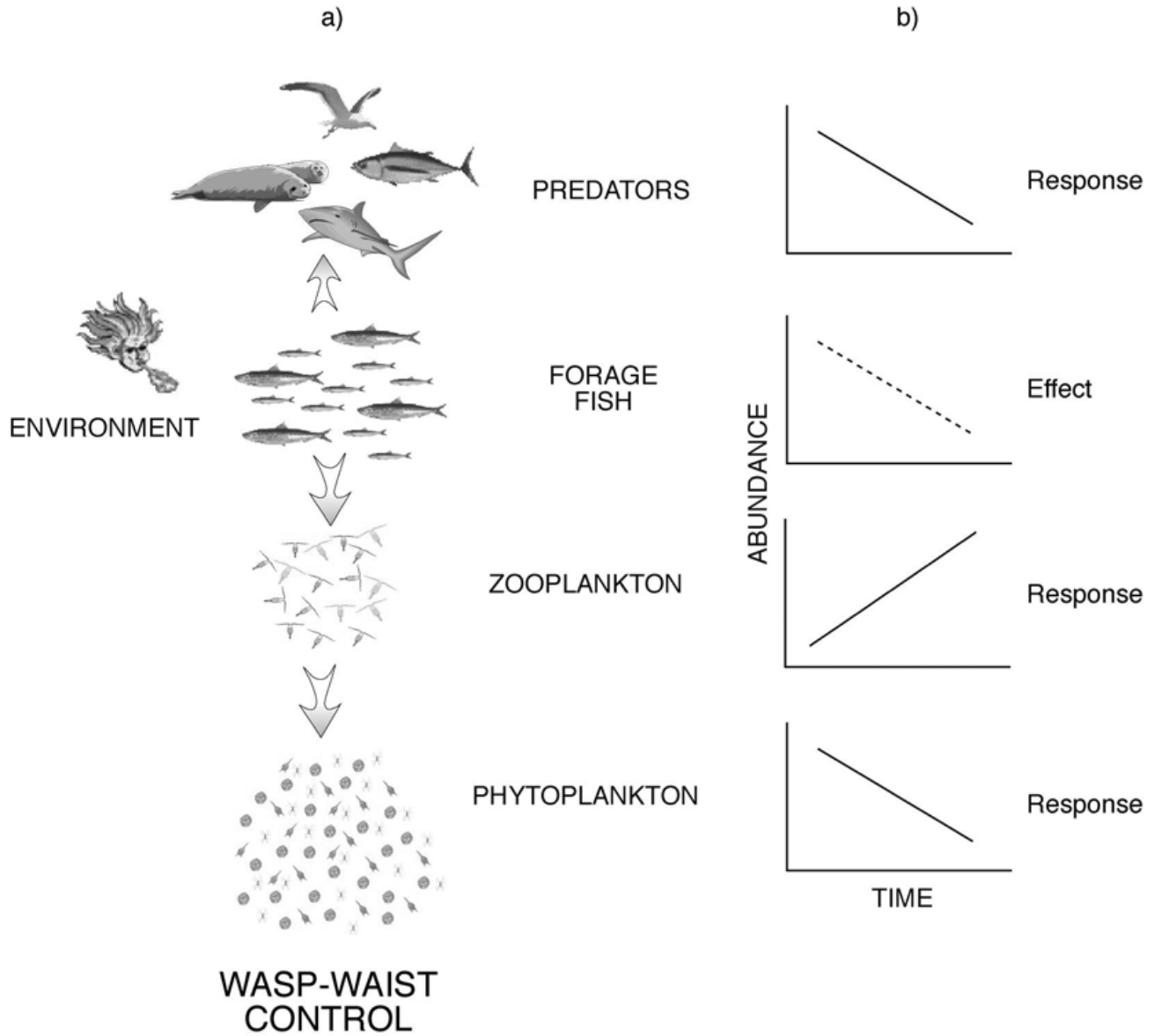


Figure 3. Illustration of wasp-waist control (from Cury et al., 2014).

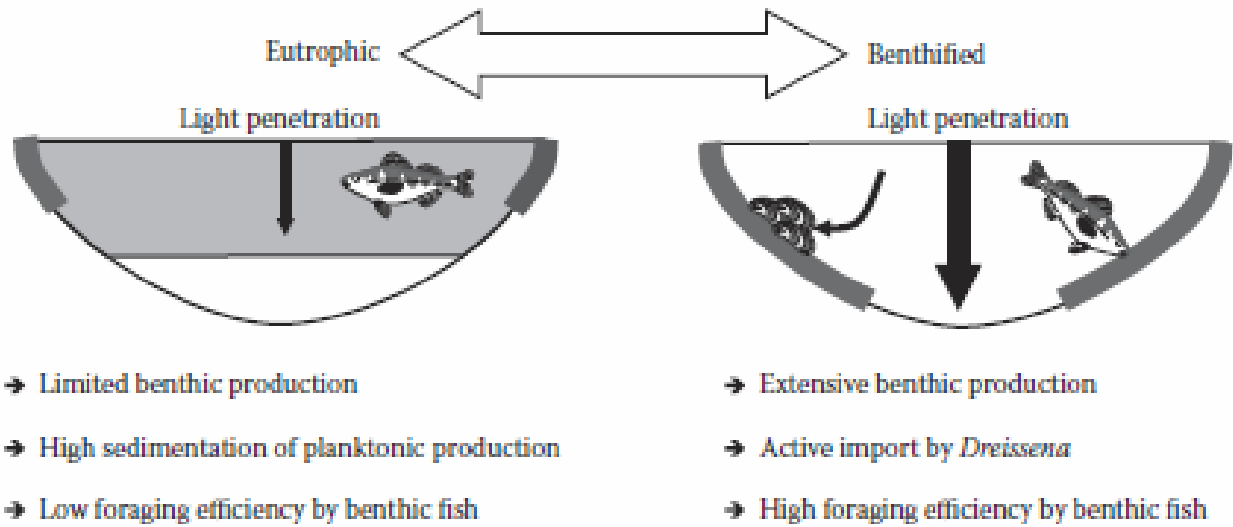


Figure 4. Illustration of benthification (from Mayer et al., 2014).

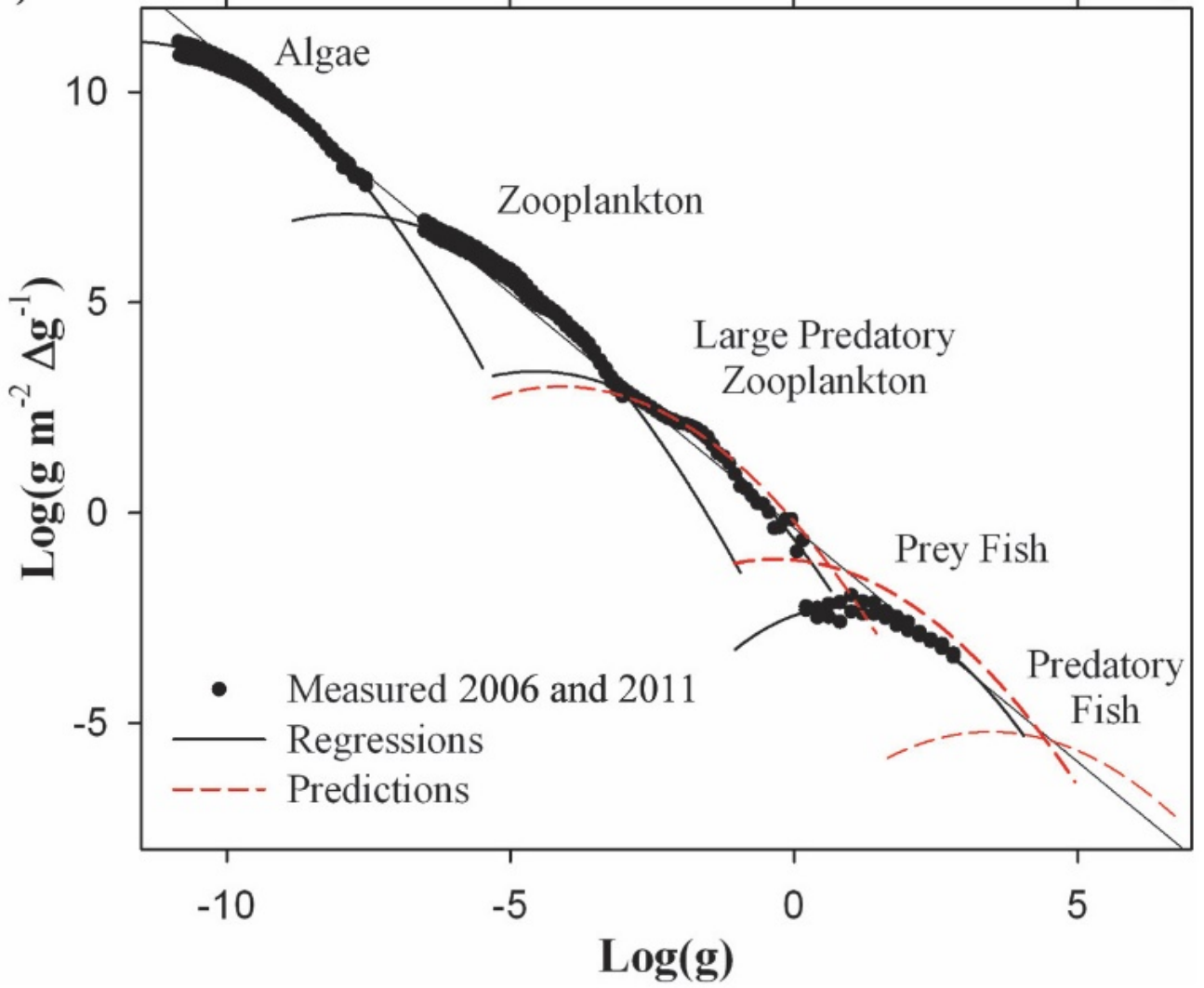


Figure 5. Biomass size-spectra for Lake Superior during 2006 and 2011 (from Yurista et al., 2014).

References

- Applegate, V.C., van Meter, H.D., 1970. A brief history of commercial fishing in Lake Erie. United States Dep. Inter. U.S. Fish Wildl. Serv. Bur. Commer. Fish. Fish. Leaflet. 630: 630, 28.
- Barbiero, R.P., Balcer, M., Rockwell, D.C., Tuchman, M.C., 2009. Recent shifts in the crustacean zooplankton community of Lake Huron. *Can. J. Fish. Aquat. Sci.* 66: 818–828.
- Barbiero, R.P., Lesht, B.M., Warren, G.J., 2011. Evidence for bottom-up control of recent shifts in the pelagic food web of Lake Huron. *J. Great Lakes Res.* 37: 78–85.
- Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., Weidel, B.C., 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. *Bioscience* 64: 26–39.
- Capon, S.J., Lynch, A.J.J., Bond, N., Chessman, B.C., Davis, J., Davidson, N., Finlayson, M., Gell, P.A., Hohnberg, D., Humphrey, C., Kingsford, R.T., Nielsen, D., Thomson, J.R., Ward, K., Nally, R. Mac, 2015. Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. *Sci. Total Environ.* 534: 122–130.
- Carpenter, S.R. (2003) Regime shifts in lake ecosystems: Pattern and variation. *Excellence in Ecology Series* (Vol. 15), Ecology Institute
- Cury, P., Freon, P., Maloney, C., Shannon, L., Shin, Y., 2014. Processes and patterns of interactions in marine fish populations: an ecosystem perspective, *The Sea*, vol. 13.
- Deines, A.M., Bunnell, D.B., Rogers, M.W., Beard, T.D., Taylor, W.W., 2015. A review of the global relationship among freshwater fish, autotrophic activity, and regional climate. *Rev. Fish Biol. Fish.* 25: 323–336.
- Dettmers, J.M., Goddard, C.I., Smith, K.D., 2012. Management of alewife using Pacific salmon in the Great Lakes: Whether to manage for economics or the ecosystem? *Fisheries* 37: 495–501.
- He, J.X., Bence, J.R., Madenjian, C.P., Pothoven, S.A., Dobiesz, N.E., Fielder, D.G., Johnson, J.E., Ebener, M.P., Cottrill, R.A., Mohr, L.C., Koproski, S.R., 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. *Can. J. Fish. Aquat. Sci.* 72: 7–23.

Hoyle, J.A., Bowlby, J.N., Brousseau, C.M., Johnson, T.B., Morrison, B.J., Randall, R.G., 2012. Fish community structure in the Bay of Quinte, Lake Ontario: The influence of nutrient levels and invasive species. *Aquat. Ecosyst. Heal. Manag.* 15: 370–384.

Kao, Y.C., Adlerstein, S.A., Rutherford, E.S., 2016. Assessment of top-down and bottom-up controls on the collapse of alewives (*Alosa pseudoharengus*) in Lake Huron. *Ecosystems* 19: 803–831.

Leach, J. H. and S. J. Nepszy 1976. The fish community in Lake Erie. *Journal of the Fisheries Research Board of Canada*, 33: 622-638.

Matson, P.A., Hunter, M.D., 1992. Special Feature: The relative contributions to top-down and bottom-up forces in population and community. *Ecology* 73: 723-723

Mayer, C.M., Burlakova, L.E., Eklöv, P., Fitzgerald, D., Karatayev, A.Y., Ludsins, S. A, Millard, S., Mills, E.L., Ostapenya, A. P., Rudstam, L.G., Zhu, B., Zhukova, T. V, 2014. Benthification of freshwater lakes: Exotic mussels turning ecosystems upside down. *In: Quagga Zebra Mussels Biological Impacts and Control* (edited by Thomas F. Nalepa, Don W. Schloesser). Chapter 36, pg. 575–586.

McQueen, D.J., Post, J.R., Mills, E.L. 1986. Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci* 43: 1571–1581.

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J., Lean, R.S., 1989. Bottom-up and top-down impacts on freshwater pelagic community structure *Ecological Society of America*. 59: 289–309.

Nicholls, K.H., Hoyle, J.A., Johannsson, O.E., Dermott, R., 2011. A biological regime shift in the Bay of Quinte ecosystem (Lake Ontario) associated with the establishment of invasive dreissenid mussels. *J. Great Lakes Res.* 37: 310–317.

Sprules, W.G., 2008. Ecological change in Great Lakes communities — a matter of perspective. *Can. J. Fish. Aquat. Sci.* 65: 1–9.

Sprules, W.G., Barth, L.E., 2016. Surfing the biomass size spectrum: some remarks on history, theory, and application 1. *Can. J. Fish. Aquat. Sci.* 73: 477–495.

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., 2014. A new look at the Lake Superior biomass size spectrum. *Can. J. Fish. Aquat. Sci.* 71: 1324–1333.

Discussion Notes

Q: Can you clarify what you mean by ecosystem change?

A: More about trophic state, but also species diversity and community structure. Literature suggests that the slope of the biomass spectra is sensitive to stressors, e.g., fishing, habitat changes.

C: There has been discussion on whether “regime shift” has happened in the Great Lakes, but really “alternate stable states” might be more accurate (“regime shift” seems to be pretty loaded, maybe think about a different term for communicating to managers and public).

C: Kao paper on Lake Huron – steady top-down pressure, changes in bottom-up are really what drove the system past the tipping point.

C: But we are not really dealing with natural system because of stocking? (But most of salmon were naturalized.) Disconnect between stocked predator and prey base, run risk of collapse because it only takes a few bad recruitment years.

C: Salmon and alewife uncoupled to begin with because recruitment success depends on what happens in streams, not what’s happening in the lake.

