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An Evaluation of the Effects of Conservation and Fishery Enhancement Hatcheries on Wild Populations of Salmon[1]

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Abstract

The historical, political and scientific aspects of salmon hatchery programmes designed to enhance fishery production, or to recover endangered populations, are reviewed. We start by pointing out that the establishment of hatcheries has been a political response to societal demands for harvest and conservation; given this social context, we then critically examined the levels of activity, the biological risks, and the economic analysis associated with salmon hatchery programmes. A rigorous analysis of the impacts of hatchery programmes was hindered by the lack of standardized data on release sizes and survival rates at all ecological scales, and since hatchery programme objectives are rarely defined, it was also difficult to measure their effectiveness at meeting release objectives. Debates on the genetic effects of hatchery programmes on wild fish have been dominated by whether correct management practices can reduce negative outcomes, but we noted that there has been an absence of programmatic research approaches addressing this important issue. Competitive interactions between hatchery and wild fish were observed to be complex, but studies researching approaches to reduce these interactions at all ecological scales during the entire salmon life history have been rare, and thus are not typically considered in hatchery management. Harvesting of salmon released from fishery enhancement hatcheries likely impacts vulnerable wild populations; managers have responded to this problem by mass marking hatchery fish, so that fishing effort can be directed towards hatchery populations. However, we noted that the effectiveness of this approach is dependant on accurate marking and production of hatchery fish with high survival rates, and it is not yet clear whether selective fishing will prevent overharvest of wild populations. Finally, research demonstrating disease transmission from hatchery fish to wild populations was observed to be equivocal; evidence in this area has been constrained by the lack of effective approaches to studying the fate of pathogens in the wild. We then reviewed several approaches to studying the economic consequences of hatchery activities intended to inform the social decisions surrounding programmes, but recognized that placing

monetary value on conservation efforts or on hatcheries that mitigate cultural groups' loss of historical harvest opportunities may complicate these analyses. We noted that economic issues have rarely been included in decision making on hatchery programmes. We end by identifying existing major knowledge gaps, which, if filled, could contribute towards a fuller understanding of the role that hatchery programmes could play in meeting divergent goals. However, we also recognized that many management recommendations arising from such research may involve trade-offs between different risks, and that decisions about these trade-offs must occur within a social context. Hatcheries have played an important role in sustaining some highly endangered populations, and it is possible that reform of practices will lead to an increase in the number of successful programmes. However, a serious appraisal of the role of hatcheries in meeting broader needs is urgently warranted and should take place at the scientific, but more effectively, at the societal level.

1. Introduction

Enhancement is increasingly seen as an important fishery management tool (Leber *et al.*, 2005a), especially in light of the worldwide decline in wild fish populations. Broadly defined as the deliberate release of cultured organisms to increase population abundance for conservation or harvest objectives, enhancement of fish and invertebrate populations has been implemented extensively since the turn of the century. However, there has been considerable debate about the efficacy of releasing cultured organisms, the impact of these organisms on conspecific wild populations, and the relevance of this approach for meeting societal needs [reviewed in Taylor (1999a) and in Section 2]. Thus, enhancement has fallen out of favour as a management technique at various periods since it was first implemented. However, improvements in seed production, rearing technology, disease control, tagging and genetic and ecological approaches to management have invigorated renewed research in the field (Blaxter, 2000). These technological improvements have coincided with a changing philosophy; namely, that enhancement should be conducted in a scientifically based and sustainable manner (Leber *et al.*, 2005a), rather than providing a means of supplying unlimited fishery resources, or replacing extirpated natural populations without addressing the reasons for the decline.

Given this shift in philosophy and the renewed interest in the field, it is not surprising that several reviews and edited volumes on the topic have been published recently. In a comprehensive evaluation of marine fish enhancement, Blaxter (2000) has shown that success depends on the life history stage, the season at release, and the size of the enhanced region. However, doubt remains over whether enhancement can be used to recover declining fish populations occurring in the high seas (Blaxter, 2000). In their introduction

to an edited symposium on the topic, Leber *et al.* (2005a) identified several key emerging issues associated with recent advances in the field, but pointed out that there are few examples of the successful implementation of these advances (Leber *et al.*, 2005b). This theme is echoed in a review of enhancement of marine invertebrates (Bell *et al.*, 2005); although programmes aim to either rebuild depleted populations or increase their productivity, objectives are infrequently identified and success is rarely measured, so any advances cannot be effectively evaluated.

A review of salmon enhancement activities adds an interesting dimension to discussions within the field. Salmon populations exhibit an extensive range of life history strategies (Allendorf and Waples, 1996; Quinn, 2005); they can be locally adapted to their rearing and spawning habitats (Taylor, 1991) and are genetically differentiated from each other on a fine scale (e.g., Waples *et al.*, 2001). Therefore, many enhancement efforts are aimed at discrete stocks or populations of salmon, and often take the form of hatchery programmes sited near spawning grounds. Additionally, programmes vary in their objectives and range from fishery enhancement to conservation hatcheries (Utter and Epifanio, 2002). There is considerable interest in the interactions between hatchery-produced fish and conspecific wild populations, many of which are endangered or declining (National Research Council, 1996; Parrish *et al.*, 1998). Above all, salmon are culturally and economically significant, and their management is usually driven by competing societal demands (Taylor, 1999a). Taken together, these issues provide a broad basis for evaluating a range of enhancement activities in a variety of species, each represented by a large number of independent stocks, and each aimed at fulfilling an assortment of societal needs.

Salmonid hatchery programmes have aroused considerable debate in the last few decades. Many critics have noted that hatcheries have failed to stem the decline of salmon stocks and, in some cases, have exacerbated this decline (Hilborn, 1992a; Larkin, 1974; Myers *et al.*, 2004; National Research Council, 1996). Biological problems that may arise following hatchery releases include changes in the genetic diversity of wild populations (Utter and Epifanio, 2002; Waples, 1991), risk of transmission of disease pathogens to wild stocks (Elliott *et al.*, 1997), exceeding the carrying capacity of streams and oceans (Beamish *et al.*, 1997; Levin *et al.*, 2001) and over-harvest of wild stocks due to mixed-stock fishing (Beamish *et al.*, 1997; Hilborn, 1985a; Unwin and Glova, 1997). On the other hand, a defence of hatchery programmes has been mounted on the basis that evidence of these problems is either lacking or the product of poor scientific rigour (Brannon *et al.*, 2004b; Heard, 2001), or that critics have specific social agendas (Brannon *et al.*, 2004b; Buchal, 1998; Robbins, 2004). The debate over hatchery programmes reached a peak in the mid-1990s, which led to advocates on both sides agreeing to rein in the rhetoric, if not substance,

of their views (Hilborn, 1999; Schramm, 1996). However, in the United States, hatchery-related disputes moved to the courts after 2000, and legal challenges have included the interpretation of the language within the Endangered Species Act and a state's right to direct recovery efforts (*Alsea Valley Alliance*, 2001; *Maine v Norton*, 2003; *California State Grange*, 2005). Admittedly, these debates are rarely as polarized outside the United States, yet the character of these contests helps to illustrate the ecological and social implications of salmonid hatcheries, and how other societies fall along the spectrum of these views and responses.

The interaction between societal demands and science in the context of the hatchery debate is a complicated one. Social advocates on both sides often selectively employ scientific papers that further their view, while science is often confined to researching systems that have been established by public demand based on material needs (such as placing dams across rivers for hydroelectric power). In light of this complicated relationship, it is important to state from the outset that it is not our aim to enter the social debate on whether hatcheries should, or should not, exist. Many commentators have pointed out that hatcheries provide one of many tools that can be used in salmonid management (e.g., Mobrand *et al.*, 2005; Waples, 1999) and, in many cases, viable alternatives have rarely been offered. Thus, we acknowledge that enhancement activities are likely to persist in the foreseeable future, given their societal framework. Rather, we confine our review to the major social and scientific issues associated with the use of hatchery-raised salmon for conservation purposes and for fishery enhancement.

This chapter focuses largely on areas in which salmonid hatcheries could impact wild stocks. It should be pointed out that it is not the intent of this chapter to suggest that hatcheries should not have a role in salmonid enhancement activities, especially where their use represents an important means to recover critically endangered stocks. For example, it is likely that certain populations might well have gone extinct by this date without captive propagation programmes that have been largely successful (e.g., the Snake River sockeye salmon in the northeastern United States; Utter and Epifanio, 2002). We also attempt to identify major knowledge gaps associated with these issues. The topic is a large one, and cannot include all aspects of the debate, and thus we initiate our treatment by first describing the focus of this chapter.

1.1. Scope of the review

The term 'enhancement' takes in a wide variety of activities that humans have engaged in on behalf of salmon species and the fisheries that capture them. Thus, it is necessary to identify the kinds of activities that we will review, and those that we will not consider.

At one end of the continuum, there are 'habitat enhancement' projects that add woody debris to streams. These 'stream enhancement' efforts may or may not succeed in increasing fish densities, depending on whether the wood that was added remained in the channel, and whether it was needed in the first place (e.g., Cederholm *et al.*, 1997; Roni and Quinn, 2001). There have also been efforts at enhancing the productivity of rearing environments. Application of inorganic nutrients or the introduction of plant material- or marine-derived nutrients to freshwater may sometimes accelerate juvenile salmon growth (e.g., Hyatt and Stockner, 1985; Mason, 1976; Mundie *et al.*, 1983; Stockner and MacIsaac, 1996). Whether or not the fast growth in freshwater is translated into more adults (the real objective) is a more complex issue (Koenings *et al.*, 1993), but we will not review these studies.

In addition to activities directed at juvenile habitat or growth, there have been three main types of projects pertaining to the enhancement of reproduction: use of in-stream egg incubation boxes, spawning channels and hatcheries. The egg incubation box is used simply to protect developing embryos during their vulnerable stage by forcing the upwelling of water through gravel, where the eggs are placed. Spawning channels are artificial channels, supplied with water diverted from natural rivers or fed by groundwater and designed to optimize the conditions for spawning and incubation of embryos. In most wild populations, the survival from egg deposition to emergence is about 10–30%, depending on density and physical factors (Quinn, 2005), but survival rates in spawning channels can be about 50–80% (Essington *et al.*, 2000; Hilborn, 1992b). In species or populations where spawning habitat is the limiting factor rather than rearing space or food, the channels can be successful. Consequently, they are most widely used for pink, *Oncorhynchus gorbuscha*, and chum, *O. keta*, salmon (species that migrate to sea after emerging from the gravel) and sockeye salmon, *O. nerka* (that migrate to lakes) rather than for the species that rear in streams (e.g., coho, *O. kisutch*; and Chinook salmon, *O. tshawytscha*; steelhead trout, *O. mykiss* and Atlantic salmon, *Salmo salar*) because the production of these latter species is generally limited by rearing capacity rather than spawning capacity. We have elected to avoid reviewing the literature on spawning channels and outplanting of egg incubation boxes, and so will only consider enhancement projects that actually remove gametes from adult salmon for incubation (i.e., hatcheries). This is a very important distinction because some (though not all) of the issues related to hatcheries stem inexorably from the circumvention of natural processes of selection on the wild fishes such as spawn timing, nest site selection, preparation and defence by females and mate choice and competition by both males and females.

Our chapter does not include operations based on deliberately domesticated salmon that are maintained throughout their life cycle in aquaculture

facilities for the purposes of food production. These types of operations have been the subject of a recent review (Naylor *et al.*, 2005). Although many of the issues associated with such activities are related to those examined here, fish from these facilities are not intended for deliberate release and it is the consequences of this management action that are the focus of this chapter.

Activities on anadromous salmonids in the genus *Salmo* (the Atlantic salmonids) and *Oncorhynchus* (the Pacific salmonids) will be examined, with a few examples from freshwater salmon within both genera and from *Salvelinus* (the charrs) (Table 2.1). However, this chapter places an emphasis on anadromous Pacific salmon for a number of reasons. First, the authors of this chapter are most familiar with this species. Many of the issues that will be addressed here are relevant to all species, and a comprehensive review of the issues in Pacific salmon, with supporting evidence from Atlantic salmon, is intended as illustrative. Second, Pacific salmon hatchery management has largely been under governmental control since the building of the first facility in California in 1871. Thus, the debate about enhancement has always been a very public one, and affected by legislation and court deci-sions. The use of Pacific salmon hatcheries involves public lands, and a large component of these operations is driven by the continued importance of commercial and recreational salmon fisheries. Third, most enhancement efforts in the eastern Atlantic are focused primarily on providing salmon for recreational fishing in the face of the decline of native populations and, to a

Table 2.1   Scientific names and common names of salmon species (family Salmonidae, subfamily Salmoninae) used frequently throughout this chapter

Genus	Common name (anadromous/ freshwater)	Scientific name
Salmo (the Atlantic salmonids)	Atlantic salmon	*S. salar*
	Sea trout/brown trout	*S. trutta*
Oncorhynchus (the Pacific salmonids)	Chinook salmon	*O. tshawytscha*
	Chum salmon	*O. keta*
	Coho salmon	*O. kisutch*
	Cutthroat trout (predominantly freshwater)	*O. clarki*
	Masou (cherry) salmon	*O. masou*
	Pink salmon	*O. gorbuscha*
	Sockeye salmon/kokanee	*O. nerka*
	Steelhead/rainbow trout	*O. mykiss*
Salvelinus (the charrs)	Arctic charr	*S. alpinus*

Infrequent examples are named in the text.

smaller extent, on harvest and conservation (Section 3). The more significant issues in Atlantic salmon are around the interactions between commercially farmed fish and wild stocks and, as we outlined above, outside the scope of our review.

Finally, we recognize that hatchery releases have substantial ecological impacts on the systems in which they operate, but do not review this aspect in detail. Instead, the chapter focuses primarily on the interactions between hatchery fish and their wild counterparts, since most hatchery operations are justified on the basis of supporting the very stocks with which they interact, either by directing harvest pressure away from wild stocks, or by supportive breeding for the recovery of weakened stocks. It is these justifications that will be largely examined here.

1.2. Motivations and objectives of hatcheries

The term 'hatchery' encompasses a broad spectrum of operations, each with different objectives and practises. Many critiques of hatchery practises fail to discriminate between these goals and hence the range of impacts that various activities will have on wild populations (Allendorf and Ryman, 1997). In order to provide a full evaluation of the state of knowledge of hatchery activities, it is therefore necessary to describe the different categories into which hatcheries fall. This attempt at definition should be qualified. It is recognized that hatcheries have rarely been categorized (Section 2) and many modern enhancement activities continue to lack clear defining objectives. Further, the purposes of hatcheries may change and yet may retain their founding broodstock. For example, a number of hatcheries in the northeast Pacific are defined as having conservation goals, but the majority of these were founded on the principle of providing opportunities for harvest. Thus, current hatchery practises are most likely to fall along a continuum of the definitions given here. Finally, many of the terms used below have been applied loosely. For example, 'supplementation' has been used to describe activities varying from conservation to fishery enhancement. 'Stocking' has been used in a generic sense to describe the release of cultured fish into the wild, but has also specific definitions in the context of enhancement, mitigation and conservation activities (Cowx, 1998). Here, we attempt to more clearly define many of these categories below.

Hatcheries are classified broadly by having either conservation or fishery objectives. The former are intended to restore extinct, endangered or threatened populations or to reduce the risk of extinction. The latter are used to increase population sizes for fishery opportunities. The aquaculture classification of Utter and Epifanio (2002) is largely followed here, with an emphasis on salmon hatcheries.

Captive broodstock hatcheries are conservation oriented, with the sole purpose of maintaining populations that cannot be supported in their wild habitat for even part of their life cycle (Utter and Epifanio, 2002). Typically, the broodstock is maintained in captivity until the population threats have been removed, at which point the captively reared fish will be restored. For example, populations of Atlantic salmon indigenous to the Iijoki and Oulujoki rivers in Finland have been maintained in captivity since dam construction removed suitable spawning habitat (Saisa *et al.*, 2003) and may be reintroduced as part of the International Baltic Sea Fishery Commission's 'Salmon Action Plan' to increase wild population returns. Sockeye salmon returning to Redfish Lake, part of the Columbia River drainage system on the west coast of North America, declined to very small numbers of returning adults from 1991 to 1996; all were taken into captivity, and a portion of the population has since been utilized in a continuing programme of reintroduction (Utter and Epifanio, 2002).

Supplementation hatcheries also share a conservation ethic. Waples *et al.* (2007) defined supplementation as 'the intentional demographic integration of hatchery and natural production, with the goal of improving the status of an existing natural population'. While the intention is to incorporate the broodstock into wild stocks, the degree of integration can vary, with different outcomes (Section 5.1). Supplementation activities have been implemented extensively on the west coast of North America in an attempt to mitigate losses due to anthropogenic activities such as dam construction, forestry, agriculture or urbanization (Section 3.1).

Production hatcheries, or *fishery enhancement hatcheries* (Utter and Epifanio, 2002), are hatcheries that seek to augment the abundance of salmon in order to increase fishing opportunities. 'Ocean ranching' has been defined as the release of 'juvenile specimens of species of fishery importance raised or reared in hatcheries and nurseries into the sea for subsequent harvest at the adult stage or manipulating fishery habitat to improve growth of the wild stocks' (Mustafa, 2003), which can often include domesticated stocks, and thus falls under this category. One potential outcome of such activities is that the resulting demographic increases may redirect harvest pressures away from natural production. In many cases, the wild populations are viable. Production hatcheries are used extensively throughout the world. For example, many European countries release anadromous Atlantic salmon and brown trout (*S. trutta*) populations; many hatchery strains are derived from exogenous stocks. The pink salmon fishing industry in Alaska is supported by releases from production hatcheries in Prince William Sound (PWS; Section 4).

Mitigation hatcheries are production hatcheries that have typically been founded to compensate for lost harvest opportunities following substantial reduction or extirpation of an indigenous stock due to losses of habitat or other anthropogenic activities (Utter and Epifanio, 2002). Such hatcheries

have been established with the understanding that the habitat that is essential for part of the salmon life cycle will not be replaced within the predictable future, and thus continuation of the population is dependant on artificial propagation. The most extensive programme in this category is the chum salmon programme operated in Japan (Section 4). In many cases, mitigation hatcheries are maintained in order to meet a mandate imposed by prior rights of a group to the fishery. For example, access to the Chinook salmon fishery was lost by the native peoples of the Columbia River Basin following the construction of the Grand Coulee Dam, and mitigation hatcheries were constructed in response to tribal treaties (Utter and Epifanio, 2002). Given increasing concern that endangered or threatened stocks may be caught in mixed-stock fisheries (Section 5.4), the release of hatchery fish at a remote acclimation site has been explored. In the Columbia River, for example, an ongoing programme has placed hatchery juveniles into a net pen at a location that has not been frequented by migrating endangered salmon stocks (ISRP/IEAB, 2005). The project's intent is that the fish acclimate and return to the remote site where they can be harvested, thus reducing risk to the endangered wild stocks.

Hatcheries providing fishing opportunities for non-indigenous fisheries (*Introduced fish*) are production hatcheries (including 'put and take' aquaculture) operated to provide harvest or recreational fishing opportunities on species that are exotic to the region in which they are released (Utter and Epifanio, 2002). For example, rainbow trout has been extensively introduced to countries in the Southern Hemisphere, and Chinook salmon has been introduced to the North American Great Lakes and New Zealand. Many of these operations involve a single introduction, while others are maintained by hatchery programmes (e.g., Chinook salmon in the Great Lakes) with the notion that the introduced species may go extinct once such activities cease.

1.3. Content overview

In the following sections, we provide a social context for an evaluation of hatchery operations through an overview of the history of hatchery activities and the political dynamics associated with hatchery programmes. We then provide a survey of the geographical extent of anadromous and freshwater hatchery programmes throughout the world. In an attempt to understand the impacts of such programmes, we evaluate in detail the types of biological risks that hatchery programmes may pose to wild stocks of salmon species and return to the social aspect of such programmes by examining the economic issues associated with hatchery programmes. The chapter ends with a discussion on the risks associated with conservation and fishery enhancement hatcheries, and on the social drivers and costs of hatchery activities.

2. Historical Overview of Hatchery Activities

Western salmonid fish culture dates to eighteenth-century Westphalia. In 1747, army officer and naturalist Ludwig Jacobi used ancient Asian techniques to fertilize and rear trout in an artificial environment, but not until he published his memoirs in 1770 did his achievements gain notice. In the next century, a number of Europeans emulated his efforts, including Karl Lund, Karl Vogt, John Shaw, Joseph Rémy and Antoine Géhin. Each refined and expanded upon Jacobi's work by innovating new methods for raising an array of freshwater and anadromous species. These were limited efforts by individual enthusiasts and scientists, people primarily interested in studying and reproducing small stocks of fish for fulfilment or profit rather than for professional or industrial interests (Marsh, 1857; Prince, 1900).

The development of a hatchery programme, in the modern sense of the systematic management of fish and fisheries, required a more institutionalized approach. France was the first to adopt this tack. In 1850, inspired by the work of Rémy and Géhin at Bresse and the writings of naturalist Armand de Quatrefages, the French Minister of Agriculture built a fish-breeding station at Huningen to repopulate the Rhine and Rhône rivers. Soon Switzerland, Germany, England and Scotland had established similar efforts to restore their fisheries. In most cases, these hatcheries were designed to serve both angling and commercial interests, and while none produced immediate, demonstrable successes in rebuilding stocks, they represented a new movement in fisheries policy that drew the attention of North Americans. Interest in fish culture began relatively late in Canada and the United States. The first documented case of reproducing trout was by Ohioan Theodatus Garlick in 1853. This work quickly gained notice. Fishmongers and anglers saw a hope for reversing decades of decline in the fisheries. As a result, they lobbied legislators throughout the eastern states to establish fish hatcheries, and from 1855 to 1857, Massachusetts, Connecticut and Vermont commissioned studies on approaches to restore local fisheries. Each report became a treatise on the technical and socio-political implications of breeding fish, and each concluded that while fish culture had not yet restored a troubled fishery, the technology held tremendous promise for ameliorating the material consequences of progress.

Government support for hatchery programmes did not begin in the United States until the end of the Civil War. In 1865, New Hampshire built the first state-run hatchery, and California, Connecticut, Maine, New Jersey, New York, Pennsylvania and Rhode Island followed by 1870 (Bowen, 1970). These operations were primarily dedicated to game fisheries. The major expansion of fish culture in the next decade was more tied to commercial interests however. In 1867, at the request of several New England fish commissions, a for-profit fish culturist named Seth Green bred

shad eggs on the Connecticut River; the next year he extended this work to the Hudson, Potomac and Susquehanna rivers (Goode, 1881; Norris, 1868). In 1871, Charles Atkins and Livingston Stone persuaded the state of Maine to build a hatchery at Bucksport specifically for hatching Atlantic salmon, and Frank Clark hatched whitefish on the Great Lakes in 1872 (Milner, 1874; Stone, 1897).

Canadian fish culture loosely paralleled American activities. In the late 1850s, Richard Nettle first hatched brook trout and Atlantic salmon in Quebec city. By the mid-1860s, enthusiasts were hatching these species and lake herring on the St. Lawrence and Great Lakes. The most prominent culturist was Samuel Wilmot, a zealous self-promoter who billed himself as the leading fish culturist in North America. In 1866, he persuaded the province of Ontario to hire him as a fishery officer and fund his hatchery at Newcastle on Lake Ontario. Two years later, the Dominion of Canada took over the hatchery and made Wilmot an officer of the Department of Marine and Fisheries. In the early 1870s, he built additional salmon hatcheries on the Restigouche (1872), Miramichi (1873), Gaspe (1874) and Tadoussac (1875) rivers, and in 1876 he was promoted to Superintendent of Fish Breeding for Canada. The Dominion built its first hatchery for Pacific salmon on the Fraser River in 1884. Wilmot overstated his achievements on occasions—he had not been the first to hatch salmon or whitefish—but he was, without doubt, the driving force behind federalization of artificial propagation in North America (Prince, 1900; Lasenby *et al.*, 2001).

Influenced by Canada's hatchery programme, the US Congress soon followed suit. It created the US Fish Commission (USFC) in 1871, and the following year the first commissioner, Spencer Fullerton Baird, assigned Livingston Stone to transplant salmon eggs from the Sacramento River to eastern streams. In 1873, Baird hired Seth Green to plant shad in Midwestern streams and the Sacramento River. Other American fish culturists refined methods for inseminating and incubating eggs, and Baird turned his USFC employees into an army of researchers, surveying habitat and species abundance, investigating egg development and experimenting with fish feeds. As in Canada, federal support for fish culture grew. By the 1880s, Congress was funding hatcheries from the Bay of Fundy to San Francisco Bay, from the Columbia River to the Savannah River and from the Gulf of Mexico to the Great Lakes. By the end of the century, Canada and the United States had built extensive hatchery programmes. Almost every major fishing stream was affected by at least one federal, state, provincial or private hatchery, and fish culture had become an intrinsic tool of managing game and commercial fisheries across North America (Allard, 1978).

Both countries also conducted extensive fish transportation programmes. The motivations for transplant programmes were complex. Some of it was driven by emigrants' desires to recreate the ecologies of

home or, as Wisconsin's Commissioners of Fisheries boasted in 1888, in hopes of creating one vast 'Summer Paradise' (quoted in Bougue, 2000; see also Lampman, 1946). Economic opportunity was another major influence in shipping salmon around the world (Taylor, 1999a), and, as Spencer Fullerton Baird himself admitted in 1877, political considerations also drove transplant projects: 'The object is to introduce [fish eggs] into as many states as possible and have credit with Congress accordingly. If they are there, they are there, and we can so swear, and that is the end of it' (quoted in Allard, 1978). Using railways and steamships, hatchery programmes sent species to every corner of the continent and beyond. In the last quarter of the nineteenth century, the USFC and Canada Department of Marine and Fisheries transplanted a menagerie of species. Pacific salmon were transplanted to the Great Lakes, South Dakota's Belle Fourche River, and the Great Salt Lake, not to mention Europe, Asia, South America and Australasia (Colpitts, 2002). By 1900, global hatchery ecology was emerging in which salmonids played a key, but hardly singular, role. Brown trout were shipped from England to California, California Chinook salmon were sent to New Zealand, Japanese koi (*Cyprinus carpio carpio*) were cultivated in Massachusetts, Rhode Island shad were released in Oregon streams, Oregon steelhead were exchanged with Germany, German carp (*C. carpio carpio*) were placed in the Great Basin and black bass were released just about everywhere (Allard, 1978; Bogue, 2000; Bowen, 1970). Salmonids were far from the only species introduced to new environments.

The paradox of most hatchery programmes was that institutional successes went hand-in-hand with ecological disaster. Despite growing fiscal support—Congress increased the Division of Fish Culture's budget from $25,000 in 1873 to $331,000 by 1900—optimism was deserting fish culturists (Cart, 1968). North American and European salmon runs had been declining for centuries (Netboy, 1980). Whitefish populations in the Great Lakes had collapsed in recent decades, as had shad and alewife stocks along the Atlantic (Bogue, 2000; McPhee, 2002; Steinberg, 1991). Shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) were colonizing west coast streams, but few markets existed for these species and some observers worried that exotics would disrupt native species. German carp were denuding rearing habitat for western North American trout (Langston, 2003), and brown trout and rainbow trout were displacing indigenous species in Australia and New Zealand (Crowl *et al.*, 1992). The more things fell apart, the more politically potent hatchery programmes seemed. By the early twentieth century crises had become fish culture's *raison d'etre*. Declining stocks and degraded habitat made artificial propagation the default solution for many governments. And if the results often fell short, the achievements of these programmes were no less significant. North American fishery agencies had become the gold standard for fishery management. The USFC had developed into a model agency for supporting fisheries

through economic surveying, scientific research and artificial propagation, and professional scientists were turning the American Fisheries Society and, after 1912, the Biological Board of Canada, into premier organizations for fisheries science (Johnstone, 1977; Smith, 1994).

The principal exceptions to the mounting problems of hatchery work were a select few game fish species. Brown trout (*S. trutta*), rainbow trout (*O. mykiss*), bass (*Micropterus dolomieu* and *M. salmoides*), catfish (*Ictalurus furcatus, I. punctatus, Ameiurus catus*), crappie (*Pomoxis nigromaculatus*), perch (*Perca flavescens, Morone americana*) and pike (*Esox lucius*) adapted well to pond culture, but, equally important, each also had enthusiastic angling constituencies. In Europe, angling had been a primary motive for planting brown trout and Atlantic salmon since the 1700s. Since the majority of streams were privately owned, most releases were performed by individuals and fishing associations. Conditions in Japan and North America were different. Most waters were publicly owned, so both individuals and the state released fish into the waterways. In Japan, for example, the Agricultural Bureau initiated hatchery work in 1878 on streams in Niigata-ken, Nagano-ken, Ibaraki-ken and Hokkaido. Budgets and plantings grew significantly by 1900 (Imperial Fisheries Bureau, 1904). Canada followed a slightly different path. At first small, privately run hatcheries operated in the Maritimes, Quebec and Ontario, and a few provinces gained some authority over fisheries by 1900. The federal government retained primary authority for oceans and ultimate authority for all other fisheries, however (Thompson, 1975). Thus, similar to Japan, the Dominion of Canada operated in support of both angling and commercial interests well into the twentieth century.

Hatchery development in the United States was more complicated due to a constitutional division of authority. The federal government held jurisdiction of seas, navigable rivers, and territories, but states ruled all other waters including the oceans within three miles of the coast. In practise, this meant that the USFC and US Bureau of Fisheries (USBF) propagated commercial species that frequented the seas or interstate waters such as the Great Lakes and Columbia River (Allard, 1978; Taylor, 1999a). Federal hatcheries planted game fish in national parks and federal forests, as well as across Alaska, but by 1900 states were taking over the primary responsibility for much of the hatchery work (Pritchard, 1999). Fishery agencies were evolving into a huge apparatus for breeding and distributing fish. Large and growing bureaucracies existed in nearly every state, and an immense amount of fish were bred and planted each year by fish culturists (Lampman, 1946; Reiger, 2001; Taylor, 1999a).

The next half-century was a period of elaboration rather than change. The size and scope of fishery agencies continued to grow as stock depletion and habit decline accelerated after 1900. The policy of compensating for problems with fish culture, begun in New England in the 1860s, extended

to the Pacific Northwest in the 1910s when Washington State adopted an 'in lieu' policy that would eschew fish-ways if the dam owner funded a hatchery (Steinberg, 1991; Taylor, 1999a). Although few governments made this formal policy, all were increasingly inclined to mitigate losses rather than restrain development. When alewife (*A. pseudoharengus*), eel (*Anguilla rostrata*), salmon, shad and sturgeon (*Acipenser transmontanus*) populations dropped because of habitat loss, agencies in Canada, France, Great Britain, Ireland, Japan, Russia and the United States responded by advocating fish-ways and hatcheries. Few wild fish populations recovered, but the bureaucracies overseeing them thrived (Netboy, 1980; Pritchard, 2001; Taylor, 1999a).

Hatchery programmes also experienced an institutional mitosis. The fisheries had been torn by rivalries for centuries. Towards the end of the nineteenth century, state legislatures in the United States began to formalize the divisions between sport and commercial interests in separate fish and game departments. Fish culture was influenced by these events as it was embedded in such agencies. Individual hatcheries began to specialize, serving the desires of constituencies interested only in market or game fish, or specifically in one species. In the Pacific Northwest, for example, Oregon's Fish Commission began to favour Chinook salmon in coastal streams where coho had been the dominant native fish, while the Game Commission planted bass and walleye (*Sander vitreus*) in inland streams where salmon and trout had predominated (Taylor, 1999a). Transplanting coho to Lake Michigan in the 1960s precipitated similar upheavals in the Great Lakes (Chiarappa and Szylvian, 2003). Institutional specialization and ecological reorganization occurred across many Northern Hemispheric fisheries during this period, including Hokkaido Island, Vancouver Island, Yellowstone National Park and the Barents Sea and White Sea (Harris, 2001; Imperial Fisheries Bureau, 1904; Pritchard, 2001).

Scientific research also became an increasingly important institutional activity. The USFC had been created as a research agency in 1871, and Commissioner Baird insisted that research remain a high priority even as fish culture dominated budgets (Allard, 1978). Annual reports included essays by top scientists, and the *Bulletin of the Bureau of Fisheries* was a science publication from its inception in 1881. The other major research publication in the United States was, of course, the *Proceedings of the American Fish-Cultural Association* and its successor, the *Transactions of the American Fisheries Society* (Smith, 1994). The Biological Board (later the Fisheries Research Board) of Canada began its own research programme in 1912 (Johnstone, 1977), and Europeans had developed a tradition of scientific cooperation long before the International Committee on the Exploration of the Seas (ICES) formed in 1902 (Rozwadowski, 2002). In addition, various state and provincial fishery agencies in the United States and Canada began their own research programmes (Taylor, 1999a).

