Further Reading

- Burgner RL (1991) Life history of sockeye salmon (Oncorhynchus nerka). In: Groot C and Margolis L (eds) Pacific Salmon Life Histories, pp. 2–117. Vancouver: UBC Press.
- Foerster RE (1968) The sockeye salmon, Oncorhynchus nerka. Bulletin of the Fisheries Research Board of Canada 162: 422.
- Groot C and Margolis L (eds) (1991) Pacific Salmon Life Histories. Vancouver: UBC Press.
- Healey MC (1991) Life history of chinook salmon (Oncorhynchus tschawytscha). In: Groot C and Margolis L (eds) Pacific Salmon Life Histories, pp. 312–393. Vancouver: UBC Press.
- Heard WR (1991) Life history of pink salmon (Oncorhynchus gorbuscha). In: Groot C and Margolis L (eds) Pacific Salmon Life Histories, pp. 120–230. Vancouver: UBC Press.
- Kals F (1991) Life histories of masu and amago salmon (Oncorhynchus masou and Oncorhynchus rhodurus).
 In: Groot C and Margolis L (eds) Pacific Salmon Life Histories, pp. 448–520. Vancouver: UBC Press.
- McDowell RM (1988) *Diadromy in Fishes*. London: Croom Helm.

- Mills DH (1989) Ecology and Management of Atlantic Salmon. London: Chapman and Hall.
- Mills DH (ed.) (1993) Salmon in the Sea and New Enhancement Strategies. Oxford: Fishing News Books.
- Mills DH (ed.) (1999) The Ocean Life of Atlantic Salmon. Oxford: Fishing News Books.
- Reddin D (1988) Ocean Life of Atlantic Salmon (Salmo salar L.) in the northwest Atlantic. In: Mills D and Piggins D (eds) Atlantic Salmon: Planning for the Future, pp. 483–511. London and Sydney: Croom Helm.
- Reddin D and Friedland K (1993) Marine environmental factors influencing the movement and survival of Atlantic salmon. In: Mills D (ed.) Salmon in the Sea and New Enhancement Strategies, pp. 79–103. Oxford: Fishing News Books.
- Salo EO (1991) Life history of chum salmon (Oncorbynchus keta). In: Groot C and Margolis L (eds) Pacific Salmon Life Histories, pp. 232–309. Vancouver: UBC Press.
- Sandererock FK (1991) Life history of coho salmon (Oncorbynchus kisutch). In: Groot C and Margolis L (eds) Pacific Salmon Life Histories, pp. 396–445. Vancouver: UBC Press.
- Thorpe JE (1988) Salmon migration. Science Progress (Oxford) 72: 345-370.

SALMONID FARMING

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Introduction

All salmonids spawn in fresh water. Some of them complete their lives in streams, rivers, or lakes but the majority of species are anadromous, migrating to sea as juveniles and returning to spawn as large adults after one or more years feeding. The farmed process follows the life cycle of the wild fish; juveniles are produced in freshwater hatcheries and smolt units and transferred to sea for ongrowing in floating sea cages. An alternative form of salmonid mariculture, ocean ranching, takes advantage of their accuracy of homing. Juveniles are released into rivers or estuaries, complete their growth in sea water and return to the release point where they are harvested.

The salmonids cultured in seawater cages belong to the genera *Salmo*, *Oncorhynchus*, and *Salvelinus*. The last of these, the charrs are currently farmed on a very small scale in Scandinavia; this article concentrates on the former two genera. The Atlantic salmon, Salmo salar is the subject of almost all production of fish of the genus Salmo (1997 worldwide production 640 000 tonnes) although a small but increasing quantity of sea trout (Salmo trutta) is produced (1997 production 7000 tonnes). Three species of Oncorhynchus, the Pacific salmon are farmed in significant quantities in cages, the chinook salmon (also known as the king, spring or quinnat salmon), O. tshawytscha (1997, 10000 tonnes), the coho (silver) salmon, O. kisutch (1997, 90000 tonnes) and the rainbow trout, O. mykiss. The rainbow trout (steelhead) was formerly given the scientific name Salmo gairdneri but following studies on its genetics and native distribution was reclassified as a Pacific salmon species. Much of the world rainbow trout production (1997, 430000 tonnes) takes place entirely in fresh water although in some countries such as Chile part-grown fish are transferred to sea water in the same way as the salmon species.