C: Disagree, fecundity depends on how many alewife they eat – density dependent mechanisms with Chinooks in Lake Michigan, tightly linked to alewife population.

C: Ji He bioenergetics model – is controversial – absolute abundance issue. Winter survival component that helped collapse alewives.

C: Kao Lake Michigan model – Chinook probably at carrying capacity in current ecosystem, so stocking more or less won’t change much. But changing stocking rate of lake trout, steelhead, will change biomass of their populations. If you want to cut lake trout to restore more chinook, it probably won’t work.

C: Chinook not eating gobies, lake trout and steelhead are. You’ll still have top predators just maybe not the ones people want.

C: Anecdotally in Lake Michigan – signs of moving toward different state, e.g., yellow perch recruitment increase, lake trout reproducing more successfully.

Re-examining relationships among nutrients, autotrophs and fish

Brian Weidel¹

¹United States Geological Survey, Great Lakes Science Center, Lake Ontario Biological Station
17 Lake St. Oswego, NY 13126

Abstract

A paradox for fisheries managers is that “cleaner” water equates to less fish. Reducing mineral nutrient loading, specifically phosphorus, has been an important management action for changing Great Lakes water quality. However, in its simplest, fish biomass is positively related to nutrient concentrations and Great Lakes nutrient concentrations have and continued to decline (Dove and Chapra, 2015). A long and rich history of correlative and experimental studies have confirmed the positive effects of nutrients on the biomass of fish and other aquatic food web components (Melack, 1976; Oglesby, 1977; Downing and Plante, 1993). Most recently, the comparisons have been made at a global level (Deines et al., 2014) finding strong evidence for the positive relationship between metrics of fish biomass and autotrophic production, which is generally limited by phosphorus (Wetzel, 2001). This is not to say nutrients or phosphorus are the only controls on lake fish biomass. A suite of alternative drivers influence fish biomass including the presence or absence of top predators (Carpenter and Kitchell, 1993), physical conditions (Hayes et al., 2009) or the morphometry of the system (Ryder et al., 1974). Studies that seek to quantify the role of these other drivers almost always acknowledge the underlying element of nutrient concentration as a controlling driver. The magnitude of change in phosphorus could influence how well it is understood as a driver. For instance, in Lake Superior, Lake Huron, and Lake Michigan total phosphorus (TP) concentration changes have been less so than Lake Ontario. Strong contrasts over time in TP and space are more likely to reveal correlation with measures of fish biomass. As the most downstream and with the largest watershed to surface area relationship Lake Ontario has undergone the most extreme changes in lake-wide phosphorus dynamics. Peak values in the 1970s were between 20 and 30 ug/l, while contemporary values range from 4-6, an approximate 80% decline. Interestingly, estimates for total prey fish biomass, which represent the vast majority of fish biomass in the lake, have apparently declined approximately 75% over this time period (Fig. 1). Comparison among the Great Lakes also shows a correlation between total fish biomass and TP (Fig. 2). So why don't most studies on changes in Great Lakes fishes acknowledge the role of nutrient declines or reducing fish biomass? Accurate measure of whole lake fish biomass are difficult and fish species respond uniquely to changes in nutrients. This complexity was captured in an early conceptual model of the relationship between fisheries yields and chlorophyll (Oglesby et al., 1987; Fig. 3). This complexity has led investigators to posit the question: “Is it top-down or bottom-up?” (Bunnell et al., 2014). This line of investigation can create a dichotomy that suggests at some level that there can only be one influence, when most studies conclude that both influences are operating non-independently. We borrowed elements from numerous studies to create a conceptual model (Fig. 4) for relating fish biomass as a positive wedged function of mineral nutrients, or primarily phosphorus. That wedge represents a wide range of fish biomass values for a given nutrient concentration, and we illustrate some of those additional drivers and their influence on biomass.

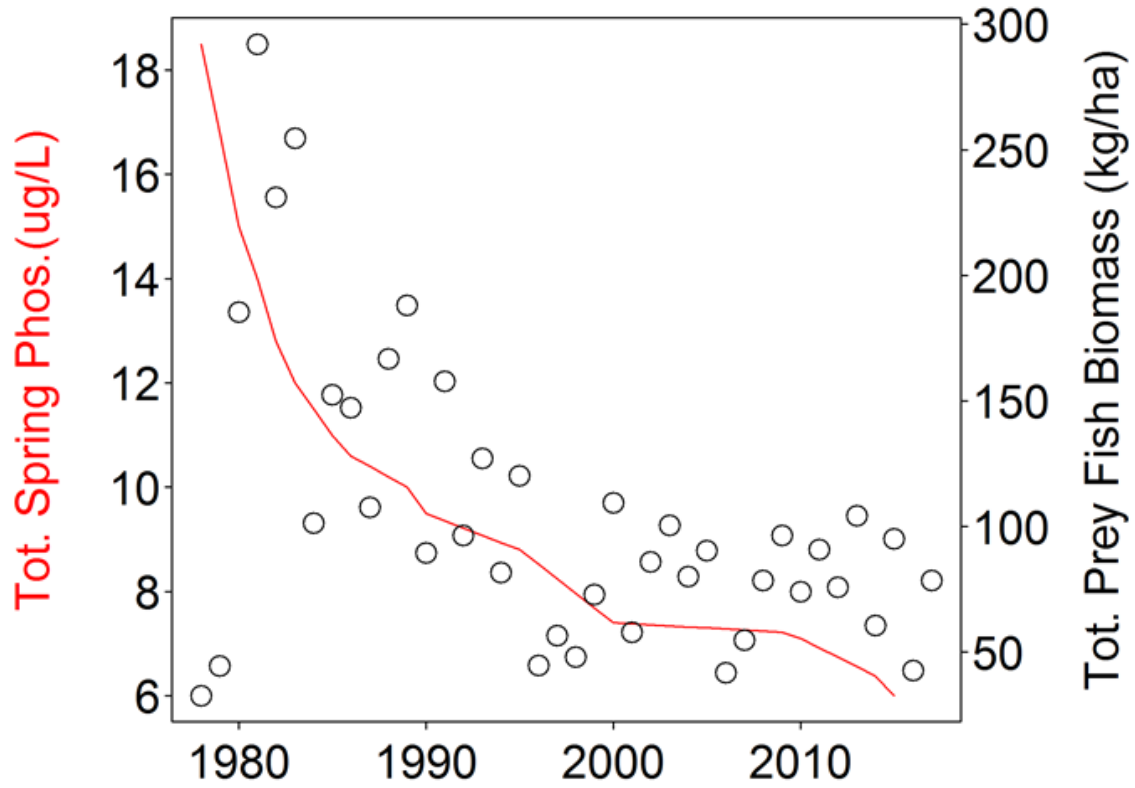


Figure 1. The relationship between measures of spring total phosphorus (estimated graphically from Dove and Chapra, 2015) and total prey fish biomass estimated from bottom trawling in Lake Ontario (unpublished data).

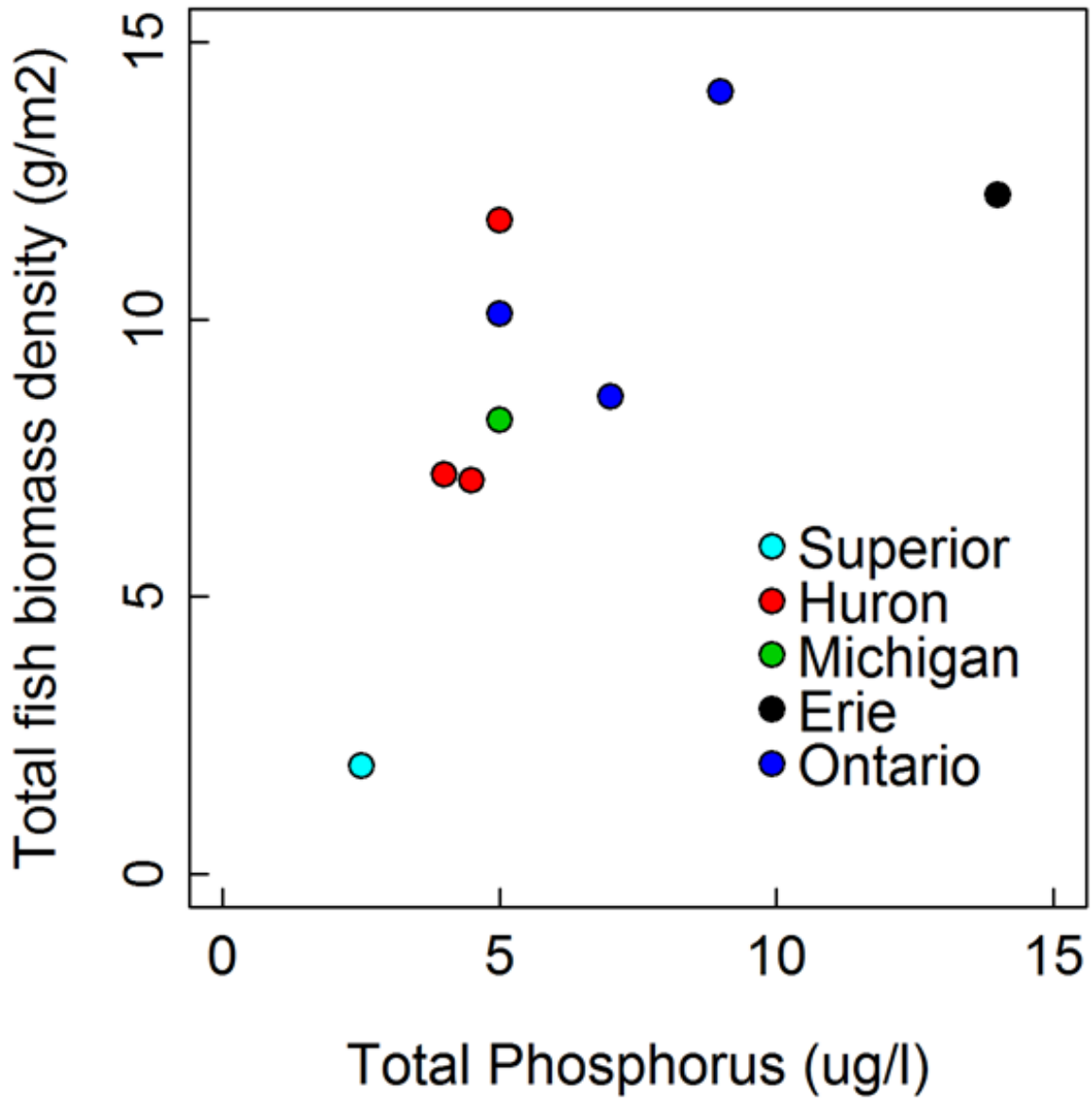


Figure 2. Total fish biomass is positively related to total phosphorus concentration for results based on nine food web mass balance models of the Great Lakes.

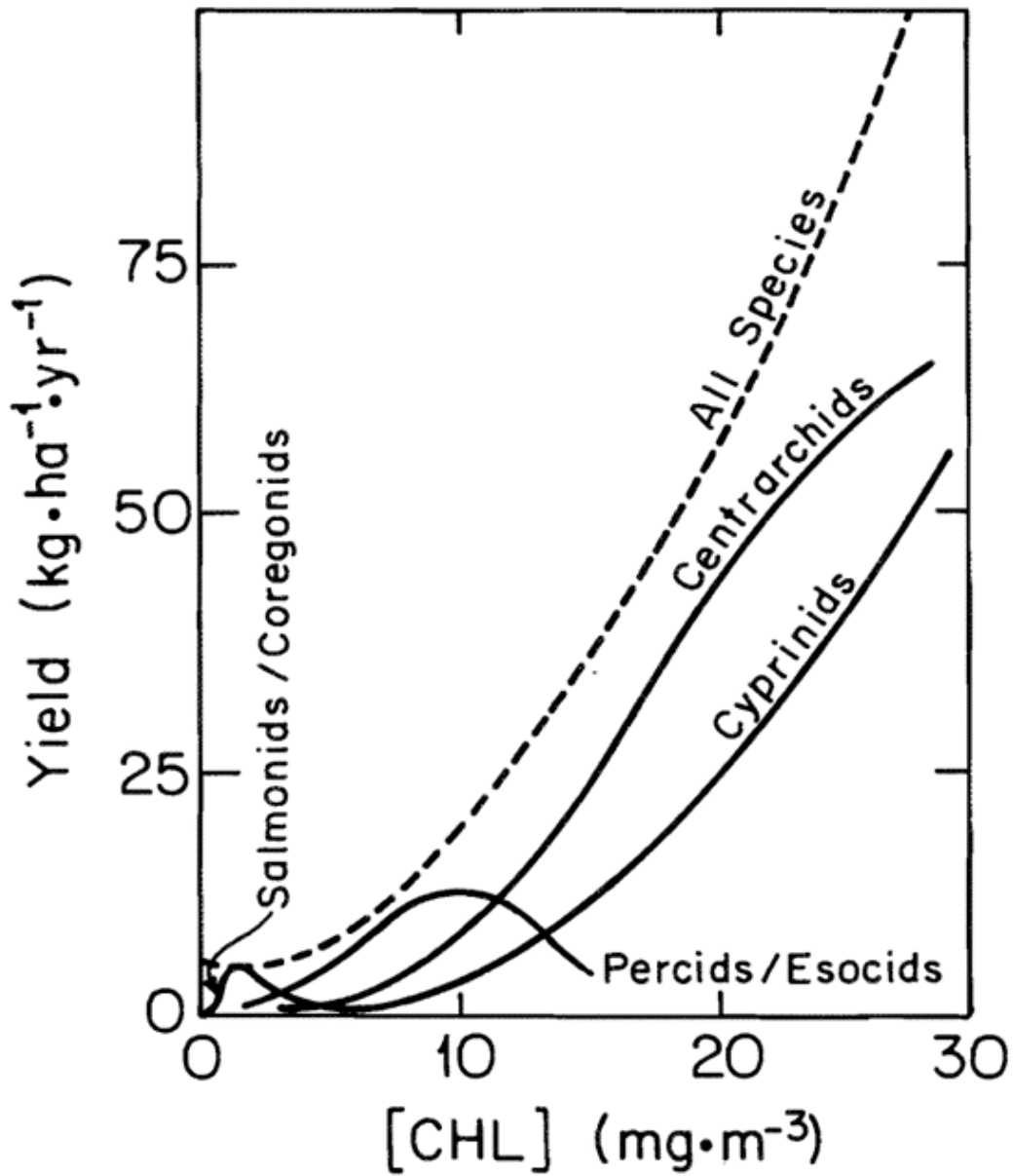


FIG. 3. Estimated distribution of fish yields among major taxa for north temperate latitude lakes.

Figure 3. A figure extracted from Oglesby et al. (1987) showing a conceptual model relating fisheries yields to measure of chlorophyll-a for different fish community guilds.

