Ecological and Genetic Effects of Salmonid Introductions in North America¹

C. C. Krueger and B. May

College of Agriculture and Life Sciences, Department of Natural Resources, Farnow Hall, Cornell University, Ithaca, New York 14853, USA


Stocking of non-native Salmonidae into North American waters began around 1870. Brown trout (Salmo trutta) from Europe established populations across North America and is the only successful inter-continental introduction. Introductions of native salmonids within North America but outside their native ranges have been common. Ecological effects of salmonid introductions include competition, predation on native salmonids and other fishes, environmental modification through digging of redds in stream bottom substrates during spawning, and introduction of parasites and disease to native fish. Direct genetic effects from stocked salmonids are caused by interbreeding with native species. Indirect genetic effects may result through selective forces and/or a reduction of effective population size, genetic drift, and inbreeding. Management actions used to remove non-native salmonid populations include chemical reclamation and construction of barriers to movement. Salmonid stocking as a management practice is appropriate for species or population rehabilitation. Continued stocking of non-native salmonids should cease where viable native salmonid populations exist. New introductions of Eurasian species should not be made because effects are unpredictable. Aquaculture and the creation of transgenic fish pose special threats to North American salmonids. The era of widespread, intentional introductions of salmonids by man justifiably is drawing to a close.

L'empoissonnement de certaines eaux d'Amérique du Nord avec des Salmonidae non indigènes a commencé aux environs de 1870. La truite brune, Salmo trutta, originaire d'Europe, dont on trouve des populations partout en Amérique du Nord, est le seul cas d'introduction intercontinentale fructueuse. L'introduction de Salmonidae indigènes, mais à l'extérieur de leur aire de distribution originale, a été courante. Parmi les effets écologiques de l'introduction de Salmonidae figurent la compétition, la prédation qui s'exerce sur des Salmonidae indigènes et d'autres espèces de poissons, les modifications environnementales attribuables au creusement de nids pendant le frai à même les matériaux formant le lit des cours d'eau et l'introduction de parasites et de maladies attaquant les espèces indigènes. Les effets génétiques directs de l'empoissonnement avec des Salmonidae résultent de la reproduction croisée avec des espèces indigènes. Les effets génétiques indirects peuvent être attribuables à des forces de sélection ou à une réduction de la taille effective d'une population, à une dérive génétique et à des croisements consanguins. Les méthodes de gestion utilisées pour éliminer les Salmonidae non indigènes comprennent l'ajout de produits chimiques pour désa枚poissonner des plans d'eau et la construction de barrières limitant les déplacements. L'empoissonnement avec des Salmonidae est une pratique de gestion qui convient au rétablissement d'espèces ou de populations. L'empoissonnement continu avec des Salmonidae non indigènes devrait être interrompu là où il existe des populations de Salmonidae viables. On ne devrait pas procéder à une nouvelle introduction d'espèces eurasiennes, car les effets sont imprévisibles. L'aquaculture et la création de poissons transgéniques constituent une menace particulière pour les Salmonidae d'Amérique du Nord. L'époque où l'homme pouvait justifier l'introduction intentionnelle et généralisée de Salmonidae tire à sa fin.

Received July 19, 1990
Accepted March 7, 1991

Widespread introductions of trout and salmon in North America began around 1870 and were common by the turn of the century. The initiation of these stocking programs corresponded with major advancements in fish cultural practices, especially the artificial fertilization and hatching of salmonids, and the construction of rapid transportation systems, most notably railroads (Bowen 1970; Moyle 1986). By the 1960's, fish cultural technology had advanced to the point that salmonid hatcheries capable of producing millions of fish annually were being used to stock bodies of water as large as the Great Lakes (Parsons 1973). Over this time period from 1870 to 1970, a variety of North American and European salmonid species were introduced outside of their native ranges. For example, 10 exotic species of Salmonidae were introduced into Michigan waters between 1873 and 1972 (Latta 1974).

The term, introduction, is used here to mean transfers of fish by man, sometimes repeatedly, into waters outside of their native ranges. Introductions may be categorized into three types based on origins of the fish used: inter-continental transfers, the stocking of native species within North America but outside of their native ranges (intracontinental transfers), and the transfer of genetically differentiated stocks within native ranges (stock transfers). Successful introductions result in the sustained

¹This paper forms part of the Proceedings of the Ecological and Genetic Implications of Fish Introductions Symposium (FIN) convened at the Great Lakes Institute, University of Windsor, Ontario, Canada, May 17–19, 1990.
naturalization of species or stocks in their new environment. Most introductions have occurred by intentional or purposeful actions to "improve" native fish communities for humans (Courtenay and Kohler 1986). Only rarely have successful introductions of salmonids occurred from the accidental release or escape of fish.

The introduction of salmonid species has had a profound and permanent effect on the native fish fauna of North America. These effects may be classified as ecological or genetic. Ecological effects involve processes or mechanisms such as competition, predation, and habitat alteration (Taylor et al. 1984; Moyle et al. 1986), and are a direct consequence of the genetic characteristics of the species introduced. Genetic effects involve processes which change the gene pools of populations and species. Ecological and genetic effects, in theory, may cause native species to (1) be eliminated, (2) have changes in growth and survival, (3) be genetically changed, (4) alter community structure, (5) exhibit combinations of the above, or (6) exhibit no detectable changes (adapted from Moyle et al. 1986). Typically, the effects of introductions have been discussed in terms of the impacts of one species on another. However, important intraspecific effects may also result from the introduction of stocks or populations that are genetically differentiated from native populations of the same species (i.e., stock transfers; Krueger et al. 1981).

The purpose of this paper is to provide a review of trout and salmon (Salmonidae: Salmoninae) introductions in North America, and to examine the evidence for ecological and genetic effects of these introductions. The primary focus will be on effects that have occurred between introduced and native salmonids. Interactions between introduced salmonids and other native fishes and other aquatic organisms such as invertebrates will be discussed minimally. The effects that have occurred on fisheries from the introduction of salmonids will not be discussed (e.g., Hansen et al. 1990).