Here, the history of salmonid culture leading to the commercial mariculture operations of today is reviewed. This is followed by an overview of the requirements for successful operation of marine salmon farms, constraints limiting developments and prospects for the future.

History

Salmonids were first spawned under captive conditions as long ago as the fourteenth century when Dom Pinchon, a French monk from the Abbey of Reome stripped ova from females, fertilized them with milt from males, and placed the fertilized eggs in wooden boxes buried in gravel in a stream. At that time, all other forms of fish culture were based on the fattening of juveniles captured from the wild. However, the large (4-7 mm diameter) salmonid eggs were much easier to handle than the tiny, fragile eggs of most freshwater or marine fish. By the nineteenth century the captive breeding of salmonids was well established; the main aim was to provide fish to enhance river stocks or to transport around the world to provide sport in countries where there were no native salmonids. In this way, brown trout populations have become established in every continent except Antarctica, sustaining game fishing in places such as New Zealand and Patagonia.

A logical development of the production of eggs and juveniles for release was to retain the young fish in captivity, growing them until a suitable size for harvest. The large eggs hatch to produce large juveniles that readily accept appropriate food offered by the farmer. In the early days, the fish were first fed on finely chopped liver and progressed to a diet based on marine fish waste. The freshwater rainbow trout farming industry flourished in Denmark at the start of the twentieth century only to be curtailed by the onset of World War I when German markets disappeared. The success of the Danish trout industry encouraged a similar venture in Norway. However, when winter temperatures in fresh water proved too low, fish were transferred to pens in coastal sea water. Although these pens broke up in bad weather, the practice of seawater salmonid culture had been successfully demonstrated. The next major steps in salmonid mariculture came in the 1950s and 1960s when the Norwegians developed the commercial rearing of rainbow trout and then Atlantic salmon in seawater enclosures and cages. Together with the development of dry, manufactured fishmeal-based diets this led to the industry in its present form.

Salmonid Culture Worldwide

Fish reared in seawater pens are subject to natural conditions of water quality and temperature. Optimum water temperatures for growth of most salmonid species are in the range 8–16°C. Such temperatures, together with unpolluted waters are found not only around North Atlantic and North

Pacific coasts within their native range but also in the southern hemisphere along the coastlines of Chile, Tasmania, and New Zealand. Salmon and trout are thus farmed in seawater cages where conditions are suitable both within and outwith their native ranges.

Seawater cages are used for almost the entire sea water production of salmonids. A very small number of farms rear fish in large shore-based silo-type structures into which sea water is pumped. Such structures have the advantage of better protection against storms and predators and the possibility of control of environmental conditions and parasites such as sea lice. However, the high costs of pumping outweigh these advantages and such systems are generally now used only for broodfish that are high in value and benefit from controlled conditions.

The production figures for the four species of salmonid reared in seawater cages are shown in Table 1.

Norway, the pioneering country of seawater salmonid mariculture, remains the biggest producer of Atlantic salmon. The output figures for 1997 show the major producing countries to be Norway (331 367 t), Scotland, UK (99 422 t), Chile (96 675 t), Canada (51 103 t), USA (18 005 t). Almost the entire farmed production of chinook salmon comes from Canada and New Zealand with Chile producing over 70 000 tonnes of coho salmon (1997 figures). Most of the Atlantic salmon produced in Europe is sold domestically or exported to other European countries such as France and Spain. Production in Chile is exported to North America and to Japan.

