A System Dynamics Model of Fish Populations in Western Lake Superior

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Abstract:

Lake Superior's fishery resources have been subject to management control for more than a century. A goal of achieving stability of fish populations has been elusive. Present goals stated by management authorities have been expressed as hopes of achieving "fish- community objectives", some of which may be impossibly exclusive in practice. A system dynamics model of major predator and prey fish populations of Western Lake Superior is discussed and demonstrated. Model simulations of fish population changes are compared to historical estimates. Model-implied results of alternate management policies are explored. Experiments applying past and alternative management policies indicate that a policy of reducing current high rates of predator stockings together with moderately increasing predator harvestings would contribute to long term population stability among both predator and prey fish populations of Lake Superior.

Index Words: *System Dynamics model, Lake Superior, predator prey interactions, lake herring, rainbow smelt, underfishing, fishery management, complex fishery systems.*

Introduction:

Lake Superior is the largest of the freshwater lakes in the Laurentian Great Lakes System. In surface area it ranks first among the freshwater bodies on the planet. Its volume exceeds that of the combined volume of the rest of the five Great Lakes. In volume of freshwater it ranks second only to Lake Baikal in western Siberia. The lake measures 380 some miles east to west and about 180 miles north to south.

In the late 19th and early 20th century human influences began to affect the fish populations comprising Lake Superior's fishery systems. Its fishery resources had been harvested for centuries by native Americans. In the mid-1800s immigrant northern European fishermen joined in the production efforts. Catch methods included the use of longlines, gill nets, seines, empoundment gear, and more recently submerged trap nets and trawling. By the mid 1940's production of all species combined reached a peak of about 20 million pounds annually, most caught on the American side. The bulk of production concerned just three species: lake trout (*Salvelinus naymaycush*), whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus artedi*). [Production totals for the WWII years may be understated. Because of OPA price control policies, substantial production may have been unreported.] Most commercial fishing operations involved small boats 15 to 40 feet in length carrying one or two fishermen aboard. In 1943 there were several hundred commercial fishing licenses issued by the state of Minnesota to fishermen along the 150 mile stretch of Minnesota's north shore.

Following World War II production levels declined, initially because of reduced fishing effort, later from falling prices, and older fishermen leaving the industry. Bronte et al., 1990 discusses changes in the fishery during these years.) A most unfortunate event was the appearance in Lake Superior in the late1940's of an exotic predator, the sea lamprey (*petromyzon marinus*), which had already caused precipitous declines in lake trout production on the lower Great Lakes, especially in lakes Michigan and Huron. The sea lamprey was believed to have gained access to the Great Lakes system when the Welland Canal was constructed in 1913 as a large-vessel shipping bypass around Niagara Falls.

The Sea Lamprey Invasion of the Great Lakes

The sea lamprey is an eel-like vertebrate predator, originally an ocean-inhabiting creature, adapted to spawning in freshwater streams. Such freshwater spawning creatures are referred to as anadromous, and like ocean salmon, are sometimes able to adapt to full lifecycle survival in fresh water. During the parasitic phase of its life cycle the lamprey attaches itself to swimming fish with a suction-cup-like mouth lined with tiers of raspy teeth. Through its mouth the lamprey draws blood and fluids from its hosts, while experiencing rapid growth during a one-year parasitic feeding period.

The sea lamprey had advanced through the lower Great Lakes, and eventually made their way into Lake Superior. Their appearance in Lake Superior was first recorded in 1938. By the late 1940's a significant fraction of larger lake trout in the commercial catch were showing signs of scarring from lamprey attacks, and by the mid-1950s few larger fish remained. Virtually all bore multiple lamprey wounds. By the late 1950's production of the larger predator species, including lake trout, siscowets (*Salvelinus namaycush* siscowet), whitefish, and burbot (*Lota lota*), had declined sharply. The rapid disappearance of the predator fish stocks were expected to have important effects upon the stocks of prey fish upon which the predators had fed. In the early 1960s management authorities around the shores of Lake Superior halted sport and commercial fishing for lake trout in most of Lake Superior. Lake trout was at the time of the fishing moratorium the most economically important species to the commercial and recreational fishery.

In 1956 an international joint commission had been created to coordinate efforts in accomplishing several objectives. The devastating effect of lamprey predation on the fish populations of the lower Great Lakes made it clear that Lake Superior might be the last stand for some of the affected species. An international convention established the Great Lakes Fisheries Commission to gather funding and to organize common efforts. Goals of the Commission included control of sea lamprey abundances in all of the Great Lakes, assistance to the commercial and sport fishing industries in the various lakes, and coordination of lake research on affected fish populations.

Recent History of Fish Populations:

Lake Superior was the last lake in the Great Lakes chain to be invaded by the lamprey, and it was the first to be successfully rehabilitated, though not without other problems arising in the meantime. Preceding the appearance of the lamprey was another non-native, the rainbow smelt, a small, anadromous, salmonid which entered Lake Superior, most likely via the St. Mary's River. The smelt had been planted in Lake Michigan by the Michigan Conservation Department, beginning in 1911 and 1913 and thereafter, serving as a forage fish to support earlier Atlantic Salmon stocking programs.

The consequences for the Great Lakes ecosystem of the smelt introductions were unimaginable, and continue to provoke argument almost a century later. Indications of the effects that the rainbow smelt have on food web interactions showed up by 1943, when a massive die-off of smelt in Lake Michigan was followed a few years later by record catches of many other species that had suddenly become scarce. By 1948 the year classes present in the record catches of whitefish, walleye pike and ciscoes consisted of those fish whose young of the year occurred in the year of the smelt die-off. But soon a new exotic preyfish, the alewife would overrun Lake Michigan.

In the mid-1960's the State of Michigan, against the advice of the Great Lakes Fisheries Commission, began programs of massive stockings of several species of Pacific Ocean salmon in Lake Michigan. The idea was to develop what was called a put-grow-take fishery. Pacific salmon would be raised in hatcheries, stocked in the lakes to feed on the lake's prey resources, and then be subject to catch. Economic benefits to Michigan of the recreational fishing activities were the prime motivator, although the bonus of commercial catch for public consumption was offered to help justify the public expense of the stocking programs.

Ecological risks, it was thought, would be minimal. It was felt that the exotic fish stockings could be halted at any time; the exotics would not adapt to natural reproduction in the open lake context, according to planners and advocates. Earlier salmonine species introductions on much smaller scales had met with limited success, unless continually supplemented with further stockings.

The initial results were wildly successful. Feeding on a huge biomass of alewife, which had become well-established in lakes Michigan and Huron, salmon increased to the point where massive spawning runs developed in Lake Michigan streams. These seasonal events were attended by crowds of sport fishermen, some using snag-hooks, spears, dip nets and other gear to gather the dying spawners that choked virtually every major stream flowing into the lakes. The chief architects of the plan, Mssrs. Tanner and Tody went on tour, speaking at sporting and civic clubs around the Midwest for many months.

In what might be viewed as a classic repetition of the "tragedy of the commons" (Hardin, G, 1968), state management authorities in Wisconsin and Minnesota soon emulated the Michigan example. Seeking to stem the loss of sport fishermen to Michigan, state management authorities of the adjacent states began their own stockings of Pacific coho salmon, Pacific chinook salmon, kamloops trout, and other anadromous salmonids. These stockings began in the western Lake Superior region in 1970s and soon had important and largely unplanned effects on forage stocks, which in turn affected native fish recruitments. The widespread stockings of competitive exotic predators were suspected to hinder the restoring of native predator species, like the coaster brook charr, in some of the upper Great Lakes. The history of the salmonine introductions into the Great Lakes has been documented extensively (Crawford, S.S., 2001).

In Lake Superior there had been no significant populations of alewife, such as those present in Lake Michigan; however, the lake had been invaded by another anadromous salmonid, the rainbow smelt (*Osmerus mordax*). These prey fish had been intentionally introduced into Lake Michigan in 1911 and 1913 by Michigan Conservation Department stockings in Crystal Lake as an additional forage fish to accompany salmon introductions. By 1930 the smelt had made their way up the St. Mary's River into Lake Superior. While the lake trout were still abundant as predators to hold their expansion in check, the smelt remained secondary. Decades later, when trout declined from lamprey predation, the smelt began to increase rapidly, finding food in the plankton, larval lake ciscoes and other small fish. This combination of favorable conditions contributed to high recruitment rates into the adult smelt stocks.

Debate continues about the importance of predation and competitive effects of the exotic smelt on the native cisco. (Selgeby, J.H. et al., 1978, Selgeby, J.H. 1982, Jacobson, L.D. et al., 1987, Cox, S.P. and James F. Kitchell, Stockwell, J. in press). The cisco had been the primary forage fish for lake trout in lakes Michigan, Huron and Superior, and had been present in considerable abundance from the earliest recorded times. For more than a century cisco abundance remained high, as evidenced by continual commercial catches. At the western end of Lake Superior commercial fishing operators had fished this species and the lake trout since the 1870's. Catches of ciscoes during the fall run amounted to 2 to 6 million pounds and more for nearly a century until the early 1950s, when catches began to decline. The presence of smelt caught by their teeth in the cisco gill nets prompted warnings from visiting Lake Michigan fishermen about a coming loss of the cisco fishery in Lake Superior. These omens were accompanied by evidence of larval and fingerling ciscoes found in the stomachs of smelt. By the time researchers began to focus attention on smelt, the relative numbers of smelt and ciscoes had shifted substantially.

