Dr. Weber

Simonson Preliminary Exam Questions

March 24, 2020

These questions are closed book and you have 10 hours to complete them. You can provide as long of a response as you like, but I suspect you will be able to adequately address each of these questions with a ~3 page response per question.

**General ecology**

1. **Describe the Green World Hypothesis and its application to shallow lakes.**

The Green World Hypothesis (GWH) describes a pattern of trophic cascades that are observed in many physically and geographically disparate ecosystems, including aquatic, terrestrial, and marine habitats. A trophic cascade occurs when the biomass of one trophic level is indirectly affected by another trophic level. The effect must occur through at least one intermediate trophic level for it to qualify as a trophic cascade. The GWH states that the primary production across the world would be decimated or eliminated by herbivores if higher trophic levels did not regulate herbivores through predation. The presence of predators and carnivores in an ecosystem prevent exponential growth in the herbivore populations, which would, according to the GWH, consume vegetation in excess of primary production and lead to less photosynthetic plant biomass over time.

The relationship between primary consumers (herbivores) and higher trophic levels is complicated. The GWH is clear when secondary consumers are the highest trophic level in a system, and the effects of these predators have a direct effect on herbivore abundance and density, but effects like these are not always so direct. There are often more trophic levels above the secondary consumers, and the dynamics of these species may reduce secondary consumer populations, which would then release primary consumers from predation pressure and lead to an increase in herbivory and less plant biomass in an ecosystem. Trophic interactions are hardly linear, and biodiversity in a system leads to niche overlap and resource competition among species, and reduction of one herbivore species may not affect plant biomass if another herbivore can fill that niche.

There are numerous examples of the GWH in closed systems, that is, the specified habitat area is closed off from significant immigration and emigration of all taxa levels. Islands are a particularly useful ecological experiment, and in many cases, direct effects of secondary consumers on herbivores are observed. Isle Royale, in Lake Superior, USA, is an example of an ecosystem in a delicate balance, with low resilience and resistance to disturbance. An introduction of the canine parvovirus led to severe declines in the wolf population on the island, and moose populations subsequently increased. During the time that plant resources were not limiting to moose, moose fecundity and condition continued to increase, which left fewer weak/young/old moose available for wolves, whose abundance and condition continued to decrease. When the island became over-browsed by moose, the wolf population was too small and too inbred to rebound enough to control moose, and Isle Royale continued to be over-browsed by an emaciated moose population at their carrying capacity. Due to climate change, the probability of new wolf immigration over winter ice from mainland habitat was unlikely, and agency staff recently re-introduced about 20 wolves to Isle Royale. Under the GWH, the primary production of the island should recover as the weakest and oldest moose are consumed by wolves. Isle Royale is undoubtedly a natural experiment with high potential for testing the GWH.

A common theme that supports the GWH is the success and dominance of many invasive species across the globe. Both plants and primary consumers have many of the population attributes that make them successful invaders. They are usually r-selected species with high fecundity and rapid generation times, adapted to disturbed environments, and tolerant of a wide range of environmental conditions. Introduced species often have not co-evolved with taxa in the habitats where they establish; thus, they commonly do not have a predator for natural biocontrol. In the case of photosynthetic plants, the lack of herbivores leads to higher primary production, as seen in the establishment of *Phragmites spp.* across coastal habitats, an example that if left unchecked or unregulated herbivory could severely reduce plant populations. The absence of an effective predator for herbivores leads to a decline in primary production, as observed when invasive insects wipe out plant communities; the lack of a higher trophic level to consume the insects supports the GWH. Lakes, especially shallow ones, are highly susceptible to invasive species and shifts in plant and herbivore communities.