Review of Salmonid Introductions

The stocking and subsequent naturalization of non-native salmonids has occurred worldwide on all continents except Antarctica. Notably successful introductions have occurred with the North American salmonids, especially the brook trout (Salvelinus fontinalis) and rainbow trout (Oncorhynchus mykiss), to Europe, South America, Africa, and Asia (MacCrimmon and Campbell 1969; MacCrimmon 1971). In contrast, the only successful inter-continental transfer of a salmonid species to North American waters has been the brown trout (Salmo trutta) from Europe (Luton 1985). Salmonid species that have been introduced to North America but failed to establish populations include the cherry salmon (O. masou; Christie 1970), the Ohrid trout (Salmo letnicus; Courtenay et al. 1984), and the Danube salmon or huchen (Hucho hucho; Crossman 1984).

Although few inter-continental transfers of salmonids have been made into North American waters, intra-continental introductions of native salmonids to areas outside their natural distribution have been extensive. Such introductions have occurred for virtually all North American species of Oncorhynchus, Salmo, and Salvelinus at one time or another. Salmonids from Pacific drainages that have established populations outside of their original ranges include: rainbow trout into the Great Lakes drainages (MacCrimmon and Gots 1972) and other Atlantic drainages from the Appalachian Mountains to Newfoundland (King 1937; King 1942; Chadwick and Bruce 1981; Whoriskey et al. 1981; Moore et al. 1983), golden trout (O. aquabonita) from the Kern River drainage in California into the high mountain lakes of the Sierra Nevada and mid-continent Rocky Mountains region including Alberta (Crossman 1984), the chinook, coho, and kokanee salmon, (O. tshawytscha, O. kisutch, O. nerka) into the Great Lakes/St. Lawrence River and other Atlantic drainages (Parsons 1973; Stoltz 1974; Symons and Martin 1978; Whitler 1982; Martin and Dadswell 1983; Emery 1985; Dumont et al. 1988), and the kokanee salmon into lakes and reservoirs throughout the west (Wydowski and Bennett 1981).

Similarly, salmonids from eastern North America (Atlantic coast to the Mississippi drainage and north) have been introduced westward. Most notable has been the naturalization of brook trout to waters from the Rocky Mountains west to the Pacific Ocean. Lake trout (Salvelinus namaycush) have also established populations in western North American lakes such as Lake Tahoe, Nevada and Lewis Lake, Wyoming, but naturalized populations of this species are less widespread outside its range than the brook trout. The Atlantic salmon (Salmo salar) has been stocked into the upper Great Lakes (Parsons 1974) westward to the Pacific drainages such as Cowichan Lake, British Columbia (introductions included salmon of North American and Scottish origins, Crossman 1984). Although establishment of Atlantic salmon populations has not occurred, their presence in lakes has been maintained by annual stocking. Species such as Dolly Varden trout (Salvelinus malma) and Arctic char (S. alpinus) have not been a part of the extensive stocking programs focused on other North American salmonids. In the west, many lakes above 1 500-2 000 m were originally barren of fish but now contain introduced populations of salmonids from eastern and western North American sources (brook, brown, rainbow, cutthroat, and golden trout; Moyle 1986).

The transfer of stocks or populations of species within native ranges has been both extensive and poorly documented. Stock transfers have probably been the most common type of introduction to occur in North America because stocking programs have been an important part of management conducted by fishery agencies. The extensive nature of these introductions can be illustrated by a genetic study of brook trout initiated by the authors and D. Perkins. This project required the sampling of brook trout populations from the waters of the Adirondack Mountain region of New York where stock transfers had not occurred. Fewer than 25 (2.3%) out of 1 100 brook trout lakes and ponds in the Adirondack region were identified as unstocked based on historic records. Species restoration programs such as those conducted for lake trout and Atlantic salmon have often used stock transfers as a management action. For example, lake trout from Clearwater Lake, Manitoba have been stocked regularly into Lake Ontario for more than 10 yr (Krueger et al. 1989). In some cases, the stocks transferred are recognized subspecies. For example, Yellowstone cutthroat trout (Salmo clarki lewisi) have been stocked for more than 35 yr into Glacier National Park waters that contained westslope cutthroat trout (S. c. bouvieri; Marnell 1988).

Inter-continental stock transfers have been rare because few species are native to more than one continent. Clearly the potential exists for species such as Arctic char, Atlantic salmon, and those in the genus Oncorhynchus to be introduced from other continents. As mentioned above, Atlantic salmon from European origins have been stocked in North America. In addition, Arctic char from France were released into Westward Lake,
Ontario and three lakes in Saskatchewan; however, these lakes did not originally contain char (Crossman 1984).

The stocking of hybrids between species has been much less common than the transfer of species or stocks. The most extensive hybrid stocking program has been one administered by the Province of Ontario as part of a fishery rehabilitation project for Lake Huron (Berst et al. 1980). Splake, the fertile hybrid between lake and brook trout, were first stocked in the 1950's as a replacement for the lake trout which was nearly extinct as a result of sea lamprey predation. Later in 1969, splake selected for early maturity and retention of swimbladder gas were begun to be stocked, as were backcrosses between selected splake males and female lake trout. Although a substantial amount of natural recruitment has not been observed, natural spawning of these hybrids has occurred in Lake Huron. Splake have also been stocked into Precambrian Shield lakes of Ontario and lakes of Alberta. A self-reproducing stock was established in Lake 17, Ontario after an initial planting of 5,460 F, hybrids (Berst et al. 1980). In 1951, Agnes Lake, Alberta was stocked with 1,000 F, splake. Natural reproduction was first confirmed in 1955 and has continued at least through 1967 (Goldberg et al. 1967).