The smelt's invasion success was accelerated in the late 1950's by the lack of presence of effective predators. Throughout the decade smelt had increased along the south shore of Lake Superior, and reaching the western end they found ideal habitat, feeding on abundant planktonic and piscivorous, mostly coregonid stocks. Though relatively small in size, rarely exceeding a tenth of a kilogram in weight, they proved to be extremely adaptable, as plankton feeders, predatory carnivores, and as cannibalistic feeders. As they had done on the lower lakes, the smelt eventually surpassed the ciscoes in abundance. Smelt quickly became the dominant fish in Lake Superior, growing to an estimated biomass of 100 to 300 million pounds by 1965. Commercial catches of smelt in Western Lake Superior exceeded several million pounds by 1966. Substantial spring catches continued for almost two decades, tonnages varying mainly with weather conditions during the spawning run and with the fishing effort expended by sport and commercial harvesters.

By the mid 1960s spring spawning runs of smelt choked nearly every stream and water outlet into Lake Superior; sport fishers drove in from hundreds of miles away to dip the fish in Lake Superior's tributary streams, and seine them on the beaches. Lakeside residents found their backyard fences and outbuildings being torn apart for beachside firewood. Populations of lakeside towns swelled by the tens of thousands during the annual spring "smelt run". This seasonal party was repeated for almost two decades, and then, as suddenly as they had come, the smelt seemed to disappear.

System Complexity:

The complex picture in Lake Superior began with predator population declines, occasioned by lamprey predation; it continued with lamprey control efforts and increased lake trout stockings in Lake Superior in the late 1960s, augmented by salmon stockings beginning in the mid 1970's. These stocking programs have continued until very recently, when a few have been abandoned for lack of measurable success and on account of high cost. [For example, a recent study by the Minnesota Department of Natural Resources found that for Chinook Salmon (*Oncorhynchus kisutch*), the most prized of the sport fish stocked by the MNDNR, the public cost per stocked fish caught by anglers exceeded $360.] (Schreiner, 2006).

Model Development:

The system dynamics model focuses on adult population numbers for the major predator and prey species, both native and introduced. The adult population is the life-stage that is of ultimate interest to harvesters and managers; it is responsible for reproduction, and much of the predation occurs between adult predators and adult prey. Most of the available data on both predator and prey abundances come from catch numbers as related to catch effort levels. Catches for both predators and prey involve the adult life stages as targets.
Starting with estimated 1940 levels of the modeled predator and prey species, we simulate the effects of reproduction, maturation, and fish stockings. Mortalities from natural causes, predation, and harvesting are included in a system dynamics model covering a period of six decades of Western Lake Superior history.

Mortalities for the earlier life stages are often available as summary value estimates, which are affected by habitat influences as well as predation and cannibalism. The magnitudes and effects of predator-prey interactions on pre-adult life stages have not been established and are only recently discussed in the research literature of Lake Superior. Fisheries managers speak of recruitment to a life-stage or cohort class to express the annual rate of entry into the life stage. Recruitment rates are used to express annual offspring survivals per existing adult. Average recruitment numbers have been used to express these rates of transition into the adult life-stages, after maturation delays.

This approach uses average estimates for early life stage mortalities expressed as a constant, when the reality is certainly that recruitment varies substantially from year to year on account of weather, temperatures and other conditions. A more detailed model than this one, a model based on year classes, not life-stages, might deal with pre-adult predation and cannibalism, for example.

The sensitivity analysis capabilities of Vensim™ can be used to examine the effects of changes in these recruitment estimates. Model simulations can compare and test for rough agreement with historically measured catches per unit effort and estimates of peak abundances. In the case of the smelt population development, recruitment estimates of 1.2 to 1.9 are necessary in order to account for the very rapid growth in numbers experienced historically.

All models involve simplifications, and it is worthwhile to review some of those that have been adopted here. The cannibalistic and predatory activities of the adult smelt upon their own species and upon other species at pre-adult stages are not specifically addressed in the model. These may be quite important, especially in a dynamic context where other processes are ongoing. For instance, it is well established that the smelt are predatory upon just about any fish up to half their length which come within their range. For another, they compete importantly with other prey fish for habitat space and food. As zooplankton feeders they devour many similar items, including the opossum shrimp *Mysis relicta* and *Diporiea* spp. that are favored by the cisco. For phytoplankton feeding the smelt gill rakers are not as efficient as those of the cisco, but they use up a share of the resource and they are predatory upon the young of their cisco competitors. Modeling all of these interactions would be difficult and might impede learning and understanding. Yet their importance may not be obvious. While it is necessary and desirable that simplifications be used in modeling, we must be aware that departures in model simulation behavior from real-world behavior can be expected as a consequence.

Carrying Capacities of Forage Species

Ultimately the lake has an upper limit to the biomasses that it can support, sometimes referred to as carrying capacities. When one component of the food web feeds upon another, biomass can accumulate among the trophic levels, with each level storing and using energy it has received as a result of feeding on the trophic level beneath it in the food chain. It might seem that an almost unlimited amount of energy could be so accumulated within a sufficiently elaborate trophic level structure. Such is not the case; oxygen is generally required, as well as other substances. Water concentrations of these critical elements is limited, and Lake Superior is noted for its pure and relatively sterile water.

Carrying capacities for Lake Superior have not been established until recently, and have been estimated in several ways. Hydro-acoustic methods currently are providing more realistic estimates than were provide formerly by spring bottom-trawl surveys (Hrabik, 2005, Mason et al., 2005). The carrying capacity estimates used in this model are based upon these recent findings. Mean pelagic prey fish biomass was found to be 15.56 kilograms per hectare for the western Lake Superior region, varying by region from 9.46 kg/ha in the open water areas to 27.98 kg/ha in the Apostle Islands to 20.22 kg/ha in the Duluth, Minnesota region. Considering the entire area of the western lake of 2 ¼ million hectares we estimate the pelagic prey carrying capacity to be at least 35 million kilograms.

Amounts of prey consumed by Lake Superior predators have been estimated and confirmed in both laboratory and sampled lake-dweller fish studies. For the most part the predators consume about 0.9% of their body weight per day. This consumption results, on average, growth of about .04% per day averaged among the salmonine predators, and amounting to about 20% per year.

A fundamental modeling difficulty presents itself in this predator prey model, wherein multiple predators are simultaneously hunting and consuming multiple prey species. In our western Lake Superior model we are concerned with at least four salmonid species in search of sustenance from two prey species. The question is: How much of each prey species is consumed by each predator species as a function of population numbers and concentrations per unit of time. The answer to this question is important because it holds keys to the long-term relative survival success among the predator and prey species.

One approach would be to deal with the predators and their prey in an aggregate way, aggregating the major predators into one group, and the two prey species into another group (Moxnes, 2005). An earlier version of the model using the Personal Learning Edition of Vensim™ showed interesting behavior with species grouping. In effect the predators were modeled as a composite predatory agent consuming an aggregate prey biomass. However, some important questions involving management policies of stocking, harvesting etc. require modeling the species individually.

The advanced versions of Vensim™ have subscripted variable capabilities (Vensim Reference Manual, Ventana Systems, 2005). These features prove to be very useful in simplifying aging and other equations so that one subscripted equation can be used to express, say, the effect of food availability on mortality for all predator species.

Fish conversion efficiencies in warm waters are often high, sometimes nearing unity. In the colder waters of Lake Superior growth is much slower. Even so, during the course of a year an adult Chinook salmon might consume several hundreds of ciscoes while doubling its weight. A salmon at maturity usually consumes somewhat more for its weight, while expending more energy than a trout for the same prey item caught. This is necessary for the salmon in order to support its increased growth rate, earlier reproductive maturity, and shorter time span as a reproducing adult as compared to the native lake trout. For salmon, more rapid metabolic processes are required to catch and process food at the higher rates that are characteristic of the ocean-based salmon.

Development of a Prey Preference Measure

The differences between the life cycle characteristics of the exotic salmon species and the lake trout have important effects upon their responses to prey availability. Both species seem to prefer the smelt when smelt are relatively abundant, as the smelt are most easily caught. As smelt populations diminish, ciscoes become relatively more important in the diets of both the exotic salmon and the native trout. For example, a recent study showed that although smelt constituted 27% of the available food biomass, smelt made up 66% to 78% of the fish found in predator stomach contents.

With a roughly equivalent amount of energy per unit of weight, the smaller average size of smelt is more than offset by the ease with which they are captured, owing to their slower average swimming speed. So we might expect that the dynamics of their population changes would be different from that displayed by herring populations. Another difference in the prey populations is related to their reproductive cycles and fecundity characteristics. The smelt reach reproductive maturity in a relatively short period of two years. The smelt females produce a large number of very tiny eggs, often exceeding 20,000 in number, which are deposited in stream beds and beaches during a spring spawning run that lasts about three weeks. The smelt eggs hatch within a few weeks following deposition.

The ciscoes, on the other hand, are fall spawners; their eggs hatch the following spring. Ciscoes must survive for 6 years before reaching reproductive age. An average female will deposit 8000 eggs, spawned in the open lake, where they are subject to a number of types of mortality. The eggs hatch in the early spring. The larval ciscoes are subject to destruction by natural causes of weather and currents, as well as predation by other fishes; among them are the smelt. The Duluth, Minnesota area at the extreme western end of the lake, and the Black Bay, Ontario regions, are areas famous for their cisco spawning grounds. Large schools of smelt have been observed on the cisco spawning grounds engorging themselves on the newly hatched larvae of young ciscoes.