Seawater Salmonid Rearing

Smolts

Anadromous salmonids undergo physiological, anatomical and behavioral changes that preadapt them for the transition from fresh water to sea water. At this stage one of the most visible changes in the young fish is a change in appearance from mottled brownish to silver and herring-like. The culture of farmed salmonids in sea water was made possible by the availability of healthy smolts, produced as

 Table 1
 Production of four species of salmonids reared in seawater cages

	1988 production (t)	1997 production (t)
Atlantic salmon Rainbow trout ^a Coho salmon	112377 248010 25780	638 951 428 963 88 431
Chinook salmon	4 698	9774

^aIncludes freshwater production

a result of the technological progress in freshwater units. Hatcheries and tank farms were originally operated to produce juveniles for release into the wild for enhancement of wild stocks, often where there had been losses of spawning grounds or blockage of migration routes by the construction of dams and reservoirs. One of the most significant aspects of the development of freshwater salmon rearing was the progress in the understanding of dietary requirements and the production of manufactured pelleted feed. The replacement of a diet based on wet trash fish with a dry diet also benefitted the freshwater rainbow trout farming industry, by improving growth and survival and reducing disease and the pollution of the watercourses receiving the outflow water from earth ponds.

It was found possible to transfer smolts directly to cages moored in full strength sea water. If the smolts are healthy and the transfer stress-free, survival after transfer is high and feeding begins within 1-3 days (Atlantic salmon).

The smolting process in salmonids is controlled by day length; natural seasonal changes regulate the physiological processes, resulting in the completion of smolting and seaward migration of wild fish in spring. For the first two decades of seawater Atlantic salmon farming, producers were constrained by the annual seasonal availability of smolts. These fish are referred to as 'S1s', being approximately one year post-hatching. This had consequences for the use of equipment (nonoptimal use of cages) and for the timing of harvest. Most salmon reached their optimum harvest size or began to show signs of sexual maturation at the same time of year; thus large quantities of fish arrived on the market together for biological rather than economic reasons. These fish competed with wild salmonids and missed optimum market periods such as Christmas and Easter.

Research on conditions controlling the smolting process enabled smolt producers to alter the timing of smolting by manipulating photoperiod. Compressing the natural year by shortening day length and giving the parr an early 'winter' results in S1/2s or S3/4s, smolting as early as six months after hatch. Similarly, by delaying winter, smolting can be postponed. Thus it is now possible to have Atlantic salmon smolts ready for transfer to sea water throughout the year. Although this benefits marketing it makes site fallowing (see below) more difficult than when smolt input is annual.

The choice of smolts for seawater rearing is becoming increasingly important with the establishment of controlled breeding programs. Few species of fish can be said to be truly domesticated. The only examples approaching domestication are carp species and, to a lesser degree, rainbow trout. Other salmon species have been captive bred for no more (and usually far less than) ten generations; the time between successive generations of Atlantic salmon is usually a minimum of three years which prevents rapid progress in selection for preferred characters although this is countered by the fact that many thousand eggs are produced by each female. Trials carried out mainly in Norway have demonstrated that several commercially important traits can be improved by selective breeding. These include growth rate, age at sexual maturity, food conversion efficiency, fecundity, egg size, disease resistance and survival, adaptation to conditions in captivity and harvest quality, including texture, fat, and color. All of these factors can also be strongly influenced by environmental factors and husbandry.

Sexual maturation before salmonids have reached the desired size for harvest has been a problem for salmonid farmers. Pacific salmon species (except rainbow trout) die after spawning; Atlantic salmon and rainbow trout show increased susceptibility to disease, reduced growth rate, deterioration in flesh quality and changes in appearance including coloration. Male salmonids generally mature at a smaller size and younger age than the females. One solution to this problem, routinely used in rainbow trout culture, is to rear all-female stocks, produced as a result of treating eggs and fry of potential broodstock with methyl testosterone to give functional males which are in fact genetically female. When crossed with normal females, all-female offspring are produced as the Y, male, sex chromosome has been eliminated. Sexual maturation can be eliminated totally by subjecting all-female eggs to pressure or heat shock to produce triploid fish. This is common practice for rainbow trout but used little for other salmonids, partly because improvements in stock selection and husbandry are overcoming the problem but also because of adverse press comment on supposedly genetically modified fish. This same reaction has limited the commercial exploitation of fast-growing genetically modified salmon, produced by the incorporation into eggs of a gene from ocean pout.