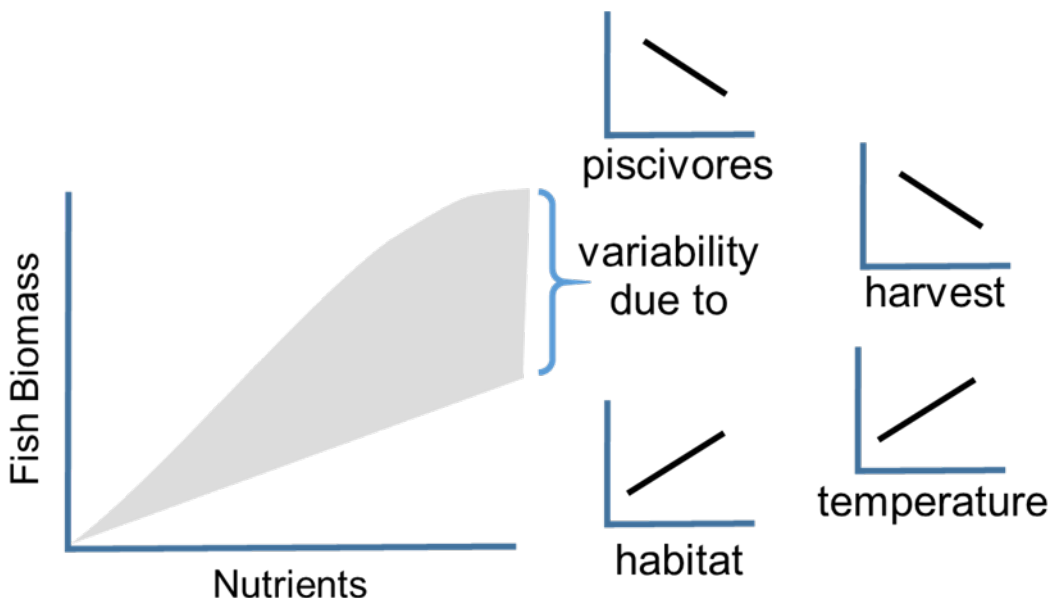


Figure 4. A conceptual model for the relationship between fish biomass and nutrients (e.g., total phosphorus) and the influence of other factors on the variability in this relationship.

References

Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., Weidel, B.C., 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. *Bioscience* 64, 26–39.

Carpenter, S.R. and Kitchell, J.F. (1993) *The Trophic Cascade in Lake Ecosystems*, Cambridge University Press.

Deines, A. M., Bunnell, D. B., Rogers, M. W., Beard, T. D., & Taylor, W. W. (2015). A review of the global relationship among freshwater fish, autotrophic activity, and regional climate. *Reviews in Fish Biology and Fisheries*, 25(2), 323–336. <https://doi.org/10.1007/s11160-015-9384-z>

Dove, A. and Chapra, S.C., 2015. Long-term trends of nutrients and trophic response variables for Great Lakes. *Limnology and Oceanography*. 60(2): 696-721. <http://dx.doi.org/10.1002/lno.10055>

Downing JA, Plante C (1993) Production of fish populations in lakes. *Can J Fish Aquat Sci* 50:110–120

Melack JM (1976) Primary productivity and fish yields in tropical lakes. *Trans Am Fish Soc* 105:575–580

Oglesby RT (1977) Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. *J Fish Res Board Can* 34:2271–2279

Oglesby R.T., Leach J.H., Forney J. (1987) Potential Stizostedion yield as a function of chlorophyll concentration with special reference to Lake Erie. *Can J Fish Aquat Sci* 44:166–170

Ryder, R.A., Kerr, S.R., Loftus, K.H. and Regier, H.A. (1974). The morphoedaphic index as a fish yield estimator: Review and evaluation. *Journal of the Fisheries Research Board of Canada*, 31, 663-688.

Wetzel, R.G. 2001. *Limnology: Lake and river ecosystems*, 3rd ed. Academic Press, San Diego, CA.

Discussion Notes

C: No buy-in from stakeholders right now because of a giant 2016 year-class of alewife, fishers don't think there's a problem anymore, they're not understanding the concept of year-class.

C: Framing around biomass, thresholds needed to support predator demand.

C: What if instead of water quality we called it "lake fertility?" Different connotation!

C: Fisheries managers don't need all the details, just need to provide public assurance that we understand the system.

C: If you've never seen changes in clarity that are broad enough, then you might not think enough about clarity's role – might need to step out of your system. "Stay out of muddled middle, look for strong contrasts."

C: Good point on habitat. A lot of what dreissenids do is habitat modification. Not just a trophic component. Changing light levels is a habitat issue, affects both primary production and fish, comes from both ends. Ecosystem engineers. Even nutrient effects are habitat related – e.g., deforestation changing shading. Pea soup and chocolate milk in western Lake Erie– you can see this habitat from space!

C: When the "wind blows, fish grow." Fish habitat groups in Lake Erie, nearshore-dominated dramatic features like plume, think more about habitat than in other lakes that are huge, offshore is dominant feature. LAMP process trying to work closer with fishery managers.

C: It's a challenge to get people to think of habitat differently

C: This is a cool conceptual model. Geometry of curve, looking at it as managers – would it be better to manage for variability? Your risk would be that you could score high, but following year would be low. Looking at conceptual curve, if relationship is like that envelope, think about managing for variability rather than population size.

C: Reminds me of a financial planner – assess risk tolerance first. Need to do this for stakeholder community. Do we want to push the envelope or play it safe?

C: We're in the muddy middle, that's where huge variability and risk lies.

C: Edge of envelope is falling off cliff, perhaps not realistic.

C: Anoxia might be an edge where you've gone too far.

C: When you reduce variability, reduce chance of bumper years, but also failed years. Upper and lower bounds of envelope – reduce risk of bad years a little, but reduce chance of good year even more. May not be a risk you're willing to take.

Bay of Quinte ecosystem responses to eutrophication and nutrient control

Marten Koops¹


¹Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada
Burlington, Ontario

Contributors: Monir Hossain, Warren Currie, George Arhonditsis, Jim Hoyle, Mohi Munawar,
Kelly Bowen, Heather Niblock, and Mark Fitzpatrick

Bay of Quinte Ecosystem Responses to Eutrophication and Nutrient Control


Marten Koops

Great Lakes Laboratory for Fisheries and Aquatic Sciences
Fisheries and Oceans Canada
Burlington, Ontario





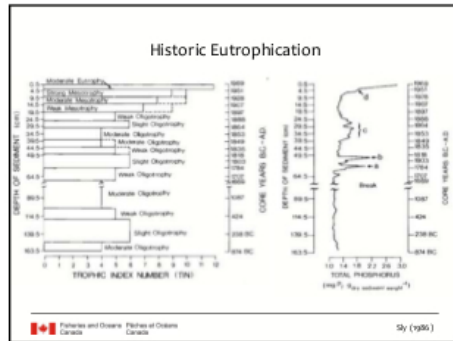
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- Monir Hossain
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- Mohi Munawar
- Kelly Bowen
- Heather Niblock
- Mark Fitzpatrick



The Bay of Quinte

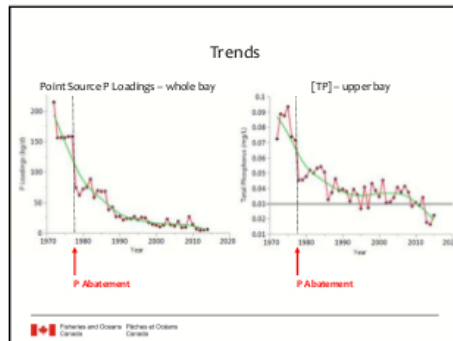
- 2-shaped embayment on north shore of Lake Ontario
- 35.4 km² surface area
- 64 km long
- Watershed > 18,000 km²
- Three general areas:
 - Upper bay: 16 km; mean depth 5.5 m; max depth 8 m
 - Middle bay: 23 km; mean depth 5.4 m; max depth 17 m
 - Lower bay: 25 km; mean depth 2.4 m; max depth 6 m
- Project Quinte initiated in 1972 to examine the effects of P reduction
- 2017 is the 45th year of sampling in the Bay of Quinte

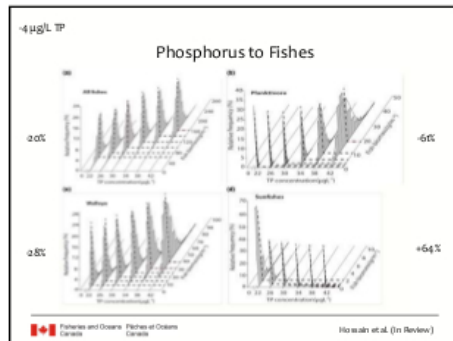
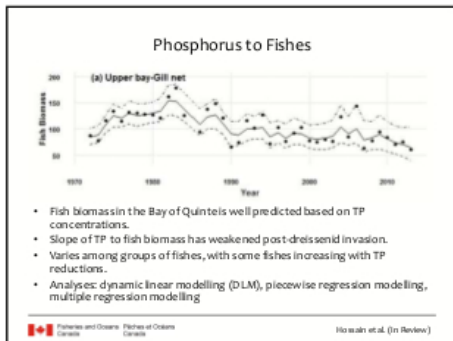
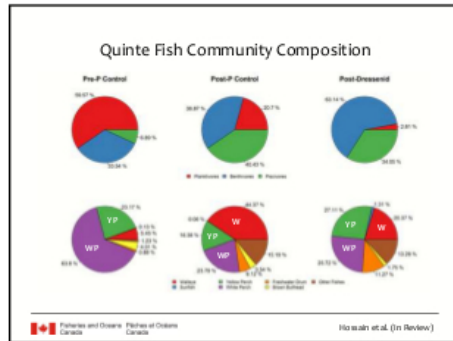
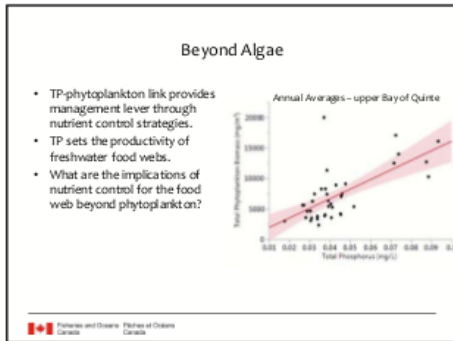
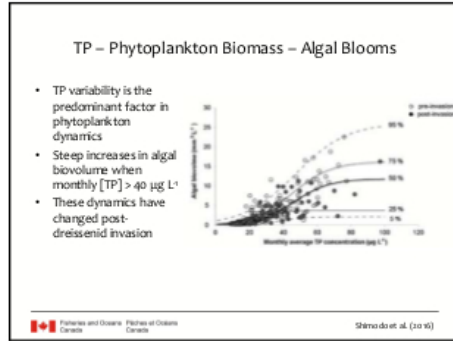




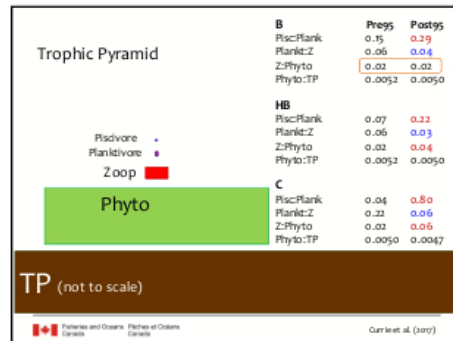
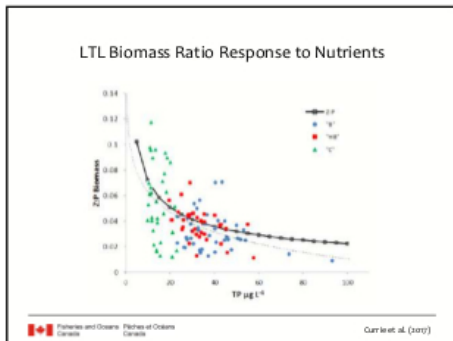
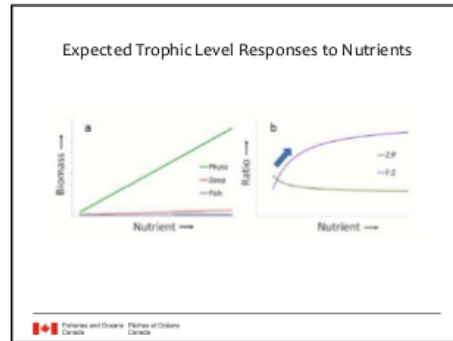
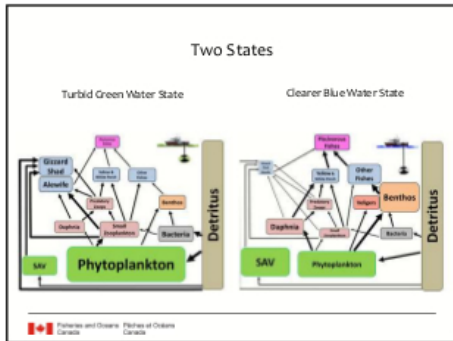
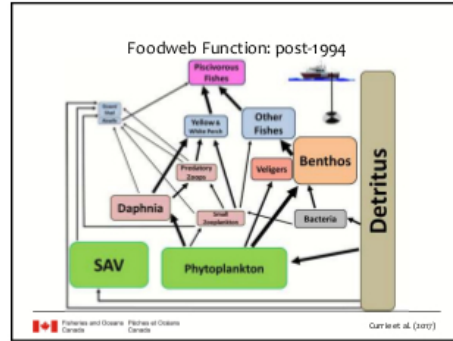
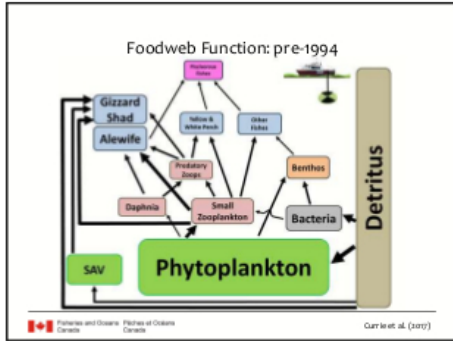
Bay of Quinte Timeline:

<ul style="list-style-type: none"> 1950-1960: Some TP inputs from agricultural practices. 1950-1970: Cultural eutrophication. Trophic state shifts from mesotrophic to autotrophic. 1971: P levels in detergents reduced. 1972: Great Lakes Water Quality Agreement (GLWQA) signed. 1972: New water treatment facilities begin operation. 1978: Cold winter. Severe Alewife & White Perch mortality. Strong Walleye cohort. GLWQA revision. 1980: Macrophyte abundance starts to increase. 1980: GLWQA revision. Areas of Concern (AOCs) created. Quinte listed as an AOC due to eutrophication concerns. 1991: Dreissenid mussels first appears in Quinte. Mt. Pinatubo eruption and La Niña produce cold summer. late 1990s: Increased zebra mussel abundance, macrophytes, water clarity, cormorants. Decreased Walleye. Cercariae invasion. early 2000s: Round Gobies invasion. 2017: GLWQA revision. 	<div style="border-left: 1px solid red; border-right: 1px solid red; padding: 0 5px; margin-bottom: 5px;">Cultural Eutrophication</div> <div style="border-left: 1px solid red; border-right: 1px solid red; padding: 0 5px; margin-bottom: 5px;">P Control</div> <div style="border-left: 1px solid red; border-right: 1px solid red; padding: 0 5px;">Post-dreissenid Clear Water</div>
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Koops et al. (2009), Wilver et al. (2011), Currie & Frank (2015)





Conclusions

- P dynamics and the production of algal blooms have likely changed post-dreissenid invasion.
- Quinte is now less reliant on pelagic foodweb pathways.
- Generally, trophic biomass ratios have increased, except in the planktivore:zooplankton ratio.
- Overall, further TP reductions likely to reduce fish biomass.
- A 4 µg/L TP reduction (30 → 26 µg/L) likely to reduce fish biomass by 20%.

Discussion Notes

Q: Why are biomass ratios important?

A: It tells you how much of upper trophic levels you expect to get for a given biomass of LTL. Not the same as transfer efficiency, but gives sense of how biomass is being converted to the next trophic level.

