A Review of

2006 Status Review for Anadromous Atlantic Salmon (*Salmo salar*) in the United States

Prepared for the Center for Independent Experts

By

Paul Bentzen*

May 14, 2006

*Professor
Department of Fisheries and Oceans Chair,
Fisheries Resource Conservation Genetics
Department of Biology
Dalhousie University
Halifax, Nova Scotia, Canada

Executive Summary

This report presents a review prepared for the Center for Independent Experts of the report “Status Review for Anadromous Atlantic Salmon (*Salmo salar*) in the United States” (Fay et al. 2006). The Status Review addresses three general issues pertaining to the Gulf of Maine Distinct Population Segment (GOM DPS) of anadromous Atlantic salmon, *Salmo salar*. First, on the basis of recent genetic data as well as pre-existing life history and zoogeographic data, the Status Report reaffirms the integrity of the GOM DPS, but also extends its definition to include several populations previously excluded from the DPS. The newly included populations comprise anadromous Atlantic salmon in three large rivers, the Androscoggin, Kennebec above the former Edwards Dam, and the Penobscot above the former Bangor Dam, as well as all associated conservation hatchery populations used to supplement natural populations within the DPS. Second, the Status Review evaluates present abundance levels in the DPS, and conducts a population viability analysis to evaluate the probability of extinction of the GOM DPS. Third, the Status Review examines the applicability of the five statutory ESA listing factors to the GOM DPS, and concludes that each of the five factors is partly responsible for the current low abundance of the GOM DPS. This review evaluates the evidence and conclusions presented in the Status Review with regard to four key terms of reference:

(a) *Is the species delineation supported by the information presented?* The key new genetic information presented comprises recent studies of microsatellite DNA that now include most rivers in the proposed DPS. The new data show that Atlantic salmon populations in the Penobscot and Kennebec Rivers are closely related to populations elsewhere in the DPS; therefore inclusion of these rivers in the DPS is strongly supported. The basis for including the Androscoggin River in the DPS is less strong, since no genetic data are available from salmon in this river, and seems at least partially at odds with the exclusion of the St. Croix River from the DPS. Neither river supports self-sustaining populations, but returning salmon in the Androscoggin are comprised entirely of stray salmon of unknown origin, whereas the St. Croix is the subject of hatchery supplementation using broodstock of Penobscot origin.

(b) *Does the Status Review include and cite the best scientific and commercial information available on the species and threats to it and to its habitat?* The best genetic data are cited in the Status Review, although some recent genetic studies relevant to the DPS delineation are omitted. Some available information on marine survival of stocked Canadian Atlantic salmon in relation to the distance between the source and recipient populations that also bears on the discreteness and significance of the DPS is not cited. Information presented on threats to the GOM DPS in terms of the five ESA listing factors is generally comprehensive and balanced, although discussion of threats posed by aquaculture and poor marine survival are relatively brief in comparison to the likely magnitude of the threats represented by these factors.

(c) *Are the scientific conclusions sound and derived logically from the results?* The key conclusion that the GOM Atlantic salmon DPS is endangered is incontestable in light of the current extremely low abundance of salmon returning to rivers within the DPS, and

the failure of concerted conservation efforts to bring about recovery to date. The scientific conclusions regarding the nature of threats and limitation to the DPS, which are that all five ESA listing factors are responsible for the decline of the DPS, are generally well grounded, although at least one listed threat, over-exploitation, is unlikely to be significantly hindering recovery. One threat to the GOM DPS, loss of genetic diversity and inbreeding depression, is largely dismissed in the Status Review on the grounds that this issue is being addressed by captive breeding, but this view fails to consider the loss of genetic diversity prior to captive breeding.

(d) *Where available, are opposing scientific studies or theories acknowledged and discussed?* Evidence for the key opposing theory, that at least some salmon populations, such as the Penobscot, are derived wholly or in part from historical stocking of Canadian salmon, is well presented in the form of stocking records that document the large number of Canadian-origin salmon that were introduced to the DPS. Minor ancillary information consistent with the 'Canadian origin' hypothesis, is also presented. The possibility that historical stocking of Canadian salmon has substantially altered the genetic composition of any populations within the DPS, including the Penobscot, is refuted by the genetic data. For other aspects of the Status Report, which deal primarily with the nature of threats to the DPS, opposing theories are not a major issue, since none of the suggested threats and limiting factors are mutually exclusive.

Introduction

In January 2006 the Atlantic Salmon Biological Review Team (BRT) submitted a report titled "Status Review for Anadromous Atlantic Salmon (*Salmo salar*) in the United States" (Fay et al. 2006; henceforth, the Status Review). This report is a review of the Status Review prepared for the Center for Independent Experts.

The Status Review includes a broad range of general biological, historical, and management information pertaining to anadromous Atlantic salmon in the United States; however, the critical parts of the Status Review deal with three major issues: (1) the delineation of the Gulf of Maine Distinct Population Segment (GOM DPS), (2) the current status and abundance of the GOM DPS and its risk of extinction, and (3) a review of the threats that apply to the GPS, particularly as they pertain to the five listing criteria identified in the Endangered Species Act (ESA). Of these three major issues, current abundance of Atlantic salmon in the DPS and associated extinction risk is the most straightforward: abundance is clearly extremely low and has remained so despite concerted conservation measures, leading inescapably to the conclusion that the risk of extinction is significant. The other two issues are more complex, and form the focus of this review.

This review is based on a close examination of the Status Review and a number of the scientific reports cited within it. The review was conducted following four key terms of reference: (a) Is the species delineation supported by the information presented? (b) Does the Status Review include and cite the best scientific and commercial information available on the species and threats to it and to its habitat? (c) Are the scientific conclusions sound and derived logically from the results? (d) Where available, are opposing scientific studies or theories acknowledged and discussed? The findings of this review are presented according to these terms of reference.

(a) Is the species delineation supported by the information presented?

Like the 1999 BRT report that preceded it, the 2006 Status Review recognizes three Distinct Population Segments for anadromous Atlantic salmon. Two of these DPSs, Long Island Sound and Central New England, are long extinct, whereas the third, Gulf of Maine (GOM) remains extant and is the focus of most of the report. The new report differs critically from the previous one, however, in the delineation of the GOM DPS. The current Status Review includes three large rivers that were previously excluded from the GOM DPS: the Penobscot above the former Bangor Dam, the Kennebec above the former Edwards Dam, and the Androscoggin, as well as conservation hatcheries used to supplement wild anadromous salmon populations within the DPS. The additional rivers are included in the DPS largely on the basis of genetic data that have become available since the previous status review. The scientific basis for the three historical DPSs and the revised definition of the remaining extant DPS is discussed in detail below.