Site Selection

The criteria for the ideal site for salmonid cage mariculture have changed with the development of stronger cage systems, use of automatic feeders with a few days storage capacity and generally bigger and stronger boats, cranes and other equipment on the farm. The small, wooden-framed cages (typically $6 \text{ m} \times 6 \text{ m}$ frame, 300 m^3 capacity) with polystyrene flotation required sheltered sites with protection from wind and waves greater than 1–2 m high.

Recommended water depth was around three times the depth of the cage to ensure dispersal of wastes. This led to the siting of cages in inshore sites such as inner sea lochs and fiords. These sheltered sites had several disadvantages, notably variable water quality caused by runoff of fresh water, silt, and wastes from the land and susceptibility to the accumulation of feces and waste feed on the seabed because of poor water exchange. In addition, cage groups were often sited near public roads in places valued for their scenic beauty, attracting adverse public reaction to salmon farming.

Cages in use today are far larger (several thousand m³ volume) and stronger. Frames are made from either galvanized steel or flexible plastic or rubber and can be designed to withstand waves of 5 m or more. Flotation collars are stronger and mooring systems designed to match cages to sites. Such sites are likely to provide more constant water quality than inshore sites; an ideal salmonid rearing site has temperatures of 6-16°C and salinities of 32-35% (parts per thousand). Rearing is thus moving into deeper water away from sheltered lochs and bays. However, there are still advantages to proximity to the coast; these include ease of access from shore bases, proximity to staff accommodation, reduction in costs of transport of feed and stock and ability to keep sites under regular surveillance. Other factors to be taken into account in siting cage groups are the avoidance of navigation routes and the presence of other fish or shellfish farms. Maintaining a minimum separation distance from other fish farms is preferred to minimize the risk of disease transfer; if this is not possible, farms should enter into agreements to manage stock in the same way to reduce risk. Models have been developed in Norway and Scotland to determine the carrying capacity of cage farm sites.

Current speed is an important factor in site selection. Water exchange through the cage net ensures the supply of oxygen to the stock and removal of dissolved wastes such as ammonia as well as feces and waste feed. Salmon have been shown to grow and feed most efficiently in currents with speeds equivalent to 1–2 body lengths per second. In an ideal site this current regime should be maintained for as much of the tidal cycle as possible. At faster current speeds the salmon will use more energy in swimming and cage nets will tend to twist, sometimes forming pockets and trapping fish, causing scale removal.

Some ideal sites may be situated near offshore islands; access from the mainland may require crossing open water with strong tides and currents making access difficult on stormy days. However, modern workboats and feeding barges with the capacity to store several days supply of feed make the operation of such sites possible.

The presence of predators in the vicinity is often taken as a criterion for site selection. Unprotected salmon cage farms are likely to be subject to predation from seals or, in Chile, sea lions, and birds, such as herons and cormorants. Such predators not only remove fish but also damage others, tear holes in nets leading to escapes and stress stock making it more susceptible to disease. Protection systems to guard against predators include large mesh nets surrounding cages or cage groups, overhead nets and acoustic scaring devices. When used correctly these can all be effective in preventing attacks. Attacks from predators are frequently reported to involve nonlocal animals, attracted to a food source. Because of this and the possibility of excluding and deterring predators, it seems that proximity to colonies is not necessarily one of the most important factors in determining site selection.

A further factor, which must be taken into account in the siting of cage salmonid farms, is the occurrence of phytoplankton blooms. Phytoplankton can enter surface-moored cages and can physically damage gills, cause oxygen depletion or produce lethal toxins that kill fish. Historic records may indicate prevalence of such blooms and therefore sites to be avoided although some cages are now designed to be lowered beneath the surface and operated as semisubmersibles, keeping the fish below the level of the bloom until it passes.

Farm Operation

Operation of the marine salmon farm begins with transfer of stock from freshwater farms. Where possible, transfer in disinfected bins suspended under helicopters is the method of choice as it is quick and relatively stress-free. For longer journeys, tanks on lorries or wellboats are used. The latter require particular vigilance as they may visit more than one farm and have the potential to transfer disease. Conditions in tanks and wellboats should be closely monitored to ensure that the supply of oxygen is adequate (minimum 6 mgl^{-1}).

