**Ph.D. preliminary exam questions for Martin Simonson (submitted by Timothy Stewart)**

1. **As you know, common carp have strong physical and biological impacts in North American wetlands and lakes. Using background knowledge of ecology, and perhaps your own research observations, predict significant ecosystem changes that are likely to occur after a carp population becomes established in a typical Midwestern USA shallow lake, and describe carp-induced mechanisms (or causes) for these changes. Address physical, chemical, and biological changes that are likely to occur in both benthic and pelagic habitats, and in both littoral and limnetic environments. If you expect that the nature and magnitude of carp effects would be dependent on population- or ecosystem-level factors (e.g., carp population density or biomass, initial lake trophic state, presence or absence of other species), describe how and why such variation in carp effects should occur.**

The establishment of non-native species result from introductions into novel habitats, and a species is considered invasive when the stages of introduction rapidly progress from initial detection to abundances and densities that are a nuisance. Common carp exhibit many of the population characteristics ubiquitous to a wide range of invasive taxa groups and carp have been described as ecosystem engineers who can alter the physical, chemical, and biological structure and function of aquatic ecosystems. Thus, the extent of impacts that carp have on shallow lakes of the Midwestern United States is an interactive effect of carp’s disturbance to natural biogeochemical cycling within a lake.

The physical effects carp can have on a shallow lake or wetland include significant impacts to the benthic zone of the lakes, in both littoral and limnetic environments. Carp feeding behavior resuspends sediments and alters the redox potential of a thin layer of microbes and algae that are critical to nutrient cycling within lakes. The behavior also destabilizes the substrate, which is detrimental to rooted macrophytes in the littoral zone, and because plants attenuate waves, the relative intensity of wave energy in the littoral zone can increase, potentially leading to more shoreline erosion.

Shallow lakes, and especially wetlands, are important ecosystems that often provide critical natural services through inherent nutrient cycle regimes. Carp reduce the capacity for these ecosystems to serve as nutrient sinks; when primary production is nutrient-limited, the release of phosphorous bound in sediments can spur an increase of primary production. It is suggested that carp can initiate positive feedback loops and, as a result, increase the stocks of nutrients in a system, when flows in and out of the ecosystem may remain the same. Eutrophication of this sort leads to shifts in flora and fauna of the lake, often stressful conditions (e.g., hypoxia) develop where carp can have a competitive advantage against other species. When nutrient pools increase in the pelagic zone of lakes, algal biomass responds positively, and rates of photosynthesis during the day and respiration at night exacerbate the diel variation in dissolved oxygen; algae blooms and die-offs can severely affect a lake’s structure and function.

True ecosystem engineers alter their habitats such that the distribution of biomass among plants, herbivores, and carnivores shift dramatically toward a new stable state or successional trajectory. Carp feeding is selective for benthic macroinvertebrates throughout the entire system, which releases many microbes and other species from competitive exclusion. However, the extent and duration of hypoxic events can be fatal to sessile benthic macroinvertebrates. The uprooting of plants from carp feeding and spawning behavior is a clear example of how carp actively change the littoral zone structure in shallow lakes. Algae blooms in the pelagic zone are subject to winds and currents, and algae can become very concentrated in some areas of the lake; algae concentrated at the surface out-competes other plants for light. Similarly, blooms that are dispersed throughout more of the water column can reduce the effectiveness of sight-feeding predators. Finally, the structure and function of a wetland or shallow lake can be affected to the point where migratory waterfowl and other terrestrial fauna suffer (e.g., bald eagles are active predators of adult carp, in clear water).

The severity and extent of all carp effects listed above are affected by the population dynamics of carp, which have many of the life history traits of successful invasive species. Namely, carp have high dispersal rates, juvenile carp experience rapid growth, they are omnivorous and tolerant of a wide range of conditions, they do well in disturbed environments, and adults have high survival and high fecundity. This population-driven feedback loop often results in the degraded condition of shallow Midwestern lakes; as carp populations increase, the magnitude of their effect on geochemical pathways affect the biotic community, usually giving carp some competitive advantages over other species.