The impact of this science on hatchery operations was uneven. Some research proved functional, such as designing efficient fish-ways and fish screens, understanding predators and parasites and refining effective and economical feeds (Bowen, 1970; Eicher, 1970; McHugh, 1970). Fish tagging studies confirmed the home-stream theory for salmon and influenced fishing treaties (Taylor, 1999a). Administrators of hatchery programmes in Canada and the United States embraced this work enthusiastically, but they rejected critical research. Harley White's study of Prince Edward Island trout (White, 1924), Willis Rich's statistical analysis of Columbia River hatcheries (Rich, 1922) and Russell Foerster's work of Cultus Lake sockeye (Foerster, 1936) all cast doubts on claims that fish culture had made significant differences in the size of salmonid populations. Although economic considerations were also important, this research did influence decisions to halt hatchery work in British Columbia and Alaska during the 1930s. Fish culturists responded by attacking White and ignoring the broader implications of his research (Johnstone, 1977; Taylor, 1998b). By 1950, salmonid hatchery programmes in North America were on a path best described as scientific yet without scrutiny (Hilborn and Winton, 1993; Lichatowich, 1999; Taylor, 1999a). Similarly aggressive hatchery programmes have been initiated around the Baltic Sea in recent decades, but here, too, familiar problems with disease, interbreeding, mixed-stock fisheries and declining wild populations have emerged (Khristoforov and Murza, 2003; Paaver *et al.*, 2003).

Research during the 1940s and 1950s created the technical and intellectual foundation of the last half-century. Studies of parasites and diseases, and advances in medical and food science led to new prophylactic treatments. Fish culturists devised ways to address epizootics, and extruding machines produced pelleted feeds that avoided age-old problems with nutritional deficiencies and contamination (Stickney, 1996). These innovations allowed fish culturists to raise more fish, more economically for far longer. As hatcheries began to raise greater numbers of much larger fish, fishery bureaucracies expanded again. Great Lakes managers started replacing failing whitefish stocks with trout, and west coast hatchery workers used new feeds to retain Pacific salmon to smoltification (Chiarappa and Szylvian, 2003; Taylor, 1999a). Meanwhile, the Scandinavians succeeded in raising rainbow trout and then Atlantic salmon from eggs to harvest. By 1960, a far more technically based era of salmonid culture had emerged (Sedgwick, 1982).

Developments in North America since 1960 have exposed lingering problems with hatchery programmes. Practises learned from the commercial farming of Atlantic salmon, rainbow trout and several Pacific salmons, and the transporting of juvenile Pacific salmon around dams with trucks and barges were regarded as significant advances in the 1960s and early 1970s. The salmon hatchery programme was even revived in British Columbia,

where Canada's Department of Fisheries and Oceans (DFO) constructed a number of production hatcheries, and the International Pacific Salmon Fisheries Commission (IPSFC) began to experiment with artificial spawning channels (Mead and Woodall, 1968; Roos, 1991). The appearance of success faded in the 1970s as worries surfaced about the deleterious effects of mixed-stock fisheries, genetic interactions with wild stocks, threats of disease transmission, mass hatchery releases out-competing wild stocks and continuing declines in many fisheries (Lichatowich, 1999; Orr *et al.*, 2002; Taylor, 1999a). Many western inland trout and Pacific salmon stocks have declined due to habitat loss, competition from and hybridization with exotic species (Cone and Ridlington, 1996; Leary *et al.*, 1995). Hatcheries on the Great Lakes produced so many lake trout and Pacific salmon that they annihilated the last significant whitefish stocks (Chiarappa and Szylvian, 2003). In addition, the collapse of Labrador's Atlantic salmon fishery in the 1970s revealed the inability of hatcheries in the eastern United States and the Maritime Provinces to compensate fully for the effects of intense harvests and declining habitat (Netboy, 1980).

During this period, hatchery programmes in Europe and Scandinavia showed mixed results. In the 1970s and 1980s commercial salmon farms in Norway, Scotland and Ireland gained a foothold in the marketplace due to declining salmon fisheries in the western Atlantic and northeastern Pacific. The Norwegian salmon farming programme at the time also aided small, outlying communities; however, a market collapse in the 1990s, caused in part by competition from a rapidly expanding Chilean salmon aquaculture industry, led to industry consolidation by a few corporations and growing concerns about the ecological impacts of industry practises (Milstein, 2003). More recently, efforts to rebuild extinct runs in Belgium's Meuse River basin revealed, once again, that the success of artificial propagation depends on healthy habitat and competent fish passage technologies (Prignon *et al.*, 1999), while work on the Asón and Nansa rivers in Spain demonstrated that transplanted salmon stocks fare more poorly than native wild stocks (Verspoor and de Leaniz, 1997). Species hybridization between Atlantic salmon and trout populations in Sweden has been attributed to the release of too many fish by hatcheries (Jansson and Oest, 1997), and hatcheries throughout the Gulf of Bothnia have contributed to genetic homogenization in wild Atlantic salmon populations (Khristoforov and Murza, 2003; Paaver *et al.*, 2003; Vasemägi *et al.*, 2005).

The persistence of these problems, most of which have plagued salmonid hatcheries for a century or more, has inspired ever more urgent calls for reform and even termination. Critics have demanded that salmonid hatcheries be independently evaluated, that hatchery managers define goals which are rigorous and testable and that administrators develop policies based on the best available science (Brown, 1982; Lichatowich, 1999; Mobrand *et al.*, 2005; National Research Council, 1996; Taylor, 1999a). At the same time,

however, it is clear that some wild salmonid stocks are in such great peril that the only hope for recovery seems to be the sort of intensive hatchery programmes that exacerbate problems within the region (Schiewe *et al.*, 1997). Thus, the last 15 years has been a period of reassessment. History casts a troubling light on the practises and goals of many salmonid hatchery programmes, but no consensus has emerged yet about the future of these programmes.

3. Political Dynamics of Hatchery Programmes

Although usually considered a scientifically based activity, salmonid hatcheries must also be understood as political technologies fundamentally shaped by economic and cultural concerns. Scientists have been key players in creating and shaping hatchery programmes, and fish culturists have conducted important research, yet the history of these programmes reveals that science has often played only a secondary, legitimizing role in policy-making, or has been implemented to maintain the *status quo*. Social and economic politics has been the primary influence on government-sponsored hatchery programmes in the last two centuries. Thus, examining the historical context of the political aspects of fish culture is essential for understanding the development and consequences of salmonid hatcheries during this period.

This historical perspective is particularly crucial in the current, highly politicized climate that surrounds salmonid hatcheries. In recent years some programmes have earned withering criticism. Scholars have cited a number of problems, including insufficient scientific rigour, economic worth and ecological viability in many enhancement programmes (Anonymous, 2004; Hilborn and Eggers, 2000; Myers *et al.*, 2004; National Research Council, 1996). With less care, critics have also tried to explain the technology's origins by variously blaming zealous founders, short-term thinking and even Francis Bacon for replacing a holistic appreciation of nature with instrumentalist thinking (Cone and Ridlington, 1996). The disparity between careful studies of technical issues and vague assertions about historical roots has hindered our understanding of why science has not been a stronger guide in hatchery policies (McEvoy, 1986).

Closer attention to the past illustrates how thoroughly blurred politics and science were in early hatchery programmes. From the beginning, proponents of hatcheries noted that manual fertilization of fish eggs produced far greater hatch rates than natural reproduction. Many were led by an arithmetical logic to predict astonishing increases in fish populations by even meagre efforts. According to US Fish Commissioner Spencer Fullerton Baird, fish culture would allow the government 'not only to maintain

the present supply of fish, but to increase it if desirable' (Baird, 1874). Framing these insights in agrarian terms, proponents argued that an acre of water was more productive than one, five, or ten acres of land. One even insisted that 'one acre of the waters of any salmon stream in Oregon . . . is worth more as a medium for the product of a food supply than forty acres of the best land in the State' (Hume, 1893). Such boasts drew notice in many countries, but what made fish culture most appealing for government officials were its political implications. Few could resist a technology that French scientist Jules Haime claimed (Marsh, 1857) was 'destined to solve one of the important terms of the great problem of cheap living' (McPhee, 2002).

The cultural context in which fish culture emerged was another factor in its popularity. Although the rhetoric surrounding fish breeding emphasized bountiful harvests, contemporary politicians were less motivated by Malthusian fears of hunger than by the growing conflicts between aquatic and terrestrial interests. George Perkins Marsh, who was squarely on one side of this contest, explained to Vermont's legislature in 1857 that 'We cannot destroy our dams, or provide artificial water-ways for the migration of fish. . .; we cannot wholly prevent the discharge of deleterious substances from our industrial establishments', nor was it probable 'that any mere protective legislation, however faithfully obeyed, would restore the ancient abundance of our public fisheries'. For Marsh and others the 'final extinction of the larger wild quadrupeds and birds, as well as the diminution of fish, and other aquatic animals, is everywhere a condition of advanced civilization and the increase and spread of a rural and industrial population' (Marsh, 1857). Destruction was thus the sad but inevitable cost of progress.

Most people exploring the feasibility of fish culture programmes were not worried about an imminent implosion of food sources. Rather, it was growing contests over dwindling fish stocks that forced politicians in many countries to address the issue. In other words, it was the *political* implications of finite resources, not hunger, which first inspired modern hatchery programmes. Conflicts among fishers led France to build a government hatchery at Huningen in 1850 to repopulate the Rhine and Rhône rivers. Lobbying by sport and commercial interests led New England states and Canada to fund trout, shad and salmon work during the 1860s (Prince, 1900; Reiger, 2001), and tourism agendas influenced Japan to build a hatchery on Lake Chuzenji in the 1890s (Imperial Fisheries Bureau, 1904).

Economic possibilities helped leverage funding, but as Spencer Baird noted in an 1875 letter to the US Senate, the tangled problems of regulation were also salient. 'In the United States', he observed, 'it has always been found very difficult to enforce laws in regard to the fisheries. When passed by the States they involve an extensive police for their execution', and, crucially, no state had built such a force. Thus he 'unhesitatingly' recommended that instead of the passage of protective laws which cannot

be enforced except at very great expense and with much ill feeling, 'measures be taken ... for the immediate erection of a hatching establishment on the Columbia river, and the initiation during the present year [1875] of the method of artificial hatching of these fish' (Baird, 1875).

Here were the political underpinnings of the modern hatchery. Government officials in many countries, most of whom knew or cared little about fish or about fish culture, nevertheless supported large government budgets for these programmes not simply because the technology promised to sustain fisheries but because Haime and Armand de Quatrefages in France, Frank Buckland in Britain, Samuel Wilmot in Canada and Marsh and Baird in the United States assured officials that hatcheries would avert the social conflicts between declining fish stocks and modern development (Bogue, 2000; Gardner-Thorpe, 2001; MacCrimmon, 1965; Prince, 1900; Taylor, 1999a). For governments and the public alike, much of fish culture's appeal emanated from its panacean qualities (Taylor, 1999a). Hatcheries seemed to alleviate the need to make hard choices about limiting access to fish or habitat.

Yet governments did make choices and did intervene, and one of fish culture's first impacts was on property rights. By 1850 many state legislatures in the United States had already forced dam owners to maintain fish-ways to protect migrating species (Steinberg, 1991). Such limitations became precedents for further restrictions to facilitate artificial propagation. Between 1861 and 1865 the British Parliament passed acts for England, Ireland, Scotland and Wales that exempted fish culturists from regulations and limited private claims on some Scottish and Irish streams (Great Britain, 1861, 1862, 1863, 1865). Americans were more hesitant. Marsh advised Vermont legislators to rely 'upon the enterprise and ingenuity of private citizens' and to create economic incentives by according property rights to fish produced by entrepreneurial hatcheries (Marsh, 1857). Vermonters did not agree, believing that fish and game should remain free until capture (McEvoy, 1986). The same held true across the United States, Canada and Japan, but experiences varied in European nations. In countries with customs of privatized fish and game, parliaments had to finely tune rules to specific bodies of water before initiating public or private hatcheries during the last two centuries (Prat, 1998).

Even then, however, fish culture did not prevent further restraints on people's interests in fish, water and land. One unavoidable conflict created by hatcheries was the need to harvest fish. The very effort to enhance fish stocks put fish culturists in conflict with other resource users. One hatchery on Oregon's Clackamas River inspired repeated conflicts because the hatchery weir blocked both migrating salmon from upstream settlers and logs floating to downstream lumber mills (Taylor, 1999a). Far more common were the ways hatcheries abetted the dispossession of resources. In Canada (the Maritimes, St. Lawrence and British Columbia), in the United

States (New England, the Great Lakes and Pacific Northwest) and in Japan (Hokkaido Island), hatcheries divided indigenous peoples from their salmon, trout and whitefish fisheries (Harris, 2001; Newell, 1993; Parenteau, 1998; Taylor, 1999a; Walker, 2001). In 1877, for example, Livingston Stone evicted Clackamas Indians from their fishery to prevent competition with his hatchery (Taylor, 1999a). Over time, hatcheries built to mitigate dams also reorganized the spaces of reproduction in ways that deprived Native peoples of their historic fisheries (Allen, 2003; Evenden, 2004; Taylor, 1999a). In a few instances, such as the introduction of Pacific salmon to the Great Lakes, exotic transplants for the benefit of recreational anglers also undermined commercial and aboriginal fisheries (Chiarappa and Szylvian, 2003). In recent years, however, the lines of these conflicts have shifted. In Europe, notably in Britain, and in North America, growing concerns about the genetic implications of declining stocks of wild salmonids have increasingly pitted conservation groups against the only remaining significant group of harvesters: anglers.

Another consequence was that salmonid hatcheries became contested prizes. Relentlessly shrinking fish stocks exacerbated existing tensions among fishers, and the rarer a population or species became, the more hatcheries became an explicit prize in political battles. In Canada and the United States, commercial and sport fishers engaged in what was essentially an ecological tug of war, battling over the control of hatcheries and the release of game and commercial species. In Oregon and Washington, industrial fishers also fought over which hatcheries and rivers would receive financial support (Parenteau, 1998; Taylor, 1999b). In the Great Lakes, Pacific Northwest and Japan, commercial and sport fishers also tried to deny aboriginal fishers access to hatchery fish (Blumm, 2002; Chiarappa and Szylvian, 2003; Shigeru, 1994). The advent of salmon aquaculture has had similar implications in Norway, where commercial fishers were excluded from harvesting Atlantic salmon to protect sport and farming interests (Otterstad, 1998). On the other hand, Alaskans chose to bar Atlantic salmon aquaculture from their state and restrict activities to 'private, non-profit' (PNP) hatcheries, fearing that the ecological and economic destabilizations that have accompanied farming operations elsewhere would negatively affect their Pacific salmon fisheries (Herbst, 2003).

Such consequences illustrate why technology must be understood within its historical context. Fish culture was not inherently racist or classist, even if some fish culturists were bigots (Chiarappa and Szylvian, 2003), but when hatcheries were used to serve the interests of some at the expense of others, then technology was politicized. This held true not only in those internecine battles that plagued sport and industrial fisheries during the last two centuries (Jacoby, 2001; Thompson, 1975), but, more insidiously, it also applied to industrialization. Fish hatcheries meshed seamlessly with an ideology of production that defined value narrowly in terms of economic

wealth and regarded development as a natural good. Once industrial growth emerged as the ultimate goal, fish culture thrived politically because it promised to enable such an agenda. This partnership between fish culture and development began very early. The first hatcheries were built in Europe and eastern North America in the 1850s and 1860s to stem declining fish stocks due to habitat loss and industrialization (Kinsey 2006; Netboy, 1968; Pisani, 1984; Smith, 1994). In western North America, fears of overfishing were the fulcrum for establishing hatchery programmes (Harris, 2001; Taylor, 1998b). In all cases, fish culture was popular because neither the public nor legislators wanted to regulate economic activity. This pattern of relying on technological solutions was a deliberate, politically influenced choice that continued throughout the twentieth century (Meffe, 1992). After 1910, state, provincial and federal governments allowed entrepreneurs to mitigate damaging activities by funding state-run fish hatcheries (Blumm, 2002; Evenden, 2004; Harris, 2001).

This 'in-lieu' policy saw its most aggressive application with dam-building programmes in Washington State on the Cowlitz, Lewis, White Salmon and Columbia rivers, but it was a popular solution from Japan to Western Europe. In 1923, Herbert Hoover declared 'We have only to preserve and increase the supplies of our fish by moderate restraint and scientific propagation' (Taylor, 2004). In the 1950s, France dammed the Rhône for navigation and hydroelectricity and hoped hatcheries would mitigate fisheries losses (Pritchard, 2001). In the 1960s, the Hokkaido Development Agency confiscated Ainu lands to build the Nibutani Dam for the sake of national progress (Sonohara, 1997). The culture that inspired each event has not changed in many cases. In 2003, the US President George W. Bush insisted that dams posed no problems for salmon runs (Reichmann, 2003). In all cases governments essentially institutionalized George Perkins Marsh's assumption that damage to wild stocks was an unavoidable consequence of progress. In a few places such as the United Kingdom, fishery institutions have begun to embrace a more risk-adverse approach to managing fragile stocks of salmonids, but in these cases the role and operation of hatcheries has also undergone significant change. Hatchery programmes have continued to thrive because they remain the most politically appealing, least controversial way to address the material consequences of development.

The political appeal of fish hatcheries was underscored by the technology's resistance to scientific criticism. Researchers have noted many basic flaws with fish culture. In the 1890s Knut Dahl, Johan Hjort, Ernest Holt and John Moore cast doubt on the efficacy of fish culture by citing poor statistics, insufficient controls and inconsistent results. These were leading European scientists, yet government officials ignored them in favour of voices that said what politicians wanted to hear (Smith, 1994). Criticism nevertheless increased with time. In the 1910s Americans Barton Warren Evermann and Willis Rich lodged similar complaints, as did Canadians

Russell Foerster, William Ricker and Harley White in the 1920s and 1930s (Taylor, 1998a, 1999a). After World War II, scientists expanded the litany of criticisms to include problems related to genetics, mixed-stock fisheries and habitat loss. Peter Larkin and James Lichatowich have been only two of many scientists who continued to point out the fundamental problems with salmonid enhancement in recent decades (Larkin, 1974; Lichatowich, 1999).

More than any other aspect of fish culture, it has been the selective acceptance of this criticism that underscores the importance of a broad historical perspective. Calls for 'better science' to guide hatchery pro-grammes sound sensible (Koenings, 2000; Parent, 2003), yet the more we consider the tangled history of science and politics, the less science seems able to resolve basic problems with these programmes. Calls for adaptive management—for framing policies around assumptions of a complex and unpredictable nature informed by incomplete and evolving knowledge—suggest growing acceptance of this messy state of affairs. Yet even this approach leaves many issues unresolved (Lackey *et al.*, 2006; Langston, 2003). An underlying assumption of adaptive management has been that, if not now then eventually, science *will* lead (Lee, 1993). The problem is not simply that science has never been a primary guide, but that our yearning for objectivity ignores the import of history. Not only has politics intrinsically shaped the agendas and practises of modern salmonid hatcheries, but the consequences of these actions have also narrowed managers' options. For example, the use of spawning channels and acclimation ponds were not simply new scientifically based technological approaches to hatchery problems but also politically based decisions to rely on environments that mimic natural conditions rather than on wild environments themselves. Longing for objective science obscures the historically produced circum-stances that continue to constrain both our policy options and the ecological and social consequences of our choices.

This is not a call to abandon dispassionate science for subjective politics, but a request that readers learn to recognize the intrinsic social and ecologi-cal implications of salmonid hatcheries. Science is a necessary tool for developing effective practises, but it cannot resolve the social politics that have framed the structure and intent of fish culture policies since the mid-nineteenth century. Thus, expectations that more science will necessarily lead to better policies tends only to mask the social implications of various policy choices, a tactic that many interests have used in the Pacific salmon crisis (Taylor, 1999a). Such approaches only perpetuate conflict because, as we have seen in fishery after fishery in North America and Europe, any policy not reached through the messy, compromise-laden process of con-sensus building quickly migrates to the courts. Many of the problems attending salmonid hatcheries can only be resolved through political nego-tiation, and a prerequisite to a stable outcome will be an understanding of the historical development of those hatchery programmes. We must first

step back and examine the historical lessons of these technologies before we can move intelligibly into the future.

4. Geographical Extent of Activities

Here, we report on the numbers of salmon released from conservation and fishery enhancement hatcheries in the northern Atlantic and Pacific oceans. This section is intended to provide an understanding of the relative numbers of fish released in different regions, and to identify the main purposes for their releases.

4.1. Enhancement of indigenous salmonids: Conservation, production and mitigation hatcheries
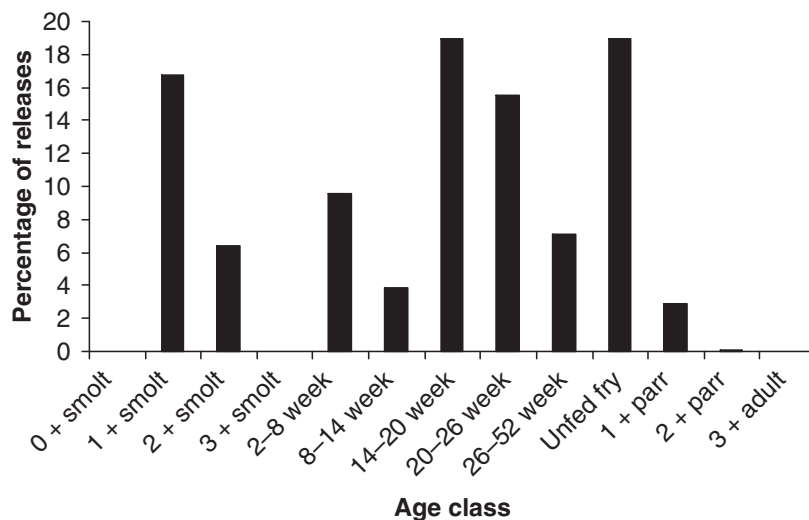
4.1.1. Atlantic salmon (*S. salar*)

Atlantic salmon have been artificially propagated and released into the wild on a large scale for more than a century. While the goals of Atlantic salmon hatcheries are as varied as Pacific salmon hatcheries (e.g., supplementation of at-risk populations, compensation for human-mediated loss of production, reestablishment of extinct populations, and increased catch), Atlantic salmon hatcheries differ in several ways from those in the Pacific. Most obviously, hatchery operations in the Atlantic are based on a few species compared to the seven species propagated in Pacific hatcheries. The scale of hatchery operations also differs dramatically. For instance, the number of Atlantic salmon smolts released is about two orders of magnitude less than releases of coho and Chinook smolts in the Pacific (Isaksson, 1988). Atlantic salmon hatcheries frequently employ a 'delayed release' technique in which out-migrating juveniles are released directly into marine waters rather than rivers (Salminen *et al.*, 1995). While this practise appears to improve survival, it may increase straying (Gunnerød *et al.*, 1988).

4.1.1.1. Western Atlantic The United States releases Atlantic salmon in an effort to recover populations that have been extirpated or severely depleted for decades. Over the last 10 years, annual releases from hatcheries in the United States have averaged greater than 10 million (M), with a maximum 15.3 M in 2000 (Fig. 2.1). The vast majority of fish releases are fry (Fig. 2.2). An analysis has shown that of the nearly 193 M salmon released in New England since 1969 (Fig. 2.2), 79% were fry, 12.4% were smolts and 8.5% were parr (US Atlantic Salmon Assessment Committee, 2003). Additionally, adult salmon that were spent, or were excess to hatchery broodstock needs, have been released into US rivers, although these numbers are low
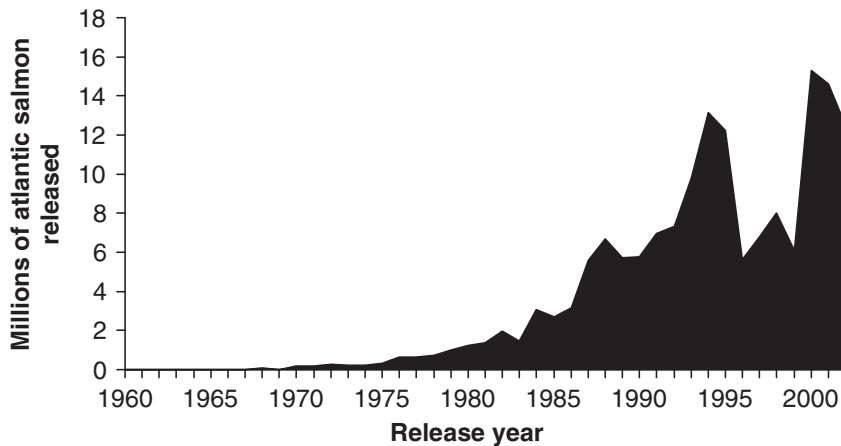
Figure 2.1 Number, in millions, of Atlantic salmon (*S. salar*) released from hatcheries into New England waters from 1960 to 2000 (all life stages). Data are from the US Atlantic Salmon Assessment Committee (2003).

Figure 2.2 Percentage of Atlantic salmon (*S. salar*) released into New England waters by age class. Data are from the US Atlantic Salmon Assessment Committee (2003).

(e.g., 3576 in 2002). Twenty river systems have routinely received hatchery Atlantic salmon, but three of these rivers (Merrimack, Connecticut and Penobscot) account for more than 80% of total releases.

Despite the many millions of hatchery fry released over the last several decades, 88% of Atlantic salmon returning to US waters originated as hatchery smolts. The remaining 12% of returning fish originated from either natural spawning fish or hatchery fry. In general, however, return rates of hatchery fish have been very low. In 2000, for instance, the return rate of hatchery smolts released in the Penobscot River was 0.10% (US Atlantic Salmon Assessment Committee, 2003).

Canadian Atlantic salmon hatcheries have been built primarily to compensate for the loss or degradation of freshwater habitat as a consequence of hydropower development or other human activities. As with US releases, returns from Canadian smolt releases have been low, ostensibly as a result of harvesting in the Greenlandic fishery (Isaksson, 1988). From 1976 to 2002 nearly 80 M Atlantic salmon were released from hatcheries in the Canadian Maritimes. Of these, most fish released were unfed or young fry, while nearly 17% were 1+ smolts (Fig. 2.3).

4.1.1.2. *Eastern Atlantic*   While Scotland, Ireland and Norway are the major worldwide producers of Atlantic salmon in commercial programmes, production of salmon reared in conservation or fishery enhancement hatcheries is small.

Legislation in Scotland governing the use of freshwater habitats limits the development of hatcheries in these environments (Thorpe, 1980). Nevertheless, about 14 M fish are released annually throughout the region, most of which comprise eyed ova, unfed and fed fry (B. Davidson, Association of Salmon Fishery Boards/Institute of Fisheries Management, personal communication). Approximately 15% are released as parr. The majority of fish released in these waters provide harvest opportunities, although some are released to compensate for habitat lost to hydroelectric power schemes. The region has seen better recovery following habitat restoration, and is turning to this approach as the primary conservation measure.

Production of juvenile salmon from Irish hatcheries is also modest relative to other countries. Unfed fry comprise the vast bulk of releases from hatcheries. Approximately 2.9 M fish were released in 2002. Releases of parr also take place, with 598,000 released in 2002 compared to 349,000 in 1999. About half a million smolts have been released each year since 1995
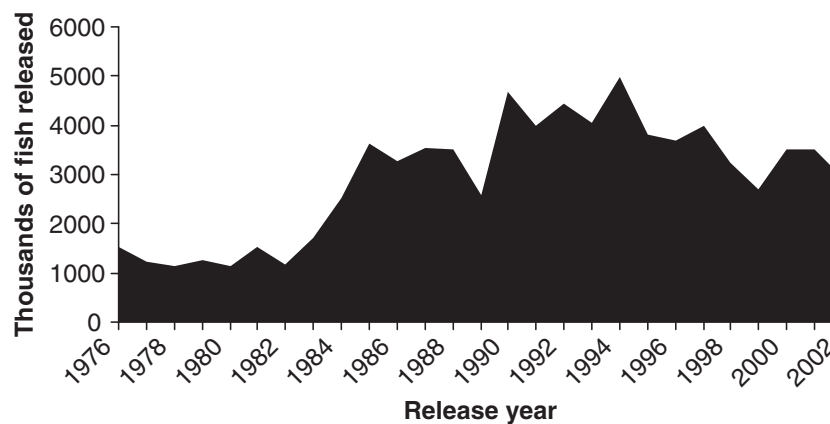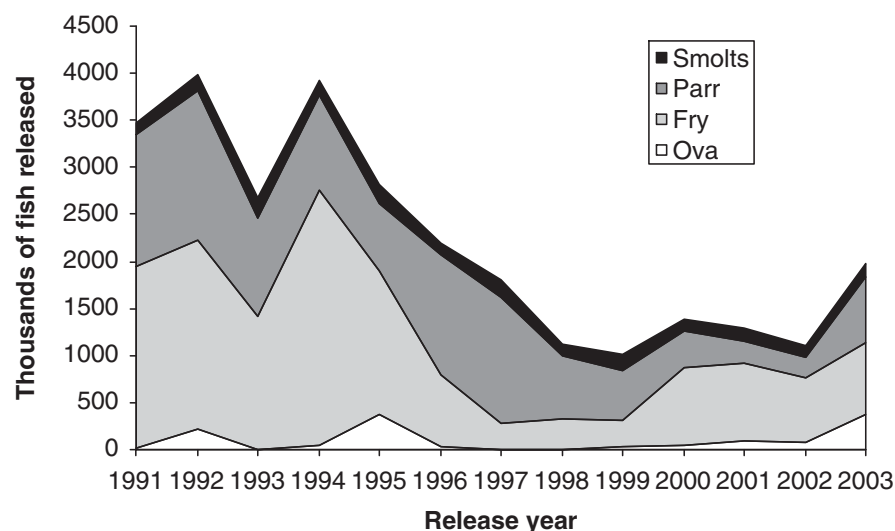

Figure 2.3   Number, in thousands, of Atlantic salmon (*S. salar*) (all life stages) released from hatcheries into waters of the Canadian Maritime provinces (Novo Scotia, New Brunswick, and Prince Edward Island) from 1976 to 2002.

(WGNAS, 2003). The major goal of these hatcheries is the preservation of fisheries which are affected by hydroelectric development (Isaksson, 1988).
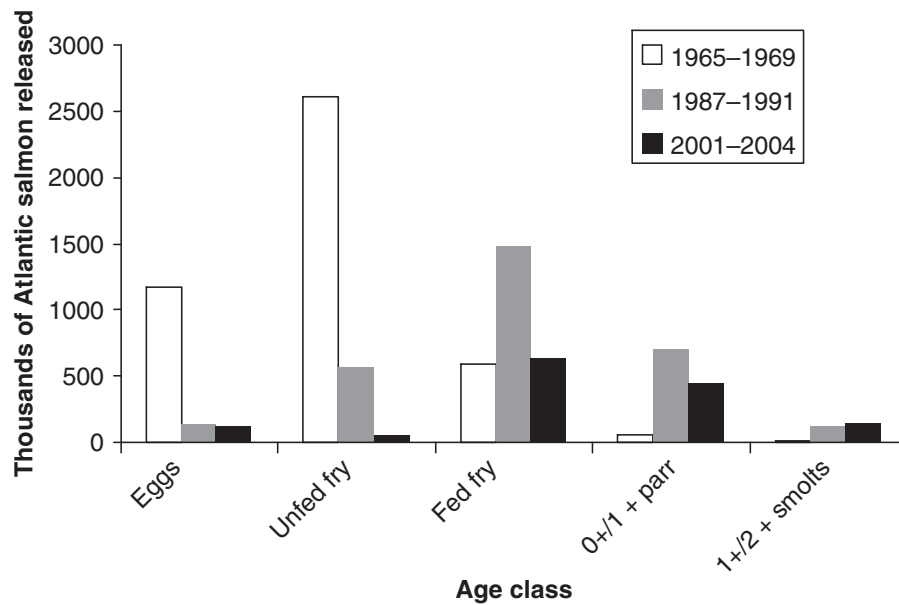
In England and Wales, releases of Atlantic salmon are modest (Fig. 2.4). Currently (2000–2004), 1.4 M salmon are released annually, of which 42% are parr and smolts (Fig. 2.5). This release size contrasts with historical releases of 4.4 M in 1965–1969 and 3.0 M in 1987–1991 (N. Milner, Environment Agency, UK, personal communication). Hatchery releases in this region are intended to recover salmon stocks that declined as a result of poor estuarine water quality and loss of spawning and rearing habitat (Milner *et al.*, 2004).

In Norway, several hatcheries release Atlantic salmon in an effort to compensate for loss of spawning and juvenile rearing areas due to hydro–power development. As with other East Atlantic countries, there was a rapid expansion of hatchery production in the 1980s, with recent annual releases of 8–9 M fry (Jonsson *et al.*, 1993). Even so, production of adult salmon from hatchery releases in Norway is small relative to other countries in the region.

Iceland is in a somewhat unique position relative to other countries in the Atlantic because salmon harvest is limited to terminal fisheries in streams (Isaksson, 1988). Iceland's hatchery programme began with experimental smolt releases in 1964 (Isaksson *et al.*, 1997; Fig. 2.6). After achieving return rates of 4–9% over the following 15 years (Isaksson, 1988), commercial releases began with the goal of supplying a privately owned terminal fishery. After a period of low return rates in the 1990s, commercial operations ended;

Figure 2.4   Number, in thousands, of Atlantic salmon *S. salar* ova, fry, parr and smolts released from hatcheries into waters of England and Wales from 1991 to 2003. Data are from Milner *et al.* (2004).