Lakes can be generally classified as oligotrophic (nutrient-poor, low production), mesotrophic (moderate nutrients and production), or eutrophic (high nutrients and primary production). Shallow lakes are usually eutrophic lakes due to higher summer temperatures, increased substrate area that receives light exposure, and a variety of landscape and watershed effects. If left undisturbed, eutrophic shallow lakes may enter one of two alternative equilibrium states: the clear-water state is characterized by high abundance of aquatic macrophytes, high zooplankton diversity and density, and higher predator abundance when compared to the turbid-water state, which has high algal biomass and lower zooplankton and predator densities. The alternative stable states hypothesis fits with the GWH such that regulation of secondary consumers (zooplankton) releases algae from predation and leads to higher primary production. If left unregulated, zooplankton have fast generation times and populations can grow exponentially if prey (algae) are not limiting. Again, it is the abundance of secondary consumers, and indirectly abundance of higher predators, that determines primary production in these lakes. However, algae have a faster generation time than zooplankton and grazing zooplankton may become satiated, reducing consumption rates of algae.

One might argue that this top-down perspective of the GWH toward aquatic ecosystem structure and function does not apply to nutrient-rich eutrophic lakes. Bottom-up regulation, where plant nutrients limit primary production, is certainly an attractive alternative hypothesis. However, a phenomenon has been documented in how plants (mainly algae) respond to increased nutrients involves selecting either nitrogen (N) or phosphorous (P) as a limiting ingredient in an experimental enclosure. Given enough time, the system will reach equilibrium with the taxa that has the lowest need for the limiting resource dominating algal biomass in a system. When grazers (zooplankton) are added, not only is the diversity of algae maintained, but an interesting effect occurs when the limiting nutrient is increased. The overall algae density does not increase over the long term because herbivore density responds positively to their corresponding increase of food resources, and algae are maintained at the same density as before. Thus, the pule of nutrients has little permanent effect on primary production because it is the primary consumers that regulate photosynthetic biomass, and the GWH is supported.

Disturbances to shallow lakes, such as nutrient addition and introduction of invasive species, are significant anthropogenic influences on the trophic structure in eutrophic systems. Under the GWH, removal of large predators in these lakes (such as sportfish) can lead to an increase of planktivores, which triggers a trophic cascade through decreasing zooplankton and increasing algae biomass. The nutrient addition experiment shows that hyper-eutrophication can lead to an increase in grazing zooplankton. The many trophic connections in aquatic food webs complicate the bottom-up hypothesis beyond primary consumers. Further, seasonal shifts in environmental conditions, algal and crustacean species diversity and abundance, and lake turnover result in periodic disturbances to these lakes that prevent shallow lakes from reaching a full equilibrium.

The Green World Hypothesis is supported by numerous natural and experimental examples; however, there are almost always exceptions to the rule. Shallow lakes are highly unique and variable, disturbances are common, and indirect non-consumptive effects between species complicate matters significantly. Still, due to the presence of this trend in a plethora of environments, the GWH is a robust framework to form experimental and observational hypotheses.

**Fisheries biology**

1. **First, do fish feel pain? It is a hotly debated topic within the profession that has major implications for how we conduct business and how our profession and the angling community may change in the future. Provide evidence for and against this argument. Finally, what do you believe and why?**

**Second, do fish sleep?**

The concept of fish perception and cognition is quite intriguing and controversial. The extension of human ethics and projection of moral values onto animals guides treatment and restrictions on the use, consumption, and management of many species. Further, the exact moral value extended to any given species is a function of culture and times. Environmentalism and expansion of moral values into biota tends to increase with affluence, while organisms farmed for food in some places are regarded as pets elsewhere. Where exactly to draw the line between which organisms do or do not receive full moral standing (harming them is “wrong”) is highly complex and variable depending on who you ask.

Many vertebrates, especially terrestrial ones, receive full moral standing. Even livestock that is raised only for slaughter are afforded some comforts and should not be exposed to human harm or abuse. Usually, this extends from similarities between an animal’s appearance and their response to what humans would classify painful stimuli. A dog whimpering with a broken leg is clearly in pain, and their facial expressions mimic ours. However, the farther away organisms are from human appearance and response to stimuli, the less moral standing they are given. Invertebrates are hardly given moral standing unless they perform some critical ecosystem service. The difference may lie in the nervous system of vertebrates, which serves as a conduit for electrochemical signaling within an organism. Even when it is acknowledged that organisms feel pain, that cost is often weighed against human benefit and organisms that do feel pain are still subject to harm by humans (e.g., laboratory mice and rats, livestock). Fish have a somewhat developed nervous system and brain, with developed societal roles, learning behavior, and decision-making skills. Why not pain?