Initial ecosystem conditions have a role to play, as well. For instance, the connectivity of a lake or wetland to other habitat types within the landscape affects carp dispersal rates and reproduction (e.g., carp have access to spawning habitat as well as nursery habitat for juveniles). Under the alternative stable state hypothesis for shallow eutrophic lakes, the initial ecosystem state (i.e., clear or turbid) has some resistance to disturbance. Using the cup and ball metaphor, shallow Midwestern lakes that existed in a clear state before carp had shallow and narrow sides; a small disturbance could push these lakes into a much more stable turbid state where feedback loops make the turbid stable state more resistant to disturbances. Lake morphology may be one of the most significant factors contributing to the shift in alternative stable states because depth, size, and amount of littoral zone habitat can affect primary production and nutrient cycling. Thus, the effects of common carp are somewhat mitigated in larger and deeper systems.

The interaction of carp with their environment leads to many direct and indirect changes to the structure and function of shallow lakes and wetlands. Alterations to physical and geochemical processes in aquatic habitats spur significant changes to the biotic community and successional trajectory of these ecosystems, often to the detriment of human use and values. Management of carp is no small undertaking!

1. **According to information presented in your dissertation proposal, bigmouth buffalo can also have strong effects in shallow lakes, and that these effects may be influenced by multiple environmental factors (again, including population- and ecosystem-level factors; see previous question for examples). Using your research observations and knowledge of ecology, describe significant impacts that bigmouth buffalo are likely to have on biophysical components of shallow lakes, and mechanisms for these effects, across a range of buffalo population densities (or biomass), and in lakes of different trophic status.**

Bigmouth buffalo are a fascinating species. The adaptations life history traits that have evolved in bigmouth buffalo as they have spread from Hudson Bay to Louisiana are no small feat. High fecundity and ability to spawn multiple times a season make them efficient dispersers in riverine systems, and potentially centenarian lifespans make their reproductive capabilities in shallow lakes adapted for frequent disturbances and population bottlenecks that are common in shallow lakes. As filter-feeding planktivores, buffalo are secondary consumers. Buffalo are adapted to consume a resource that is rarely limiting in shallow lakes and can exert minimal effort in searching for food; essentially, they are grazers of grazers.

In general, the mechanisms by which buffalo impact the biophysical components of shallow lakes are a result of their feeding behaviors. To a lesser extent, bioturbation from spawning activity may influence littoral zone structure in lakes, but the primary source of biophysical change by bigmouth buffalo in shallow lake ecosystems is zooplanktivory. Nearly all juvenile fish in shallow lakes depend on zooplankton for development in the post-larval stage, and competition from buffalo for a shared resource may directly affect the growth and development of other fish taxa in the lake.

A trophic cascade can be induced when buffalo populations grow, and subsequent increases to predation suppress the zooplankton community (especially large-bodied cladocerans), and when algae are released from grazing pressure, primary production increases. Under the Green World Hypothesis, the predation of algae by zooplankton is, in part, determining the abundance and diversity of algae in shallow lakes. When released from grazing pressure, interspecific competition leads to the dominance of the best competitor in that niche. These shifts in primary production often incur changes to nutrient and chemical cycles in the epilimnion and hypolimnion of shallow lakes.

Although the effect per individual is small in both oligotrophic and eutrophic lakes, the bioturbation from spawning is proportional to the amount of buffalo in the lake, combined with substrate type (e.g., silt remains suspended in the water longer than sand) and amount of littoral area. The disturbances from this behavior can include uprooting of macrophytes, destruction of other fish species’ spawning beds or refuge habitat, and burying/exposure of benthic macroinvertebrates. Again, although the effect per individual is small, the cumulative effect of high buffalo densities can be a significant periodic disturbance to the littoral zone of shallow lakes.

Oligotrophic lakes are usually characterized by relatively high zooplankton biomass and few planktivores; therefore, if an external disturbance (e.g., nutrient inputs from the watershed, invasive species) leads to a shift in the distribution of biomass among trophic levels, buffalo may be able to acquire zooplankton resources faster. This competitive advantage leads to increased condition and reproductive success, which in turn leads to population growth, and the trophic cascade begins, and the oligotrophic lake may be shifted out of its stable state. Another factor that may spur this trophic cascade is the nutrient-limited condition of oligotrophic lakes. That is, primary production may remain the same, but when predation by primary consumers is suppressed, overall plant biomass increases.