The numbers of smolts stocked into each cage is a matter for the farmer; some will introduce a relatively small number, allowing for growth to achieve a final stocking density of $10-15 \text{ kg}^{-3}$ whereas others stock a greater number and split populations between cages during growth. This latter method makes better use of cage space but increases handling and therefore stress. Differential growth may make grading into two or three size groups necessary. Stocking density is the subject of debate. It is essential that oxygen concentrations are maintained and that all fish have access to feed when it is being distributed. Fish may not distribute themselves evenly within the water column; because of crowding together the effective stocking density may therefore be a great deal higher than the theoretical one.

As with all farmed animals the importance of vigilance of behavior and health and the maintenance of accurate, useful records cannot be overemphasized. When most salmon farms were small, producing one or two hundred tonnes of salmon a year rather than thousands, hand feeding was normal; observation of stock during feeding provided a good indication of health. Today, fish are often fed automatically using blowers attached to feed storage systems. The best of these systems incorporate detectors to monitor consumption of feed and underwater cameras to observe the stock.

All of the nutrients ingested by cage-reared salmonids are supplied in the feed distributed. Typically, manufactured diets for salmonids will contain 40% protein (mainly obtained from fishmeal) and up to 30% oil, providing the source of energy, sparing protein for growth. Although very poorly digested by salmonids, carbohydrate is necessary to bind other components of the diet. Vitamins and minerals are also added, as are carotenoid pigments such as astaxanthin, necessary to produce the characteristic pink coloration of the flesh of anadromous salmonids. The feed used on marine salmon farms is nowadays almost exclusively a pelleted or extruded fishmeal-based diet manufactured by specialist companies. Feed costs make up the biggest component of farm operating costs, sometimes reaching 50%. It is therefore important to make optimum use of this valuable input by minimizing wastes. This is accomplished by ensuring that feed is delivered to the farm in good condition and handled with care to prevent dust formation, increasing the size of pellets as the fish grow and distributing feed to satisfy the appetites of the fish. Improvements in feed manufacture and in feeding practices have reduced feed conversion efficiency (feed input: increase in weight of fish) from 2:1 to close to 1:1. Such figures may seem improbable but it must be remembered that they represent the conversion of a nearly dry feed to wet fish flesh and other tissues.

The importance of maintaining a flow of water through the net mesh of the cages has been emphasized. Mesh size is generally selected to be the maximum capable of retaining all fish and preventing escapes. Any structure immersed in the upper few meters of coastal or marine waters will quickly be subjected to colonization by fouling organisms including bacteria, seaweeds, mollusks and sea squirts. Left unchecked, such fouling occludes the mesh, reducing water exchange and may place a burden on the cage reducing its resistance to storm damage. One of the most effective methods of preventing fouling of nets and moorings is to treat them with antifouling paints and chemicals prior to installation. However, one particularly effective treatment used in the early 1980s, tributyl tin, has been shown to have harmful effects on marine invertebrates and to accumulate in the flesh of the farmed fish; its use in aquaculture is now banned. Other antifoulants are copper or oil based; alternative, preferred methods of removing fouling organisms include lifting up sections of netting to dry in air on a regular basis or washing with high pressure hoses or suction devices to remove light fouling.

The aim of the salmonid farmer is to produce maximum output of salable product for minimum financial input. To do this, fish must grow efficiently and a high survival rate from smolt input to harvest must be achieved. Minimizing stress to the fish by reducing handling, maintaining stable environmental conditions and optimizing feeding practices will reduce mortalities. Causes of mortality in salmonid and other farms are reviewed elsewhere (see Mariculture Diseases and Health). It is vital to keep accurate records of mortalities; any increase may indicate the onset of an outbreak of disease. It is also important that dead fish are removed; collection devices installed in the base of cages are often used to facilitate this. Treatment of diseases or parasitic infestations such as sea lice (Lepeophtheirus salmonis, Caligus elongatus) is difficult in fish reared in sea cages because of their large volumes and the high numbers of fish involved. Some treatments for sea lice involve reducing the cage volume and surrounding with a tarpaulin so that the fish can be bathed in chemical. After the specified time the tarpaulin is removed and the chemical disperses into the water surrounding the cage. Newer treatments incorporate the chemicals in feed and are therefore simpler to apply. In the future, vaccines are increasingly likely to replace chemicals.

