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December 23, 1996

Dr. Catherine Carlson
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CANADA

Dear Dr. Carlson:

I received a copy of your reply to my New England salmon article and was asked to respond. Let us consider my response as dialogue, opening lines of communication to better delineate differerences of opinion.

First, I endorse the generation of controversy in such issues as the historical (and prehistorical) abundance of New England salmon regardless of the motives of the provoker. New ideas, new paradigms, and progressive change cannot come about unless conventional wisdom and the status quo are vigorously challenged.

I will avoid the terms science or scientific. The only "scientific" tests of your hypotheses concerns your hypothesis that salmon did not occur in New England before about 1500 A. D. (which would be refuted by documenting archaeological or fossil remains of Salmo salar before this time) and your hypothesis that climatic warming commencing in the late eighteenth century is the cause of New England salmon extinction, not dams and pollution (there are historical records that refute this hypothesis).

When salmon first came to North America and what was their historical abundance are questions for which only indirect evidence can be used and this requires interpretation and professional judgement.

In your paper, "The (in) significance of Atlantic salmon," you state that you analyzed "30,000 fish bones" from prehistoric sites of aboriginal people (and no salmon bones were found). Did you make a concerted effort to find scales and

otoliths? Typically, otoliths are the most durable bones in a fish, often the only remnants left after thousands of years. Sifting for otoliths with fine mesh screening is time consuming and often ignored in archaeological studies.
I assume you have read a 1993 paper by Peteet, et al. published in Quaternary Science Reviews, vol. 12, pp. 597-612, that mentions fossil scales from New Jersey that match the scales of S. salar. This paper does not illustrate these reputed salmon scales, but I received further information and a photograph (enclosed is xerox of photo). One scale was taken from a deposit dated to 11,500 years ago. The other is dated at 9,000 years. These dates approximate the retreat of the glacier front from this area (the edge of a southern or Atlantic glacial refugium for fishes). The scale is far from perfect and as an archaeologist with a specialty in fish remains, I assume you are more knowledgeable in scale identification than I am; but, do you know of any family of North American freshwater fishes except Salmonidae that lack radii or any form of sculpturing on their scales? If these fossil scales from New Jersey are from a salmonid fish, the only possible species would be brook trout or Atlantic salmon. The scale in the photo is definitely not from a brook trout.

Concerning your hypothesis that climatic change doomed New England salmon to extinction with or without dams and pollution, we can assume from your line of reasoning that during the period from about 1800 to about 1900, New England salmon were rapidly declining toward extinction in all rivers with and without dams. You cited 29 references in your paper but you omitted the best documented historical account of New England salmon, that by W. C. Kendall published in 1935 in the Memoirs of the Boston Society of Natural History, vol. 9, no. 1.

Commercial fishing for salmon in the Connecticut River apparently began about 1700. Catches were not recorded, but Kendall cites a price of a penny a pound in Hartford (a glut on the market?). Connecticut River salmon were sold in New York City (local markets saturated?) until dams eliminated all salmon by 1797. Samuel Mitchill (1816, Fishes of New York) mentioned that in former years the New York City market was supplied by Connecticut River salmon, but now they are shipped in on ice from the Kennebec River (Maine).

Kendall cited the Kennebec River as the second most productive New England river (after Penobscot). The Kennebec lost its salmon in 1872 when a dam was constructed at Augusta. The Androscoggin River, Maine, probably the third most productive New England River, also lost its salmon to blockage by a dam about the same time. In 1888, the total commercial salmon catch in Maine was 205,149 pounds. Most of this (75-80%) must have been Penobscot salmon because it and several small rivers were the only rivers still maintaining salmon. The Penobscot, by this time, was badly impaired by dams and toxic pollution from pulp mills--it was operating at a much reduced capacity. Amazingly, in 1930, when the Penobscot reached the stage of advanced, almost terminal degradation as a salmon river, it produced a commercial catch of 88,295 pounds.

A reading of Kendalls' history of the loss of salmon in New England rivers after dam construction does not allow for a reasonable conclusion that climate not dams caused the demise of New England salmon. For detailed documentation of the demise of salmon in the Merrimack River associated with dams and pollution, see Stolte (1981) "The Forgotten Salmon of the Merrimack," U.S. Dept. of Interior.

Although I agree with you that New England salmon were never as abundant as implied in folklore, they were probably much more abundant than you seem to believe. Their abundance under pristine conditions based on my very gross estimate is that about 90% of the time (9 years out of 10) total numbers of salmon on spawning runs to the 30 or so New England rivers would have ranged between 100,000 (poor years) to 500,000 (good years). This is a conservative estimate based on area available for egg to smolt production compared to European Rivers where data are available. I would also point out that in 1930, the Miramichi River, Canada, which has a watershed area less than the Penobscot (about 30% smaller and only about half the area of the Connecticut River basin) had a run of about 250,000 salmon. If one examines the latitude of the Miramichi (ca. 47° N. Lat.) with Maine rivers, it will be seen there is not a great difference (ca. 1°). Thus, any inexorable climatic shift operating since the late eighteenth century to doom New England salmon certainly should have been apparent on the Miramichi by 1930. If the Miramichi with only about 10% of the watershed area of all New England salmon rivers could have runs of this magnitude, a maximum run size of 500,000 for all New England rivers before dams, pollution, and watershed degradation, is conservative.

Concerning the timing of the arrival of Atlantic salmon in North America, before or after the last glacial epoch, in lieu of definitive archaeological or fossil evidence, I use indirect evidence of genetic divergence. I cited a consistent difference in chromosome numbers between North American and European salmon to argue for a preglacial timing. You cite a 1989 paper by Davidson, et al. and personal communication with Dr. Davidson that the genetic evidence does not preclude your premise that salmon first came to North America (that is, separated from European salmon) only about 1,000 to 10,000 years ago.

I would cite a paper by Taggart, et al., 1995, Canadian Journal of Fisheries and Aquatic Sciences, vol. 52, pp. 2305-2311, concerning DNA markers. In this study, 2847 salmon from Spain, France, Ireland, Great Britain, Sweden, Norway, and Iceland were compared with 247 salmon from Maine, Nova Scotia, New Brunswick, and Newfoundland. Virtually complete separation was found between European and North American salmon. "North American" markers (in 96.5% of North American salmon) were not found in any European salmon. The dominant European marker (in 99.9% of European salmon) was found in 3.6% of North American salmon. This degree of separation strongly argues for preglacial separation of European and North American salmon (the "European" marker in North America could be interpreted to indicate some continuing postglacial movement from Europe to North America). It seems logical to assume that the salmon of Norway and Iceland have not mixed with the salmon of Spain for 10,000 years or more, yet they share the identical "European" DNA marker. You should have this paper critically analyzed by salmon genetics experts and see if they would not now agree that the genetic evidence overwhelmingly supports an hypothesis that European and North American salmon have been separated since at least the beginning of the last glacial epoch (that is Atlantic salmon were in North America prior to the last glaciation and they persisted in one or more refuge sites during glaciation).

Note that the DNA marker study does not rely on a "molecular clock" to support preglacial separation of European and North American salmon. It is based on common sense and professional judgement assuming that the separation of ancestral salmon stocks into North American and European groups occurred before the evolution of the diagnostic North American and European DNA markers, and these present markers evolved into distinct differences in Europe and in North America after the separation of the two groups. The consistency of identity among all European salmon from Spain to Norway and Iceland strongly indicates ancient (preglacial) separation of North American and European salmon.

Of course you are correct that total abundance of Atlantic salmon, considering their entire range of distribution, in the best of times, pales in comparison to Pacific salmon (especially pink, chum, and sockeye salmon). In 1995, commercial harvest of Pacific salmon in Alaska alone was 217 million fish. If the average weight were only five pounds, this would be more than a billion pounds of salmon caught only in Alaska. The 1996 returns were even greater, canneries reached capacity, prices for pink and chum salmon dropped to five cents per pound, salmon were given away free on the streets of Anchorage and carcasses kept piling up in spawning rivers.

I will co-chair a session at an Atlantic salmon workshop in Scotland in March. My session addresses the topic, "why aren't (or weren't) there more Atlantic salmon?" My estimates for the greatest total commercial catch of Atlantic salmon in the best years barely exceed 50 million pounds. The limitations imposed by their freshwater life history and differences between the North Atlantic and North Pacific as salmon foraging grounds, determines that total abundance of Atlantic salmon can only be a tiny fraction of that of Pacific salmon. This relative rareness along with elegance of form and sporting quality embodies the tradition associated with aristocracy and elitism.

Cage-cultured Atlantic salmon because of their artificiality and commonness, lack the mystique and therefore the aura of aristocracy associated with wild salmon-- my analogy of an original masterpiece and a mass produced replication.

I suggest that you rethink your comments indicating a devisive dichotomy between the aristocracy ("noble sports fishermen") and the peasantry ("the working class") related to Atlantic salmon as implied in your letter (some poor commercial fisherman lose income so that more wealthy anglers can catch more salmon). The latest figures I have for total production of cage-cultured Atlantic salmon indicate a 1995 world output of about one billion pounds (Idaho Aquaculture News, 1996 no. 2). Such production makes Atlantic salmon one of the more moderately priced fish in the market, now quite available and affordable to the working class.

I'm sure you are aware of economic studies on the relative values of salmon (Atlantic, coho, chinook and steelhead) in commercial and sport fisheries. Much more income and many more jobs are created for the working class by angler-caught fish compared to the same number of fish taken in a commercial fishery. You say that your brother is an expert steelhead angler and runs a business dependent on anglers fishing for salmon and steelhead. Ask his opinion on the consequences of diverting most of the fish on which his business is based into a commercial fishery.

I hope you take my comments as intended, in a helpful, not agonistic manner. I would much enjoy going steelhead fishing with you and your brother sometime.

Sincerely,

Robert J. Behnke
Professor of Fishery Biology

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Jan. 31, 1997

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Dear Dr. Behnke,

Thank you very much for your letter of Dec. 23 which I received on Jan. 9 at the start-up of classes and a busy teaching schedule; hence my delay in writing to you. Many of the questions you raise were not addressed in the short summary article I published in *Federal Archaeology* magazine, but are considered in my dissertation, published through University Microfilms, Ann Arbor, Michigan (1992).

I couldn't agree with you more that the documentation of *Salmo salar* in archaeological or paleontological sites for the early to mid-Holocene or Late Pleistocene would falsify my hypothesis of a late Holocene colonization of temporary duration, caused by the temporary Little Ice Age cooling (AD 1450 - 1750). The point is that evidence has not been found for Atlantic salmon despite evidence for other fish species, and any suggestions of differential preservation cannot be supported (the focus of my reply in *Trout*); i.e., their absence is significant. The demise of salmon in the late 18th century fits better with a model of climatic change (warming at the end of the Little Ice Age), than one of anthropogenic causes (dams, pollution), in my view. The warming trend after the Little Ice Age may also explain why salmon restoration hasn't been successful in re-establishing the fish in New England. That it has been successfully introduced to other cooler regions, such as the south island of New Zealand and the northern Pacific Northwest (where farmed Atlantic salmon in British Columia are escaping into the wild and surviving as fully mature ripe individuals to compete with Pacific salmon stocks -- a scarey phenomenon that makes me question the whole fisheries field, but that's another matter), suggests that the species can be introduced in suitable watersheds (of which, in my view, New England no longer is since the end of the Little Ice age.)

I am fully aware of the historical accounts that state that dams were the cause of the salmon's demise. I reviewed those accounts in my research (all are mid-19th century or later), but a review of fish legislation records for fishways of the 18th century indicates that fish runs were being protected at least up until the 1790s. Once the salmon dwindled however (as I believe because of climate change), this legislation disappeared (no longer any need for it), and then only after that did people blame the dams as the culprit. After the fishways legislation ceased, then certainly remnant runs further north such as in the Kennebec and the Androscoggin were thereafter not well protected, and the dams likely put the "last nail in their coffin", so to speak. So mainstem dams without fishways had some negative affects, but they were not fundamental to salmon decline, in my interpretation. Within the larger context of dams and their affects, that the shad runs didn't ever disappear, even without the benefit of being "leapers" like the salmon capable of negotiating the small tributary dams of the 18th century, has also never been fully explained by advocates of the dam-and-salmon-decline theory.

I cite the important Kendall 1935 article in my dissertation, but because it is a 20th century secondary compilation (of historical "facts" and hearsay), it doesn't serve to illustrate the points I highlight in the short *Federal Archaeology* article confined to citation of the 17th century primary accounts. I am also familiar with, and have cited Stolte's work, have corresponded with him, and he appears quite open to accepting my ideas regarding climate affects and effects. Perhaps you should write to him.

Regarding scales and otoliths - in my sampling methodology I use fine-mesh sieves and whole matrix column samples to recover tiny elements. I have never encountered scales in an archaeological assemblage, and they are very rare everywhere in archaeologcial sites except dry settings (and peat and water-saturated deposits/cores). Otoliths I have recovered and analyzed from New England, although they are not nearly as durable as bone, as you suggest, being made almost entirely of calcium carbonate (aragonite). I don't know of the assemblages you refer to composed entirely of otoliths.

I am familiar with the Peteet et al. (1993) article regarding the possible *S. salar* scale from Allamuchy Pond, New Jersey, I corresponded with one of the authors, Robert Daniels, in 1995 about the scale, and I admittedly dismissed it for various reasons. The article was quite vague about this single scale's species identification (saying it was abnormal with many characteristics not typical of salmonids), and despite its alleged significance touted at the end of the article, provided no photograph of it, but photos of other scales instead. (Unfortunately, because I have never worked with fish scales, I can't answer your question about radii and sculpting on the photo you were able to obtain of the scale). More seriously, the authors waffled through the course of the article about its identification: in the Abstract it is listed as trout; on page 608 it is stated that the scale matches a photo of *S. salar* - but didn't identify it in comparison to an actual scale, or claim that it definitely was *S. salar*; on page 611-12 it is stated that the pond assemblage of "sunfish, minnow, trout, and yellow perch," "present during the late-glacial and early Holocene is not unlike the assemblage found in ponds throughout the northeast today" - without mentioning Atlantic salmon; then finally after all this vagueness state on page 612 that the scale "identified as as scale from *Salmo salar*" is interesting and an "important find and indicates that this species migrated north with the glacial retreat." (!) They also had trouble identifying some of the other scales (e.g., the ctenoid scale that on page 606 is identified to the genus *Lepomis*, but becomes *Micropterus* or *Pomoxis* on page 612, even though they are not native to the area either). Finally they never clearly corollated the scale to a specific pollen zone so I made nothing much of the "conclusion" or claim for importance, having not been impressed with their "science". Perhaps I dismissed it too quickly, and the salmon story may have involved some earlier extinctions. I wouldn't rule out the possibility of a Pleistocene presence on the Atlantic seaboard (although in my dissertation I look at possible refugia and Pleistocene stream characteristics on the mid-Atlantic continental outwash plain that indicate substantial sand but not gravel deposits necessary for salmon spawning redds; I have a MSc. in Quaternary science from the University of Maine, hence my interest). I have been working on a site from Kamloops Lake, BC with Pacific salmonid bones dating between 18,000 and 15,000 B.P. (I enclose a recent publication on that site for your interest).

I compared salmon prices to shad in the 18th century in my dissertation and salmon was "expensive" in comparative perspective.

Regarding the Miramichi, I have no idea whether or not a one degree latitude difference is significant or not, but it might be, particularly if combined with cooler ocean currents, or air masses, that influence water temperatures (both ocean and river) in the Maritimes that are different from the Gulf of Maine.

In terms of the genetic evidence, I am aware that genetic markers have been isolated to separate European and Canadian stocks. I have very little genetics background, however Dr. William Davidson explained that these genetic "distinctions" need not require great periods of time, and as I quote Robert Kendall, no genetic clock is established for salmon stock separation. I am not sure why you think that it is logical to assume that Norwegian and Spanish salmon have not mixed?, and "common sense" and "professional judgement" mean different things to different people. The issue of timing for stock divergence is somewhat important, but not paramount. Labrador/Greenland stocks may have migrated and genetically diverged from European stocks even as early as the Late Pleistocene, but when they migrated and colonized New England rivers is a separate issue.

Aristocracy or elitism in salmon sportsfishing is a cultural phenomenon (I know scientists like to believe their science is uninfluenced by their own cultural context), and elitisim is not confined to Atlantic salmon. The sportsfishermen who book "trips" with my brother in BC are generally very wealthy individuals, Califoria winery owners, even Bob Hope; and Pacific salmon have never been rare. My point in addressing the issue of sportsfishing elitism is that it is the sportsfishing lobby, and not commercial fishing lobbies, that have kept the salmon restoration funding going in New England; and that surprised me when I first realized it. Yes, farmed Atlantic salmon sold in the grocery store is available at reasonable cost; sportsfishing for them, however, is not. Also, in the Pacific Northwest, the commercial salmon fishery (run by the "working class") is a much bigger industry than sportsfishing (run largely by and for elites). In fact, the sportsfishing industry on the BC coast is relatively new (didn't become dollar-wise significant until the Yuppie period of the 1980s), compared with commercial fishing, canneries, etc. that began in the mid-19th century, and continue today as the backbone of the British Columbia economy. The majority of salmon harvested in BC are from commercial boats. I spent a summer working on a commercial salmon troller in 1978, and believe me, it's a very working class, non-environmentally aware, culture, with big money and fish involved.

My brother, Chris Carlson, has started a new yacht-based sports fishing operation for this season rather than his usual land-based operation (an old BC Packers cannery) out of Namu on the central British Columbia coast. He is presently doing "shows" in San

Francisco and Seattle as I write, and if you would like, I'll get him to contact you with his new brochures. Noting your Colorado address reminds me that Chris was actually born in Boulder, and I went to elementary school in Boulder until I was ten years old.

The conference in Scotland sounds most intriguing, and I often wish that I was better connected to fisheries conferences. A salmon conference is being held at Simon Fraser University in Vancouver in February that I hope to find the time to attend. Unfortunately inter-disciplinary research has never really caught on in fisheries science has it?

Thank you for your letter. The dialogue is interesting and worthwhile. I have long been familiar with your research and publications.

Sincerely,

Catherine Carlson

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February 18, 1997

Dr. Catherine Carlson
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Dear Catherine:

Thank you for your letter of January 31. Enclosed is a copy of a draft prepared for the Atlantic salmon workshop next month. You can note how, by improper use of extrapolation and induction, an estimate of New England salmon abundance can be made that comes close to that of Rostlund's gross overestimate.

Evidently, questions on cost-benefits of New England salmon restoration have been effectively propagated. Also, ~~enclosed~~ are pages from Fisheries recounting values people are "willing to pay" to save, protect, or restore rare fishes. Surprisingly, Atlantic salmon, the king of fishes, fares no better than ordinary minnows. The reason for this is that this evaluation was based on 1,000 residents of Massachusetts resulting in numerous "zero protest votes" (I wouldn't give a cent to continue to pour down that rathole, might be a typical protest vote). It is surprising that so many of the general public would be informed on such an issue. I suspect your opinions and those of others raising questions on restoration were picked up by the media.

We both agree that an inordinate amount of money has been spent on salmon restoration in relation to the benefits. We would disagree that climatic change alone determines lack of success. Based on Pacific salmon and steelhead studies, it is well-documented that a race native to a certain river has much greater (10 fold or more) survival than fish of the same species, but native to a different river when both are stocked together. See citation to Mayama 1989, in my draft. The point is that New England salmon restoration has been based on non-native races. Wherever eggs could be obtained, they were hatched and stocked. Numerous salmon from Iceland were stocked in the Connecticut River, where I doubt they would have much chance to survive and return as adults. The fact is, my comments on page 6 concerning the significance of hereditary-based adaptations was not understood or appreciated by the people involved in New England salmon restoration. Although I am not personally familiar with the administrative structure of New England salmon restoration, I believe it would be a good bet that any program representing a diversity of state and federal agencies, each pursuing autonomy or doing their own thing, is a recipe for failure. In addition, most of the rivers of New England and their watersheds have been unalterably changed.