It is easy for society to extend moral standing and quantify pain in organisms with more developed nervous systems than “less developed” or “less evolved” species. Fish with a developed brain and nervous systems respond to stimuli (e.g., visual cues and predation, taxis based on temperature and oxygen thresholds), however many invertebrate taxa, even plants, protists, and fungi, experience some form of taxis in relation to stimuli. Without being able to quantify a qualitative and indiscrete response such as pain in fish, it is remarkably difficult to use pain as a basis for which to give fish moral standing or not. Blood and tissue chemicals, respiration rates, physical and even behavioral analysis can all be used to determine if stress is impacting or has impacted a fish, but these methods fall short of quantifying pain levels in fish.

However, I believe that fish experience pain. Consider an anadromous fish species that is biologically compelled to swim far inland from a marine environment and undergoes an incredible amount of stress. The evolution of this behavior as a form of parental care that results in increased recruitment aside, this migration has a significant impact on the fish. They must cross oxygen and salinity gradients, requiring a shift in osmotic regulation. They must swim against the current for long distances, literally swimming uphill and jumping over barriers. Finally, finding spawning habitat, exhausted fish die from the cumulative stress of the migration. In each step, there are analogs to what mammals or humans would also experience: muscle stress and buildup of lactic acid from exertion, organ pain from altered salinity/chemical/nutritional conditions, although I concede that the vigorous reproduction behavior culminating in death is an exception (although that would likely be painful, in my opinion).

Perhaps also consider electrofishing as a fish sampling technique. The pulsed electrical DC is critical to stunning, and not killing, the fish. Early attempts with constant and direct current resulted in high fish mortality. Fishes have a lateral line system of highly sensitive nerves just below the skin, leading to the brain of fish. These nerves detect minute movements and vibrations in the water, which resonate farther in water than in air. Because the electricity dissipates in the water, at first fish experience low levels of shocking and have positive taxis toward the source of electricity, but soon are wholly immobilized by strong electrical current. The conduit of water leading to the sensitive nerves of the lateral line is a likely source of pain due to the sensitive nature of the organ. I believe this is quite analogous to, say, putting a nearly dead 9-volt battery on one’s tongue and feeling a tickling sensation compared with being shot by a Taser and subject to complete immobilization via electricity. I hear the latter is quite painful.

If fish did not experience pain, stressful experiences would cause them to respond primarily by taxis to areas of less stress. However, there are still electrochemical cues that alter fish behavior, such as muscle fatigue, causing a fish to slow movement and the gulping of air when a fish is suffocating out of water. Finally, fish exhibit learning behavior and decision making (to some extent), and the cues for that behavior can come from pain stimuli as well as physiochemical cues and interactions with other organisms. I am pretty solidly in the fish feel pain camp.

But do fish sleep? Poikilotherms naturally metabolize at a rate subject to environmental temperatures. Fish, as a rule, cannot be in perpetual motion, with a possible exception to the rule being large tuna species, but I believe they have adaptations to raise their body temperatures slightly. Due to the diel variation in water temperatures during summer, periods of warmth, light, and high primary productivity would be conducive for feeding and metabolism, while cold and dark periods when respiration exceeds production tend to favor lower metabolism. It would be selectively advantageous, in this case, for a species to lower their metabolism below the maximum rate allowed by temperature and minimize the net loss of energy during periods when fish cannot consume prey. During winter seasons, when temperatures are at their lowest, and many food resources become limiting, a species’ fitness would be higher if they could reduce metabolism below the maximum allowed by temperature, much like bears and amphibians that undergo torpor.