Predation by smelts on coregonids has been documented over the years (Loftus, D.H., et al.,1986). but the extent and importance for fish population web dynamics has been unclear. The situation in Black Bay, Ontario served as an example area where smelt and lake herring were both present in great abundance for at least three decades up until 1990 (Bronte, Charles. R., et al., 2003, Fish community change in Lake Superior 1970-2000, p. 1559-1560).

In many areas throughout the world smelt have been found to be instrumental in affecting populations of fish much larger in size than themselves. In the Great Lakes a report in the 1957 AFS publication indicated their influence when, in the aftermath of an extensive smelt die-off in 1943, there appeared unusual abundances of whitefish, walleye pike, and lake trout in 1949-53. The spikes in stocks of these various fishes all were related to year classes, the young-of-the-year of which had occurred in the year of the smelt die-off of 1943. Other studies of smelt, some going back more than a century, had shown similar effects when smelt were superabundant.

The model's central problems involve the equations for the predator consumption of prey. The magnitudes of the predation mortalities are related both to prey abundance and to predator numbers. Even when prey are readily available, prey consumption by predators is limited by predator satiation, food handling and metabolic constraints. When prey are relatively scarce, energy expenditure during searching may be the limiting factor. The precise relationships may not be as important as the general features of predation, which involve reasonable limits to rates of consumption.

In 1995 an important study of predator-prey population relationships was published in the North American Journal of Fisheries Management, a publication of the American Fisheries Society. The article was entitled, Bioenergetics Modeling as a Salmonine Management Tool Applied to the Minnesota Waters of Lake Superior (Negus, M.T., 1995) Her work investigated the energy transfers that prey fish populations must have supplied to predators in order to accomplish observed growths in biomass of the lake's predator fish populations. It was a single-year study of major predator populations' growth in biomass. Prey population mortalities were inferred from the predator growth figures.

This was an initial application of bioenergetics modeling to estimation of predation mortalities for Western Lake Superior. One conclusion was that prey populations might have been much higher than had been estimated in former prey population studies. The modeling results indicated that predation mortality would have consumed the entire stock of prey, and more. The paper's author suggested that high predation mortalities brought into question the advisability of the continuous heavy stockings of predators. She offered that "in many cases stocking quotas have been determined by historical production levels and hatchery capacities rather than by analysis of [fish] community dynamics."

Using several of the natural mortality parameters from Mary Negus's study, this modeling effort presents a long term view of the lake ecosystem. It looks at the population dynamics using a limited number of parameters in a model that shows the overall dynamic behavior of the populations as determined by the feeding, mortality and reproductive characteristics of the individual fish species as agents and actors.

A preliminary model involving a single average predator population feeding on a single composite prey fish population showed dynamics that bore considerable resemblance to population changes experienced during the aftermath of the lamprey invasion, lamprey control efforts, and trout rehabilitation periods of lake history. The stocking programs which followed upon mixed success of lake trout rehabilitation were added as timed inputs to the model. This seemed to further clarify the picture and explained in part the sudden collapse of the seemingly limitless smelt populations seen during the 1960's and 1970's.

The substantial exotic predator populations that currently exist are regarded by some fishery managers to be unrelated to levels of the forage base biomass. Even the significantly reduced growth rates among predators were described as undetermined in cause by a recent research study funded by the Great Lakes Fisheries Commission (Johnson, T.B., 2001). Other clues are manifested in the historically high stocks of plankton. The presence of these stocks is confirmed in hydro-acoustic studies. Research vessels make lake-wide transits during summer months. The implication is that predators may have the effect of suppressing the plankton-feeding prey stocks.

Conclusions

There may be no extant fishery management protocols with which to address the situation of relatively high levels of predators versus their prey on a large-lake scale (Stewart, D.J. and Myriam Ibarra, 1991). Aquaculture managers deal successfully with this situation on a regular basis, though on a scale where consequences of policy decisions are more quickly realized. The primary focus of fishery management on the Great Lakes continues to concentrate upon achieving ever increasing abundances of those predator species that are of particular interest to recreational fishermen. Changes in predator stocking quotas are regularly discussed, as are restrictions on harvesting; but increases in harvesting are virtually unheard of as a management tool, except in the case of siscowets. To speak of achieving longer term increases in future predator abundances by means of increased harvesting in the present may be contrary to current thinking among today's Great Lakes fishery management professionals, who must contend with immediate demands for more predators from varied stakeholder groups.

Lake Superior may well be a vast, underutilized resource. The sunlight which fuels the lake productivity continues to fall upon the lake; water quality remains superb, plankton levels are high. Perhaps it is fisheries management that has failed, not the intransigent behavior of the resource. If industrial pollution had caused the reduction of fisheries production in Lake Superior to current rates that are a fraction of historic harvests then, presumably, a serious problem with the causative agent would be recognized. When expert human management achieves this same dire result, confusion of cause and effect is common. It is hoped that experimenting with a lake system dynamics model will help concerned parties to increase their understanding of this complex fishery system.

This model has been shown and explained to a group of fishery managers at the Minnesota DNR's North Shore fishery management center at French River. The model was also seen by the Minnesota Lake Superior [Fishery] Advisory group, made up of representatives of various stakeholders, including sport fishermen, charter boat captains, Save Lake Superior Association, water quality scientists, university fishery department academics and representatives of the public. There were many questions and several follow-up presentations to fishery stakeholder groups. The model has served to focus discussions in ways that seemed to be helpful to many participants.

After completing a two-year process of monthly meetings attended by representatives of dozens of stakeholder groups, a management plan for Minnesota's waters of Lake Superior was completed in late 2006 (Schreiner, 2006). Parts of the plan which would have allowed a resumption of a limited commercial fishery for lake trout, allowing the taking of 3000 fish, were soon quashed by unidentified but top-level authorities at the Minnesota DNR offices in the State capitol. In May, 2007, bills in both houses of the Minnesota legislature restored the Lake Superior Advisory Group's plan to allow the resumption of limited commercial fishing for lake trout and whitefish along the northernmost section of Minnesota's Lake Superior shore. This event occurs almost 50 years after management authorities imposed a "temporary" halt on commercial fishing for lake trout and whitefish.

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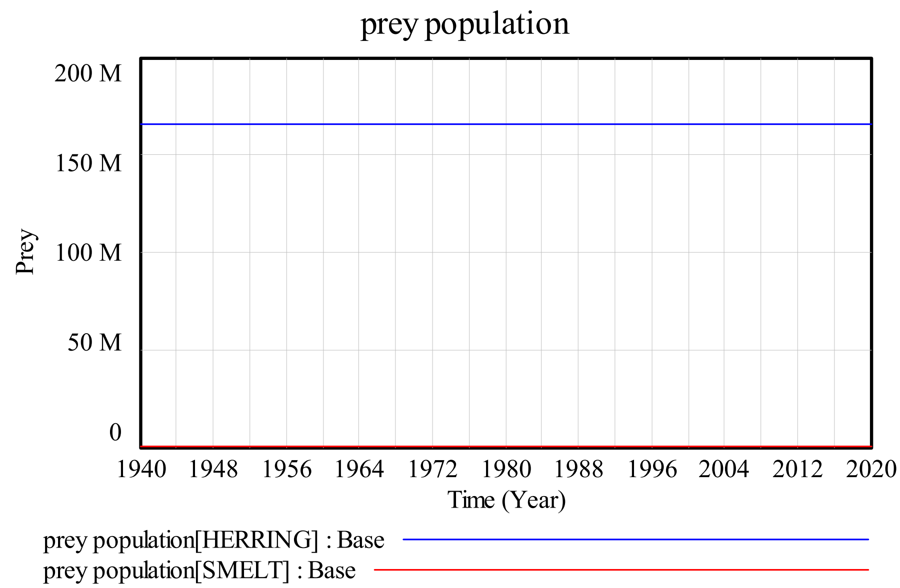
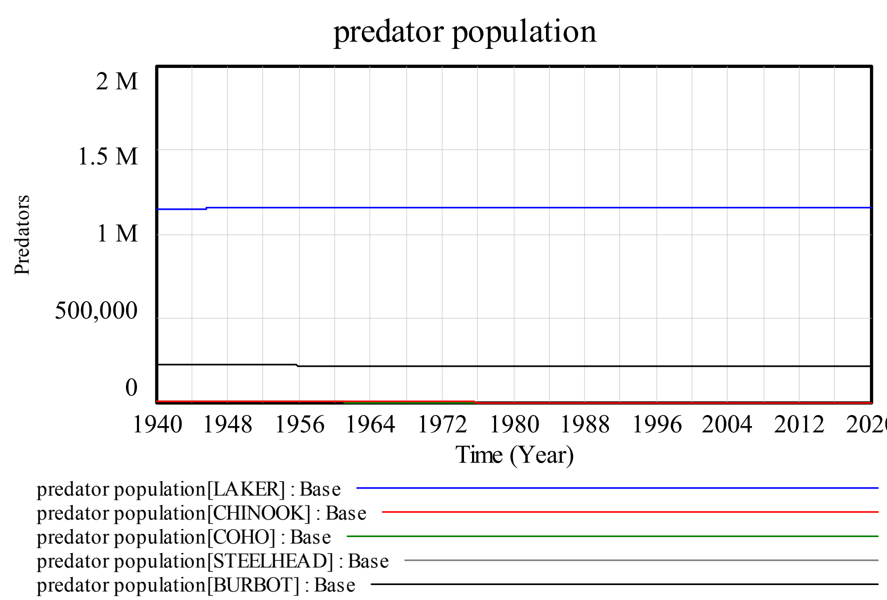
Base Model Runs:

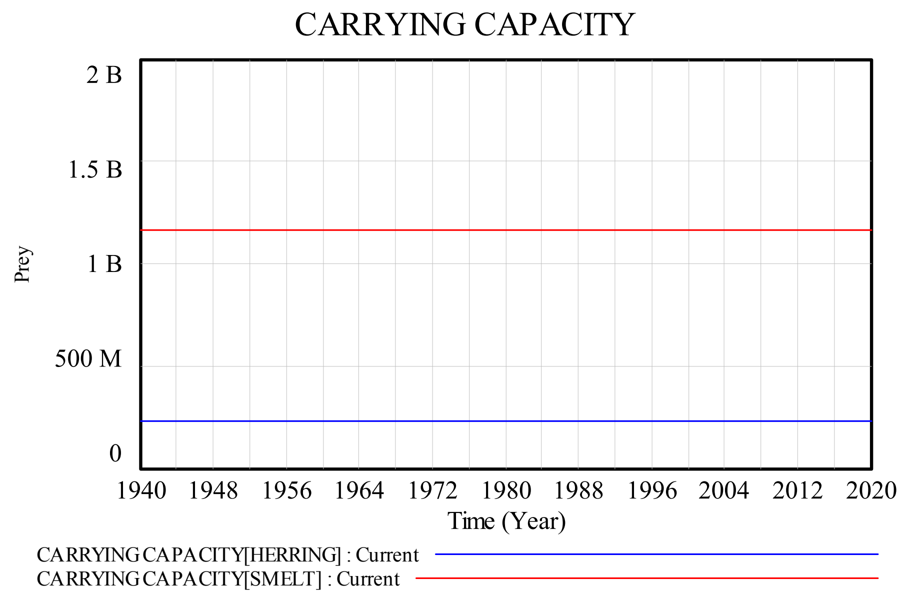




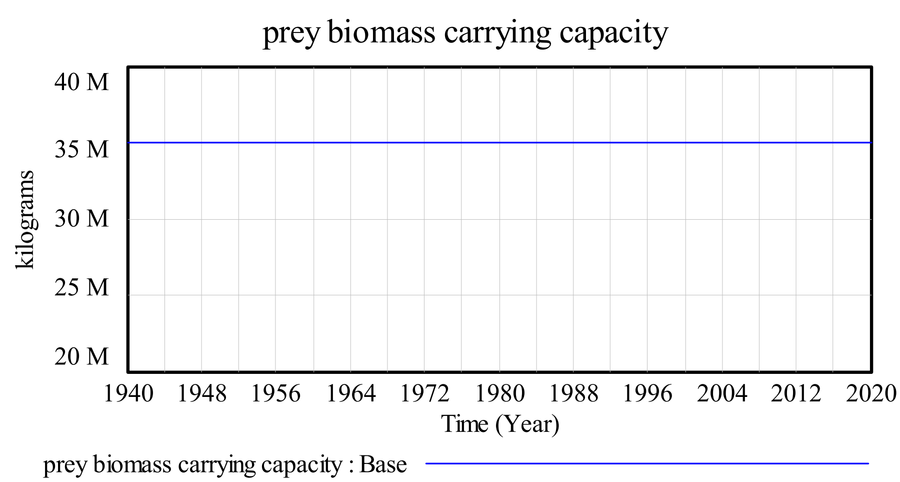
Base Runs: lamprey invasion=0; smelt recruitment=0; predator stockings are not active. There are no predator or prey harvests. No exotic ocean species are present in the lake.

Fisheries were subsistence-based until about 150 years ago when lake trout (siscowets) were sought by American Fur Company, and rendered for fish oil. Lake herring are at 70% of carrying capacity. There are no smelt in the lake until the 1920s or 1930s.

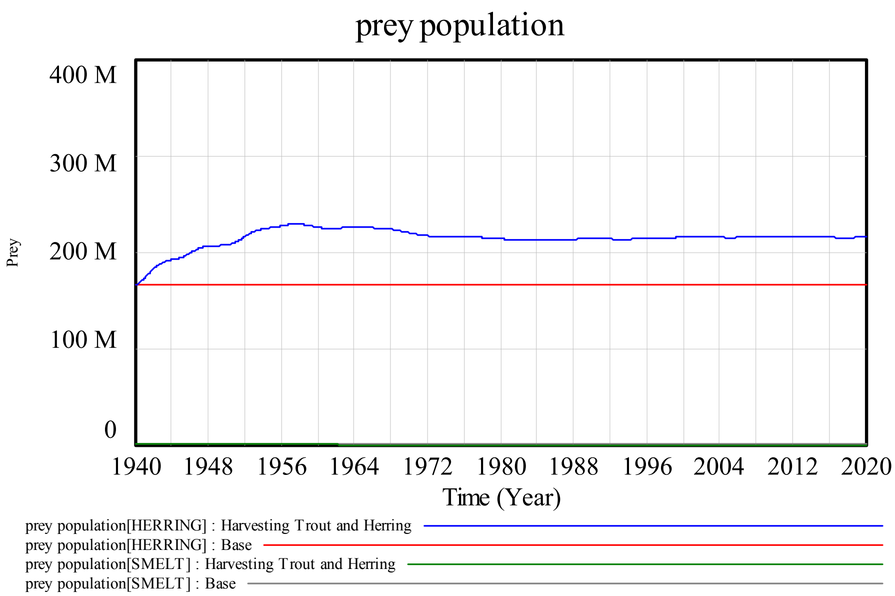
Carrying capacity in numbers of adult fish for cisco, also known as {lake herring}, and smelt {rainbow smelt}:

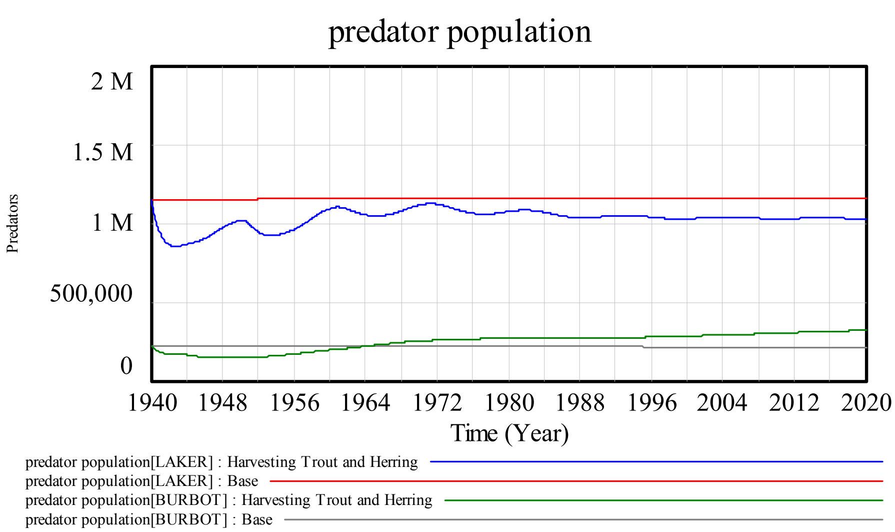


Carrying capacities in numbers of individual fish shown above have been converted from carrying capacity for the lake in millions of kilograms, shown below:



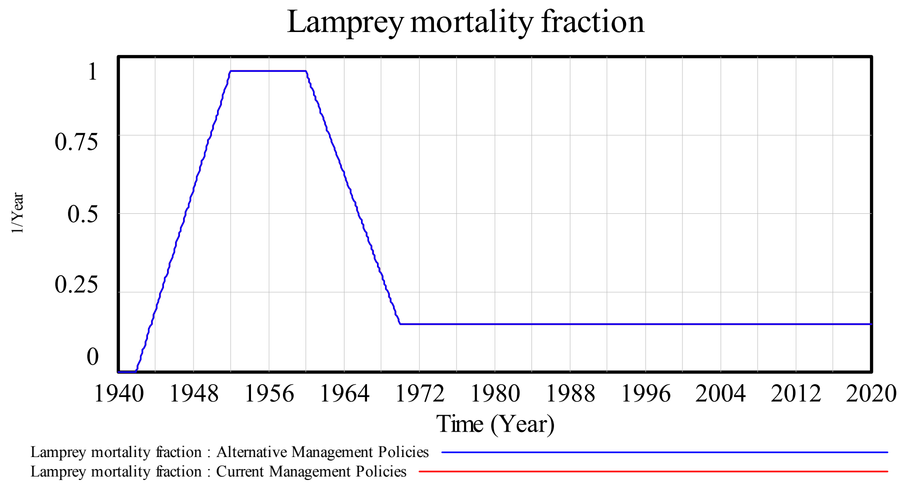
Harvesting Run: Lake Trout and Burbot are harvested-25% of adult stocks annually. Harvesting Run: lamprey=0; stocking policy=0; annual harvesting level is 25% of adult stock. Note that for these assumed conditions, the cisco {HERRING} population increases, lake trout population declines along with burbot, which, having the slightly higher recruitment rate than lake trout, later returns to pre-harvest levels. This might resemble the situation had no lamprey or smelt invasions occurred.