In recognizing three DPSs for anadromous Atlantic salmon, the Status Review follows the conclusions of the 1999 Status Report, which described the DPSs on the basis of broad geographic, physiographic and ecological considerations, but also builds on these considerations by adding or elaborating on several additional criteria. The first criterion invokes Olivero's (2003) concept of Ecological Drainage Units (EDUs), which aggregates basins on the basis of similarities in zoogeographic history, physiography, and climate. The three DPSs include six EDUs of varying geographic scale, ranging from portions of the Connecticut River drainage to groups of rivers further north, but in no case does a single EDU span the boundary between two proposed DPSs. The second criterion considered by the 2005 BRT is ground water temperature, under the rationale that groundwater temperature provides an average measure of climate, and closely reflects geographic variation in the growth rates of juvenile salmon, and consequently, variation in life history attributes. Differences in ground water temperature distinguish (cooler) northern from southern New England. The third criterion considered by the 2005 BRT is the near shore marine community, with the rationale that differing predator assemblages and thermal regimes will influence life history attributes such as run timing. Offshore areas are not regarded as relevant, because these are thought to be similar for all northwest Atlantic salmon stocks. The marine community criterion defines a split between areas south and north of Cape Cod.

The evidence cited in the Status Review for these DPS delineation criteria appears to provide a comprehensive summary of available information, and a convincing basis for the recognition of three DPSs; however, since two of the three DPS are extinct, the information embodied in them is primarily of use in defining a historical context for the remaining DPS, the Gulf of Maine. A fourth criterion considered in the report, biological and genetic information on extant salmon populations is of primary importance for determining the integrity and boundaries of the surviving DPS.

The Status Review cites two general lines of biological evidence to support the integrity of the GOM DPS. The first line of evidence is the familiar natal philopatry exhibited by all salmon. As noted in the report, natal homing need not be perfect for distinct, locally adapted population units to evolve; indeed, some straying is essential to avoid inbreeding and permit recolonization of habitats following severe disturbances. However, the issue of concern is not natural straying, but human mediated gene flow brought about by many years of deliberate stocking of non-native salmon from sources outside of the DPS, primarily the Miramichi River in northern New Brunswick, but also the Saguenay and St. Jean Rivers in Quebec. The long-term effects, if any, of these introductions can only be assessed with genetic data.

The other line of biological evidence cited in the Status Review relates to life history: Maine Atlantic salmon are well known to return primarily (>80%) as two sea winter (2SW) fish, whereas Canadian stocks exhibit a much higher proportion of 1SW fish, also known as grilse. In nearby Canadian outer Bay of Fundy populations, about 55% of returning salmon are grilse, and in the inner Bay of Fundy, about 93% of salmon return as grilse (Hutchings and Jones 1998; Amiro 2003). As noted in the Status Review, higher proportions of grilse seen for Penobscot salmon from the 1960s-early 1990s has been suggested to be evidence of successful return of Canadian origin stocked salmon (Bernier et al. 1995), but an alternative explanation invokes heavy interception in the West Greenland fishery during this period of salmon that would otherwise have returned as 2SW fish. Again, genetic data can provide the only answer about the long-term outcome of the Canadian salmon introductions.

Genetic data thus emerge as the most important evidence bearing on the biological integrity of the GOM DPS, as well as its exact delineation – that is, whether the newly included portions of the Kennebec, Penobscot and Androscoggin Rivers belong in the DPS. The Kennebec had been excluded from the earlier version of the DPS because native salmon in that watershed are widely accepted to have been extirpated and eventually replaced by straying salmon from unknown sources. The mainstem Penobscot had been excluded from the earlier version of the DPS because of uncertainty about the effects of past stocking from Canadian sources. The Status Review cites a number of genetic studies that bear on these questions, the most relevant of which are King et al. (2001) and Spidle et al. (2001; 2003; 2004). These studies are all based on microsatellite data. Microsatellites are currently the most widely used genetic markers in population genetic studies, and are generally considered the most sensitive markers available because of the high levels of polymorphism (many alleles) they exhibit (Wright and Bentzen 1994) and because the ability to accurately resolve population relationships is closely related to the number of alleles that are surveyed (Kalinowski 2002; 2004; 2005; see also for example Winans et al. 2004).

In considering genetic data, the Status Review relies most heavily on Spidle et al. (2003). This is reasonable, since this is the most recent and comprehensive genetic study covering the GOM DPS, and includes some data from King et al. (2001). The latter study, which covered a wide range of U.S., Canadian and European populations, is the most comprehensive range-wide genetic study of Atlantic salmon ever published utilizing microsatellite markers. The Status Review focuses on three types of analysis reported in the Spidle et al. (2003) study: a multidimensional scaling (MDS) plot based on transformed genetic distance (1- genetic distance), neighbor-joining (NJ) dendrograms based genetic distance, and assignment tests. Both the MDS plot and the NJ tree use the same input data, the genetic distance D_A (Nei et al. 1983), but the two analyses have different strengths and weaknesses. MDS has the ability to portray complex relationships in two (or more) dimensions, without the constraint of depicting all relationships as bifurcating branches in a single dimension. The NJ analysis does impose this constraint, and therefore is less accurate in its depiction of some genetic distances. For this reason, the MDS plot is arguably the best visual representation of genetic distances among all populations, but it offers no means to test hypotheses regarding the relationships of groups of populations. By contrast, NJ analysis does provide a means to test hypotheses, because the data can be bootstrapped to provide statistical measures of confidence for groupings of populations that appear on the tree.

The Status Review attempts to describe the MDS plot in Spidle et al. (2003), which given the ‘visual’ nature of the analysis, is somewhat ineffectual in the absence of the plot itself; it would have been very helpful to include the actual figure in the report. The report then goes on to summarize the NJ analysis, although herein there is some confusion: the report appears to introduce the NJ analysis in paragraph 3 on p. 49, but actually begins discussing the NJ results in the previous paragraph. Also reflecting some confusion is the second sentence in the third paragraph on p. 49 ["Although genetic differences were small, Maine populations clustered together."] Small genetic differences are precisely what make populations cluster together. Nonetheless, the report correctly captures the main point: that with the arguable exception of the Kenduskeag and Cove Brook populations, all Maine populations cluster very closely together. The Status Review cites Spidle et al (2003) further to note some structure within the Maine population cluster; that is, some populations appear more closely related than others. These distinctions in degrees of relatedness may make sense in terms of the history of inter-basin stocking and the relative sizes of populations (small populations are likely to be more divergent than larger ones, because of genetic drift), but statistical support for these distinctions is minimal, and in any case, the minor differences in relatedness are irrelevant to the key point: that, (with two possible exceptions) all Maine populations are closely related to each other and genetically distinct from other North American (i.e., Canadian) populations.