Finally, observing fish in the aquarium in 215 Science II has led me to believe that fish sleep. Many of the benthic species in the tank will rest on a substrate or in cubby holes, other fish float with nearly imperceptible fin movements that seem to be just as unconscious as taking dissolved oxygen from the water through gills. One fish, in particular, begins floating sideways when it sleeps, and when I enter the darkened room early in the morning and turns on the lights, it takes that fish 15-30 seconds to “wake up” and recognize that a change occurred in its environment. Assuming sleep is defined as a period of reduced metabolism and brain energy, while still subconsciously maintaining minimum respiration and homeostasis, then fish sleep.

**Fisheries management**

1. **Describe what is meant by fisheries induced evolution, the processes involved, how it may affect populations, and what can be done to mitigate it. How may fisheries induced evolution affect the populations you are working on in NW Iowa, if at all. How would you go about testing for fisheries induced evolution for your study species?**

Fisheries Induced Evolution (FIE) is the process by which artificial selection through the harvest of fish stocks drives an evolutionary shift in a species. The phenotypic plasticity of fish species, along with the type and magnitude of exploitation, may create genetic bottlenecks that spur microevolution of a species (e.g., individual traits gradually drift to a single phenotypic form). Although present in large systems, this is more likely to occur in smaller, isolated systems subject to high fishing exploitation. Therefore, FIE is a result of abiotic factors as well as artificial selection as a result of fishing practices.

Microevolution may occur more frequently in closed systems when immigration and emigration are limited, and there is little to no gene flow among metapopulations. Generally, microevolution occurs faster in r-selected species with shorter generation times; however, it is often the larger k-selected fish species that are sought for commercial and recreational harvest. This presents the first genetic bottleneck for k-selected species: older, larger individuals contribute more to recruitment, but as those size and age classes are exploited, the individuals with shorter time to reproduction are selected for as their genes are more likely to persist through generations. If the exploitation of k-selected fish species includes individuals that are not sexually mature, then a fishery collapse is likely to occur.

The total amount of fishery exploitation is a function of many factors, many of which are independent of the fishery itself. For instance, the frequency and magnitude of commercial harvest events may be somewhat influenced by the proximity of a system to a fish market or an angler’s warehouse or a decent hotel. Catchability is continually improving through technological developments. Recreational harvest may be influenced by a chamber of commerce marketing campaign, human population density, access, and so on. Although very few fish are truly k-selected species in the sense of internal embryonic development and parental care, there is a trend that larger and older individuals have more significant contributions to the reproductive success of a species. Thus, the frequency, magnitude, bycatch, species selection, and catchability of a species all factor into reproductive genetic bottlenecks that may drive FIE.

The implications of FIE can cause shifts in species assembly, primarily if niche overlap and interspecific competition for resources exist. A negative feedback loop could develop when the exploited population becomes a less efficient competitor to the growing unexploited population. The hypothesis by Pauly that humans are “fishing down the food web” is an exciting take on FIE because when commercial fisheries induce a fishery collapse, the same commercial fishing operations often begin to exploit the most abundant species of the next lowest trophic level, and so on. For inland waters where metapopulations are variably isolated and connected, the exploitation of fishes can remove the capacity of source animal populations to migrate and supplement other metapopulations. Alternatively, they could increase the draw of sink metapopulations where species migrate into but are harvested. In terms of island biogeography theory, this could lead to higher rates of local metapopulation extinction and, therefore, another genetic bottleneck to fish populations.