In most cases, introductions of salmonids have been intentional as part of stocking programs intended to “enhance” aquatic communities for fishing. In some instances, remarkable sport fisheries have resulted from these stocking programs such as for Pacific salmon in the Great Lakes (Hansen et al. 1990). Enhancement or supplementation programs to benefit commercial fisheries for anadromous species have also been successful. For example, sockeye salmon (O. nerka) have been stocked extensively in Pacific drainages and expanded the range for this species (e.g., Blackett 1979). Stock transfers for this purpose may be increasing along the Pacific coast (Helle 1981). A notable exception to intentional stocking was the accidental introduction and subsequent wide-spread establishment of the pink salmon (O. gorbuscha) from the Pacific Ocean to Lake Superior and their subsequent spread downstream to other Great Lakes and Atlantic drainages (Emery 1981; Kwan and Lawrie 1981; Randall 1984). Escapement from pen-rearing aquaculture operations (e.g., Atlantic salmon along the Pacific coast) will likely serve as a new source of introductions in the future.

Ecological Effects of Salmonid Introductions

Competition

Salmonids introduced into lakes and streams may compete with native fish faunas for food and space. Competition here refers either to the use of resources that are in short or inadequate supply with respect to the potential demand (exploitation competition) or to the use of a resource by a species that interferes with the use of that resource by another species regardless of supply (interference competition). Competitive interactions may lead to (1) the extinction of one species, (2) fluctuating coexistence as the environment alternately favors one species then the other, and (3) niche shifts (Moyle and Vondracek 1985). Competition in streams may occur as species attempt to secure territories for adequate space and, therefore, food and cover (Chapman 1966). Interspecific competition may be most intense during late summer in years of high population abundance when stream flows are often low, and space and food are minimal (Griffith 1988). Under other circumstances, stream populations of salmonids may be more likely regulated through climatic factors such as droughts, floods, or severe winters. Competition between species may be more intense in lakes than in streams because climatic factors are presumed to be less effective regulators of fish populations. This increase, however, may be balanced by reduced territorial behavior in lake habitats because of the increased spatial dimensions and an absence of current (Griffith 1988).

Competition is the most commonly invoked process used to explain the ecological effects of salmonid introductions. For example, native brook trout have disappeared from many waters in eastern North America, especially streams, over the past 100 yr and have been replaced by the recently naturalized, European brook trout. Competition between the species has often been suggested as the process that caused the species shift. Both species occupy similar stream habitats and appear to have considerable diet overlap (e.g., Metzelaar 1929; Nyman 1970; Johnson 1981). In one study, brown trout dominated and excluded brook trout from preferred resting positions in streams during the summer which may reflect a form of interference competition between these species (Fausch and White 1981). Studies of winter habitat preferences have also indicated considerable overlap between the two species; however, interaction at this time of year may be reduced by the lack of agonistic behavior at low temperatures (Cunjak and Power 1986). Competition for space and food in a fluctuating stream environment has been offered as a partial explanation for the replacement of brook trout by brown trout in a Minnesota stream over a 15-yr time period (Waters 1983). Competitive advantages of brown over brook trout may have been enhanced by widespread changes in habitat that have occurred in this region (e.g., deforestation and summer warming of streams).

In other streams of eastern North America, the brook trout has been replaced by rainbow trout introduced from Pacific drainages. These streams have headwater regions that contain only brook trout, followed by a middle zone of sympathy between rainbow and brook trout, and downstream sections dominated by rainbow trout. As with the brown trout, competition between the species often has been suspected as the cause of the displacement of brook trout. However, the potential competitive advantages of rainbow trout over brook trout often have been unclear. For example, brook trout seemed to dominate rainbow trout in environments of low water velocity and temperature (13°C), while no advantage for either species occurred in high water velocity and temperature (19°C; Cunjak and Green 1983, 1984, 1986; see discussion by Fausch 1988). In contrast, Gibson (1981) reported, based on experimental observation, that rainbow trout were more aggressive and could displace brook trout from preferred stream areas. Cunjak and Green (1983) suggested habitat segregation between brook and rainbow trout may be a function, in part, of competitive interactions; however, Fausch (1988) has argued that their data better support the conclusion that genetically fixed differences in fundamental niche may exist between these species that minimize competitive interaction. Several studies also have been conducted over many years on sympatric populations of brook and rainbow trout in Sagehen Creek, California (Gard 1961; Gard and Seegrist 1972; Seegrist and Gard 1972; Gard and Flittner 1974; Erman 1986). Population abundance of these species has fluctuated considerably over time in this stream. Though competition may have played a role in the dynamics of the trout populations, the effects of beavers (Castor canadensis) on habitat, and floods and droughts on recruitment processes, may have been more important factors (see Can. J. Fish. Aquat. Sci., Vol. 48 (Suppl. 1), 1991}
The disappearance of brook trout from streams of the southern Appalachian Mountains may have been caused by competition with naturalized rainbow trout (King 1937; Larson and Moore 1985). Growth rates of both species have been observed to be about equal until spring of the second year of life when rainbow trout gain a growth advantage over brook trout (Whittworth and Strange 1983). This advantage results in a larger size-at-age rainbow trout over brook trout that then continues for the rest of their lives. Also, rainbow trout appear better able than brook trout to occupy the shallow riffles and pools that characterize this region's streams (Larson and Moore 1985). These authors observed that brook trout shifted to unfavorable positions away from main currents when rainbow trout were abundant. The shift in position by brook trout, presumably away from optimal feeding stations, could be the source, or may contribute to, the growth rate differences observed between the species. The size advantage that rainbow trout gain as a result should further enhance the ability of this species to occupy preferred positions in streams. In another study in four Appalachian streams, rainbow trout population densities were reduced an average of 88% by electrofishing (no. 100 m⁻²). In response, brook trout standing stocks (kg ha⁻¹) substantially increased in all four streams over a 6-yr period, and did not follow the changes in density observed in three allopatric control sections (Moore et al. 1983; Moore et al. 1986). These field studies provide some of the best evidence available for competition between rainbow and brook trout (see review by Fausch 1988); although, processes such as predation in addition to competition could also have contributed to their outcomes.