The two 'possible exceptions' to the tight clustering of all Maine populations require further consideration. One of these populations, the Kenduskeag, is said in the Status Review (in reference to the MDS plot) to be "as similar to other Maine populations as the Miramichi and St. John populations from Canada". This represents a mis-interpretation of the MDS plot. Dimension 1 and dimension 2 on an MDS plot (Figure 2 in Spidle et al. 2003) are not necessarily equivalent in scale, so it is not possible to compare divergence in one dimension with divergence in the other dimension without knowing the proportion of the total genetic variance each dimension explains (this information is not provided in Spidle et al. (2003)). Canadian populations tend to differentiate from U.S. populations in both dimensions, but primarily in dimension 1, whereas anadromous U.S. populations are differentiated almost exclusively on dimension 2, which is likely smaller than dimension 1. The best way to quantify distinctions such as which pairs of populations are more or less differentiated is with tabulated pairwise values of actual genetic distances, which unfortunately are not presented in Spidle et al. 2003. In the absence of that information, only the NJ analysis and the assignment tests can be used to judge the relationship of the Kenduskeag population to other Maine populations, and as the Status Review correctly reports, both of these analyses support the close relationship of Kenduskeag to other Maine populations.

The second genetic outlier among Maine populations is Cove Brook, an unstocked tributary of the Penobscot. Cove Brook appears as an outlier (on dimension 2) of the MDS plot, and as noted in the Status Review, clusters with >90% bootstrap support with several Canadian populations. The report suggests as one possible explanation for this result that Canadian salmon stocked in the Penobscot strayed to and reproduced in Cove Brook. This explanation makes little sense, since it implies that 'Canadian' salmon are a homogenous group. In fact, Canadian salmon are much more genetically diverse than anadromous Maine salmon (King et al. 2001; Spidle et al. 2003, and noted on p. 50 of the Status Review), in accord with their much larger geographic spread. The Canadian populations that Cove Brook groups with are Newfoundland and Labrador populations, which are themselves very diverse, and quite distinct from the New Brunswick and Quebec populations that were stocked in the Penobscot. A second explanation proposed in the Status Review, that the similarity of Cove Brook to the Canadian stocks is "a random event or an artifact of small population size and a genetic bottleneck event" is much more plausible. Allelic diversity (not cited in the Status Review) over all 11 microsatellite loci is much lower (60) for Cove Brook than it is for other Maine populations (mean = 82, range = 72-88; Spidle et al. 2003). This indicates a small effective population size for Cove Brook, and implies the likelihood that Cove Brook has diverged from other Maine populations through genetic drift that has been accelerated by population bottlenecks, as has also been suggested by Lage (2003).

The third category of analysis carried out by Spidle et al. (2003) and summarized in the report is assignment tests. As correctly summarized in the Status Review, the assignment tests also provided evidence of the distinctiveness of Maine populations from the remainder of the North American range. Individual salmon from Maine were correctly assigned back to river, nation, and to GOM DPS with substantially higher success than expected by chance alone. Further, there were very few mis-assignments between GOM populations and any of the Canadian source populations used historically for stocking. The very low rate of mis-assignments with these populations is typical of mis-assignment rates between populations that have not been the subject of historic transfers. Finally, the rate of correct assignment to the GOM DPS increased when Penobscot was added to the DPS, a result that further emphasizes the genetic similarity of the Penobscot to other Maine populations.

The Status Review also considers evidence of the GOM DPS' biological and ecological significance. Evidence for two criteria, (1) "persistence of the DPS in an ecological setting unusual for the taxon" and (2) "evidence that the loss of the DPS would result in a significant gap in the range of a taxon" is readily evident in the position of the DPS at the southern limit of the species range in the NW Atlantic. Evidence for a third criterion supporting biological and ecological significance (3) "that the GOM DPS differs markedly from other populations of the species in its genetic characteristics" comes from the extensively discussed microsatellite genetic data, as well as from the unproven, but reasonable supposition that Maine salmon are uniquely adapted to life at the southern range limit of the species. As noted in the report, although southerly adapted salmon stocks also exist in Europe, these are known to be highly genetically divergent from North American Atlantic salmon (King et al. 2001).

In summary, the genetic data reviewed in the Status Review strongly support the conclusion that the GOM anadromous Atlantic salmon DPS are discrete and biologically significant; in fact, some key evidence in the cited literature is actually stronger than represented in the Status Review (see section b below). However, the evidence cited to support the inclusion of 'new' rivers in the DPS (mainstem Penobscot, Kennebec and Androscoggin) is subject to two significant caveats. The first caveat is that direct genetic evidence supporting inclusion in the DPS are only available for two of the rivers previously excluded from the DPS, the mainstem Penobscot and Kennebec (represented by two tributaries, Bond Brook and Togus Stream). The genetic evidence for the inclusion of these two rivers in the revised definition of the DPS is compelling, but the case is less strong for another river included in the proposed DPS, the Androscoggin, which is not represented in genetic data sets. Inclusion of this river in the DPS is based on the inference that salmon returning to this river are likely to be genetically similar to those in other Maine rivers that are part of the DPS. This inference is reasonable, but also leads to the second caveat: there are inconsistencies in the logic applied to the delineation of the two opposite DPS boundaries.

According to Maine Rivers (http://www.mainerivers.org/index.htm), the Androscoggin does not harbor a self-sustaining salmon population and is not subject to a hatchery based restoration program; mature salmon seen there are strays from unknown sources. As noted above, it is reasonable to assume the stray salmon in the Androscoggin are from the same source(s) that refounded the nearby previously extirpated Kennebec River population, and therefore of the same genetic type as those that make up the DPS. However, on the other side of the DPS, the Status report excludes the St. Croix River from membership in the DPS, despite the fact that it has been and continues to be stocked with salmon that are ultimately of Penobscot origin, and that salmon produced in hatcheries for the purposes of population restoration are otherwise included in the DPS. The basis for the exclusion of the St. Croix from the DPS gets little explicit discussion in the Status Review, but appears to rest on genetic data (Spidle et al. 2003) that show Dennis Creek (a tributary that enters the St. Croix estuary) clustering with the Saint John, Miramichi and other Canadian populations in the NJ analysis. The argument made is that Dennis Creek, represented in the Spidle et al. (2003) study by parr collected in 1995, is representative of the original, native St. Croix population, just as lower drainage tributaries of several other rivers are considered surrogates of their respective mainstem river populations. Although this argument is reasonable in the other cases cited, there are problems with the argument as it applies to Dennis Creek and the St. Croix River. First, the genetic analysis is based on a single year of parr samples from Dennis Creek (a population now regarded as extirpated). Second, it is possible that the Dennis Creek parr sample included the progeny of aquaculture strays, a possibility not considered in the Status Review. The St. Croix estuary is adjacent to the largest concentration of salmon farms in the GOM/Bay of Fundy region, and in the nearby Maguagadavic River in New Brunswick, 57% of mature salmon in 1996 were escapees from salmon farms (Lacroix and Stokesbury 2004). Escaped farm salmon are known to be spawning successfully in Bay of Fundy Rivers (P. O'Reilly, DFO Canada, personal communication). The majority of farmed salmon in the region are of a strain derived from the Saint John River population, so inclusion of parr of derived from the aquacultural strain could account for the clustering of the Dennis Creek sample with the Saint John population. Finally, it is important to note that Dennis Creek occupies a basal position in the 'Canadian' cluster in the Spidle et al. (2003) NJ analysis, and statistical support for its inclusion in that cluster is weak (<70%). In sum, genetic evidence to exclude the St. Croix River from the DPS is at best tenuous, and thus the logic that includes Androscoggin in the GOM DPS, but excludes St. Croix, is questionable.