Eutrophic lakes, on the other hand, may exist in turbid states independently of buffalo biomass densities. Bottom-up dynamics from primary production may be a more reasonable explanation for the algal-dominated state of eutrophic lakes. Epilimnetic photosynthesis in shallow eutrophic lakes may have developed independently of buffalo biomass, and zooplankton selection for eukaryotes and nitrogen limitation may lead to the success of nitrogen-fixing cyanobacteria. Juvenile and young-of-year buffalo may have a competitive advantage in eutrophic lakes because sight-feeding predators have a reduced capture probability of these fish. Finally, the turbidity of eutrophic lakes gives adult bigmouth buffalo a competitive advantage due to filter-feeding behavior because buffalo expend less energy to capture prey than piscivores.

Although bigmouth buffalo exhibit traits that can induce trophic cascades, alternative stable state theory suggests that buffalo alone will not initiate a shift in the trophic state, rather, an external disturbance is most likely to cause the change in ecosystem structure and function. Throughout their evolution, bigmouth buffalo appear to have adapted well to a range of environments and disturbances, including lentic and lotic, oligotrophic and eutrophic, large and small. The proliferation of this species across such a wide geographic range is a testament to buffalo perseverance and adaptability. I think buffalo are a very underappreciated species.

1. **Is there a practical way, in your opinion, to manage populations of invasive common carp in shallow lakes on a long-term basis? Is it possible to reduce and subsequently maintain carp population density at a level whereby adverse impacts of this species are significantly reduced, and if so, what is the most effective method for achieving this goal? Is this plan likely to be cost-effective? In other words, what economic benefits and costs are likely to be associated with or result from this plan?**

Common carp management in the Midwest is undoubtedly complicated. In order to be successful, fisheries managers will have to take a multi-faceted approach. Particularly under the alternative stable state hypothesis, a “severe disturbance” initiated by fisheries managers may be required to push shallow lakes into a clear-water state. In other words, a significant initial input of time, energy, and capital are necessary to complete the transition from turbid- to clear-water state, but once in the clear-water state, less effort would be required to maintain carp populations. One of the most significant factors that will determine the success of carp management is public engagement and support from stakeholders across the Midwest.

Supplementing predator populations through fish stocking implements a biocontrol approach that is an essential component of carp management. In systems where piscivore abundance is low, the suppression of juvenile carp may not be effective. When characteristically top predators like walleye and muskellunge have a relatively low impact on carp recruitment, stocking will be necessary. Also, bluegill are adept predators of carp eggs, which adhere to submerged and emergent vegetation in the littoral zone of lakes. In Lost Island Lake (Palo Alto County, Iowa), bluegill stocking was effective at increasing biocontrol of carp reproduction and meeting the public demand for an improved bluegill fishery.

An emerging form of possible biocontrol by engaging the public is the growing popularity of bowfishing. Bowfishing is more effective in clearer water, and thus, once a lake renovation is successful, a marketing campaign and other outreach that emphasizes consumptive use of carp but not native species could not only supplement population control of carp but increase angler recruitment and involvement in conservation. Mechanical removal, or harvest, of common carp remains a popular biocontrol method across the Midwest and is certainly more effective at removing carp than bowfishing. However, current harvest regimes have had limited success in controlling carp populations. Prescribing removals by setting capture quotas or by increasing catchability using the Judas fish technique to locate aggregated carp within a lake are likely to act as severe disturbances, and subsequent carp removals under the current commercial angling setup may be effective at sustained carp management over the long-term.

Restrictions to carp spawning success may be effective tools for long-term population management as well. Because carp seek shallow, vegetated wetland zones of lakes to spawn, careful placement of fish barriers may inhibit carp reproduction and migration. However, this technique may not always be feasible given lake morphology and life history of other fish taxa in the lake. Chemical controls of carp that either initiates sex reversal or result in “daughterless” carp are other emerging techniques, but the effectiveness of these techniques is still being tested and described. Finally, fry electrofishing has been suggested as a potential tool for carp management, using boat electrofishing immediately after carp spawning can “fry” the fry, severely reducing carp recruitment.