Figure 2.5   Number, in thousands, of Atlantic salmon (*S. salar*) released into waters of England and Wales by age class. Data are from Milner *et al.* (2004).
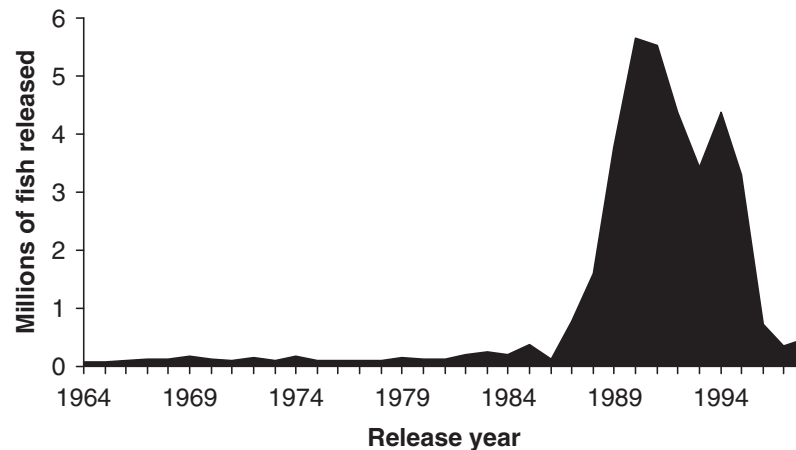
Figure 2.6   Number, in millions, of Atlantic salmon (*S. salar*) smolts released into Icelandic waters. Data redrawn from Isaksson *et al.* (1997).

however, there is still ongoing enhancement to increase abundance for angling (Isaksson and Oskarsson, 2002).

4.1.1.3. Baltic Sea   Since the early 1950s, several extensive hatchery programmes have been in place throughout the Baltic Sea region with the aim of preserving and maintaining fisheries for Atlantic salmon stocks that have been drastically reduced by hydropower development and other forms of habitat degradation (Eriksson and Eriksson, 1993; Salminen and Erkamo, 1998). Specifically, countries surrounding the Baltic Sea have developed a

'Salmon Action Plan' (ICES, 2005), which aims to restore healthy runs of Atlantic salmon and sea trout. A number of rivers in Finland, Sweden, Estonia, Latvia, Lithuania and Russia have been identified for population restoration efforts (including hatchery intervention), with the eventual goal of creating self-sustaining populations of both species.

By the mid-1980s, natural production of Atlantic salmon had been largely replaced by artificial propagation throughout the Baltic [Eskelinen and Eriksson (1987) cited in Isaksson (1988)]. For instance, in 2001 total smolt production for the Baltic region was 7.9 M Atlantic salmon, of which 6.6 M (83.5%) were of hatchery origin (ICES, 2002). However, the proportion of hatchery-reared fish varies substantially among regions, with the proportion of hatchery-reared smolts as high as 98.4% in the Gulf of Finland (ICES, 2002).

Sweden began releasing hatchery fish during the 1950s and over the next decade the number of released smolts increased to about 1.5 M (Fig. 2.7). By the middle of the 1980s Swedish hatchery production increased to about 2 M (mainly 2-year-old) smolts. In the early 1970s, Finland began a smolt release programme that grew rapidly in the 1980s. In recent years, Finland has released nearly 2.5 M smolts into the Baltic (Fig. 2.7; ICES, 2005).

A number of other Baltic countries have hatchery programmes, and their contribution to regional hatchery production increased in the late 1980s. In 2001, in addition to Sweden and Finland, Poland, Latvia, Estonia and Russia released salmon into the Baltic (Fig. 2.8). Denmark and members of
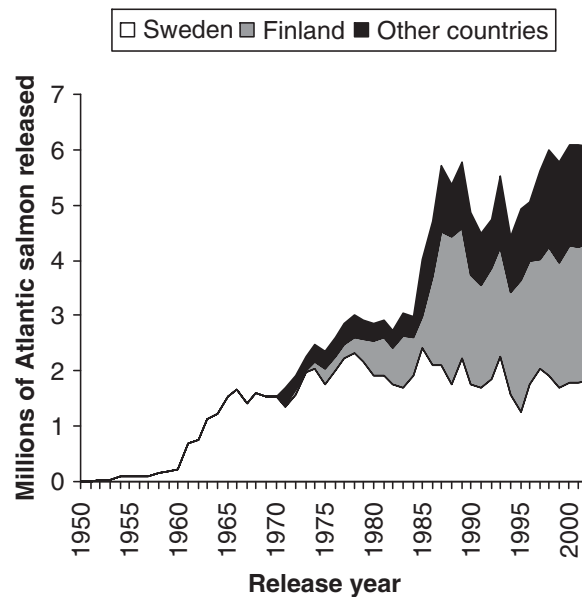
Figure 2.7   Number, in millions, of hatchery-raised Atlantic salmon (*S. salar*) smolts released into the Baltic Sea. Data extracted from Eriksson and Eriksson (1993) and ICES (2002).
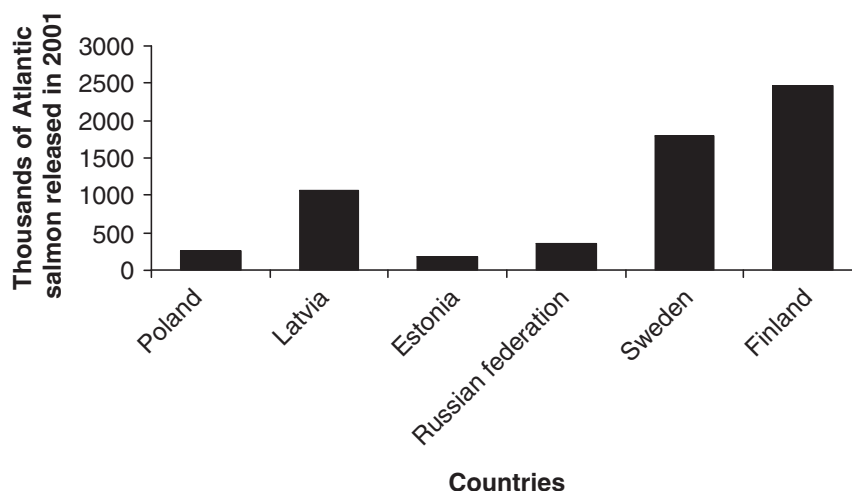
Figure 2.8 Number of hatchery-raised Atlantic salmon (*S. salar*) smolts released by country into the Baltic Sea. Data from ICES (2002).

the European Union also released small numbers of salmon in the 1990s (ICES, 2002). Mixed-stock analysis using genetic approaches have shown that hatchery fish comprise 20–75% of the total Finnish catch, depending on the region harvested (ICES, 2005).

4.1.2. Sea trout (*S. trutta*)

Sea trout the anadromous form of *S. trutta* are subject to hatchery production, but this is small in most countries. There are two exceptions.

The Baltic Sea countries release sea trout to compensate for spawning habitat lost through anthropogenic activities such as pollution, harvest, damming and dredging. The majority of hatchery fish support fisheries, although a few are used to rehabilitate threatened or extirpated populations (ICES, 2005). All early life history stages (to 2-year-old smolts) are released. Hatchery production has been fairly constant since 1988 (Fig. 2.9); Sweden, Poland and Finland are the greatest contributors of hatchery fish to the Baltic Sea. Finland and Estonia release about half of their smolt production directly to the coastline, while the remaining fish are released in dammed rivers. The majority of countries collect broodstock from naturally returning fish, but Poland's production relies almost entirely on hatchery fish; the wild populations are believed to be very small in this country (ICES, 2005).

In Ireland sea trout fisheries were, before the late 1980s, very important sport fisheries, but they collapsed dramatically due to the impacts of sea lice infection associated with marine salmon farming (Whelan and Poole, 1996). Similar decline occurred in Scottish west coast sea trout fisheries, also linked to salmon farming.
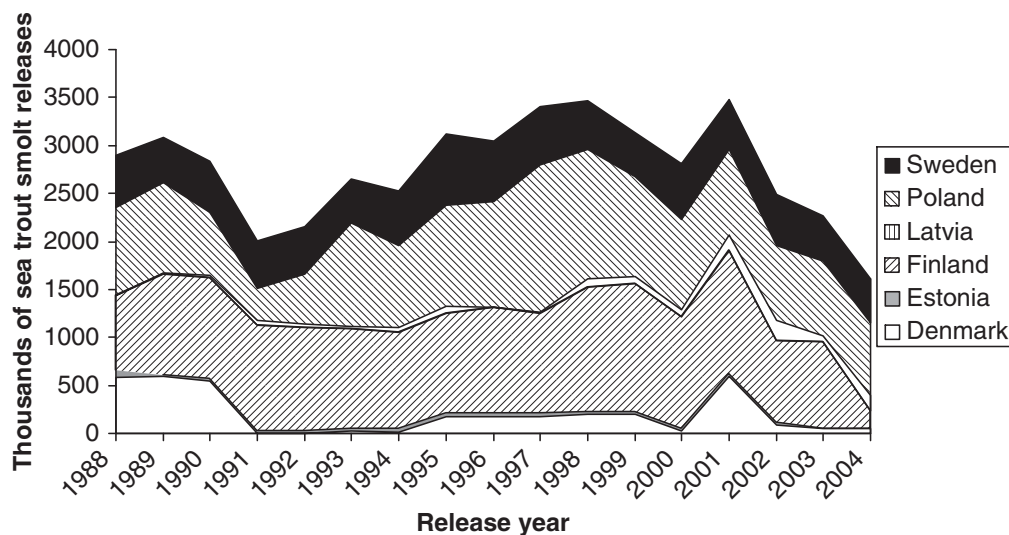
Figure 2.9 Number of hatchery-raised anadromous sea trout (*S. trutta*) smolts released into the Baltic Sea by country from 1988 to 2004. Russia and Lithuania released small numbers in the early years of this time series but are not included here. Data from ICES (2005).

4.1.3. Pacific salmon (*Oncorhynchus* spp.)

Salmon hatcheries in the Pacific date from the 1870s, when the US Fish Commision established a hatchery on the McCloud River in California (Lichatowich, 1999). Early hatcheries were directed towards the enhancement of depleted stocks or mitigation for habitat loss, but these hatcheries achieved limited success because nearly all operations relied on releases of young fry that had low survival rates (Mahnken *et al.*, 1998). Important innovations in feeding technology, disease control and rearing early life history stages occurred in the 1950s and 1960s leading to releases of larger fish with higher survival rates (Lichatowich and McIntyre, 1987), and since this time, hatcheries have played a major role in the management of Pacific Rim salmonids.

4.1.3.1. British Columbia Hatcheries have existed in British Columbia since the first sockeye (*O. nerka*) hatchery began production in the 1890s. These early hatcheries were substantial, with total output in 1910 around 500 M fish (Peterson *et al.*, 2002), more than the current production in British Columbia (Fig. 2.10). Hatchery production ceased after a couple of decades because it was difficult to demonstrate any increase in production as a result of artificial propagation (Section 2; Wood *et al.*, 2002), but began again in the 1960s (Section 2). In 1977, the Salmon Enhancement Programme (SEP) of Canada was started with the aim of doubling the catch of Pacific salmonids by protecting, rehabilitating and enhancing fish stocks throughout British Columbia. Artificial propagation has played a major role in the hatcheries formed under the SEP; spawning and rearing
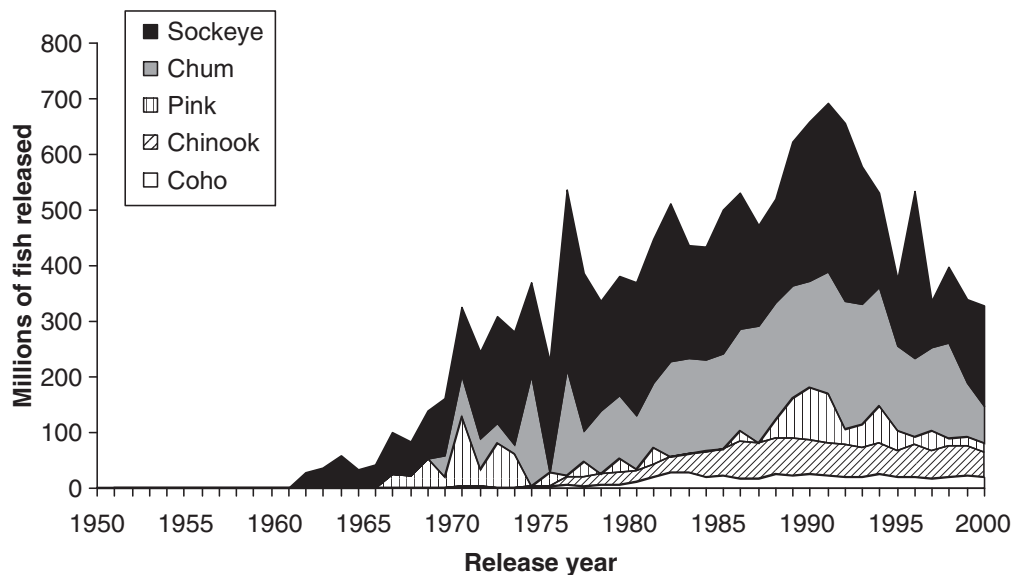
Figure 2.10 Number of hatchery fish by species (all life stages) released from British Columbia hatcheries and spawning channels. Included are sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon. Data from the North Pacific Anadromous Fish Commission (http://www.npafc.org/).

channels and in-stream incubation boxes are intended to speed the recovery of depleted stocks. British Columbia currently has 38 federally operated hatcheries and an additional 150 public involvement projects (e.g., classroom hatcheries or classroom incubators; Wood *et al.*, 2002).

Production from British Columbia hatcheries and spawning channels peaked in 1992 when nearly 700 M fish were released (Fig. 2.10). Since then production has declined, with recent releases totalling around 330 M fish. Throughout the time series examined here, sockeye and chum (*O. keta*) have dominated hatchery and spawning channel production, with sockeye comprising 41% (mostly spawning channel production) and chum 34% of production in recent years. Additionally, an average of 20 M coho, 53 M Chinook (*O. tshawytscha*) and 41 M pink salmon (*O. gorbuscha*) have been released in recent years [Fig. 2.10; North Pacific Anadromous Fish Commission (http://www.npafc.org/)].

4.1.3.2. Japan   Japan operates the most extensive hatchery operation in the world, with the goal of supporting its salmon fisheries. Japanese hatchery programmes date from 1888, when the Chitose River Central Hatchery was built in Hokkaido (Johnson *et al.*, 1997). Within 12 years, 45 chum salmon hatcheries were constructed. However, as in other regions of the Pacific Rim, fish culture practises were not well developed and the majority of releases comprised unfed fry. Beginning in the 1960s, improvements in feeding led to an increase in the size of juveniles, and as the percentage of fed

fry increased, return rates to hatcheries also increased substantially, reaching 2.3% after 1966 (Isaksson, 1988; Mahnken *et al.*, 1998).

Currently more than 300 chum salmon hatcheries are located on the islands of Honshu and Hokkaido, and at least 262 rivers are managed almost entirely for artificial propagation. Over 2 billion salmon are released annually from these hatcheries. Chum salmon have made up about 93% of recent releases (Fig. 2.11). Additionally, an average of about 132 M pink and 15 M masu salmon (*O. masou*) have been released annually into Japanese waters over the last decade (North Pacific Anadromous Fish Commission, http://www.npafc.org/).

4.1.3.3. Russia The first salmon hatcheries in Russia began production in the 1920s in tributaries to the Amur and Kamchatka rivers. At this time, the Japanese also built hatcheries on Sakhalin Island and the Kuril Islands, which came under Russian control after World War II (Johnson *et al.*, 1997). By the 1960s, 25 hatcheries operated in Russia and recently 44 hatcheries have produced 500–550 M salmon annually in an effort to enhance fisheries (Environment and Natural Resources Institute, 2001). Production is almost entirely based on chum and pink salmon and is approximately evenly distributed between the two species (Fig. 2.12). In addition, close to 3 M coho, 5 M sockeye, 400,000 Chinook and 200,000 masu have been released annually (Environment and Natural Resources Institute, 2001).
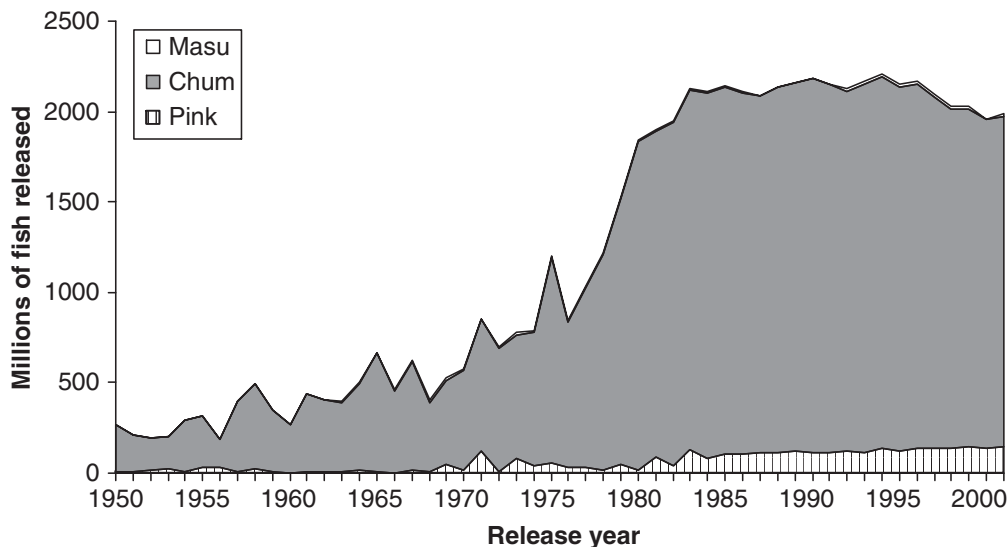
Figure 2.11 Number, in millions, of hatchery fish by species (all life stages) released from Japanese hatcheries from 1950 to 2000. Included are masu (*O. masou*), chum (*O. keta*) and pink (*O. gorbuscha*) salmon. Data from the North Pacific Anadromous Fish Commission (http://www.npafc.org/).
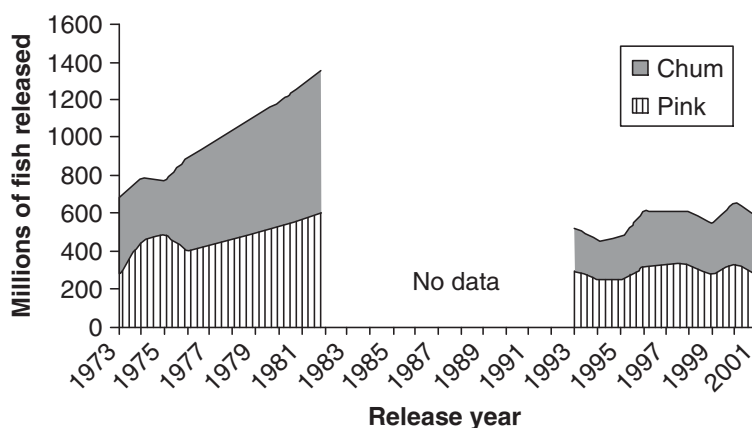
Figure 2.12   Number of hatchery chum (*O. keta*) and pink (*O. gorbuscha*) salmon (all life stages) released from Russian hatcheries from 1973 to 2001. Sockeye, masu, chinook and coho are not included; see text for numbers released during this period.

Russian hatcheries differ from Japanese programmes in that they were not constructed to manage rivers exclusively for hatchery fish. Consequently, Russian hatcheries generally have used local fish for broodstock and there is no attempt to prevent natural spawning. Even so, natural production was not afforded a high priority as, historically, eggs were widely exchanged among hatcheries and excess hatchery fish were allowed to spawn with wild fish. In recent years, however, hatchery managers have recognized the problems associated with egg transfers and such exchanges have been reduced (Johnson *et al.*, 1997).

4.1.3.4. *Alaska*   Construction of hatcheries in Alaska began in the early 1900s, but they were often badly sited and had poor water quality. As a consequence, these hatcheries achieved little success and by 1936 Alaska's hatcheries ceased production (Roppel, 1982). However, after a protracted decline in salmon catches in the early 1970s, the Alaska Department of Fish and Game developed a coordinated SEP and the state of Alaska passed legislation that encouraged 'PNP' hatcheries. Over the next several years, there was an explosion of hatchery construction (Fig. 2.13; Farrington, 2003) and corresponding hatchery releases (Fig. 2.14). A unique feature of Alaska's hatchery system is that most hatcheries are operated by private associations of fishers, environmentalists and local civic interests (Heard *et al.*, 2003). These associations can not only build and operate hatcheries, but they also assist the Alaska Department of Fish and Game in the development of regional salmon plans, authorize taxes on salmon catches to support hatcheries and sell returning hatchery fish to offset operational expenses (Heard *et al.*, 2003). Currently, there are eight regional aquaculture associations in Alaska.
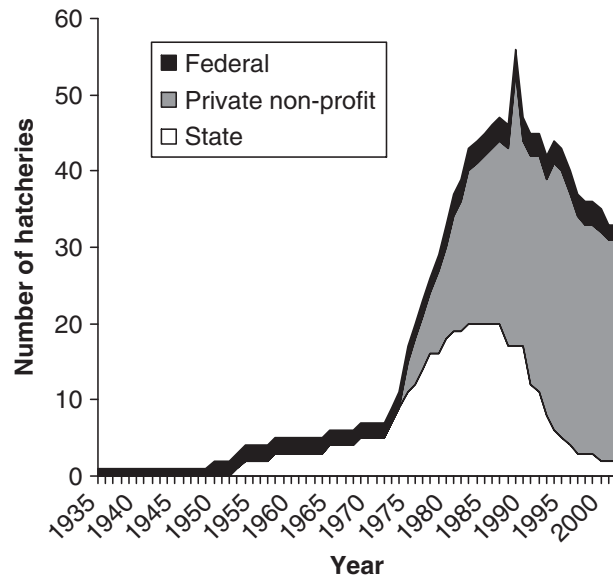
Figure 2.13 Number of federal, state and private Pacific salmon (*Oncorhynchus* spp.) hatcheries operating in Alaska (Farrington, 2003).
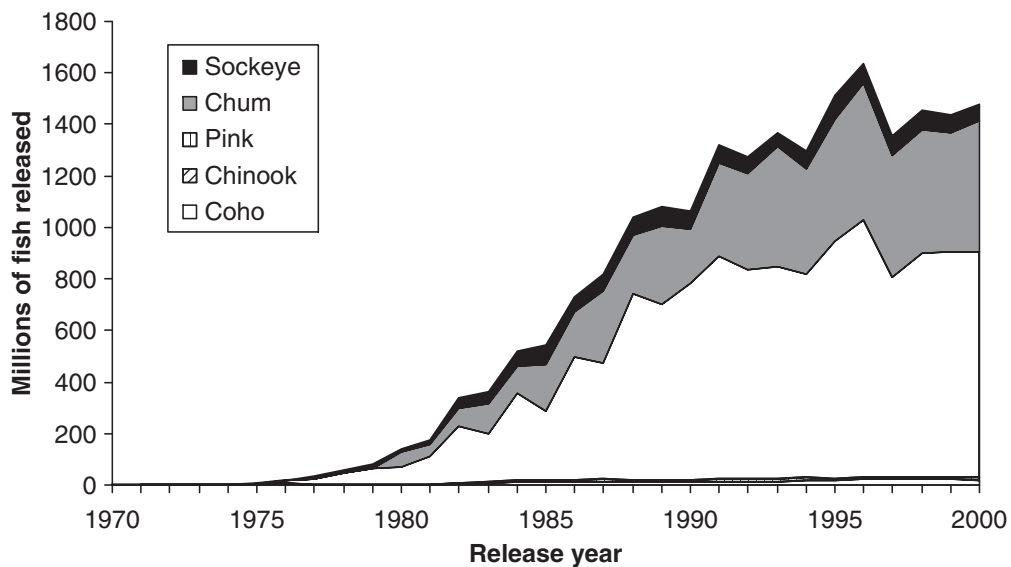
Figure 2.14 Number, in millions, of hatchery salmon by species (all life stages) released from Alaska hatcheries. Data from the North Pacific Anadromous Fish Commission, 2003 (http://www.npafc.org/). Included are sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon.

Pink and chum salmon have made up the bulk of the salmon produced in Alaska hatcheries (Fig. 2.14). In recent years, more than 1.4 billion salmon have been released annually; 61% are pink and 32% are chum, respectively. In addition, recent annual sockeye releases have averaged more than 70 M (5%), coho releases have averaged about 18 M (1.3%)

and Chinook releases have averaged nearly 9 M (0.6%). The PWS and Southeast Alaska regions are the largest producers of hatchery salmon. The Prince William Sound Aquaculture Corporation releases more than 400 M pink salmon each year and operates the largest hatchery operation in North America (Environment and Natural Resources Institute, 2001).

Hatchery-produced fish appear to contribute significantly to harvest levels in Alaska. In 2000, hatchery fish comprised 42% of Alaska's pink, 64% of chum, 19% of Chinook, 24% of coho and 4% of sockeye catches (Heard *et al.*, 2003). However, the proportion of hatchery fish in the catch varied greatly among regions. For instance, 82% of the pink and 88% of the chum harvest in PWS was of hatchery origin. In contrast, hatchery fish comprised only 10% of the total salmon harvest (2% pink, 0% chum) in Cook Inlet (Heard *et al.*, 2003).

4.1.3.5. *United States, Contiguous Pacific States*

Salmon hatcheries in the US Pacific Northwest have played an increasingly prominent role in salmon management. Most public hatcheries were originally constructed to rebuild depleted stocks and to mitigate for loss of natural spawning habitat, and their goal was simply focused on enhancing the harvest of adults in the commercial fisheries (Flagg *et al.*, 2000). The number of hatcheries increased gradually throughout the first half of the twentieth century; facilities were constructed at a rate of about 1.5 per year from 1900 until 1950. However, the pace of construction increased rapidly in the latter part of the century, at a rate of nearly 6 per year from 1951 to 2000.

Total hatchery production peaked in the early 1980s with the release of nearly 600 M salmon (Fig. 2.15). More recently, total annual hatchery releases have averaged about 400 M. Chinook salmon dominate the releases in the Pacific Northwest with average annual releases of 256 M fish from 1990 to 2000. The centre of Chinook production is the Columbia River Basin, which accounts for about 27% of the world's total Chinook release (Mahnken *et al.*, 1998). Coho and chum are also produced in large numbers, with annual average releases from 1990 to 2000 of 77 and 66 M fish, respectively. Additionally, hatcheries in the region annually release steelhead (*O. mykiss*; 28 M per year), sockeye (11.6 M per year) and pink salmon (1.8 M per year). Interestingly, hatchery releases do not correspond directly to the number of hatcheries constructed (Fig. 2.16). For Chinook, for example, there appears to be a step function, with average annual production increasing abruptly in the 1950s and subsequently varying around a greater mean than in previous years (Fig. 2.16).

While salmon hatcheries operate in California, Idaho, Oregon and Washington, the majority of hatchery fish are produced in Washington. In 1998, more than 70% of Pacific salmon released in the mainland United States originated from Washington hatcheries, with 16% from California, 10.4%
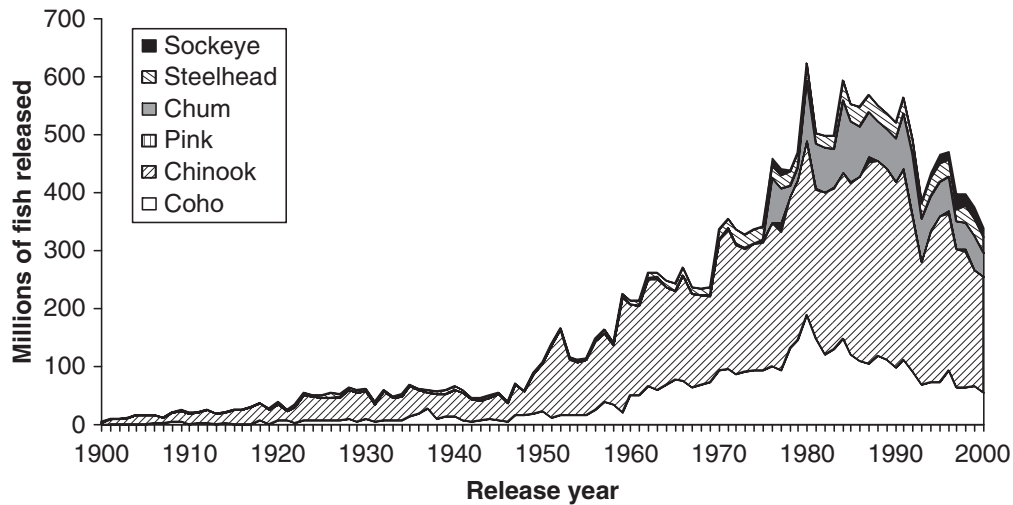
Figure 2.15 Number, in millions, of hatchery Pacific salmon (*Oncorhynchus* spp.) (all life stages) released from hatcheries in the continental United States. Data from the North Pacific Anadromous Fish Commission (http://www.npafc.org/) and Mahnken *et al.* (1998). Included are sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon.
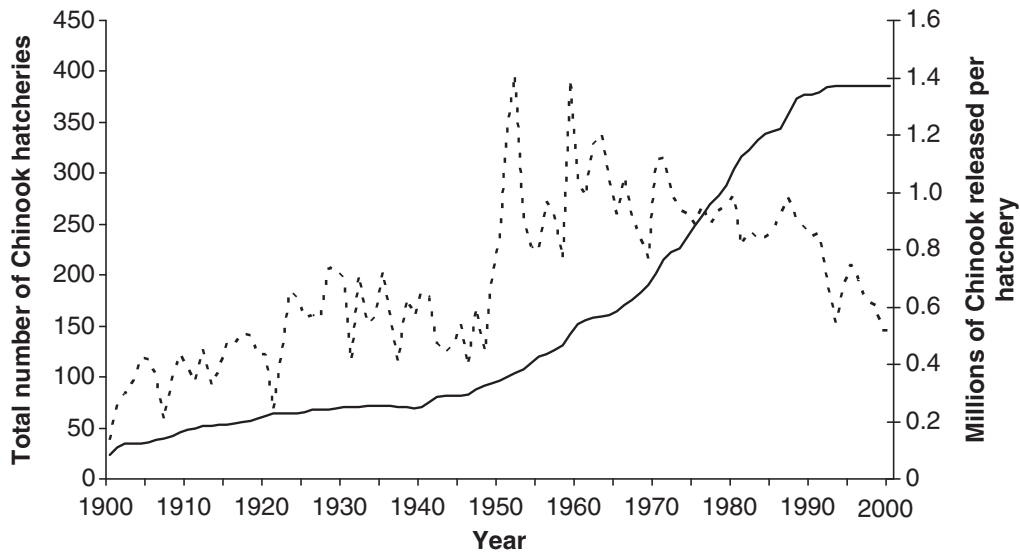
Figure 2.16 Cumulative number of Chinook salmon hatcheries (solid line) and the average number of hatchery Chinook salmon *O. tshawytscha* (dashed line) released into continental US water per hatchery from 1900 to 2000. Data extracted from Myers *et al.* (1998) and the North Pacific Anadromous Fish Commission (http://www.npafc.org/).

from Oregon and 2.7% from Idaho (North Pacific Anadromous Fisheries Commission Statistical Yearbook, available at http://www.npafc.org/).

As part of the management process in the Pacific Northwest, hatcheries are required to state the purpose of their operations (Drake *et al.*, 2003). We grouped these operational goals into three of the categories outlined earlier

(Section 1.2): mitigation, supplementation or production hatcheries. The purpose of hatcheries varied greatly among species (Fig. 2.17). The stated purpose of most coho and steelhead hatcheries, for example, was production, while conservation was the primary purpose of most chum hatcheries.

Drake *et al.* (2003) also reviewed available published literature and unpublished studies and subjectively classified hatchery stocks based on the amount of genetic divergence between the hatchery and wild stocks and the source of the hatchery stock relative to wild stock. The hatchery fish were classified as local or non-local, and if the latter, as within or outside evolutionary significant units (ESUs; Waples, 1995).