In some Lake Superior tributaries, brook trout are abundant upstream from waterfalls that prevent access to spawning, non-native rainbow trout from the lake. Downstream from these falls, rainbow trout juveniles are typically more abundant than brook trout. In a study conducted on a Lake Superior tributary, growth of young-of-the-year brook trout was significantly suppressed after emergence of rainbow trout fry in June (Rose 1986). Exploitative and interference competition between rainbow and brook trout for invertebrate foods was suggested as a likely cause for the results. Competition by the rainbow trout may explain part of the reason for the displacement of brook trout in this region. Brook trout populations in Great Lakes tributaries may also be threatened by competition for food and space from recently introduced coho salmon which emerge earlier, are larger, and have similar habitat preferences as brook trout juveniles (Fausch and White 1986; Gibson 1981). Many cutthroat trout populations declined precipitously in western North America after non-native salmonids were introduced about 100 yr ago. Competition has often been inferred as the mechanism that caused displacement of cutthroat trout by non-natives; however, changes in habitat and fishing pressures often have contributed to these declines as well (see review by Griffith 1988). Few studies have been conducted to identify the competitive mechanisms involved between cutthroat trout and non-native species. In Yellowstone National Park, the introduction of the brook trout has nearly always resulted in the disappearance of Yellowstone cutthroat trout (Varley and Gresswell 1988). Similarly, brook trout displaced Lahontan cutthroat trout between 1960–70 in Pole Creek, a tributary to the Truckee River, California (Gerstung 1988). The larger size of brook trout over cutthroat trout of similar age may confer a competitive advantage. In northern Idaho streams, brook trout maintained a 20 mm size advantage over cutthroat trout of the same age groups due to their earlier emergence (Griffith 1972). Introduced rainbow, brown, and lake trout have also displaced cutthroat trout at many locations; however, mechanisms that caused the disappearance of cutthroat trout are conjectural (Moyle and Vondracek 1985; Gerstung 1988). For example, cutthroat trout disappeared from the Henrys Fork of the Snake River, Idaho within 8 yr after the introduction of rainbow trout (Griffith 1988). Rainbow trout may have a competitive advantage over cutthroat trout because they appear to be more aggressive than equal-sized cutthroat (Nilsson and Northcote 1981). Kokanee salmon introduced in lakes may also compete with cutthroat trout for plankton food (Gerstung 1988; Marnell 1988).

The golden trout has also suffered from introductions of non-native salmonids presumably through competition. This species was originally endemic to the Kern River watershed in the eastern Sierra Nevada Mountains of California (Schreck and Behnke 1971). Introduced brown, brook, and rainbow trout have displaced golden trout, possibly through competitive mechanisms (Pister 1991). The brown trout, in particular, appeared to successfully defend territories and out-compete golden trout for space in the upper South Fork of the Kern River (Pister, E. P., California Department of Fish and Game, personal communication).

Predation

Predation by introduced salmonids on native salmonids or other aquatic organisms has been little studied in North America. A few references exist, often without details, that note predation by non-native salmonids. For example, lake trout introduced to lakes in Glacier National Park may be a significant cause of mortality of native westslope cutthroat trout through predation (Marnell 1988). Introduced chinook and coho salmon in the Great Lakes also have been noted for their predatory effect on alewife (Alosa pseudoharengus, Stewart et al. 1981). European brown trout are known to be piscivorous and feed upon native brook trout. For example, stomachs of brown trout larger than 30 cm from the North Branch of the Au Sable River, Michigan were found to contain high proportions of fish, notably brook trout (Alexander 1977). A significant increase in brook trout larger than 22.9 cm occurred when 40–66% of brown trout of this size were removed and American mergansers (Mergus merganser) were harassed and chased from a section of this river (Shetter and Alexander 1970). Brown trout were also suspected to be an important predator of golden trout in the Upper Kern River drainage in California (Pister, E. P., California Department of Fish and Game, personal communication).

The effects of introduced salmonids on non-salmonid fishes have been rarely investigated. In a Virginia stream, large (>28 cm) and small (<28 cm) brown trout were experimentally stocked in the spring and changes in the fish community were monitored over the summer and fall (Garman and Nielsen 1982). While small brown trout rarely ate fish, large trout ate five species of fish consistently through the study period of May–November. Abundance of the major prey species, the tor-
rent sucker (*Moxostoma rhoeoecum*), decreased in the section stocked with large trout but remained constant over the same time period in a reference section. Similarly, predation by brown trout on a threatened native sucker species (*Catostomus microstomus*) from northern California may be a mechanism that affects abundance of the sucker population (Moyle and Marciotti 1975). We conclude, based on these studies, that large brown trout can alter the abundance of native fish fauna in North American waters through predation.

Introduced non-native salmonids may also feed upon and affect the abundance of native invertebrates and amphibians. The disappearance of three pelagic cladocheran species of zooplankton in Lake Tahoe has been attributed, in part, to predation by naturalized kokanee salmon (Morgan et al. 1978). Introduced salmonids are also known to feed on benthic invertebrate populations (e.g., Wurtsbaugh et al. 1973), but little documentation of the effects of predation on abundance and distribution of invertebrates has occurred. Such effects may be important, especially in barren lakes. For example, four species of trout and salmon introduced over many years into fishless mountain lakes in California were reported to have altered native invertebrate and amphibian populations (Herbold and Moyle 1986).