The health of cage-reared salmonids can be maintained by a site management system incorporating a period of fallowing when groups of cages are left empty for a period of at least three months and preferably longer. This breaks the life cycle of parasites such as sea lice and allows the seabed to recover from the nutrient load falling from the cages. Ideally a farmer will have access to at least three sites; at any given time one will be empty and the other two will contain different year classes, separated to prevent cross-infection.

Harvesting

Most of the farmed salmonids reared in sea water reach the preferred harvest size (3-5 kg) 10 months or more after transfer to sea water. Poor harvesting and handling methods can have a devastating effect on flesh quality, causing gaping in muscle blocks and blood spotting. After a period of starvation to ensure that guts are emptied of feed residues the fish are generally killed by one of two methods. One of these involves immersion in a tank of sea water saturated with carbon dioxide, the other an accurate sharp blow to the cranium. Both methods are followed by excision of the gill arches; the loss of blood is thought to improve flesh quality. It is important that water contaminated with blood is treated to kill any pathogens which might infect live fish.

Ocean Ranching

The anadromous behavior of salmonids and their ability to home to the point of release has been exploited in ocean ranching programs which have been operated successfully with Pacific salmon. Some of these programs are aimed at enhancing wild stocks and others are operated commercially. The low cost of rearing Pacific salmon juveniles, which are released into estuaries within weeks of hatching, makes possible the release of large numbers. In Japan over two billion juveniles are released annually; overall return rates have increased to 2%, 90% of which are chum (*Oncorhynchus keta*) and 8% pink (*Oncorhynchus gorbuscha*) salmon. The success of the operation depends on cooperation between those operating and financing the hatcheries and those harvesting the adult fish. The relatively high cost of producing Atlantic salmon smolts and the lack of control over harvest has restricted ranching operations.

See also

Mariculture Diseases and Health. Ocean Ranching. Open Ocean Convection. Salmon Fisheries: Atlantic; Pacific.

Further Reading

- Anon (1999) Aquaculture Production Statistics 1988–1997. Rome: Food and Agriculture Organization.
- Black KD and Pickering AD (eds) (1998) Biology of Farmed Fish. Sheffield Academic Press.
- Heen K, Monahan RL and Utter F (eds) (1993) Salmon Aquaculture. Oxford: Fishing News Books.
- Pennell W and Barton BA (eds) (1996) Principles of Salmonid Culture. Amsterdam: Elsevier.
- Stead S and Laird LM (In press) Handbook of Salmon Farming Praxis. Chichester: Springer-Praxis.
- Willoughby S (1999) Manual of Salmonid Farming. Oxford: Blackwell Science.

SALT MARSH VEGETATION

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Introduction

Coastal salt marshes are intertidal features that occur as narrow fringes bordering the upland or as extensive meadows, often several kilometers wide. They occur throughout the world's middle and high latitudes, and in tropical/subtropical areas they are mostly, but not entirely, replaced by mangrove ecosystems. Salt marshes develop along the shallow, protected shores of estuaries, lagoons, and behind barrier spits. Here, low energy intertidal mud and sand flats are colonized by halophytes, plants that are tolerant of saline conditions. The initial colonizers serve to enhance sediment accumulation and over time the marsh expands vertically and spreads horizontally, encroaching the upland or growing seaward. As salt marshes mature they become geomorphically and floristically more complex with establishment of creeks, pools, and distinct patterns or zones of vegetation.

Several interacting factors influence salt marsh vegetation patterns, including frequency and duration of tidal flooding, salinity, substrate, surface elevation, oxygen and nutrient availability, disturbance by wrack deposition, and competition among plant species. Moreover, the ability of individual flowering plant species to adapt to an environment with saline and waterlogged soils plays an important role in defining salt marsh vegetation patterns. Morphological and physiological adaptations that halophytes may possess to manage salt stress include a succulent growth form, salt-excreting glands, mechanisms to reduce water loss, such as few stomates and low surface area, and a C4 photosynthetic pathway to promote high water use efficiency. To deal with anaerobic soil conditions, many salt