C: Almost like per capita food availability.

Q: What would you say to a guy at a bar?

A: When you have highly eutrophic systems, you're getting less zooplankton biomass per unit of phytoplankton biomass. When you push down P concentrations, you get more zooplankton per unit phytoplankton.

Q: Then you would predict that high P concentrations would have less efficient systems?

A: Yes.

C: Other trophic biomass ratios have increased with less TP.

Q: What is the history of anoxia in the bay?

A: Historically occurred, but don't get that now.

Q: What would you speculate is the mechanism for further TP reductions reducing fish biomass?

A: Definitely different species are responding differently. It's a food web energy dynamics thing, treating food web like a black box; stuff happens, and we get fish out.

C: We see wonderful statistical relationships, but when you try to explain to stakeholder you could have less credibility, how do you explain?

C: It's not satisfying enough to say "not enough food to support certain species", as food limitation could be happening at different life stages.

C: Changes are initiated at bottom of the food web, cascade up, too complex to explain with one mechanism operating at one level, it is like the "butterfly effect" in food webs.

Comparing estimates of trophic transfer efficiencies among the Great Lakes: Any insights?

Tom J. Stewart¹

¹39 Elm Street, Kingston, Ontario, K7K 1M8

Contributors: Henrique Giacomini, Monir Hossain, Yu-Chun Kao, Martin Koops, Bryan Matthias, Ed Rutherford, Brian Weidel, Dan Yule, Hongyang Zang.

Abstract

Trophic transfer efficiency (TTE) is a measure of the efficiency of energy transfer from one trophic level (TL) to the next and is estimated as the production at TL n divided by the production at TL $n-1$. It can be determined directly from field studies (Lindeman, 1942; Schulz et al., 2004), calculated from mass-balance Ecopath models (e.g., Kao et al., 2016), or from size spectrum theory (Jennings et al., 2002; Trebilco et al., 2013). TTE was estimated to vary from 3.7 to 42% (Gaedke and Straile, 1994; Jennings et al., 2002; Schulz et al., 2004). To examine variation in TTE in the Great Lakes, Ecopath models and biomass size-spectra were assembled from published and unpublished studies. Size-spectra analysis determined that Great Lakes TTE ranged from 3 to 22% depending on what assumptions were used to relate size-categories to production (Fig. 1). Analysis of 16 Great Lakes mass-balanced Ecopath models suggest TTE declined with TL and only approximated the “10% rule” (Pauly and Christensen, 1995) for transfers from TL-3 to TL-4 (Fig. 2). Consistently, systems with high TTE at the lowest TLs were also estimated to have high TTE at the higher TLs (Fig. 3). This phenomenon has been observed in experimental studies and referred to as a carry-over effect (Dickman et al., 2008). The mechanism driving this effect in the Great Lakes requires further investigation. There was no apparent consistent effect of dreissenid establishment on TTE, but it may be difficult to detect on a whole lake scale using these methods. Lake Superior and Lake Ontario had higher TTE than the other lakes suggesting that very different food web structures can be equally efficient in transferring lower trophic production to fisheries.

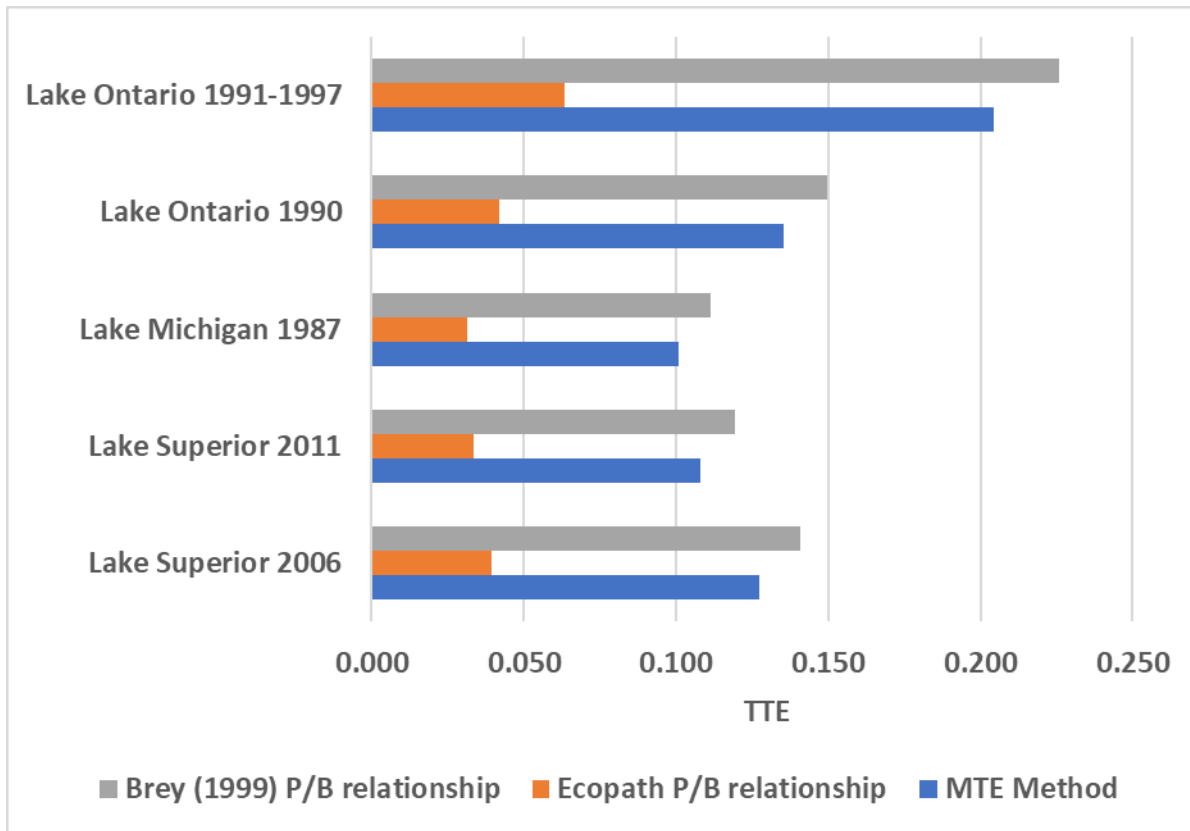


Figure 1. Estimate of Great Lakes trophic transfer efficiency (TTE) derived from published biomass spectra. Different estimates for each lake are based on different assumptions to convert estimates of biomass to estimates of production based on size. These include a general relationship between body size and production to biomass ratios (Brey, 1999), and a similar relationship developed from Lake Ontario Ecopath data (unpublished), and an alternative method based on metabolic theory (MTE).

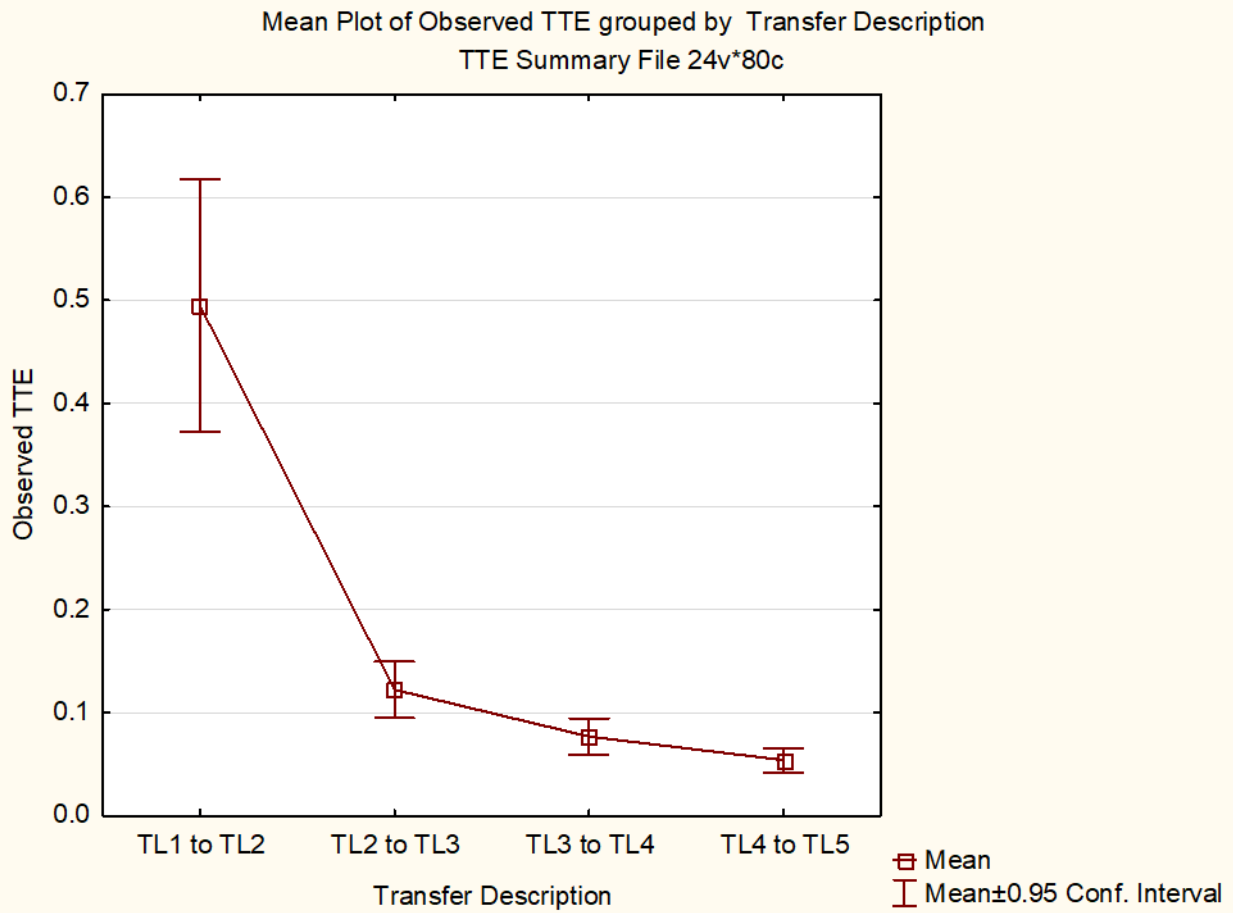


Figure 2. Mean and confidence interval of trophic transfer efficiency (TTE) derived from 16 Great Lakes Ecopath models.

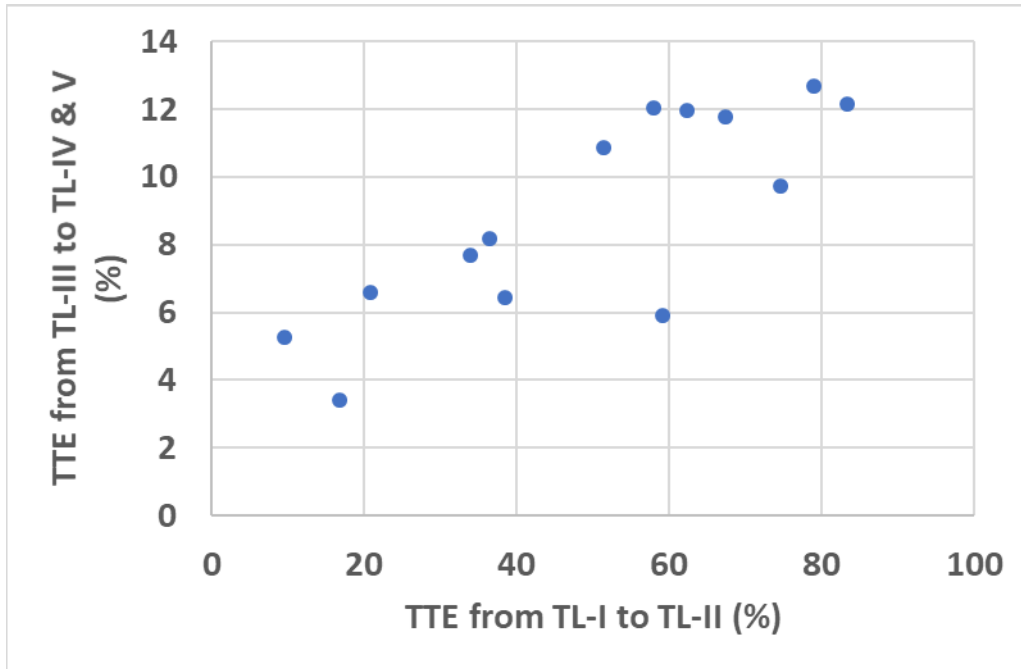


Figure 3. Relationship between trophic transfer efficiency (TTE) for transfers from trophic level 1 (TL-1) to trophic level 2 (TL-2) and TTE from trophic level 3 (TTL-3) to combined trophic levels 4 and 5 (TL-IV & V).

References

Brey, T. 1999. A collection of empirical relations for use in ecological modelling. NAGA ICLARM Quart. 22: 24–28.

Dickman, E.M., Newell, J.M., González, M.J., Vanni, M.J., 2008. Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. Proc. Natl. Acad. Sci. U. S. A. 105: 18408–18412.

Gaedke, U., Straile, D., 1994. Seasonal-changes of trophic transfer efficiencies in a plankton food-web derived from biomass size distributions and network analysis. Ecol. Modell. 75: 435–445.

Jennings, S., Warr, K.J., Mackinson, S., 2002. Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. Mar. Ecol. Prog. Ser. 240: 11–20.

Kao, Y.C., Adlerstein, S.A., Rutherford, E.S., 2016. Assessment of Top-Down and Bottom-Up Controls on the Collapse of Alewives (*Alosa pseudoharengus*) in Lake Huron. Ecosystems 19: 803–831.

Pauly, D., and Christensen, V. 1995. Primary production required to sustain global fisheries Nature, 374: 255-257.

Schulz, M., Koschel, R., Reese, C., Mehner, T., 2004. Pelagic trophic transfer efficiency in an oligotrophic, dimictic deep lake (Lake Stechlin, Germany) and its relation to fisheries yield. Limnologia 34: 264–273.

Trebilco, R., Baum, J.K., Salomon, A.K., Dulvy, N.K., 2013. Ecosystem ecology: Size-based constraints on the pyramids of life. Trends Ecol. Evol. 28: 423–431.

Discussion Notes

C: Models are focused on upper trophic levels, lots of detail about feeding habits of fish, less on zooplankton and other lower trophic levels; need to understand consequences of that.

C: Good example is the microbial loop, but many updated models include that component.

C: If the “carry-over effect” is not a modelling artifact, invoking nutritional differences seems suspect because stoichiometry of animals is much more constrained than primary production. Need certain amount of nitrogen for example. To see that clear of a signal doesn't make sense based on stoichiometry.

C: Could be related to food web structure, but still not clear how that might work.

C: When dealing with only a few trophic levels, a lot of models mash together zooplankton as one group. Really each zooplankton species has a complicated life history, just as much trophic complexity as fishes if not more (particularly specialization of microzooplankton).

C: Many of the models do capture some of this complexity, for example, a proportion of zooplankton production is assigned to TL-4 in some cases.

C: When species are combined as one group, you take difference in diet and difference in consumption into consideration.

Taking it to the fish: A conceptual model of trophic transfer efficiency

Tom J. Stewart¹

¹39 Elm Street, Kingston, Ontario, K7K 1M8

Contributors: Monir Hossain, Yu-Chun Kao, Martin Koops, Bryan Matthias, Ed Rutherford, Brian Weidel, Hongyang Zang, Doran Mason.

