Chapter 8

SMOLT PRODUCTION

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INTRODUCTION

Hatcheries for production of salmonids were well established during the latter part of the last century (*see* Chapter 1). For the most part, these pioneering efforts concentrated on the production of fry and fingerlings for release into streams. During the last four decades, large-scale hatchery programs involving rearing of smolts for release have been established in Europe, North America and Asia. More recently, a large international salmon farming industry has come to depend upon the production of millions of smolts for stocking into netpens and rearing to a marketable size.

"As the winter's chill is taken off the waters by the warm sun of spring, the fry grows and grows, escaping all kinds of dangers, and increasing in weight and strength, till it is gratefully recognized by the juvenile angler as the little parr, clad in a very gay livery, and which nobody believed, till lately, would ever become a salmon. An interesting episode occurs when the little fish attains the first year of its age – one-half of the shoal becoming smolts, eager for change of scene; the other half remaining in the parr state for a year longer" (Anonymous 1861).

When this description of juvenile development was written, naturalists were just beginning to understand the life cycle of Atlantic salmon (*Salmo salar*). More than a century later, we now recognize that the transformation of the stream-dwelling parr to

the silvery smolt entails many behavioral, morphological and physiological changes that prepare juvenile salmonids for their feeding migration to the sea (Hoar 1988).

This understanding has been achieved through considerable experimentation, particularly with Atlantic and coho salmon (*Oncorhynchus kisutch*) as is evident in several symposia on salmon smolting (Bern and Mahnken 1982; Thorpe et al. 1985; Hansen et al. 1989; Saunders et al. 1994*a*). The emphasis on these two species is due to both their economic importance and their well-defined parr-smolt transformation, which is amenable to study.

However, the classic description of smolting as developed from studies of Atlantic and coho salmon does not pertain to all anadromous salmonids because there is considerable variation among species (Hoar 1976; McCormick and Saunders 1987; McCormick 1994; Clarke and Hirano 1995). Smolts vary not only with respect to the size and age at which they are able to thrive in seawater but also in the seasonal environmental cues which synchronize their development. On the one hand, pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon enter the ocean soon after emergence to grow for only a year or more; on the other, Arctic charr (*Salvelinus alpinus*) enter the sea for a brief period of a few weeks or months during the summer.

In this chapter, we review the biology of the parr-smolt transformation in the major anadromous species that are under cultivation, indicating the features that they share and the differences among them. These differences have led to varying techniques for rearing them.

The first salmon hatchery in the U.K. was established in 1868 (*see* Chapter 1). Salmon hatching techniques were introduced to Japan in 1876 and by 1888, the Chitose Central Salmon Hatchery was established near Sapporo, Hokkaido (Kaeriyama 1989). The first salmon hatchery in North America was built by Samuel Wilmot at Newcastle on Lake Ontario. Upon Wilmot's recommendation, in 1866 the Government of Upper Canada, by an order-in council, reserved Wilmot's Creek for the natural and artificial propagation of Atlantic salmon (Dunfield 1985). Wilmot was later superintendent of fish culture for the federal government from 1876 to 1895 and established 15 hatcheries across Canada. The Craig Brook salmon hatchery near East Orland, Maine was established in 1871 and it is still open today.

The first salmon hatchery in western North America was built in 1872 on the McCloud River in California under the direction of the U.S. Fish Commission. It incubated chinook salmon (*Oncorhynchus tshawytscha*) eggs to the eyed stage and then shipped them by stage coach and train across the U.S. for stocking rivers on the Atlantic coast. Numerous hatcheries were then established in Washington and Oregon beginning in 1877 (Nash 1995). The first salmon hatchery in British Columbia was built at New Westminster, near the mouth of the Fraser River in 1884 and by 1910 there were eight such facilities (Gough 1991). The first of many Alaskan hatcheries was built on Kodiak

Island in 1891 and by 1901, one with a capacity of 110 million eggs was built on Revillagigedo Island near the southern tip of the Alaska panhandle. The hatcheries in British Columbia and Alaska concentrated on the production of sockeye salmon (*Oncorhynchus nerka*). By 1929 there were 72 hatcheries from California to Alaska; the cumulative releases of fry up to 1928 were in excess of 12 billion (Wahle and Smith 1979).