Did you present estimates on prehistoric or historic changes in water temperatures in freshwaters and marine waters in your dissertation? A point you may not be aware of is that the Atlantic salmon is one of the most thermally tolerant salmonid species (see enclosed pages from fisheries text). They are much more tolerant of high temperatures than brook trout yet brook trout persisted throughout New England. In regards to sea temperatures, the St. John's River enters the Gulf of Maine (same latitude as Maine rivers) and has consistently supported large runs of salmon in the nineteenth and twentieth centuries. In the late nineteenth century, Atlantic salmon were stocked in the Delaware River and adult returns were documented.

I should have pointed out that Kendall's early references to dams on New England rivers were based largely on reports of C. G. Atkins and E. M. Stilwell. The primary source is the first report of the U.S. Fish Commission for 1872-73. The earliest dam blocking salmon is given as 1680. By 1870, virtually every salmon river had dams; many runs were completely eliminated by then.

My comments on the durability of otoliths is based on sediment cores, both marine and from lakes, where otoliths are retrieved to study fish species composition (and sometimes growth rate) over different time periods.

Many thanks for reprint documenting salmon in Kamloops Lake 18,000 years ago, several thousand years earlier than believed possible by contemporary thinking on glacial dating. According to my references, the period from 18,000 to 23,000 years BP was the coldest of the cold. This information is important for dating dispersal of rainbow and cutthroat trout. I note Mark Wilson has a paper in the same volume on Eocene fishes. Anything new on Eosalmo?

Your letter arrived on February 11, just after my return from Seattle. I was meeting and signing agreements with people from Moscow University in regards to studies on Kamchatkan trout (to be funded by anglers allowed to fish for steelhead on Kamchatka). I was at the Seattle Sportsman's show (we had a booth on Kamchatka), Saturday, February 8. If I had known, I would have looked up your brother and introduced myself.

One last question. It is clear from Dunfield's work (also Kendall) that Native Americans actively sought salmon in New England, typically using special spears from canoes in the seventeenth and eighteenth centuries (also on tributaries to Lake Ontario). Have you or anyone else examined historical sites where salmon were known to be harvested to look for salmon remains?

Sincerely,

Robert Behnke
Professor of Fishery Biology

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Sincerely,

Robert Behnke
Professor of Fishery Biology

# ATLANTIC SALMON, AGAIN: REPLY TO BEHNKE

**(Revised shortened version Dec. 1996)**

Catherine Carlson
University College of the Cariboo

It was more than a little irritating to find Mr. Behnke implying that my motivations are not to advance scholarship, but to "get attention" by proposing "outrageously wrongheaded" explanations for the demise of Atlantic salmon in New England. I have given seminars over the years to salmon restoration biologists, sent them reprints of my dissertation and articles, have had telephone calls from heads of state and federal agencies concerned with salmon restoration, and have been interviewed by the media; -- but always there are attempts to ignore my research because of the political implications, the monies and careers at stake, and the inability of applied science to administer skepticism or self-criticism. I know that I am as popular as a "skunk at a tea party" in salmon restoration circles, as one retired biologist recently wrote to me in support of my research. I welcome new ideas that would support or refute my science, but unfortunately Mr. Behnke does not do that.

Mr. Behnke's primary criticism of my research is that my explanation for the lack of salmon bones in Indian middens ignores the soil conditions in New England that are too acidic to preserve salmon bones. He quotes Dennis Stanford, an archaeologist who works with mammoth and bison bone sites on the Great Plains that, "it is possible that bone remains once existed in New England but have since disintegrated." My 1992 Ph.D. dissertation from the University of Massachuetts at Amherst addresses this question, and it is absolutely true that in acidic soils you don't get good bone preservation. However, as any archaeological textbook attests, one of the best types of archaeological site for bone preservation is shell middens with alkaline soils caused from the leaching of calcium carbonate. The excellent preservation of fish bones in New England is demonstrated by the fact that from the 75 sites in New England that I analyzed (most of which are shell middens), the bones of over 40 species of fish were identified, although not salmon. Shad bones have far more delicate skeletons than salmon, so if these fish's bones managed to survive in these sites, then there is no reason to suspect that the salmon's shouldn't have also. There is also a misconception that because fish bones are small, they're not durable. My grandmother prepared home-canned salmon in a pressure cooker under far greater heat than an aboriginal stew or smoke fire. One of the reasons that I disliked eating salmon sandwiches made from my grandmother's salmon was because she left the salmon vertebrae in the meat, so I was constantly having to spit out those hard little (pressure cooked) bones.

In the Pacific Northwest, large quantities of salmon were traditionally fished by aboriginal peoples as they schooled along the ocean shore before entering the rivers to spawn, and the coastal shell middens contain large quantities of salmon bones; but not so in New England. Also on the Pacific Coast, aboriginal peoples harvested salmon once they entered the estuaries and rivers, and the archaeological sites reflect this; but not so in New England. Even in some sites in New England where dense middens of shell are absent (for example, the Turners Falls site on the Connecticut River, the Eddy site at Amoskeag Falls on the Merrimack River, and the Eddington Bend site on the Penobscot River), fish are preserved, probably because of the saturation of the soils with organics and fish oil at these excellent shad fishing locations.

One conclusion of my research is that salmon were not present in prehistoric times. However, I also noted that the historical accounts tell a different story, i.e., that salmon were present during the Colonial period. Mr. Behnke quotes Steve Brooke as stating that, "We know they [salmon] existed in <u>large numbers</u> during historic times," (emphasis mine) but I have argued that we don't *know* that at all. Whereas salmon are noted in the historical accounts of fish, their numbers are open to interpretation because the accounts are not quantitative. In addition, there is the fact that the predictions of vast salmon runs of the past were based on later 19th century historical accounts of a secondary nature (i.e., rewritten reguritations of original 16th and 17th century primary documents), and that their numbers may have been embellished because salmon was a high status fish to the English and the early colonial "promotors" of the region. Furthermore, there's additional potential for "salmon inflation" in the accounts because before Linnean classification, unfamiliar species were described in European terms, such as the shad as "white salmon."

"Large" is also highly subjective and relative. By Mr. Behnke's estimates there were 500,000 salmon in the combined runs of New England during optimum time (although how he arrives at this figure is unclear if the maximums of the three largest rivers was only 170,000). But even if 500,000 is reasonable, the amount is tiny compared with last year's (1995) combined species salmon run in the Fraser River in British Columbia, where even in a situation of declining stocks, there were approximately 20 million fish for this single river system.

However, even if salmon were not as abundant as the secondary historical accounts suggest, salmon were, nonetheless, present historically, and this is a quantitative leap over the prehistoric record. Since the historical presence of salmon indicates that environmental conditions must have provided favorable salmon habitat, I investigated climate records of the historic period and discovered that the Colonial period corresponded with a temporary climatic cooling called the Little Ice Age (AD 1450 - 1800). I proposed that because salmon are a cold water species, the conditions during the Little Ice Age would have created favorable salmon habitat, causing a southern expansion of their range into the rivers of New England where they had not been prehistorically. This neatly explains why there were no salmon bones in archaeological sites (because conditions were too warm prior to the Little Ice Age), but also why we see them referenced in the historical accounts. During the warming trend that ended the Little Ice Age (in the late 1700s), conditions became again unfavorable, and significantly, the extinction of the salmon corresponds in time to the termination of the Little Ice Age. This suggests that it was climate change and not dam construction (which happened historically after the fact of salmon decline), that was the cause of salmon extinction. The salmon restoration program has failed to recognize that the salmon situation today is due to a complex set of climatological variables, and less so with the effects of industrialization (dams and pollution).

Despite the fact that the paleontological record of fishes from the Pleistocene also shows negative evidence for salmon, Mr. Behnke argues that this can be over-ruled because the genetic evidence supports its presence before this last prehistoric glacial period. Since I had also proposed mechanisms for the colonization of North American rivers by stocks originating in Europe, and the potential for glacial refugia, I also reviewed genetic evidence of stock divergence. I discussed this with Dr.William Davidson at Memorial University, who at the time (1991) told me that the genetic evidence on salmon stock divergence is ambiguous; however, he agreed that there was nothing to rule out the possibility of a very recent origin (migration), within the last 1,000 years, of salmon to North America. More recently, in a letter to me (1995), Dr. Robert Kendall (American Fisheries Society) noted that in regards to the genetic evidence for stock divergence, "As far as I know, no genetic clock has been properly calibrated for fishes, and all estimates of time since the divergence of populations are speculation."

I have never felt that it is my role (or expertise), as an archaeologist, to evaluate public policy on salmon restoration; but as a citizen of the United States, I can legitimately ask about the way in which public tax dollars are spent to "protect" and "enhance" salmon, including the building of research facilities named after prominent politicians at the expense of other, possibly more real, environmental problems in archaeological and fisheries science. My inter-disciplinary research suggests that salmon restoration is an expensive experiment with little hope of returns in the post-Little Ice Age climate. In attempting to understand why it is that salmon restoration continues in its rut of failed attempts since 1870, I have come to understand the social role of sportsfishing and the status of the "aristocratic salmon". That class and aristocratic sportsfishing *still* has everything to do with it is evident in Mr. Behnke's final comment that states that, "For a connoisseur of the arts [read 'noble sportsfishermen'], such comparison valuation [between wild and hatchery reared salmon] would be simple: an original Van Gogh compared to a mass-produced facsimile. Others, such as a commercial fisherman [read 'the working class'], however, might have a very different value system." Don't get me wrong, however - I'm not against sportsfishing. My grandparents were avid salmon sportsfishers; I learned to tie flies at the age of twelve; and my brother, one of the best steelhead fishermen in B.C., runs a sports salmon fishing business where I too have experienced the sing of the reel. It's the reinvention of Nature that I find problemmatic.

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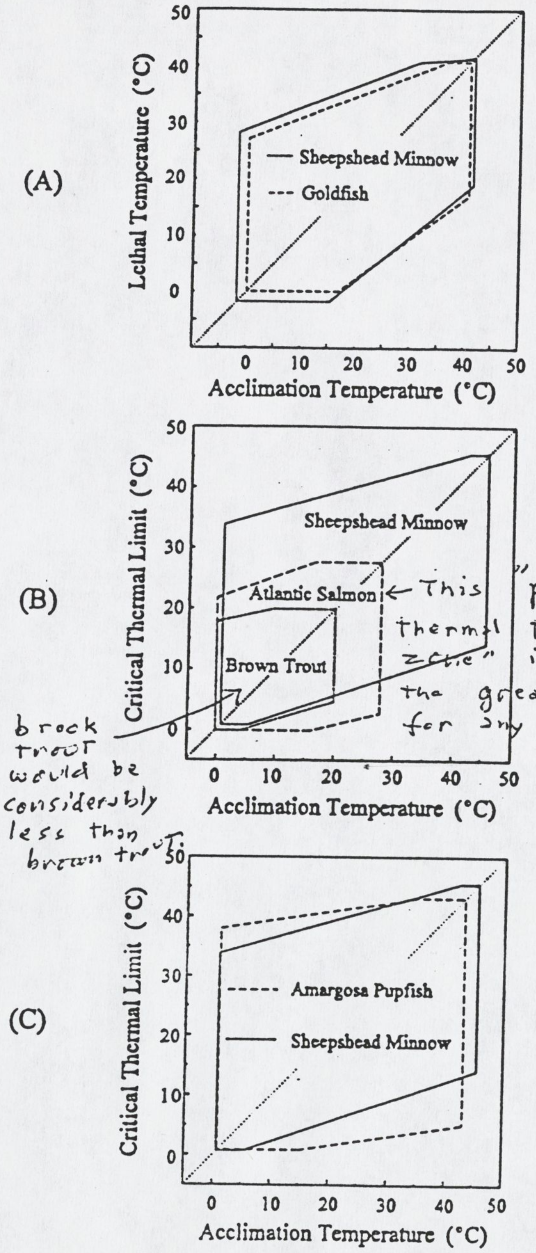
## Discussion

The physiological thermal tolerance zone of the sheepshead minnow (1380 $C^2$) is the largest ever measured for a fish. It exceeds the previous high mark of 1220 $C^2$ reported for the goldfish, *Carassius auratus*, by more than 13% (Fry et al., 1942). Direct comparison of both species' static polygons (Fig. 4A) reveals that the acclimation range of the sheepshead minnow is approximately 3 C larger than that of goldfish. The pupfish also demonstrates a greater acclimation scope than goldfish across most of its acclimation range. Both fishes could be considered eurythermic on the basis of their static polygon areas alone. By comparison, Antarctic icefishes, *Trematomus* spp., studied by Somero and DeVries (1967) have polygon areas of less than 100 $C^2$, the smallest known among fishes (Brett, 1970).

In addition to unparalleled physiological tolerance, sheepshead minnows are more resistant to thermal extremes than are other fishes. Strawn and Dunn (1967) found sheepshead minnows to be the most heat resistant of the more than 25 fish species they compared (including goldfish) from 12 families. Sheepshead minnows are also more heat resistant than Salt Creek pupfish, *Cyprinodon salinus* (Otto and Gerking, 1973), and more resistant than the Amargosa pupfish, *Cyprinodon nevadensis mionectes*, to both high and low temperatures. Amargosa pupfish acclimated at 27 C have MLETs of 6 and 2 min when plunged into 38 or 8 C (Hirshfield et al., 1980), whereas sheepshead minnows acclimated at 25 C and exposed to 38 or 8 C have an MLETs of nearly 10 and 74 h, respectively (Table 1). This unusually high, i.e., orders of magnitude, thermal resistance enables sheepshead minnows to survive short-term temperature extremes in nature that are otherwise lethal.

High temperature resistance of sheepshead minnows is further enhanced with increasing ambient salinity. Strawn and Dunn (1967) found that MLETs of sheepshead minnows acclimated at 35 C and plunged into 43 C nearly tripled (from 18 to 50 min) as salinity was increased from 0–20‰. Our resistance time data (Table 1) predict a further increase in MLET to 12 h for fish acclimated to 35‰. Osmo mediated increases in thermal resistance clearly benefit pupfish in tidal pools where temperature and salinity are likely to increase simultaneously.

Sheepshead minnow CTMaxima predicted from our regression of CTMax on acclimation temperature are remarkably similar to other cyprinodontid values where LOE is the experi-




← This "physiol. thermal tolerance zone" is probably the greatest known for any salmonid species

brook trout would be considerably less than brown trout

Fig. 4. (A) Comparison of physiological thermal tolerance zones of sheepshead minnows and goldfish. Goldfish data from Fry et al. (1942). (B) Comparison of ecological thermal tolerance zones from sheepshead minnow with brown trout and Atlantic salmon. Salmonid data from Elliott (1981, 1991, respectively). (C) Comparison of ecological thermal tolerance from sheepshead minnow with the Amargosa pupfish. The Amargosa pupfish polygon was derived from thermal scope data presented by Feldmeth (1981).

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WORKSHOP 1: PREDICTING PATTERNS OF CHANGE IN ATLANTIC SALMON:
Relative to Atlantic salmon, How do we anticipate change?

Suggested Outline

A. BACKCASTING: What information do we have on fluctuations/declines in Atlantic salmon populations or changes in community structure that affect Atlantic salmon over the last 50-100 years that would allow us to project forward?

1. What is the current state of our information regarding the status of Atlantic salmon populations?

- How good are our data on trends in population abundance throughout the range of their occurrence?

2. What do we know about abiotic and biotic factors and ecological interactions that affect Atlantic salmon?

- Have any cause & effect relationships regarding population fluctuations and community dynamics been established, and how conclusive is the evidence?

- Are there other mechanistic interactions that will help us understand past, present, and future trends both in the freshwater and marine habitat?

- Can we relate population trends to ecological mechanisms?

3. What human impacts have affected salmon over the past 50-100 yrs (e.g. land use, dams,hatcheries, pollution, habitat fragmentation)?

4. What are the critical gaps in our current understanding of population and community dynamics of Atlantic salmon and of their environmental mileu that would allow an effective management plan to be formulated?

e.g. Have distinctive population groupings been identified (ESU/GCG's [evolutionary significant units/gene conservations groups, and do we know the status of all core groupings?

5. Can we identify or even guess at critical threshold levels in population levels of Atlantic salmon & their prey base to allow system recovery from perturbation?

6. What are the major impediments to our present and future understanding of populationtrends and community interactions? Are any of the stumbling blocks tractable?

a) Have we extracted from available case studies (successful or unsuccessful) all relevant information?

b) Are predictive models or modelling techniques available that can untangle some of the complexities of the natural world, including indirect effects, nonlinear population responses, cumulative effects of multiple perturbations? What can we learn from predictive models developed in other areas (e.g. weather, economic, etc.)

c) Can we link impacts across freshwater and marine environments?

d) Improvements in research design:

i) Can we better match the spatial & temporal boundaries of studies to allow separation of systematic from random variation?

ii) Might new technologies be employed or more effectively utilized that could reduce errors in estimating population/ecosystem parameters or in conveying spatial pattern (e.g. GIS)?

iii) What statistical techniques offer the most promise for revealing pattern or relationships?

B. FORECASTING: Can we make some stabs at what lies ahead for Atlantic salmon?

1)What specific research, management, and policy questions relative to Atlantic salmon are we interested in answering in the future? How will we assess our success or failure relative to the questions?

2) What changes can be anticipated in the socio-economic (demographic projections, per capita resource consumption, environmental attitudes, political arena) and environmental milieus (e.g. global warming, acidification) that are most likely to impinge on salmon?

Over what time frame are each of these changes expected to occur?

3) What specific effects are these likely to have on the major risks (mortality factors) to salmon associated with harvesting, hatcheries, habitat quality, hydropower, and the oceanic rearing environment?

4) What non-lethal effects are these human impacts likely to have in the future (e.g. in addition to the above, changes in land use, dams, pollution, habitat fragmentation)?

5) Can we quantify the trajectories of these changes on population sustainability through time?

C. MANAGEMENT IN THE FACE OF UNCERTAINTY: How can we revise our research agendas, monitoring & management programs to accomodate uncertainity?

1) Can we suggest guidelines for a monitoring program to track changes in the status of Atlantic salmon populations and in the quality of their supporting habitats?

- in terms of spatial & temporal boundaries
- in terms of specific variables to be tracked
- in terms of sampling protocol & data analysis
    - in terms of an organizational structure that:

1) incorporates peer review of the monitoring program;

2) establishes collaborative opportunities among agencies, institutions, & the interested public;

3) that supports adaptive management approaches

2) Can we suggest ways to restructure management activities or programs so that they can be treated as experiments?

**Atlantic Salmon Work Group 2: Can we develop a general theory of life history variation for Atlantic salmon?**

**I. Salmonid life history, compared to other fish taxa**. Although we may ultimately want to concentrate on life history variation within the Atlantic salmon, we may gain some greater depth of understanding by beginning with a broader approach. We should first understand the pressures and constraints that led to general salmonid life histories, then the pressures driving Atlantic salmon life histories differentially from other salmonids, and finally, the pressures and processes driving the expression of particular life histories and range of variation in these traits within Atlantic salmon. Without understanding the life history constraints (or at least life history starting points) associated with phylogeny, we can not hope to understand the evolution of species-specific and population-specific life histories.

A. What characterizes salmonids?

1. common occurrence of diadromy, specifically, anadromy
2. large eggs
3. low numbers of eggs, relative to many other taxa
4. common occurrence of semelparity
5. ???

B. What has driven the evolution of salmonids toward these life histories?

**II. Atlantic salmon life history, compared to other salmonids**. Within the salmonids, what generally characterizes Atlantic salmon life histories and distribution? What distinguishes them from other salmonids? What has driven these characteristics?