(b) Does the Status Review include and cite the best scientific and commercial information available on the species and threats to it and to its habitat?

DPS discreteness and biological and ecological significance

In general, the Status Review does cite the best scientific evidence regarding the discreteness and biological and ecological significance of the GOM DPS; however several omissions are notable.

One omission is the failure of the status review to cite several recent studies that reported allozyme genetic data for North American Atlantic salmon populations. Cordes et al. 2005 reported on allozyme variation in seven populations belonging to the GOM DPS. Verspoor 2005 described allozyme variation among 53 Canadian populations, and Verspoor et al. 2005 combined data from the previous two data sets with comparable genetic data from European populations. These studies revealed similar levels of genetic variation in the Maine and Canadian salmon populations, and also showed that Maine populations were significantly differentiated from all Canadian populations. NJ and MDS analyses based on D_A genetic distances depicted complex relationships among populations (Verspoor et al. 2005). Maine populations were most similar to outer Bay of Fundy and Gulf of St. Lawrence populations, and neither Maine nor Canadian populations necessarily clustered according to geographic proximity in the NJ analysis. By contrast, a principal component analysis of arcsine transformed allele frequencies depicted Maine populations as relatively divergent from all Canadian salmon populations. Overall, although the allozyme data are useful in that they confirm that Maine populations are genetically differentiated from Canadian populations, the population relationships suggested in Cordes et al. (2005) and Verspoor et al. (2005) deserve less weight than those presented in King et al. (2001) and Spidle et al. (2001;2003;2004), because the latter studies resolved much more genetic variation than observed in the allozyme studies, and thus are expected to provide more robust estimates of population relationships (Kalinowski 2002; 2005).

One striking line of evidence supporting the discreteness and biological significance of the GOM DPS is only briefly alluded to in the Status Review. This is the fact that the landlocked Maine Atlantic salmon populations branch with the anadromous Maine salmon populations with >70% bootstrap support in the Spidle et al. (2003) NJ analysis. This is doubly significant. First, this is evidence that the anadromous salmon in Maine retain evidence of co-ancestry with local, native non-anadromous populations. In other words, the NJ analysis suggests a closer relationship between anadromous Maine salmon and landlocked populations that diverged from them thousands of years ago than between the anadromous Maine populations and most other (Canadian) populations with which they could have been experiencing recent (both natural and anthropogenic) gene flow. Second, in the NJ analysis, anadromous Maine salmon (with the exception of Cove Brook) are separated from all other anadromous populations in North America (except for Gold River) by at least two successive nodes with >70% bootstrap support (one of these nodes is the branch leading to the landlocked populations). Hence, if the landlocked populations had not been included in the NJ analysis, bootstrap support for the anadromous Maine cluster would likely have been substantially stronger than 70%. The fact that the Gold River sample also branched with the Maine anadromous and landlocked samples does not negate the significance of the genetic similarity of the landlocked and anadromous Maine populations. The Gold River sample was based on fry and parr collected over two successive years, and appeared divergent from other populations. Its position on the NJ tree could be a random consequence of the same factors (genetic drift driven by small population size and relatedness among the juveniles comprising the sample) that may have influenced the position of the Cove Brook sample; alternatively, it could reflect historical affinities between Maine populations and the populations of southwestern Nova Scotia.

The Status Review also fails to cite important evidence that GOM DPS salmon are uniquely adapted (and therefore both discrete, and significant with respect to the species as a whole). Early on (p. 15) the Status Review cites Reisenbichler (1988) for evidence (from coho salmon) that when salmon are transplanted away from their source population, their marine survival varies in inverse relationship to the geographic distance between donor and source population. The Status Review fails to cite an even more relevant report that shows compelling evidence for the same phenomenon in North American Atlantic salmon (Ritter 1975). That study showed that geographic distance between donor and source population explained 66% of variance in arcsine transformed tag recovery rate (a proxy for marine survival. Figure 1 shows that Atlantic salmon experience relatively undiminished marine survival if stocked within a few hundred km of the donor population, but at donor vs. recipient population distances of >1,400 km, tag recoveries (and therefore, presumably marine survival) approach zero. The distance between the Miramichi River (a major source population for stocking) and the Penobscot River is of this approximate magnitude, and the distance for the other Canadian source populations (in Quebec) is even greater. Thus, one would expect extremely low returns for Canadian-origin salmon in Maine, which is precisely what was observed. As summarized in Spidle et al. (2003), heavy stocking of the Penobscot with Miramichi salmon from 1948-1967 produced returns only on the order of tens of fish per year, whereas adult returns rebounded when stocking was subsequently switched to GOM-origin (Machias and Narraguagus) salmon (1968-1971), and finally to salmon bred from returning Penobscot fish from 1972 onward. Likewise, as reported in Spidle et al. (2004) attempts to restore the Connecticut River salmon population using Canadian-origin salmon produced almost no returns; whereas, return rates increased substantially when Penobscot broodstock were subsequently used. The history of Penobscot and Connecticut River stocking programs is tantamount to experimental evidence that GOM-origin Atlantic salmon experience higher marine survival than Canadian-origin salmon when they are stocked anywhere in New England, and therefore is evidence of the locally adapted nature of Gulf of Maine salmon, and hence of the distinctiveness of the DPS.

Threats to the DPS and its habitat

The Status Review provides a comprehensive description of threats and limiting factors that apply to the freshwater range of the DPS. A strong case is made that dams pose the largest threat in the freshwater habitat to recovery of the DPS, although a long list of other threats and limitations are discussed. These include water pollution, pesticides, acidification, water diversions, diseases and parasites, exotic predators and competitors, and not least, deleterious ecological consequences of the diminution and loss of runs of other anadromous fishes that once co-occurred with Atlantic salmon.