Environmental Modification

Some introduced fishes can modify their environments through feeding and other activities and adversely affect native fishes. The common carp (*Cyprinus carpio*) and the grass carp (*Ctenopharyngodon idella*) are well-known examples of non-native introduced fishes that can remarkably alter their aquatic environments. These fish can cause a reduction in aquatic macrophytes and an increase in turbidity often to the detriment of native fishes (Taylor et al. 1984). Similar types of environmental effects from introduced salmonids seem unlikely due to the behavioral patterns characteristic of this family. However, salmonids that spawn in streams do modify their habitat by digging redds in the stream bottom for incubation of their eggs. In streams, population size can be regulated by habitat variables, such as the availability of spawning gravels and juvenile rearing space, that affect recruitment to the next generation. As a result, the number of spawners each year will tend to be in some form of equilibrium with the available spawning habitat. Stocking of salmonids can decouple the feedback mechanisms that naturally control spawner density and result in unusually large numbers of spawners using the available habitat. By their digging activities, these fish could significantly reduce invertebrate production by dislodgement or destruction, disturb redds of native salmonids that spawn at the same time of year, or disrupt habitat for fish species such as sculpins (*Cottus* sp.). The massive stocking of coho and chinook salmon in the Great Lakes has often resulted in exceptionally large spawning runs of salmon up rivers in the fall. In the Platte River, a Lake Michigan tributary, invertebrate populations of 12 taxa decreased significantly in terms of number and weight m^-2^ after the spawning of introduced coho salmon (Hildebrandt 1971). As a result, food supplies for native fishes in this region could be affected negatively through the spawning activities of introduced salmon. The possibility also exists that Pacific salmon from the Great Lakes, through modification of spawning habitats, could physically destroy eggs of native brook trout which are deposited at about the same time in the fall.

Introduction of Parasites and Disease

Stocking of non-native salmonids may result in the inadvertent introduction of parasites and pathogens to indigenous salmonid populations. Disease transmission to wild fish populations may also occur from fish that escape from pen-rearing operations used in commercial aquaculture (Barinaga 1990). If a native population has little natural immunity or resistance to a disease, the results of infection can be disastrous to the population. Stocking of Atlantic salmon smolts from Sweden in 1975 likely caused the introduction of a parasitic fluke (*Gyrodactylus salaris*) to wild populations in Norway (Johnsen and Jensen 1986; Sattaur 1988). Since the initial introduction, the distribution of the parasite in 26 infected rivers has been closely associated with stocking from six infected Norwegian hatcheries (Johnsen and Jensen 1986). In these rivers, a dramatic reduction of populations of salmon parr has occurred and catches of adults in later years have sharply declined. The existence of all wild Atlantic salmon populations in Norway is now considered threatened by this parasite (Hindar et al. 1991).

Documentation of disease introductions in North America from the stocking or escape of salmonids has been uncommon. Dumont et al. (1988) cites a report of infectious pancreatic necrosis in non-native coho salmon in Lake Ontario but not its transmission to native salmonids. In Wyoming, bacterial kidney disease (BKD) has been transmitted from stocked infected hatchery trout to naturalized non-native brook, brown, and rainbow trout populations (Mitchum et al. 1979). Whirling disease, caused by the protozoan, *Myxosoma cerebralis*, was introduced from Europe to North America from a shipment of frozen rainbow trout (see reviews by Hoffman and Schubert 1984 and Marnell 1986). The disease has been found to be pathogenic to rainbow and brook trout in North America. A wild brook trout population in Michigan has been reported to be infected with whirling disease downstream from an infected hatchery (Yoder 1972).

Diseases have been introduced from North America to other locations through transfers of salmonids. For example, infectious hematopoietic necrosis virus (IHNV) was introduced from Alaska through a shipment of sockeye salmon eggs to a hatchery in Hokaido, Japan (Rohovec et al. 1988). The disease subsequently spread to cultured and wild populations throughout the country.

Release or escape of diseased fish from hatcheries or aquacultural operations does not always result in an epidemic among wild fish or detectable transmission of the disease to the wild. In two studies that used experimental stockings of infected hatchery brook trout, BKD and furunculosis were minimally transmitted to wild resident brook trout (Allison 1961; McDermott and Berst 1968). Similarly, the stocking of brook trout, that were carriers of infectious pancreatic necrosis virus, into an Alberta lake resulted in little transmission of the disease into other salmonids present (Yamamoto and Kiliitoff 1979). Hatchery water, after being used for rearing BKD infected Atlantic salmon, did not readily infect wild salmon when discharged into the Margaree River, New Brunswick (Pippy 1969).

Lack of disease transmission was certainly a fortunate outcome of these studies.

Development of disease control programs among management agencies has been encouraged to reduce the risk of disease introduction from infected fish destined for stocking (Goede 1986). Concern about disease transmission from introduced salmonids, especially from Pacific drainages, has been an impor-
naturally occurring, typically infertile F₁ hybrids is rare and short lived (no future generations), and therefore the ecological effects from their presence in fish communities is probably minimal. However, artificial techniques are now available to produce large quantities of viable but infertile triploid interspecies hybrids (see Thorgaard 1983). Triploid hybrids may pose a more serious threat to native salmonids and could cause important ecological effects or indirect genetic effects if stocked.

**Interspecific introgression**

Introgression is the flow of genes from one species gene pool into the gene pool of another species (or subspecies). Frequently, genes are transmitted through introgression to both species (or subspecies) if a narrow contact zone occurs between their geographical distributions. If only a small amount (<0.1%) of gene flow occurs, introgression may be viewed as increasing the capability for adaptation because the process introduces new variation upon which natural selection can operate. A larger amount of gene flow may disrupt the adaptive gene complexes which have evolved over time to permit the native species to effectively use its particular environmental niche. The ultimate threat of introgression is that the flow of genes never stops, and that eventually one gene pool is effectively replaced by that of the other species (or subspecies). Even if the flow of genes is stopped, the effects of introgression may be significant over evolutionary time scales.