Abstract

In a workshop breakout group, participants discussed how to best to communicate insights from the synthesis of Great Lakes Ecopath models to fisheries managers. The group focused on the concept of “primary production required” (PPR), a routine in Ecopath that deconstructs consumptive flows to calculate how much primary and detrital production is required to support species-group production (Christensen and Pauly 1993). To compare among fish species-groups and ecosystems, a new production efficiency index was proposed that calculates the amount of PPR to produce a unit of standing stock biomass (B/PPR). Fish species-groups vary in their efficiency, with smaller species able to produce higher biomass for the same consumptive use of primary production (Fig. 1). Variation among ecosystems suggest that the new index may capture the influence of food web structure on species-specific production. For example, Lake Huron Chinook salmon B/PPR index was much lower during 2006-2009 compared to early years (Fig. 2). The participants speculated that the B/PPR index would vary as a doomed shaped function of trophic state. Each species-group may have an optimal trophic-state (measured as total phosphorus levels) associated with higher levels of production efficiency. Data synthesized for Chinook salmon was consistent with this concept, but this is an oversimplification based on limited data (Fig. 3). Further research and synthesis is required.

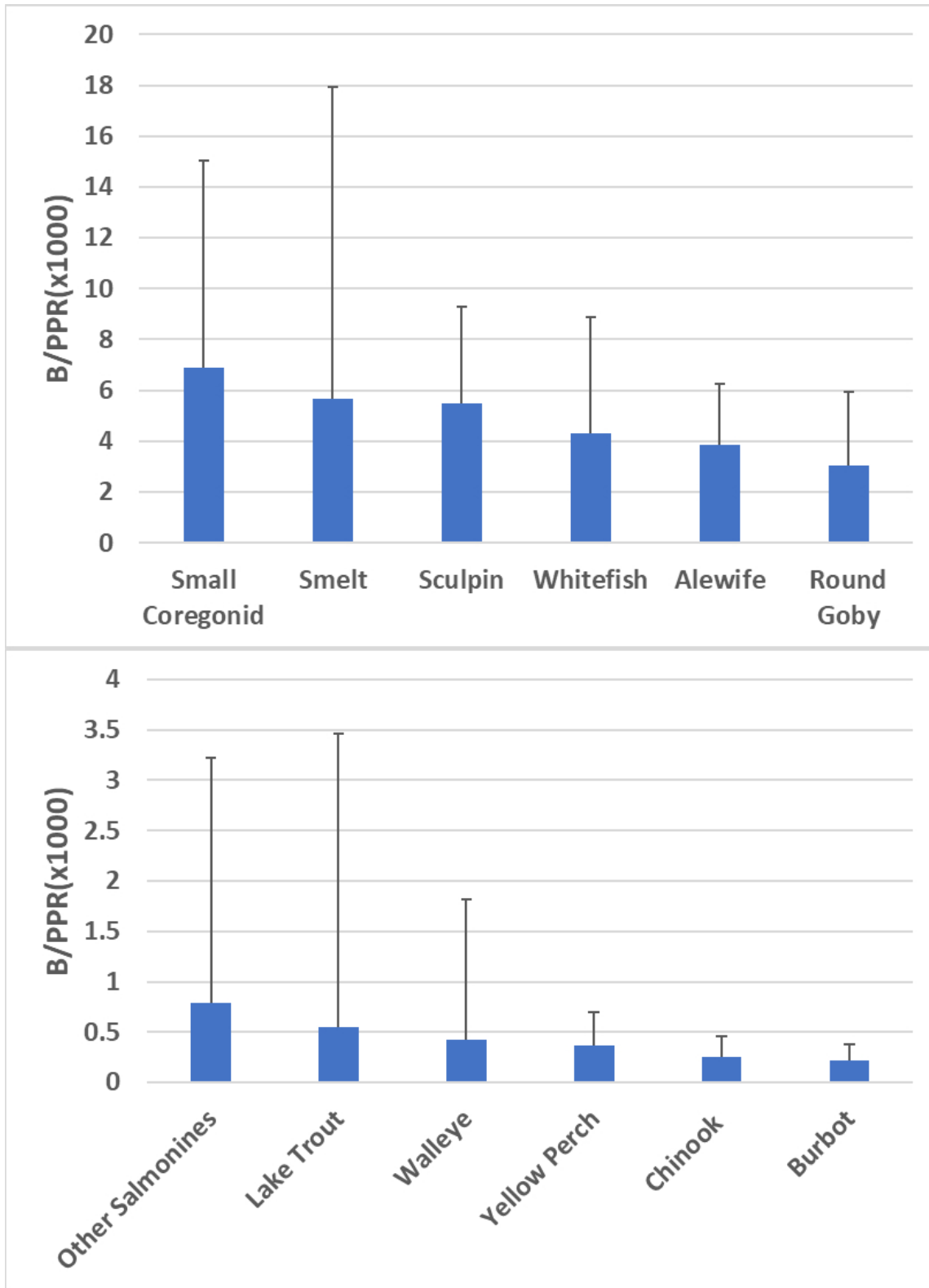


Figure 1. B/PPR index for selected species-groups across the Great Lakes. Bars are one standard error.

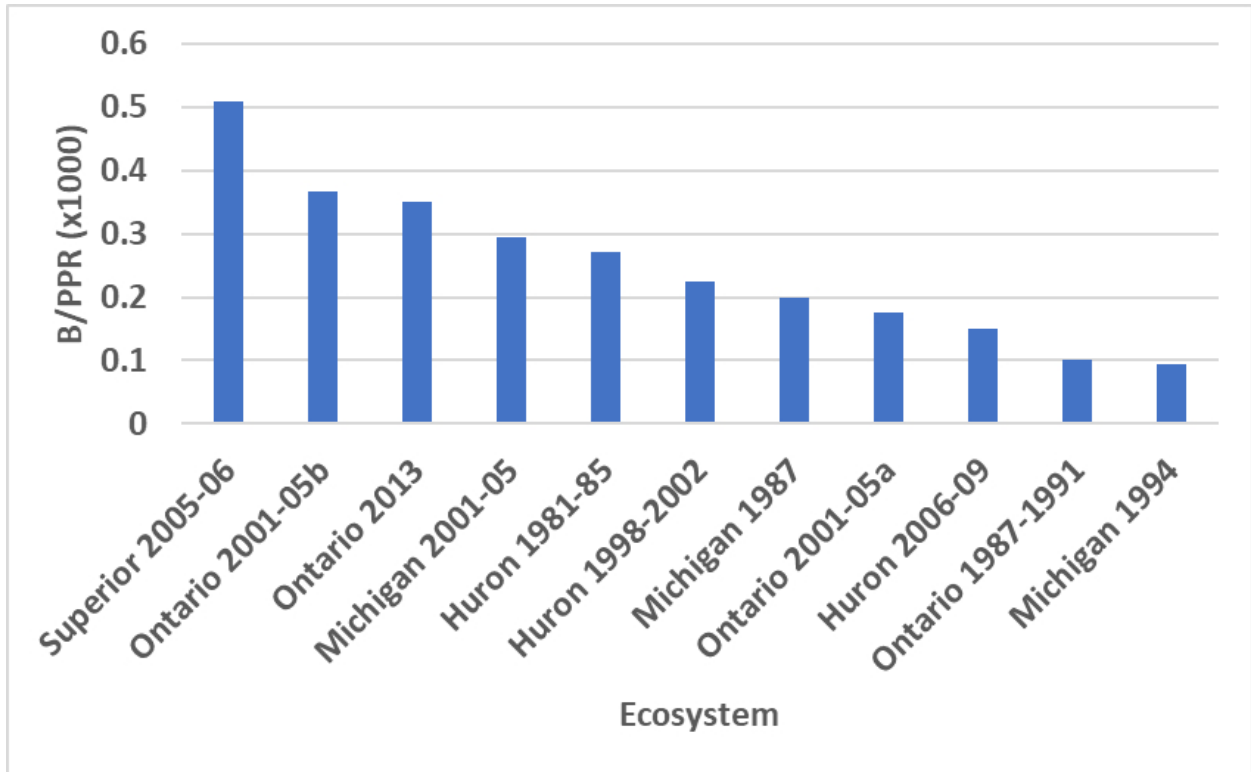


Figure 2. B/PPR index (species-group biomass/species-group PPR) for Chinook salmon across modeled ecosystems representing different time-periods and Great Lakes.

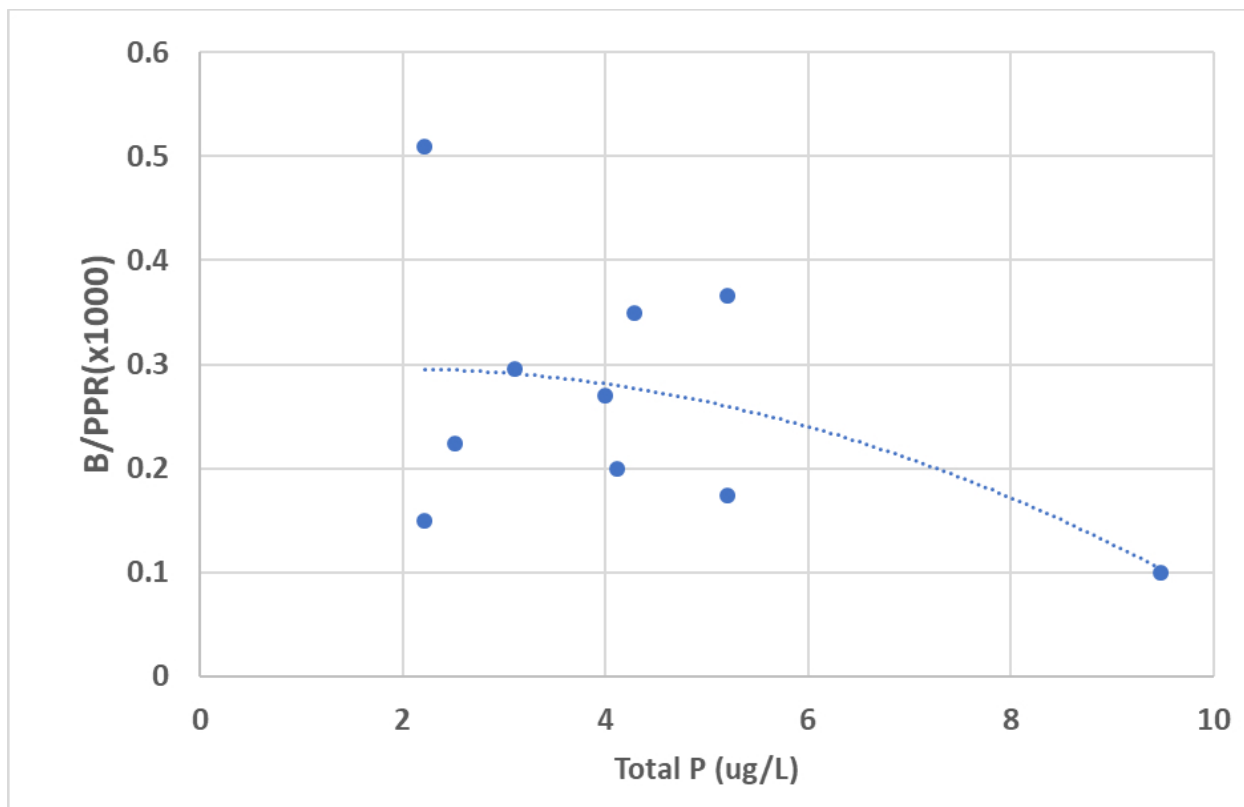


Figure 3. Relationship between total phosphorus (spring and summer combined, Great Lakes National Program Office, unpublished data) and Chinook salmon B/PPR for selected Great Lake ecosystems (excludes Lake Erie and embayment ecosystems).

References

Christensen, V. and Pauly, D. 1993. Flow characteristics of aquatic ecosystems, p. 338-352. In V. Christensen and D. Pauly (Eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Discussion Notes

Q: Implication is that maintaining food web structure that can efficiently utilize PP and detritus can benefit fisheries?

A: Yes, and not only that, the high TTE associated with both Lake Ontario and Lake Superior suggests that very different food web structures can both result in high TTE.

C: Models are focused on upper trophic levels, lots of detail about feeding habits of fish, less on zooplankton and other lower trophic levels; need to understand consequences of that.

Understanding the trophic consequences of reduced phosphorus and dreissenid mediated increases in water clarity on Great Lakes fish communities and fisheries

David “Bo” Bunnell¹

¹United States Geological Survey, Great Lakes Science Center, 1451 Green Rd, Ann Arbor, MI 48105

Contributors: Rick Barbiero, Tomas Höök, Roger Knight, Stuart Ludsin, Christine Mayer, Ed Rutherford, and Hank Vanderploeg

Abstract

Water clarity was chosen as a workshop focus because it is a feature of the Great Lakes that is easily understandable and observable to anglers and fishery managers and declines in offshore phosphorus (accelerated by proliferation of dreissenid mussels) have led to increased water clarity in Lakes Ontario, Michigan, and Huron. Given a goal of the scientific workshop was to help inform fishery managers, our emphasis was on the consequences of increased water clarity on fish and fisheries and not on the mechanisms underlying the changing water clarity. As an introduction, we used monitoring data from US EPA to establish increasing trends in offshore water clarity for the three aforementioned lakes: Ontario is 43% more clear since 1990, Huron is 49% more clear since 1998, and Michigan is 37% more clear since 2001 (see Fig. 1). The increasing water clarity is a result of the declining phytoplankton in these lakes, owing to both long-term declines in phosphorus inputs and grazing by invasive dreissenid mussels. To understand the consequences of changing water clarity to fish and fisheries, we developed a conceptual model through a process that began prior to the workshop (over conference calls) and continued through workshop breakout group discussions. Our final model (Fig. 2) focused first on how water clarity would influence aspects of the food web (i.e., especially those that could influence fish distribution and abundance), which ultimately shapes fish community composition and the fishery. Increased water clarity can cause zooplankton to shift to deeper waters during the daytime to avoid planktivores (Dodson 1990). For example, water clarity is so high in Lake Michigan that visual-feeding predatory *Bythotrephes* are no longer light limited and can feed on daphnids and other zooplankters down into the metalimnion (Vanderploeg et al. 2015). Many zooplankton species respond by occupying colder hypolimnetic waters during the day, which can limit their productivity (Pangle et al. 2007). Given that nearly all fish during some part of their first year of life are planktivorous (and others for their lifetime), water clarity can affect the spatial overlap between fish and a key prey resource. Increased water clarity can also reduce light limitation for benthic algae and increase their primary production. This change could favor herbivorous fish species, such as suckers or carp but also generally favor more benthic oriented species such as round gobies, freshwater drum, or even lake whitefish. Increased light penetration can also increase macrophyte production in the nearshore which, in turn, can increase spawning and nursery habitat for some fish species. Water clarity can also directly influence the fish community by affecting foraging success or predation risk for individual fishes. These factors contribute to each species theoretically having an ideal light environment under which

conditions for feeding while avoiding predation are optimized. Although these light conditions are not well described for most species, Lester et al. (2004) illustrate how catch-per-unit-effort for walleye fisheries is higher in more turbid environments than clear environments (see Fig. 3 from Lester et al. 2004 below). Mechanistically, empirical work with yellow perch in the Great Lakes provides another example of how water clarity influences both rates of both foraging and predation. Wellington et al. (2010) demonstrated how larval yellow perch consumed less food under high turbidity conditions caused by phytoplankton than under high turbidity conditions caused by sediment. Likewise, Reichert et al. (2010) revealed that the risk of predation for larval yellow perch was higher in clearer water than in turbid water in western Lake Erie. Hence, the net outcome of foraging success and avoiding predation should contribute to the water clarity vs. fish abundance that Lester and others have established for walleye which, in turn, will shape the types of fish communities that occur in lakes with different water clarities. Our discussions during the workshop also highlighted how changing water clarity could influence catchability of fishing gears used in either fishery-independent assessments or by recreational anglers and commercial fisheries. Although there is limited research on this topic in the Great Lakes, research in other systems indicates light intensity can affect catchability of bottom trawls (e.g., Buijse et al., 1992) and gill nets (e.g., Hansson and Rudstam, 1994), two commonly used gears in assessments and commercial fisheries. Furthermore, angler behavior can shift based on the changing distribution or community composition of fishes, and they might change their fishing gears (baits) and deployment of their baits (e.g., depth, time of day) in response to changing water clarity. Forecasting of fishery performance is important to fishery managers and is dependent on their understanding of fishery behavior under varying environmental conditions.