The source of most Chinook stocks was found to be local or non-local but within the ESU (Fig. 2.18). In general, Drake *et al.* (2003) determined that while there were moderate to few wild fish in most Chinook hatchery brood-stock, there was no more than moderate divergence of the hatchery stocks from the wild fish. Additionally, the ratio of hatchery Chinook to the natural population was high for a number of stocks. This result meant that there were substantial numbers of natural origin fish in the Chinook broodstock and there was minimal divergence between hatchery and wild fish. A minority of hatchery stocks comprised broodstock whose source was outside the ESU, and in these stocks, there was extreme divergence between hatchery and wild fish. A similar pattern emerged for steelhead; many hatchery stocks exhibited little divergence from natural populations, but a significant number of stocks showed substantial or extreme divergence (Fig. 2.18). This latter result may be partly explained by the use of a deliberately domesticated hatchery stock with a different return timing from wild populations. Coho hatchery stocks generally had no more than moderate divergence from wild stocks, and chum hatchery stocks showed little divergence from fish of natural origin.
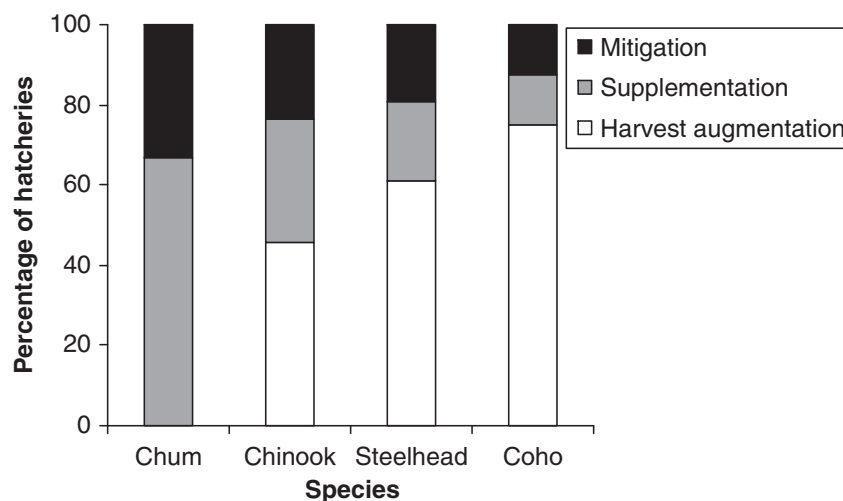
Figure 2.17   Declared purpose of hatcheries for each of four species of Pacific salmon in the Pacific Northwest. Data are from Drake *et al.* (2003).
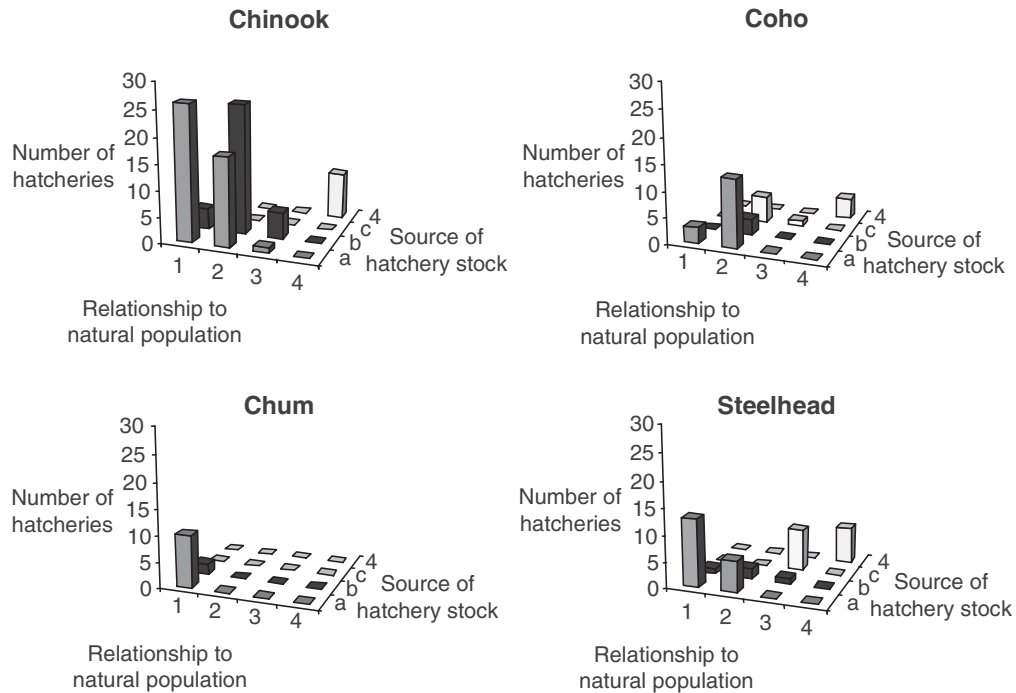
Figure 2.18 Number of steelhead (*O. mykiss*), Chinook (*O. tshawytscha*), coho (*O. kisutch*) and chum (*O. keta*) salmon hatcheries organized by the amount of genetic divergence between the hatchery and wild stocks (relationship to natural population) on a scale of 1–4, and the source of the hatchery stock relative to wild stock (source of hatchery stock) on a scale of a–c for stocks within an ESU, and 4 for those outside an ESU. Data are from Drake *et al.* (2003).

4.2. Enhancement of non-indigenous salmon and trout: Introductions

The literature on worldwide salmon and trout introductions is extensive, and will be reviewed elsewhere. Several general conclusions relevant to our discussion can be drawn from these findings. First, data on release sizes for anadromous salmonids in conservation, production and mitigation hatcheries were not readily obtained (Section 4.1), and similar data on introductions were not available in most cases. In addition, it appears difficult to discriminate between those introductions that were successful versus those that were not. Second, there were inconsistencies in the scales over which the data were reported, and these scales varied historically. Third, it appears that the extent of introductions worldwide has declined, possibly because most potential sites for salmon fisheries have been explored. However, there is a paucity of data on ongoing 'put and take' hatcheries based on non-indigenous salmon, and it is difficult to gauge the level, extent and impact of these activities. Finally, the ongoing tension between economic and ecological incentives is identified as being a primary determining force as to

whether exotic introductions will continue. We do not explicitly address the consequences of non-indigenous salmon introductions in most of the risks that we review. However, the introduction of exotic salmon may result in extreme outcomes of these risks; for example, competition with local species, the introduction of a non-endemic pathogen or hybridization with vulnerable indigenous species.

5. Potential Consequences of Enhancement Activities

5.1. Genetic risks associated with salmon hatchery programmes

The genetic effects of hatchery programmes have been the subject of substantial review in the literature. Most authors agree that releases can have detrimental effects on wild populations (e.g., Allendorf and Ryman, 1997; Aprahamian *et al.*, 2003; Busack and Currens, 1995; Cross, 2000; Hindar *et al.*, 1991; Utter, 1998; Waples, 1991) and others have suggested management steps that may be taken to reduce such effects (Hard *et al.*, 1992; Mobrand *et al.*, 2005; Waples and Drake, 2005). The debate in this area is not around whether hatchery programmes pose a threat to wild populations, but whether the risks are sufficiently large to compromise wild populations and if true, whether they may be reduced or avoided through correct management actions (Brannon *et al.*, 2004a; Campton, 1995; Waples, 1999).

The aim of this section of the chapter is not to simply repeat the information provided in many of the papers written on this topic, but to update and evaluate our understanding of the genetic consequences of hatchery programmes. First, we will review the current knowledge of the genetic risks involved. Second, most would argue that the varying objectives of hatchery programmes will pose different types and magnitudes of effects on wild populations, and so we will examine the impacts of hatchery programmes in the context of their release objectives (conservation or fishery enhancement hatcheries, following the classification outlined in Section 1). Finally, we will identify research directions that will assist designing management steps that may be taken to reduce the genetic risks associated with different salmon hatchery programmes.

5.1.1. Genetic risks associated with hatchery fish

The potential genetic outcomes of rearing and releasing hatchery fish into the wild fall broadly into three categories: the effect of hatcheries on hatchery fish, the direct effect of hatchery fish on wild fish and the indirect effect of hatchery fish on wild fish (Campton, 1995; Hindar *et al.*, 1991;

Waples, 1991). The latter occurs through processes such as competition, disease transfer and increased fishing mortality on the wild component of a stock, all of which result in demographic changes or selection in the wild populations. The first two factors will be reviewed in detail below, primarily because much is known about these factors, while the third has not been empirically studied to any significant extent (Campton, 1995; Waples, 1991), and so will not be discussed further in this section.

5.1.1.1. *The genetic effects of hatcheries on hatchery fish*

Procedures implemented in the collection, mating, rearing and release of hatchery salmon may lead to a change and perhaps a reduction in genetic diversity of the source population in two ways. First, as the population size decreases, the random loss of genetic variation in a population can be expected to increase. A loss of genetic variation may lead to inbreeding and an associated decrease in fitness, termed inbreeding depression. Second, the hatchery environment can be a poor imitator of wild conditions, and hatchery fish may become adapted to their environment through a process known as domestication selection. The result of both effects may ultimately lead to the release of a genetically altered population that may interact negatively with any wild stocks present, by decreasing the overall fitness of the combined populations.

5.1.1.1.1. *Loss of genetic diversity and inbreeding*

The genetic diversity relevant to the long-term survival of a species is quantitative in nature, that is, several gene loci interact with each other and with the environment to create a range of phenotypes. Quantitative genetic diversity is difficult to measure at present (Hard, 1995), although substantial advances are being made in characterizing this functional diversity (reviewed in Danzmann and Gharbi, 2001; Vasemägi and Primmer, 2005). Thus, effective population size is often used as a proxy metric for quantitative genetic diversity because the theoretical link between this measure and loss of genetic variation is well known (Frankham *et al.*, 2002).

The effective population size, N_e, is the size of an ideal population whose genetic composition is influenced by random processes in the same way as a real population. It is important to realize that N_e can be very different from the census size, N_c, of a population, and the ratio of N_e to N_c can be affected by factors such as sex ratio, family size, fluctuations in population size, overlapping generations and variance in reproductive suc–cess. The measurement of N_e in salmon populations is usually confounded by overlapping generations, seen in most species; hence N_b, the number of breeders corrected for generation length, is often the preferred measure (Waples, 1990, 2004). The ratio of N_b (or N_e) to N_c in wild salmon populations is often low (e.g., Shrimpton and Heath, 2003), and has been

noted to vary between 0.01 and 0.71 (Bartley *et al.*, 1992; Hedrick *et al.*, 1995; Waples *et al.*, 1993).

A number of practises associated with the management of hatchery fish may lead to a decrease in N_e (Busack and Currens, 1995). For example, hatcheries may cause accelerated growth, which in turn may cause early maturation in male salmon and thus skew male to female ratios (Larsen *et al.*, 2004). Spawning protocols that deviate from 1:1 sex ratios are known to reduce N_e (e.g., Allendorf, 1993). Genetic variation may also be lost at the founding of the hatchery strain, during a bottleneck or during prolonged periods of reduced population size. Most studies have not examined the underlying causes of a decline in genetic diversity, but such decreases of diversity in hatchery strains have been reported at neutral genetic markers (Jones *et al.*, 1997; Koljonen *et al.*, 1999; Nielsen *et al.*, 1997; Primmer *et al.*, 1999; Tessier *et al.*, 1997; Was and Wenne, 2002). Where a decrease in N_e has been directly measured, it is often possible to attribute the decrease to broodstock practises that may be avoidable (Koljonen *et al.*, 2002).

On a positive note, it is widely recognized that if management steps are taken to avoid a loss of variation, then the N_e to N_c ratio within a captive population can be higher than that in the wild. For example, if founder population sizes are adequate (Allendorf and Ryman, 1997; Frankham *et al.*, 2002), sex ratios are equalized at mating (Campton, 2004), family sizes are also equalized (Allendorf, 1993) and long-term fluctuations in population sizes are avoided, then N_e to N_c ratios can exceed 1.0. Thus, captive populations may be used to enhance the genetic diversity in a depleted wild population (Hedrick *et al.*, 2000).

However, a loss of genetic variation may be unavoidable in some cases. The inevitable consequence is that a self-perpetuated broodstock will eventually comprise individuals with higher average relatedness, and mating between these individuals will result in inbreeding (identity by descent). Inbreeding by itself does not result in a change in gene frequencies; it does, however, result in an increase in homozygotes. Inbreeding is often associated with a decline in fitness-related phenotypes (Keller and Waller, 2002), termed inbreeding depression, which in turn may lead to a reduction in population size and a change in gene frequencies through genetic drift (Bijlsma *et al.*, 2000; Saccheri *et al.*, 1998). Inbreeding depression is usually more prevalent in life history traits than in morphological traits (DeRose and Roff, 1999) and tends to be more severe in wild than in captive populations (Crnokrak and Roff, 1999; Kalinowski and Hedrick, 1999).

The manifestation of inbreeding depression is usually attributed to one of two mechanisms, either the loss of dominance ('masking' of deleterious alleles) or of over-dominance (heterozygote advantage) at genetic loci encoding fitness traits (Frankham *et al.*, 2002). Deleterious alleles may increasingly occur in the homozygous state following inbreeding, thus reducing the dominance interactions between advantageous and deleterious alleles

in heterozygotes. It has been argued that a fitness decline is controlled by the *rate* of inbreeding because deleterious alleles occur more frequently as homozygotes in small populations, and are no longer masked by positive or neutral dominant alleles. Selection can then act by 'purging' these alleles from the population. However, many researchers have demonstrated that selection against deleterious alleles cannot be relied on to decrease the rate of extinction because these alleles can also become fixed in a population through genetic drift (Reed *et al.*, 2003). An alternative explanation for a decline in fitness is attributed to the advantage conferred by over-dominance at heterozygous loci; that is, the sum of two alleles at a locus may outweigh either of the two homozygotes. If heterozygotes are lost, then overall fitness will decline in a population. If over-dominance is the underlying mechanism for inbreeding depression, then purging cannot be implemented as a management tool and in fact, the over-dominance hypothesis may partly explain why this approach is unpredictable in many cases.

Wang *et al.* (2002) provided several examples of inbreeding depression in their review of inbreeding in salmonids. Perhaps their most significant finding was that experimental designs have varied, and general inferences about the incidence and manifestation of inbreeding depression in the salmonids cannot easily be drawn. There are three major approaches to testing inbreeding depression in a population (Keller and Waller, 2002): (1) the experimental comparison of inbred with outbred lines, (2) the outcrossing of small inbred populations to examine whether an increase in heterozygosity results in an increase in fitness, and (3) the comparison of the phenotypic values of related versus unrelated individuals within a population. Inbreeding studies on salmonids have favoured the first method and have differed in the rates of inbreeding reported (Wang *et al.*, 2002). In a typical experiment using sexually reproducing organisms, inbred individuals are produced only after at least two generations of mating. Such experiments can be especially protracted in salmon, most of which reach maturity after several years. Hence, most studies have generated individuals with high inbreeding values as early as possible. Wang *et al.* (2002) proposed that the contradictory results seen by different researchers at the same traits and in the same species can be explained by the rates of inbreeding, most of which are not characteristic of wild populations. For example, Gjerde *et al.* (1983) reported inbreeding depression in adult body weight of rainbow trout *O. mykiss* under fast inbreeding, whereas Pante *et al.* (2001) do not observe this outcome under slower inbreeding. This contrast supports the notion that purging may play a role in avoiding fitness declines in salmonids, a view which needs to be verified by further research.

Other equally important factors may also affect the manifestation of inbreeding depression in the reported studies. For example, the initial inbreeding coefficient, F, of the baseline population may differ between

experimental populations (Wang *et al.,* 2002), as may the prevailing environmental or social conditions (Gallardo and Neira, 2005). Inbreeding depression also varies by the trait measured (DeRose and Roff, 1999) and this trend certainly appears to be supported within salmonids. For example, early growth-related traits and survival appear to be more prone to inbreeding than adult weight and size (Wang *et al.*, 2002), and inbred Chinook salmon have been found to be more susceptible to the pathogen *Myxobolus cerebralis,* but not to *Listonella anguillarum* or infectious hematopoietic necrosis virus (IHNV; Arkush *et al.*, 2002).

Perhaps the most conspicuous point here is that the majority of such studies have been carried out on cultured fish. If the incidence of inbreeding depression in salmon increases in the wild, as in other taxa (Crnokrak and Roff, 1999; Kalinowski and Hedrick, 1999), then more emphasis on wild populations is needed. The design of such experiments should be systematic, include both resident and anadromous forms and populations with inbreeding history and those without. Such broadened studies likely will be more amenable to generalizations about the effects of inbreeding in systems incorporating hatchery releases.

5.1.1.1.2. Domestication selection   Domestication selection that arises in a supplementation programme is often unintentional, resulting from 'natural' adaptation of the species to the hatchery. Simply, life history theory predicts that selection imposed by a novel environment will rapidly alter the genetic architecture of life history traits of a population, and lead to divergence between the founding and the new population. The strength of this change will be dependent on the selection regimes between the hatchery and the wild environment, the numbers of generations that the broodstock are held in captivity and the magnitude of genetic variation underlying the fitness trait under selection. Thus, the opportunity for domestication selection to produce divergence between wild and captively reared individuals is largest when the latter are cultured throughout their life histories for many generations (Hard, 1995). However, simulations have shown that domestication selection in hatchery fish can have rapid and substantial negative genetic effects on targeted wild populations, even when wild captive breeders are always used (Lynch and O'Hely, 2001; Ford, 2002).

Examples of differences between hatchery and wild fish are widely published. However, it should be noted that in many of these cases it is difficult to implicate domestication selection alone. For example, a series of experiments have demonstrated behavioural and morphological differences between wild populations and hatchery coho salmon (Fleming and Gross, 1992, 1993) and Atlantic salmon originating from aquaculture facilities (Fleming and Einum, 1997; Fleming *et al.*, 1994, 1996). While many of these experiments serve to demonstrate the rapid phenotypic divergences that may be obtained following deliberate domestication, the cultured

strains used in some of these studies were not derived from the same watershed as the wild populations. In fact, Reisenbichler and Rubin (1999) pointed out that the prevalence of this experimental design in most studies, and the fact that many researchers examine only one or two fitness-related traits, has resulted in the charge that domestication selection has yet to be demonstrated in hatchery salmonids. On the west coast of North America, hatchery coho salmon have been compared to their wild source counterparts. Juvenile cultured coho salmon are less aggressive at emergence and adult hatchery fish are not as successful at mating as wild hatchery fish (Berejikian et al., 1997, 1999, 2001a). The two groups also differ morphologically (Hard et al., 2000). However, in an informative series of experiments, dissimilarities between hatchery and wild steelhead (*O. mykiss*) have been substantially reduced by rearing hatchery fish in enriched environments (Berejikian et al., 2000, 2001b). Thus, an explanation for many of the variations observed between hatchery and wild fish is that the different rearing environments have acted to change the phenotypes without substantially changing the underlying genotype, thus confounding a genetic interpretation of the results of these studies. However, there are cases where the evidence indicates that a hatchery population diverged from the wild population from which it was derived (e.g., anti-predator and aggressive behaviour of juvenile steelhead trout Berejikian, 1995; Berejikian et al., 1996). In addition, the adults selected for spawning in a hatchery are often the early arrivals, with the result that the distribution of spawning may change, often quite dramatically (Flagg et al., 1995; Ford et al., 2006; Quinn et al., 2002). Such differences in spawning date are likely to have large fitness consequences, as this trait is closely linked to the prevailing regimes of temperature, flow and productivity of the ecosystem.

The *genetic* outcomes of domestication selection and their potential solutions have rarely been tested empirically in salmonids due, in part, to the fact that such experiments require a breeding design and these species are long lived. Even in those populations in which domestication selection has been reported in controlled experiments, few studies have been designed to detect this phenomenon directly. An experiment conducted over several generations (Hershberger et al., 1990) implicated domestication selection for increased weight in coho salmon cultured over four generations in marine net pens. However, the underlying genetic model in this study has been criticized (Hard, 1995) because the experiment did not maintain controls that may have discriminated environmental versus genetic changes during culture.

In a seminal study, wild steelhead embryos released in small streams generally had a higher survival to 1 year than those of either hatchery or hybrid offspring (Reisenbichler and McIntyre, 1977). In this case, hatchery fish were derived from the wild population and separated for only two generations. Results differed between streams, suggesting a genotype by

environment interaction that was magnified in some environments but not others (Hard, 1995). Hence, the severity of domestication selection can be expected to vary in wild environments. As a comparison, in a recent experiment mimicking the experimental design of Reisenbichler and McIntyre (1977), differences in growth and survival were not seen between the offspring of wild brown trout, a sea-ranched strain and their hybrids when they were reared in the wild (Dahl *et al.*, 2006; Dannewitz *et al.*, 2003). The sea-ranched strain had been separated from its source population by seven generations. These contrasting examples highlight the importance of experimental design—the sea trout experiments were conducted in a common environment, were replicated and took into account genetic effects that may explain variation between individual families comprising each cross type.

It is quite clear that the risks posed by domestication selection have not been quantified in a *systematic* fashion. In articles examining genetic changes in hatchery salmon populations, many authors have recognized domestication selection as a potentially significant problem (Busack and Currens, 1995; Waples, 1999), but have concluded that scant evidence exists to evaluate its significance to management approaches. Little is known about the relationship between selection on specific fitness traits and population size, the number of generations in captivity that may lead to genetic differences with the wild population and whether such selection is reversible or avoidable through different management approaches. Such knowledge is essential for conservation planning, and there is an urgent need for research on the extent and consequences of domestication selection in salmonids, as well as steps that may be taken to reduce its effects.

5.1.1.2. Hatchery regime effects on wild fish   If the hatchery regime results in a change in the genetic composition of the captive population, then such changes can have negative consequences on the wild populations with which they interact. These changes can be demographic in nature; the release of a genetically under-represented hatchery population into the wild can reduce the overall effective population size N_e of the two components together or decrease the existing population structure. The changes can also affect the fitness traits of a wild population through hybridization with less fit hatchery fish. Taken together, the results of these processes can lead ultimately to the decline and extinction of an endangered wild population.

5.1.1.2.1. Changes in effective population size   A simple simulation based on the Ryman–Laikre model (Ryman and Laikre, 1991) can be used to illustrate the effects of hatchery release size on a population's effective size, N_e (Hedgecock and Coykendall, 2007). The model examines the effect of hatchery recruitment to a wild population over a *single* generation, and relies

on known values of effective size for hatchery (N_{eh}) and wild (N_{ew}) fish. Outcomes vary with the relative proportion of hatchery fish in the total census population (Fig. 2.19). Intuitively, supplementation with a hatchery population with a large N_e is beneficial when the wild population has a small N_e (Fig. 2.19A), but detrimental with the opposite scenario (Fig. 2.19C). The most interesting lesson to be learned from this model, however, is that the effects of hatchery supplementation can be very detrimental to wild populations of moderate effective size (Fig. 2.19B).

One needs to keep in mind that N_e is less than N in most cases. For example, the Ryman–Laikre method assumes that all fish are spawning adults, but many hatcheries release smolts with different return rates than the wild fish. Similarly, it is assumed that hatchery and wild fish have an
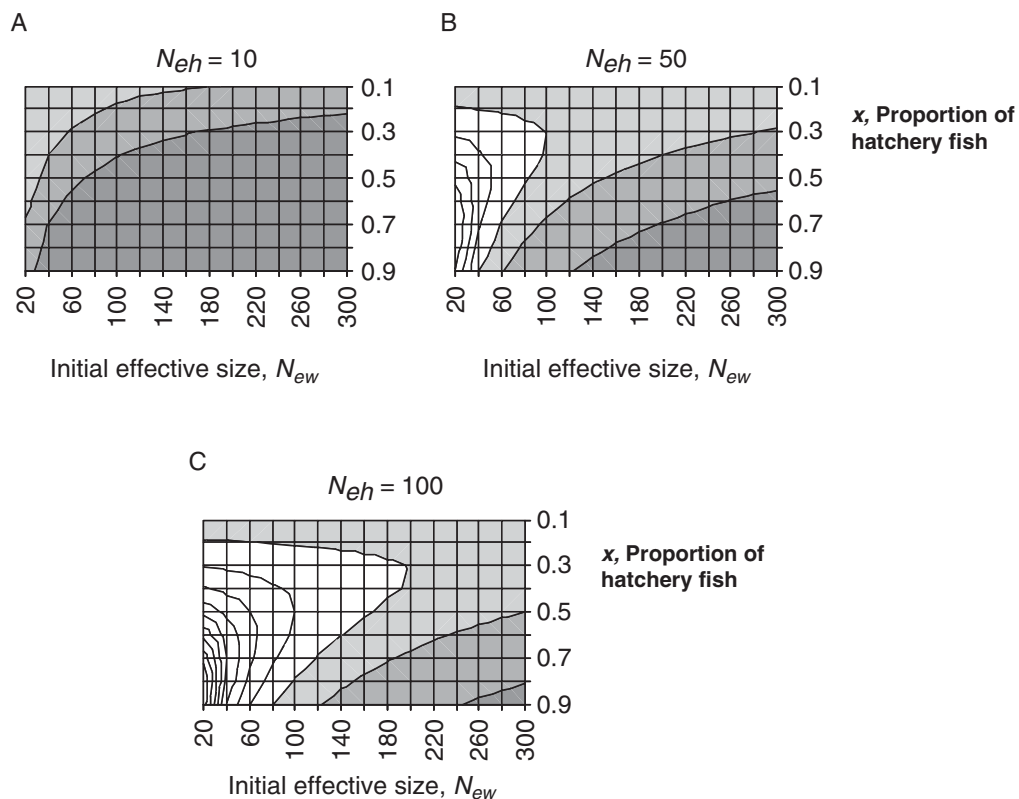
Figure 2.19 Proportional change in the effective population size of a supplemented population (N_{es}), following a single release of a hatchery population of varying effective sizes (N_{eh}). Shaded areas represent decreases in the effective size of the supplemented population. Each contour line represents a proportional increase or decrease by a factor of 2. Based on approaches developed by Ryman and Laikre (1991) and Hedgecock and Coykendall (2007) where $N_{es} = (N_{eh}N_{ew})/(x^2 N_{ew} + y^2 N_{eh})$, and N_{ew} is the effective size of the wild population prior to supplementation, x is the relative proportion of hatchery-origin fish, y of wild fish, and $x + y = 1.0$.

equal chance of reproducing successfully, but many studies have shown that this is not the case. The approach also assumes that the numbers of progeny from captive or wild fish are distributed binomially, and that there are no overlapping generations. This model has been further developed, taking many of these caveats into account, and the newer models will be discussed in a later section. The central point to be made from this model, however, is that attempts to increase the growth rate of a population may be detrimental to the genetic diversity of a population if few individuals are used to recover that population (Ryman and Laikre, 1991).

5.1.1.2.2. Hybridization and outbreeding depression   The impacts of hatchery releases may be limited to a change in effective population size if the hatchery stock is genetically identical to the wild population with which it interacts. However, if genetic variation in hatchery stocks changes following inbreeding or domestication selection, or if hatchery fish are exogenous to the wild system, then hybridization between the cultivated fish and the wild fish may have unintended consequences. Hybridization between unrelated populations can lead to a reduction in fitness, known as outbreeding depression. Outbreeding depression has been attributed to two mechanisms, each of which can have different long-term consequences.

First, outbreeding depression can result from a loss of local adaptation (known as ecological outbreeding depression). Populations can become adapted to a specific environment following selection. Such 'local adaptation' is extensive in the salmonids (Allendorf and Waples, 1996; Taylor, 1991; Waples *et al.*, 2001), and there is substantial concern that hybridization will result in its loss (Allendorf and Waples, 1996; Busack and Currens, 1995). If individuals from unrelated populations mate, hybrids have only half the 'adapted' alleles in either parental environment and are not as fit as the parental populations. This reduction in fitness is often seen in the first (F1) hybrid generation. Second, outbreeding depression may follow a disruption of interactions between co-adapted genetic loci underlying fitness traits (known as physiological outbreeding depression). These epistatic interactions can arise either through selection, which can act concurrently on genes that are inherited together, or through chance associations (Lynch and Walsh, 1998; Templeton, 1986). Significantly, co-adapted gene complexes can differ between populations occupying similar environments, and recombination between divergent genomes can disrupt such complexes. Typically, hybrid vigour (heterosis) observed in the F1 hybrids is a poor indicator of the performance of subsequent generations (Lynch and Walsh, 1998) because recombination between the parental chromosomes occurs for the first time in this generation.

It has been hypothesized that the underlying mechanisms for outbreeding depression will have different outcomes for hybrid populations. Simulations have shown that a disturbance of local adaptation results in a greater initial

fitness decline than a disruption of co-adapted gene complexes (Edmands and Timmerman, 2003). However, the simulation results differ over the long term. Much of the genetic variation explaining local adaptation is additive and provides a better opportunity for population recovery through selection than does the epistatic variation that results from co-adapted gene complexes. Epistatic variation arises through genetic drift and indirect selection (Lynch and Walsh, 1998).

The severity of outbreeding depression is expected to change with a number of parameters and there is a considerable body of literature investigating whether such parameters can be used to predict the outcomes of hybridization. For example, the incidence of outbreeding depression is expected to increase with greater genetic distance between hybridizing taxa (Emlen, 1991; Lynch, 1991). This prediction is true across a wide range of species, but not in others (Edmands, 2002). Declines in fitness may depend on prevailing environmental conditions (Lynch, 1991). These environments may fluctuate temporally and results may vary accordingly (Gharrett et al., 1999; Gilk et al., 2004). Most studies investigating the consequences of hybridization are on first generation hybrids only, but outbreeding depression can be expected to vary across generations (Edmands and Timmerman, 2003). Thus, fitness increases in first-generation hybrids are not necessarily repeated in the second generation (Fenster and Galloway, 2000), and population recovery can vary (Edmands and Timmerman, 2003; Templeton, 1986). Finally, the expression of outbreeding depression differs across fitness traits (Andersen et al., 2002).

A meta-analysis on several studies in fishes has shown that the outcomes of hybridization are difficult to predict (McClelland and Naish, 2007). Response varies across traits, taxon and generation but, significantly, genetic distance based on neutral genetic markers cannot be used reliably as an indicator of the incidence of outbreeding depression. Such an outcome can be explained by the unpredictable nature of the different mechanisms underlying outbreeding depression (Lynch and Walsh, 1998), but also by the fact that a measure of genetic distance at fitness traits may be more appropriate for this task (McClelland and Naish, 2007). In a recent review, Utter (2001) proposed that the *complexity* of life history might be a better predictor of outbreeding depression because introgression is more likely in freshwater than in anadromous salmonids, and hybrids of the latter may be less likely to survive.

In salmonid fishes, both increases and decreases in fitness have been observed in the F1 generation. Decreases have been observed in pink salmon homing ability (Bams, 1976), disease resistance in coho salmon (Hemmingsen et al., 1986), salinity tolerance in kokanee hybrids (Foote et al., 1992), growth rate in coho salmon (McClelland et al., 2005; Tymchuck et al., 2006) and rainbow trout (Tymchuck and Devlin, 2005) and development rate in coho (Granath et al., 2004). However, such

decreases were not seen in the F1 of pink salmon (Gharrett and Smoker, 1991; Gharrett *et al.*, 1999).

A few studies have followed outbred populations through to the F2 or subsequent generations (McClelland and Naish, 2007), and individual case studies have shown a continuation in reduced fitness in these generations (McClelland *et al.*, 2005; McGinnity *et al.*, 2003; Tymchuck and Devlin, 2005; Tymchuck *et al.*, 2006). In all of these examples, fitness loss was attributed to genetic mechanisms underlying ecological outbreeding depression. However, it is the systematic treatment of hybridization over varying evolutionary distances that will provide researchers with the ability to predict the genetic outcomes of mixing populations. In a series of experiments on pink salmon populations, researchers in Alaska have per-formed crosses between populations of varying genetic distance with the intent of detecting the point at which outbreeding depression will no longer be demonstrable. At one extreme, reproductively isolated pink salmon returning strictly in either the odd or the even years were crossed and released. The survival of their F1 hybrids in the wild was comparable to the controls (Gharrett and Smoker, 1991; Gharrett *et al.*, 1999), but the F2 hybrid survival rate was severely depressed (Gharrett *et al.*, 1999). In this case, outbreeding depression was attributed to a breakdown in co-adapted gene complexes, which is perhaps not surprising. The odd and even year pink salmon return to similar habitats and any genetic differences that accumulate between them must be due, in large part, to genetic drift. In contrast, a second experiment has demonstrated that the second mecha-nism underlying outbreeding depression is loss of local adaptation. Pink salmon from the same year class that were spatially separated by about 1000 km were hybridized and both the F1 and F2 generations exhibited outbreeding depression (Gilk *et al.*, 2004). In contrast to these findings, coho salmon spawning populations separated over spatial distances of 130–340 km and displaying different development rates showed no change in fitness over two generations following hybridization (Smoker *et al.*, 2004), although the authors point out that the power of the data may not have been sufficient to detect outbreeding depression.

These experiments serve to illustrate the potential outcomes of hybri-dizing unrelated populations, but are most useful when they are systematic in nature. The continuation of experiments such as those conducted on pink salmon over different distances will provide a very interesting insight into whether evolutionary distance can be used as a predictor of the potential for outbreeding depression within a single anadromous salmonid species, a point relevant to effective management.

5.1.1.2.3. Population structure   Increasingly, attention is being paid on the effects of hatchery releases on metapopulation structure of a wild population (Utter, 2004; Ward, 2006). Hatchery activity may affect

population structure through two means: by transfers between different locations and by continued release of hatchery fish. For example, Vasemägi *et al.* (2005) demonstrated that ongoing releases of non-indigenous Atlantic salmon resulted in homogenization of population structure of wild fish over time. The impact of the *number* of fish transferred and released on population structure has not been frequently reported, and yet an understanding of this relationship is important for risk assessments. In coho salmon, it has been shown that the number of fish transferred might reduce population structuring, even between closely related populations (Eldridge and Naish, 2007). More importantly, the numbers of fish released from hatchery programmes that collect broodstock locally resulted in a reduction in fine scale population structure in this species (Eldridge and Naish, 2007), a finding that has clear implications for ongoing hatchery programmes. Population structure reflects evolutionary processes, some of which lead to local adaptation, and levels of migration between neighbouring populations are related to the long-term genetic viability of a species as a whole (Waples, 2002). The greater the spatial diversity of a species, the more likely that species will exhibit resilience to extinction risk (McElhany *et al.*, 2000). Ongoing hatchery programmes may need to control the size of their release and numbers of fish transferred between programmes in order to reduce their impact on this resiliency.