Introgression from introduced salmonids has played and continues to play a role in the evolution of native salmonid gene pools, especially in western North America. The principal recipient native species in this region have been the golden trout and various subspecies of cutthroat trout. The principal donor species has been the ubiquitously introduced rainbow trout. Documentation of introgression is much easier in this case than for intraspecific gene flow (between stocks or populations) since the degree of genetic divergence is greater at the species or subspecific level than typically occurs among populations. For example, introgression between the introduced rainbow and native golden trout in California has been reported from field observations of morphological characters (Schreck and Behnke 1971; Moyle 1976). Based on allozyme analysis, introgressive hybridization has been documented between the introduced rainbow trout and native Paiute cutthroat trout of California (S. c. selenis, Busack and Gall 1981). Introgression with rainbow trout has also been detected in native cutthroat populations located in Montana (8 of 16 samples from the Yellowstone River drainage) and Utah (7 of 39 samples) based on allozyme analysis (Allendorf and Leary 1988; Martin et al. 1985). Analyses of mtDNA coupled with allozyme variability has readily permitted the estimation of the degree of introgression among subspecies of cutthroat trout. For example, Gyllensten et al. (1985) have shown that cutthroat trout in Forest Lake, Montana represented a hybrid swarm of native westslope (S. clarki lewisi) and introduced Yellowstone (S. c. bowvieri) cutthroat trout based on mtDNA and allozyme analyses. Gene flow through introgression has occurred to both subspecies gene pools and breeding has been essentially random. This population now no longer represents either subspecies, but will continue to evolve into a new subspecies as long as it remains isolated from other populations. Similar evidence for introgression between native and introduced subspecies of cutthroat trout has been reported for other populations in Montana (Marnell et al. 1987; Allendorf and Leary 1988).
**Intraspecific gene flow**

By far the most difficult category of genetic effects to document are those that involve different populations of the same species. The difficulty in documentation occurs because the parentage of progeny from interstock matings usually are unrecognizable morphologically and biochemically. However, this type of genetic effect may be common because stocking programs have been a common and widespread practice of fishery management throughout North America.

Interbreeding between introduced and native populations will result in a reduction of genetic variability between the populations (a "homogenizing" effect) and outbreeding depression. Populations evolve to maximize their fit to the ecological niche which they occupy. Such evolution leads to changes in the gene pool of a population that cause it to be suited to a particular environment. If a source of fish, genetically different from the population in the receiving waters, is introduced and successfully breeds with the resident fish, genetic differences between the populations will decline. If the stocking program is widespread and interbreeding frequent, locally adapted native stocks will be replaced by larger more homogeneous populations (Allendorf and Leary 1988). Outbreeding depression will be a consequence caused by interbreeding of populations and will result in a decline in fitness (their capability to reproduce new generations). Initially the F1 generation may exhibit increased fitness as coadapted gene complexes from both parents remain intact and may provide substantial benefit to the progeny (heterosis or hybrid vigor). However, recombination in later generations (F2 and beyond) will disrupt these gene combinations and cause fitness to be lower than either parental population. The genetic danger to native salmonids from outbreeding depression is substantial; however, few studies have documented its occurrence as a result of interbreeding between hatchery and wild salmonids (Gharrett and Smoker 1991).

Most fishery management agencies practice some form of fish population enhancement via stocking. In many cases this activity involves planting of young fish, progeny of hatchery broodstocks, into streams or lakes that have naturally reproducing populations. The hatchery strain typically bears little genetic similarity to the wild population except as members of the same species (see review by Allendorf and Ryman 1987). The genetic differences between hatchery and wild fish often translate into important differences in physiological, behavioral, and other traits related to fitness (e.g., Reisenbichler and McIntyre 1977; Swain and Riddell 1990; Johnsson and Abrahams 1991). Stocked strains often have a long, undocumented history in a hatchery system and have been derived from fish of various geographic origins (e.g., the McCloud River hatchery strain of rainbow trout used in many hatchery programs; Needham and Behnke 1962). In some cases the introduced stock represents an outcross of a hatchery strain to a widely divergent gene pool in order to maximize first generation heterozygosity and potential hybrid vigor (Flick and Webster 1976). This practice, however, does not take into account the subsequent breakdown of hybrid vigor in later generations as described earlier (outbreeding depression).

While extensive documentation exists regarding the success of plantings as measured by catch records (e.g., Lachance and Magnan 1990), the genetic contribution of these fish to the next generation is usually unknown (see Chilote et al. 1986; Marden et al. 1989). In order to detect this second generation effect one needs to be able to examine genetic characters that distinguish populations and are transmitted to subsequent generations. Interbreeding has been documented between native and introduced populations of rainbow trout in the Yakima River of Washington based on allozyme data (Campbell and Johnston 1985). Similar results were shown for a population of rainbow trout in the Kootenai River drainage of western Montana (Allendorf et al. 1980). A loss of inter-populational genetic diversity appears to have occurred among rainbow trout (steelhead) populations of the Olympic Peninsula, Washington as a result of hatchery stocking since the 1940's (Reisenbichler and Phelps 1989). Genetic differences among Olympic Peninsula populations were much less than those observed among populations in British Columbia where little stocking has occurred (Parkinson 1984). A similar reduction in gene diversity may have occurred among chinook salmon populations of the lower Columbia River which have experienced an extensive history of stocking (Simon 1972; Utter et al. 1989).

Some studies have not found evidence for interbreeding and gene flow between hatchery and wild fish. For example, native populations of rainbow trout in southwestern Idaho (Wishead et al. 1984) and brook trout in Wisconsin (Krueger and Menzel 1979) appeared to have experienced gene flow with stocked fish. In an extensive survey of 86 populations of chinook salmon from British Columbia to California, the distribution of genetic variation was associated with probable historic routes of recolonization after glaciation even though massive stockings of salmon have occurred recently in some regions (Utter et al. 1989). If interbreeding between hatchery and wild chinook salmon was common these historic relationships should have been disrupted. Lack of evidence for interbreeding between hatchery and wild salmonids for the reasons that follow (adapted from Steward and Bjorn 1990):

*interbreeding and gene flow has not occurred or been extensive because of poor survival or other life history or genetic mechanisms effectively blocking spawning success of hatchery fish.