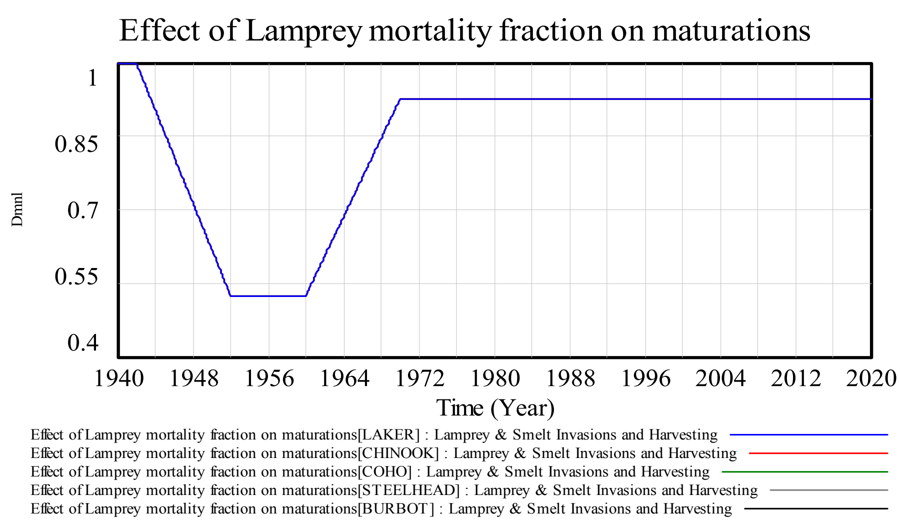
Lamprey Mortality:

A. Lamprey Mortality on Adult Predators



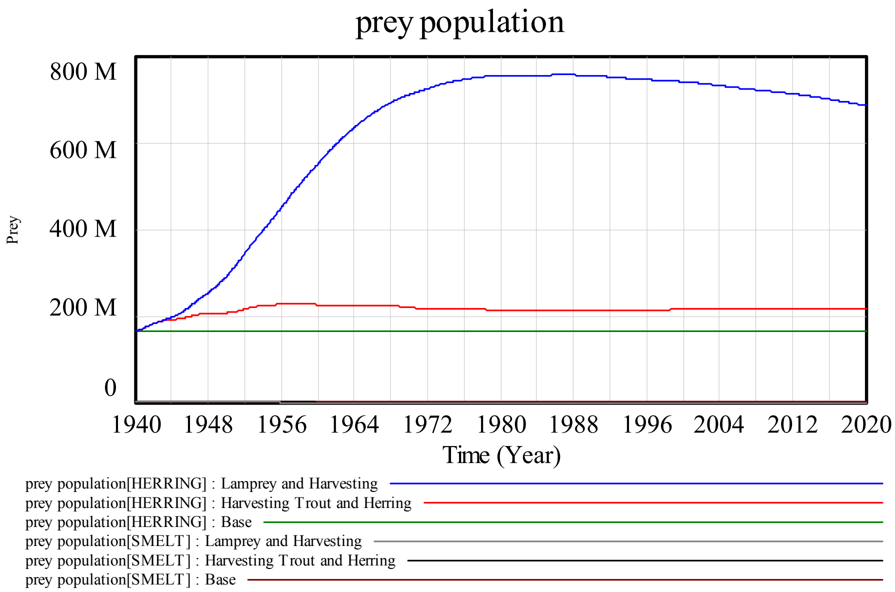
Mortality of 95% among adult predators is approached by 1952 and continues until 1960 when lamprey control programs begin to take effect. Since 1970 mortality is assumed to be 15%.

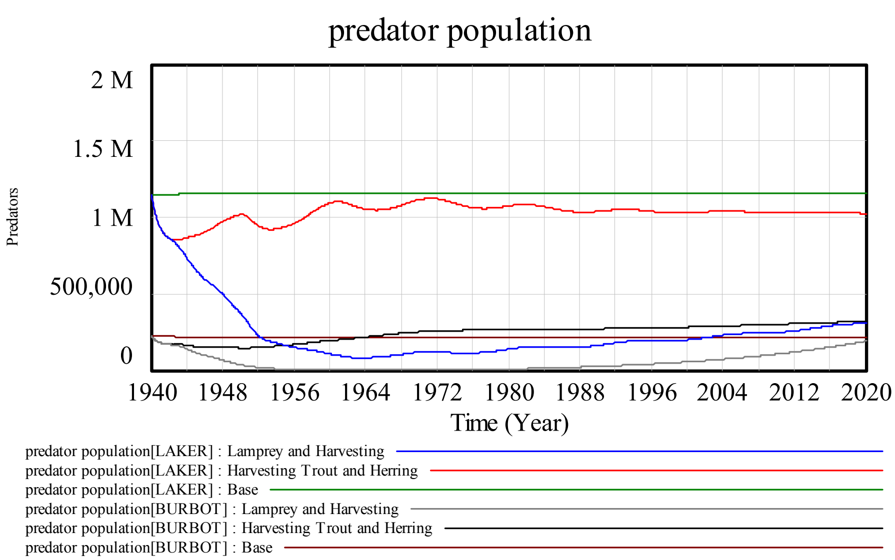
B. Effect of lamprey upon maturations of predators:



Lampreys are believed to attack pre-adult predators, reducing predator maturation rates. Magnitude of the effect is modeled at 0.5 times that of the adult mortality.

Lamprey Invasion Runs:

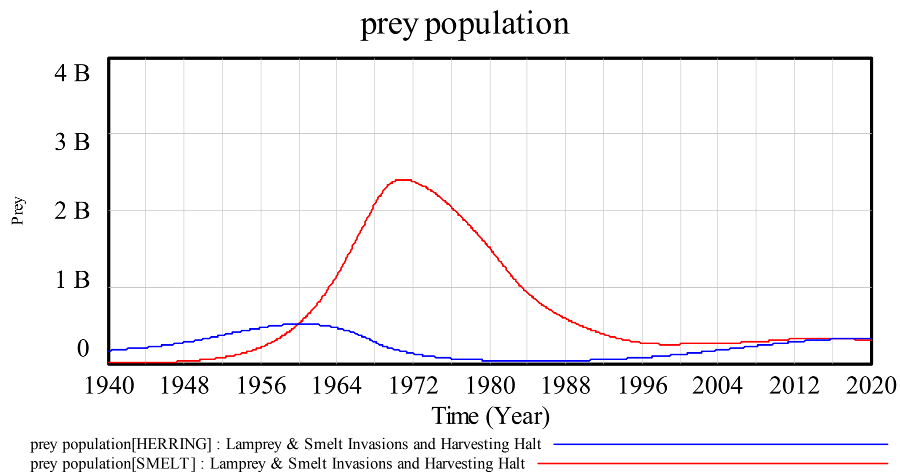


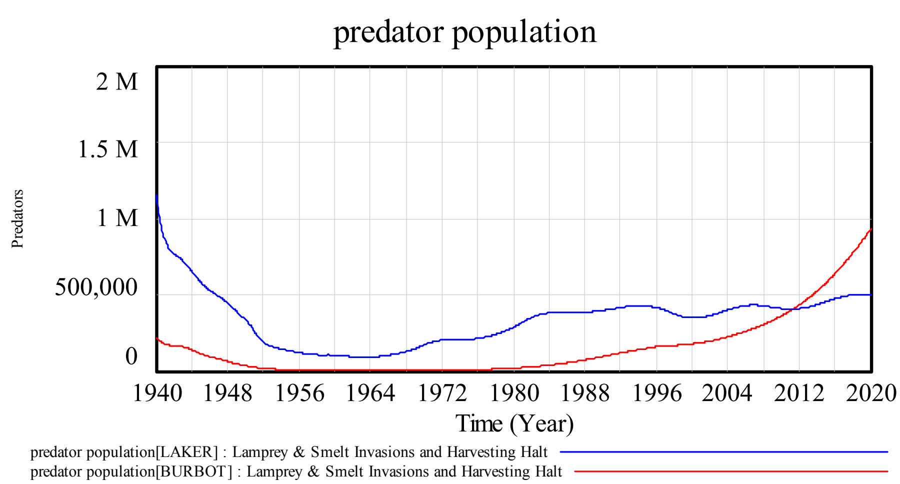


Lamprey Invasion Run Comments: Trout and burbot harvesting at 25% continues, and herring population increases substantially. No predator stocking programs are in place, but control programs beginning in early 1960s reduce mortality from lamprey to 15%

annually. Burbot population recovers after seven decades, but lake trout lag. No smelt have entered the picture in the above run.