**A.** Description of general life cycle for Atlantic salmon.

**B.** What characterizes Atlantic salmon?

**C.** What has driven the evolution of Atlantic salmon toward this life histories?

**III. Life history variation within Atlantic salmon.** Our first goal is to synthesize the current state of thinking on Atlantic salmon life histories. This should include identification of patterns in life history variation (e.g., geographical patterns) in Atlantic salmon, explanation of probable causes of these patterns, what constrains Atlantic salmon life history variation, etc.

**A.** What traits will we include in our discussions? e.g.,

age/size at smoltification
age/size at first reproduction
freshwater growth rate
growth rate at sea
egg size
egg number
timing of spawning
timing of return to freshwater
return rate
sex ratio of anadromous fish
frequency of different male reproductive strategies
survival rates
prevalence of iteroparity

**B.** What type of information on the current knowledge of those traits do we want to synthesize? e.g.,

1. general state of that trait in Atlantic salmon
2. geographic variation
3. variation across environmental gradients
4. changes through time
5. correlation with other traits
6. ???

(Items 2-5 may begin as descriptive information but should lead the discussion toward underlying selection pressures and constraints causing patterns in variation and correlation among traits.)

**C.** Fill in a grid addressing what is known about each type of information (**B**) about each life history trait (**A**). (Jeff Hutching's talk on Monday should put us well on our way toward this goal.)

**D**. Identify what we yet need to know about each trait, identifying *important* gaps in our knowledge. (An empty cell in our grid merely reflects a *lack* of information, not an *important* gap in information.)

**E**. What qualitatively different approaches have been taken and should be taken in the study of these life histories? Some of these approaches will be aimed at better defining the state of these traits, and others will have the goal of revealing the causes of observed states of the traits and, possibly, predicting future changes that might accompany future environmental changes.

**F**. In-depth discussions of how to fill gaps in our knowledge. This will involve combining information from **D** and **E**. For example, we may want to discuss use of quantitative genetic models to predict life history changes in response to changes in environment. Or we may want to discuss use of coordinated large-scale (i.e., large geographical scale) empirical experiments to test ideas about how life history traits should and do vary.

********************************************************************************

**Preliminary Schedule**

Monday evening (1.5 h). Discuss and define general goals of workgroup. Define life history states that describe salmonids in general, and what has led to the evolution and expression of those traits. Define how Atlantic salmon fit within the salmonids in general. (sections **I** and **II** above)

Tuesday (2 h). Fill in grid of current knowledge about specific life history traits of Atlantic salmon. (section **III.A-C**)

Tuesday evening (1.5 h). Identify gaps in knowledge. Identify approaches to filling in these gaps. Define focus of next part of discussion: specific approaches applied to specific questions. (i.e., define which questions we will focus our discussion on and which approaches to those questions.)

Wednesday (0.6 h). Open House.
Wednesday (2.5 h). Detailed discussion of different approaches applied to specific gaps in our knowledge (as defined in Tuesday discussion).

Thursday. Workgroup Summaries

Thursday (2 h). Wrap up discussion. Focus workgroup output. What have we learned? How will we communicate this to others?

# THE ECOLOGICAL BASIS OF MANAGING FLOW REGIMES FOR RIVER FISH

**Claudio I. Meier**

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## 1. Introduction

About one out of every three species or subspecies of North American freshwater fish is endangered, threatened, or deserving of special concern (Williams et al., 1989, cited in Allan and Flecker, 1993). In the U.S., 34 % of fish species are as classed as rare to extinct, whilst 20 % of the world's freshwater fish can be conservatively classed as extinct or in serious decline (page 59 in Naiman et al., 1995). If evolutionary units (populations that maintain their identity at appropriate temporal and spatial scales, within a unique evolutionary lineage; Nielsen, 1995) are considered instead of species, these figures would be much higher. Consider for instance, the multitude of life-history forms in Pacific salmon species (what we usually call "salmon runs").

Allan and Flecker (1993) propose that the following six factors are of critical importance for biodiversity in lotic environments: habitat loss and degradation, spread of exotic species, overexploitation, secondary extinctions, chemical and organic pollution, and climate change. In their study of North American freshwater fish extinctions, Miller et al. (1989; cited in Allan and Flecker, 1993) found that habitat loss and species introductions were the main culprits, involved in 73 and 68 % of all cases, respectively. It is interesting to note that altered flow régimes usually lead directly to habitat loss, and can indirectly affect native species by favouring the dispersal of exotics.

Fish habitat in rivers and streams is altered, lost, or degraded by many different factors, such as land-use changes (e.g., disforestation for agriculture). Here, we will focus on the effects of altered flow régimes due to dams, diversions, and channelisation works, which appear to have impacted river fish more than any other human activity.

## 2. Common impacts of hydraulic works

Large-scale hydraulic works cause a suite of impacts on the hydrology, morphology, and ecology of a river system (for reviews on this subject, see Petts, 1984; Brookes, 1988; Gore and Petts, 1989; Collier et al., 1996). Two general effects have been found worlwide (Stanford et al., 1996):

i.) Habitat diversity is substantially reduced: Flow and sediment régimes are altered, so that the fluvial processes that create heterogeneous channel and habitat patches are changed. The longitudinal connectivity is interrupted by barriers and by dewatering.

Seasonal flow variability is reduced, but discharges can fluctuate at shorter time-scales. The natural temperature régime is lost. Channelisation procedures and constant flows disconnect the wetted channel from its floodplain, altering baseflow/groundwater interactions, degrading riparian habitats, impeding seasonal floodplain inundation, and creating an homogeneous wetted channel. The lack of flooding allows woody vegetation to encroach upon the once-active channel, and the riparian zone becomes then less diverse. Summarising, these projects create discontinuities along all three spatial dimensions of a river system, and homogenise channel and floodplain habitat, to the detriment of native biota.

ii.) Native diversity decreases whilst exotic species proliferate: The altered hydrologic, sediment, and temperature régimes do not provide adequate conditions for most native species, adapted to the natural régimes. On the other hand, homogenisation of habitats allows exotics to compete better (or to compete at all). For example, some desert fish are adapted to extreme flow and temperature régimes, where no exotic generalist species could survive (Minckley and Meffe, 1987), but if the flow is regulated by a dam, then the non-native can outcompete the native species (Edwards, 1978).

Of course, the right course of action would be to restore the natural flow régime (Poff et al., 1997), but this is difficult, if not impossible for some types of hydraulic works. The changes in the natural hydrologic régime depend very much on the nature and operation of the project. The most common are: constant subtraction or addition of flow due to diversions, decreased peak flows and increased low-flows due to regulating dams, and fluctuating flows due to hydropeaking.

Upper Laramie - compact in Cache La Poudre.

**3. Some fish adaptations to natural flow régimes**

Some species have evolved quite specialised strategies for spawning during flooding stages, for example, over flooded meadow grasses or in the inundation forest ( see chapter 8 in Petts, 1984). Other species depend on the flooded forest for food (Goulding, 1980).

Salmonid species have evolved to local hydrologic conditions, so that spawning and emergence are timed to minimise entrainment of eggs and larvae by floods. This could explain the failure or success of particular trout introductions around the world. The lack of high, flushing flows can result in sedimentation of spawning beds, but ill-timed flooding can scour the bed material, entraining eggs or larvae. Fluctuating flows can result in severe mortality due to stranding of individuals, even those of larger sizes.

Discharge also acts as a migration stimulus for many anadromous and potamodromous fishes. Sometimes though, "creating" floods by releasing water from dams does not elicit movement, so that factors other than flow must be involved (Trépanier et al., 1996). LKT

Altering flows:

- Change 3D connectiveness
- Allow LWD to grow

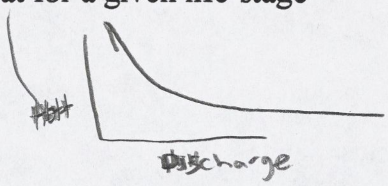
## 4. Controlling factors of fish distribution and abundance

Orth (1987) proposes that river and fish ecology should be taken into account when developing and applying instream flow-habitat models. He reviews the ecological factors that control fish populations in streams. These are energy source (food), water quality, temperature régime, physical habitat structure, flow régime, and biotic interactions. It is important to realise that these are definitely not independent !

Another way of looking at the impacts of river regulation on fish is through the hierarchical framework of causation proposed by Petts (1984). This further illustrates the complexity of the river system, even before the lateral and vertical dimensions of the fluvial system are considered (Petts and Amoros, 1996).

## 5. Crash course in instream flows methods

Jowett (1997) reviews the different types of instream flow methodologies.These can be somewhat arbitrarily classified as hydrologic (or historic) methods, that only consider historic hydrologic records; hydraulic methods, that only look at the hydraulic characteristics (depth, width, wetted perimeter, etc) of stream cross-sections; and habitat methods, that attempt to estimate the availability of physical habitat for a given life-stage of a given species.




## 6. Can we prescribe flow regimes for river fish?

There have been numerous criticisms of instream flow methods, including "state of the art" habitat methods such as PHABSIM (Orth, 1987; Castleberry et al., 1996). Indeed, it has been found for the vast majority of cases, that habitat availability is not correlated, or is even negatively correlated with fish abundance.

A big concern is the choice of "target species". How can we determine an adequate flow régime for the whole community? And for the whole ecosystem?

Moyle et al. (1998) used qualitative models to determine an instream flow régime for Putah Creek, and did manage to convince at least one judge, without needing elaborate computer models of fish habitat. Their strategy was based on requesting four different components of the flow régime: sufficient water to keep a continuous flow to the mouth of the creek, seasonally enhanced flows for spawning and rearing of native fishes, habitat maintenance flows every three to five years (to improve habitat and reduce exotics), and seasonally enhanced flows for anadromous salmonids. How different would this be from the optimal condition, the natural flow régime?

Do you think it is possible to compromise between conservation of native species and maintenance of recreational fisheries?

How important are biotic influences on fish community structure? When could one expect them to become important or prevail?

Can we prescribe instream flow régimes for fish communities?

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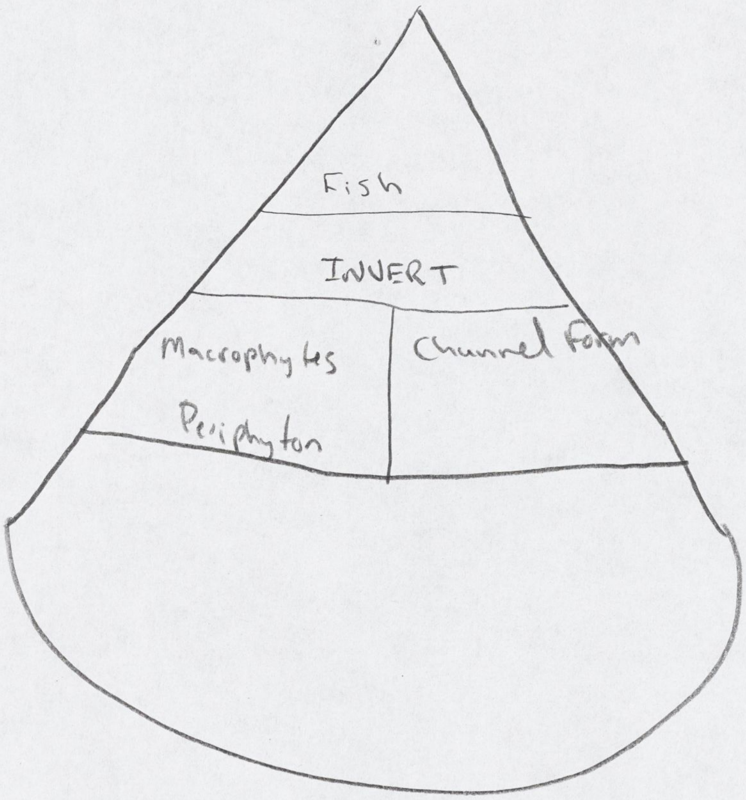

**Breeding behaviour and reproductive dynamics of Atlantic salmon: responses to temporal and spatial heterogeneity**

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For Atlantic salmon, reproduction is the ultimate goal of life and as the link between generations, it creates the genetic structure of their populations. The breeding behaviour and tactics of Atlantic salmon are shaped principally by natural selection for offspring production and sexual selection for access to mating opportunities. These evolutionary forces operate with differing intensities in the two sexes, shaping the mating system and reproductive dynamics of Atlantic salmon. Female breeding success is largely dependent on egg production, access to breeding territories and nest quality and survival. Egg production represents more than half the female's energetic investment during reproduction (i.e., maturation, upstream migration and spawning). By contrast, gamete production represents less than a tenth of the anadromous male's energetic investment. For males, breeding success is largely determine by the ability to gain access to ovipositing females, which they may do using a variety of tactics. Asynchronous female spawning and the male ability to spawn rapidly and repeatedly results in male-biased operational sex ratios that generate intense male competition for mates. This has been responsible for the evolution of specialised traits, including secondary sexual characters and alternative reproductive tactics (e.g., parr maturation). The mating system of Atlantic salmon shows many similarities to that of other salmonids, yet important differences remain that create unique reproductive dynamics. Using data from a series of rivers in the North Atlantic, the degrees of temporal heterogeneity in adult population size, sex ratio and body size are examined. These parameters affect reproductive dynamics, as revealed by the results from experimental studies, and shape the populations. Altered environments, in particular, can severely impact many reproductive parameters and have important ramifications for Atlantic salmon populations.

**LEGACIES AND LAGTIMES WITHIN FLUVIAL SYSTEMS**

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Atlantic Salmon are considered as symbols of a 'healthy' river; the restoration of migratory salmonids to rivers throughout the UK is seen as a primary objective in most catchment management plans. The primary cause of the loss of migratory salmonids in eastern England is commonly associated with the legacy of pollution which causes anoxic conditions in the estuaries in summer. However, both short-term and long-term changes have impacted upon salmon stocks. Short-term impacts include stocking and fishing practices; channel alterations; and flow regulation policies. Long-term impacts include runoff, water-quality and sediment yield changes following catchment-scale landuse changes. All of these are superimposed upon climatic changes (a) following the Little Ice Age of 1550-1850 and (b) global warming. The inability to model the nested hierarchy of human impacts upon salmon stocks remains a fundamental problem for managers.

*Stocked salmon* are fish that have had artificial spawning and/or rearing techniques applied at some point of their life cycle and/or originate from intentional releases to the wild.

*Escaped salmon* are fish that have spent some or all of their life cycle undergoing artificial propagation and originate from accidental or unplanned releases into the wild.

Although the analytical tools are not currently available to distinguish between native and wild salmon beyond the parental generation, the Working Group recommends that native salmon populations be given special consideration.

Native, wild, naturalized, stocked and escaped fish are potential components of a salmon population. Native and wild salmon, in that order, are the most valuable because of their genetic robustness and the value society places upon them. However, naturalized and stocked salmon may be genetically similar to wild salmon, although lacking the full benefits derived from natural selection.

Escaped salmon are most likely to negatively affect native, wild, naturalized and stocked salmon populations because of the unplanned and uncontrolled nature of their arrival in the wild. Where unacceptable risks or impacts are identified, appropriate actions should be taken to eliminate or limit future escapes, and, where possible, to remove escaped fish from the wild.

## 13 EVALUATION OF METHODS USED IN THE ESTIMATION OF UNREPORTED LANDINGS

The processes utilised in collecting information on unreported salmon catches in the North Atlantic as well as the types of information gathered were identified and are summarised in Table 13.1. In most countries the values provided are based upon the local knowledge of fishery managers or bailiffs who are familiar with the fisheries. The values are generally termed 'guess-estimates', indicating that they are not derived from annual surveys of fisheries or analyses of catch data. However, these guess-estimates are usually supported, in part at least, by observations of landings, knowledge of legal and illegal fishing activity, recoveries of illegal fishing gear, prosecutions, etc. In Canada, Ireland, UK(England & Wales) and UK(Scotland) estimates are the sum of values obtained for different fishery areas.

Various surveys have been conducted in Canada, Norway, UK(Scotland), UK(Northern Ireland) and UK(England & Wales) to estimate the proportion of catches reported by netsmen and anglers. This has involved comparing the reported catches with independent estimates of the landings in certain fisheries obtained by fisheries managers, regional staff and observers using log-books and other surveys. In several countries observations made during microtag scanning programmes have been used to estimate the accuracy of reported catches. In UK(England & Wales) estimates of catch reporting rates by anglers have been obtained from the analysis of catches reported after repeat reminders were sent to licence holders.

The Working Group was unable to evaluate the accuracy of the methods used for developing the estimates of unreported catches, although it considered that the data provided represented the best available information. It is important that assessments are based upon estimates of the total fishing mortality and this should therefore include unreported catches wherever possible. The Working Group recommended that all countries should continue to improve their estimates of unreported catches based upon surveys and sampling programmes.

## 14 CHANGES IN GROWTH RATE, MEAN WEIGHT AT AGE AND PROPORTION OF DIFFERENT SIZE GROUPS

This Section is related to Section 7.1. The context in which inter-relationships among growth rate, size at age and sea-age at maturity must be considered and the possible confounding effects of other variables are described there.

### 14.1 Growth Rate

No full data sets for growth rate are available. Although growth rates can be inferred from mean weight estimates at specific sea-ages, the underlying growth patterns are not evident in these sets. Life-history theory suggests that these patterns may be important in the pre-maturity growth phase. In addition, size-specific mortality is expected to distort the relationships between growth, mean weight and age in fish surviving to the abundance is overestimated at the end of the time series. This is also seen in the time series of residuals which appear to be serially correlated (Figure 10.2.2.4). There are a number of statistical issues that need to be addressed before these data can be applied in predictive models.

This relationship is remarkably similar to the relationship observed for the North American non-maturing stock complex. The overlap in the location of critical thermal habitat area suggests that non-maturing stocks from both continents are being acted upon by the same oceanic conditions by their first winter at sea. The same analysis was performed for the Northern European complex which yielded weaker correlation. However, the areas of greater relevance to the life history of northern stocks were not thoroughly investigated. The Working Group recommends that investigation of the relationship between ocean climate and pre-fishery abundance of European stocks be continued.

### 10.2.3 Development of catch advice

The assessment of pre-fishery abundance provides only a rough indication of trends in stock abundance and no predictions can be provided for the forthcoming season. In addition, the Working Group is still not able to provide spawning targets for all rivers in the NEAC area. As a result no mechanism is available for providing managers with numerical catch options. However, it appears likely from the pre-fishery abundance estimates that stocks of non-maturing 1SW salmon, the component forming the majority of the catch in the Faroes area, have shown an overall downward trend over the past 15 years despite measures being taken to reduce exploitation in most areas. As a result the Working Group recommends that managers should adopt a conservative approach in setting quotas until information is available to show that an alternative strategy will adequately safeguard salmon populations.

## 11 COMPILATION OF TAG RELEASE AND FINCLIP DATA FOR 1995

Data on releases of tagged and finclipped salmon in 1995 were provided by the Working Group and will be compiled as a separate report. A summary of national markings is given in Table 11.1. In 1995, a total of just over 3.35 million salmon were marked, a substantially lower number than in 1994 (4.42 million). The number marked was also low compared to 1993 (3.62 million). Finclips (2.29 million fish) and microtags (0.91 million) were the most frequent marks used. Most marks were applied to reared parr and smolts (3.27 million) and with only small numbers of wild parr and smolt (0.065 million) and adult fish (0.019 million) being marked.

An additional 1783 salmon were tagged at sea in the Faroes area with Norwegian Lea tags. These have not been included in the tables.