*effects of gene flow cannot be distinguished from changes caused by natural selection or genetic drift.

*available technology is inadequate to discern the extent of gene flow that has occurred.

*genetic differences between hatchery and wild stocks may be small; hatchery practices may not have altered historic genetic compositions in the comparatively short time that hatchery fish have been cultured.

As a result, a lack of evidence for interbreeding and gene flow can lead to several alternative explanations, only one of which is that it has not occurred.

**Indirect Genetic Effects**

The introduction of a non-native salmonid may cause one or more indigenous species or populations to decline in numbers or range such that their gene pool is changed. Reductions in effective population size increase rates of genetic drift and inbreeding which can produce changes in allelic frequencies. These changes may occur as random increases in unfavorable alleles which could reduce the overall genetic adaptability of the population (or species). A reduction in fitness may contribute to ecological processes such as competitive displacement and result in the ultimate extinction of the species or population. Reductions in native range will undoubtedly lead to reductions in the overall genetic variability of the species, without necessarily leading to changes in the individual gene pools of the remaining populations.

Indirect genetic effects have probably occurred in native populations of brook trout in the Appalachian Mountains, where populations have declined sharply over the past 60 yr due to introductions of rainbow trout (discussed earlier). Gene flow is now substantially reduced, if not prevented, between these remnant populations in this region which are confined to only the headwater areas of streams. These populations are important because they probably represent a geographically restricted, separate subspecies of brook trout (Stoneking et al. 1981). The end result of the displacement of brook trout in this region is that the overall gene pool of brook trout has been significantly reduced and that the remaining populations have reduced numbers and are disjunct from one another. A similar situation exists for many of the native cutthroat trout populations in western North America.

A second type of indirect genetic effect is an alteration of selective forces caused by introduced salmonids in the environment (Krueger and Menzel 1979). New forms of competition, predation, environmental modification, and parasites and disease caused by non-native salmonids each may contribute to a modification of selection pressures. If selective pressures are modified, native fish gene pools must evolve in order for the populations or species to survive. Documentation of the nature and extent of this type of genetic effects is difficult to prove and remains as a challenge to future investigations.

**Management of Unwanted Salmonid Introductions**

Management actions used to reverse or prevent the negative effects of salmonid introductions have included population reduction through massive chemical reclamation and the construction of barriers to fish movement. Less than total eradication of an introduced species may be inadequate to reduce interactions with native fish to the level desired. For example, although removal of approximately 60% of the large brown trout in a Michigan river appeared to cause an increase in brook trout, the investigators concluded that brown trout would have to be reduced to considerably lower levels to improve the sport fishery (Shetter and Alexander 1970).

Total eradication of non-native salmonids has occurred in some instances. Concern over the competitive interactions between introduced brook trout (discovered in 1985) and native cutthroat trout in Aramco Creek, a direct tributary to Yellowstone Lake, resulted in a chemical treatment to remove all fish (Gresswell and Varley 1988). Subsequent surveys in 1987 indicated that brook trout appeared to have been eradicated from the Aramco Creek drainage. Even more extensive has been the program implemented to protect the native golden trout in California from the negative effects of interactions with non-native salmonids (Pister, E. P., California Department of Fish and Game, personal communication; Pister 1991). Hundreds of kilometers of stream have been chemically treated to eradicate brown and rainbow trout in the South Fork of the Kern River drainage and brook and rainbow trout in the Little Kern River drainage. Major barriers to fish movement were also constructed to prevent re-invasion from downstream areas. Although eradication of non-native species has been successful in these cases, the costs for such programs have been substantial. Sometimes, eradication of a naturalized species may be technologically impossible when the species occurs over a wide geographic area (e.g., sea lamprey, *Petromyzon marinus*, in the Great Lakes; Smith and Tibbles 1980).

**Conclusion**

Introductions of non-native salmonids have had serious deleterious ecological and genetic effects on native salmonids at some locations in North America. Best studied have been the effects of the introduction of rainbow trout on native cutthroat and golden trout in the western part of the continent and on brook trout in the east. Competition, predation, and hybridization by the introduced species appear to be the primary processes which affect native salmonids. If the statistical power of field studies has been characteristically weak (see Peterman 1990), then the actual effects of salmonid introductions could be much worse than reported here.

Unequivocal evidence is lacking in most cases to support the conclusion that competition is an important mechanism that causes displacement of native species. Often studies of competition have to be simplified in design and time frame, and conducted under comparatively artificial conditions due to logistical practicality. Subsequently, results must be interpreted and extrapolated to natural conditions. The difficulties of this approach may be illustrated by the results reported by Cunjak and Green (1984, 1986) that suggested rainbow trout had little competitive advantage over brook trout in experimental channels, yet field observations suggest otherwise in Appalachian streams (Larson and Moore 1985) and Great Lakes tributaries. If possible, studies should be conducted through the direct manipulation of species densities in replicated stream sections (Fausch 1988) similar to those conducted on the effects on brook trout numbers when rainbow trout were removed from Appalachian streams (Moore et al. 1983, 1986). This approach should also be useful in elucidating the role of introduced salmonid predators (e.g., Shetter and Alexander 1970).

Clear documentation does exist for hybridization between native and introduced salmonids because of the availability of laboratory techniques such as allozyme analyses that unequivocally identify species and their hybrids. In contrast, data that provide indisputable evidence for the inter-breeding of stocks of the same species are generally lacking. Similar to studies of competition, examination of the potential for inter-breeding would best be conducted through replicated manipulative experiments conducted in natural environments with genetically distinct stocks rather than the correlative approaches used in the past (e.g., Krueger and Menzel 1979). Few data exist regarding the second generation contributions of intraspecific hatchery plantings which constitute by far the largest category of salmonid introductions. The potential negative impact on the resident gene pool argues that management agencies should try to measure the genetic effects of their stocking programs.