Between 1929 and the early 1940s, all but three of the 18 U.S. federal salmon hatcheries were closed or turned over to state governments. The hatcheries in British Columbia, Alaska and California also were closed but most hatcheries operated by the States of Washington and Oregon remained in operation.

Decline in support for hatcheries came with the realization that they were contributing little if anything to the fisheries. The standard practice of the early hatcheries was to release fry soon after the eggs hatched, when the yolk sac had been absorbed (Wahle and Smith 1979). In the absence of scientific knowledge of basic husbandry, staff of the early hatcheries learned by trial and error. Improvement of techniques for producing smolts for release evolved gradually from the early empirical practices. Over time, it was learned that larger, older juveniles had a much higher rate of survival to adulthood than did fry. A major breakthrough in this area was the introduction of effective manufactured diets in the early 1960s which greatly improved growth and health of presmolt salmon (Cleaver 1969). Current fish husbandry techniques based on systematic investigation of salmon biology have evolved in concert with the expansion of hatcheries for stock restoration since the 1950s and 1960s and more recently with the growth of commercial salmon farming.

There was a resurgence of hatchery construction in the Columbia River basin in the 1940s following construction of the Grand Coulee Dam that prevented Pacific salmon from migrating to spawning areas in the upper portions of the river. Numerous additional hydroelectric dams constructed throughout the lower basin resulted in a number of new hatcheries being established with the aim of restoring the wild stocks caused by habitat alteration (Wahle and Smith 1979). Similarly, large-scale hydroelectric development on major salmon rivers in Sweden after World War II stimulated the construction of hatcheries rearing Atlantic salmon smolts to compensate for lost natural production (Lindroth and Larson 1985). With the advent of improved techniques for production of smolts, many hatcheries in Alaska were re-opened beginning in the 1950s and in British Columbia in the late 1960s and early 1970s.

BIOLOGY OF THE PARR-SMOLT TRANSFORMATION

An understanding of the physiological basis for the parr-smolt transformation (or smoltification) is required for the effective operation of salmon hatcheries. Whether they

are producing smolts for release in support of fisheries or for transfer to netpens for growout, hatcheries must provide coordinated environmental cues to ensure that smolt development is synchronized for a successful transition to seawater.

Changes Associated with Smolting

Life History and Anatomical Changes (*see also* Chapters 2 and 3). Changes in body form and colouration are most obvious in species such as the Atlantic salmon (McCormick et al. 1985) and the coho salmon (Gorbman et al. 1982; Winans and Nishioka 1987). In these species, the deep-bodied, cryptically coloured stream-dwelling parr becomes a slender, silvery smolt with darkly pigmented margins of the dorsal and caudal fins. The development of silvering is caused by the deposition of guanine and hypoxanthine in two layers beneath the scales and deep in the dermis (Markert and Vanstone 1966; Johnston and Eales 1967).

Atlantic salmon occur in rivers flowing into the northeast Atlantic from Spain and Portugal north through France, the U.K., Ireland, Norway, Sweden, Finland, Russia, across to Iceland, Greenland, and down through rivers on the western side of the Atlantic Ocean through Canada and the U.S. as far south as Connecticut. In some European rivers, Atlantic salmon may smolt at age 1+ (i.e., S1), but most are two years old. Smolts in eastern North America are rarely under two years old; four- and five-year-old smolts are not uncommon in the northern part of the range (Power 1961). Atlantic salmon smolts range from 125 to 180 mm fork length, depending on age and stock.

As with Atlantic salmon, brown trout (*Salmo trutta*) exist in both anadromous (often termed sea trout) and resident forms. Anadromous and non-anadromous fish of both sexes can occur in the same river and are apparently the same genetic stock (Hindar et al. 1991). Smolts develop after two to six years and range in size from 110 to 200 mm fork length. The downstream migration occurs in spring and adults spend from one to three years at sea before returning as mature spawners (Økland et al. 1993; L'Abee-Lund 1994).