## 12 DEFINITION OF WILD SALMON

Aquaculture, sea ranching and large scale enhancement and re-establishment programs are taking place throughout the natural distribution area of Atlantic salmon resulting in the presence of artificially bred fish in the wild. It would be advantageous to be able to unambiguously distinguish among these various groups of salmon; unfortunately, this is not currently possible. Since these salmon of different origins occur throughout the North Atlantic, it is important to establish a common understanding of what is meant by the term wild salmon, and to define the other stock components that might occur. Declines in the abundance of wild salmon may be masked by an increase in abundance of intentionally or accidentally stocked salmon unless it is possible to distinguish stocked from wild fish.

The Working Group defined the following classes of salmon, based upon parental origin and how much of their life cycle was spent in the wild:

***Wild salmon*** are fish that have spent their entire life cycle in the wild and originate from parents which were also spawned and continuously lived in the wild.

***Native salmon*** are wild salmon which are members of a population with no known effects from intentional or accidental releases.

***Naturalized salmon*** are fish that have spent their entire life cycle in the wild and originate from parents, one or both of which, which were not wild or native salmon.

Perhaps there is nothing more misunderstood in the "spirit" world than single malt scotch. While all single malts are made from only one grain, malted barley, they gain a multitude of flavors from their surrounding environments. Some may pick up the flavor of the sea right through their casks, others develop sherry flavors left behind by the original occupant of the cask, while others may become smoky or peaty from the water used in their production. And still others may have all these flavors in stages throughout their ageing process. No trip to Scotland is complete without experiencing first hand some of the multitude of examples offered to the weary traveler, but with hundreds to chose from this can become a daunting task. The following list is by no means complete or the final word on single malt. It is meant only to introduce the newcomer to the classics and some of the local single malts you will find to give the reader some ideas of where to start. You could spend a lifetime sampling all the single malts in Scotland, perhaps, a lifetime well spent.

## The Classics

### Cragganmore

From the Speyside region, this is a very complex malt. The nose is sweet with an almost herbal fragrance. Medium bodied with a lingering floral/herbal finish. Personally, this is maybe my favorite malt.

### Glenkinchie

This malt comes from the Eastern Lowlands, near Edinburgh. A soft, sweet nose starts this malt, followed by a light, very clean palate. The finish is spicy and warming.

### Glenmorangie

The Scots pronounce this Northern Highlands malt to rhyme with "orangey". This is the biggest selling malt in Scotland, but the distillery is still small. There are many varieties and ages offered, all are well worth your time.

### Lagavulin and Laphroaig

The most famous of the malts from The Isle of Islay. Its many products are very full of character. Drinkers either love or hate the iodine, salty, almost medicinal flavor prevalent in these very bold offerings. Certainly worth a try to round out any malt experience.

## Local Interests

### Lochnager

Right in your backyard, this Eastern Highland distillery was visited by Queen Victoria. I highly recommend trying this most local offering. Lightly smoky, it derives the most flavor from its malt backbone.

Since the Speyside region is the most densely populated by distilleries, you will find many smaller malts not available in the U.S.. All the classics above are widely available back home but offer a great starting place for the novice. Remember, the best source of information will probably be your bar keep, so ask for recommendations and if your lucky, you may also get some local history and lore. To Your Health!

Return-Path: <mather@forwild.umass.edu>
Date: Thu, 23 Jan 1997 11:22:50 -0500
From: mather@forwild.umass.edu
Subject: Att: Robert J. Behnke, Two month update
To: donna@picea.CNR.ColoState.EDU
X-Vms-To: IN%"donna@picea.CNR.ColoState.EDU"

MASSACHUSETTS COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT
DEPARTMENT OF FORESTRY AND WILDLIFE MANAGEMENT
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DATE: January 17, 1997

TO: Participants - "Integrating across scales: predicting patterns of change in Atlantic salmon"

FROM: Martha Mather, 413-545-4895, mather@forwild.umass.edu

RE: A general update

TWO MONTHS TO GO. Less than two months remain until our workshop entitled "Integrating across scales: predicting patterns of change in Atlantic salmon" will be held in Braemar, Scotland. At this end, everything is going great. Donna, Carol, and I are looking forward to a stimulating and enjoyable meeting and hope you are too.

MANUSCRIPT DRAFTS. To receive your airline ticket, I must receive a reviewable manuscript draft ONE MONTH PRIOR TO THE MEETING, I.E. THE WEEK OF FEBRUARY 17. Workgroup co-leaders should send me preparatory materials that will ensure an insightful and productive workgroup, as outlined in the October 1 letter, by the same date. If you want to make changes to these documents in late February or early March, you can replace the manuscript/outline you send me now with a revised version before/at the meeting. Be sure that your manuscript or preparatory materials include an abstract as that is what will be circulated to other participants.

TRAVEL ARRANGEMENTS. We ask that all travel arrangements be finalized by January 31, 1997. If you haven't returned your completed, signed itinerary to Annette yet, please contact her at Carroll Travel, "carroll@javanet.com", PH 413-256-8931, FAX 413-256-8165, as soon as possible.

WORKGROUPS. Each of you should have received an outline and list of potential discussion questions from your workgroup co-leaders. If you have not provided them with your feedback, please do this as soon as possible. Everyone will also receive a packet of preparatory materials, e.g. background readings, a workgroup agenda, final discussion questions, and individual assignment, from your workgroup leader in about a month.

If you are having trouble contacting other workshop participants, please let me know. I may have revised address material that will help you.

FUTURE UPDATES. In about a month, I will be sending you plane tickets, information on how to get from the airport to the hotel, hotel brochures, some background information on the area, general meeting information, an agenda, abstracts, and some recommendations on how you might best meet your spouses and friends after the meeting.

In the meantime, if I can provide any additional information, please do not hesitate to contact me. Best wishes.

What can be done? -+ -+ - artificial culture - smolt + - grilse +.
genetics
- cage culture

I How life history variation affects abundance, biomass
1-2-+ smolt age
1-2 + sea to maturity
% repeat spawners
- "races" (re. Col. R. chinook)

II I - Wild stock, cause decline
FW vs. marine.

'III - 'Scale' - FW - more local - regional
Marine - whole N. Atl. - both Europe - N. Am.

IV - Evol. perspect. -
constraints -

BPA - report

Focus talks ~ 1 pollutants
2. Dispersal, recruitment, migration
3, interaction - behavior, physiol. in determining performance in early life
*- enhance success of fry stocking -
4. pop. dynamics I - yr. class strength
5 pop. dynamics II - density, energetics,
6 keystone habitats
what characterizes - smolt / unit density (R. Burb)
7 Restoration & rehabilitation - [illegible] II - physical hab 10%
8. II - populations
9 - pop. genetics *- Ricker - Huntsman statement
- 10

* Natural Systems

II

Europe - N. Am
trout & ocean : fertilizer!
greatest impact
why are trout vs. salmon

lake rearing

'Integrating'?

→ Work Group

papers
5 ...
19 ...
4 Pins ...

III 5 -

Larsen
Friedland's Ocean survival - when? - postsmolt - temp. correlates

Compet. interference
herring
mackerel

WORKGROUP 4

HOW DO WE APPLY THE CONCEPTS PRESENTED HERE?

The areas to be considered have been arranged into a series of units. Because our workgroup will be responsive to the deliberations of the overall workshop, it will not be sensible to take these units in a strict chronological order. Unit 1 forms a basis for defining the scope of our deliberations and will continue throughout the workshop. We will deal with Unit 2 early on and return to it at the end in Unit 5, the review. Units 2 and 3 will proceed as the concepts are defined and the workshop progresses.

Unit 1. What are "the concepts presented here"?

The workshop covers a very broad range of issues relating to the biology of Atlantic salmon. Within the time available, it will not be possible to consider all of these issues. However, we will be in a position to identify the most important issues arising from each topic, and to consider these in some detail. So the first specific question to be addressed is:

for each of the 5 plenary talks and 19 focus talks, what is the single most important a) conclusion/finding, b) untested hypothesis and c) missing data?

This question should be considered by each member of the workgroup. The results of this process will form a basis for Units 3-5 of the workgroup sessions.

Unit 2. General issues relating to the application of concepts

There is a wide range of general issues relating to the application of science to management, both in developing policy and in the practical manipulation of fisheries resources. These can be discussed independent of the specific concepts derived in unit 1. Discussion of these issues may come up with some interesting new insights into management processes but could undoubtedly go on for a long time (much longer than we have time available). However, we should attempt at least to address the following points fully:

What call is there for science-based management structures in the "real world"?

Should we, and how can we, focus science on providing the basis for pragmatic "rule-of thumb" management procedures?

How can we best communicate science to managers and politicians such that they have confidence in its practical value?

What is the current relationship between scientific theory and salmonid management and how, if at all, might incorporation of scale dependent processes into the theory influence the nature of this relationship?

The answers to these questions should provide a framework in which to consider more detailed applications of knowledge in following units.

Unit 3. Specific topics

For each of the conclusions/findings, untested hypotheses and missing data identified in Unit 1, assess the relevance to practical management and policy development bearing in mind the conclusions of Unit 2. In particular:

To which aspects of policy/management practice is this finding relevant?

Are current applications of the finding adequate or is there scope for improvement?

How critical might the untested hypothesis be, is it pivotal or incidental to management needs?

How critical are the missing data? How should they best be collected and integrated into our current framework of understanding?

Unit 4. Integration

It may be possible to identify links between the issues discussed in Unit 3 and in so doing to develop our thoughts into something of a general framework. This could be achieved in a number of ways, perhaps by considering components of the salmon life-cycle or by considering sub-groups of populations inhabiting different habitat types. Certainly, in keeping with the theme of the workshop, it will be necessary to relate findings to temporal and spatial scales of management. We will have complete flexibility in this regard until we have a better idea of the output of other units at the workshop. However, we can focus on the following questions:

What links are there between conclusions/untested hypotheses/missing data from different topics?

Are there areas of salmon biology that are particularly well understood or for which knowledge is particularly weak?

Can we identify critical gaps in the knowledge base to which future research might best be addressed?

Is it possible and sensible to integrate our deliberations into a general framework or is a piecemeal approach more realistic?

Unit 5. Review

Following Unit 4, we should have a list of important conclusions and research requirements, hopefully formulated into a general framework. We should have identified possibilities and requirements for implementing some of the concepts as components of management plans and policies. In the final topic we will re-assess the application of concepts taking on board any modification arising from Unit 4. We should consider:

Are there conflicting requirements for implementing different management needs?

What are the outstanding obstacles in applying integrated management proposals?

Looking beyond the issues of pure science, what skills, knowledge and political climate are necessary to apply effectively the concepts discussed here?

In light of the dynamic nature of science, how do we facilitate a regular interchange between the scientific and management components of the integrative framework proposed?

Suggested reading (will be posted to workgroup members)

1. Chapter 4 from "The Freshwater Imperative: A Research Agenda" by Bob Naiman et al. The chapter is titled "Linking Research, Management and Policy" and is a general overview of the problem and one approach to dealing with it.

2. Chapters 1-3 from "Compass and Gyroscope: Integrating Science and Politics for the Environment" by K.N. Lee. These chapters first give an overview of sustainability of resources, especially salmon, in the Columbia River basin. With the Columbia River salmon as a case study, Li then lays out an approach he calls "adaptive management," for integrating science and managment when dealing with sustainability of resources in large complex ecosystems.

UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE
NORTHEAST REGION
One Blackburn Drive
Gloucester, MA 01930-2298

March 25, 1997

Robert Behnke
Department of Fishery and Wildlife Biology
Colorado State University
Fort Colllins, CO 80523

Dear Dr. Behnke:

We are requesting your assistance as a peer reviewer of two reports on the status of Atlantic salmon in the U. S. The purpose of both of these reviews is to summarize the status of Atlantic salmon populations in Maine under the Endangered Species Act. The two reports come to different conclusions and we are soliciting your expert analyses of the two summaries. The first document is Section 4 (pages 17-26) of the draft Status Review for Anadromous Atlantic Salmon in the United States (January 1995). The second document is the Report of the Salmon Genetics Committee of the Maine Governor's Atlantic Salmon Task Force (December 1996; eighteen pages). The NMFS and USFWS must base their listing decision on the best available science and the constructs of the ESA. For guidance on ESA issues we have included copies of the joint USFWS-NMFS policy on listing Distinct Population Segments (February 7, 1996) and a review manuscript by Waples (1991). We would like to request your independent review of these two documents and your analysis of the applying the policy for delineating distinct population segments to Atlantic salmon utilizing existing data. We are anticipating the release of a report from the USGS Biological Resources Division that will provide additional genetic information and would like to also request your review of that document when it becomes available.

For your information, the following is a brief summary of the history of this issue. In the fall of 1993 the National Marine Fisheries Service and the U.S. Fish and Wildlife Service (the Services) were petitioned to list Atlantic salmon throughout their entire historic range as endangered under the Endangered Species Act (ESA). The Services determined that categorizing all U.S. Atlantic salmon as a single distinct population segment for consideration under the ESA was not appropriate given that some populations had persisted over time while others have been extirpated and are being restored with exogenous stocks. Service biologists used genetic and life history data to delineate a distinct population segment of Atlantic salmon that appears to meet the reproductive isolation and evolutionary significance criteria. That distinct population segment is comprised of Atlantic salmon populations in the Sheepscot, Ducktrap, Narraguagus, Pleasant, Machias, East Machias and Dennys Rivers. On September 29, 1995 the Services published a proposed rule to list this distinct population segment of Atlantic salmon as threatened under the ESA. The State of Maine commented in strong opposition to the proposed rule and submitted a report from the Salmon Genetics Committee of the Governor's Maine Atlantic Salmon Task Force (December 19, 1995). The Genetics Committee submitted a revised report dated December 1996 (enclosed) which concludes that the seven river populations of Atlantic salmon do not meet the reproductive isolation and evolutionary significance criteria. Several state and federal representatives, have requested that these materials be reviewed by independent sources. At present, the Services are compiling all comments sent by interested parties, prior to making a final listing decision.

It would be of great benefit to the Services and the State of Maine to receive additional input on this topic from fish genetic and salmonid experts such as yourself. We hope that you are able to participate. Please return the check-off sheet in the enclosed envelope indicating whether or not you will be able to assist the Services in this task.

Thank you in advance for your time and assistance. Please feel free to contact me at 508-281-9116 if you have any questions or would like any additional information to assist you in your review.

Sincerely,

Mary Colligan

Mary Colligan
Fishery Biologist

# Report of the Salmon Genetics Committee
# Governor's Maine Atlantic Salmon Task Force

December 19, 1996

Irv Kornfield, Chair
John Bailey
Ken Beland
Chuck Ritzi

SUMMARY

Presented below is a summary of our conclusions regarding the proposed listing of Atlantic salmon as threatened in the seven Downeast rivers, and comments on State/Federal management plans for salmon.

We conclude that formal listing of salmon in these rivers is not justified on the basis of the scientific information presented in the Proposed Rule. For our evaluation, we used a metapopulation perspective whereby definition of Maine Atlantic salmon is dependent upon the magnitude of temporal persistence of individual populations and exchanges of fish among them. Consideration of all available data and population genetic and demographic theory suggest that the proposed listing is not based on objective evidence, but rather on a general "conservative scientific philosophy." By extension, this conclusion implies that additional rivers in the State, and, specifically, the four rivers of concern, should also not be listed. The principal observations supporting this position are: (1) the magnitude of past stocking of Maine rivers with Atlantic salmon of synthetic origin facilitated introgression and eliminated local variability, and (2) current "natural" or "wild" reproduction is likely that of offspring from hatchery fish rather than "native" strains. Because of these historical alterations, the Proposed Rule seeks to list organisms that no longer represent an evolutionary significant component of this species.

Regardless of the listing question, we believe that the integrated State/Federal management plan for Atlantic salmon presently being implemented is a proactive, well formulated guide that will achieve its principal objectives. On the basis of genetic and historical evidence, we suggest that some modifications to this plan are necessary. River-specific broodstock management for the Penobscot, Narraguagus, and Machias will provide the degree of isolation necessary to generate local adaptations under a metapopulation paradigm. However, based on genetic and historical evidence, we strongly suggest that river-specific management is not warranted for the Sheepscot River, and that such management be reviewed for the Dennys, East Machias, and Pleasant Rivers following a series of well defined genetic tests.

## Evaluation of Proposed Rule

The genetic status of Atlantic salmon in waters in the State of Maine is exceedingly complex. Fortunately, several recent publications provide some guidance for the interpretation of available genetic and historic data (Johnson et al., 1991; Avise, 1994; NRC, 1995; Weitkamp et al., 1995).

Like several species of West Coast salmonids, Atlantic salmon in Maine may be viewed as constituting a metapopulation. A metapopulation is a dynamic aggregation of discrete populations which are periodically connected and isolated from each other; constituent geographic populations may occasionally go extinct, but can be reestablished via colonization from other populations over ecological or evolutionary time periods (see Hunter [1996] for an overview). Atlantic salmon in <u>all</u> Maine rivers, as well as geographically proximate rivers in New Brunswick, Canada (see below), constitute this metapopulation. In some systems, a temporally stable or "core" population may act as a reservoir for much of the available genetic variation. Atlantic salmon in the United States have the Penobscot as the "core" population. It is important to note that at certain periods in the past, this core population was propagated through hatchery operations rather than simple maintenance in the wild.

In contrast to natural systems, immigration and emigration among constituent units of the Atlantic salmon metapopulation have been achieved by intentional movement of fish from natural populations and stockings of hatchery fish over an extremely short period of time (Figure 1). Regardless of refinements to

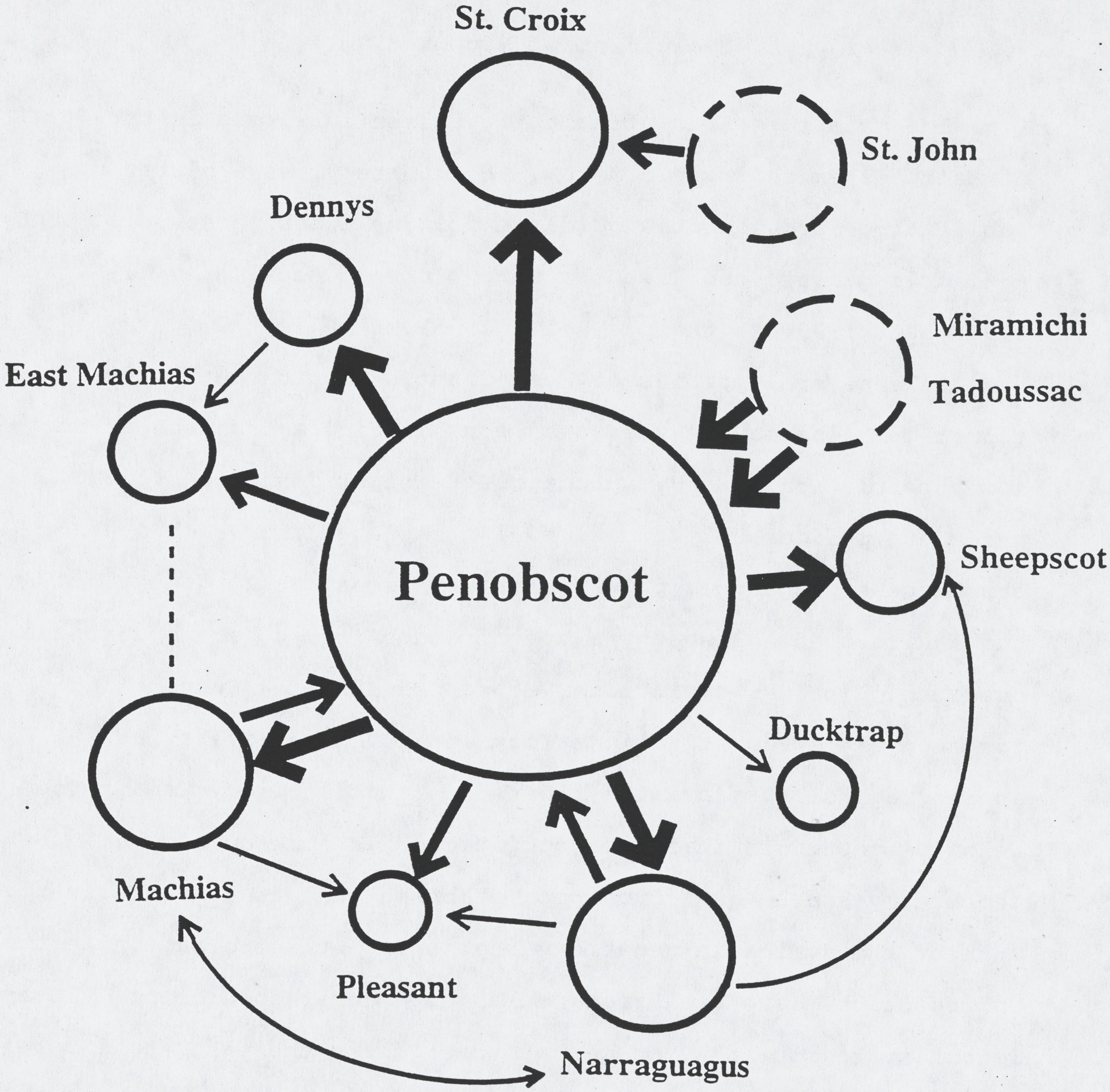


Figure 1. Metapopulation structure of Atlantic salmon in Maine. This diagram summarizes the history of population connections since the late 1800's. Circles represent discrete rivers, solid lines represent directed stocking, and dashed lines represent natural straying. Contributions of rivers to hatchery strains are indicated by arrows directed to the Penobscot. Symbols are proportional to the magnitude of population size and stocking history (see Table A). Several of these rivers lost natural salmon runs and were subsequently restored by stocking from the Penobscot. Note the extent of introductions from distant Canadian rivers (dashed circles); many direct introductions from the Miramichi, in particular, were made to other Maine rivers (see Table A). The St. Croix River is part of the Maine metapopulation; the St. John River population may also be included.

this figure, it serves as a heuristic to appreciate the extent of fish exchanges that have taken place since the late 1800s as well as a quantitative statement of the **cummulative magnitude** of intentional movements.