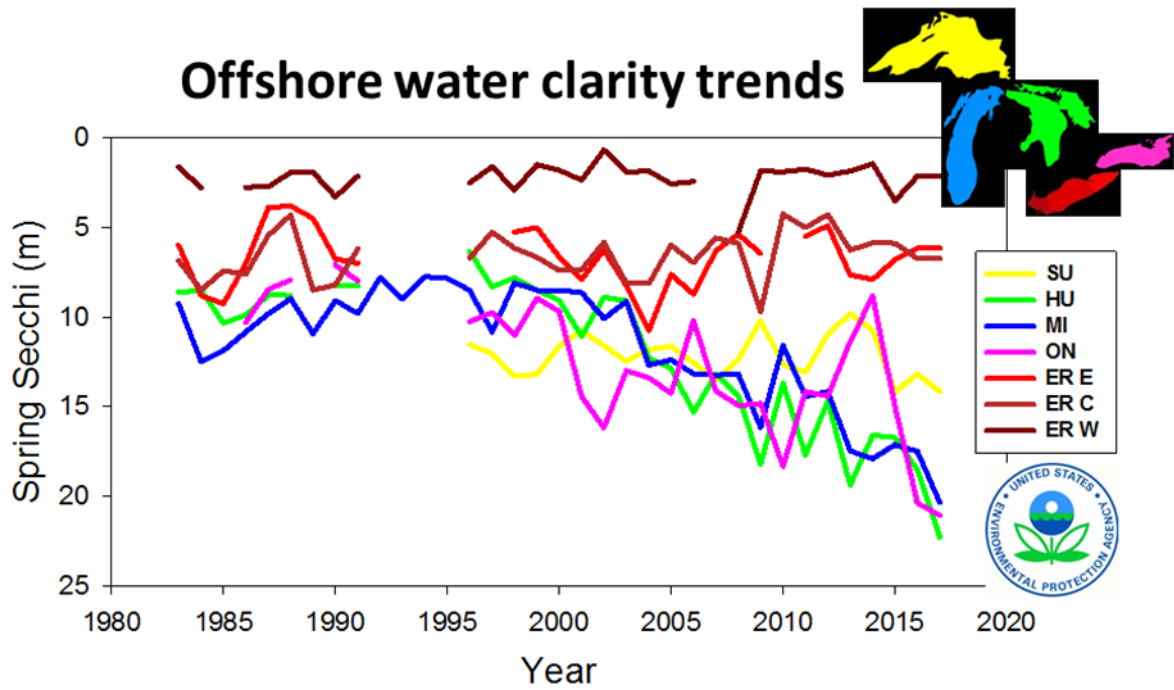


Figure 1. Mean Secchi disk depth in the Great Lakes demonstrating increasing water clarity (deeper Secchi) in Lake Michigan (MI), Huron (HU), and Ontario (ON). Data courtesy EPA-GLNPO.

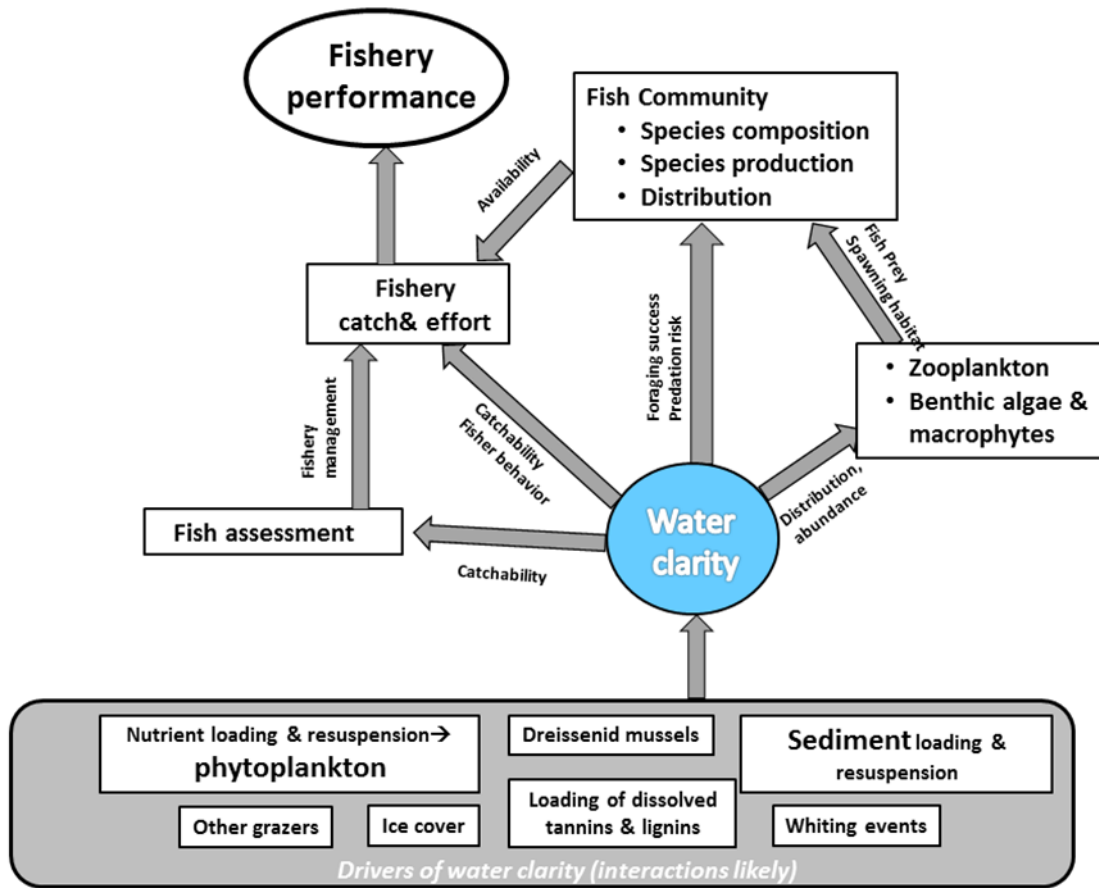


Figure 2. Conceptual model of how water clarity influences the food web (zooplankton, benthic algae, macrophytes, fish), the ability of scientists and managers to assess the fisheries, and the ability of anglers to catch the fish. The lower gray box depicts the factors that contribute to changing water clarity, but these exact drivers were not the focus of our discussions.

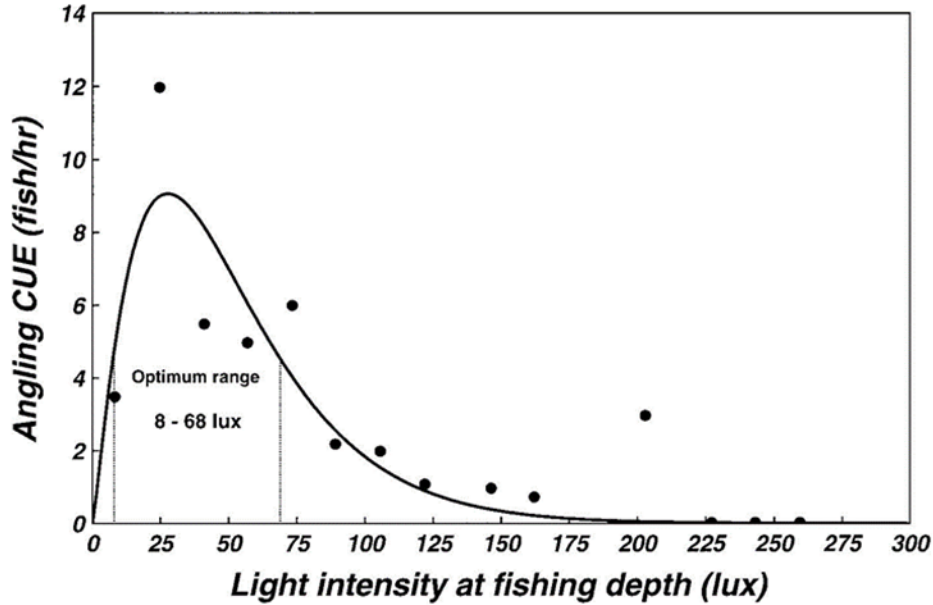


Figure 3. Angling catch-per-unit-effort (CUE) of walleye as a function of light intensity, demonstrating higher walleye CUE in more turbid waters (from Lester et al., 2004). Walleye CUE by anglers is presumed to positively related to walleye abundance.

References:

Buijse, A.D., Schaap, L.A., and Bult, T.P. 1992. Influence of water clarity on the catchability of six freshwater fish species in bottom trawls. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 885-893.

Dodson, S. 1990. Predicting diel vertical migration of zooplankton. *Limnology and Oceanography* 35: 1195-1200.

Hansson, S., and Rudstam, L.G. 1994. Gillnet catches as an estimate of fish abundance: a comparison between vertical gillnet catches and hydroacoustic abundances of Baltic Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). *Canadian Journal of Fisheries and Aquatic Sciences* 52: 75-83.

Lester, N.P., Dextrase, A.J., Kushneriuk, R.S., Rawson, M.R., and Ryan, P.A. 2004. Light and temperature: key factors affecting walleye abundance and production. *Transactions of the American Fisheries Society* 133: 588-605.

Pangle K.L., S.D. Peacor, and O.E. Johannsson. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology* 88: 402-412.

Reichert, J.M., Fryer, B.J., Pangle, K.L., Johnson, T.B., Tyson, J.T., Drelich, A.B., and Ludsin, S.A. 2010. River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 987-1004.

Vanderploeg, H.A., S.A. Pothoven, D. Krueger, D.M. Mason, J.R. Liebig, J.F. Cavaletto, S.A. Ruberg, G.A. Lang, R. Ptacnikova. 2015. Spatial and predatory interactions of visually preying nonindigenous zooplankton and fish in Lake Michigan during midsummer. *Journal of Great Lakes Research* 41(Suppl. 3): 125-142.

Wellington, C.G., Mayer, C.M., Bossenbroek, J.M., and Stroh, N.A. 2010. Effects of turbidity and prey density on the foraging success of age 0 year yellow perch *Perca flavescens*. *Journal of Fish Biology* 76: 1729-1741.

Discussion Notes

C: Water clarity as predictor – what examples do we see where clarity can have an effect on these vital rates or population rates of fish?

C: Should species composition be added to the conceptual model?

Q: What's driving the change to more algal blooms now?

A: Maumee River loading combined with climate (warming). Trend to higher proportion of dissolved reactive phosphorus – agriculturally derived P.

C: More effective delivery rather than more effective application (tile, climate, less tillage = more broadcasting...better connection to lake rather than changes in agricultural practices.

C: We often focus on nearshore-offshore but different nearshore areas of Lake Michigan are different – e.g., northwest and southeast Lake Michigan see increasing chlorophyll concentration nearshore, but there have been declines in southwest Lake Michigan.

C: Regarding the Mayer et al., 2014 slide describing benthification related to increased water clarity – all these lakes are shallow.

Q: How useful would information on drivers of water clarity be to fisheries managers?

A: It is important but they don't need high level of detail. Amount of detail in the current conceptual model is sufficient.

C: Drivers of changes in water clarity (nutrients/herbivory vs. sediment loading) have different effects on fish production. Reduced sediment loading could lead to more production.

C: Think Secchi depth is most useful, and if you have measure of chlorophyll you can know what kind of turbidity. You also have seasonal trends (e.g., western Lake Erie early season = plume, late season = algal bloom).

C: Perhaps large fish are more affected by turbidity.

C: Inside and outside of sediment plumes and HABs, for larval fish (yellow perch, gizzard shad, shiners, white perch) there is no difference in consumption. We don't know if this is because fish captured in bloom are hiding during day and coming out during crepuscular period. Think they're using blooms as refuge. But diet items are different inside and outside.

C: Wiley, 1984 paper on optimal macrophyte density for fish production is relevant – can get at the fish reproduction piece.

Appendix A: Workshop Agenda

Date	Time	Activity	Presenters
Monday, August 28	13:00	Introduction to the workshop	Tom Stewart and Lars Rudstam
	13:15	Managers perspective on lower trophic level change and fisheries	Roger Knight
	13:50	The Lake Constance experience	Roland Roesch
	14:40	Update on IJC Lower Trophic Level and Fish Synthesis	John Bratton
	15:15	Great Lakes lower trophic level indicator trends	Beth Hinchey
	15:50	Recent changes in Great Lakes Nearshore	Todd Howell
	16:25	Review of some key hypotheses and case-histories of lower trophic influence on fish and fisheries	Tom Stewart and Lars Rudstam
	17:00	Adjourn	
	18:00	Dinner and Social	
Tuesday, August 29	8:30	Flashing new insights from last night's discussions	Facilitator
	9:00	Re-examining relationships among nutrients, autotrophs and fish	Brian Weidel
	9:40	Bay of Quinte: Phosphorus, fish and dreissenids	Marten Koops
	10:15	Trophic consequences of Great Lakes nutrient declines, dreissenids and water clarity	Bo Bunnell
	11:15	Comparing estimates of trophic transfer efficiencies among the Great Lakes: Any insights?	Tom Stewart
	12:00	Lunch	
	13:30	Discussion and assignment to themes	Facilitator
	14:00	Taking it to the fish: A conceptual model of trophic transfer efficiency	Break-out groups

Appendix A: Workshop Agenda

	14:00	How to produce fish: A conceptual model of fish production and yield	
	14:00	Isn't it transparent: A conceptual model of the trophic consequences of oligotrophication	
	18:30	Dinner and Social	
Wednesday, August 30			
	8:30	Break-out group presentations and discussion	Break-out group nominee & Facilitator
	11:15	Wrap-up and next steps	Tom Stewart
	12:00	Adjourn (optional lunch)	

Appendix B: Discussion notes following breakout group reporting

Taking it to the Fish: A conceptual model of trophic transfer efficiency

C: Take the species assemblage with overall production plot – focusing on high-value species, how much energy does it take to grow those, and how does it change over time. Tells you about efficiency of food web across lakes and within a lake across time.

C: May be a different relationship after you correct Lake Michigan 1994.

Q: How many models can we get for one lake to get at the time scale?

A: You can export simulated Ecopath models over time. If you really want to do that, and with Ecosim, you can simulate primary production (PP) required for every year.

Q: Lake Huron is predominantly picoplankton now – what does that mean? Could we figure that out?

A: Yes. Could see relative change. Would be interesting. Suspect less efficient.

C: Small/benthic fishes are more efficient than large or pelagic.