5.1.2. Evidence for the genetic impacts of different types of hatchery programmes

In an interesting evaluation of the genetic risks associated with hatchery practises, Campton (1995) raised two key points that are often ignored when evaluating whether hatchery fish can be effectively used as a management tool for conservation or harvest. First, most studies fail to discriminate between the underlying biological or management-based causes of any detrimental effects. In the years between Campton's and this chapter, this distinction has rarely been elucidated. Second, there is a paucity of data providing a clear understanding of the biological causes of such effects. In Section 5.1.2, we examine the evidence for the genetic outcomes of hatchery practises in the context of hatchery type and programme goals, the risks associated with such goals and the evidence, if any, for impacts that may be attributed to biological effects rather than to management effects.

5.1.2.1. Captive broodstock   The greatest genetic risks associated with the maintenance of an entirely captive broodstock in culture over long periods of time are the loss of within-population genetic diversity and domestication selection. Losses due to genetic drift may be avoided by maintaining high N_e/N_c ratios and inbreeding can be reduced for as long as possible by maintaining pedigrees and minimizing kinship during mating (Rodriguez-Clark, 1999). In very small populations, selection theoretically becomes

almost negligible (unless the selection differential is very high), and some authors have suggested that captive endangered populations be managed as fragmented subpopulations in different rearing facilities in order to avoid domestication selection (Margan *et al.*, 1998). This strategy is risky because significant reductions can be incurred if subpopulations are lost and to date, the approach has been supported empirically in experimental populations of fruit flies only (Woodworth *et al.*, 2002). Perhaps some of the best management steps that can be taken to avoid domestication selection in a captive broodstock are the reduction of the number of generations held in captivity (initiating reintroduction as soon as possible), and decreasing selection differentials between hatchery and wild environments as far as possible.

The scientific community has started to accumulate evidence on the consequences of genetic drift, inbreeding and domestication selection in captive salmon populations, but there are few studies that examine the effectiveness of management steps in mitigating these risks in fishes, let alone salmonids. For example, studies comparing modern to archival samples, such as that conducted on captive Atlantic salmon in the Baltic region (Saisa *et al.*, 2003), demonstrate that long-term programmes have resulted in reduced genetic diversity and effective sizes. However, the extent to which such losses could have been avoided through careful management has not been determined, especially since our awareness of the risks has post-dated the initiation of such programmes. Realistically, the mating of relatives (and hence inbreeding) is inevitable in a closed system despite the best measures (Myers *et al.*, 2001). An inbreeding rate of around 1% is generally deemed acceptable in benign agricultural environments (Franklin, 1980), but this tenet has yet to be tested in salmonids that will eventually be released to the wild.

5.1.2.2. Supportive breeding through supportive breeding   The goal of many conservation-oriented hatcheries is to support declining populations and, thus, most seek to enhance numbers without compromising the genetic diversity of the wild populations. This goal may be difficult to attain because a change associated with broodstock collection and release is probably inevitable (Waples, 1999). Supplementation hatcheries face similar challenges as those described for captive broodstock, but have an advantage in some cases. Many genetic changes such as inbreeding and domestication selection can be theoretically reduced by replenishment from the wild populations, and many recommendations focus on this practise (e.g., Mobrand *et al.*, 2005). However, these programmes may also have a major disadvantage: through their practises, they could alter the genetic composition of the wild stocks with which they interact. This alteration may occur through a change in effective population size, homogenization of locally adapted stocks or through outbreeding depression, and can affect the ability of the vulnerable populations to adapt to a changing environment.

Systematic treatment of the genetic effects of supportive breeding has only occurred through theoretical modelling. Earlier, we described how a single generation of supplementation could result in a decrease in the effective population size of a wild population, even if supplementation leads to an overall increase in the census size (the Ryman–Laikre effect). This first model was important in alerting managers to an important risk associated with supportive breeding, but examined the outcomes of supplementation over a single generation only. Supportive breeding programmes are usually carried out over several generations and are typically considered successful if the programme results in a viable, self-sustaining population.

In a series of modelling exercises, a number of authors have examined the genetic impacts of supplementation under different management and demographic scenarios. The approaches used can be divided into two groups: one focused on effective size or inbreeding and the related effects on drift (Duchesne and Bernatchez, 2002; Wang and Ryman, 2001; Waples and Do, 1994), and the other on measures related to fitness differences between the two components of the population (Ford, 2002; Lynch and O'Hely, 2001; Theodorou and Couvet, 2004). All models were based on several necessary assumptions and attempted to identify the conditions under which supplementation programmes are detrimental or beneficial to vulnerable wild populations. Both groups have implicit links to the other, but an integrated model that addresses the effects of both drift and domestication (or relaxation of selection) has yet to be developed.

All of the studies demonstrated conditions under which supplementation would be negative. For example, Waples and Do (1994) showed that if a small number of breeders were used in a hatchery, an 'inbreeding crash' would result in the wild population after the cessation of an unsuccessful programme. The relaxation of selection in a hatchery may lead to the accumulation of deleterious mutations through drift (Lynch and O'Hely, 2001), which may in turn compromise any numerical gains in the population. A wild population's mean phenotype can rapidly change towards that of a captive population (Ford, 2002) even when migration between the two is small.

Several management steps such as increasing the N_e of the hatchery population may reduce genetic risks associated with releases, but some theory has shown that this benefit is realized only if the census size of the entire population increases (Wang and Ryman, 2001) or if the contribution of captive populations is moderated (Theodorou and Couvet, 2004). The rate of inbreeding could be reduced if N_e/N_c ratios were high in the hatchery population (Waples and Do, 1994). Steps such as increasing the migration rate between the hatchery and wild stocks through broodstock replenishment from the wild have the advantage of reducing negative genetic changes (Duchesne and Bernatchez, 2002; Ford, 2002; Wang and Ryman 2001), but the outcomes of using exclusively wild fish for

broodstock are complex and depend on the scenarios modelled (Duchesne and Bernatchez, 2002; Wang and Ryman, 2001).

Many models point towards an optimal programme duration. At the initiation of a program, supplementation could be detrimental to the N_e of the wild population because the initial demographic effect of sampling wild individuals to create a broodstock may be negative, and must be compensated for by several generations of support (Duchesne and Bernatchez, 2002; Wang and Ryman, 2001). On the other hand, all the studies caution that supportive breeding programmes may not be genetically beneficial in the long term in many situations. For example, in the selection model of Ford (2002), it was demonstrated that a shift in a wild population's phenotype can still occur within 50 generations in some scenarios modelled, even if hatchery broodstock comprise natural spawners, and that outcomes may depend in part on population growth rate and carrying capacity in the native environment.

Perhaps the strongest message derived from a reading of these six studies is that the outcomes of supplementation are difficult to predict and may be programme-specific [an examination of the scenarios modelled by Duchesne and Bernatchez (2002) supports this view]. Although some broad conclusions could be drawn, each study has caveats even if the model assumptions are correct. Thus, strong emphasis must be placed on monitoring changes in genetic diversity very closely and in developing meaningful performance measures for hatchery programmes.

Little empirical proof supports theoretical predictions of the outcome of management practises, partly because most of this theory is very recent, and many supplementation hatcheries have existed for longer than our awareness of the genetic risks involved. However, several case studies support theoretical predictions; namely, that genetic diversity can be maintained or reduced by hatchery founder numbers (Primmer *et al.*, 1999), sex ratios at mating (Tessier *et al.*, 1997), hatchery population size (Hansen *et al.*, 2000) and effective population size of released hatchery fish (Eldridge and Killebrew, 2007; Hedrick *et al.*, 2000; Tessier *et al.*, 1997). Heggenes *et al.* (2006) reported that measures of neutral genetic variation and population structure did not significantly change after 20 years of supportive breeding, an outcome attributed to the use of overlapping year classes and frequent integration of wild fish into the broodstock. On the other hand, some studies do not fit predictions. In Sweden, a hatchery population of sea trout received no new broodstock from its source wild populations for approximately seven generations (Palm *et al.*, 2003), but was used to supplement the wild populations, thereby creating unidirectional gene flow. Effective population size was high in the captive population and, while small genetic differences were seen between both captive and wild fish on a yearly basis, these differences were outweighed by temporal variation (Palm *et al.*, 2003). The hatchery stock used in this study was the same

population that showed little sign of domestication selection described earlier (Dannewitz *et al.*, 2003).

Studies on stray rates from supplementation hatcheries are rare and the extents to which fish from such programmes interbreed with wild fish are unknown. There are several examples of close genetic relationships between locally derived hatchery fish and their wild counterparts (e.g., Hansen *et al.*, 2000; Primmer *et al.*, 1999) and one case in which a wild Chinook population in the Columbia River appears to have maintained its integrity in the face of supplementation in nearby rivers (Marshall *et al.*, 2000). In contrast, Williamson and May (2005) suggested that releases of supplementation hatchery fish in areas that do not correspond to their natal spawning grounds have led to reduced imprinting and widespread straying and homogenization of Chinook populations in California.

A key question relevant to evaluating the potential risks and benefits of supportive breeding is whether hatchery fish are as fit as their wild counterparts and whether they may effectively contribute to conservation efforts (Berejikian and Ford, 2004; ISAB, 2002). Two studies based on measuring the reproductive success of locally derived hatchery fish provide some information on their relative lifetime fitness over the short term. Locally derived coho salmon (Ford *et al.*, 2006) and steelhead (Araki *et al.*, 2007) reared in a hatchery to the smolt stage and released were as successful reproducing in the wild as naturally produced wild fish. These results provide a clear contrast with the reduced reproductive success of exogenous, domesticated Atlantic salmon (aquaculture escapees; McGinnity *et al.*, 1997, 2003) and steelhead (Araki *et al.*, 2007) that have been propagated over several generations. While both studies on the locally derived broodstock provide a somewhat optimistic outlook for conservation programmes, there are caveats attached to both. Ford *et al.* (2006) pointed out that their study was performed on a system which had experienced hatchery releases for over 60 years, and the naturally produced fish were themselves likely propagated in a hatchery in the previous one or two generations. Araki *et al.* (2007) reported that hatchery fish reproducing with each other in the wild produced fewer offspring than expected, which has implications for cumulative fitness losses over several generations of propagation. Both studies emphasize that the long-term effects of supportive breeding programmes are still unknown.

Returning to our stated aim of evaluating whether negative biological effects can be avoided by correct management practises, we conclude that there is insufficient empirical data available, although recent studies on relative fitness of locally derived hatchery fish provide some insight on their possible contribution to conservation efforts, and should be replicated and continued over several generations. The theoretical information has demonstrated that there are scenarios under which correctly managed hatcheries may benefit declining populations, and empirical studies should

be carried out within the framework of this theory. However, it is quite clear there are few general statements that are applicable to supportive breeding programmes. Theory has shown that the 'window of opportunity' for rehabilitating populations may be limited to short time periods, and practically, programmes must be accurately monitored to avoid negative effects. The permanent use of conservation-based hatcheries may be risky, since there appear to be substantial genetic risks associated with the failure to sustain large and genetically diverse populations. The maintenance of such hatcheries therefore depends on risk trade-offs that necessarily relies on clear dialogue between science and policy (Waples and Drake, 2005).

5.1.2.3. *Production hatcheries in the presence of wild stocks*   The typical production hatchery practise of releasing a closed, and at least partially domesticated, population for harvest opportunity can result in introgression. Introgression may, in turn, lead to a change in the mean phenotype towards that of the hatchery fish, to outbreeding depression and to complete displacement of the wild population.

Although the effects of production hatcheries on wild fish have not been explicitly modelled, many of the theoretical treatments examined above provide insight on the outcomes of such programmes. If a closed, captive population makes a large contribution to the breeding pool, genetic load may increase substantially over the long term (Lynch and O'Hely, 2001; Theodorou and Couvet, 2004), but even low levels of gene flow from the hatchery to the wild populations can move the optimal wild phenotype towards that of the hatchery fish (Ford, 2002). None of the theoretical studies explicitly model the use of exogenous and domesticated stocks that have been typically used in production hatcheries. Some recent empirical evidence for the outcomes of releasing hatchery fish are summarized in Table 2.2, but few general trends can be inferred from the systems studied because release numbers, duration of releases and broodstock management have been poorly documented. Hatchery releases pre-date any concerted scientific studies and in many cases in Europe stocking has been practised for 150 years or more (Berrebi *et al.*, 2000a; Laikre, 1999).

There is extensive evidence that hatchery–wild hybrids from production hatcheries are less fit than wild fish (Table 2.2) and rates of introgression vary with life history strategies. For example, studies in brown trout indicate that introgression rates are higher in resident than anadromous forms. The more complex life history of the anadromous forms probably precludes completion of the life cycle (Ruzzante *et al.*, 2004). In a review paper, Utter (2001) noted that anadromous fish from different evolutionary lineages are less likely to hybridize with each other than those within lineages. In support of this view, Ford *et al.* (2004) reported that introduced coho populations from Washington State did not appear to persist in Oregon, whereas transfers between closely related populations appear to have affected population

Table 2.2 Summary of genetic effects of hatchery fish on wild fish, categorized by source of hatchery fish and species

Species and life history	Region	Outcome	Study
Exogenous source of hatchery fish			
S. trutta, anadromous	Denmark	Reduction in fine-scale population structure, level of introgression correlated with intensity of release activity	Fritzner *et al.*, 2001; Ruzzante *et al.*, 2001
		Low incidence of released fish. Hatchery fish provided little harvest opportunity for the anadromous population, but introgressed with the resident forms	Hansen, 2002; Hansen *et al.*, 2002
		Decline in incidence of domesticated fish following cessation of releases	Fritzner *et al.*, 2001; Ruzzante *et al.*, 2004
	Norway	Mortality of hatchery fish at early life history stages was higher than wild fish, may reduce incidence of introgression	Borgstrom *et al.*, 2002
S. trutta, resident	Norway	Hatchery fish hybridized with wild fish, but survival of hybrids was lower than wild	Skaala *et al.*, 1996
		Little impact of hatchery on wild fish population structure, despite 40 years of stocking	Heggenes *et al.*, 2002
	Spain	Extensive introgression in all populations studied, reduction of population structure	Cagigas *et al.*, 1999; Garcia–Marin *et al.*, 1998; Machordom *et al.*, 1999, 2000

(continued)

Table 2.2 (*continued*)

Species and life history	Region	Outcome	Study
		Release of hatchery fish did not improve population size	Machordom *et al.*, 1999
		Straying of hatchery fish from areas that received releases versus ones that did not. Hatchery genotypes persisted after cessation of releases	Cagigas *et al.*, 1999
		Lower incidence of introgression in harvested regions than in protected areas	Garcia-Marin *et al.*, 1998, 1999
		Decline in alleles of domesticated origin 7 years after cessation of releases	Almodovar *et al.*, 2001
	France	Some selection against hatchery fish, but cessation of releases for 6 years did not lead to recovery of wild genotypes	Poteaux *et al.*, 1998a,b
		Levels of introgression varied with intensity of release activity	Aurelle *et al.*, 1999; Poteaux *et al.*, 2000
		Incidence of introgression was small annually, but accumulation of hybrid genotypes increased over time. Incorporation of locally derived broodstock may have maintained population variation	Berrebi *et al.*, 2000a

	Switzerland	Introduction of domesticated strain reduced reproductive barriers between two indigenous forms	Largiader and Scholl, 1995
		Degree of admixture was site specific and may be linked to management actions—intensity of release activity and fishing	Largiader and Scholl, 1996; Mezzera and Largiader, 2001a; Mezzera and Largiader, 2001b
		Hybrids between hatchery and wild fish were less fit than wild fish, mortality of hybrids greater between age 1+ and 2+. Hybrids were more vulnerable to fishing	Mezzera and Largiader, 2001a,b
	Italy	Reduction in genetic diversity and structure, replacement of wild subspecies with hatchery fish	Marzano *et al.*, 2003
S. salar, anadromous	North America, east coast	Evidence that past release activities reduced stock structure in some drainage systems	King *et al.*, 2001
	Denmark	Translocations or hatchery releases have had little effect on long-term population structure	Nielsen *et al.*, 1999
	Estonia	Release of hatchery fish compromised recolonization of restored habitat by indigenous populations	Vasemägi *et al.*, 2001
O. mykiss, anadromous	United States, west coast	Increased straying by non-native hatchery fish	Schroeder *et al.*, 2001

Table 2.2 (*continued*)

Species and life history	Region	Outcome	Study
		Hatchery females had lower reproductive success than wild fish	Kostow *et al.*, 2003
		Introduced summer run hatchery fish hybridized with indigenous winter run populations	Mackey *et al.*, 2001; Kostow *et al.*, 2003
		Hatchery fish were more abundant on spawning grounds and produced more offspring, despite lower reproductive success	Kostow *et al.*, 2003
O. mykiss, resident	United States, west coast	Introgression led to a reduction in disease resistance in indigenous population	Currens *et al.*, 1997
O. clarkii, resident	United States, west coast	Rainbow trout/cutthroat trout hybrids were difficult to detect in generations later than the F1 in the wild, provided a mechanism for undetected introgression	Campbell *et al.*, 2002
O. tshawytscha, anadromous	United States, west coast	Population structure persisted, despite extensive hatchery releases	Utter *et al.*, 1995
Salvelinus umbla, resident	European Alps	Extent of introgression was small and varied across environments	Brunner *et al.*, 1998
		Higher introgression of hatchery fish in a lake disturbed by pollution than one that remained undisturbed	Englbrecht *et al.*, 2002
Salvelinus nyamacush, resident	United States, southeast	Extent of introgression with non-native northern form varied from replacement to	

		no detectable hybridization. Erosion of population structure, level of introgression not related to intensity of release activity	Galbreath *et al.*, 2001; Hayes *et al.*, 1996;
Endogenous source of hatchery fish			
S. trutta, anaromous	Poland	Reduction in genetic diversity within hatchery stocks	Was and Wenne, 2003
S. salar, anadromous	Ireland	No differences in survivorship observed between hatchery and wild fry at 18 months	Crozier and Moffett, 1995
		Locally derived hatchery fish exhibited similar return numbers but different life history. Translocated population from neighbouring drainage had lower return rates	McGinnity *et al.*, 2004
O. tshawytscha, anadromous	New Zealand	Significant changes observed in male life history characters and in return timing. Population was introduced from California	Unwin and Glova, 1997
O. gorbuschi, anadromous	Alaska	Hatchery derived from local broodstock appeared to have no affect on wild population structure in the same locality	Seeb *et al.*, 1999

structure in the same species (Eldridge and Naish, 2007). The incidence of hybridization within freshwater salmonids appears to vary greatly (Table 2.2). Hybridization between hatchery and wild fish can be extensive and detrimental (Cagigas *et al.*, 1999; Garcia-Marin *et al.*, 1998), with little benefit to the population size (Machordom *et al.*, 1999). On the other hand, descendants of hatchery fish may be undetectable even after a long period of hatchery releases (Heggenes *et al.*, 2002). Many studies report greater introgression with higher release numbers (Aurelle *et al.*, 1999; Mezzera and Largiader, 2001a), but others did not (Hayes *et al.*, 1996). Some authors observed a decline in hybrid genotypes after releases are stopped (Almodovar *et al.*, 2001), but these genotypes persisted in other areas (Poteaux *et al.*, 1998a). There is also some evidence that the incidence of hybridization may be environmentally or ecologically dependent. Arctic charr (*Salvelinus umbla*) released into an undisturbed lake in the Alps were less successful at becoming established than those released into a historically polluted one (Englbrecht *et al.*, 2002).

Management strategies for production hatcheries have been proposed in order to avoid the negative impacts of hatchery fish on wild populations (ISAB, 2002; Mobrand *et al.*, 2005; Utter, 2004). Utter (2004) has suggested that the domestication of hatchery broodstock can be expected to lead to substantially reduced fitness of hatchery fish in the wild. The release of such stocks may be beneficial under management scenarios that are aimed at deliberately segregating hatchery and wild fish, because reduced fitness of hatchery fish would minimize concerns about the impacts of colonization and hybridization. There is not yet sufficient data to determine whether this is a viable strategy; while many studies report hybridization between less-adapted hatchery and wild fish (Table 2.2), there have been few concerted efforts at deliberately domesticating 'maladapted' hatchery fish for segregated programmes and tracing their reproductive success in the wild. There are some existing approaches that may support this goal, however. For example, certain steelhead production hatcheries in the United States have introduced non-native populations that differ in their run timing and spawn timing from indigenous populations. While the effects of these programmes have not yet been fully characterized, it appears that the life histories of the hatchery fish may change in response to the new environment and in some examples, return timing and spatial distribution have been seen to overlap with that of the wild fish (Mackey *et al.*, 2001), making introgression with wild individuals possible, but in one case, limited (Kostow, 2004). Cutthroat trout (*O. clarki*) are deliberately hybridized with rainbow trout (*O. mykiss*) because the hybrids can be identified from the parental species phenotypically and can be targeted by anglers. However, hybrid individuals of generations later than the F1 cannot be reliably identified and hence escape capture, leading to ongoing inter-specific introgression (Campbell *et al.*, 2002). Segregation can be controlled, to some extent,

by complete harvest of the hatchery population. Brown trout hatchery fish in one study appear to be more susceptible to angling (Poteaux *et al.*, 1998a), and a review of programmes in Spain showed that there are lower levels of introgression in harvested than protected regions (Garcia-Marin *et al.*, 1998). However, such an approach relies on efficiency of capture.

Given these caveats, Mobrand *et al.* (2005) have recommended that an alternative strategy could be considered, the integration of hatchery fish and wild fish. Fish surplus to the maintenance of the wild population may be harvested. The use of endogenous sources of broodstock for production hatcheries has both positive and negative aspects. Using native stocks may reduce losses associated with the production of less fit hybrid individuals typical of exogenous fish releases. For example, a pink salmon hatchery using locally derived broodstock appeared to have had little effect on the population structure of indigenous wild populations (Seeb *et al.*, 1999). A second hatchery collects broodstock migrating into PWS destined for different regions, and the hatchery fish released comprised a mixture of stocks with greater potential to affect local populations. On the other hand, it may also be argued that exogenous fish are more likely to be purged from a wild population, especially if a programme is terminated. There is also some evidence for change in life histories, even when endogenous fish have been used and fish have been reared for part of their life cycle in the hatchery (McGinnity *et al.*, 2004) sometimes causing a subsequent shift in such traits in the wild population (Unwin and Glova, 1997). Finally, theoretical approaches have shown that long-term integration between hatchery and wild stocks is not always a sustainable strategy, which is further exacerbated if that stock is subject to harvest (Goodman, 2005). These studies emphasize the need for further research on the impact of broodstock management and release.

In summary, published studies show that production hatcheries have been detrimental to local wild populations where the two populations interact, although there are many examples where distantly related popula–tions do not appear to have persisted. It should be noted that many genetic studies have focused primarily on reporting levels of introgression only, and results are rarely correlated with the size of release. It is also possible that less fit hybrid individuals may have reduced the overall effective population size and structure of wild fish, thus causing changes in the life history of wild populations, and this aspect should also be studied in greater depth. It is still difficult to ascribe outcomes of production hatcheries to manage-ment or biological causes. Management strategies for production hatcheries advanced thus far would be to maintain the hatchery and wild fish as separate populations (Mobrand *et al.*, 2005; Utter, 2004), or to integrate hatchery and wild populations (Mobrand *et al.*, 2005), but the efficacy of these approaches over the long term has yet to be demonstrated empirically.

5.1.2.4. Introduced species   The greatest genetic risk associated with the introduction of a new salmon species to a habitat is hybridization with native indigenous populations. Hybridization in this case has three primary genetic outcomes: introgression, repeated introgression leading to hybrid swarms in which neither of the parental genotypes persist, or sterility and hence lost reproductive potential (Allendorf *et al.*, 2001; Leary *et al.*, 1995).

Hybrids of brown trout and Atlantic salmon tend to be unidirectional and may compromise one species through introgression, but not the other (Garcia-Vazquez *et al.*, 2004; McGowan and Davidson, 1992). Hatchery releases have led to hybridization between these two species (Jansson and Oest, 1997), and although outside the realm of this chapter, has increased following escapes from salmon farms in Europe (Matthews *et al.*, 2000). The widespread introduction of rainbow trout for angling has threatened the genetic integrity of many western freshwater species in North America (Leary *et al.*, 1995; Scribner *et al.*, 2000). For example, rainbow trout form fertile hybrids with cutthroat trout (Allendorf and Leary, 1988) and introgression can be greater in regions of hatchery introduction than in areas where the two species co-occur naturally (Docker *et al.*, 2003). Many populations have been replaced by hybrid swarms (Allendorf and Leary, 1988; Williams *et al.*, 1996), which are of no evolutionary or conservation value (Allendorf *et al.*, 2001). Similar results have been recorded in Europe, for example, in areas where brown trout have been introduced to marble trout (*S. marmoratus*) habitats (Berrebi *et al.*, 2000b). Interactions between native bull trout (*Salvelinus confluentus*) and introduced brook trout (*Salvelinus fontinalis*) result in unidirectional hybridization (Kanda *et al.*, 2002), and reproductive effort is substantially compromised in the former species because bull trout tend to be the maternal contributor. The majority of fish are F1 hybrids, with very few backcrosses detected (Kanda *et al.*, 2002). Therefore, bull trout populations are demographically compromised by the reduced reproductive output following the introduction of brook trout for fishing purposes. Finally, the introduction of a new species for harvest opportunity may also have indirect genetic effects on native populations through competition and restriction of the ranges of native populations.

5.1.3. Can management practises negate genetic impacts?

To summarize this section of the chapter, we evaluate whether the current state of knowledge provides guidance on management steps that may be taken to reduce the genetic risks associated with different salmon hatchery programmes. In the decade since Campton (1995) noted that distinction between management and biological risks were rarely elucidated, the majority of research has shown that hatcheries can affect genetic diversity within hatchery populations, and that interactions between hatchery and wild populations can be detrimental. However, a growing number of studies have shown that specific steps in broodstock management have led

to both negative and positive outcomes. In recent years, a shift in the research is beginning to move from reporting problems associated with individual case studies towards researching possible solutions, driven in part, by attempts to reform hatchery practises. A key need in this area, therefore, is the development of a strong understanding of the *degree* to which specific activities pose a risk and whether proposed management approaches are effective at reducing these risks.

If we consider the diverse biological outcomes of hatchery rearing, there are still a significant number of unanswered questions. Accumulating evidence has shown that inbreeding in salmonids leads to fitness declines, and these declines vary by the trait measured. However, the relationship between inbreeding and the point at which inbreeding depression becomes manifest is still unclear. In other words, at what population sizes and generation can we expect a decline in fitness due to inbreeding? The answer is unlikely to be simple and can be extended to exploring how the incidence of inbreeding depression is related to historical inbreeding levels, to different wild environments, to life history strategy and to rate of inbreeding. The related management questions would therefore be concerned with developing strategies to both avoid and recover a population from suffering inbreeding depression.

Domestication selection remains a controversial topic, and research thus far has been directed at describing individual case studies that provide evidence of this phenomenon. Measuring the *magnitude* and *direction* of domestication selection under different selection regimes typical of hatcheries, and testing whether the genetic outcomes are reversible if selection is relaxed, is necessary. Research relevant to management should be directed towards evaluating strategies to reduce the magnitude of domestication selection by integrating wild individuals into the broodstock, as well as understanding the relationship between selection and population size and generation number in order to gain an understanding of the duration over which hatchery programmes should be maintained.

Theoretical treatments of the demographic and fitness effects of hatchery releases on the genetic variation and effective population size of wild populations have proved very informative and have illustrated the potential of various management approaches. It is important to provide empirical support of steps aimed at maximizing effective size and reducing demographic effects of releases on the wild populations. Systematic approaches are ambitious and long-term, but can be accommodated by close monitoring of a large range of existing hatchery programmes.

Fitness declines associated with outbreeding have been clearly demonstrated in a large number of studies. However, if a threatened population requires rehabilitation by the introduction of new broodstock, it is still unclear how closely related donor and recipient populations should be in order to avoid outbreeding depression. It appears that genetic distance may

prove an unreliable measure, but few studies have examined the relationship between measures of a range of evolutionary distances and the probability of outbreeding depression within a given salmonid species. Management-related research should be directed towards determining acceptable levels of introgression and understanding how evolutionary distances relate to these levels.

Many of these questions are difficult to answer, particularly because they require prolonged experimental periods and substantial support. We emphasize that hatchery-directed research has thus far focused on reporting the genetic outcomes of specific programmes, with only recent exploration of the relationship between these results and management actions. In our chapter [and that of Campton (1995)], we have found little evidence of this delineation and, unfortunately, little insight into whether research programmes are now being directed towards exploring this relationship. This weakness has been exploited by opposing viewpoints on whether hatchery fish should be permitted to spawn in the wild (Brannon *et al.,* 2004a; ISAB, 2002).

If we accept the likely outcome that hatchery programmes will persist, then two general research directions should be implemented in order to provide practical management advice. The first should focus on developing a clear understanding of the relationship between genetic risks involved in hatchery releases, and steps to reduce these risks, even if these experiments are expected to take place over several generations. Most hatcheries have been established without research programmes, and a strong emphasis should be placed on devoting at least a portion of the rearing space to experimental releases. It is only by directly comparing a network of experiments in hatcheries with similar goals that many of the risks and management approaches may be quantified. The second direction should focus on developing a risk averse approach to management, as advocated by Waples (1991, 1999), which implements strict monitoring protocols. These protocols should track fitness changes in hatchery and wild populations using a mixture of approaches. Such data could also contribute significantly to a large meta-analysis that would allow evaluation of the genetic risks posed by releasing cultured fish into the wild. Hatchery programmes have existed for many decades, yet surprisingly, a large programmatic approach to answering many outstanding questions about genetic risks and remedial management practises has yet to be executed. We strongly advocate such research.

Finally, it is important at this point to raise the social context in which research in this discipline is conducted. Waples (1999) and Waples and Drake (2005) pointed out that genetic changes associated with hatcheries are inevitable. Research will likely determine the genetic consequences of hatchery programmes, but societal values must be consulted to determine the degree to which these consequences are acceptable. Efforts to improve the interaction between the two are strongly encouraged.

5.2. Behavioural and ecological interactions between wild and hatchery-produced salmon

There are important implicit (though seldom explicit) assumptions of hatchery programmes regarding ecological and behavioural processes. Violation of these assumptions may result in lower than anticipated production either from the hatchery or from the region that includes hatchery and coexisting wild populations. First, it is assumed that the hatchery increases the abundance or survival of salmon populations during the life history stage that limits the wild population size and that subsequent stages are not limiting. Second, it is assumed that there are no significant interactions between wild and hatchery fish that would limit the enhancement effort. This section briefly reviews these issues, with emphasis on competition between wild and hatchery fish, and a brief consideration of predation.

5.2.1. Competition between wild and hatchery fish

The majority of lifetime mortality in salmonids generally takes place during the period from fertilization to emergence from the gravel several months later. Much of this mortality results from poor circulation of water or low dissolved oxygen concentration (often related to fine sediment), scour from flooding, desiccation or freezing and disturbance by the digging of other female salmon (Quinn, 2005). It has been known for well over a century that salmonid eggs and milt can be taken from adults, mixed and the embryos incubated with higher survival rates than commonly occur in nature [reviewed by Bottom (1997) and Lichatowich (1999); see also Section 2]. Early hatchery programmes were predicated on the assumption that increased number of fry released into the rivers would produce commensurate increases in adults. However, the extent to which this is true depends on the species involved. Almost all salmonid species characteristically emerge from stream gravels and rear for months or years in the stream before migrating to the sea, a lake or a larger river. The generally low productivity of streams caused these species (e.g., coho and Chinook salmon, rainbow and cutthroat trout, Atlantic salmon, brown trout, Arctic charr) to evolve territorial behaviour. Juveniles defend territories from conspecifics and heterospecifics with stereotyped displays and overt aggression. Decades of research have indicated that food and space limit the density of juveniles and production of smolts from streams (Bradford *et al.*, 1997; Chapman, 1966), though habitat quality (e.g., Sharma and Hilborn, 2001) and environmental conditions cause production to vary among sites and years.

The ability of individuals to acquire and retain high-quality feeding territories depends on a number of interrelated factors. Not surprisingly, larger fish dominate smaller ones, and even a small size disparity is sufficient to determine the outcome of a contest, but territorial possession also

strongly influences competition (e.g., Abbott *et al.*, 1985; Huntingford and Garcia de Leaniz, 1997; Rhodes and Quinn, 1998). Both of these factors favour early emerging fry because they will hold territories and will have grown by the time that later emerging fry try to compete with them (Einum and Fleming, 2000), though predation may serve as a countervailing pressure (Brännäs, 1995). There are many other factors affecting dominance relationships, including recent experience in territorial bouts, individual recognition, sibling recognition and metabolic rate. However, individuals that are unable to obtain territories may adopt non-territorial 'floater' behaviour patterns (Nielsen, 1992) or be forced to emigrate (Chapman, 1962).