As many fishery resource managers have at least acknowledged fishery collapses, if not FIE, these bottlenecks are sometimes mitigated by maximum allowable catches and by augmenting catchability (e.g., restricting fishing to certain seasons, restricting gear types). Setting a minimum allowable size to catch may help prevent a fishery collapse, but microevolution could still occur as smaller, slower-growing individuals with younger age at maturity have a selection advantage. In recreational fisheries and endangered species situations, fish may be propagated and stocked to supplement recruitment. Although this may be a source of new genetics for a population, most fish reared at hatcheries have relatively low genetic diversity from limited broodstocks. Further, the mortality of stocked fish is usually very high. Therefore, stocking fish may be a temporary band-aid that slows, but does not prevent, fishery collapses. Hybridization of species is another possible compensation to the genetic bottlenecks, but if the hybrids are highly similar to the exploited species, they may under the same selection pressure and will not have higher fitness relative to the parental lineages. Blue pike (*Sander spp.*) were present in eastern Lake Erie at the turn of the 20th century, and it was believed that they could interbreed with other lake walleye, but through geographical isolation, they rarely interbred with the tributary spawning lake walleye. Overfishing induced a fishery collapse, and the overall genetic diversity of genus *Sander* was reduced.

In the shallow, natural lakes of NW Iowa, common carp (*Cyprinus carpio*) and bigmouth buffalo (*Ictiobus cyprinellus*) have proliferated in nearly all systems, and it can therefore be inferred that in the absence of commercial harvest, common carp and bigmouth buffalo have a competitive advantage over other species which have overlapping niches. Mechanical removal of these two species, along with freshwater drum (*Aplodinotus grunniens*) has been occurring to some extent in NW Iowa for nearly a century, and yet the fisheries do not completely collapse. However, genetic bottlenecks could still occur. The higher amount of phenotypic variation that I’ve observed in some of my study systems compared to others leads me to believe that in some systems, genetic bottlenecks from commercial fishing of carp and buffalo have caused gene drift.

In Storm Lake, for example, there is a high number of “mirror carp” and “leather carp,” individuals that have enlarged scales in reduced number, or few to no scales at all. Although this mutation may or may not contribute to overall fitness, the random removal of commercial harvest put this carp population through a genetic bottleneck, and perhaps at some point (or at repeated points), a higher number of mirror carp survived commercial harvest. Since fish have been excluded from most of Little Storm Lake, an ideal spawning location for common carp, another natural bottleneck may have conferred a reproductive advantage for mirror and leather carp, leading to their higher abundance.

A test of this hypothesis would be difficult without historical data, and like many bottlenecks, it may be a pure, random chance that mirror and leather carp persisted in passing on their genes. I am not too familiar with fish genetics, but I would expect that the results among lakes might yield impressive results. In essence, frequency and magnitude of carp and buffalo harvest in these lakes would be the primary factor to test against genetic diversity, and covariates could include connectivity of systems and watershed size, which might be positively correlated with genetic diversity; smaller systems might have lower genetic diversity compared to larger lakes.

Removal of these carp and buffalo is highly size-selective for larger individuals, leaving small individuals in the lake. A possible mechanism behind the lack of fishery collapses for carp and buffalo could be the variable recruitment success of fishes each year, and the potentially exponential success per individual when spawning conditions are perfect. These strong year classes could allow the fish to perpetuate, as relatively few large individuals need to remain in the population for the population to rebound when conditions are met.

Under this hypothesis, a possible test would be to measure gonadal:somatic indices (GSI) of carp and buffalo in varying size and age classes. A higher index value indicates highly fecund individuals, and if the oldest fish have higher indices, then that species is likely adapted to many repeated spawning events with low success, but few that are highly successful; overfishing of these individuals could lead to more genetic bottlenecks and reduced genetic diversity. If smaller carp and buffalo had higher GSI values, then perhaps a lower age at maturity and higher abundance of smaller fish (in a harvested system) would be the main factor sustaining the populations and recruitment overfishing is not a factor in the FIE of that system.

Overall, predicting the probability of Fisheries Induced Evolution in NW Iowa would be highly problematic. In addition to market variability, gear and size selectivity, stress and occasional failure of fish containment areas, and highly variable catchability (although with technological advancement it generally increases), natural selection pressure and artificial selection are highly intertwined. Failure to account for the different sources of selection pressure could lead to bias and unreliable data/results. Long-term projects (>10 years), high-frequency sampling(> 1x per year), and broad geographic study areas (across state lines) would probably be most effective at capturing trends in FIE, but logistical constraints would make such a project prohibitive.