The extensive past movements of Atlantic salmon have engendered genetic homogeneity (King and Smith, 1994; Kornfield, 1994; May et al., 1994; Schill and Walker, 1994) which is antithetical to evolutionary adaptation. We note, in particular, that the magnitude of genetic (allozyme) differentiation associated with coho salmon ESU listings (Weitkamp et al., 1995; Fed. Reg. 60(142):38011-38030) is substantially greater than those observed in Atlantic salmon (May et al., 1994). Against this benchmark, there is no genetic justification for protection of Maine Atlantic salmon as a threatened distinct population segment (DPS) of this taxon.

To qualify for protection as a distinct population segment or, alternatively, evolutionary significant unit (ESU), two related criteria must be met (Waples, 1991): (a) populations must be reproductively isolated from conspecifics and (b) populations must be biologically significant. Simply put, the frequency and magnitude of stocking that has been practiced in Maine waters has, in aggregate, compromised both the isolation and the genetic integrity of native Atlantic salmon necessary to qualify for protection as a threatened DSP. The effects of stocking were not addressed appropriately in the Proposed Rule; the probable genetic effects, in particular, were not considered.

The most substantive feature of the management of the entire

Atlantic salmon fauna in the State of Maine has been the introduction of hatchery reared fish (stocking or outplanting) to all waters to offset the effects of dams, pollution, and overfishing. Stock enhancement has been practiced on virtually all salmon waters in the State for varying periods of time. An impressive (but partial) history of stocking is provided in the Status Review for Anadromous Atlantic salmon in the United States (Anon., 1995) associated with the presentation of river specific data. For example, the Narraguagus River has been stocked since 1918 with over 2.5 million fry, parr and smolts. Three general features of such stocking are significant to explicit statements about genetic isolation and integrity included in the proposed rule.

First, until 1969, much of the enhancement effort included introductions of fish of Canadian origin, i.e., strains from outside Maine drainages. It is generally accepted that there are several life history characteristics which distinguish Canadian and U.S. fish. From scattered field observations, some of these exotic introductions produced undesirable results (many of the returning salmon were small, late-run grilse), but these phenotypic traits did not persist. However, given the extent and duration of stocking, there is a reasonable probability of direct incorporation of some genetic material (introgression) from these fishes into native Maine strains. This introgression, by itself, might be sufficient to disqualify these seven rivers as an ESU or DPS. It is most important in this regard to recognize that Atlantic salmon in the St. Croix River are part of the Maine metapopulation because of the close geographic proximity of this river to Downeast rivers in Maine. Indeed, it is possible that Atlantic salmon from additional Canadian rivers, such as the St. John, should also be included. However, it is clear that geographically distant Canadian populations or those occupying different habitats are not part of this metapopulation, e.g., the Miramichi River.

While Atlantic salmon from the St. John are genetically indistinguishable from proximate Maine populations (May et al., 1994), they differ in life history attributes correlated with age at reproduction (e.g., proportion of returning two sea-winter fish). Is this phenotypic difference sufficient to distinguish all Maine populations as constituting a separate group (and thus potentially a separate DPS)? Two opposing factors must be considered. First, such characters as age at maturity have a high heritability in Atlantic salmon (Gall, 1993). This means that a portion of such physiological differences is genetic in origin. However, it has been established that changes in such attributes may be strongly influenced by local regimes of natural selection and that life history adaptations can evolve extremely rapidly (Quinn and Unwin, 1993). For other phenotypic characters such as timing of individual runs, it is clear that local thermal histories can potentially explain much of the observed variation.

Second, for many years, Atlantic salmon were directly exchanged among isolated rivers systems in the state (Anon., 1995). For example, fry, parr, and smolts originating from the salmon lineage in the Penobscot, Narraguagus, and Machais Rivers were introduced into the seven rivers of the proposed DPS.

Finally, "Maine" strains of Atlantic salmon, notably the Penobscot strain, have been artificially synthesized, propagated in hatchery culture, and used for extensive stocking of rivers throughout the State and other areas of New England. The origin of the current Penobscot strain is complex (Roberts, unpubl.), but includes genetic material from residual stocks in the Penobscot, Narraguagus, and Machias Rivers as well as Canadian Atlantic salmon from different drainages (Anon., 1995; Roberts, 1970). Since adult salmon were virtually absent from the Penobscot River for an extensive period during the 1950s, broodstock for propagation of the current "Penobscot" strain came from other areas. Thus, the strain of fish widely introduced into all of Maine waters is genetically homogenized from several Maine sources and may include components originating outside the United States. Simply put, if the Penobscot strain of fish were a dog, it would not be recognized by the American Kennel Club. This does not imply that the current Penobscot strain is unacceptable for restoration activities any more than it would imply that a mixed-breed makes an unacceptable pet.

Some of the changes associated with hatchery culture and introduction are predicted by population genetics theory (NRC, 1995; Slatkin, 1985). First, extensive introductions from common hatchery sources should act to dedifferentiate populations. Consistent with this, estimates of migration between rivers (Nm) based on analysis of allozyme electrophoretic variation by May et al. (1994) suggest high levels of gene flow; we suggest that such gene exchange is that resultant from past stocking. Note that periodic stocking from a common source population and exchanges frequencies among rivers (Bentzen and Wright, 1992). This effect is exaggerated by variation in the number of individuals stocked and low population sizes. Further, there is a high probability that the Penobscot strain has experienced multiple genetic bottlenecks associated with hatchery operations; the number of broodstock used in recent years may not have exceeded 30 individuals at times, and unequal sex ratios and mass spawning have occurred (E. Baum, pers. comm.). These factors act in a nonlinear manner to decrease effective population sizes (NRC, 1995; Hartl and Clark, 1989) and are of particular concern for broodstock maintenance of very small rivers that can naturally support only limited effective population sizes. Further, effective population size within a metapopulation framework is particularly sensitive to changes in numbers of local populations (Gilpin, 1991).

The most significant aspect of the genetic exchanges summarized above concerns the actual fate of introduced fishes. In particular, regardless of genetic makeup, stocking of Maine rivers has been partially successful: hatchery reared Atlantic salmon have now been observed reproducing in the wild and the probable progeny of these fishes have been routinely captured in the wild (Beland, unpubl.). In contrast to the stocked individuals, their offspring carry no signatures of their hatchery origins; they bear no fin clips or thermal marks to their scales or otoliths. Thus, these progeny of synthetic origin, now reproducing in the wild, would occur sympatrically with, but be indistinguishable from, any native fish. We conclude that the present stock is most likely a mixture arising via hybridization between feral and native components. In the Proposed Rules under evaluation here, there was no discussion of either stocking (and its potential ramifications), or the criteria used for distinguishing "native" stocks from the offspring of hatchery reared fish which are now reproducing in the wild. Instead, the Rule (and Status Review) assumes that all naturally spawning salmon carry some native genetic component important to local adaptation.

From a genetic perspective, listing of Atlantic salmon in Maine rests on two critical assertions in the Proposed Rule: that there has been "...continuous persistence of a substantial component of **native stock** reproduction" and, that "Gene flow between **wild populations**, or stock transfers, was determined not to have been sufficient to have eliminated **all historic differences** [our emphases added]." We conclude that because of (1) the extensive stocking history of Atlantic salmon in this region and, (2) the inability to distinguish between the offspring of hatchery fish reproducing in the wild from "native stocks" or "wild populations", the two above assertions from the Proposed Rule have no empirical support. However, it could be argued that low observed rates of straying constitute evidence of isolation. Two arguments can be advanced against this position. First, generally accepted rates of salmonid straying of 1-5% (Stabell, 1984; O'Connell et al., 1995) provide sufficient gene flow to prevent local differentiation unless natural selection is intense (Hartl and Clark, 1989). Second, significant local rates of straying have been periodically detected; straying of some groups of Carlin-tagged hatchery smolts released in the Machias exceeded 15% in the Narraguagus (Baum and Spencer, 1990), presumably because those rivers are only separated by about 25 km. More importantly, it is extremely difficult to document background straying rates when local adult runs are small and reporting relies on the recreational fishery. Again, we note that salmon in the wild carry no distinguishing marks of their origins.

The history of Atlantic salmon in Maine coupled with basic genetic theory strongly support the position that significant genetic changes have been induced by human activities. Thus, the criteria necessary for recognition of Atlantic salmon in these seven Maine rivers as a DPS or ESU are not met. Listing of this taxon in Maine waters, including the four Rivers of Concern is not supported. The genetic composition of the populations proposed for listing is such that they no longer represent an evolutionary significant biological component of the biological species; this situation is similar to that of coho salmon in the lower Columbia River (Johnson et al., 1991; Fed. Reg. 58(124):29553).

## Management implications

We believe that the Maine Atlantic Salmon Restoration and Management Plan, 1995-2000 is a carefully crafted, proactive approach to manage the State's salmon resources. Clearly, operational plans will need to be modified as the State's position on listing and the Federal reaction become solidified.

However, it is obvious to us that the basic plan will provide the degree of river isolation necessary to allow local adaptations to occur under a metapopulation paradigm (NRC, 1995). Given this perspective three general points should be noted. First, all rivers in Maine that support Atlantic salmon are part of the metapopulation. The potential roles and contributions of these waters should be continually evaluated. Second, specific genetic tests are central to an objective evaluation of the significance of several Maine rivers (see below). These tests will require refinement and modification of genetic studies which are currently in progress. Finally, it is obvious that on-going local adaptation of specific populations can be impacted by Atlantic salmon originating from commercial aquaculture. Such populations must be protected from the potential effects of releases from aquaculture.

To evaluate the management implications of the seven rivers proposed for listing, we developed a matrix which highlights those genetic and demographic parameters critical to recovery; many of these parameters have a strong, documented historical base. In addition, we considered currently available genetic information and projected what new genetic information could be critical for future management decisions.

Our summarization of historical demography and current status (Table A; see also Fig. 1), as well as genetic information suggests an hierarchy strategy for management of the seven Downeast rivers. First, given its small absolute population size and the possibility of retention of aboriginal genetic material (Kornfield, 1994), the **Ducktrap River** should be protected but

## Genetics Working Group River Analysis Matrix

### Part A. The 7 rivers proposed for Threatened status under ESA.

| River (references) | Prob. of bottleneck in wild (years) | Prob. of bottleneck in hatchery | Extent of stocking (sources) | Evidence of past straying | Strain currently in hatchery | Estimated ($N_e$) in current broodstock (per cohort) | Salmon Habitat ($100m^2$) units | Adult returns @ 2 smolts/unit and 3% sea survival | Potential for aquaculture strays |
|---|---|---|---|---|---|---|---|---|---|
| Dennys (1, 2, 3, 5, 11, 12, 15) | High - 1889-1920's High - 1990's | Moderate - multiple strains | High P, MR, M, N, C | Yes Aqua-culture 1990's | Yes | Moderate SR kelts <10 1992-1995 captive parr 25-75+ | 2,415 | 150 | High |
| East Machias (1, 2, 3, 8, 12, 15) | High - early 1800's Moderate 1860's-1940's | High - for 1940 release Moderate - multiple strains | High P, D, EM | Yes Aqua-culture 1980's and 1990's low #'s of hatchery origin | Yes | Moderate 1993-1995 captive parr ≤ 50 | 2,145 | 125 | High |
| Machias (1, 2, 3, 10, 12, 15) | High 19th century Moderate 20th century | Moderate - multiple strains | High P, M, MR, N, | Yes low #'s of hatchery origin | Yes | Moderate SR kelts <10 1992-1995 captive parr 50-125+ | 6,685 | 400 | High |
| Pleasant (1, 2, 3, 12, 15) | High- 1860's-1940's Moderate - 1980's High - 1990's | Moderate - multiple strains | High P, C, M?,N? | None | Yes | Low 1995 parr age-1 <25 age-0 <10 | 1,085 | 75 | Moderate |
| Narraguagus (1, 2, 3, 4, 6, 12, 15) | High 19th and early 20th centuries | Moderate - multiple strains | High P, N, MR, M, C | Yes low #'s of hatchery origin | Yes | Moderate captive parr 1992-1995 100-150+ | 6,015 | 350 | Low |
| Ducktrap (1, 3, 7, 15) | High - Dams 19th century Historically small #'s | No | Low- (P) | None | No | N/A | 585 | 35 | Low |
| Sheepscot (1, 2, 3, 7, 12, 13, 14, 15) | High - 1870's -1952 and 1990's | Moderate - multiple strains | High - (P,N,M, MR,C) | Yes | Yes | Low 1995 SR adults < 15 1993-1995 captive parr 30-40+ | 2,845 | 250 | Low |

Note: $N_e$ for the current broodstock cohorts held in the hatchery is based upon the following:

Sea Run adult broodstock - Number currently being held in hatchery.

Captive parr cohorts - Estimated number of sea sun adults spawning in river two years prior to capture.

P - Penobscot River
M - Machias River
N - Narraguagus River
EM - East Machias River
D - Dennys River
MR - Miramichi River (Canada)
C - Unknown Canadian Egg Source

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should not be enhanced by any introductions; the population size is too small to establish a genetically prudent broodstock program (Busack and Currens, 1995; NRC, 1995). Second, for the **Sheepscot River**, single locus fingerprinting data (Kornfield, 1994) strongly suggests that the current population has passed through a recent population bottleneck; the effective number of alleles is significantly less than that observed in all other Maine rivers and, in contrast to those rivers, no unique alleles were observed. Given that the natural Atlantic salmon run in this river was virtually absent for a period in excess of 70 years (Kendall, 1935; Meister and Foye, 1963), the current salmon population is assuredly of Penobscot origin. It is inappropriate to maintain a river-specific broodstock program for the Sheepscot. Third, given its small population size, probable past bottlenecks and proximity to the Narraguagus, we believe that river-specific broodstock management of the **Pleasant River** may not be warranted. Instead, salmon from Narraguagus program could potentially be stocked here. We suggest that an appropriate genetic assay using hypervariable microsatellite loci could provide information necessary to more rigorously evaluate this strategy. In particular, **using a minimum of three <u>hypervariable</u> microsatellite loci (McConnell et al., 1995; Slettan et al., 1995), river-specific management would not be warranted if a population sample of Pleasant River Atlantic salmon were statistically indistinguishable (Zaykin and Pudovkin, 1993) from either the Narraguagus or the Penobscot, or was demonstrably depauperate in variation compared to other Maine rivers.** We stress that the microsatellite loci to be used **must** contain a large number of alleles with intermediate frequencies; loci with few (< 4) alleles or those with alleles near fixation are not capable of providing the sensitivity demanded by these tests (see McConnell et al., 1995). The same management perspective and genetic tests should be applied to both the **East Machias River** (where the appropriate comparison would be with the Machias River and the Penobscot River) and the **Dennys River** (where comparisons should be made with the Machias, St. Croix, and Penobscot). Finally, within the framework of management using the metapopulation perspective, we recognize that river-specific broodstock and management be applied to Atlantic salmon of the **Machais River**, **Narraguagus River**, and **Penobscot River**. Such programs will provide opportunities for long-term adaptation under the metapopulation model.

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Why Aren't There More Atlantic Salmon?

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ABSTRACT

As a species, Salmo salar is now more abundant than during its entire existence. Virtually all (ca. 98% of biomass) of this present abundance, however, is due to artificial culture of a food fish. Wild Atlantic salmon, whose value is based on its qualities as a sport fish, has been in a general downward cycle. Evolutionary constraints decree that S. salar never was and never can be as abundant as some species of Pacific salmon. Its Pacific basin analogue is the steelhead, Oncorhynchus mykiss.

Extrapolation from commercial catch records indicate a maximum abundance of all wild and hatchery supplemented adult Atlantic salmon throughout their range during the past 50 years to be in the range of 25,000 to 35,000 tonnes. In ancient times, during a high abundance cycle when all rivers throughout the historical range were unimpaired, maximum abundance should have been about twice that of the maxima of recent times.

Fish professionals must serve the fish as the primary customer.
A conclusion of the American Fisheries Societies' Point-Counterpoint Debates

In an era of biodiversity awareness, such a statement is indeed environmentally correct. It is obvious, however, that we serve some fish species more than others. All fishes are not equal in the eyes of the public, and it is public perception that ultimately determines the amount of funding and emphasis on selected fish species. Consider the volumes of literature produced, the employment of biologists, managers, and administrators, the number of symposia, conferences, and workshops, and the private organizations devoted to protecting and enhancing the well-being of a fish species in regards to Salmo salar as opposed to an "ordinary" fish such as the slimy sculpin, Cottus cognatus. In addressing the question of Atlantic salmon abundance, we must recognize a sharp dichotomy within S. salar; the wild (and hatchery supplemented) salmon of legend and folklore and the fish reared in pens like cattle fattened in a feedlot.

There is now several fold greater abundance of Atlantic salmon than likely ever existed since the origin of the species. According to the Idaho Aquaculture News (Second Quarter 1996), European production of cultured Atlantic salmon reached 375,000 tonnes (270,000 from Norway) in 1995. If the production of North America and, especially, Chile is added, world output of cultured Atlantic salmon is now about 500,000 tonnes or greater. With North Atlantic stocks of wild salmon in a downward cycle (hopefully beginning recovery), the current biomass ratio between cultured and wild, adult Atlantic salmon (returning to spawn) is about 50:1.

Particularly in areas of intensive cage culture, there are impacts of cultured salmon on wild salmon such as interbreeding of escaped fish leading to outbreeding depression in wild populations and proliferation of pathogens and parasites. The positive aspect of cultured salmon in relation to wild salmon has been the lower price of Atlantic salmon as a food fish; now one of the more reasonably priced fish on the world market. This lower market value is a disincentive for the commercial harvest of wild salmon and a powerful argument to maximize the return of spawners to their home rivers to maximize regional economic benefits by maximizing the value of S. salar as a sport fish.