All species of Pacific salmon are propagated in hatcheries for release in order to support commercial and recreational fisheries. Chinook and coho salmon are also produced for stocking netpens in commercial salmon farms.

The masu salmon (*Oncorhynchus masou*) occurs only in Asia, specifically in Japan, eastern Korea and northward to the Sea of Okhotsk. In northern areas such as the Island of Hokkaido, it is mainly anadromous but in the southern part of its range it completes its life cycle entirely in the rivers as "yamame". The stream-dwelling juveniles are deep-bodied and have prominent parr marks. The smolts are readily distinguished by a loss of parr marks, development of a silver colour and a more slender body form. In Hokkaido, the peak downstream movement of masu salmon smolts occurs during the

first half of May of the second spring (Kato 1991). The smolts average 110-130 mm fork length. Many rapidly growing underyearling males become sexually mature in autumn; they do not become smolts in the following spring but remain in the river (Aida et al. 1984). The amago salmon (*O. rhodurus*) is closely related to the masu salmon and is considered to be a subspecies by some authors (Numachi 1984; Robins et al. 1991). The amago salmon has a very limited distribution in rivers along the eastern coast of central Honshu Island and on nearby Shikoku Island, Japan (Kato 1991). Juvenile amago salmon grow in streams during the first year. Many males become sexually mature in autumn of the first year and are not able to acclimate to seawater, while a variable proportion of the larger sexually immature fish become smolts in late November and December (Nagahama et al. 1982). Closely related to the amago is the "biwamasu", a lake-dwelling form from Lake Biw" on southwestern Honshu Island, Japan. Fry of the biwamasu become partially silvered during their first spring and migrate downstream into Lake Biwa where they grow for three to five years until they return upstream to spawn. When held under pond conditions, biwamasu grow more slowly and exhibit less intense body silvering and darkening of the outer margins of the dorsal fin than do amago (Fujioka 1987).

The coho salmon is most common along the west coast of North America where it is found from California to Alaska; on the Asian coast it occurs from the Bering Sea south to Sakhalin Island and the northern part of Hokkaido Island in Japan (Sandercock 1991). Juvenile coho salmon usually spend at least a year in fresh water, often in small coastal streams. The seaward migration of smolts occurs from late April to June. As with the masu, the stream-dwelling parr are cryptically coloured with prominent parr marks while the smolts are silvery.

The chinook salmon occurs in medium and large rivers from California to northern Hokkaido (Healey 1991). There are two major juvenile life history forms: "ocean-type", which enter the sea as underyearlings, and "stream-type", which spend one or more years in fresh water. Ocean-type juveniles migrate downstream either soon after emergence as fry or after several months as fingerlings and remain in low salinity waters of estuaries for one or two months until they reach a size of 70 mm fork length. Subsequently, they move offshore. The stream-type life history pattern is predominant in Asian and Alaskan populations and occurs also in headwater tributaries, particularly in larger rivers, elsewhere in North America (Taylor 1990; Healey 1991). They reside in rivers for one or more years until they reach a size of 75-125 mm fork length and undertake the seaward smolt migration; unlike the ocean-type juveniles, they do not reside for an extended time in estuaries, but disperse into marine waters. Chinook fry have large parr marks. Unlike coho, ocean-type chinook do not undergo as distinct a transformation from parr to smolt while in fresh water; instead they gradually become more silvery as they grow in estuarine areas. In contrast, the stream-type chinook smolt is readily distinguished from the parr stage by its silvery colour, elongated shape and darkly pigmented margins of the dorsal and caudal fins.