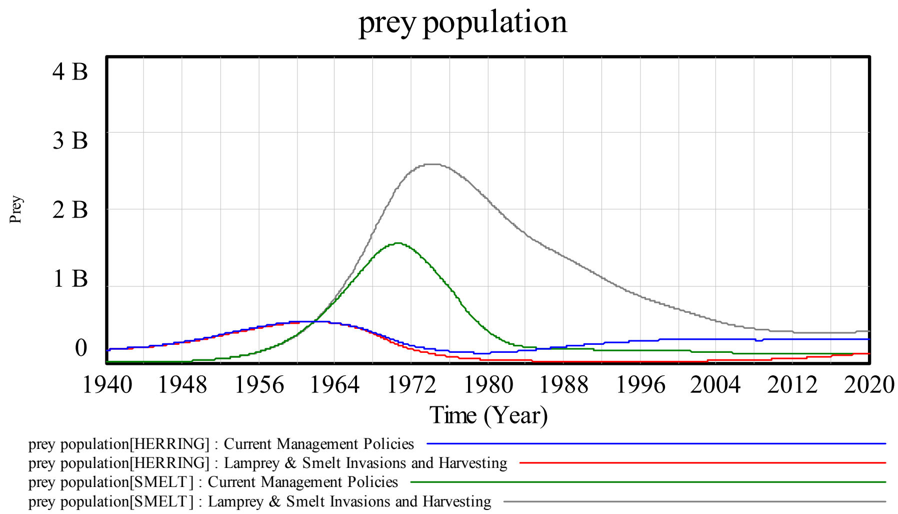
Runs comparison: Lamprey Invasion Accompanied by Smelt Invasion

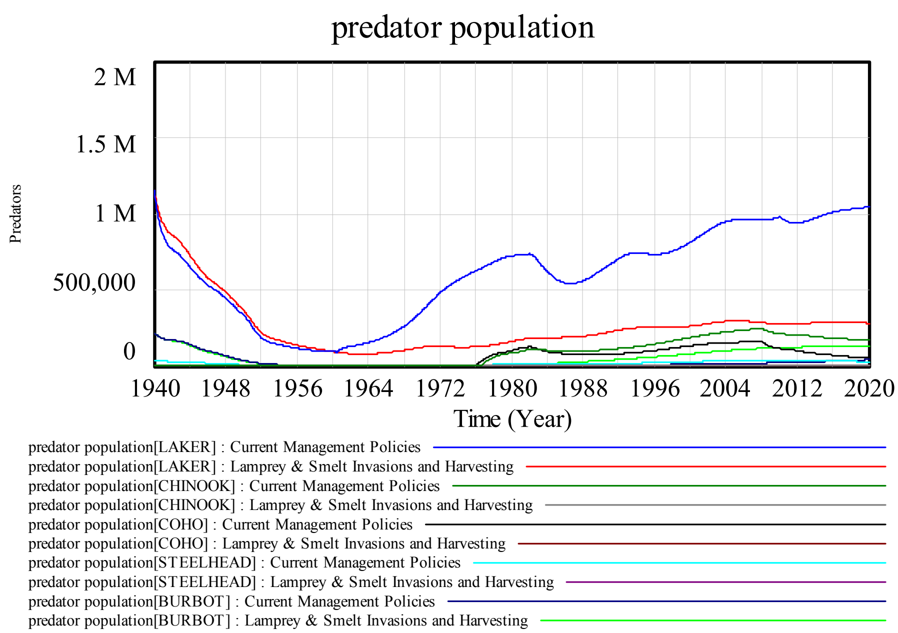




Lamprey & Smelt Invasions Comments: In this run lampreys destroy much of the predator population; smelt reach peak abundances more than 2.5 times higher than in the absence of lamprey predation. No stocking programs for trout or salmon.

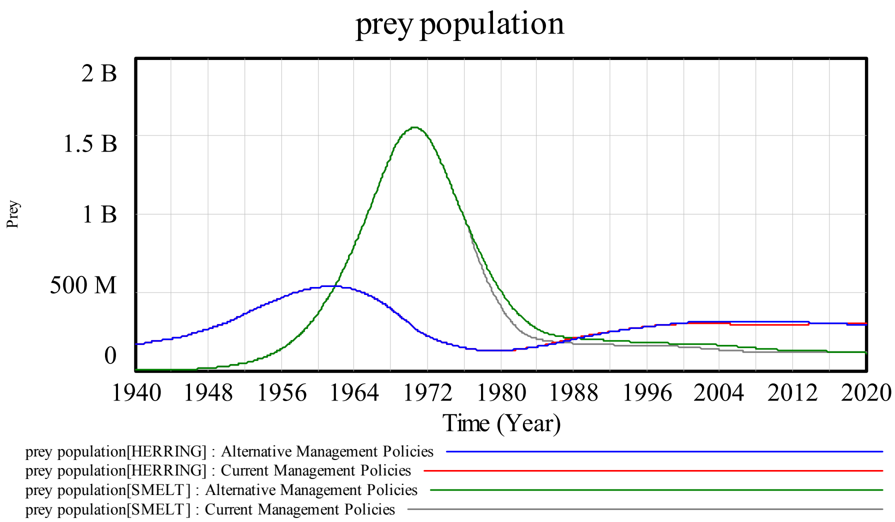
Current Management Policies Run: Halt commercial but not sport predator harvesting, stock lake trout and Pacific Ocean salmon. Implement lamprey control programs.

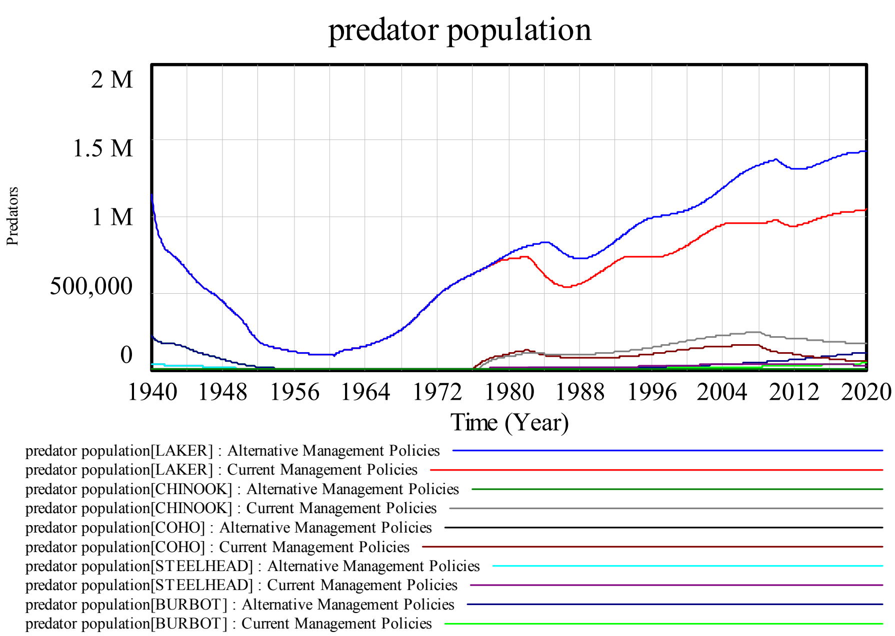




Current Policy Run Comments: The lamprey-caused reduction of predators allows smelt to increase rapidly resulting in abundant available biomass. Lake trout recovery is improved by harvesting halts.

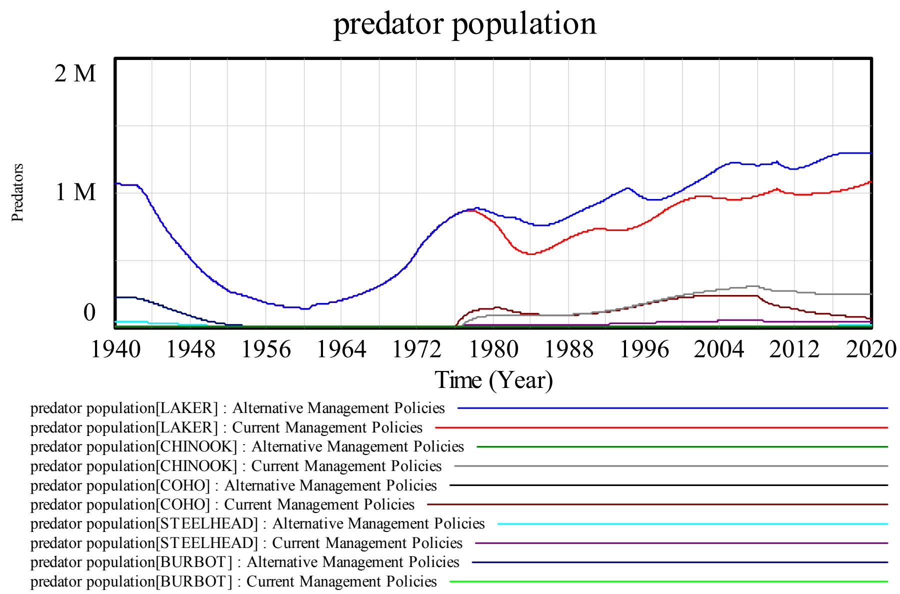
Alternative Management Policies Run:





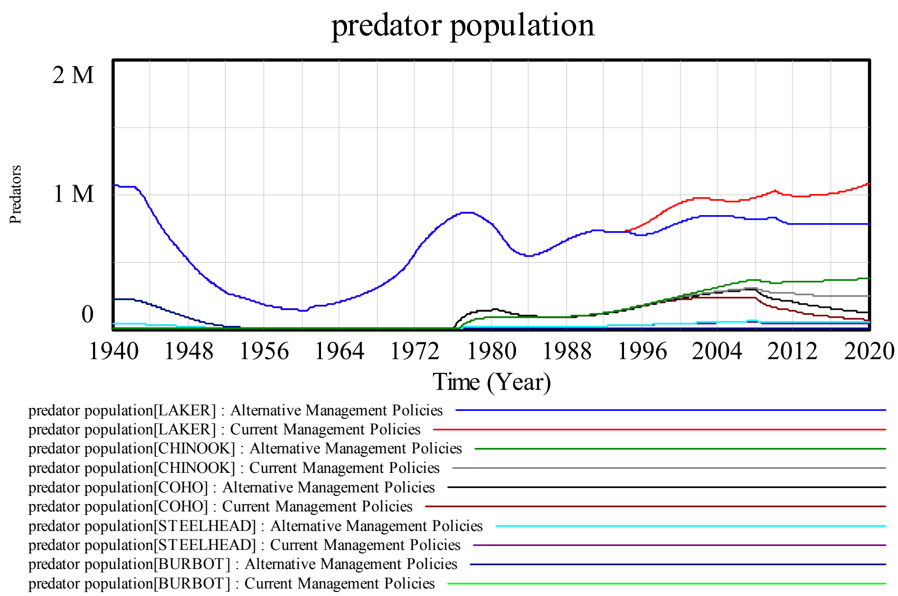
Alternative Policies Run Comments: Elimination of exotic Pacific Ocean salmon stockings has little effect on magnitude of prey populations. However, reduced competition for the prey resources allows lake trout restoration to be achieved more than a decade sooner on account of increased food availability for trout.

Alternative Policies Run: Halt Exotic Stockings, Resume Commercial Harvest in 1994



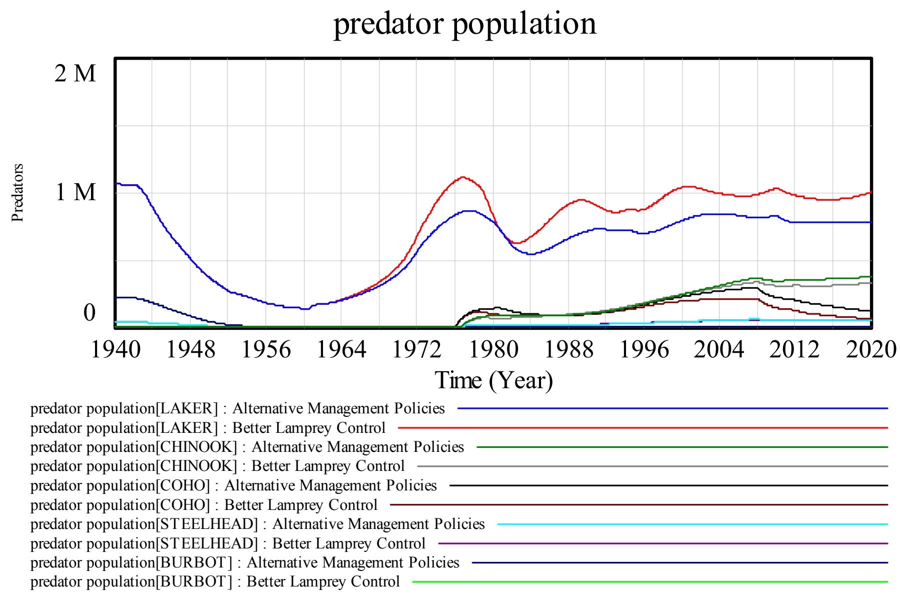
This fishery management scenario is similar to the previous one, except that in 1995 commercial fishing is resumed. Thus, a commercial harvest of 10% of the adult stock is taken additionally. (The 10% sport harvest is presumed, and 15% lamprey mortality is presumed, also). This harvest would not be sustainable in the presence of continued salmon stockings, as we shall show in the next simulation.

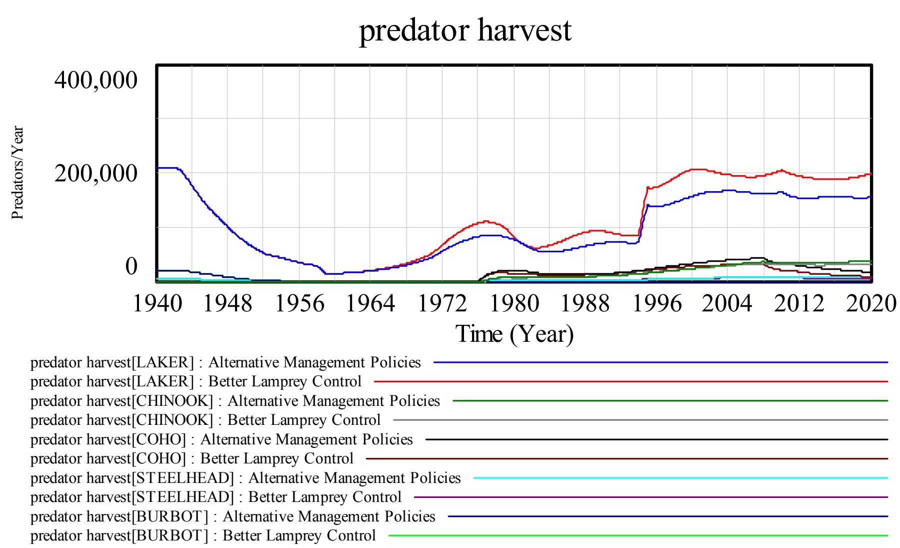
Alternative Policies Runs: Same as previous, except continue to carry on salmon stockings. Thus our alternate policy is a variant of CURRENT MANAGEMENT POLICY, except that we resume commercial harvesting.



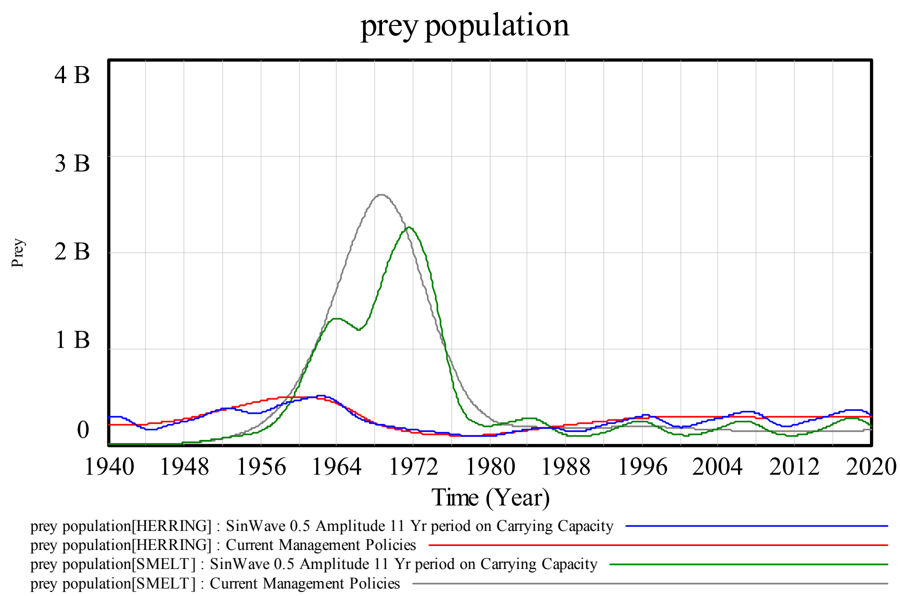
This policy is barely sustainable. In the late 1970s lake trout recovery is briefly reversed by competition from stocked salmon. In 1994 harvesting is resumed and the blue path is the result. In our next simulation we will show how more effective lamprey control would alter this picture.

Better Lamprey Control Run: Same as previous, except that lamprey mortality has been reduced from the currently assumed 15% to the 5% goal level sought by the Fish Community Objectives Plan.





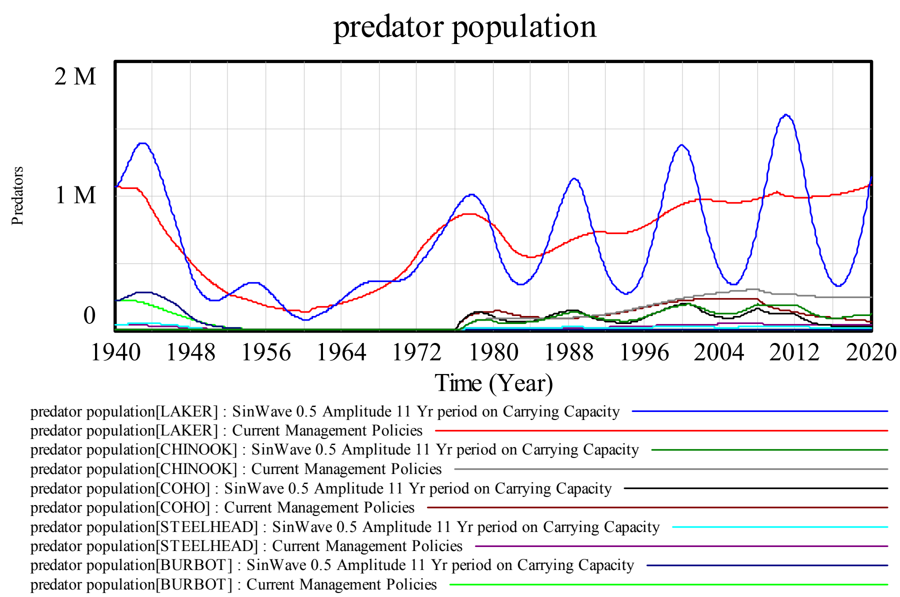
Carrying Capacity Experiment: Biomass carrying capacity is modulated by a 0.5 amplitude sin wave of sunspot cycle period. The results show that the prey fish members of the fishery web system appear to be quite robust to perturbations.