In contrast to the extensive description of threats that apply to the freshwater habitat, two other categories of threat considered in the Status Review, salmon aquaculture and reduced marine survival receive much briefer treatment, and deserve further comment.

As described in the Status Review, farmed salmon pose a number of threats to native salmon. The Review also notes the large numbers of escaped aquacultural salmon that have returned to the St. Croix, Dennys and Narraguagus Rivers, but makes no explicit link between this fact and the particularly poor returns of spawners to these rivers noted elsewhere in the Review (e.g., Dennys and Narraguagus, Table 7.1.4; St. Croix, p. 57). An important aquaculture-related threat is outbreeding depression that occurs when aquacultural salmon escape and spawn in nearby rivers. The Status Review cites some studies that bear on this threat (e.g., Hindar et al. 1991; Fleming and Einum 1997; McGinnity et al. 1997; Gross 1998), but fails to highlight one important point. Evidence in the cited studies has concerned genetic interactions between farmed and wild salmon of the same continental race; whereas, at least a proportion of the aquacultural salmon escaping into Maine rivers have presumably have been of the European origin Landcatch strain. Outbreeding depression between native wild North American salmon and aquacultural salmon of at least partial European origin is likely to be more severe than situations where both wild and domestic fish are of the same continental race. Aquacultural salmon of European origin are known to have reproduced and produced up to 10% of juveniles sampled in at least one Bay of Fundy river, the Big Salmon (P. O'Reilly, DFO Canada, personal communication). Although use of European origin salmon in aquaculture is no longer permitted, considerable harm may already have been done. There is also recent scientific evidence, not cited in the Status Review, of deleterious fitness effects from hybridization between Saint John River derived aquacultural salmon and Nova Scotia populations of wild salmon. F1 crosses between the aquacultural strain and non-domesticated salmon showed a decrease in survival, and an increase in variance in survival among families (Lawlor 2003; Lawlor and Hutchings 2004). It is important to note that fitness effects are expected to be worse in F2 generation hybrids, because of the break-up of co-adapted gene complexes.

The section in the Status Review on marine survival is remarkably brief in relation to its likely importance as a threat to the GOM DPS. This undoubtedly reflects, at least in part, the relative paucity of information on this subject in comparison to the wealth of information available on threats in the freshwater environment. Nonetheless, there is more information that could be cited on the subject. For example, although it is cited elsewhere in the Status Review, a study by Chaput et al. (2005) that documents a phase shift in marine productivity of Atlantic salmon is not discussed in the section on marine survival. Chaput et al. (2005) document an abrupt decline in marine survival of Atlantic salmon that began around 1991, has persisted until present, and involves all northwest Atlantic salmon stocks – and hence is likely to be an important factor in the failure of the

GOM DPS to recover despite the many recovery efforts that have been undertaken. The majority of references to marine survival cited in the Status Review cover time periods before 1991, and thus are of limited relevance to recent and current recruitment of Maine Atlantic salmon.

A group of nearby Atlantic salmon populations, known as the inner Bay of Fundy (iBoF) Atlantic salmon designatable unit (DU, a Canadian term closely analogous in meaning to a DPS) was listed as Endangered by the by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2001, and under the Canadian federal Species at Risk Act (SARA) in 2003. Given their relatively close geographic proximity to the GOM DPS, and their similar conservation status, there are useful comparisons to be made between the iBoF Atlantic salmon DU and the GOM DPS, but such comparisons are not made in the Status Review. Although some freshwater habitat for iBoF salmon has been lost due to dams and other blockages, much the habitat remains available and has been judged relatively healthy. There is little industrial pollution, acidification is not a concern (because of the well buffered bedrock geology), exotic species are not thought to pose a serious threat, and runs of other anadromous species, including smelt, alewife and shad remain relatively healthy. Several publicly available reports (not cited in the Status Review) identified low marine survival as a key limiting factor for iBoF Atlantic salmon (National Recovery Team 2002; DFO 2003; Amiro 2003). For example, marine survival of hatchery smolts for an iBoF river, the Big Salmon, declined from an average of 6% during 1966-1991, to 0.3% for the 2002 smolt year class (Gibson et al. 2004). Marine survival rates for another iBoF river, the Stewiacke, were 0.02-0.42% in 1991-1993 (Amiro and Jefferson 1996). Such return rates are well below replacement levels (Amiro 2003), and iBoF salmon are currently being maintained in a captive gene banking program comparable to the one employed for the GOM salmon.

Of course, iBoF salmon may not be perfectly comparable to GOM salmon, for reasons including differences in the near shore marine environments of the two areas and possible differences in marine migration routes. On the other hand, the two population groups probably overlap in their marine distribution in the outer Bay of Fundy and Gulf of Maine. Moreover, as noted above, the decline in marine survival has affected most, if not all, of northwest Atlantic populations. For example, Reddin et al. (2000) reported at least a 50% decline in marine survival in two Newfoundland rivers between the 1970s and the 1990s. Wide scale declines in marine survival beginning in the 1980s have also been reported for Europe (Potter and Crozier 2000).

A decline in marine survival may therefore also pose the leading threat to the survival of the GOM DPS. Although the many factors identified for the freshwater environment in Maine undoubtedly limit the potential for recovery of the GOM DPS, poor marine survival may be the greatest proximate threat, a suggestion supported by the failure of spawner escapement to even approach conservation escapement goals scaled to the amount of currently available freshwater habitat (e.g. Status Review Table 7.1.4).

As noted in the Status Review, the causes of marine mortality remain poorly understood. One possible explanation for an increase in marine mortality is a climate-driven North

Atlantic regime shift post-1991(Chaput et al. 2005). Another possibility is a more-or-less concurrent transition to an alternate continental shelf ecosystem driven by historical over-exploitation of groundfish stocks in the northwest Atlantic (Choi et al. 2004). A third possibility, particularly relevant to populations of salmon in the Gulf of Maine and adjacent Canadian areas that have seen some of the worst declines in marine survival, is that growth of the aquaculture industry has also contributed to the decline in marine survival. Sorting out these competing, but not mutually exclusive possibilities should be a priority for further research.

Finally, one more category of threat to the GOM DPS deserves comment. The loss of genetic diversity can impair population fitness, and small numbers of breeding individuals can lead to inbreeding, and further loss of fitness. Given the recent demographic history of GOM salmon in the smaller rivers such as the lower Penobscot tributaries and the Downeast rivers, such genetic risks to population health are clearly a concern; yet the Status Review appear to largely dismiss such concerns (p. 164-165) on the basis that the captive breeding program is effectively managing genetic diversity in these populations. This is certainly true in some degree, but ignores two points. First, a situation where the continued genetic health of several populations is largely dependent on human intervention can only be regarded as precarious. Second, this view fails to consider the loss of genetic variation prior to the captive breeding program. Lage (2003) offers evidence of population bottlenecks affecting Kenduskeag and Cove Brook, and documents a historical decline in genetic diversity in the Dennys River. The latter information is not cited in the Status Review.