C: Might be useful to ignore PP as x-axis and compare how efficient species are at converting PP into a gram of their own tissue.

Q: Are native species more efficient than introduced species?

A: This is not evident in the data, introduced species may be successful because they are efficient at exploiting resources.

C: Simple units and comparisons will be most compelling to the public – e.g., totally making up these numbers, “in today’s Lake Michigan, it takes 50 lbs of PP to produce one lb of Chinook, but only 10 lbs of PP to produce one lb of lake trout.” “It used to take 20 lbs of PP to produce one lb of Chinook in Lake MI, but now it takes 50 lbs,” etc.

C: Is it better to compare species within models than compare across models? Due to model artifacts, different assumptions across models, etc?

C: Take home message to anglers might be – if salmon or predator of interest is converting more efficiently, does that mean more or bigger fish?

C: Means more for given nutrient level. Expensive in terms of nutrients to grow a big fish. Relevant to questions around which coregonids to reintroduce for restoration. Walking through this in a food web model would be interesting, there are implications for alewife or potential predators.

C: We can also use isotopes to get at trophic level. Couldn't you use isotope value as a surrogate for TTE?

C: Disagree with the idea that native species will be more efficient than exotic. Example in Lake Champlain with exotic alewife, native smelt. Predators got more efficient feeding on alewife.

C: The environment in which evolution is working on them matters, some invaders came from oligotrophic environments. And why do invasive species succeed? These are already adapted well, might be very efficient.

How to produce fish: A conceptual model of fish production and yield

Q: Shouldn't the relationship decline at high nutrients?

A: Agree with idea but not over this range of data. Phytoplankton become light-limited instead and it just plateaus out. May have to include a qualifying statement – this applies only the Great Lakes.

Q: Does predator curve need to be more complex?

A: Yes, in actuality you can lose prey production with excessive harvest or excessive predation. But need to balance this reality with the need to be conceptually simple

C: Oligotrophication – is connectivity going to be more important as this happens? Is a message to managers that we have to up our game? Concentrate more on habitat? Is predator/prey balance going to be more of a challenge? Restoration of species more conducive given oligotrophication?

C: Nutrient reductions give fisheries community support for the argument to take more actions to move up and down the y-axis (habitat restoration, cut stocking, etc.).

C: Lake Constance oligotrophication more of a socioeconomic response (cage aquaculture). An oligotrophic lake in China (missed name) – also developed cage culture.

C: Should y-axis be fish biomass? But production is more important for harvest. People really think about species. That relationship is dome-shaped for walleye (see Oglesby).

C: There are models for species of interest. As you increase nutrients, e.g., for Saginaw Bay walleye, will drop biomass and potential harvest. Connected to land use. This is a good tool to talk about restoration, what people can do. Land management is a huge thing that is the source of nutrients. Would be good to highlight examples from places and species that people are familiar with.

Q: Nutrient loading is mechanism of model. Do you have data though?

A: Model is calibrated to landings and biomass data. Species change is probably due to interactions in community.

C: Some disagreement as to whether more nutrients in cage culture = more salmon – in absence of other species.

C: Illustrate how an invasive species like dreissenids can drop production given same nutrient loading.

C: What's the western Lake Erie story for walleye from the 1970s? They declined, this counters Lars' point that more nutrients always = more fish.

C: Might be possible to generate lake-specific curves. Emphasize modifiers specific to each lake. General conceptual model that we tailor to each lake.

C: Response variable – fish production, could do biomass, or could do fisheries yield. Relationships would be same general form, but evidence for lack of decline on back end – is that being driven by fish biomass? We rarely actually measure fish production – many of these relationships probably use biomass or yield. Don't want some element of conceptual model that is loaded.

C: You can build high biomass somewhere like Superior with low production.

C: The spread allows you to address biomass differences. Relative change in spread compared to nutrient change – increase slope and keep wide, or keep it flatter and narrower (could do a little of both)?

C: Put some data on it?

C: What if all nutrients are moved into non-consumable materials like mussels or macrophytes? This takes us to lower end of envelope. Or high predators.

C: What about fishing intensity? “Human predators.”

C: Can we turn this into a dynamic “dashboard?” Tipping points project is trying to do this. Very data-intensive. How much can this be conceptual vs. data-based?

C: There should be an asymptote (plateaus).

C: Vollenweider (1974)– nutrient load equation plotted, PP across five Great Lakes in 1970s. It does asymptote, but we've moved left.

C: Habitat connectivity – all sorts of improvements would allow you to move up and down on y-axis. Creating spawning habitat. Not just connectivity. Lots of play on y-axis, are you harvesting predators or planktivores? Connectivity is a loaded term; “Habitat availability,” “Habitat quality and quantity,” or just “habitat?”

C: Managers get to modify this. We can present it as a draft and they may have language that helps.

C: Envelope – range of ways a system could be configured. Fine with that as conceptual – but don't lose the point that variability is important to managers. Instead of envelope being different ways system could be configured, look at interannual variability given nutrient level. Can you pull out estimates of variability at different nutrient levels?

C: Bay of Quinte analysis (Koops and Hossain), if you just play with nutrients maybe variability does what we expect, but not when you start considering other factors, e.g., zooplankton biomass ratio.

C: Variability is particularly important as it applies to high-value species.

C: Regier 1969 paper on Lake Erie walleye– high recruitment events are a signal of stressed system. Could “stress” be oligotrophication? Depends on community.

C: Is it easier to manage in certain regimes than others? What is the “management climate” of different systems?

C: Should sea lamprey be in conceptual model as a predator? Drives some of variability. Mentioning sea lamprey would help.

Isn't it transparent: A conceptual model of the trophic consequences of oligotrophication

C: Need to consider the “and, but, therefore” paradigm for communicating a compelling story. The “therefore” is missing from this.

C: Effect of clarity on bass selection. 2002 review article by Vanderploeg – mussels providing food and habitat for gobies, light intensity increases predation. Beaver Island – giant bass feeding on gobies. Hasn't been explicitly explored but there is anecdotal/observational stuff.

C: Can we look at responses of fisheries to water clarity – gillnet catchability coefficients? Lake Erie example. Deepwater trawling affected? Anglers – trolling picked up in Lake Erie as water cleared. Tighter schools? Walleye more easily spooked. Catch-per-unit effort became higher for trolling vs. casting. Relevant to assessment as well.

C: May not be more salmon, just increased catchability. We can say to anglers: we have all seen water clarity changes, you've modified your fishing activity because of that. Have we thought about what that means to how we manage? Clarity is associated with reduced productivity.

C: This might be a good discussion for the management group...think about the fisheries effects.

C: Only need to acknowledge the complicating factors but focus on what we see with the fisheries. Need a synthesis.

C: Plot lakes through time? Barbiero's graphic. Will look at ways to represent how things are changing.

C: Make phytoplankton and sedimentation even bigger under "drivers" to emphasize importance?

C: Add benthic algae in with macrophytes.

C: Deep pelagic offshore systems – structuring food web differently, communities are deeper, effects of lower temperatures. UVB radiation with water clarity, surface avoidance?

C: This would be in review paper, but does UV need to be in the manager conceptual model?

C: We should at least mention distribution and abundance (this is wrapped up in zooplankton). Also interactions with *Bythotrephes*, increased range of predation depth. Has depth at which people catch salmon/trout changed? Winter alewife distribution.

C: Important to communicate to managers the struggle scientists have in working changes in clarity into our paradigms. We're trying to adapt science and investigative models; you also need to adapt management. We're highly suspicious that we are experiencing changes in predator-prey dynamics and anglers are a predator.

C: Cod fishery example with catchability – failed to adapt to change in catchability. Decision analysis with two indices. Consequences of assumptions of one index...there was uncertainty presented and managers ignored.

C: Catchability models – use this generally to say, this is when you should start thinking about catchability issues.

C: Disadvantage is once you say that we don't always know what we're measuring, and it is changing as the environment changes, then it's a free-for-all – you lose credibility with stakeholders.

C: Water clarity and stratification – light is driving temperature. Changing density of prey fish in foraging arena.

C: Have not seen a change in temperature at depth in GLNPO data. Have only analyzed to 2003. Think this is more wind-driven than light-driven.

C: Lake Ontario evidence is that the thermocline is getting shallower, counter to theory. August thermocline depths are decreasing. Air temperature is important. We see this in Lake Michigan as well.

C: Trophic changes are clearly directional, but engineering changes in system (biotic or nutrients) – lots of different things happen.

C: Water clarity leads to change in human behavior. Add another box for fishing behavior, catchability? Add a “fisheries yield” box at top?

C: Clarity is an aesthetic that non-anglers associate with higher-quality environment. There are studies on this. Economic negatives associated with mussels – but property values went up because of clear water. We have to deal with a constituency that likes this aesthetic – need to be even more adaptive in management and communication.

C: With any sort of water quality measures, we have perceived benefits of improving water clarity/quality; benefits of this are not fisheries-based. There are trade-offs. We can care about fish, but we’re always going to lose this argument. If you could compare water quality vs. fish economically, suspect we’re going to lose.

C: What can we do as managers to enhance ecosystem services associated w/fisheries benefits? Not expensive to have initial effect, have to spend more and more money and effort to get marginal effects. Maybe we don’t want to keep spending lots of money to improve water quality a little bit more, because it is expensive and will have negative impacts on fish. No one was talking about phosphorus and fish, what’s to say pendulum can’t swing the other way? What if people start publishing on that, noting it, saying it? Would they continue to put money into reducing Lake Michigan nutrient loads?

C: Developing nutrient loading/chlorophyll/P model for Lake Michigan. Next step we want to take – maybe we shouldn’t be messing around with Grand River. No *Cladophora* in nearshore zone due to wave action and sand substrate. Don’t want nutrients where you have hard substrate and get *Cladophora*. Where do you want to put your pipe?

C: Need a handle on where water quality issues are regionally. Drive home that if you can make efforts on nutrient reduction as targeted as you can on nutrient and geography, you may be able to achieve nutrient reductions (shotgun approach) and water quality outcomes while having less effect on fisheries. Really empower fisheries community to go up the y-axis (on Weidel’s graph). Dialogue that finds ways to optimize outcomes to both communities.

C: Water quality issue will win out when it comes to harmful algal blooms; maybe not for *Cladophora*? Need to quantify the problem.

C: Manager’s workshop – this should be a module.

C: Formal position statement issued by Lake Erie Committee that led to trophic level monitoring program –do we need a formal position statement the other way? Challenge is to turn this into a positive conversation.

C: Not to say that fisheries needs to trump water quality issues, but when we make decisions around water quality we need to take into account fisheries effects. Fishery managers need to be at the table. Get LAMP coordinators at manager’s workshop?

C: Is the goal restoration, or a put-and-take fishery? In Lake Michigan the impression is that the fishery industry is biggest, most important contributor to economy.

C: In places like Green Bay water quality may trump fisheries. This comes up in LAMP process and with the conservation community quite a bit. Seems to be at odds with goals of fish community. “Whose lake is it?” Whoever has the most clout? Fishermen say it’s our lake to fish Pacific salmon. Our clients are usually fishermen.

C: Western Lake Erie example – water clarity as an example of an essential component of habitat. People don’t often think about open water as habitat. This might be important story to tell.

C: Tend to think of zooplankton as having habitat and temperature preferences that determine where they are in the water column, but water clarity could be important.

C: Top things related to water clarity to tell managers:

- Fish composition
- Co-varies with productivity
- Clarity (distribution and abundance of primary producers, primary consumers, macrophytes) affects vital rates (growth, predation risk)
- Oligotrophication is like cutting down trees – difference between a forest and a grassland, or an old-growth vs. new-growth forest. It’s a fundamentally different ecosystem and you have to manage it differently. Don’t expect to find the same animals in a grassland as forest!
- With increased water clarity, food resources shift deeper (either change deep chlorophyll layer or benthification).
- Water clarity will affect composition, distribution, size/growth, recruitment of fishes.

C: Ignore sediments – P/nutrient issue is what managers care about. But we’re supposed to think about every lake. Sediment resuspension important in other lakes in nearshore.

C: No handle on what drives fish recruitment in large lakes, but some indication that upwelling events important; would like to keep sediments in.

C: Is a “decision tree” a better way to organize?

C: Seasonal vs. long-term effects (cutting down tree vs. temporary weather events). “Non-linear” and “trade-offs” – idea for a unimodal distribution of fish responses across gradient of trophic state/clarity. Can show where each lake is on curve and what direction it’s moving in. Then the mechanistic relationship/model can explain where each species is on curve/how its particular curve is shaped.

Appendix C: Workshop themes and rationale

A. Comparative analysis of independent measures of trophic transfer efficiency (TTE):

Rationale: TTE can be easily understood by fisheries managers and has analogies in agriculture and economics. It can potentially be used in a general conceptual model relating LTL change to fish and fisheries. The general effect (increase/decrease) on TTE by invasives, zooplankton community structure, prey fish community structure shifts, or non-edible algal blooms can potentially be described. It is possible to quantify TTE using different independent methods which could lead to testing or development of some interesting hypotheses.

General methods to calculate TTE:

Size-Based: TTE metrics can be either size-based or species-based. Size-based metrics can be derived from biomass size spectra and empirical or theoretical relationships between size and trophic position and P/B ratios (Gaedke and Straile 1994; Jennings et al. 2002). Size spectra, estimates of P/B, and both diet and isotope based estimates of trophic position are available for a number of Great Lakes. Syntheses of these data to derive the required empirical size-based relationship specific to the Great Lakes would be possible.

Ecopath Balanced Models: A complete Ecopath balanced model has all the elements to calculate either aggregate TTE (i.e., trophic levels I to II, II to III, III to IV) or species specific TTE (e.g., PP to Zoo, PP to Mysis, Zoo to Prey-fish, Zoo to Alewife etc.)

Empirical Indicators: Generally, and especially across the Great Lakes, species-specific P/B ratios are assumed to vary much less than estimates of biomass. This means that biomass might be a surrogate for production for some species or species-groups. Isotope data is becoming more prevalent and might be applied to quantify differences in trophic position of key groups (zooplankton, Mysis, Alewife) across the lakes. By combining these data it should be possible (have to think a little more on this) to compare indicators to TTE across the Great Lakes or over time.

B. Predicting commercial fisheries yield and fish biomass and production from measures of LTLs

Rationale: Fisheries managers have long understood that primary production can directly influence the productive capacity of fish. They also understand that fish production, commercial fisheries yield, prey fish biomass, angler CPUE can also be greatly influenced by other factors (e.g. harvest policy, weather, predation). It is still apparent that fish managers want to be able to demonstrate to themselves and others that changes in primary production can influence fisheries outcomes (positively and negatively). This can help with fishing management planning and fish community objectives by allowing for some evidence-based anticipation of changes in potential yield or carry capacity.

General Methods: Approach would be to assemble data bases describing commercial fisheries yield, fish biomass, and indicators of primary production and look for correlations. Additionally,

we would compare these relationships to literature analyses (e.g. Deines et al. 2014). Synthesis data from ECOPATH mass balance models would also be assembled that relate mass balanced estimates of primary production to mass balanced estimates of prey fish production and biomass.