Sockeye salmon are found along the North American coast from the Klamath River in California to the Yukon River in Alaska and along the coast of Asia from the northern Bering Sea south to the northern shore of the Sea of Okhotsk (Burgner 1991). Sockeye salmon exhibit a variety of life history patterns. At one end of the spectrum is the kokanee, a permanent freshwater resident form of sockeye salmon that may occur in sympatry with anadromous populations or in lakes which are not accessible from the sea. Kokanee are found naturally in lakes from Idaho around to Hokkaido but their range has been extended considerably by introductions. Juvenile sockeye usually reside in lakes for at least one or two years before migrating seaward as smolts from April to June. However, in some river systems without lakes, there are "ocean-type" populations of sockeye salmon that enter the sea as underyearlings and "river-type" populations that inhabit river channels for at least one year (Birtwell et al. 1987; Wood et al. 1987). Sockeye fry have short parr marks and black spots on the back. The pelagic feeding stage in lakes has a darker back and the parr marks become less distinct with silvering of the sides. At the time of smolting, they become more silvery and streamlined.

The chum salmon is found along the Pacific and Arctic coasts of North America from California to the Mackenzie River and in Asia from the Lena River in the Arctic south to Korea (Salo 1991). Juvenile chum enter the sea as underyearlings, usually soon after emergence at a size of 35-45 mm. However, in some populations, migration may be delayed and the fry grow to 60 or 70 mm in length in the river or estuary (Sparrow 1968; Mason 1974). In the Amur River, juvenile chum salmon may grow to a size of 90 mm. Although chum salmon fry have small parr marks, there is no distinct morphological transformation to the smolt stage.

The pink salmon has an extensive range from California to the Arctic coasts of North America and Asia and along the western Pacific coast to Korea on the Japan Sea (Heard 1991). Juvenile pink salmon migrate seaward very soon after emergence from the gravel at a size of 28-35 mm fork length and 130 to 260 mg in weight. Juvenile pink salmon lack typical parr marks; the fry are green on the back and silver on the sides from the time of emergence.

Steelhead trout (*Oncorhynchus mykiss*) are the anadromous form of rainbow trout. They are found in North American rivers from California to Alaska and in Asia, mainly on the Kamchatka peninsula (Burgner et al. 1992). Throughout this range, they co-occur with non-migratory rainbow trout. Juveniles reside for one to five years in fresh water before entering the sea as smolts during late April and early May at sizes ranging from 125-225 mm fork length. Smolts acquire a silvery colour and become more slender.

Most populations of brook trout (also termed brook charr, *Salvelinus fontinalis*) are resident in fresh water although there are anadromous populations in many coastal rivers of northeastern North America (Naiman et al. 1987). In northern latitudes, brook charr migrations are characterized by spring emigrations of 2- to 4-year-old fish that

remain in seawater for only two to four months. In the southern portion of its range, seaward migration is more variable, and often occurs in the autumn.

Arctic charr occur as both anadromous and resident populations in a circumpolar distribution in rivers surrounding the Arctic Ocean. Anadromous populations are usually found north of latitude 60°N. Anadromous stocks of Arctic charr typically migrate to the sea for the first time after three to seven years in fresh water at a length of 170 to 260 mm (Finstad et al. 1989*a*). Smolting is not obvious externally in Arctic charr. Unlike salmon, charr do not over-winter in the sea but usually return to fresh water after as little as a month. Another contrast with salmon is that the upstream migrants are frequently not sexually mature (Johnson 1980).

Physiological Changes. An essential part of the parr-smolt transformation is an increase in euryhalinity which allows the smolt to live in salinities varying from soft fresh water to full strength seawater. Although the timing of development of hypo-osmoregulatory capacity differs among species, the physiological mechanisms which prepare salmon for life in the sea are common to all.

The body fluids of salmonids have an osmotic concentration approximately one-third that of seawater. While salmonids are in fresh water, the concentration gradient favours entry of water into the body and loss of salts by diffusion (i.e., they are hyperosmotic to the external water). Most of these movements occur across the gill surface because the rest of the body surface is relatively impermeable. To counter these passive flows, the fish excretes the excess water as a dilute urine and obtains salts from the food as well as by active uptake across the gill surface. Once salmonids enter salt water, the osmotic gradient is reversed (i.e., they are hypo-osmotic to the external water). Loss of water and diffusion of salts into the body are restored by drinking seawater; urine flow is reduced to conserve water and salts are actively excreted across the gill by mitochondrial-rich cells called "chloride cells" (*see* Chapter 2). The excretion of salts is accomplished by means of an enzyme, Na^+,K^+-adenosine triphosphatase (ATPase), that is often measured as an indicator of smolt quality (*see* page 545).