(c) Are the scientific conclusions sound and derived logically from the results?

The soundness and logical basis of the scientific conclusions pertaining to the delineation of the DPS has already been discussed extensively under the first two terms of reference. In general, the conclusions are sound. One exception, however, occurs on p. 52 of the report where it is stated that “Based on genetic analysis…four primary groups of North American populations…are evident”. The report lists these ‘primary’ groups as the anadromous GOM populations, non-anadromous Maine populations, Canadian populations, and the Connecticut River population. The genetic data in King et al. 2001 and Spidle et al. (2003; 2004) do not support such a division. Inspection of the NJ tree (Figure 3) in Spidle et al. (2003) suggests at least three major anadromous salmon groups, two Canadian plus the Maine DPS. Given its extremely recent derivation and subtle genetic differentiation from the Penobscot stock (Spidle et al. 2004), the Connecticut River population is clearly (in terms of its genetic affinities) a member of the ‘Maine’ group. The landlocked Maine populations definitely represent a divergent group, but the same would almost certainly be true of a number of other, unrelated landlocked populations in Canada. A recent genetic study of 53 Canadian rivers (Verspoor 2005) based on allozyme data revealed six major population groups, each likely to be as differentiated from each other as the Maine populations are from the Canadian populations.

The key conclusion that the GOM Atlantic salmon DPS is endangered is incontestable in light of the current extremely low abundance of salmon returning to rivers within the DPS, and the failure of concerted conservation efforts, including captive breeding and population supplementation, to turn the situation around thus far.

The scientific conclusions regarding the nature of threats and limitation to the DPS are generally well grounded. The report discusses evidence for a long list of threats including habitat degradation, pollution, historical over-exploitation, ecological effects, aquaculture and poor marine survival and inadequate regulations, as they apply to the five ESA listing criteria, and concludes that all five criteria apply in at least some degree to the status of the DPS. This is certainly true, on at least a historical basis. At least one factor, over-exploitation is likely not a significant current threat, in light of the fact that the west Greenland fishery has been greatly curtailed, all fisheries targeted on the GOM Atlantic salmon are closed, and groundfish fisheries in Atlantic Canada that previously caught GOM Atlantic salmon as bycatch, are either closed or greatly curtailed. The small St. Pierre and Miquelon fishery is the one remaining targeted salmon fishery that could catch GOM salmon; the number of GOM salmon that it intercepts is unknown but likely very small.

(d) Where available, are opposing scientific studies or theories acknowledged and discussed?

For the delineation of the GOM DPS, the key opposing theory is that current salmon populations in this DPS are derived wholly or in part from historical stocking of Canadian salmon. The main evidence in support of this theory, the large numbers of Canadian-origin salmon that were stocked over an extended period in the 20^{th} century, is well documented in the Status Review. As discussed earlier in this report a suggestion by Bernier et al. (1995) that an apparent increase in grilse return rates from the 1960s to the early 1990s was evidence of introgression by Canadian salmon is discussed in the Status Review, as is the opposing suggestion that this apparent trend was a consequence of selective removal of 2SW-type salmon in the West Greenland fishery. Likewise, the Status Report authors suggest reproduction by stray Canadian-type salmon as a possible alternative explanation for the anomalously divergent nature of the Cove Brook population, in addition to the more likely possibility that the divergence of Cove Brook is due to genetic drift accelerated by a small population size.

For other aspects of the Status Report, which deal primarily with the nature of threats to the DPS, opposing theories are not a major issue, since none of the suggested threats and limiting factors are mutually exclusive. As already discussed, except for what is arguably an under-emphasis on threats related to aquaculture and poor marine survival, the Status Report does an excellent job of reviewing possible threats to the DPS.

References

Amiro, PG. 2003. Population status of Inner Bay of Fundy Atlantic salmon (*Salmo salar*), to 1999. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2488. 44p + vi.

Amiro, PG and EM Jefferson. 1996. Status of Atlantic salmon in Salmon Fishing Areas 22 and 23 for 1995, with emphasis on inner Bay of Fundy stocks. Research Document 96/134, Canadian Stock Assessment Secretariat, Department of Fisheries and Oceans, Halifax, N.S.

Bernier, K, D Billings, N Dube, C Fay, S Hall, L Horvath and B Stetson. 1995. Report of the Penobscot River Subcommittee. Four Rivers Technical Working Group, Governor's Maine Atlantic Salmon Task Force. 147 p.

Chaput, G, CM Legault, DG Reddin, F Caron and PG Amiro. 2005. Provision of catch advice taking account of non-stationarity in productivity of Atlantic salmon (Salmo salar L.) in the Northwest Atlantic. ICES Journal of Marine Science 62:131-143.

Choi, JS, KT Frank, WC Leggett, and K Drinkwater. 2004. Transition to an alternate state in a continental shelf ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 61:505-510.

Cordes, JF, DL Perkins, HL Kincaid and B May. 2005. Genetic analysis of fish genomes and populations: allozyme variation within and among Atlantic salmon from Downeast rivers of Maine. Journal of Fish Biology 67 (supplement A):104-117.

DFO. 2003. Atlantic Salmon Maritimes Provinces Overview for 2002. Stock Status Report 2003/026, Department of Fisheries and Oceans.

Fay, C, M Bartron, S Craig, A Hecht, J Pruden, R Saunders, T Sheehan and J Trial. 2006. Status Review for Anadromous Atlantic Salmon (Salmo salar) in the United States. Report to the National Marine Fisheries Service and the U.S. Fish and Wildlife Service. 283 pages.

Fleming, IA and S Einum. 1997. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES Journal of Marine Science 54:1051-1063.

Gibson, AJF, RA Jones, SF O'Neil, JJ Flanagan and PG Amiro. 2004. Summary of monitoring and live gene bank activities for inner Bay of Fundy Atlantic salmon in 2003. Research Document 2004/016, Canadian Science Advisory Secretariat, Department of Fisheries and Oceans, Dartmouth N.S.

Gross, MR. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl. 1):131-144.

Hindar, K, N Ryman and F Utter. 1991. Genetic effects of cultured fish on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48(5):945-957.

Hutchings, JA and MEB Jones. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 55 (Supplement 1):22-47.

Kalinowski, ST. 2002. How many alleles per locus should be used to estimate genetic distances? Heredity 88:62-65.

Kalinowski, ST. 2004. Genetic polymorphism and mixed-stock fisheries analysis. Canadian Journal of Fisheries and Aquatic Sciences 61:1075-1082.

Kalinowski, ST. 2005. Do polymorphic loci require large sample sizes to estimate genetic distances? Heredity 94:33-36.