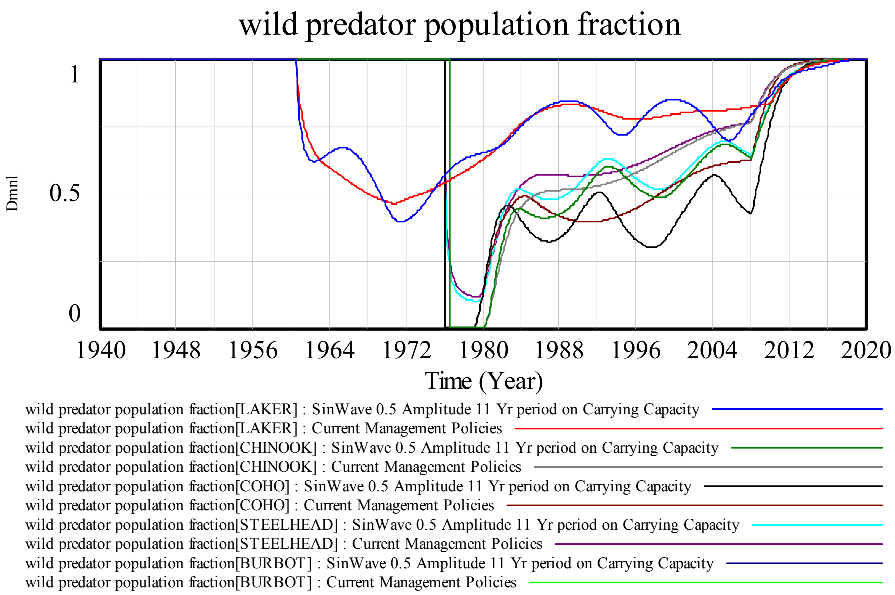
As it happens in this experiment, the ascent of the smelt population towards its peak in year 1968 is interrupted by biomass carrying capacity variation. Note that peak is delayed, and that slope of descent of smelt population is increased in this case. This delay of peak is just a coincidence; a different cycle period might have reversed the order of peaks.

Carrying Capacity Experiment, continued:

The 0.5 amplitude, 11-year period sin wave modulating the biomass carrying capacity has effects which pass from carrying capacity to the prey populations to the predator populations.



The increasing amplitude of the laker population may show how the system amplifies the effects of food availability upward through the trophic levels of the system.



Wild predator population fractions can serve as a reality check.

Many other experiments are possible, using the system dynamics model. Several interesting ones might include the following:

1. What are the effects of noise on recruitment rates of predators and preys?
2. What is the effect of stocking prey fish, or of restricting prey fish harvesting on predator fish populations over time?
3. If lamprey hadn't caused the collapse of lake trout, would commercial fishing have done so? Is it fair to state that the collapse was due to overfishing and lamprey predation?
4. What is the effect of the sequence and timing of the arrivals of lamprey and smelt in western Lake Superior?
5. Are fishery managers wise to consider the long run effects of policies? How can the consequences of policies be estimated without a model, mental or otherwise, that relates the structure of the system to system behavior over time?

This model is a continuing development effort. Improvements-in-progress will include modeling the lamprey population as a level variable. Further modeling effort is needed on the mutual effects of smelt and coregonid species, and on intra-species cannabalism.

The following tables summarize the commercially important predator fish and prey fish populations, their origins and their current abundances and commercial status:

Table 1. Important Predator Species of Lake Superior

Predator Species:	Origin:	Comments:	Commercial Status:
lake trout (salvelinus naymaycush)	native	former commercial species continuously stocked since 1920's, now restored after lamprey devastation	commercial fishing halted, sport fish continued
coaster trout	native	prized sport fish intermittent stockings.	never a comm'l fish
steelhead trout	introd. 1895*	important sport fishing species, mostly seasonal stream fishing.	never commercial
kamloops trout	introd. 1978*	continuously stocked stocking recently halted	ne'er comm'l
coho salmon	introd. 1977*	continuously stocked 30 year stocking program failed Unplanned-for self-sustaining stocks now present in Lake Superior.	never a comm'l fish
chinook salmon	introd. 1979*	continuously stocked stocking to be halted 30 year stocking program failed Unplanned self-sustaining stocks are now present.	never a comm'l fish

* Crawford, S.S 2001 — Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects Canadian Special Publication of Fisheries and Aquatic Sciences (132), 2001. 205 pp.

Table 2. Commercially Important Prey Species of Lake Superior

Prey Species:	Origin:	Comments:	Commercial Status:
cisco {lake herring}	native	important commercial fishery in western Lake Superior in Wisconsin South Shore and in Minnesota North Shore region Important forage species for predators	quota restricted

whitefish	native	important commercial species no sport harvest never stocked, now very abundant and the most important commercial species in Lake Superior in terms of value of catch and in abundance of stocks.	only Native American harvesting at present
rainbow smelt (osmerus mordax)	introd. 1930*	formerly important commercial fishery. substantial remnant populations exist sport harvesting at low levels commercial production levels less than 2 % of peak harvests of the 1970's Continues to be an important forage species	Seasonal harvest

* Ebener, M.T. 2002

Appendix A: Prey Preferences:

The predator fish differ in their preferences for the prey fish available to them. But how do we quantify the choices that are made? In order to approach this problem I have relied on certain characteristics that are distinctive. The smelt as prey offer a roughly similar energy content per unit of weight to that which is offered by the cisco. However these prey species differ substantially in average size as adults, and their swimming speeds for fish of the same size is quite different. The smelt are slow swimmers, moving at less than .02 m/s, while the ciscoes move much more rapidly, often faster than .07 m/s. The ciscoes are capable of much higher burst speeds.

On the other hand, the predator fish vary substantially in activity levels and growth rates over their adult life span. The salmon are faster moving and more energetic. The salmon must grow more rapidly in order to reach reproductive maturity in less than 4 years, after which they spawn and expire. The lake trout reach maturity only after 7 to 11 years, and may continue their reproductive lifetimes indefinitely, spawning annually for more than a decade. These differences are important in understanding the long term survival prospects of the two species groups.

Research suggests that predator gape size establishes an upper limit on the size of prey fish that are likely to be consumed. The size preference curve resembles a dome shape, with the greatest preference being for prey fish about ¼ the length of the predator, provided the gape can surround the prey fish's girth. (Lundvall, et al., 1999) Such a large capture size preference may mean that the predator can thereby maximize his predatory efficiency in terms of energy profit per unit time.

In the case of our Lake Superior species we have a situation where the predator and prey species are similar in shape and prismatic coefficient. Thus an optimal size of prey at $1/4^{th}$ predator length would mean that the preferred prey would weigh in at about $1/64^{th}$ the weight of the predator. Studies have shown that our predator fish have been found to consume about .005g/g of body weight per day. We are thus able to express the rates of predator consumption of prey in terms of numbers of prey fish consumed, without reference to the actual size or growth stage of the predator. The expected numbers of fish consumed will often be greater than these estimates, particularly in the case of the smelt, which will never reach a mass of $1/64^{th}$ that of a large lake trout. The same holds true for ciscoes in the case of the largest predators.

The ratio of weights between the two prey fish of approximately 5.0 has been used in order to convert biomass to numbers of prey fish. For example, the average adult count of smelt might be 15 to the pound, while herring might be 3 to the pound. This ratio has also been used to estimate the annual food requirements for each of the prey species.

Appendix B. Recruitment Rates

The rates for lake trout and other predators are those that may have been useful averages during the years prior to the lamprey invasion. Rates chosen for smelt were arrived at in order to explain the very rapid increase in smelt numbers during the 1950s. Recruitment rates are often found to be highly variable, with a few year classes showing very high values, and many other years showing low values. Since these rates are averages which are affected in the model by other variables we have chosen to use average rates which have applied over several years' time.

Predator Species:

Species	Initial Population	Recruitment Rate	Stocked Survival Fraction
Lake Trout	1.06 Million	0.5	.034
Burbot	215,000	0.4	not applicable, none stocked
Chinook	0	0.5	.03
Coho	0	0.5	.03
Steelhead	40,000	0.5	.03

Prey Species:

Species	Initial Population	Recruitment Rate	Stocked Survival Fraction
Cisco	CC * 0.89	0.7	.1
Smelt	CC* 0.0001	1.2	.1 entry via St.Mary's River

Final Remarks:

Other constants and table functions can be accessed in the .vmf file for the model of the western Lake Superior system, which is titled FORAGE 30.vmf and is included as part of the submission. Because of the extensive use of the array functions and subscripted variables capabilities of Vensim™, the model simulations of FORAGE 30 will require the Professional or the DSS versions of Vensim™.

Much of the documentation for the model is internal. With the main influence diagram in view, you may place your cursor over any variable or constant to read a comment and to see what is the variable's unit of measure. Right-clicking on the variable gains access to its defining equation. Changing from sketch to text view will show a complete list of all the equations of the model.

This model could be re-parameterized for any of the Great Lakes regions, and of course for other defined bodies of productive water.

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