**What about the future? Should introductions of new salmonid species or stocks continue?** Below we offer five recommendations about future salmonid introductions. The recommendations were developed on the premise that the risks or costs associated with salmonid introductions should be borne by society and not by native species or populations.

First, some introductions are acceptable, especially those used in restoration programs for populations or those used in threatened or endangered species programs. Examples include the restoration of lake trout in the Great Lakes and of Atlantic salmon in rivers along the Atlantic coast. Considerations for stocking fish will be different depending on whether or not local extinction or severe population depletion has occurred (Krueger et al. 1981; Williams et al. 1988). If local extinction has not occurred, stocking strategies should seek to protect the original
native gene pool that remains. Unusual man-made or man-altered environments, such as reservoirs, may also provide acceptable locations for stocking programs. The fish species used for these introductions should have the characteristics suggested by Li and Moyle (1981).

Second, we recommend termination of the continued stocking of non-native trout and salmon species or strains if these fish will have direct access to or contact with wild native salmonid populations. This type of introduction poses unacceptable ecological and genetic risks. Implicit within this recommendation is the belief by the authors that native salmonid species and strains have a priority for existence and perpetuation over non-native forms. If societal pressures on fishery management requires implementation of put-grow-take, enhancement, or supplementation programs, then local native species and stocks should be used for propagation and stocking. If these stocking programs occur in bodies of water where other species are being restored, careful consideration must be given to determine whether the two programs conflict with each other. We argue that if a choice is to be made between the two types of programs, native species or population restoration should be given the highest priority. In some circumstances, following this recommendation may not be straightforward. For example, “What is a native species or stock?” Anadromous rainbow trout were introduced approximately 100 yr ago to Lake Superior and have developed self-sustaining populations that support a highly prized sport fishery. Many anglers in the region consider rainbow trout a native and the more recently introduced chinook salmon an exotic. In this case, the distinction between native and exotic species by society appears dependent on the time since introduction, with the transition from exotic to native measured, at most, in a few human generations rather than glacial epochs.

Third, we suggest that no new introductions of European or Asian salmonid species should occur in North America because of the unpredictable ecological and genetic effects on native species. Further, new intracontinental transfers of salmonid species or stocks is also discouraged. Lakes and streams can be considered as islands of aquatic environments in a sea of land (Magnuson 1976; Brown 1989). Their community dynamics are likely to operate similarly to the processes and concepts used to explain island biogeography (MacArthur and Wilson 1967). This theory predicts that such islands are more susceptible to successful invasion by alien species with subsequent extinction of native species than larger, less isolated, and more complex environments. Waters suitable for salmonids may be even more prone to vulnerability from invasion than other lakes and streams because they are typically oligotrophic and have low species diversity. Li and Moyle (1981) suggest that these waters are simply not good sites for new introductions due to the potential negative effects on native fauna. Thus, ecological theory predicts that native salmonids and their aquatic communities appear to be at a higher risk of extinction through interactions with introduced fish than would occur in other aquatic communities. The amount of information needed to develop better quantitative predictions of the effects of introductions would be more than is available for any vertebrate species (Brown 1989). Simply stated, the risk posed by new introductions to native faunas is too high and unpredictable to justify further introductions.

Fourth, technology must be developed and policies enacted that help minimize the risk from escape of cultured salmonids into the wild. Salmon and trout that escape from the salmon pen or cage culture industry pose important ecological and genetic risks to wild populations. Fortunately, lost fish pose important economic costs to the industry, thus a strong incentive exists to consider measures to prevent escape.

Fifth, transgenic fish, those that have had foreign DNA inserted into their genomes, pose yet another threat to wild salmonid populations. Measures need to be in place to prevent the release or escape of these fish into the wild (see discussions by Tiedje et al. 1989 and Kapuscinski and Hallerman 1990). For example, Atlantic salmon populations are already at risk from this type of introduction as the antifreeze protein gene has been reported to have been successfully transferred into the Atlantic salmon genome (Fletcher et al. 1988).

Certainly, not every introduction of non-native salmonids has caused a permanent ecological or genetic effect on native North American fauna. The lack of detectable effects on native salmonids from introductions has been reported (e.g., Miller 1958; Pollard and Bjornn 1973; Peterosky and Bjornn 1988) and has been argued to be the most common result of introductions in general (Simberloff 1981). Regardless, the chronic, long-term practice of stocking non-native salmonids over the past century has contributed major, and seemingly permanent, changes in the native salmonid species of the continent. The pervasive and permanent nature of such biological contamination of aquatic communities by exotic species and the difficulty of remediation makes the risk from non-native introductions too high.

For approximately 100 yr after 1870, the manipulation of aquatic communities by the introduction of non-native species was viewed as ethically acceptable by fisheries professionals in North America. Undeniably, the stocking of non-native salmonids resulted in the development of important sport fisheries throughout the continent. Since that time, fishery science has questioned the continued acceptability of such practices on the basis of ecological and genetic theory (e.g., Magnuson 1976; Li and Moyle 1981). The legitimacy of new introductions appears to have declined considerably among fishery professionals as policies and measures have been developed to control future introductions of fish (e.g., Welcomme 1985; Kohler and Courtenay 1986; Hallerman and Kapuscinski 1990). In a broader context, a new discipline has concurrently emerged since 1970, known as conservation biology, that explicitly places high value on natural assemblages of organisms and their protection, and discourages non-native introductions (e.g., Soulé 1986). Clearly, the era of widespread, intentional introductions of salmonids and other fish species as a fishery management activity justifiably is drawing to a close.

Acknowledgments

This paper benefited from helpful, critical reviews of an earlier version received from R. L. Eshenroder of the Great Lakes Fishery Commission and A. J. Garrett of the University of Alaska.

References