King, TL, ST Kalinowski, WB Schill, AP Spidle and BA Lubinski. 2001. Population structure of Atlantic salmon (*Salmo salar* L.): a range-wide perspective from microsatellite DNA variation. Molecular Ecology 10:807-821.

Lacroix, GL and MJW Stokesbury. 2004. Adult return of farmed Atlantic salmon escaped as juveniles into freshwater. Transactions of the American Fisheries Society 133:484-490.

Lawlor, JL. 2003. Genetic differences in fitness-related traits among populations of wild and farmed Atlantic salmon, *Salmo salar*. MSc Thesis, Dalhousie University, Halifax.

Lawlor, JL and JA Hutchings. 2004. Consequences to fitness-related traits of hybridization between farmed and wild Atlantic salmon, *Salmo salar*. Journal of Fish Biology, 65 (Supplement A):319.

McGinnity, P, C Stone, JB Taggart, D Cooke, D Cotter, R Hynes, C McCamley, T Cross and A Ferguson. 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES Journal of Marine Science 54:998-1008.

National Recovery Team for Inner Bay of Fundy Atlantic Salmon Populations. 2002. FINAL DRAFT: National Recovery Strategy for Inner Bay of Fundy Atlantic Salmon (*Salmo salar*) Populations. National Recovery Strategy, Recovery of Nationally Endangered Wildlife (RENEW), Ottawa.

Nei, M, F Tajima and Y Tateno. 1983. Accuracy of estimated phylogenetic trees from molecular data. Journal of Molecular Evolution 19:153-170.

Olivero, AP. 2003. Planning methods for ecoregional targets: freshwater aquatic ecosystems and networds. The Nature Conservancy, Conservation Science Support, Northeast and Caribbean Division. Boston, MA. 55 p.

Potter, ECE and WW Crozier. 2000. Perspective on the marine survival of Atlantic salmon. Pages 19-36 *in* D. Mills, editor. The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Fishing News Books, Oxford.

Reddin, DG, J Helbig, A Thomas, BG Whitehouse and KD Friedland. 2000. Survival of Atlantic salmon (*Salmo salar* L.) related to marine climate. Pages 88-91 in D. Mills, ed. The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Fishing News Books, Oxford.

Ritter, JA. 1975. Lower ocean survival rates for hatchery-reared Atlantic salmon (*Salmo salar)* stocks released in rivers other than their native streams. ICES CM 1975/M:26, 10.

Spidle, AP, WB Schill, BA Lubinski and TL King. 2001. Fine-scale population structure in Atlantic salmon from Maine's Penobscot River drainage. Conservation Genetics 2:11-24.

Spidle, AP, ST Kalinowski, BA Lubinski, DL Perkins, KF Beland, JF Kocik and TL King. 2003. Population structure of Atlantic salmon in Maine with reference to populations from Atlantic Canada. Transactions of the American Fisheries Society 132:196-209.

Spidle, AP, TL King and BH Letcher. 2004. Comparison of genetic diversity in the recently founded Connecticut River Atlantic salmon population to that of its primary donor stock, Maine's Penobscot River. Aquaculture 236:253-265.

Verspoor, E. 2005. Regional differentiation of North American Atlantic salmon at allozyme loci. Journal of Fish Biology 67 (supplement A):80-103.

Verspoor, E, JA Beardmore, S Consuegra, C García de Leániz, K Hindar, WC Jordan, M-L Koljonen, AA Mahkrov, T Paaver, JA Sánchez, Ø Skaala, S Titov and TF Cross. 2005. Population structure in the Atlantic salmon: insights from 40 years of research into genetic protein variation. Journal of Fish Biology 67 (Supplement A):3-54.

Winans, GA, MM Paquin, DM Van Doornik, BM Baker, P Thornton, D Rawding, A Marshall, P Moran and S Kalinowski. 2004. Genetic stock identification of steelhead in the Columbia River basin: an evaluation of different molecular markers. North American Journal of Fisheries Management 24:672-685.

Wright, JM and P Bentzen. 1994. Microsatellites: genetic markers for the future. Reviews in Fish Biology and Fisheries 4:384-388.

APPENDIX 1: Materials provided by the Center of Independent Experts

Fay, C., M.Bartron, S.Craig, A Hecht, J Pruden, R.Saunders, T.Sheehan, and J. Trial (2006) Status Review for Anadromous Atlantic Salmon (***Salmo salar***) in the United States. Report to the National Marine Fisheries Service and US Fish and Wildlife Service. 283pp.

Selected references from Fay et al. (2006).

APPENDIX 2: Statement of Work

Consulting agreement between the University of Miami and Dr. Paul Bentzen

April 24, 2006

Atlantic salmon status review

Background

The purpose of this technical review is to ensure that the scientific information presented and analyzed in the Status Review for Atlantic salmon in the United States is the best available scientific data.

On November 17, 2000, the National Marine Fisheries Service and the U.S. Fish and Wildlife Service (the Services) issued a final rule to list the Gulf of Maine Distinct Population Segment of Atlantic Salmon (GOM DPS) as endangered under the Endangered Species Act (ESA). The GOM DPS was defined as all naturally reproducing wild populations of Atlantic salmon, having historical river-specific characteristics found north of and including tributaries of the lower Kennebec River to, but not including the mouth of the St. Croix River at the United States-Canada border and the Penobscot River above the site of the former Bangor Dam. Populations which met these criteria were identified as being in the following rivers: Dennys, East Machias, Machias, Pleasant, Narraguagus, Sheepscot, Ducktrap, and Cove Brook.

In the final rule listing the GOM DPS, the Services deferred the determination of inclusion of fish that inhabit the main stem and tributaries of the Penobscot River above the site of the former Bangor Dam. The deferred decision reflected the need for further analysis of scientific information, including a detailed genetic characterization of the Penobscot population. In addition, the Services were committed to reviewing data regarding the appropriateness of including the upper Kennebec and other rivers as part of the DPS. In late 2003, the Services assembled a Biological Review Team (BRT) comprised of biologists from the Maine Atlantic Salmon Commission, Penobscot Indian Nation, NMFS, and USFWS. The BRT was charged with reviewing and evaluating all relevant scientific information necessary to evaluate the current DPS delineations and determining the conservation status of the populations that were deferred in 2000 and their relationship to the currently listed GOM DPS.

NOAA Fisheries is required to use the best available scientific and commercial data in making determinations and decisions under the ESA. The first question that must be addressed is what the appropriate species delineation is for consideration of conservation status. The ESA defines an endangered species as “any species which is in danger of extinction throughout all or a significant portion of its range,” and a threatened species as “any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." A species may be determined to be threatened or endangered due to any one of the following factors:

(1) the present or threatened destruction, modification, or curtailment of its habitat or range;
(2) overutilization for commercial, recreational, scientific or educational purpose;
(3) disease or predation;
(4) the inadequacy of existing regulatory mechanisms; and
(5) other natural or manmade factors affecting its continued existence.