For those involved with management, enhancement, and restoration of Atlantic salmon, the great difference in values between cultured and wild salmon should be understood so that programs can be explained and defended. In terms of tonnes of S. salar and the values associated with tonnes of fish, there is an enormous chasm between cultured and wild Atlantic salmon, as if they were two different species--a noble species and an ordinary species.

## Evolutionary Constraints on Abundance

Probably in the Miocene a common ancestral species separated into two isolated groups, one in the North Pacific basin and one in the North Atlantic basin. The North Pacific isolate gave rise to the genus Oncorhynchus and the North Atlantic group to Salmo (Behnke 1992). A similarity in ecological divergences between the Atlantic and Pacific evolutionary lines is the trend toward increased anadromy in the six species of Pacific salmon and in the Atlantic salmon, and the trend to expand the inland, freshwater range in rainbow and cutthroat trout (O. mykiss and O. clarki) and their derivatives in western North America and the brown trout, S. trutta, in Europe (including its spread to Asia and North Africa). Although the rainbow trout, as a whole, is the western North American equivalent of the brown trout, the anadromous form of O. mykiss, the steelhead, in regards to determinants of abundance, such as smolt density per unit area, is the equivalent of Atlantic salmon.

A major difference between evolution in Oncorhynchus and in Salmo is the much greater diversity of extant species. This difference is not so pronounced between Pacific and Atlantic trout as it is between the single species of Atlantic salmon versus the six species of Pacific salmon. Pacific salmon evolution reflects a consistent trend to reduce dependence on the freshwater environment and increase the potential for marine growth--from O. masou, with many resident freshwater populations and with anadromous populations in which half or more of the life span occurs in freshwater, to pink and chum salmon, O. gorbuscha and O. keta, that smolt and enter the ocean soon after emergence. The sockeye salmon, O. nerka, maximizes smolt production per unit rearing area by specializing as a lacustrine planktivore. This adaptation led to many resident freshwater populations called kokanee. In southern Alaska and on Kamchatka, sockeye salmon also have stocks that are not dependent on lakes and migrate to the ocean from rivers as young-of-the-year. Coho salmon, O. kisutch, typically spend one year in rivers before smolting (in spring of their second year), and return to spawn after about 15-16 months of marine growth, comparable to Atlantic salmon grilse. Chinook salmon, O. tshawytscha, express highly variable life histories in different parts of their range and in different populations in the same river basin, such as the Columbia. Smolts typically migrate to the ocean as young-of-the-year in the southern parts of the range, and as yearlings in the more northern rivers and in some far-inland populations. The typical period of ocean growth for most chinook populations is two to four years. The Pacific salmon radiated into six species with diverse life history forms evolving a semelparous life history along the way (all die after spawning except for resident populations of O. masou). Compendiums of life history information on all species of Pacific salmon is found in Groot and Margolis (1991). The Atlantic salmon is the sole extant species of the evolutionary line leading to anadromous specialization in the North Atlantic basin. The divergence of S. salar and S. trutta occurred long ago (probably in Pliocene) which suggests some extinctions occurred along the way. In any event, the trend to increase adult abundance by reducing dependency on freshwater and increasing smolt production per unit area in Pacific salmon is not apparent in Atlantic salmon. For this reason, the abundance of naturally reproduced Atlantic salmon never was and never will be comparable to that of Pacific salmon, especially pink, chum, and sockeye salmon. Atlantic salmon abundance is comparable to steelhead abundance in comparable spawning and rearing rivers because of their similar life histories. The Columbia River, historically, was the most productive river for both steelhead and chinook salmon. According to Chapman (1986), under intensive fishery exploitation, the greatest commercial catch of Columbia River steelhead was 2,200 tonnes in 1892. Peak commercial catch of chinook was 19,540 tonnes in 1883, about a nine-fold difference in maximum abundance as expressed in biomass. The steelhead can be a useful surrogate for Atlantic salmon especially in the development of techniques for enhancement and restoration.

A similarity between Pacific salmon and rainbow and cutthroat trout on one hand and Atlantic salmon and brown trout on the other is that Atlantic salmon and all species of Pacific salmon, with the exception of O. masou of Taiwan and southern Japan and one Japanese population of O. nerka, have no glacial or preglacial relict populations outside the range of anadromous populations. A great amount of evolutionary diversity is found in the 14 subspecies of cutthroat trout occurring far inland to the headwaters of the Columbia, Missouri, Colorado, and Rio Grande river basins. Primitive forms of rainbow trout occur in Mexico far south of anadromous populations (Behnke 1992). Brown trout left relict populations around the Mediterranean and Adriatic seas and extended their range inland to the Black and Caspian sea basins and to the Amu Darya drainage of the Aral Sea. Regan (1938) was so convinced that S. salar must have left a relict somewhere during a glacial epoch that he considered Salmothymus obtusirostris, a trout-like fish endemic to a few eastern Adriatic rivers, to be such a relict, even classifying obtusirostris as a subspecies of Salmo salar. Regan believed this to be an example of pedogenesis, or sexual maturation in the parr stage as an adaptation to a freshwater life history. Reference to obtusirostris as a glacial relict derivative of S. salar is still found in contemporary literature (Mills 1989). Although Salmothymus obtusirostris could reasonably be classified in the genus Salmo, it is not derived from nor closely related to S. salar (Behnke 1968).

Evidently, specializations for anadromy has restricted the evolutionary options of S. salar to diverge into a multitude of life history forms and geographical races comparable to O. mykiss or S. trutta. Atlantic salmon, within the range of anadromous populations, has given rise to resident lake salmon in a few European lakes and numerous North American lakes in postglacial times. The greatest life history diversity as expressed in age at maturity, growth, life span and maximum size is found among lake salmon populations inhabiting waters with very different food resources. The Atlantic salmon native to Lake Ontario (extinct for the past 100 years) attained maximum weights to 20-21 kg (Parsons 1973). Resident salmon occurring in some acidic ultraoligotrophic ponds in Newfoundland with inadequate forage sexually mature at about 15cm and have maximum sizes of from 20 to 25 cm (Leggett and Powers 1969; Barbour et al. 1979). Only one ~~known~~ entirely fluvial Atlantic salmon population is known. It occurs in the River Namsen, Norway, above a barrier with no other fish species (Berg 1985).

The most ancient geographical separation of the species is between the Atlantic salmon of North America and Europe. Although genetic analysis have shown high similarity among all S. salar, the study by Taggart et al. (1995) on DNA markers revealed a highly consistent differentiation between European salmon from Spain to Norway and Iceland and North American salmon from Maine and Canada. The consistency of differentiation between European and North American DNA markers indicates that Atlantic salmon were in North America prior to the last glaciation and persisted somewhere during the glaciation.

Although S. salar can be considered as a "genetically consolidated" species compared to the magnitude of disjunct, geographically divergent groups of S. trutta or O. mykiss, there are, certainly, important hereditary-based differences in life history adaptations among populations of S. salar that are not apparent from data of molecular genetics. An understanding of the hereditary basis of phenotypic (or quantitative) adaptive traits is important for proper salmon management at the population level (Behnke 1995; Hard 1995 a, b; Healy and Prince 1995). As shown by Mayama (1989) for two O. masou populations in neighboring rivers on Hokkaido, a small hereditary difference in life history (timing of smolt migration) can result in a major difference in marine survival. A most important goal for Atlantic salmon management is to maintain hereditary distinctions intact and in place, regardless of molecular genetic data on "identity."

## Historical Abundance

Erhard Rostlund, an anthropologist, attempted to estimate the total fisheries resource available to native Americans in prehistoric times. For historic Atlantic salmon rivers of the U. S. (About 28-30 rivers from the Housatonic to the St Croix) he made an assumption that..."If the Atlantic salmon ran in quantity per unit area somewhat like the Pacific salmon, about 14,000,000 or 15,000,000 pounds of salmon would represent the possible annual yield." (Rostlund 1952). If "annual yield" represented 50% of the total spawning runs, then total abundance of Atlantic salmon returning to New England rivers each year would have been on the order of 12,000 to 14,000 tonnes according to Rostlund's calculations. This would have been the abundance of legend and folklore, but it is a gross overestimate and such an assessment must be considered in the realm of "scientific" folklore. As discussed above, the "quantity per unit area," or smolt density, is quite different between Atlantic salmon and Pacific salmon. If steelhead were used as a surrogate for quantity per unit area, Rostlund might have come close to reality.

It is possible to take a best-case scenario, playing a game of "ifs," with each "if" based on a highly improbable assumption then make a great leap of induction to arrive at a greatly inflated estimate for historic abundance of New England salmon--comparable to court testimony of a clever, but unprincipled expert witness.

Crozier and Kennedy (1993) presented data on the River Bush, Northern Ireland, that must be one of the most productive Atlantic salmon rivers in the world as expressed in per unit area of smolt density and survival to returning spawners (virtually all spawners are grilse). The watershed of the River Bush is 33,700 ha. Stream water surface area is 84.5 ha, of which, 41 ha is usable salmon habitat. This amount of usable habitat equals 4100 habitat units of 100 $m^2$ each. From 1973 to 1991, smolt migrations ranged from 14,509 to 44,958, or from about 3 to about 11 smolts per habitat unit. Marine survival, calculated from catch and escapement of grilse returning the following year ranged from 25% to 36%, averaging 33%. A best-case scenario for the River Bush would be about four returning salmon per habitat unit.

According to estimates of the U.S. Fish and Wildlife Service and the National Marine Fisheries Service (1995), historically, the Connecticut River contained 262,500 habitat units for Atlantic salmon spawning and rearing. The total for all other New England rivers is about 300,000 habitat units. According to these estimates, about 562,000 Atlantic salmon habitat units were once available for freshwater salmon production in New England. At four returning salmon per unit, the run to the Connecticut River would have been more than 1 million and more than 2.2 million to all New England rivers. Given that New England salmon averaged about five kg (virtually all were multi-winter fish) (Kendall 1935), total annual abundance in biomass would have been about 11,000 tonnes according to this improbable scenario of extrapolation, induction, and "ifs." It is interesting to note, however, that this fantasy estimate is rather close to Rostlund's estimate.

The indirect method of assessing historic (or prehistoric) abundance by habitat units and assumptions on marine survival contain obvious flaws for attempts to arrive at an overall estimate of abundance through time for the species as a whole. All habitat units are not equal in smolt production among rivers or in the same river in different years. Marine survival can be highly variable. There are short-term and long-term cycles influencing both the freshwater and marine phases of life history. The most direct quantitative data on overall abundance is commercial catch statistics. Catch statistics, however, require assumptions on escapement to estimate total abundance and such data are not available over a broad geographical region. For better precision, catch statistics should be based on salmon caught in or near the mouths of their home rivers, at the time of their maximum weight before spawning. Open sea fisheries such as off of Greenland and north of the Faroes, introduce inherent errors. For example, what would be the survival and weight gain until the time of return to home rivers of salmon if they were not taken in the open sea fishery?

Catch data based on coastal and river fisheries should ideally apply only to sexually mature salmon returning to spawn. If only grilse are involved, estimates of catch plus escapement would be assumed to essentially represent total marine biomass (recognizing that the present year's smolts may have entered the sea one to three months before the grilse return). With multi-sea winter salmon (and repeat spawning salmon that may skip a year between spawnings), considerable biomass of immature salmon remains in the sea, not accounted for in abundance estimates based on catch plus escapement. This is comparable to abundance estimates for Pacific salmon based on catch plus escapement. Each year during the harvest of chinook salmon returning to spawn, several year classes are still growing in the ocean.

Mills (1989 fig. A1) depicted total North Atlantic commercial salmon catch from 1960 through 1987. The catch data indicate a high abundance cycle from the mid 1960's to the mid 1970's, with catch maxima of about 12,000 tonnes in 1967 and 1973. During this period, the open sea fishing on immature salmon peaked, reaching a maximum of about 3,000 tonnes. If these salmon were not caught in the open sea and returned to their home waters the following year, the total biomass of sexually mature fish in the 1965-1975 period should have been higher. Reddin and Friedland (1993 fig. 4.1) presented a graph of total commercial North Atlantic salmon catch from 1960 through 1991. They separated Canadian catch from that of other countries. Their figure generally agrees with Mills' figure except for maxima of about 10,000 tonnes compared to about 12,000 tonnes. When the graph is extended beyond 1988, a consistent downward catch trend into the 1990's is apparent.

No comprehensive, basin-wide escapement data are available for total abundance estimates of sexually mature salmon. During periods of past high abundance, it can be expected that the commercial fishery was intensive and exploitation rates of the most abundant runs was high. Crozier and Kennedy (1993) give exploitation rates for the River Bush salmon runs from about 60% to about 90% over ~~on~~ many years. If an overall exploitation rate of 60% is used for the North Atlantic basin as a whole during catch maxima of about 12,000 tonnes, then total abundance in biomass of all salmon returning to their home rivers would be on the order of about 20,000 tonnes. If the salmon of the Barent and White seas of the Arctic Ocean of northern Russia and salmon of the Baltic Sea are added to the North Atlantic estimates, the total maximum biomass of all S. salar returning to spawn during the past 50 years could have been on the order of 25,000 to 35,000 tonnes.

Figure 4.1 of Reddin and Friedland (1993) shows a rather consistent correlation between the Canadian catch and the European catch of salmon. This correlation indicates that throughout the range, ocean conditions, rather than freshwater conditions, is the most pervasive and significant determinant of abundance of adult salmon. This same figure shows that, on average, the Canadian catch was about 30 to 35% of the total catch of the North Atlantic basin during 1960-1991.

The greatest Canadian commercial catch of record was about 6,000 tonnes in 1930 (Dunfield 1985). A scenario based on a Canadian catch of 6,000 tonnes and the assumption that this represented 33% of the total North Atlantic catch, would give an estimate of 18,000 tonnes of Atlantic salmon harvested in the North Atlantic basin in 1930. At 60% exploitation, total abundance of North Atlantic salmon would have been about 30,000 tonnes. This could be considered as a one in 100 year maximum. Baltic and Arctic Ocean salmon would add several thousand additional tonnes.

What might have been the abundance of Atlantic salmon before the impact of human civilization? Before dams and pollution of rivers and gross modifications and degradation of watersheds, Atlantic salmon occurred in Europe southward to the Duoro River of Portugal and southward to the Housatonic River in North America. Salmon became extinct in many rivers, including large rivers such as the Connecticut in North America and the Rhine of Europe, and were reduced to small remnants of original abundance in most other rivers in the southern parts of the range. Abundance of salmon when all rivers in the historic range were operating at maximum salmon-producing capacity, and during period of favorable ocean conditions is a matter of speculation, but it must have been considerably greater (twice greater?) than the maxima of the twentieth century.

For total historic abundance of S. salar, resident lake ("landlocked") populations should also be considered. Compared to anadromous salmon, lake salmon, at maximum abundance, would make up only a small fraction of the species' abundance. This abundance, however, could have been a significant amount considering the magnitude of the waters once inhabited. The three largest lakes of Europe, Ladoga and Onega in Russia, and Vänern in Sweden, have a combined surface area greater than 3,000,000 ha and all have native populations of lake salmon. Hundreds of North American ponds and lakes have or had native lake salmon. North American salmon lakes, in total, have about twice the surface area of the three largest European lakes, but Lake Ontario, where the native salmon is long extinct, is responsible for most of this amount. Considering all waters that historically had native populations of resident freshwater Atlantic salmon, and assuming that overall salmon biomass averaged only 0.1 kg/ha then the total biomass of all nonanadromous salmon in historic (or prehistoric) times would have been at least 1,000 tonnes.

Any estimates of maximum abundance of Atlantic salmon, even with best-case scenarios and speculative extrapolations, would still pale in comparison to Pacific salmon. In 1995, the commercial catch of Pacific salmon in Alaska alone was 217 million fish (ca. 500,000 tonnes or more) (Holmes and Burketet 1996). This catch (and abundance) must have been exceeded in 1996 when canneries reached capacity, markets became saturated, fishing ceased, and millions of carcasses piled up in spawning streams (mostly pink and chum salmon). One river system in Alaska, the Kvichak, with Lake Iliamna, has had runs of sockeye salmon estimated up to 42 million (catch plus escapement). With an average weight of 2.4 kg, the biomass of sockeye salmon returning to the Kvichak River alone can reach 100,000 tonnes (Dunaway and Fleischman 1996).

There is an inverse relationship between abundance and value per salmon. Beyond a certain point of abundance, each additional fish becomes devalued as expressed in commercial prices or anglers willingness to pay to catch each additional salmon. Although I don't expect greatly increased abundance of Atlantic salmon to create a serious problem, and most would happily embrace such a problem, elimination of commercial fishing combined with favorable ocean conditions, should result in returns of salmon to many rivers that will be several fold greater than during the recent past. The challenge would be to maintain maximum economic value for each salmon caught by anglers. That is, to avoid the inverse relationship between abundance and value, but this is a matter of economics and business management, not biology.

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(1) A major difference between coho smolts and Atlantic salmon smolts is in their size. Coho smolt size varies in different rivers and in the same river in different years but ranges from about 75mm to about 125mm, mostly in the range of 80 to 110mm, considerably smaller than Atlantic salmon smolts, especially in relation to weight and size of territories. For comparable rivers, coho smolt density can be several times that of Atlantic salmon. Bradford et al. (1997) lists coho smolt abundance reported from many rivers. The Situk River, Alaska, is 69km in length and produced 213,000 coho smolts. Barrett Creek, draining a tiny watershed in British Columbia of 37ha, produced 5006 smolts. Thus, in smolt production per unit area, coho salmon can enormously exceed the output of Atlantic salmon.

(2) It was long assumed that the only entirely freshwater flervical population of Atlantic salmon occurred above a barrier in the River Namsen, Norway (Berg 1985). Gibson et al. (1996), however, found several populations of drawf flervical salmon occurring with brook trout in Newfoundland.

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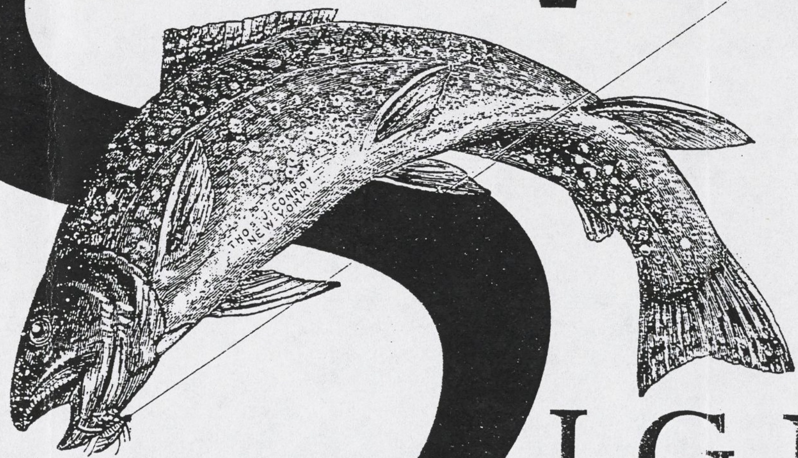
# The {in} Significance of Atlantic Salmon



Common folklore in New England holds that Atlantic salmon (*Salmo salar*), a highly prized game and food fish in both Europe and North America, were once so abundant in the rivers that early colonists could walk across the backs of the fish as they ran up the rivers in spring to spawn. There are tales that people became so tired of eating them that a law was passed requiring poor servants and laborers to be fed the fish no more than twice a week.