C. Understanding the trophic consequences of reduced phosphorus and dreissenid mediated increases in water clarity on Great Lakes fish communities and fisheries

Rationale: Reduced phosphorus levels, increased water clarity, dreissenids and round goby establishment and the loss of *Diporeia* are co-occurring and related phenomena. Coincident changes include increased depth of the euphotic zone, altered fish habitat, changes of fish distribution and fish community shifts which have changed energy and material flow within Great Lakes food webs. Several mechanistic hypotheses have been proposed linking these observations. Many of the related observations, for example, increased water clarity, are obvious to both fisheries managers and their stakeholders. Fisheries managers could benefit from a succinct and easily understood summary of these changes and possible mechanistic explanations. What fish and fisheries effects can be confidently attributed to these interacting influences and what aspects are less certain? Can the trophic consequences of these changes be described and quantified?

General Methods: Key syntheses and hypotheses focused papers (e.g. Barbiero et al. 2011, Stewart et al. 2014, Vanderploeg et al. 2014, Mayer et al. 2014) will be reviewed and summarized in a general conceptual model focusing on the trophic consequences of dominant influences (e.g. sequestering of material by dreissenids, changes in primary productivity, increased water clarity, expansion of round goby). Case histories (e.g., Bay of Quinte, Saginaw Bay, Great Lakes offshore and nearshore time series) will be drawn on as supporting examples). Indicators of the trophic consequences of these changes (e.g. fish growth, diets, TTE, algal edibility, zooplankton community structure, species or species-group production) will be proposed and evaluated for supporting evidence.

D. Supporting Data and Literature Syntheses

In addition to the above syntheses themes, individuals or teams will be assigned to assemble key indicator data to be available to workshop participants.

1. Offshore LTL indicators
2. Nearshore LTL indicators
3. Selected prey fish trend indicators
4. Selected predator fish trend indicators
5. Commercial fishery yields
6. Summary white-paper describing literature hypotheses, case-histories, glossary relating LTL to fish and fisheries

References

Barbiero, R. P., Lesht, B. M., & Warren, G. J. (2011). Evidence for bottom-up control of recent shifts in the pelagic food web of Lake Huron. *Journal of Great Lakes Research*, 37(1): 78–85. <https://doi.org/10.1016/j.jglr.2010.11.013>

- Deines, A. M., Bunnell, D. B., Rogers, M. W., Beard, T. D., & Taylor, W. W. (2015). A review of the global relationship among freshwater fish, autotrophic activity, and regional climate. *Reviews in Fish Biology and Fisheries*, 25(2): 323–336. <https://doi.org/10.1007/s11160-015-9384-z>
- Gaedke, U., & Straile, D. (1994). Seasonal-changes of trophic transfer efficiencies in a plankton food-web derived from biomass size distributions and network analysis. *Ecological Modelling*, 75: 435–445. [https://doi.org/10.1016/0304-3800\(94\)90038-8](https://doi.org/10.1016/0304-3800(94)90038-8)
- Jennings, S., Warr, K. J., & Mackinson, S. (2002). Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Marine Ecology Progress Series*, 240: 11–20. <https://doi.org/10.3354/meps240011>
- Mayer, C.M., Burlakova, L.E., Eklöv, P., Fitzgerald, D., Karatayev, A.Y., Ludsin, S. A, Millard, S., Mills, E.L., Ostapenya, A. P., Rudstam, L.G., Zhu, B., Zhukova, T. V, 2014. Benthification of freshwater lakes: Exotic mussels turning ecosystems upside down. In: *Quagga Zebra Mussels Biological Impacts and Control* (edited by Thomas F. Nalepa, Don W. Schloesser). Chapter 36, pg. 575–586. doi:10.1201/b15437-44
- Stewart, T. J., Rudstam, L., Watkins, J., Johnson, T. B., Weidel, B., & Koops, M. A. (2016). Research needs to better understand Lake Ontario ecosystem function: A workshop summary. *Journal of Great Lakes Research*, 42(1): 1–5. <https://doi.org/10.1016/j.jglr.2015.10.017>
- Vanderploeg, H. A., Pothoven, S. A., Fahnenstiel, G. L., Cavaletto, J. F., Liebig, J. R., Stow, C. A., and Bunnell, D. B. (2012). Seasonal zooplankton dynamics in Lake Michigan: Disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. *Journal of Great Lakes Research*. 38: 336-352

Appendix D: List of participants

Name	Affiliation
Roland Roesch	LAZBW, Fisheries Research Station, Argenweg 50/1, 88085 Langenargen, Germany
David (Bo) Bunnell	U.S. Geological Survey - Great Lakes Science Center
Hank Vanderploeg	NOAA - Great Lakes Environmental Research Laboratory
Ed Rutherford	NOAA - Great Lakes Environmental Research Laboratory
Roger Knight	Great Lakes Fishery Commission
Julie Hinderer	Great Lakes Fishery Commission
Tom Stewart	Ontario Ministry of Natural Resources and Forestry-retired
Lars Rudstam	Cornell University
Elizabeth Hinchey	U.S. EPA Great Lakes National Program Office
Brian Weidel	U.S. Geological Survey - Great Lakes Science Center
Marten Koops	Fisheries and Oceans Canada
Todd Howell	Ontario Ministry of Environment and Climate Change
John Bratton	LimnoTech
Stu Ludsin	Ohio State University
Thomas Hook	Purdue University
Christine Mayer	University of Toledo
Rick Barbiero	DynCorp Environmental
Yu-Chun Kao	Michigan State University
Hongyan Zhang	University of Michigan
Jim Watkins	Cornell University
Toby Holda	Cornell University
Annie Scofield	Cornell University
Monir Hossain	Fisheries and Oceans Canada
Doran Mason	University of Florida

Appendix E: Ecopath models, PPR calculations and correlations

The influence of food web structure relied on a summary of published and unpublished Great Lakes Ecopath models (Table 1). Ecopath models use data on species-group biomass, biomass-specific rates of species-group production and diet to derive mass-balanced static description of food webs (Christensen et al. 2008). Production for each trophic levels (TL) was determined from the ``trophic level decomposition`` routine in the Ecopath `Network analysis` tool (Christensen et al. 2008), TTE from one TL to the next was estimated as the production at TL n divided by the production at TL n-1.

The ``primary production required`` (PPR) was calculated from the ``Consumption`` analysis tool in Ecopath (Christensen et al. 2008). By back-calculating along all trophic pathways determined by diet and rates of consumption, the routine determines the accumulated total amount of primary production and detrital production necessary to support the production of a species-group, or combination of species-groups in a food web. The percent of PPR (%PPR) was calculated by dividing the species-group PPR by total system primary production and detrital production combined. Initial analysis and workshop discussions indicated that this metric might explain variation in the biomass and production of different species-groups and species-guilds. Assignment of species-groups to species-guilds was based on grouping species from the same taxonomic family, life-history characteristics and size (Table 2). If more than one life-stage of a species-group was represented in the food web description all biomass, production, and PPR metrics were summed to give a complete life-history representation on the species group. Graphs suggested a power function of the form $Y = aX^b$ where Y is species-group biomass and X is PPR or % PPR. Simple regression analysis was used to fit the model to the data (Table 2).

Table 1. Ecopath models and sources used in the food web analysis.

Lake	Area	Time Period	Source
Erie	Central	1996	Unpublished, H. Zhang
Erie	Whole lake	1999	Unpublished, H. Zhang
Erie	West	1999-2001	Zhang et al. 2016
Huron	Whole lake	1998-2002	Kao et al. 2016
Huron	Whole lake	1981-1985	Kao et al. 2016
Huron	Whole lake	2006-2008	Unpublished , Y. Kao
Huron	Saginaw Bay	1990	Kao et al. 2014
Michigan	Whole lake	2001-2005	Kao et al. 2018
Michigan	Whole lake	1987	Rogers et al. 2014
Michigan	Whole lake	1994-1995	Unpublished, E. Rutherford
Ontario	Hamilton Harbour	2004-2008	Hossain et al. 2012
Ontario	Whole lake	2001-2005	Stewart and Sprules 2011
Ontario	Whole lake	1987-1991	Stewart and Sprules 2011
Ontario	Whole lake	2001-2005	Currie et al. 2012
Ontario	Whole lake	2013	Unpublished, B. Weidel
Superior	Whole lake	2005-2006	Unpublished, B. Matheson

Table 2. Model parameters and correlations coefficients between species-group biomass and primary production required (PPR) for Ecopath mass-balance models (Table 1). See text for model description. Correlation coefficients in bold are significant ($P < 0.05$).

Species Group	Species	N	PPR			% PPR		
			a	b	R ²	a	b	R ²
Alewife	<i>Alosa pseudoharengus</i>	14	0.021	1.057	0.961	0.143	1.132	0.946
Smelt	<i>Osmerus mordax</i>	15	0.021	0.604	0.634	0.250	0.619	0.508
Alewife and Smelt	<i>Alosa pseudoharengus</i> , <i>Osmerus mordax</i>	29	0.004	0.962	0.881	0.159	1.023	0.852
Sculpin	<i>Cottus cognatus</i> , <i>Myoxocephalus thompsonii</i>	15	0.060	0.955	0.786	0.426	0.485	0.266
Salmon and Trout	<i>Oncorhynchus tshawytscha</i> , <i>O. mykiss</i> , <i>O. kisutch</i> , <i>Salvelinus namaycush</i> , , <i>Salmo trutta</i> ,	42	0.001	0.748	0.764	0.025	0.762	0.645
Percids	<i>Perca flavescens</i> , <i>Sander vitreus</i>	15	0.001	0.939	0.921	0.043	0.955	0.743
Whitefish	<i>Coregonus clupeaformi</i>	11	0.010	0.795	0.591	0.310	0.583	0.429
Coregonids	<i>Coregonus clupeaformi</i> , <i>C. kiyi</i> , <i>C. hoyi</i> , <i>C. artedi</i>	20	0.010	0.829	0.610	0.321	0.551	0.370

References

- Christensen, V., Walters, C.J., Pauly, D., Forrest, R., 2008. Ecopath with Ecosim version 6 User Guide. Fish. Centre, Univ. Br. Columbia, Vancouver, Canada 281, 1–235.
- Currie, W.J.S., Cuddington, K.M.D., Stewart, T.J., Zhang, H., Koops, M.A., 2012. Modelling spread, establishment and impact of bighead and silver carps in the Great Lakes. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/113 3848, vi + 74.

- Hossain M, Arhonditsis GB, Koops MA, Minns CK. 2012. Towards the development of an ecosystem model for the Hamilton Harbour, Ontario, Canada. *Journal of Great Lakes Research*. 38, 628–642.
- Kao Y-C, Rogers M. W. , Bunnell D. B. 2018 Evaluating stocking efficacy in an ecosystem undergoing oligotrophication. *Ecosystems* 21: 600–618.
- Kao, Y.C., Adlerstein, S., Rutherford, E., 2014. The relative impacts of nutrient loads and invasive species on a Great Lakes food web: An Ecopath with Ecosim analysis. *J. Great Lakes Res.* 40, 35–52. doi:10.1016/j.jglr.2014.01.010
- Kao, Y.C., Adlerstein, S.A., Rutherford, E.S., 2016. Assessment of Top-Down and Bottom-Up Controls on the Collapse of Alewives (*Alosa pseudoharengus*) in Lake Huron. *Ecosystems* 19, 803–831. doi:10.1007/s10021-016-9969-y
- Rogers MW, Bunnell DB, Madenjian CP, Warner DM. 2014. Lake Michigan offshore ecosystem structure and food web changes from 1987 to 2008. *Canadian Journal of Fisheries and Aquatic Sciences* 71:1072–1086.
- Stewart TJ, Sprules WG. 2011. Carbon-based balanced trophic structure and flows in the offshore Lake Ontario food web before (1987–1991) and after (2001–2005) invasion-induced ecosystem change. *Ecological Modelling*. 222, 692–708.
- Zhang H, Rutherford ES, Mason DM, Breck JT, Wittmann ME, Cooke RM, Lodge DM, Rothlisberger JD, Zhu X, Johnson TB. 2016. Forecasting the Impacts of Silver and Bighead Carp on the Lake Erie Food Web. *Transactions of the American Fisheries Society*. 145, 136–162.

Appendix F: Participants' key messages to fisheries managers

Participants were asked near the end of the workshop to submit a few key messages to convey to fisheries managers regarding the influence of lower trophic levels of fish and fisheries. Their responses were edited and categorized.

It's simple, really...

- P is responsible for the level of fish production
- Nutrient loading to the lake sets the potential for fish biomass, community composition and harvest.
- No plankton, no fish
- Biomass / production is reduced overall. (Smaller buffer/window)
- Greater proportion of production is subsurface, cooler water.
- At really low levels, production is driven by nutrient input sources.
- LTL are important because they form the foundation of the architecture of food web.
- What fishers catch and how much fishers can catch depend on LTL.

...but complex at the same time

- There is a general connection between P loading and fishery production, but there are a lot of factors and stressors that alter this simple relationship.
- Invasive species (eg. quagga mussels) may alter the relationship between nutrient loading and fish production, community composition and harvest. For example, invasive mussels have increased water clarity, macrophyte growth and production rate and biomass of some benthic taxa, while reducing chlorophyll and biomass of small zooplankton that are first foods for larval fish (cyclopoid copepods, rotifers).
- Other stressors may interact with nutrient fish relationships in complex ways. For example, warming temperatures and episodic rainstorms may interact with invasive mussels to increase frequency and magnitude of blue green algal blooms in Lake Erie.
- LTL play an important role at fish nursery habitat. Too low zooplankton will decrease larval fish growth and abundance, while too high productivity will cause turbidity that interferes larval fish consumption.
- More nutrients produce more fish, but they might not be the fish you want, and you might not be able to drink the water.
- If nutrients change, the lake will change. It will be a different type of ecosystem that you may have to manage differently. Get ready to adapt.
- Effects of changes in LTL on fisheries depends on the food web architecture.

Context matters

- Impact of various stressors such as invasive species and climate that are context dependent that is dependent on the lake and fish community concerned.
- The relative impacts of invasive species vary across productivity gradients – higher in more oligotrophic systems, lower in more eutrophic systems.
- Mesotrophic ecosystems have highest trophic transfer efficiency (TTE), while TTE decrease as ecosystems become either more oligotrophic or more eutrophic.
- Native fishery fish species prefer oligotrophic conditions than eutrophic conditions

Managers have limited ability to control, or even predict, effects of LTLs

- Fisheries management is not able to increase maximum sustainable yield above the given productivity
- There is much we don't know about how the LTL functions and how it connects to upper trophic levels to make meaningful prediction in many situations.

Assessment and monitoring are important

- Sampling and monitoring the lower trophic levels requires effort and investment to do properly. This is partly driven by the higher temporal resolution needed from the sampling.
- While an understanding of LTL is not needed when things are going well, when the system changes or the fishery goes poorly, understanding the LTL can be used to understand the changes and how management may need to adapt.
- If tracked properly, due to faster response rates, LTL can provide early indications of change.

Appendix G: Scientific names of fish species referred to in report

alewife: *Alosa pseudoharengus*

bloater: *Coregonus hoyi*

brown trout: *Salmo trutta*

chinook salmon: *Oncorhynchus tshawytscha*

dreissenids: *Dreissena polymorph* and *Dreissena bugensis*

lake trout: *Salvelinus namaycush*

whitefish, lake whitefish: *Coregonus clupeaformis* or *Coregonus lavaretus* (Lake Constance)

stickleback, ninespine stickleback: *Pungitius pungitius*

smelt, rainbow smelt: *Osmerus mordax*

rainbow trout (steelhead): *Oncorhynchus mykiss*

goby, round goby: *Neogobius malanostomus*

sea lamprey: *Petromyzon marinus*

perch, yellow perch: *Perca flavescens* or *Perca fluviatilis* (Lake Constance)