Clearly, the consequences of each tool to control carp populations incur varying levels of economic and ecological costs and benefits. Stocking, for instance, could be an expense that is incurred indefinitely, whereas fish barriers have a high up-front cost but low maintenance costs over the long-term. Fry electrofishing, coupled with regular population monitoring, could be cost-effective but the risk to native fish fauna should be weighed against the benefits of killing off juvenile carp. Chemical manipulation and release of fatal carp diseases (e.g., carp herpesvirus) can be prohibitive in terms of cost and public acceptance. Public input and cooperation are integral to a successful carp management plan.

I think that habitat-based management is one of the most robust tools for ecosystem restoration, especially in the context of alternative stable states in eutrophic lakes. Therefore, an ideal population management regime would necessarily incur high up-front costs to quantify carp abundance and prescribe harvest quotas, install fish barriers, and supplement predator populations. If the harvest quotas are implemented as an incentive-based contract program, the years where bonuses are provided to fish harvesters might be a net loss of revenue, but subsequent harvest contracts would hopefully accumulate, with positive net income over the long-term. Income from commercial fishing can be used to offset the costs of other restoration projects. I think that the human dimensions of any carp management plan are critical; commitment from the public can be strengthened through communication and outreach of lake restoration progress. Developing a new recreational fishery for carp, either through bowfishing, fly fishing, or other angling, has the potential for increased angler recruitment and retention, which is a primary objective of many state natural resource agencies.

Assuming the goal of reaching a clear-water state is achieved, public media campaigns to emphasize the message that carp are “bad” and native rough fish are “good” can help maintain the stable state of a lake by increased fishing pressure and per-person harvest. The popularity of sustainable food sourcing can be leveraged to encourage people to eat carp (maybe even make their own pet food or garden fertilizer). Up to this point, the discussion has revolved around general carp management techniques as applied to a single system or group of systems. Spreading out restoration projects across large geographic areas can be problematic, “random acts of conservation” are generally less effective than plans that focus on restoring ecosystems through an organized pattern across the landscape. Therefore, a genuinely effective carp management regime would include the application of this process, under adaptive management principles, in a systematic way that results in cumulative benefits of restoration that transcend a single lake or watershed.

1. **Name an active scientist in your field of study whose work has influenced your research in a substantial way. Describe how this person’s work has impacted research questions you have addressed, hypotheses of research outcomes, and methodologies employed.**

Kristin K. Arend, Ph. D. is a researcher that I met while working on my MS degree at The University of Toledo. She became a bit of a role model as I began to interact with her and her work at the Old Woman Creek National Estuarine Research Reserve (OWC for short). As director of research for the reserve, Kristin is jointly employed by Ohio DNR and NOAA. She designs, implements, and communicates research for OWC itself and in partnership with state, federal, and non-government agencies. As the only freshwater NOAA National Estuarine Research Reserve, OWC provides a unique study system for wetland and estuarine dynamics in the Great Lakes.

Kristin achieves local impact with her research by implementing projects that directly improve natural resource management along much of Ohio’s Lake Erie coastline. Application of theoretical ecology to a small estuary within a small watershed (in Lake Erie terms) has led to developments in restoration and conservation of coastal ecosystems. Kristin organizes public outreach campaigns, publishes technical bulletins, and creates partnerships with municipalities throughout the Great Lakes to help restore coastal ecosystems. Personally, Kristin has an eco-centric moral alignment and is highly motivated to be a responsible steward of the earth through individual actions and, broadly, through her research.

Kristin served on my MS graduate committee and therefore had a significant impact on my research questions and hypotheses regarding the nearshore fish community in Lake Erie. Beyond that, her approach to restoration and stewardship of natural resources attracted me to my current research project on carp and buffalo. Some of her community-based studies influenced the structure of my dissertation chapter, describing the effectiveness of carp and buffalo removal as a lake restoration tool. My career goal is to work in a capacity similar to Kristin: using localized research to improve natural resource conservation through outreach and cooperative partnerships, effectively “moving the needle” in the conservation of aquatic ecosystems.