The scientific and commercial information contained in the Status Review will likely contain essential factual elements upon which the agency could base its ESA determination. Accordingly, it is critical that the Status Review contain the best available information on the species and the threats, that all relevant information is identified and included, and that all scientific findings be both reasonable, and supported by valid information contained in the document.

Objectives of the CIE Review

As stated above, the Status Review has been prepared by the BRT. The Center for Independent Experts (CIE) shall review the Status Review Report to ensure that its contents can be factually supported and that the methodology and conclusions are scientifically valid.

There are several primary issues related to this species that must be addressed, and, therefore, reviewers with the following expertise are required to ensure the best available information has been utilized:

1. Life history and population dynamics of Atlantic salmon;
2. Atlantic salmon genetic, physiological, behavioral, and/or morphological variation throughout the species' range;
3. Habitat requirements;
4. Predation and disease;
5. Regulatory mechanisms for managing the species;
6. Other natural or manmade impacts affecting Atlantic salmon;
7. Aquaculture; and
8. Conservation actions including restoration efforts and recovery activities (including the conservation hatchery program).

Familiarity with ESA is also highly desirable. Each reviewer will be supplied with the Status Review Report prepared by the BRT. Any of the reports and papers cited in the Status Review Report will be made available to the reviewers upon their request.

Specific terms of reference for the CIE review:

a. Is the species delineation supported by the information presented?

b. Does the Status Review include and cite the best scientific and commercial information available on the species and threats to it and to its habitat?
c. Are the scientific conclusions sound and derived logically from the results?
d. Where available, are opposing scientific studies or theories acknowledged and discussed?

Specific Activities and Responsibilities

The CIE shall provide four reviewers to conduct a letter review of the Status Review Report. Each reviewer's duties shall not exceed a maximum of five work days. Each reviewer shall analyze the Status Review Report and develop their report in response to the above terms of reference. The reviewers shall conduct their analyses and writing duties from their primary locations. Each written report is to be based on the individual reviewer's findings, and no consensus report shall be accepted. See Annex I for additional details on the report outline.

No later than May 15, 2006, each reviewer's report shall be submitted to the CIE for review[1]. The reports shall be sent to Dr. David Sampson, via email at david.sampson@oregonstate.edu, and to Mr. Manoj Shivlani, via email at mshivlani@rsmas.miami.edu.

[1] Each written report will undergo an internal CIE review before it is considered final.

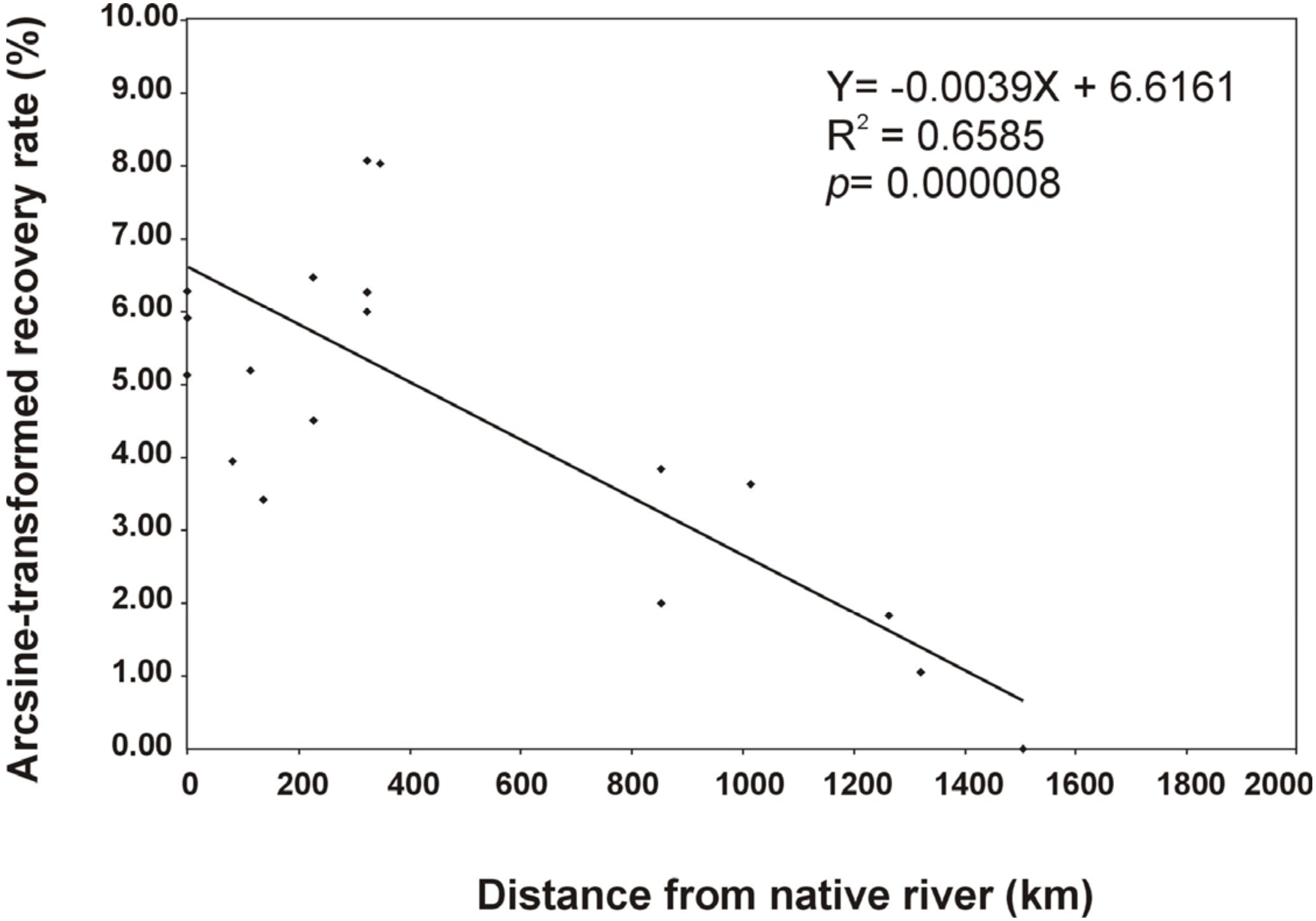

Figure 1. Lower ocean survival rates for hatchery-reared Atlantic salmon *(Salmo salar)* stocks released in rivers other than their native streams. Source: Ritter, 1975. Reproduced by permission of Carolyn Harvie, Department of Fisheries and Oceans, Canada