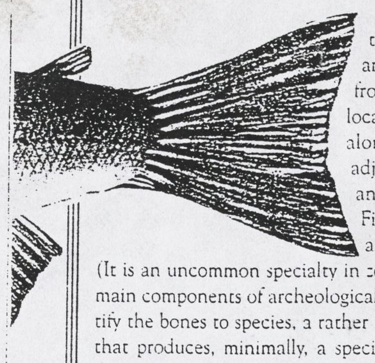
Based on such accounts, restoration biologists have written that "the Atlantic salmon rivaled the cod as an important and reliable source of protein to the early New England colonists."[1] The anthropologist Erhardt Rostlund argued that "there is theoretical reason for thinking that Atlantic salmon, per unit area, was at least as plentiful as Pacific salmon."[2]

When Europeans first arrived in northeastern North America, the Atlantic salmon was reportedly found in every river not barred by impassable falls, from northeastern Labrador to the Housatonic River, and possibly into the Hudson River.[3] John Smith commented in 1616 that "on the western shores of the Atlantic, it [salmon] is found from Greenland to the Hudson, but is exceedingly rare in the latter river, and never penetrates farther south."[4] Common belief holds that at the turn of the 19th century, increasing pollution in the rivers (sewage, mills, etc.), weir fishing at the mouths of the rivers, and the construction of large main stem dams across the rivers (for example, at South Hadley and Turners Falls on the Connecticut River in 1794 and 1798) caused salmon to become extinct in the rivers of southern New England and severely depleted in northern New England. Fisheries biologists contend, on the basis of their interpretations of historical accounts, that the Atlantic salmon resource today is a mere remnant of the fishery prior to the introduction of dams and pollution in the rivers; for this reason, restoration programs to "bring back the salmon" have been, and continue to be, an extensive and ongoing effort supported by an effective sports fishermen's lobby.

To an anthropologist, the importance of the reportedly dense salmon runs of New England in the past is the valuable food resource that the fish would have provided the native peoples of the area long before the Europeans arrived. In the Pacific Northwest, where vast runs of Pacific salmon have survived up to the present day, aboriginal peoples harvested, preserved, and stored enormous quantities of the fish such that it enabled them to free their time from the everyday subsistence activities typical of most hunter-gatherers without agriculture. This contributed to the development of highly complex cultural and social institutions, art, ritual ceremonies, sophisticated technologies, trade networks, and permanent villages; it also supported high population densities. The basic cultural pattern of the Northwest Coast aboriginal peoples was impacted by Europeans so much later than in the New England region that most of their traditional culture survived to be described by ethnographers as late as the turn of the 20th century. This is unfortunately not so for the Atlantic seaboard where introduced European diseases had such a devastating impact on the aboriginal peoples as early as the 15th century that little remained of their way of life, culture, and population.[5] Hence, it is mostly only through archeology that we can attempt to reconstruct the cultural traditions in this region. The possibility that the New England aboriginal cultures may have had access to a salmon resource comparable to that in the Pacific Northwest is therefore of interest in archeological reconstructions, and the past presence of a salmon resource has been assumed by numerous archeologists working in the region.[6]

In 1980 the author began a study of the prehistoric fisheries of the Boothbay region of the Maine coast through archeological analysis of the fish bones excavated from pre-

By Catherine C. Carlson



historic middens. The initial study involved the analysis of the fish remains from 21 archeological sites located in the estuaries and along the coast of Maine adjacent to the Sheepscot and Damariscotta rivers.[7] Fish bone had never been analyzed for New England. (It is an uncommon specialty in zooarcheology.) One of the main components of archeological faunal analysis is to identify the bones to species, a rather technical process, but one that produces, minimally, a species list and relative abundances, eventually providing an understanding of the relative importance and abundances of certain fish species to the diet of prehistoric aboriginal peoples. Analysis of 30,000 fish bones revealed a lack of salmon bones in the site assemblages, an unusual circumstance in view of the quantity and dominance of salmon bones at similar sites in the Pacific Northwest (British Columbia). A possible explanation was that the small drainages of the Sheepscot and Damariscotta rivers did not support salmon runs (even though there were historical accounts of runs in the Sheepscot), and that cod, rather than salmon, were the principal seafood resource for the aboriginal peoples of the region.

However, the lack of salmon in the Maine sites remained an unanswered question requiring a broader regional approach to the study of prehistoric fishing.[8] As research proceeded, it became apparent that there were no salmon bones in site after site in New England, although bones of numerous other species were recovered. Eventually, the analysis or review of bone remains from over 75 New England sites[9] revealed only two possible salmon vertebrae at Kidder Point and Lindquist[10] and possibly two at Frazer Point[11] (all of which may be trout). How could this be, given that the historic accounts describe such vast quantities of the fish? Did aboriginal peoples not catch them, perhaps because they lacked suitable fishing gear, or because they did not like them as a food item? Do the bones not survive in the soil conditions of New England? Were the historical accounts of salmon grossly inaccurate, embellished fish tales? Did the salmon runs not really exist in the rivers of New England, or were they so minimal as to be undetected archeologically? If there really were no salmon, then what were the implications for archeological reconstructions based on analogies with the Pacific Northwest?

DID THE SALMON RUNS NOT REALLY EXIST IN THE RIVERS OF NEW ENGLAND? THEN WHAT WERE THE IMPLICATIONS FOR ARCHEOLOGICAL RECONSTRUCTIONS BASED ON ANALOGIES WITH THE PACIFIC NORTHWEST?

Essentially the problem was one of a discrepancy between historical accounts of vast quantities of salmon in New England rivers and the archeological record that showed virtually a complete absence of the fish. The possibility that aboriginal peoples lacked suitable technology for harvesting salmon, or that they found them disagreeable as a food item, could not be supported.[12] Likewise, the suggestion that the bones do not survive in the soils of New England was also discredited because of the fact that so many other fish species with equally fragile bones have been preserved, and salmon certainly have been preserved in great quantities in archeological sites in the Pacific Northwest. How then to account for the absence?

One part of solving the problem was to review critically the primary historical documents about fish. The sources claiming vast quantities of salmon were 19th- and 20th-century syntheses and compilations made long after fishing events, and frequently based on hearsay, and were therefore subject to bias or error in interpretation due to their derivative nature. Anthony Netboy's unreferenced statement that in colonial New England, salmon "were sometimes so thick in the rivers that they overturned small boats,"[13] or A. G. Huntsman's report of an 1879 account in Lake Ontario that the salmon were once so abundant that women "seined them with flannel petticoats"[14] are undoubtedly examples of embellishment—the classic "fish story"—that cite nothing other than hearsay. Likewise, the story that poor laborers should not be made to eat salmon more than twice a week because of its cheap abundance was investigated by Newton Brainard and discredited: "Let us review the old story of the apprentice agreements which were supposed to have protected the poor by a clause stipulating that he was not to be required to eat salmon more than twice a week. This story was intended to show how plentiful and cheap salmon was here [Connecticut River], and has been generally accepted as true. As a matter of fact, it is an English or Scotch tradition which is not true, even in the land of its origin. As long ago as 1867 the *London Field* offered a reward of



THE QUESTION OF THE ABUNDANCE OF ATLANTIC SALMON IN NEW ENGLAND PRIOR TO ITS DEMISE AROUND A.D. 1800 HAD ESSENTIALLY NEVER BEEN THOROUGHLY INVESTIGATED THROUGH A CRITICAL ANALYSIS OF PRIMARY DOCUMENTS.

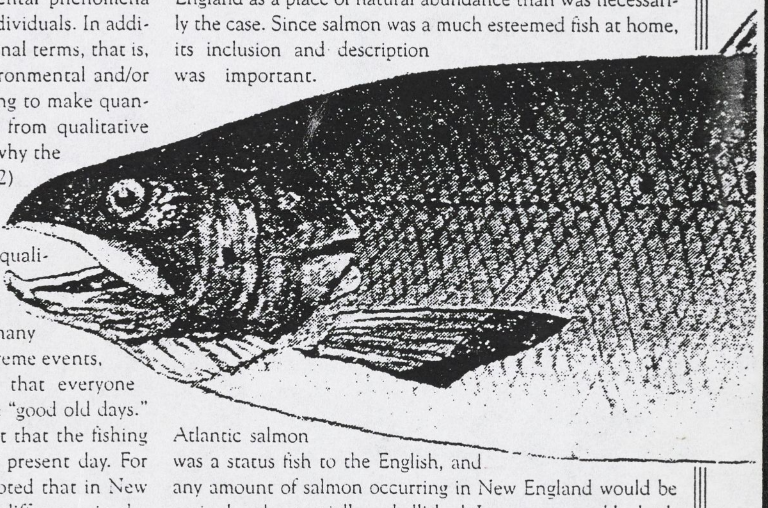
five pounds to anyone who would produce one of these agreements. The reward was withdrawn a year later, unclaimed."[15]

It was clear that the question of the abundance of Atlantic salmon in New England prior to its demise around A.D. 1800 had essentially never been thoroughly investigated through a critical analysis of primary documents.

Numerous problems can also exist for primary documents, and all historical written sources are not equally reliable. M. J. Ingram and others have described how even in the case of first editions of published manuscripts, there can be error. Authors of natural history accounts "often copied earlier [unpublished] manuscripts, mostly without acknowledgment, frequently misunderstanding and distorting the earlier materials . . . . Legends, rumors and downright fabrications were on occasion included to swell the story."[16] One of the major problems in attempting an analysis of the relative abundances of salmon in the New England rivers during the colonial period is that the primary accounts are not quantitative (i.e., measured or counted systematically). Therefore the task was to make quantitative-like interpretations from highly subjective qualitative accounts that were influenced by personal and cultural biases. Perception of environmental phenomena can vary among different societies and individuals. In addition, they can change over time in relational terms, that is, in comparison with other changing environmental and/or social conditions. Therefore, in attempting to make quantitative estimates of salmon abundance from qualitative sources, it was necessary to evaluate (1) why the material was originally documented; (2) how the phenomena were categorized, and how the categories fit into modern ones; and (3) what the significance is of qualitative terms of degree, as, for example, such statements as "once salmon runs were as great as . . . ," given that many accounts are biased toward recording extreme events, such as the one good run of salmon that everyone remembers years later as the norm in the "good old days." People throughout the ages have thought that the fishing in earlier times was better than in their present day. For example, as early as 1753, Peter Kalm noted that in New England "many old people said that the difference in the quantity of fish in their youth in comparison with that of today was as great as between day and night."[17]

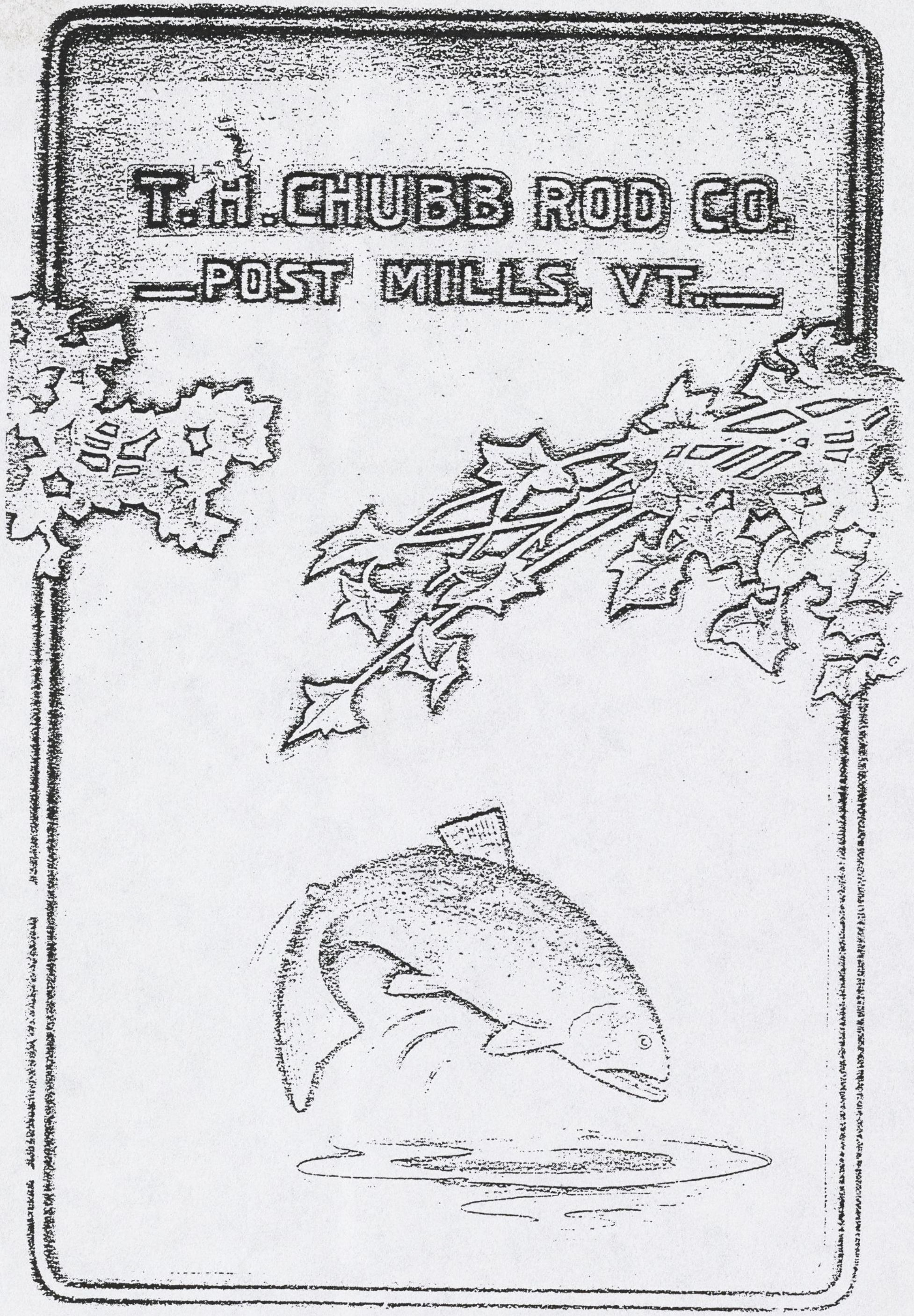
A further problem relates to the use of language because early descriptions of fish drew on a variety of vernacular terms applied before the Linnean system of binomial classification came into use after 1735. There was often a lack of vocabulary to describe particular North American species, and attempts were made to relate them to familiar Old World fish. For example, two 17th-century explorers' lengthy accounts of fish in the region—those of John Josselyn[18] and James Rosier[19]—cite "white salmon," which were undoubtedly shad. The latter were probably mistaken for salmon by early explorers and colonists with some frequency, creating "salmon inflation" in early and later derivative accounts. By the time that major systematic study of the natural history of the fishes of North America began in the 19th century, the Atlantic salmon runs of southern New England had long since disappeared.

Could the accounts of salmon also have been subject intentionally to embellishment? This is highly likely because the earliest writers were in reality "promoters" who would be biased in having strong motives for presenting to the folks back in the old country a considerably brighter image of New England as a place of natural abundance than was necessarily the case. Since salmon was a much esteemed fish at home, its inclusion and description was important.



Atlantic salmon

was a status fish to the English, and any amount of salmon occurring in New England would be praised and potentially embellished. It was esteemed by both gourmets and sports fishermen among the gentry. R.W. Dunfield remarks that Izaak Walton's *The Compleat Angler*






began "the campaign to set both angler and salmon apart from common man and common fish."[20] Walton accounted salmon the "king of fresh-water fish."[21]

To evaluate objectively the issue of salmon abundances, a survey was made of the primary historical documents of the 17th and 18th centuries, the time prior to extensive dam construction reputedly responsible for the salmon's demise. Since actual figures on numbers of salmon are nonexistent in these accounts, the statements regarding salmon abundance were compared with those of other fish species in order to achieve a general impression of relative abundance within the larger context of fish abundances—an issue that secondary historical syntheses have not addressed since they were reading the accounts from the perspective of assumed great salmon abundances.

In general, the primary accounts reviewed included entries by explorers and merchants ("promoters") and miscellaneous diaries and travelers' descriptions. The evidence indicated that while a number of accounts demonstrate that some salmon were present historically (and that is certainly a quantitative leap over the prehistoric record, both archeological and paleontological), they do not support the notion of abundant salmon runs in New England in the way that they are often made out to do.

For example, when the species of fish are listed or described, salmon, if mentioned at all, tend to fall towards the middle or end of a species list, suggesting their lesser significance. Some of the accounts go into considerable detail in describing each particular species of fish, and all are much more brief in their references to salmon than to other species. Furthermore, it was interesting to note that a number of sources did not even mention salmon.

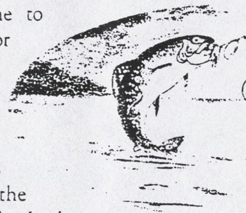
Put within the context of cod, or shad, or alewives, or sturgeon, salmon appears to have been quite minor. It was not even commercially marketable, as was the case for the Pacific salmon for which a major industry was developed in the Northwest. William Douglass in 1749 reported that "this salmon [of the Merrimack and Connecticut rivers] is not of a good quantity and is not so good quality and is not so good for a market as the salmon of Great Britain and Ireland."[22]

Of all the secondary accounts of salmon, only one, Brainard's two page article in the Connecticut Historical Society *Bulletin* presents the idea that salmon were never more than a minor species. He wrote that "the sparse early records fail to indicate any excessive number of salmon in the Connecticut River, even in the early days."[23] It is likely that the romantic folklore of once vast salmon runs is in fact myth and legend, a tall fish tale that has influenced all thinking about salmon in this century.

IT IS LIKELY THAT THE ROMANTIC FOLKLORE OF ONCE VAST SALMON RUNS IS IN FACT MYTH AND LEGEND, A TALL FISH TALE THAT HAS INFLUENCED ALL THINKING ABOUT SALMON IN THIS CENTURY.

While a conclusion that salmon was not a major, but a minor, resource is interesting, it only goes part way to explain why the prehistoric archeological record of fish indicated its virtual absence. One hypothesis is that salmon did not begin to colonize New England streams until the historic period, corresponding to a more favorable period of climatic cooling known as the Little Ice Age (A.D. 1550-1800).[24] At the end of this period, the climatic warming created less favorable environmental conditions for salmon, and hence their range retracted. Salmon are basically a cool water species that have a very narrow temperature tolerance range for developing eggs and smelts, and New England is the southern extent of its range. The idea that initial colonization did not occur until this time, and then only as a temporary range expansion, explains (1) the lack of salmon in prehistoric sites, (2) the apparent limited abundances of salmon historically, and (3) the extinction/depletion of the fish at the end of the 18th century. Since this is fundamentally a natural climatic explanation for both salmon appearance and disappearance as opposed to an anthropogenic one (dams and pollution), its implications for the modern salmon restoration programs should not be ignored. Fish biologists maintain that the resource can be restored by improving salmon habitat in the rivers through pollution control and construction of fish ladders.

In order to investigate a climatically induced hypothesis for salmon appearance and disappearance, environmental and climatic factors affecting range shifts and the mechanisms of migration in salmon were studied. Harsh glacial conditions during the Pleistocene (the last period of the great Ice Ages ending 12,000 years ago) resulted in an environment not conducive to salmon survival until about 10,000 years ago when modern warm Holocene environmental conditions began. Salmon must have migrated from Europe after the end of the Pleistocene, across Atlantic currents, during periods of suitable ocean conditions of temperature and food. Immediately prior to the Little Ice Age, the medieval warming period known as the Little Climatic Optimum (A.D. 900-1300) diminished sea pack ice around Iceland and Greenland.[25] It is possible that salmon may have migrated during this time to Davis Straits between Labrador and Greenland, an area that today is still an important feeding ground for both European and American salmon populations. This got them to the shores of North America; then as the medieval warming waned, and the Little Ice Age set in, cooler conditions south of the Labrador coast initiated salmon range expansion into the waters of the New England region. Unfortunately, the mechanisms by which Atlantic salmon colonize new streams are poorly understood and there is little reported research on the subject. Nevertheless, salmon do have the ability, despite their innate programming, to return to the stream of their birth to spawn, to colonize new streams. Research on salmon in Swedish rivers indicates a "rate of strays" of around 2 percent, suggesting that colonization of new drainages can occur relatively rapidly in suitable environmental conditions.[26]



THE ENVIRONMENTAL IDEOLOGY THAT GRANTS OMNIPOTENCE TO HUMANS . . . CAN BLIND US FROM RECOGNIZING THAT NATURAL ENVIRONMENTAL FLUCTUATIONS . . . ARE PROBABLY MORE SUBSTANTIVE ON A LONG-TERM SCALE THAN HUMAN-INDUCED ONES.