Given the limited food and space in streams, salmonids evolved under high levels of competition among juveniles. Even under some fishing pressure, far more juveniles emerge from the gravel than can be supported in the stream. Thus, for these species it is the fry to smolt period rather than the egg to fry period that is really the limiting life history stage, assuming an adequate number of adults return to spawn. Therefore, the release of hatchery-produced fry or parr into a stream may not increase the number of seawards migrating smolts due to simple competition. However, the hatchery fish may differ from the wild fish in phenotypic traits affecting dominance. For example, if they are fed for some period in the hatchery prior to release then they may be larger than the wild fish. In addition, the timing of spawning in many hatchery populations diverges, commonly becoming earlier than the wild population from which it was derived (e.g., Flagg *et al.*, 1995; Quinn *et al.*, 2002). This difference would magnify any disparity in size between wild and hatchery fish. Nickelson *et al.* (1986) studied 30 streams, half of which had received presmolt coho salmon from hatcheries, and half were unaffected by such activity. Hatchery releases increased the overall density of coho salmon but decreased the abundance of wild coho. Similar numbers of adult salmon returned to the two types of streams but the hatchery-origin fish tended to return earlier in the season and produced fewer offspring, so the hatchery releases failed to increase the productivity of the recipient streams. The authors of this finding suggested that competitive displacement may have been a mechanism underlying this outcome, but this mechanism was not explicitly tested in their study.

There have been many comparisons between the behaviour of wild and hatchery fish in laboratory experiments and also many field studies of the effects of adding hatchery fish to a population of wild or naturally rearing fish, for example, brown trout (Berg and Jorgensen, 1991; Jorgensen and Berg, 1991) and coho salmon (Rhodes and Quinn, 1999). The latter type of study is relevant but, as Weber and Fausch (2003) pointed out, very few have distinguished the effects of competition per se from the effects of increased density. In most cases, growth or some other performance measure was recorded in a population of wild fish, and compared to that in a group of wild fish to which hatchery-produced fish were added. In such

cases a 'substitutive' experimental design that controlled for overall fish density might be more informative about the processes of competition, though perhaps less representative of the normal management practise.

Competition for food and space in streams may limit many salmonid species, but this is not the case for pink, chum and sockeye salmon. These species commonly spawn at much higher densities than the other species of Pacific salmon and are much more numerous overall. Pink and chum salmon migrate directly to sea after emergence and make little or no use of streams for rearing, whereas sockeye salmon typically migrate to lakes. Conventional wisdom had maintained that salmonids were limited by freshwater constraints but that the ocean had the capacity to rear more salmonids than the rivers could produce. Thus, increases in production of juvenile pink and chum salmon should be accompanied by proportional increases in adults; sockeye salmon might be limited by either spawning or lacustrine rearing capacity. However, between the streams and the ocean lies the estuary, a habitat whose role in salmonid ecology is not fully understood (Thorpe, 1994). Is the estuary a critical habitat, merely a highway through which they must migrate or possibly a hazardous place filled with predators? Generally speaking, the species that enter the estuary at a large size move through it more rapidly than smaller salmonids. Atlantic salmon and sea trout are large when they migrate to sea, as are steelhead, cutthroat, sockeye, coho and yearling Chinook salmon. Chum salmon smolts are small, as are populations of Chinook salmon that migrate to sea in their first year of life, and these species make the most extensive use of estuaries (Healey, 1982a; Simenstad et al., 1982). Pink salmon are something of a paradox as they are the smallest in size on entry into the ocean but seem to move through estuaries faster than chum salmon. Size of smolts and growth in the estuary provide an advantage in survival at sea (Healey, 1982b; Neilson and Geen, 1986; Reimers, 1971). Though growth rates in estuaries are often rapid, the vast majority of juvenile salmonids leave after a few days or weeks, and there is evidence for food limitation in estuaries (Reimers, 1971; Sibert, 1979; Wissmar and Simenstad, 1988). However, the extent to which estuaries present a bottleneck may vary among species. In the Columbia River in the northwestern United States, for example, steelhead, coho, sockeye and yearling Chinook salmon tend to swim in the pelagic zone and remain for only a short time, whereas the under-yearling Chinook salmon are primarily in the littoral zone and are present over a much longer period (Dawley et al., 1986). We know of no systematic, controlled study of the effects of density on wild salmon, or of interactions between wild and hatchery salmon, nor on the duration of estuarine residence and survival of salmon, though such effects might occur.

It is plausible that the estuary is a limiting habitat, given the many millions of smolts that may enter over a short period of time, but can the ocean also be a limiting habitat? Mathews (1980) used data on density, growth

and survival of coho salmon in Puget Sound and the Columbia River in the northeastern Pacific to test the hypothesis that increased numbers of hatchery-produced fish depressed the growth or survival of the species, but the data were equivocal. Rogers (1980) noted the strong environmental controls over growth at sea but he concluded that there was a density-dependent reduction in growth of sockeye salmon in Bristol Bay, Alaska, an area where this species is very abundant. Subsequent to that report, a body of evidence developed indicating that the density of salmon at sea affected their growth and age at maturity. Within large 'stock complexes' such as Bristol Bay sockeye salmon and Japanese chum salmon, years with high abundance were usually associated with smaller size (e.g., Kaeriyama, 1998; Rogers and Ruggerone, 1993), though interactions with physical conditions (e.g., temperature) were also noted. For example, the increases in abundance of chum salmon from Hokkaido hatcheries were accompanied by reduced size at age and increased age at maturity (Kaeriyama, 1998). Rogers and Ruggerone (1993) found that the growth of Bristol Bay sockeye salmon was depressed in the final period at sea by their own density but was not affected by other salmon (they were especially interested in possible growth reduction related to the abundance of Japanese chum salmon). However, McKinnell (1995) and Pyper and Peterman (1999) both reported evidence of competition between stock complexes of sockeye salmon.

There is evidence, at least for some of the very large stock complexes, of density-dependent growth. Thus increases in hatchery production might be associated with smaller size and lower survival of those fish, and perhaps for sympatric salmon of the same and even other species (Levin and Williams, 2002), and authors such as Cooney and Brodeur (1998) have discussed the possible implications of marine carrying capacity for salmonid enhancement efforts. However, the extent to which these effects occur in areas with more dispersed production and lower overall densities is unclear. Perhaps more fundamentally, does high density depress only growth or survival as well? Evidence on this crucial point is much less clear, but recently Ruggerone *et al.* (2003) reported that not only the growth but also the survival of Bristol Bay sockeye salmon was depressed by the abundance of Asian pink salmon. In addition, Levin and Schiewe (2001) concluded that under conditions of naturally low ocean productivity, high densities of hatchery Chinook salmon depress survival rates of wild conspecifics. In general, the 1980s and 1990s have seen high abundance and survival rates of Pacific salmon from the northern part of their North American range, and 'predator swamping' effects might lead to a positive relationship between abundance and survival rather than a negative one. Indeed, earlier analysis indicated a positive relationship between survival of Babine Lake sockeye salmon in British Columbia and the abundance of juvenile pink salmon (Peterman, 1982). However, the question certainly needs further work before this finding can be accepted as a general conclusion.

In addition to the potential competition for food and space between wild and hatchery-produced juvenile salmon in streams, and for food in estuaries and the ocean, there are possible competitive effects and behavioural interactions on the spawning grounds. If all wild fish spawned in the river where they originated, and all hatchery fish returned and were spawned in the hatchery where they were produced, these interactions would not occur. However, this kind of segregation seldom occurs. First, there is some straying of hatchery-produced fish into other rivers (Candy and Beacham, 2000; Labelle, 1992; Quinn *et al.*, 1991). Moreover, even if the salmon return to their river of origin, there are often opportunities for exchange between wild and hatchery populations. Nicholas and Downey (1983) reported that the proportion of hatchery-produced Chinook salmon entering Elk River Hatchery, Oregon, averaged 22.8% over a 9-year period (range, 5.9–52.2%). Hence, in most years, the majority of fish produced in the hatchery did not spawn there but rather in the river. In another case of interaction between wild and hatchery salmon, Nicholas and Van Dyke (1982) estimated that 2022 (64.7%) of the 3124 wild coho salmon returning to the Yaquina River watershed in 1981 entered the Oregon Aqua-Foods hatchery. Such decoying of wild salmon into hatcheries both reduces the number of wild fish in the stream and contributes to genetic mixing.

On the other hand, hatchery fish commonly spawn with naturally produced fish and can outnumber them in some systems. In an extreme example, Nicholas and Van Dyke (1982) estimated that 6% of the adult coho salmon returning after release from the Oregon Aqua-Foods, a private production hatchery, strayed to spawn in the Yaquina River watershed, Oregon. However, they were so numerous (and the wild fish so scarce) that hatchery fish constituted 74% of the naturally spawning coho salmon in 1981 (Nicholas and Van Dyke, 1982) and 91% in 1985 (Jacobs, 1988). If a stream's carrying capacity has already been met by the wild salmon, then the addition of hatchery-produced fish will diminish the productivity of the group as a whole, even if there are no functional differences between wild and hatchery fish.

Just as juvenile wild and hatchery salmon differ in phenotype and genotype, with complex implications for their behavioural and ecological interactions, adults differ as well. The nature and extent of the differences vary greatly, depending on whether the wild and hatchery populations have been managed as a single unit (e.g., wild salmon used for spawning in the hatchery and hatchery-produced salmon allowed to spawn naturally, and all salmon subjected to common fisheries) or managed separately. For example, in Washington State, salmon hatcheries have tended to employ the former approach. Until recently, most hatchery-produced salmon were not marked, so fisheries operated equally on wild and hatchery fish, and there was considerable exchange between populations. In such cases the wild and hatchery populations may be essentially the same, and most differences between them may result from culture practises. For example, hatchery

smolts are often larger than wild smolts, and this tends to reduce the age at maturity (e.g., Norris *et al.*, 2000), and hence overall size.

On the other hand, steelhead in Washington State have been managed under a very different set of goals. Hatchery steelhead have been selectively bred to return and spawn earlier in the winter than wild fish (e.g., Ayerst, 1977). This approach was initially implemented to lengthen the growing season for juveniles in the hatchery so they could reach a suitable size for smolt transformation and release after 1 year rather than 2 years as is typical of wild steelhead. However, the high genetic variability underlying return date allowed managers to select early returning fish, and hence open early fisheries that targeted the hatchery-produced fish and close the fisheries later if the wild populations needed protection. In this situation, when the hatchery-produced fish spawn in the river, they do so earlier in the year than the wild fish. This approach may expose the hatchery fish to less favourable physical conditions (e.g., flow, temperature or loss of redds to later-arriving wild adults) since presumably the wild fish evolved an optimal spawning season to maximize embryo survival or fry growth. It is therefore perhaps not surprising that the hatchery fish do not produce as many surviving offspring per capita as do wild fish when spawning in the river, as indicated by genetic analyses (e.g., Leider *et al.*, 1990).

5.2.2. Predation

Although most research on behavioural interactions between wild and hatchery-produced salmon has emphasized competition, predation is another important ecological interaction. Salmonids tend to eat invertebrates (e.g., insects in streams and zooplankton in lakes) when they are small but they become more piscivorous once they reach about 10–20 cm (Keeley and Grant, 2001). Studies in freshwater (e.g., Hunter, 1959) and at sea (e.g., Parker, 1971) identified coho salmon as a significant predator on pink and chum salmon. Coho smolts (usually about 10- to 12-cm long) can easily consume newly emerged members of the other species (about 3–4 cm). As the pink and chum salmon grow they become progressively less vulnerable (Hargreaves and LeBrasseur, 1986), but recently Briscoe *et al.* (2005) reported that the survival of Auke Creek coho salmon was positively correlated with the numbers of pink and chum salmon fry released from nearby hatcheries. Likewise, coho salmon in lakes can be a significant predator on sockeye salmon (Ruggerone and Rogers, 1992), and Arctic charr can congregate and eat sockeye salmon smolts (Ruggerone and Rogers, 1984). These latter studies were conducted on wild populations, but releases of large numbers of hatchery-produced coho salmon coincident with the presence or migration of wild salmon could result in significant mortality. Pearsons and Fritts (1999) reported that juvenile coho could eat Chinook that were over 40% of their length (e.g., a 140-mm coho ate a 64-mm Chinook).

There has been a tendency to focus on predation by hatchery-produced smolts on wild fry, but other kinds of predator–prey interactions involving wild and hatchery fish can occur as well. For example, in Lake Washington, Washington State, there is a large population of adfluvial cutthroat trout that prey heavily on wild and hatchery-produced sockeye salmon fry (Nowak et al., 2004). The presence of hatchery fry might buffer predation on the wild fry (as predation is buffered by the abundance of longfin smelt, an alternative forage species for trout), assuming that other factors limit the abundance of trout. However, if the availability of hatchery-produced salmonids increases the abundance or modifies the distribution of predators, increases in predation on wild fish might occur.

5.3. The effects of harvest on wild salmon populations

The underlying principle in the theory of sustainable salmon harvesting is the stock concept. Due to their ability to home to their natal streams, salmon have adapted to a wide range of freshwater habitats, and consist of thousands of reproductively isolated stocks (Helle, 1981; McDonald, 1981). The population dynamics of each stock will be determined by the habitat it uses, and a convenient metric of the overall productivity of each stock is the potential recruits per spawner. A stock that spawns in good gravel with stable flows, little scouring and few fine sediments can be expected to have higher egg to fry survival than a stock spawning in an unstable stream with frequent floods and scour, siltation and intense predation. Similarly, through the rest of the freshwater and marine life history, a stock using better habitat would be expected to have higher survival rates. Higher survival through their life history results in more individuals surviving to return to spawn for every spawner in their parental generation.

On average, a habitat that has less than one recruit per spawner would not be able to support a stock of salmon without frequent immigration. Stocks in good habitat can often produce two to ten recruits per spawner from adults spawning at low density. The sustainable harvest rate for a population depends on the number of recruits per spawner. A population producing two recruits per spawner can be harvested at 50%, one spawner produces two adults, one is harvested and one remains to replace the parental generation and complete the cycle. A population with three recruits per spawner can be harvested at 66%, and a population with four recruits per spawner can be harvested at 75%.

In the absence of harvesting, populations would be expected to increase until competition for resources (breeding space for adults or food and space for their offspring) reduces the recruits per spawner to 1.0; that is, populations cannot grow forever. Thus, when we attempt to estimate the productivity of a salmon population, we normally attempt to estimate the potential recruits per spawner at low densities. Table 2.3 shows the estimated

potential maximum recruits per spawner and the exploitation rate at maximum sustainable yield (MSY) for a range of natural populations of Pacific salmon. These estimates were derived from data sets accumulated by R. Myers (Dalhousie University, Canada), and represent only stocks that have been well studied and have survived many generations of harvesting. Therefore, the estimates are almost certainly biased towards the higher end of natural productivity.

Salmon enhancement projects intervene at specific life history stages to improve the survival rates, and thus ideally increase both the recruits per spawner and the potential sustainable harvest rate. For example, if a population of salmon produced 1600 eggs per spawner, and egg to fry survival and fry to adult survival rates were 5% and 2.5%, respectively, the population would produce two recruits per spawner and could be harvested at 50%. The same stock, if placed in a hatchery with 90% egg to fry survival, would produce 36 recruits per spawner, and could be harvested at 97%. Table 2.4 shows how the sustainable harvest rate depends on the release to adult survival for a hatchery population with 1600 eggs per spawner and 90% egg to release survival.

Table 2.3   Maximum recruits per spawner for some Pacific salmon populations

Species	Number of stocks	Average maximum recruits per spawner	Exploitation rate at MSY (%)
Chinook	6	4.4	67
Chum	7	3.0	55
Pink	52	2.8	54
Sockeye	23	3.5	60

Included are Chinook (*O. tshawytscha*), chum (*O. keta*), pink (*O. gorbuscha*) and sockeye (*O. nerka*) salmon.

Table 2.4   Sustainable harvest rate for hatchery fish as function of smolt-to-adult survival

Ocean survival (%)	Sustainable harvest rate
0.08	0.13
0.10	0.31
0.50	0.86
1.00	0.93
2.00	0.97
3.00	0.98
5.00	0.99

An extensive tagging programme using coded wire tags since the 1970s has tagged tens of millions of hatchery fish each year in North America, allowing us to estimate the survival rate of hatchery fish for most hatcheries. Figure 2.20 shows the distribution of survival rates from hatchery released Chinook and coho salmon from this database. The average sustainable harvest rate for these three species is between 86% and 98%, far in excess of the sustainable harvest rate for wild stocks.

5.3.1. Sustainable harvest in mixed-stock fisheries

When SEPs are technologically successful, the stocks they produce can be harvested at very high rates, and this creates one of the primary problems in management of enhancement programmes. When natural stocks with lower
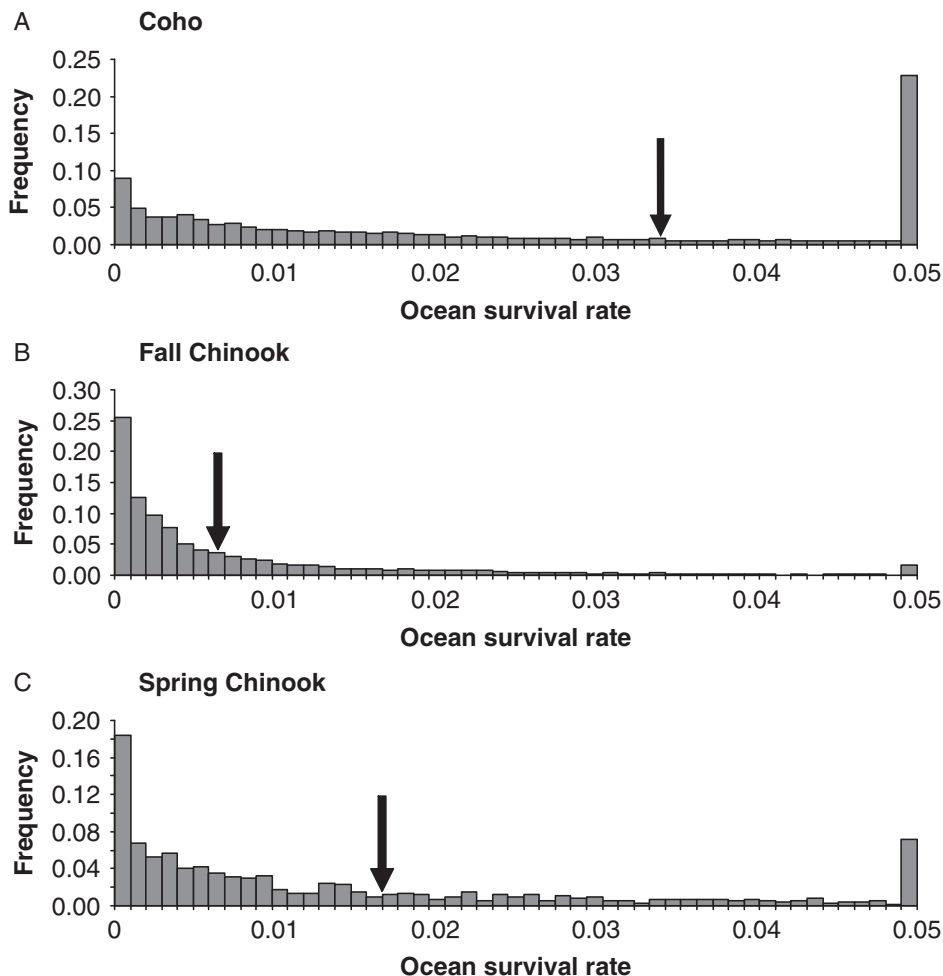
Figure 2.20   The frequency of ocean survival rates for hatchery release groups of coho (*O. kisutch*) (A), fall Chinook (B) and spring Chinook (C) (*O. tshawytscha*) from all hatchery releases in the Pacific salmon Coded Wire Tag database (Magnusson, 2002). The arrows show the average value for the salmon species.

sustainable exploitation rates are mixed in the same fisheries, how do you harvest the hatchery stocks without over-harvesting the naturally producing stocks? In theory, we would like to harvest each stock individually, be it wild or hatchery. In such an ideal world, this practise would allow us to harvest the hatchery stocks at very hard rates and the wild stocks at the appropriate rate. Unfortunately, two factors prevent this practise from happening.

First, for historical reasons, most salmon harvesting does not take place where the different stocks (natural and hatchery) are separated. This separation often takes place within a river system, since most enhancement facilities are located well above tidewater, and by tradition most commercial and recreational harvesting takes place in salt water. In the extreme of large river systems in North America such as the Sacramento, Columbia, Fraser, Skeena, Copper and Yukon, dozens (or hundreds) of discrete stocks are found in the watersheds, often diverging from one another at spawning grounds hundreds of miles upstream. A primary reason most commercial fisheries take place in salt water is that the quality of the flesh deteriorates as the fish enter freshwater, reducing their economic value. Thus, for commercial reasons, freshwater harvesting is very undesirable. It is an unfortunate fact of life that most salmon fisheries are to some extent mixed-stock fisheries, and the majority of enhanced salmon populations will be harvested with naturally producing fish when fishery enhancement takes place in a geographic region with natural production.

The problem of harvesting stocks of differential productivity in a common fishery is commonly called the 'mixed-stock harvesting problem', and has long been recognized and analysed (Hilborn, 1976, 1985b; Kope, 1992; Paulik *et al.*, 1967; Ricker, 1958; Shaklee *et al.*, 1999; Walters, 1988). Figure 2.21 shows the relationship between harvest rate and sustainable yield for a weak wild stock with potentially 1.5 recruits per spawner, and a stronger hatchery stock that produces 6 recruits to the fishery per spawner. Panel (A) shows the case where the wild stock has a potential return of 1000 spawners and the hatchery stock of 100. Fishing near the optimum rate for the wild stock (about 20%) maximizes the total harvest from the mix of stocks. However, if the hatchery is larger (panel B), its potential return is 600 spawners (still well below the potential return of the wild stock), and harvesting at about 70% maximizes the yield. This harvest rate is near the optimum for the hatchery stock but drives the wild stock extinct.

5.3.2. Salmon harvesting and impacts of hatchery fish on wild fish

Salmon fisheries can be broadly divided into two types: terminal fisheries near river mouths targeting fish as they return to a particular watershed, and mixed-stock or 'interception' fisheries that harvest a range of stocks that are intermingled. Most fisheries near the mouths of larger rivers are actually
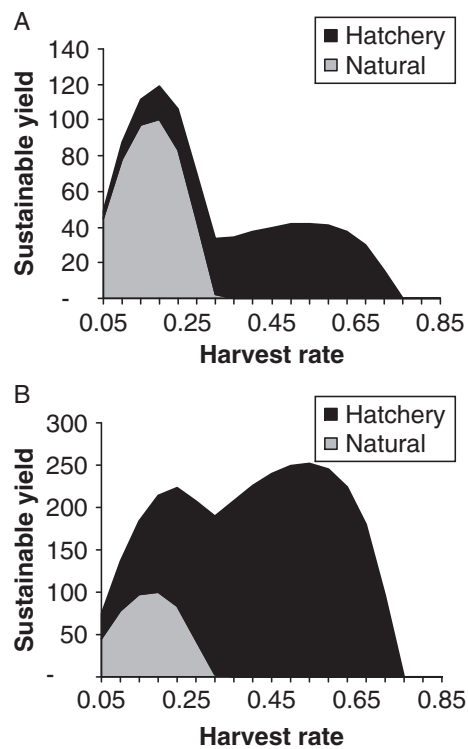
Figure 2.21 Total sustainable yield (TSY) for a fishery with a mix of a weak natural stock and a hatchery stock. TSY when (A) the hatchery stock is small ($N = 100$) relative to the wild stock ($N = 1000$) and (B) when the hatchery stock ($N = 600$) is just over half as large as the wild stock ($N = 1000$).

mixed-stock fisheries, since there is normally a range of stock complexes within any river system. But we generally do draw a contrast between the mixed-stock fisheries for immature Chinook and coho salmon that are highly intermingled along the west coast of North America, with the much more terminal (and less mixed) fisheries that take place in river mouths. Similar problems are found in the Atlantic, where many of the traditional fisheries take place on stocks of very mixed origin (Crozier *et al.*, 2004).

The Chinook fisheries are a very good illustration of the mixed-stock problem. Figure 2.22 shows the distribution of exploitation rates on Chinook salmon from four specific hatcheries: Robertson Creek, located on the west coast of Vancouver Island; Big Qualicum, located on the east coast of Vancouver Island in the Straight of Georgia; the Nisqually hatchery located in southern Puget sound and the Upriver Brights (URB) from a hatchery located on the Hanford Reach of the Columbia River. The fig. shows that the distribution of exploitation rates for different stocks differs spatially, with the Robertson Creek stock caught primarily in northern British Columbia and Alaska, the Big Qualicum and Nisqually stocks caught primarily in the more local sport and commercial fisheries of the interior waters of British
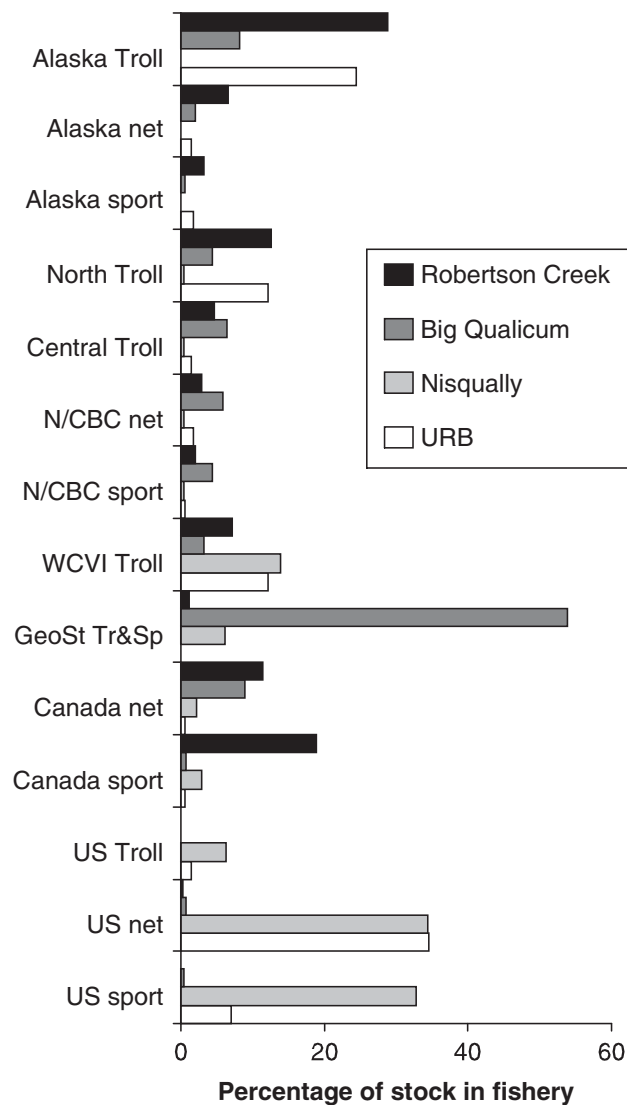
Figure 2.22 Distribution of Chinook salmon (*O. tshawytscha*) stocks in mixed–stock fisheries on the west coast of North America.

Columbia and Washington, while the URB stock is caught over most of the outer coast. Data suggest that wild stocks from the same geographic locations have similar distributions of catch, indicating that almost all of the major Chinook fisheries are heavily mixed. In other words, harvesters cannot put their lines or nets in the water without catching fish from many locations, including a mix of wild and hatchery fish.

It is these mixed-stock fisheries that pose the primary problem for wild stock managers faced with significant hatchery production. More importantly, the rise in hatchery production of Chinook and coho in the 1960–1980s led to high harvest rates in the coastwide fisheries that led, in turn, to over-harvest of the wild fish.

Figure 2.23 shows the historical pattern in exploitation rates on Big Qualicum hatchery Chinook as estimated from coded wire tagging data. Each year almost all hatchery stocks on the Pacific coast have a significant portion of their released fish tagged with small wire tags (coded wire tags), and catches and escapements are sampled to determine survival after release, harvest rates and stock contribution to mixed–stock fisheries. When the data became available, it was clear that the harvest rate on this stock was high, and indeed higher than that sustainable by wild fish (Pacific Salmon Commission Joint Chinook Technical Committee, 2002). The pattern observed for Big Qualicum hatchery fish was generally consistent with patterns of most wild Chinook stocks on the east coast of Vancouver island; that is, the harvest rates in the 1970s and 1980s were in excess of the sustainable rates for wild fish, and it was only in the 1990s that the harvest rates were reduced.

As we have seen (Section 3), most hatchery programmes on the west coast of North America have produced Chinook and coho salmon, the major exception being the recently established large programmes for pink salmon in PWS in Alaska (Hilborn and Eggers, 2000; Pinkerton, 1994). There are no fisheries for pink salmon outside of PWS, but the nature of the fisheries within this area is complex and there are significant concerns that the harvesting of hatchery fish has impacted the wild stocks. The nature of the geography and the migration of stocks have certainly posed significant concerns to the area managers. There is a tension between the desire of the managers to harvest the hatchery stocks as close as possible to the hatchery to reduce mixing with wild fish, and the economic desire to harvest the fish away from the hatcheries while the flesh quality is higher. Hilborn and Eggers (2000, 2001) showed that the advent of the large pink salmon hatchery programme in PWS coincided with a decline in the abundance and productivity of the wild fish at the same time that other wild pink salmon populations in Alaska were increasing. They suggested that the
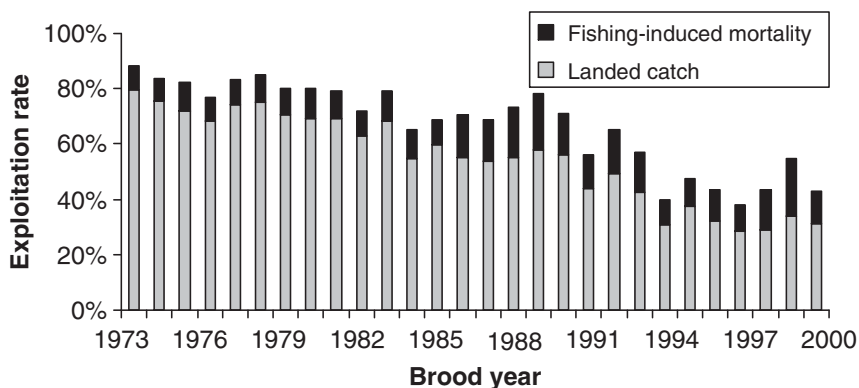
Figure 2.23 Historical exploitation rates on Chinook salmon (*O. tshawytscha*) from the Big Qualicum hatchery, British Columbia, from 1973 to 2000.

primary impact of the hatchery programme in PWS was to replace wild with hatchery fish rather than to significantly increase total pink salmon returns.

There is general agreement that fisheries agencies, in their desire to maximize the harvest of wild fish, systematically overfished many wild stocks, which led to the development of wild fish policies in Oregon and Washington in the 1990s. In 1997, the environmental impact statement for the Washington Department of Fish and Wildlife's Wild Salmonid Policy stated bluntly that 'current fish management plans and practices overfish 89 wild stocks in order to harvest co-mingled hatchery fish at rates that are not sustainable by wild populations' (Washington Department of Fish and Wildlife, 1997). This problem was not at all unique to Washington and has been found in every salmon jurisdiction that has had significant hatchery production.

5.3.3. Selective harvesting

Possible solutions to the mixed-stock harvesting problem include (1) continuing the overexploitation of wild stocks and relying on hatchery production, (2) closing of hatcheries, (3) reducing mixed-stock fishery exploitation rates to levels sustainable by wild stocks and (4) attempting to selectively harvest hatchery fish, in many cases by permitting fishermen to retain only hatchery fish (Lawson and Sampson, 1996; Zhou, 2002). Management agencies on the west coast of North America have mostly chosen to reduce exploitation rates while trying to selectively harvest hatchery fish at the same time. Selective fishing relies primarily on marking hatchery fish and encouraging fishermen to release unmarked fish, often by law. Thus, in some jurisdictions, all hatchery fish released have their adipose fin clipped and fishers can only retain adipose clipped fish. Selective fishing requires not only the ability to identify hatchery fish, but also that the survival rate of released fish is high.

5.3.4. Impacts of harvest: Summary

When hatchery programmes first became successful at producing significant numbers of fish for harvesting, the harvest of wild fish in mixed-stock fisheries was a very serious threat to the viability of the wild stocks. In the 1990s, growing recognition of the problem, aided both by better data from marking programmes and increasing concern about wild fish, led to a significant change in harvest policies in the Atlantic and the Pacific. The adoption of formal policies for protection of wild salmon has led to dramatic reductions in harvest rates in mixed-stock fisheries that should allow wild stocks to rebound where their freshwater habitat remains suitable and ocean conditions are favourable. There remains much discussion and controversy over the ability of selective fishing to continue to harvest hatchery surpluses without adversely affecting wild stocks. It remains to

be seen if these efforts will be successful and, should the results prove negative, whether society will respond accordingly by reducing or redirecting demand for harvestable fish.

5.4. Disease effects of salmonid enhancement

In a strict sense, disease can be defined as a departure from normal and may include alterations in histology, physiology, behaviour or function. Diseases may have either infectious (e.g., tuberculosis, hepatitis) or non-infectious (e.g., botulism, cystic fibrosis) causes. Although fish provide many interesting examples of disease resulting from non-infectious etiologies (Leatherland and Woo, 1998), for the purposes of this chapter we will not consider diseases of non-infectious origin because they typically are not transmissible between fish. Nevertheless, there is concern that hatchery practises can affect levels of non-infectious diseases among wild fish by amplifying diseases that have a genetic etiology (e.g., certain cancers) or by the release of chemicals or pollutants. As an example, the use of malachite green for control of fungus infections in hatchery fish has been largely discontinued in Europe and North America due to its demonstrated carcinogenicity and concern about its release into the environment via the hatchery effluent (Srivastava et al., 2004).

Disease is a natural process and one of the factors (along with age and predation) that determines rates of population mortality. It is important to remember that infectious disease is a normal component of ecosystems and that all species live in association with a broad suite of pathogens. Nevertheless, the presence of a pathogen in nature does not inevitably lead to infection and, should infection occur, it does not inevitably lead to disease. Thus, infections of fish can be acute, subacute, chronic or unapparent, and the infected fish may die, recover or become long-term carriers.

Several factors control the disease process in both wild and cultured populations of fish. These factors rest with the host, the pathogen and the environment (Hedrick, 1998). For the host, factors might include the species, stock, age, immune status and nutritional state. For the pathogen, factors include virulence, number and strain. In a normal environment, most endemic pathogens are in a relatively balanced relationship with their natural hosts. Both innate and adaptive immune mechanisms help protect the host against endemic pathogens, although pathogens with a high rate of mutation (e.g., RNA viruses) can be described as being in an 'arms race' with the host immune system. Because fish live in close association with their environment, changing environmental factors can have important effects in altering the balance of the host–pathogen relationship. Such factors include the presence of stressors, adverse water quality and abnormal water temperatures. The anthropogenic and natural stressors that reduce resistance or exacerbate disease in wild fish are typically local, for example,

hydroelectric dams, thermal effluents from power plants, contamination from mining or industrial activities and altered flows or water temperatures from natural causes or agricultural practises (Arkoosh *et al.*, 1991); however, global or large-scale effects may also cause changes in disease ecology (Kocan *et al.*, 2004).

5.4.1. Infectious diseases of salmonids

A wide variety of viruses, bacteria, parasites and fungi can cause disease in salmonids and for more detailed information the reader is referred to various fish health texts (e.g., Hoffman, 1999; Noga, 2000; Plumb, 1999; Roberts, 2001; Wolf, 1988; Woo, 1995; Woo and Bruno, 1998). While the initial exposure of a population to an exotic disease is often devastating (e.g., whirling disease in rainbow trout), differences in the host specificity, virulence and the nature of the resulting disease are frequently seen with different strains of endemic pathogens as well. For example, IHNV is endemic among a wide range of anadromous salmonids on the west coast of North America; however, significant genetic differences have been shown among the different strains of IHNV that infect sockeye salmon, Chinook salmon, and the rainbow and steelhead trout (Kurath *et al.*, 2003). This finding underscores the need for caution to avoid the translocation of both exotic pathogens and non-native strains of endemic pathogens with the movement of hatchery fish. In addition, there are significant differences in the innate resistance to a given pathogen among the various salmonid species (Nichols *et al.*, 2003; Vincent, 2002) and even among stocks of the same species (Vincent, 2002). Finally, differences in environmental conditions and other factors (e.g., strains of alternate hosts) can affect the distribution and ecology of disease in various geographic areas. An example is the difference in the severity of whirling disease among populations of naturally spawning rainbow trout in different regions of the United States (Kerans *et al.*, 2004).

5.4.2. Infectious diseases in wild and hatchery salmonids

Typically, the sources of pathogens that can infect fish are endemic among free-living, facultative pathogens in the aquatic environment (e.g., *Flavobacterium psychrophilum*, the causative agent of bacterial cold water disease) or from obligate pathogens that are maintained among reservoirs in free-ranging aquatic animals (e.g., *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease). Except for a few specific instances where exotic pathogens have been introduced to a new area by the intentional movement of hatchery fish (see below), these natural sources and endemic reservoirs among wild fish are the origins for the infectious diseases that affect both wild and hatchery salmonids (Amos and Thomas, 2002; Anderson *et al.*, 2000; Mitchum and Sherman, 1981; Olivier, 2002).

Although infectious diseases are common in populations of wild salmonids, their effects are hard to observe (especially in the ocean) and difficult to study. Many infectious diseases in wild fish occur at chronic or relatively low levels unless a significant environmental stressor is present or the population reaches an abnormally large size. Disease outbreaks that have resulted in large-scale mortality events among wild fish have been documented for several marine fish species (Hedrick *et al.*, 2003; Rahimian and Thulin, 1996) and some populations of free-ranging salmonids (Williams and Amend, 1976). In some cases, these outbreaks have resulted in losses approaching 90% of the wild stock.

Not surprisingly, much of what we know about infectious diseases of salmonids comes from experience with captively reared fish, where disease outbreaks are easily observed and there is an incentive for action, and because, at least in some cases, various disease control options may be available. As a result, most research on infectious diseases of salmonids has focused on those infectious agents causing large economic losses at commercial aquaculture facilities or large impacts at salmonid hatcheries supporting state, tribal and federal fisheries programmes. This has led some to the incorrect, but common, perception that fish disease is a hatchery phenomenon.

In addition to being more easily observed, when infectious diseases occur among fish in hatcheries, they are frequently found to have a higher prevalence or intensity than among wild stocks, although exceptions have been noted (Elliott *et al.*, 1997). Hatchery fish may experience greater impacts from infectious diseases due to higher densities, higher levels of stress and poorer water quality leading to an increased level of susceptibility and lowered ability to recover from infection. Other reasons that outbreaks of disease are more commonly observed in hatcheries might include a lower level of genetic diversity in some cases, and the fact that hatcheries typically rear the most susceptible life stages of fish, especially fry and juveniles.

5.4.3. Disease risks associated with salmon hatchery programmes

While an important area of concern, there are but a few well-documented cases in which hatchery fish have been shown to affect directly the health or infectious disease status of wild stocks (McVicar, 1997). Nevertheless, this remains a considerable area of debate and a major source of scientific uncertainty requiring additional research. However, there are several potential mechanisms by which hatcheries could affect the disease status of wild stocks.

5.4.3.1. Introduction of exotic pathogens While principally associated with the intentional movement of cultured fish harbouring an undetected infectious agent, this remains the most dangerous and best-documented threat to the health of wild stocks. Often cited examples include the introduction

and distribution of *M. cerebralis*, the causative agent of whirling disease, and *Gyrodactylus salaris*, the causative agent of gyrodatylosis. Both of these important salmonid diseases have impacted wild or free-ranging stocks, sometimes with devastating consequences.

Whirling disease was believed to have been initially introduced into cultured rainbow trout in the United States sometime in the 1950s either by direct importation of infected fish from Europe where the causative agent is endemic or by use of imported fish as trout food (Bartholomew and Reno, 2002). Now present in both captive and free-ranging salmonids in at least 23 states, the parasite continues to spread both by natural means and by the intentional or unintentional movement of infected fish by commercial farms and fisheries agencies. Among wild-spawning rainbow trout in the western United States, declines approaching 90% have been observed in certain populations (Baldwin *et al.*, 1998). Because several species of anadromous salmonids are highly susceptible, there is significant concern for wild stocks of Chinook salmon, sockeye salmon and steelhead trout in the western United States (Hedrick *et al.*, 2001).

G. salaris is a trematode parasite that is cited as having caused significant damage to wild Atlantic salmon populations in 44 Norwegian rivers (Peeler and Murray, 2004). Spread from endemic areas by the movement of infected fish used in commercial aquaculture (Johnsen and Jensen, 1986), the parasite is now present in many rivers in Norway with little chance of eradication.

While the greatest risk of introducing exotic pathogens is associated with the deliberate movement of infected fish between watersheds, other pathways have been postulated. These include birds, anglers, ballast water and straying fish (Bartholomew *et al.*, 2005; Peeler and Thrush, 2004). The operational plans of most conservation hatcheries preclude many of these risks because they rely on local stocks, have good fish health inspections and restrict the movement of fish to the same, or nearby, watersheds. Because fish pathogens are detected most readily when they affect stocks in hatcheries, it is common to assume that a newly discovered pathogen is a result of an introduction, however, this is frequently not true (Mork *et al.*, 2004).

5.4.3.2. *Amplification of endemic pathogens in hatchery fish*   A second method by which hatcheries are assumed to impact the health status of wild stocks involves the creation of a point source of infection from disease outbreaks that occur in hatchery fish. Since hatcheries often contain high densities of susceptible fish, such outbreaks can result in the release of significant quantities of infectious agents in the effluent (Watanabe *et al.*, 1988); although high levels of pathogens can also be released from wild salmonids in natural systems (Mulcahy *et al.*, 1983). The threat to wild stocks from pathogens in hatchery effluents is related to the number and concentration of infectious units that are released, the dilution of the

effluent by the receiving waters, the stability of the infectious agent in the environment and the opportunity to contact a susceptible wild fish. An example of this type of risk is the amplification of sea lice (*Lepeophtheirus salmonis*) by commercial Atlantic salmon farms in Europe and North America (Krkosek *et al.*, 2005; Morton *et al.*, 2004; Peeler and Murray, 2004; Tully *et al.*, 1999), and the dramatic collapse of sea trout stocks on the west coasts of Ireland and Scotland has been attributed to infection of post-smolts during their migration past such farms (Butler and Walker, 2006; Gargan *et al.*, 2006). However, others suggest that the role of commercial salmon farms in contributing to local infections is less clear and that infection pressure on wild fish depends on multiple factors (Brooks, 2005; Costelloe *et al.*, 1998). It should be noted that few, if any, examples are reported in which fishery enhancement or conservation hatcheries rearing Pacific salmon have been shown to amplify endemic pathogens in a manner that has resulted in an increase in disease prevalence or intensity among wild stocks in the watershed. However, because the same, or very closely related, strains of endemic pathogens infect both hatchery and wild stocks, it is currently difficult or even impossible to determine the origin of the infectious agent with certainty (Todd *et al.*, 2004). Nevertheless, a large hatchery operating on a small watershed that contains a substantial number of susceptible wild fish could present a source of risk to the wild cohort.

5.4.3.3. *Intentional release of infected fish that contact wild stocks*   In addition to the release of pathogens in hatchery effluents, conservation hatcheries will typically release fish into systems at times or in ways that attempt to mimic the natural production cycles. In some cases, these captively reared fish may be undergoing a disease outbreak or harbouring pathogens that can result in a greater than normal risk of infection for the wild stock. While some fraction of naturally produced fish may also be infected with the same endemic pathogens, there may be times or circumstances when highly infected hatchery fish will be in close proximity with wild stocks having lower levels of infection. In such cases, concerns about disease transmission from hatchery to wild fish have been raised. One example is the possibility of increased disease transmission during barging of salmon around dams in the Columbia River, where both wild and hatchery-reared salmonids are held together in close proximity and in a relatively stressful environment during collection and transportation (Elliott *et al.*, 1997).

5.4.3.4. *Reservoir for exposure of wild fish at abnormal times*   Another way in which a fishery enhancement or conservation hatchery might affect the health of wild fish is to serve as a long-term reservoir of infection. In this way, captive stocks that are chronically infected might continually release, albeit at low levels, pathogens that could initiate infections among wild fish

during life stages in which they are most susceptible or do not normally encounter the pathogen in nature. For example, in western North America, IHNV is commonly found in spawning adult sockeye and is spread among these highly susceptible fish through the water where high levels of virus have been detected (Mulcahy *et al.*, 1983). Out-migrating fry are also highly susceptible to infection with IHNV, but by the time of fry emergence, adult carcasses have largely been removed from the system and the infection pressure on fry is low. A hatchery that provided a significant source of IHNV to the watershed at these times could have an adverse effect on this highly susceptible life stage in a manner not typical in nature.

5.4.3.5. *Genetic effects of hatchery releases on disease resistance of wild stocks*   There are several methods by which hatchery operations could affect the innate disease resistance of wild stocks, including the stock or strain chosen for rearing in the hatchery. While less common at hatcheries using local stocks and exercising care to prevent inbreeding, stocks of hatchery fish having lower resistance to endemic pathogens could spread less favourable alleles at genes involved in resistance following interbreeding with wild fish (Currens *et al.*, 1997; Lawlor and Hutchings, 2004). This effect might be more likely for hatchery stocks having relatively modest differences in susceptibility compared to wild stocks because hatchery programmes choosing to rear and release stocks with significantly lower disease resistance than the wild stock have experienced very poor returns when such hatchery stocks undergo intense negative selection by endemic pathogens such as *Ceratomyxa shasta* (Bartholomew, 1998).

There is an increased effort to determine the genetic basis of disease resistance in fish. As an example, some alleles have been identified that are associated with increased resistance to IHNV, while others are associated with increased susceptibility (Miller *et al.*, 2004). Thus, even if local stocks are used, it is possible that hatcheries with highly effective disease control methods for endemic pathogens (e.g., a pathogen-free water supply) may provide a form of relaxed selection, leading to a greater frequency of alleles associated with susceptibility among the population of hatchery fish. If large numbers of these fish are released and do not encounter sufficient levels of infection in the wild, they can be expected to survive and return. If these hatchery fish are allowed to spawn with the wild stock, this relaxed selection might, over time, lower the overall resistance of the population.

While the genetic diversity of populations helps ensure survivors, hatchery diseases can exert intense selection. Some hatchery stocks that were founded from a natural population have been shown to have significantly greater resistance after a few generations of selection by disease (e.g., Chinook salmon in the Great Lakes). Such strong selection by one pathogen may be accompanied by a loss of resistance to a second pathogen (Hard *et al.*, 1992).

5.4.3.6. Release of unexposed stocks from hatcheries   Hatcheries with effective disease control programmes and a source of pathogen-free water are able to rear and to release large numbers of uninfected fish. While this is generally assumed to be highly desirable, these unexposed fish may remain susceptible and could become infected with certain endemic pathogens following release. If large numbers of such fish suffer a significant disease outbreak while co-habiting with wild stocks (e.g., during barging operations), they could generate sufficient infection pressure to produce an added risk to the unexposed portion of the wild stock; although the magnitude of this risk is unknown. Such fish, infected later than their wild cohort, could also serve as carriers during in-river or ocean migration to infect portions of the wild stocks in areas where the disease is not endemic or at times at which it does not normally occur.

5.4.3.7. Introduction of pollutants or stressors that alter disease ecology   A final method by which hatcheries could increase disease risk to wild stocks is by altering the ecology of a watershed. Naturally, this would be most likely for large hatcheries on small watersheds (Tervet, 1981). Effects could range from changes in stream temperature by large inputs of hatchery water, or phosphorous or organic matter that can increase algal growth or lower dissolved oxygen levels. Such stressors could be expected to affect the host–pathogen relationship for endemic diseases among wild fish.

Naturally, different types of hatcheries will show differing levels of these effects. In fact, each situation is probably unique. Compared with commercial aquaculture, conservation hatcheries can be expected to have significantly fewer of the most serious risks because they typically do not transport fish from outside the watershed and because they rear species, stocks and life stages that are usually derived from local, wild stocks. Nevertheless, additional research to assess the magnitude of these risks is needed.

5.4.4. Approaches to reduce effects of disease in hatcheries
Unlike their wild counterparts, there are many approaches that can be used to control the risk or reduce the severity of infectious diseases among hatchery fish. The choice, however, will depend to a significant degree on the type of facility involved. For example, disease control strategies that substantially increase overall costs tend to find few applications in commercial aquaculture but may be very appropriate for conservation hatcheries attempting to help recover threatened wild stocks. Hatcheries involved in recovery of local stocks are usually not involved with the movement of fish from distant watersheds and the associated risk of the introduction of exotic pathogens or new strains of existing pathogens. For these facilities, good fish health practises include good sanitation, sound nutrition, regular health examinations and disease monitoring (American Fisheries

Society, 2004; Winton, 2001). Further benefits can be achieved through reduction of stress by controlling fish density, water flow and temperature (Wedemeyer, 1998), and, when necessary, by careful application of drugs and chemicals (Stoskopf, 1993), vaccines (Leong and Fryer, 1993; Newman, 1993) or immunomodulators (Iwama and Nakanishi, 1996). Whenever possible, improvements to hatchery facilities should be a high priority, including using a pathogen-free water supply or disinfecting of incoming water (e.g., with ozone or ultraviolet light) and effluent treatment in some cases.

5.4.5. Application of risk assessment tools for disease management and control

In recent years, a topic of increasing interest is the application of the tools of risk assessment to the management and control of aquatic animal diseases (Bartholomew *et al.*, 2005; Office International des Epizooties, 2003). In addition to assessing the risk of the introduction, establishment and likelihood of adverse effects from the spread of a disease into a new geographic area via the movement of fish, the principles and methods of risk assessment can also be applied to help analyse ways to reduce disease risks for wild fish. While the reduction of disease in hatchery fish can lead to lowered risk for wild fish, the idea is not to simply compare the risks of hatcheries versus natural rearing, but to assess the various types and levels of risk posed by different strategies and to identify factors under management control that can affect risk.

5.4.6. Future work and knowledge gaps

As can be seen, there is considerable uncertainty surrounding many aspects of the disease risk posed by hatchery operations to wild stocks. Additional research or effort is needed in the following areas:

1. Improved methods for the detection of important salmonid pathogens (including non-lethal sampling techniques) and increased disease surveys of wild fish stocks to gain a better understanding of the distribution and level of these pathogens in nature. Additional work is also needed to validate these standard methods to ensure uniformity.
2. Studies to determine the host specificity and virulence of various strains of important viral, bacterial, protozoan and fungal pathogens affecting both wild and cultured salmonids.
3. Research to better understand the genetic basis of host resistance among salmonids and to map these traits on the salmonid genome in order to identify the genes involved in susceptibility and resistance. Genetic tools are needed to assess the levels of diversity required to maintain healthy populations, the heritability of resistance to infectious disease of salmonids and the genetic changes associated with the development of

resistance, domestication and interbreeding between hatchery and wild fish.

4. New information on the nature of the innate and adaptive immune systems of salmonids, including development of novel tools and assays to assess the factors that control the susceptibility of various species and strains of salmonids to various classes of pathogens.

5. Research to develop new vaccines to protect fish in hatcheries. This includes new-generation vaccines (e.g., DNA vaccines) and novel delivery methods.

6. Improved knowledge of the environmental factors that affect the ecology of infectious diseases of wild salmonids.

7. Improved and standardized legislation to prevent introduction, movement or spread of exotic pathogens and strains of endemic pathogens between watersheds.

8. Information on the risk to wild fish from the various types and levels of pathogens released from hatcheries. This includes studies on the pathogen shedding rate from infected fish, the environmental stability of the agent, effective dose/infection pressure that occurs in the wild and the transmission efficiency between fish in the wild.

9. Develop methods of risk reduction for various modifications in facilities or operations. These include effluent treatment, vaccination, disinfection, disease management and stress reduction. Apply risk analysis approaches to the introduction of exotic pathogens. Analyse and compare pathways and risks from aquaculture, ballast water, anglers, birds and other factors.

5.4.7. Conclusions

Infectious disease is an important component of the environment that affects both wild and cultured salmonids. Infections of salmonids may occur in watersheds, estuaries and the open ocean and, where stocks or species of wild and hatchery-reared salmonids overlap, many of the same pathogens will be shared by both. While hatchery operations can have impacts on the level of disease in wild fish that range from devastating (e.g., introduction of exotic pathogens) to inconsequential, the origin of infectious disease in hatcheries is nearly always from the aquatic environment itself or from reservoirs of infection that are maintained among free-ranging wild stocks. Additionally, the application of sound hatchery management practises and application of effective disease control strategies can do much to reduce the disease risk to wild stocks. This is especially true for conservation hatcheries where threats from introduction of exotic pathogens or different levels of disease resistance are lessened by the use of local stocks. Nevertheless, additional research is needed to provide information to better understand and quantify the risks to wild fish from infectious disease.

6. Economic Perspectives on Hatchery Programmes

Salmon enhancement efforts programmes absorb large amounts of economic resources, and they often claim to provide substantial benefits in terms of commercial fisheries harvest, recreational fishing or conservation benefits. Because hatcheries constitute but one means of conserving wild broodstocks, or enhancing fisheries, economic assessments typically focus on estimating their costs and benefits, or their cost-effectiveness. The result can help salmon enhancement planners to select projects that achieve substantial results at reasonable cost. Successful economic assessments require comprehensive information on programme costs, reliable and quantitative measures of outcomes achieved and a means of measuring the economic value of outcomes. The assembling of reliable and adequate information covering all programme dimensions is relatively rare. Consequently, this section cannot provide a comprehensive economic summary of worldwide salmon hatchery programmes. It will lay out the basic conceptual framework for an economic assessment, summarize a handful of economic studies and provide some insight into complicating factors that make conclusive economic assessments difficult in practise.

Each of the salmon hatchery types that have been described in Section 1 has a characteristic operational pattern, incurs costs associated with operations and, frequently, a blend of objectives. Figure 2.24 provides a useful scheme for evaluating hatcheries by type of operation, based on broodstock origin (hatchery origin, wild origin or permanent captive broodstock), release location, release objectives and location where the adult hatchery fish return to a fishery or spawning site, and provides a basis for economic analyses of the operations. Project outcomes can be measured in physical
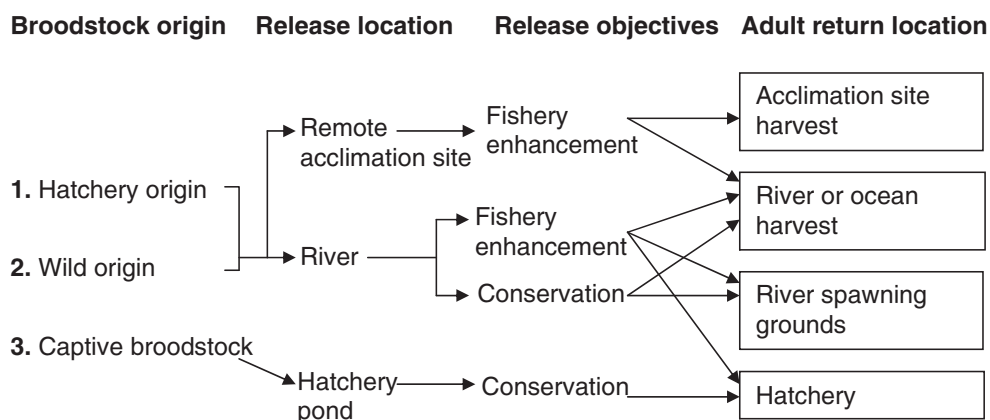
Figure 2.24 Depiction of various origins, handling routes and destinations for hatchery-spawned salmon.

terms (juveniles released, adult returns or size of broodstock preserved) as well as in economic terms (increased value of fisheries or benefits to the public). When enhancement projects are motivated by legal requirements or multi-purpose objectives that are not easily assigned an economic value, outcomes are expressed only in physical or biological units (e.g., number of returning spawners or increase in survival at some life stage). In such cases, it is useful to pursue cost-effectiveness analysis (CEA) of alternative projects or facility designs (see IEAB, 2002). The CEA reveals which projects provide the most performance for the cost incurred. When both project costs and economic benefit estimates are available, enhancement projects can be appraised via benefit-cost analysis (BCA). The BCA approach is most applicable for programmes that aim to augment or enhance fisheries or to establish or protect a salmon run with known value to people. To better inform policy makers, both BCA and CEA may need to be augmented by evaluation of other consequences such as regional employment or income impacts to account for broader socio-economic consequences (Fraser and Friedlander, 1980).

We could find few examples of economic analyses in Europe, and therefore we focus this discussion on SEPs in western North America. These programmes include private and public hatcheries that release juvenile fish for both enhancement of fisheries and conservation of wild stocks. For example, Wahle et al. (1974) and Wahle and Vreeland (1978) evaluated the Columbia River enhancement programmes, Boyce et al. (1993) assessed Alaska's salmon hatchery programme based on the increased economic value of the fisheries and Pearse (1994) evaluated costs and benefits of diverse projects in the salmon stock enhancement programme in British Columbia. In this chapter, we review some of these studies and comment on the use of economic evaluation of the hatchery and other enhancement facilities. Economic assessment methods can be applied to any form of salmon stock enhancement, including riparian habitat restoration and fish passage improvements (Paulsen and Wernstedt, 1995; Willis et al., 1998; Wu et al., 2000). Generally, an economic assessment is contingent on, and may be severely limited by, the availability of quantitative predictions of key biological outcomes of enhancement projects. Where the effects of enhancement projects on salmon populations cannot be quantified, an economic assessment may be premature.

6.1. Measuring costs, effectiveness and benefits

6.1.1. Costs
Project costs include both capital costs and annual operating costs. The capital costs comprise all initial and periodic investment expenses associated with planning, design, construction, equipment installation and replacement and land acquisition for the facilities. Operating costs involve salary

and wages, personnel benefits, transportation, utilities and routine maintenance associated with the activities of trapping and holding adult spawners, hatching eggs, rearing fry and juveniles, maintaining water supply and quality, and research and monitoring. The costs are typically revealed in budget documents of the responsible agencies, but annual budgets often do not place expenditures in the accounting categories needed for economic analysis. Agencies rarely maintain accurate capital investment and depreciation accounts, and the lack of this information makes project assessment difficult. Also, administrative, monitoring and research costs are often assigned to separate offices rather than to individual hatchery operations. To provide an accurate synopsis of individual hatchery programmes, the costs that are shared among a number of hatcheries (often administration and research) need to be allocated on some basis to individual projects. To properly account for capital costs, both start-up costs and periodic maintenance or replacement costs of a facility need to be annualized over appropriate time spans. This is typically done by treating the capital cost as the principle on a loan, and calculating the annualized capital cost as equivalent to the payment required to pay off (or amortize) the loan over a specified period. For example, the capital cost could be annualized over a 30-year period with an annual interest rate of 5%. Annualizing the capital cost facilitates comparison of annual costs (operating and capital costs) with the value of the hatchery's contribution to the fishery.

The full costs may be assembled into a summary table, displayed in accounting categories (such as labour, materials, transportation, utilities, feed, maintenance, capital expense). Where costs for a large number of similar projects are available, the results may be a statistically derived functional relationship between total or component project costs and fish release numbers, fish species, hatchery type, location and other variables that influence costs (Loomis and Fix, 1999). The accounting display provides a detailed snapshot of a particular project (or class of projects), while the functional cost equation provides a means to forecast how costs vary with hatchery size or design.

6.1.2. Effectiveness

Effectiveness should be measured to reflect the main purpose, or purposes, of the enhancement project. A fishery enhancement hatchery could be judged by the magnitude of the run size increase or harvest contribution. A conservation hatchery might be judged by the magnitude of increase in a wild salmon population. To be a useful planning device, CEA must incorporate information from a range of alternative enhancement projects. If a fixed budget for enhancement were available, a cost-effective group of projects would be those that achieve the most effectiveness for the budget. On the other hand, if a fixed enhancement objective were firmly established, the CEA would assist in selecting a mix of projects that achieves that

objective at lowest cost—that is, a programme that meets the objective cost-effectively.

Measuring the contribution of a hatchery to the size of salmon populations is a difficult research task, involving tag release and recapture data, smolt–to–adult survival estimates, harvest rate estimates (often for several geographically separate and mixed–stock fisheries) and hatchery return and straying estimates. Further, where a hatchery brood interacts with wild stocks or other hatchery stocks (via competition for food and space, disease transmission or interbreeding and genetic modification), the contribution of the hatchery to run size and harvests must be adjusted to account for possible negative changes in the other stocks. When a hatchery depends on continued capture of natural spawners for broodstock, the net increase in run size attributed to the hatchery should reflect the hatchery-origin run minus any reduction in natural spawning run.

6.1.3. Benefit-cost analysis

BCA tackles the more complex task of estimating economic value of the project outcomes. For production hatcheries aimed at commercial fishing (e.g., the Alaska SEP), the benefit is simply the net economic value of increased fish harvests (i.e., sales value minus increased harvesting cost). Where recreational fisheries take some or all of the fish, recreation benefits can be assessed using recreational demand models based on the travel cost method (see Brown *et al.*, 1983) or one of the more sophisticated recreational choice models (see Berman *et al.*, 1997). Subsistence fishing, especially treaty-obligated fishing by Native peoples, presents a more difficult conceptual task that has, frankly, not been addressed adequately by salmon economics research. Further, people who appreciate the existence or preservation of unique salmon runs hold non-use values, which do not depend on harvesting fish. Non-use values can be assessed using actual or hypothetical payments in response to questions posed in surveys, using the contingent valuation method (see Bell *et al.*, 2003). In some circumstances, salmon enhancement projects may sometimes produce all four types of benefits—commercial, recreational, subsistence and non-use value—making the benefits assessment a challenge. Further, conservation hatcheries typically provide benefits through an increase in wild stocks, and all the types of economic benefits would be applicable to these as well.

6.2. Cost-effectiveness of hatchery programmes

Two recent attempts at CEA serve to illustrate the method and the complications associated with the method. The Northwest Power Planning Council's Independent Economic Analysis Board (IEAB, 2002) assessed cost-effectiveness of six hatchery programmes and one acclimation and release programme in the Columbia River Basin. The IEAB's objective

was to provide advice regarding expenditures in the Council's Fish and Wildlife Programme, which spends roughly $40 M a year on salmon enhancement projects. The initial phase of that work studied five ongoing production hatcheries, including a lower river fall Chinook hatchery; an upper Snake River summer Chinook hatchery in Idaho; a multi-hatchery complex in the upper Columbia at Leavenworth, Washington; a steelhead hatchery in the mid-Columbia and a fall Chinook hatchery operated by a public utility district. The resulting short report and technical appendix (IEAB, 2002) were reviewed by the agencies and other technical staff. At about the same time, the Audits Division of Oregon's Secretary of State examined Oregon's hatchery programmes for cost–effectiveness. This study focused on 12 coho and Chinook hatcheries in western Oregon (Oregon Secretary of State, 2002). In both of these reports, each project was characterized by total releases, estimated smolt–to–adult survival, estimated total catch (all fisheries combined) and annualized costs. The costs are summarized in three forms: cost per fish (or pound) released, cost per adult survival and cost per adult caught. As with the BCAs discussed below, neither of these CEAs incorporates the effects of hatchery fish impacts on wild stocks.

An example of this type of economic analysis pertains to a salmon hatchery in McCall, Idaho, operated for fishery enhancement by the US Federal government. The hatchery rears summer Chinook in a facility with 2, large outdoor ponds, 14 indoor rearing tanks and incubation facilities. Initial construction costs in 1981 for the facilities were $5,453,000. Updating this fig. to 2000 by applying the US Gross National Product (GNP) price deflator yields a capital cost of $10,755,424. Annualizing this cost over 50 years at a 3% interest rate generates an estimated annual capital cost of $418,015. The costs and the production of smolts, the smolt–to–adult survival rates (SARs) and harvest rates were obtained for a 13–year period, brood years 1984–1997. The average cost per smolt released for that period was $1.09, the average cost per adult fish returning (to the fishery or the hatchery) was $271.80 and the cost per fish caught in the fishery was $1051.01. This cost occurred during a period of time when the salmon were experiencing relatively low ocean survival rates. The cost might be significantly lower during other periods of time.

The IEAB research results found that the costs per smolt (measured in 2001) varied from $0.08 for fall Chinook (sub–yearling smolts) released at a mid–Columbia public utility district hatchery to $2.60 for Chinook released as yearling smolts from the Nez Perce tribal hatchery. Based on both the data and discussions with hatchery managers, the IEAB found that the cost of producing sub–yearling smolts (fall Chinook) was substantially lower than cost per yearling smolts (spring and summer Chinook, steelhead, coho) for the obvious reason that the yearlings are reared and fed for a longer period. The cost per adult survivor ranged from a low of $12 for mid–Columbia fall Chinook to $3707 for spring and fall Chinook from the Nez Perce tribal

hatchery. Again, the two lowest cost per adult estimates were for fall Chinook hatcheries. Finally, using estimated contribution rates to fisheries, the cost per adult fish caught ranged from a low of $23 for Priest Rapid fall Chinook to $68,031 for spring Chinook from an upper Columbia river hatchery on the Entiat River. The wide range of cost-effectiveness estimates suggest that reallocation of funds to better-performing facilities would offer an opportunity to achieve more harvest enhancement per dollar spent. On the other hand, the fig. for cost per harvest were the least reliable of the cost-effectiveness measures because the sampling of tags from in-river fisheries was of unknown accuracy. Further, the Nez Perce tribal hatchery has just begun production and has focused on supplementation (conservation) of local runs, not harvest per se. The objective of that programme is not simply to produce some fish for catch somewhere but to produce a particular sub-stock returning to a particular tributary. Hence, comparability across hatch-eries is not as transparent as the numbers might suggest.