Paleontological fossil specimens of fish add empirical evidence by extending the record of northeastern fish further back in time than archeological specimens and provide evidence of the fish fauna in the region during the end of the Pleistocene. Many fossil fish specimens come from the Green Creek nodules in glacial Lake Champlain deposits near Ottawa, Ontario.[27]

The fossils provide information on what fish species survived the harsh glacial conditions of the Pleistocene. To date, smelt, cod, sculpin, whitefish, lake trout, lump fish, stickleback, and sturgeon are the predominant species; there is no evidence from paleontology that salmon were present during the Pleistocene, which supports the later archeological record of the Holocene (post-glacial conditions).

The issue of landlocked salmon, those populations of fish that remain in inland lakes throughout their life cycle without migrating to the sea, also required investigation. There has been some suggestion that they may have become introduced to inland lakes at the end of the Pleistocene when sea levels were higher as the ice sheets were melting and then subsequently have been trapped or "landlocked" as sea levels dropped, making them what biologists call "glaciomarine relicts," a possibility that would override the negative paleontological record. Only in four lakes in Maine (Sebago, Green, Sebec, and Grand lakes) are there natural indigenous landlocked populations; the rest have been introduced through fish stocking. In all four lakes, the fish had free access to the sea prior to the construction of dams. These fish are therefore considered to be voluntarily landlocked, a natural process poorly understood, but nevertheless, not the result of Pleistocene sea level changes.

Recent research by geneticists on the composition of European and Atlantic salmon stocks indicates no genetic markers differentiating the two geographical populations, supporting the idea that the evolutionary divergence of the two stocks is recent. The possibility that salmon colonized the rivers of New England only in the last 600 years cannot be refuted by the genetic data that support a recent origin of the fish to North America.[28]

In summary, Atlantic salmon are likely to be very recent colonizers to North America, particularly to New England, and their presence short and relatively insignificant. Their initial colonization and subsequent retreat may have been due largely to climatic fluctuations over the last 1,000 years from the medieval-period Little Climatic Optimum to the Little Ice Age and to the modern 19th and 20th centuries, that controlled habitat conditions in both the marine and riverine environments for migration, stream colonization, and range retraction.

It is fashionable in western culture today to view human impact on the natural environment as often the major contributing factor in environmental change. Faunal and floral extinctions, ecological "imbalance" due to exotic species introductions, deforestation, greenhouse gases for climate change, and even in the archeological literature blaming the extinction of the North American Pleistocene megafauna on over-hunting by Paleoindian hunters—are just a few examples. It is also fashionable to suggest that science can "fix" or undo anthropogenic environmental change. While humans unarguably have impacts on the natural environment, and have done so for as long as their four-million-year evolutionary history on the earth, the environmental ideology that grants omnipotence to humans over the environment can blind us from recognizing that natural environmental fluctuations in climate and species distributions or extinctions are probably more substantive on a long-term scale than human induced ones. One needs only to look at the paleoenvironmental, paleobotanical, and zooarcheological records of the past to fully appreciate this.



THE GENERAL LACK OF SUCCESS IN SALMON RESTORATION PROGRAMS, DESPITE FISH LADDERS AND HABITAT IMPROVEMENT, SUGGESTS A MORE FUNDAMENTAL ECOLOGICAL CAUSE FOR IMPOVERISHED SALMON RUNS IN NEW ENGLAND.

This article ultimately is concerned with how the issue of disappearing Atlantic salmon in southern New England, and its considerable depletion in the north, is an example of too great a focus on anthropogenic environmental change. Today's fish and wildlife managers appear to have largely ignored the paleoenvironmental databases that present long-term records of climatic change in concert with animal and plant species range changes, and even total extinctions, because of their preoccupation with the effects of industrialization. While biologists such as D. W. Lufkin have stated that "the circumstances causing the demise of *Salmo salar* are relatively simple to identify. . . [as] dams, pollution, logging practices, and over-fishing,"[29] this article argues that causes behind its demise are more complex, with ecological and climatological bases. If pollution and dams were the major cause of their extinctions, then why were the runs not made extinct on the Penobscot, a heavily dammed and polluted river in Maine? Also unaccounted for is why salmon runs became extinct downstream of the dams on the Connecticut River. The general lack of success in salmon restoration programs over the last two centuries, despite fish ladders and habitat improvement, suggests a more fundamental ecological cause for impoverished salmon runs in New England than an anthropogenic one.

We also need to examine more closely how social and cultural values can fashion a natural creature, in this case the salmon, in ways that identify it with high-ranked social positions such that it unwittingly influences our thinking in everything from the establishment of fisheries societies and restoration facilities to archeological reconstructions of prehistoric societies. The romantic allure of the king of fish colors the visions of prestigious sportsmen, biologists, and politicians. The political correctness of "environmental awareness," in which salmon has become the symbol for clean rivers, whether justified or not, becomes a factor in the judgments being made. The lowly codfish appears to be a more appropriate fish symbol for New England and one that is presently environmentally threatened; the politicians supporting salmon restoration have apparently forgotten about the "great cod" that hangs in the halls of the Massachusetts statehouse and its historical significance.

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# NAGPRA NEWS

## Implementing the Native American Graves Protection and Repatriation Act

### The Future for the Unidentifiable?

The NAGPRA Review Committee, convening in Anchorage October 16-18, addressed the issue of what to do with culturally unidentifiable human remains and funerary objects.

The committee's *Draft Recommendations on the Disposition of Culturally Unidentifiable Human Remains and Funerary Objects* had prompted 120 comments from museums, tribal groups, and the scientific community. Committee members expressed their gratitude to those who took the time to provide their observations, which will be taken into account as the second draft is composed. The committee hopes to have this document ready to discuss at the next meeting and will publish another request for comments at a later date.

Other business at the committee's tenth meeting included the review of written documentation on two disputes and a first-hand look at NAGPRA's progress in Alaska. The first dispute involved the Oneida Tribe of Indians of Wisconsin, the Oneida Indian Nation (of New York), and the Field Museum of Natural History. Formal testimony will be heard at the next committee meeting. The second was among representatives of Chief Satanta (White Bear) Descendants and the Phoebe A. Hearst Museum of Anthropology at the University of California, Berkeley. The committee deferred further action on this dispute pending additional information and consultation among the parties.

Also reviewed was a request from the Hood Museum of Art, Dartmouth College, for a recommendation regarding disposition of culturally unidentifiable human remains believed to be affiliated with the Missisquoi Abenaki Tribe (Western Abenaki), a non-federally recognized Native American group in Vermont. The committee recommended that the museum publicize the Western Abenaki's repatriation request in local New Hampshire and Vermont newspapers as notification to other possible claimants. If no other claimants express interest in repatriating the remains, the committee suggested that the Hood proceed with the repatriation process.

Ten representatives from Alaskan museums and Native communities described to the committee the broad range of NAGPRA involvement in the state. Awareness of NAGPRA in Alaska varies from groups that are actively researching claims and negotiating repatriations to those that are still trying to come to terms with the idea of dealing with the remains of long-dead ancestors. All of the speakers commented on the difficulties peculiar to Alaska, with numerous culturally distinct groups spread across vast distances.

Plans for the next review committee meeting (tentatively scheduled for early spring) are in progress.

### NAGPRA Rule Published

The final rule implementing the Native American Graves Protection and Repatriation Act was published in the *Federal Register* on December 4.

The rule establishes procedures for protecting and determining disposition of Native American human remains, funerary objects, sacred objects, and objects of cultural patrimony that are intentionally excavated or inadvertently discovered on federal or tribal lands. It also establishes procedures for conducting summaries and inventories and repatriating human remains, funerary objects, sacred objects, and objects of cultural patrimony in museum or federal agency collections.

The final rule was prepared by the DOI departmental consulting archeologist for the Secretary of the Interior in consultation with the Native American Graves Protection and Repatriation Review Committee as directed by section 8 (c) (7) of the act. The rule was initially published in the *Federal Register* as a proposal on May 28, 1993, to solicit public comment. The extensive preamble to the final rule addresses each of the substantive comments received during the comment period.

The text of the final rule is available on the National Archeological Data Base (http://www.cast.uark.edu/d.cast/nadb.html). The *Federal Register* is also available at most large libraries.

### Native Federation Proposes Steering Group, Closing Smithsonian 'Loophole'

The Alaska Federation of Natives, also meeting in Anchorage in October, authorized the creation of a statewide steering committee to examine the question of what is to be done with unidentified or unclaimed ancestral remains. The first of three NAGPRA-related resolutions by the federation, it also calls on the Keepers of the Treasures, Alaska, to act as a liaison with the committee. Alaska native organizations were urged to participate in the planning and coordination for the disposition of such

# A Tale From the Boneyard

IF YOU BELIEVE THE HISTORY BOOKS, ATLANTIC SALMON WERE ONCE SO ABUNDANT THAT THE COLONISTS COULD WALK ACROSS THE BACKS OF THE FISH AS THEY RAN UP RIVERS IN THE NORTHEASTERN UNITED STATES TO SPAWN.

It's also been long accepted that pollution, main-stem dams, poaching, and high seas commercial fishing have all played major roles in severely depleting salmon populations in some New England rivers and caused them to become extinct in others.

BUT ACCORDING TO archeologist Catherine C. Carlson, there is **no evidence that Atlantic salmon were *ever* abundant** in the rivers of New England. This startling allegation appeared in an article entitled, "The [IN] Significance of Atlantic Salmon," published in the 1996 fall/winter issue of *Federal Archeology*. Carlson, who is assistant professor of archeology at the University College of Cariboo in British Columbia, bases her belief on the analysis of thousands of fish bones from more than seventy-five prehistoric sites in New England. This study, part of a research project designed to learn more about the New England aboriginal peoples, revealed that though the remains of many kinds of fish were found, there were no salmon bones.

A REVIEW OF THE HISTORICAL DOCUMENTS further revealed that **early tales of huge salmon runs were often based on hearsay,** such as a claim that in colonial New England, salmon were sometimes so thick in rivers that they "overturned small boats," or an 1879 account that women seined salmon in Lake Ontario with flannel petticoats. The story about poor laborers being fed too much salmon also turned out to be apocryphal. In fact, a survey of historical documents from the 17th and 18th centuries—before the offending dams were built—turned up no evidence that Atlantic salmon had ever been abundant in that region.

**So what does all this mean?** Carlson suggests the story in the fish bones may have broad implications. "It is fashionable in western culture today to view human impact on the natural environment as often the major contributing factor in environmental change," she writes. "It is also fashionable to suggest that science can 'fix' or undo anthropogenic environmental change. [But] the general lack of success in salmon restoration programs over the last two centuries. . . suggests a more fundamental ecological cause for impoverished salmon runs in New England. . . . "

In plainer English, Carlson concludes that the research on aboriginal garbage dumps in New England, which began in 1980, shows "it is likely that the romantic folklore of once vast salmon runs is in fact myth and legend, a tall fish tale that has influenced all thinking about [Atlantic] salmon in this century."—DUNCAN BARNES AND MAGGIE NICHOLS

PHOTOGRAPH BY R. VALENTINE ATKINSON; CARTOON BY W. HARDBARK McLOUGHLIN

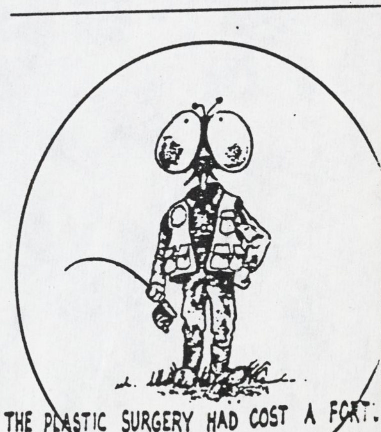
**YOU KNOW YOU'RE IN HUNTING COUNTRY WHEN...** the D.J. on the local rock station (KRXL in Kirksville, Missouri) gives the following weather report at 5 A.M. on an April morning: "Highs in the 70s today, so the morel mushrooms should be popping up. All you turkey hunters keep an eye out in the woods today. . . ."
—PHILIP BOURJAILY

## TRUE

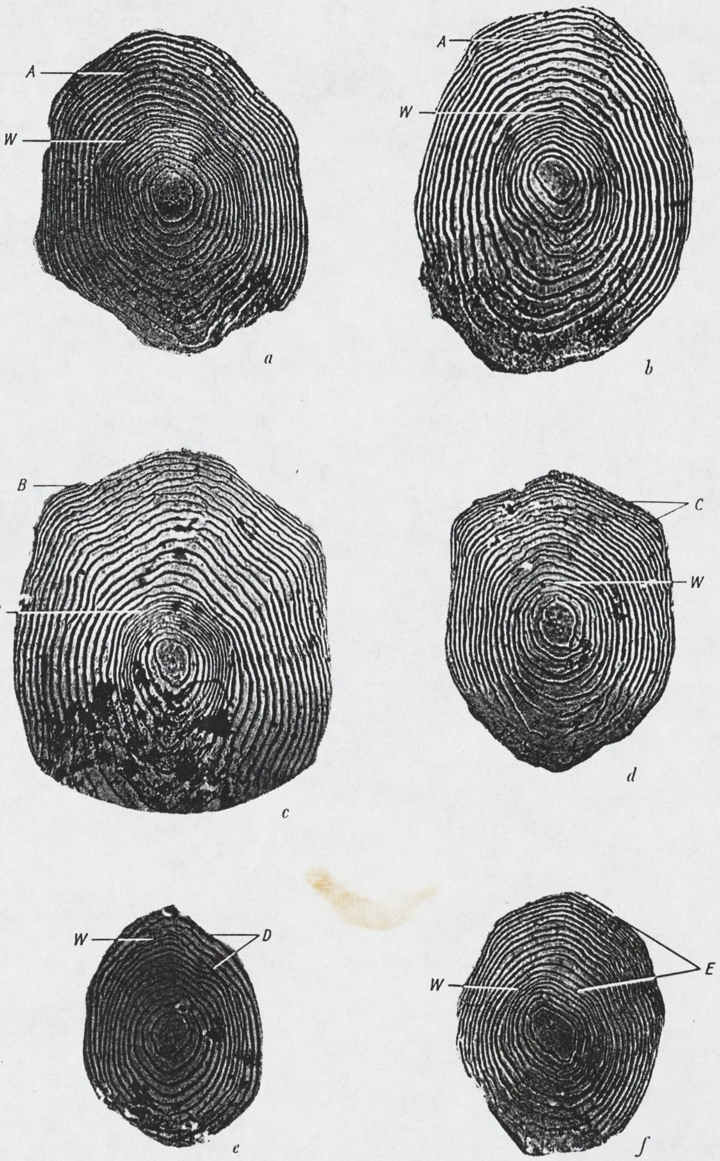
THE NEXT TIME YOU REPAINT YOUR DUCK OR GOOSE DECOYS, TRY MIXING SOME TEXTURIZING AGENT (SUCH AS PERMATEX) IN WITH THE PAINT. THIS MAKES THE DECOYS' SURFACE EVEN FLATTER THAN USUAL, PREVENTING SHINE, AND AT THE SAME TIME MAKES THEM EASIER TO PICK UP AND HANDLE WHEN WET.

TWO HINTS: PAINT THE BODIES ONLY WITH THIS MIX—THE HEADS DON'T NEED IT—AND USE THE GRIT ONLY WITH THE BODY BASE COAT, SO YOU DON'T HAVE TO MIX IT WITH SO MANY COLORS.

ALSO, DON'T USE THE HARD MINERAL GRIT SOLD FOR NONSLIP FLOOR SURFACES; IT WILL TURN YOUR DECOYS INTO SANDING BLOCKS. THEY'LL ALSO GRIND EACH OTHER'S FINISH AWAY WHEN JOSTLED IN A BOAT OR BAG. THE SOFTER TEXTURIZER IS SAFE, CHEAP, AND EASY TO MIX AND APPLY.—Don Bronk

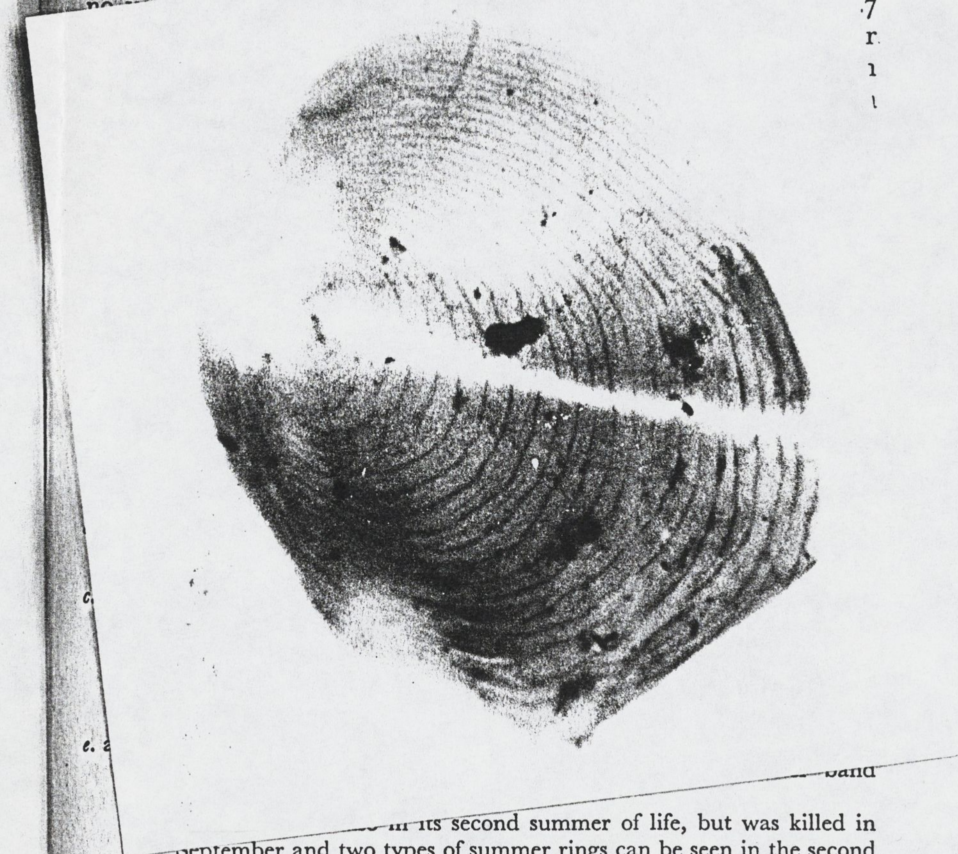


THE PLASTIC SURGERY HAD COST A FORT... BUT AT LAST VERNON MATCHED THE HATC...






salt-content of the body, otherwise the salts might reach a lethal concentration. Keys and Wilmer found that the gills of the eels contain some special "chloride-excreting cells", which apparently secrete chloride ions into the surrounding water. Copeland found similar cells in *Fundulus;* if this fish had been acclimatized to sea water, the cells had in them vesicles ... ht to be excretory and to ... ld



... band ... in its second summer of life, but was killed in September and two types of summer rings can be seen in the second summer band of rings, the wide ones following immediately on the first winter band (*W*) and the narrow summer rings towards the edge of the scale. (*Irvine and Fleming*)