The Oregon cost-effectiveness audit found cost per pound of fish released to vary from $4.08 to $9.09 (measured in 2001); cost per adult survivor (hatchery return plus catch) ranged from $14 (Salmon River fall Chinook) to $530 (coastal coho at Bandon, Oregon) and cost per adult caught ranged from $27 (Salmon River fall Chinook) to $1442 (coastal coho at the Trask River). As with the Columbia Basin hatcheries, yearling releases are more expensive than sub-yearling releases, and the cost per fish caught depends strongly on both SAR and harvest rate. Harvest rates in Oregon salmon fisheries are geared to protect the weak stocks, and they have been tightly regulated in recent years to protect coastal coho and Columbia River Chinook stocks that are listed as threatened or endangered under the Endangered Species Act. Hence, a hatchery with a reasonably low cost per adult survivor may have a high cost per adult caught simply because their fish mix with protected wild fish and harvest rates are kept low. To change the locations or operations of hatcheries to improve the future harvest rate (and to lower the cost per catch) would require adapting to future fishing regulations that will respond to perceived depletion of various salmon runs with shorter fishing seasons and lower catches.

One way to lower the cost per fish caught would be to move the smolts from the hatchery location to an acclimation site away from protected stocks, with the intent of getting the fish to return to a site where they can be fished at a high rate. The Clatsop County Economic Development Council in Oregon funded a project of this sort starting in 1977 to enhance the lower Columbia River gillnet fishery. In recent years, this project has acclimated salmon in net pens in Young's Bay, west of Astoria (IEAB, 2002). The programme includes fall and spring Chinook and coho from various sources and fish are released at sites in the Columbia River estuary. The cost per fish caught from the programme range from $14 for coho to $233 per spring Chinook.

6.3. BCA of hatchery programmes

An early BCA of salmon hatcheries was conducted by the US National Marine Fisheries Service on the Columbia River Development Programme (Wahle and Vreeland, 1978; Wahle *et al.*, 1974). These studies were tied to very ambitious mark–recapture research efforts that provided estimates of hatchery contributions from 13 Chinook and 20 coho hatcheries to ocean and river fisheries. The ocean fisheries ranged from southeast Alaska to California, and the river fisheries include commercial gillnet, sport fishing and Native peoples' fishing. Total estimated contributions to coho harvests were 1.13 and 1.05 M fish for the 1965 and 1966 brood years, and contributions to Chinook harvests ranged from 11,000 to 602,000 fish for brood years 1963 through 1966. The capital costs (costs associated with design and construction of the facilities) were annualized over 30 years at a 3.5% interest rate. Operating costs were compiled for the spawning, hatching and rearing for two brood years of coho salmon (1965 and 1966) and four brood years for Chinook salmon (1963–1966). The commercial harvests were valued by multiplying the number of fish contributed to harvest, multiplied by the estimated weight per fish and the current ex-vessel price. Recreational harvests of coho were valued by dividing the economic value per angler day of $20 (estimated by Brown *et al.*, 1983) by catch per day and then multiplying by number of fish caught by sport fisheries. Recreational harvests of fall Chinook were valued at a straight $18.35 per fish.

Overall, Wahle *et al.* (1974) estimated economic benefits for the coho fisheries at $9.07 and $8.51 M for the two brood years. When compared to the coho hatchery costs of $1.29 and $1.23 M, the benefit-cost ratios were 7.4 and 6.6 for the 1965 and 1966 brood years, respectively. For the fall Chinook hatchery programme, annual estimated benefits ranged from $1.3 to $5.2 M, while the annual hatchery costs fell in a narrow range of $659,000–$748,000. Benefit-cost ratios for the fall Chinook hatcheries ranged from 2.0 for the 1962 brood year to 7.2 for the 1963 brood year, and had a 4-year average of 4.2. Of equal interest is the estimated variation in benefit-cost ratios for individual hatcheries that ranged from 11.2 for the Spring Creek hatchery to 0.3 for the Elokomin hatchery (1961 brood year only). In principle, reliable estimates of benefit-cost ratios for individual hatcheries, or even individual batches of fish within a hatchery, could be used to score and rank the underlying rearing regimes, locations and species. This information would feed into subsequent decisions regarding design and allocation of funds within the hatchery programme.

A drawback of these Columbia River hatchery studies is the use of ex-vessel price for economic value per pound of harvest. The logic for this procedure, outlined in Wahle *et al.* (1974), is that because the hatcheries are augmenting the harvest of an open access and economically inefficient fishery, the additional catch will add little or nothing to the harvesting cost.

Normally, economists would subtract additional harvesting cost from the additional catch, assuming that an increase in gross revenue from the fishery (especially in an open access fishery like the salmon fisheries of the 1960s) would attract additional fishing effort, thus increasing costs. Had this been done for these hatchery projects, the benefit–cost ratios would have been substantially lower.

The State of Alaska began a major SEP in the early 1970s, encompassing both state-run projects, under the new Division of Fisheries Rehabilitation Enhancement and Development (FRED) of Alaska Department of Fish and Game, and PNP hatcheries owned and operated by regional aquaculture associations (see also Section 5.3). During 1972–1992, the State appropriated $210.3 M to the new FRED division, and total expenditure by PNP hatcheries was just over $200 M (Boyce et al., 1993). About 42% of PNP funds came from the State and the rest came from landings fees and cost-recovery fisheries. Cost-recovery fisheries, which are organized by the PNP hatchery associations, involve contract harvest for the association with sales revenue used to cover the costs of operating the hatcheries. In 1992, the Alaska State Senate sponsored the research reported by Boyce et al. (1993) in order to evaluate seven alternative actions being considered, including eliminating the pink and sockeye salmon hatcheries, and increasing or decreasing the two species' production levels by 15%.

The BCA analysis was approached using an Alaska accounting stance (Boyce et al., 1993), that is, only costs and benefits accruing to Alaska fishermen, processors and agencies were counted. The authors used a biological model (Collie, 1993) to project catches by species and region over a 30-year time period. The prices for salmon under each alternative were computed from an international salmon market model (Herrman, 1993), and the benefits to the fishing industry were defined as the total revenue from sales of fish minus the costs of harvesting the fish. The net economic benefits to the State equal the benefits to fishers minus the costs of the enhancement programme. With these assumptions and estimates they estimated the following 30-year, statewide totals for the existing system (Alternative 1): total catch (includes all wild and hatchery fish), 353 million kilograms; gross revenue, $557 M; benefit to industry, $222 M; hatchery costs, $23.4 M and net benefits of $199 M to Alaska.

The main results were associated with Alternatives 2 and 3, which eliminated the pink and sockeye salmon enhancement facilities, respectively. For Alternative 2 (eliminating pink salmon hatcheries), gross revenues dropped by $5.5 M, industry benefits increased by $9.7 M, hatchery costs dropped by $6.4 M and Alaska net benefits increased by $16.1 M. The implied negative net benefit from pink salmon hatcheries occurred outside of PWS, where major pink salmon hatcheries generate benefits for the local fishery. Alternative 3 (eliminating sockeye hatcheries) reduced gross revenues by $8.75 M, increased industry benefits by $ 8 M, decreased hatchery

costs by \$4.1 M and caused an increase in state benefits of \$12 M. Overall, this analysis suggested that Alaska would be better off economically without the pink salmon and sockeye salmon enhancement facilities. The report, however, warned that no recreational or subsistence fishing benefits were evaluated and that there may be some un-analysed strategic value to maintaining hatchery production to fend off the expanding salmon farming business in Europe and South America.

Canada's SEP in British Columbia was launched in 1977 with the objective of doubling salmon catches on Canada's Pacific coast through construction of hatcheries, spawning channels and other works. Over 17 years they spent \$526 M, built more than 300 facilities and expanded the fish harvests by roughly 14,000 metric tons, or 13% of the annual salmon catch. This was somewhat of a disappointment, given the ambitious goal of the SEP. A very broad and creative BCA was performed by Peter Pearse for the DFO's Internal Audit and Evaluation Branch (Pearse, 1994). The Pearse report followed a series of previous evaluations by a Royal Commission, a Ministerial Task Force and three previous audits.

Pearse (1994) estimated the catch contributions, gross and net harvest values (for commercial, Native and recreational fishing) and lifetime costs (construction and operating) for the SEP facilities. The catch contribution due to SEP was estimated at 17,361 metric tons (50% chum, 19% sockeye, 10% pink, 12% coho and 9% Chinook). These contributions were not adjusted to account for interactions between hatchery and wild stocks because Pearse (1994) was unsuccessful at getting a consensus expert judgement on the extent of interactions. For the commercial fishery, net benefits were the sum of three pieces: vessel owner benefits (50% of gross revenue minus crew share), crew benefits (crew share minus estimated labour cost, valued at mean wage) and cannery benefits (50% of wholesale value minus fish costs minus variable costs of canning operation). The Native fishery benefits were valued at the 1993 ex-vessel price, with no deductions for harvest costs. The recreational fishery was valued by multiplying increased coho catch by \$14 and increased Chinook catch by \$54. Finally, Pearse (1994) used an 8% interest rate to value past costs and benefits as of 1993 and to discount future costs and benefits (out to 2017) back to 1993. Overall, the estimated present value of SEP in 1993 costs (\$1.51 billion) exceeded the estimated net benefits (\$919.9 M) by \$592 M, leaving the programme with a benefit–cost ratio of 0.6. The benefit–cost ratios varied widely among enhancement projects; the spawning channels had a 2.2 benefit–cost and the lake fertilization projects a 1.3 benefit–cost ratio.

Pearse (1994) also provided a reasonable approach to additional decision making by dropping the past capital costs (the 'sunk' costs) and the benefits occurring before 1993. The result was an evaluation of the project from 1993 on, which is an important perspective for decision makers at that point in time. For this short-term decision framework, the benefit–cost ratio for

the overall SEP programme rose to 1.6, with a net benefit of $165.3 M. In other words, given that the costs of investing in the facilities are irretrievable, there are net benefits to continuing the programme over the expected lifespan of the facilities. If we could go back in time to the programme start-up date, possessing the economic assessment produced in 1993, we might decide not to start the programme at all. Further, because the report contains specific estimated benefits for each major project, it is useful information for planning and adapting the content of the SEP.

6.4. Complicating factors

Several conditions add to the complexity and unreliability of SEP evaluations in practise. First and foremost, measuring programme effectiveness is absolutely reliant on biological and ecological modelling and analysis. As is evident from other sections of this chapter, the full impact of hatchery releases on aggregate run size depends on interactions among stocks, and particularly the effects of hatchery smolts on wild smolts and the effect of straying hatchery-origin spawners on natural spawning populations. These effects are often only roughly quantifiable and frequently controversial among experts. The economic studies reviewed above basically assume that the hatchery run represents a net increase in the volume of salmon returns from the ocean, despite evidence that this is not true in some cases (Hilborn and Eggers, 2001). A second complication is that large volumes of returns to hatcheries can affect market prices for salmon, at least within the region impacted and during the harvest season (Herrman, 1993). When the market price varies with the hatchery output, the economic benefits to consumers should be measured as the increased consumer surplus (i.e., the increased area under the estimated demand curve as the price falls). This measure requires additional research on the market demand for the salmon products.

A third complication is that enhancement projects can have a range of complex objectives that defy even concerted attempts at quantification. Experimental and research hatcheries focused on supplementation of endangered populations that may contribute to the long-term survival of listed species. While economists have estimated non-use values for salmon protection and restoration (Bell *et al.*, 2003; Loomis, 1996), it remains difficult to attribute specific values to specific projects that protect narrow sub-populations with known levels of risk. Further, many of the hatcheries in the Columbia River Basin were authorized in conjunction with multi-purpose river development projects (hydropower dams and irrigation projects). The construction and operation of the hatcheries represent a portion of the multi-purpose project objective to preserve some specific salmon or steelhead runs in the affected tributaries. Some observers note that the associated costs are attributable to the other project objectives, and that

the trade-offs made in designing and authorizing the projects should not be recalculated later based solely on the performance of the hatcheries. There is necessarily a political balancing and negotiating aspect to these decisions that is not transparent in the economic analysis. Hence, the most that can be claimed for the economic assessment is that it is useful information for decision making when trade-offs among quantifiable objectives are being weighed.

6.5. Conclusions

Given the size and costs of public salmon hatchery-release programmes, careful and extensive benefit-cost and cost-effectiveness analyses would appear to have a useful role in salmon enhancement project selection and programme design. US Federal and State laws require that new programmes be evaluated for both environmental and economic consequences. However, salmon hatchery programmes have generally not been subjected to standard benefit-cost or cost-effectiveness analyses. Salmon hatcheries in the Pacific Northwest, British Columbia and Alaska are justified on other diverse grounds such as: (1) to mitigate for loss of spawning/rearing habitat, (2) to meet requirements of treaties, (3) to compensate for destruction of a natural salmon run via dam construction, (4) to augment commercial or recreational fishing and (5) to support threatened or endangered stocks. Only the short-lived commercial 'salmon ranching' operations in Oregon had the simple economic objective of producing harvestable fish that could sell for more than the cost of production. Hence, it is not surprising that the standard economic project evaluation techniques are rarely aimed at public salmon hatchery programmes. Nevertheless, it is also clear that SEP decisions strongly influence the magnitude of economic costs and benefits and that these decisions need not be made in ignorance of the economic consequences. The benefit–cost and cost-effectiveness analyses reviewed in this chapter show that a moderate research effort, using information normally collected for hatchery fish monitoring and budgetary purposes, can provide a reasonably constructed economic assessment of SEPs.

7. DISCUSSION

This chapter joins a growing number of papers that attempt to collate information on enhancement activities (National Research Council, 1996) and to evaluate the available evidence for the biological effects of such activities. We have presented the historical context and political underpinnings of hatchery programmes, reviewed the current level of releases from hatchery facilities in the North Pacific and Atlantic, discussed possible

outcomes of interactions between hatchery and wild fish and have evaluated economic issues associated with the design and running of hatchery programmes.

Broadly, our chapter points to three major issues. First, decisions to initiate or sustain hatchery programmes are typically motivated by political objectives, which are rooted in historical contexts. These decisions are infrequently revisited and are rarely driven by biological or ecological reasoning. A holistic view of the effects of the production of salmonids on the ecosystem has not, in most cases, been taken into consideration. Rather, the effects have tended to be viewed in isolation. Second, there remains a dearth of information on the consequences of interactions between wild and hatchery fish despite the fact that hatchery programmes have been operating for since the nineteenth century. Third, the outcomes of hatchery releases and management steps are not fully understood because robust, systematic and coordinated scientific assessments are rare.

Such broad statements, of course, are only constructive when key gaps in the state of knowledge are identified, and placed in context of the objectives of conservation and fishery–enhancement hatchery programmes. We attempt this task here, while acknowledging that reviewers examining the same data sets often reach different conclusions (e.g., Brannon *et al.*, 2004a; Myers *et al.*, 2004). Nevertheless, recent political events have motivated individual scientists and advisory groups to formulate guidelines for the management of these types of hatcheries (Mobrand *et al.*, 2005; Waples and Drake, 2005), and we examine below some of these guidelines in the context of our assessment of the major knowledge gaps in the field.

7.1. Release objectives and release sizes

We initiated the review by providing a classification system for enhancement activities in recognition of the fact that differing objectives for hatchery programmes would lead to a range of biological outcomes. We then pointed out that these objectives have rarely been identified and subsequently enacted upon (Section 4). Without these defining objectives, individual programmes cannot be held accountable if they do not have a clear set of measurable guidelines. The same issue has been raised by a number of authors (Waples and Drake, 2005; Waples *et al.*, 2007), and has been identified as a key guiding principle in formulating recommendations for hatchery programme reform (Mobrand *et al.*, 2005).

We noted an absence of standardized approaches towards the collection and archiving of data on hatchery release sizes. This outcome is not surprising since hatchery activities are defined by political boundaries. We also noted that data quality varied across the countries we surveyed. Reporting would be most useful to the scientific community if the release goals of hatchery programmes were clearly identified and if attempts were

made by the international community to centralize release data in a readily accessible format. The effects of hatchery programmes likely transcend watersheds and international boundaries and the development of a clear understanding of the extent of these effects would be well served by the collation of large data sets. It is particularly important to identify the relevant scale at which this data should be collected. Ideally, data sets should be collated hierarchically; levels of production and survivorship should be reported at the freshwater, estuarine and oceanic stages. Hierarchical data sets will be valuable for identifying the relevant scales over which interactions between hatchery and wild fish should be appraised. Finally, we noted that the effects of hatchery releases on the ecosystem were difficult to evaluate because of the paucity of data collected at this level.

7.2. Interactions between hatchery and wild fish

The literature on interactions between wild and hatchery fish was examined by exploring genetic effects, competition, harvest interactions and disease transmission. We acknowledged that this list was incomplete, but we also noted that there have been few concerted experimental approaches to understanding the outcomes of these interactions.

7.2.1. Genetic issues

Most examples of the genetic interactions between hatchery and wild fish have been retrospective and case specific, and have rarely been defined in terms of their release goals. While these studies point to a frequent outcome—that releases are often detrimental or unsuccessful—there is still a strong need to gain an understanding of the degree of risk posed by hatchery fish, and whether these risks can be reduced by correct management. Recent experimentation and a change in philosophy towards solution-based research appear promising. Part of the problem associated with research in this area is that most experiments require several generations of returning adults, and the resources needed to complete such experiments have seldom been available.

Relatively new guidelines have been presented by a scientific advisory group in the Pacific Northwest (Mobrand *et al.*, 2005). One recommendation aimed at reducing genetic impacts is that hatchery broodstock be either integrated with, or segregated from, wild populations (Mobrand *et al.*, 2005). This guideline is based on theoretical treatments that examined changes in fitness traits with varying levels of migration between hatchery and wild fish (reviewed in Section 5.1; modified from the model proposed by Ford, 2002), and is aimed at preventing the negative outcomes of reproduction between wild fish and hatchery fish that have been subject to domestication selection. The authors also point out that issues such as genetic drift, inbreeding, changes in effective size (the Ryman–Laikre effect) and

outbreeding depression might be reduced by correct management of brood-stock collection, mating and rearing protocols and individuals released (Section 5.1; see also Waples and Drake, 2005).

The recommendations of Mobrand *et al.* (2005) promote active management approaches rather than risk-averse measures, and will likely be debated in the scientific community over the next few years. For example, it has been noted that the impact of an integrated release on a fine scale metapopulation structure is unknown (Utter, 2004), especially if the other components are demographically unstable. It is also uncertain whether hatchery fish may be practically segregated from spawning wild fish once they have been released to the wild, although it has been argued that domesticated, less fit individuals might pose lower risks (Utter, 2004). Discussion on new management approaches are likely to be lively in the coming years, but recommendations such as those proposed by Mobrand *et al.* (2005) provide a framework for future experimentation on 'problem solving' approaches, and such research is strongly supported here.

It is quite clear that genetic issues have been placed at the heart of the 'hatchery–wild' debate. If one concern has been identified in this chapter, it is that many hatchery programmes continue to be operated with few objectives, and with a poor understanding of the magnitude and importance of the impacts of genetic effects of hatchery releases and the role of this information in informing remedial actions. The field has been invigorated by recent hatchery reform initiatives, but management recommendations that are implemented broadly without an experimental approach and without identifying long-term goals will continue to perpetuate this problem, possibly with the negative consequences that have been widely reported to date.

7.2.2. Competition

We identified two key assumptions that are embedded in the philosophy underlying hatchery operations. The first assumes that captive rearing is appropriately directed at the most limiting life history stage. For many species, this limitation is not at the egg to smolt stage at which most operations are directed, but during the juvenile rearing period in freshwater streams or perhaps during their estuarine or early ocean stage. The second assumption is that competition between hatchery fish and their wild counterparts does not counteract the aims of the hatchery programmes. If, as was pointed out, the carrying capacity of the environment is limited (and this has been demonstrated in a broad range of studies in freshwater and a limited number in estuarine and marine environments), then competitive interactions between the two components can have negative outcomes.

The nature and level of behavioural interactions between hatchery and wild fish may vary with the type of hatchery programme. If conservation-based hatcheries are considered first, then the primary aim of recovering a

threatened population would be best served by producing hatchery fish whose distribution in physical form and life history characters (and, by implication, in genetic composition) does not differ from that of their wild counterparts. The simple notion would be that competitive interactions would not favour one component over the other. However, many programmes have been established to recover weakened populations without considering the underlying causes of the population decline, and specifically, which element of the habitat has proven limiting. Thus, releases of wild-type hatchery fish under this scenario may not result in the intended demographic boost if the original limitation is not addressed. Hatchery fish released for fisheries augmentation may differ from wild fish in a number of physical and life history traits and may differ in abundance. These differences can have complex outcomes, depending on the extent of spatial and temporal overlap between hatchery and wild fish.

Practically, authors have suggested that negative behavioural interactions can be avoided in a number of ways that depend on the nature of the hatchery programme (Mobrand *et al.*, 2005; Waples and Drake, 2005). If the aim is to segregate the hatchery fish from the wild, then interactions during early freshwater stages can be reduced by releasing smolts that migrate rapidly to sea or by producing larger smolts that utilize different habitats than the wild fish. Marine carrying capacity should factor into estimates of release size, although it is acknowledged that calculations based on this parameter are unlikely to be realistic over the short term and only relevant to changes in ocean regimes related to large-scale climate cycles (Mobrand *et al.*, 2005). Competition for spawning habitat may be eased by siting hatcheries away from spawning grounds and by maximizing imprinting to the hatchery itself. However, as was pointed out in Section 5.2, it is unclear to what degree competition and straying by hatchery fish on the spawning grounds can be alleviated by these measures, and generally, the locations of hatcheries are largely fixed.

While each of the approaches identified above may provide some solutions for segregated hatcheries, their utility is less clear for integrated hatcheries geared towards conservation because most of the steps will result in genetic differentiation between hatchery and wild components. For example, the release of fish larger than those found in the wild can be expected to change a suite of life history characters within the run, most notably age at maturity. The issue here is whether hatcheries can produce 'wild-like' fish in numbers that do not exceed the carrying capacity of the habitat and do not compromise the wild populations.

Our chapter collated a rapidly growing body of literature that points towards detrimental behavioural interactions between hatchery and wild fish. More is known about these interactions in freshwater rearing habitats than in estuarine and marine environments. There is also, however, a paucity of information on whether risk avoidance measures are effective at

reducing competition and predation and, as far as we know, little attention is directed towards carrying capacity when the size of release is considered.

7.2.3. Harvest

The impact of harvest on wild populations becomes important when fishery-based hatcheries are considered. In theory, increasing the survival of a specific life history stage will support elevated harvest rates on the hatchery component of the population. The success of the programme will rely on the efficient segregation of the hatchery fish from the wild, which in turn is largely dependent on where and when the fish are harvested. Although two types of fisheries are recognized—terminal fisheries near the mouth of a river and interception fisheries in open waters—in practise, both target mixed stocks (although the former fishery likely comprises fewer populations than the latter). Commercial demand favours fishing at sea because flesh quality is higher during this life history phase. Ocean stocks do, of course, include a mixture of separate spawning populations, and overproduction of hatchery fish can lead to overexploitation of weaker stocks (often wild fish) within this mixture.

Several solutions to the 'mixed-stock harvesting problem' have been identified. The most controversial would lead to over-exploitation of the wild stocks and dependence on the hatchery component of the run for the persistence of the species, or almost as contentious, the termination of all production hatchery programmes. Most management agencies have instead relied on reducing exploitation rates to those sustainable by the weaker wild stocks and on selectively harvesting hatchery fish, which relies on efficient mass marking.

The success in setting appropriate exploitation rates depends on the accurate identification of a wild 'stock' so that appropriate forecasting and in-season management can be implemented. In Europe, it is recognized that the use of genetically isolated units within rivers is impracticable, and groupings based on populations experiencing similar abundance trends are being implemented instead in some places (Crozier *et al.*, 2004). Researchers monitoring mixed populations of Pacific salmon in the high seas often depend on genetic definitions of stocks (Beacham *et al.*, 2004; Seeb *et al.*, 2004).

Selective fishing requires that hatchery fish are accurately identified and that the survival rates of hatchery fish are high prior to harvest. Mass marking methods have, to a large degree, been successfully implemented in North America when the marks are clearly visible. However, the use of approaches such as otolith marking does not permit identification of hatchery fish until they are dead and, thus, they are of limited utility.

Several data sources point towards mixed success in consistently producing hatchery fish with high survival rates. Shifts in ocean regimes and marine productivity affect these rates with unintended consequences. If survival

rates are low, then fisheries may inadvertently be redirected towards vulnerable wild stocks. On the other hand, excess fish escaping the fishery in a productive year can return to the spawning grounds, raising heated debates about the fate of those individuals (ISAB, 2002). In this case, interest groups have argued that returning hatchery fish can augment declining wild populations, but this view ignores the negative outcomes that are the subject of this chapter. Regardless, social dimensions often intervene, and fish from production hatcheries have been allowed to spawn in the wild in the past (examples given in ISAB, 2002). Finally, to our knowledge, there are no studies evaluating whether selective harvesting has been effective in reducing harvest risks to wild populations, and research on this issue is needed.

7.2.4. Disease

Historical movement of infected fish or contaminated eggs and the practise of using raw, unpasteurized salmon viscera as fish food have contributed significantly to the introduction or spread of many fish pathogens. However, awareness of these issues, implementation of strategies to control infectious agents in hatcheries and development of standards and guidelines for movement of aquatic animals have done much to reduce the spread of pathogens and the impact of infectious disease (Winton, 2001). The more controversial aspect of the 'hatchery-wild' debate is around the role of hatchery fish in amplifying and/or transmitting *endemic* pathogens to susceptible wild populations. While this issue is often raised as a criticism against hatchery operations, very little is actually known about this specific source of risk to wild fish.

Our lack of understanding in this area is explained partly by the fact that standard methods have been developed for the detection of fish pathogens (American Fisheries Society, 2004; Office International des Epizooties, 2003), there are few published studies that have determined levels of pathogens in populations of wild fish or in environmental samples and fewer still that have tried to assess the risk that infected hatchery fish or contaminated hatchery effluents might pose to wild populations. Current methods for epidemiological strain typing of pathogens typically cannot distinguish hatchery from wild origin, and thus it has been difficult to demonstrate the direction of transmission for pathogens affecting both hatchery and wild fish. Similarly, there is a poor understanding of the factors that control the ecology of infectious disease among populations of wild fish, the likelihood that wild fish will develop disease following exposure to a pathogen under natural environmental conditions or the effect of disease on the survival of salmonids in either freshwater or marine environments. What is clear from the few examples given in Section 5.4 is that the disease interactions between hatchery and wild fish are complex and may be case-specific.

Several approaches for reducing disease risks to wild fish include the following hatchery practises: sound sanitation, routine screening of spawning adults for pathogens, disinfecting fertilized eggs, maintaining families separately to reduce horizontal transmission and frequent disease monitoring during the rearing period. Additionally, lower rearing densities and good nutrition can reduce stresses that exacerbate disease. Finally, hatchery water supplies should be from pathogen-free source and the hatchery effluent treated, wherever feasible. Many of these practises are in place at a wide range of hatcheries (Waples and Drake, 2005).

In summary, the role that hatchery fish play in affecting the disease ecology of wild salmonid populations is highly equivocal. Research focused on the factors controlling the disease cycle in wild fish is needed to assist in determining the risk, if any, that hatchery fish pose to their wild counterparts.

7.3. Economic issues

To adequately consider the economic consequences of SEPs, at least two lines of inquiry need to be pursued further. First, the standard project evaluation and selection tools—BCA and CEA—are designed to assist in setting priorities and choosing projects for funding. As noted earlier, these emphasize efficiency in decision making and proper balancing of government funding when outcomes are quantifiable and economic consequences can be measured. Our review of past BCA studies shows that public salmon hatchery programmes generate economic consequences from high to low in terms of a benefit-cost ratio. By applying BCA to the sub-parts of the British Columbia salmon fishery enhancement programme, Pearse (1994) found some elements with high benefit-cost ratios even though the programme as a whole performed poorly by this standard. This information should assist in the selection of fishery enhancement projects that yield positive economic benefits. Existing CEAs show that hatcheries in the Columbia basin and Oregon have widely varying costs, ranging from $23 to $68,031 per additional fish caught. Clearly, where projects aim to increase fish harvests, hatcheries achieving a lower cost per fish represent a better public investment in fishery enhancement.

Because these objectives for conservation hatcheries and mitigation hatcheries (e.g., fishing opportunities for Native Americans) are less easily quantified in economic terms, BCA is less relevant to selecting projects of this type. Still, CEA is an appropriate decision tool where a range of alternatives is being considered for species protection or fisheries enhancement. Second, the project selection process inevitably triggers shifts in locations of government facilities and expenditures, and these fuel local economic impacts. Hence, impacts on small, rural communities become a focus for government decisions when salmon enhancement projects are

being considered. This brings the discussion of hatchery openings and closing directly into the political crossfire as those most likely to be affected raise their concerns through democratic processes. Overall, since little economic analysis has been included in the design and project selection process for SEPs, it is not surprising that these programmes are not demonstrated to be strong contributors to our economic prosperity. Inclusion of improved economic analysis in project design and selection could improve the situation.

7.4. Moving forward: Scientific and social dimensions

Most enhancement activities are operated under the principle of 'adaptive management' (Section 3), that is, that hatchery practises should change as new scientific information becomes available. Practically, attempts to address many of the knowledge gaps we identify in our review have only recently been implemented and thus hatcheries have been slow to reform. We note, too, that there has rarely been a coordinated and programmatic approach to managing hatcheries within a given region. Throughout this chapter, it has been difficult to identify whether hatchery risks are due to inherent biological problems or due to poor management decisions. This criticism is not new (Hilborn, 1992a; Rich, 1922). Rarely have programmes been set up to effectively track any question, and, although a difficult goal to fulfil, they have not generated sufficiently systematic data to prove success or failure.

In some cases, political developments have led to a growing number of attempts to reform hatchery practises. We mentioned earlier that an independent scientific panel was mandated to review hatchery programmes in the Pacific Northwest and provide broad recommendations and guidelines for reforming existing hatcheries (Mobrand *et al.*, 2005). The process identified several key guiding principles that the nature and objectives of hatchery programmes must be clearly identified and programme success be measured against these goals, that operations and establishment of programmes should be scientifically defensible and that hatcheries should respond rapidly to new information as it becomes available.

While few people will quibble with such clear recommendations based on scientific principles, it is important to consider the social and political contexts in which the recommendations were made (Section 1). The reader is reminded of the arguments presented on the political aspects underpinning hatcheries (Section 3); namely that it is not science, but economic and cultural issues that motivate hatchery programmes. The hatchery reform process inherently acknowledges *a priori* that hatcheries have a role to play in recovering threatened populations or in enhancing fisheries, and it is in this political framework that the science is conducted. The alternative, that all hatcheries be closed, is unlikely to be seriously considered in the near future.

Thus, the successful implementation of any scientific approach is dependent on sustained political support.

Recent attempts to reform hatchery practises are a positive move. However, if the political process does not include ongoing attempts to answer the key knowledge gaps (some of which are identified above) then hatchery management will not have the appropriate tools for long-term monitoring and will continue to be managed without a sound scientific foundation. Without these tools, the larger question of whether hatcheries can, in fact, support conservation and harvest activities while minimizing risks to wild populations in a socially acceptable framework will remain largely unanswered. (This is not a trivial question: the counting of hatchery fish in listing decisions under the Endangered Species Act has been debated in court, and has resulted in policy reformulations in the United States; *Alsea Valley Alliance v. Evans; NOAA Federal Register June 2005*.) It should be noted, too, that the reform process attempts to change the practises of existing programmes and should not be interpreted as an excuse for creating new ones. Yet this is a possible outcome. The social and economic processes driving hatchery reform will inevitably use different measures of success than will biological approaches, and the formulation of a set of recommendations may be seen as that success. It should be emphasized that the reform of hatchery practises inevitably involves trade-offs between different risks (e.g., reducing competition between hatchery and wild fish in freshwater by releasing hatchery fish at outmigration may increase genetic changes due to domestication; Waples and Drake, 2005). The weighting of these risks will likely occur at the societal level. Finally, it should be noted that the implementation of hatchery reform is limited to the regions of the world in which the tenor of the political debate is at its strongest. It is still unclear whether there is sufficient social impetus to implement such changes worldwide, and yet it is clear that they are needed.

7.5. Conclusions

We conclude by restating the intent of this chapter. The subject matter has focused largely on areas in which hatcheries could adversely impact wild stocks. We do not suggest that hatcheries should not have a role in salmon enhancement where their use represents an important means to recover critically endangered stocks. In Section 1, we list several populations (e.g., the Snake River Sockeye in the Pacific Northwest) that would be extinct without a captive propagation programme.

However throughout this chapter, it has been difficult to separate biological factors from social factors in problems associated with salmon hatchery programmes. Despite the fact that hatcheries have been operated over many decades, it is still unclear whether such activities can support conservation and fishery goals. A greater emphasis should be placed on

experimental approaches to reforming hatchery practises by conducting coordinated research within the existing and extensive hatchery system using appropriate controls. This research should be supported by a climate of active debate about the role of salmon hatcheries in today's society.

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