Hormonal Control of Smolting

Although changes in many hormones are associated with smolting, the actions of most are not well understood. Only the major hormones associated with smolt development that have been most intensively studied are reviewed (*see* Chapter 2 for more information on the endocrine glands and the hormones they secrete).

Thyroid Hormones. Smolting involves a number of developmental changes including growth, body shape, behaviour, pigmentation and an increase in euryhalinity. It is perhaps not surprising then, that the thyroid, which has long been known to have important developmental effects in vertebrates, is involved in smolting. Destruction of

the thyroid gland was found to depress growth of juvenile steelhead trout and chinook salmon; normal growth was restored following treatment with thyroxine (Norris 1969). Activation of the thyroid in Atlantic salmon smolts was first described by W. Hoar in 1939 but the more recent discovery of a surge in circulating thyroid hormone levels in coho and masu salmon smolts (Dickhoff et al. 1978; Nishikawa et al. 1979) stimulated renewed interest in the role of the thyroid. Although treatment with thyroid hormones usually has little effect on acclimation to seawater, it does cause the increases in silvering and growth rate usually associated with smolting. Triiodothyronine has been administered in the diet in a number of species to accelerate growth and appearance of smolt characteristics (McBride et al. 1982; Shelbourn et al. 1992; Boeuf et al. 1994a). Juvenile coho salmon that are transferred prematurely to seawater become stunted and have a number of differences in hormone function compared with typical smolts (Clarke and Nagahama 1977; Nishioka et al. 1982). The thyroid of stunts appears inactive and plasma thyroid hormone levels are reduced (Folmar et al. 1982). Thyroid hormones are also involved in the olfactory imprinting of smolts which facilitates their return to their natal stream as sexually mature adults (Scholz et al. 1985; Morin et al. 1989).

Cortisol. A steroid hormone secreted by the interrenal tissue, cortisol plays a major role as an osmoregulatory hormone in teleosts and is immunosuppressive during stress (Mazeaud et al. 1977; Barton et al. 1985; Barton and Iwama 1991). It has long been known that the interrenal cells are hypertrophied in juvenile Atlantic and coho salmon at the time of smolting (McLeay 1975; Olivereau 1975; Specker 1982). Cortisol treatment assisted regulation of plasma electrolyte concentrations in juvenile sea (brown) trout, Atlantic salmon and coho salmon after transfer to seawater (Richman and Zaugg 1987; Madsen 1990; Bisbal and Specker 1991). Cortisol is known to act directly on the gill to induce differentiation of chloride cells and stimulate increased Na^+,K^+-ATPase activity (McCormick and Bern 1989). Cortisol also influences changes in lipid metabolism that occur in smolts, such as the reduction in total lipid and triacylglycerol content of dark muscle and liver tissue (Sheridan 1989).

Growth Hormone. Pituitary growth hormone not only promotes growth of juvenile salmon but also increases survival in seawater. Although growth hormone is not considered an important osmoregulatory hormone in most teleosts, it has been shown to facilitate regulation of plasma ion concentrations in juvenile salmonids after transfer to seawater (Komourdjian et al. 1976; Clarke et al. 1977; Miwa and Inui 1985; Bolton et al. 1987; Hirano et al. 1987; Madsen 1990) and to stimulate the development of gill Na^+,K^+-ATPase (Richman and Zaugg 1987). Secretion of growth hormone increases following entry of salmonids into seawater. Growth hormone stimulates production of insulin-like growth factor I (IGF-I) in the liver, gill, and kidney, which in turn stimulates an increase in gill Na^+,K^+-ATPase (Sakamoto et al. 1993, 1994). Growth hormone also stimulates conversion of thyroxine to triiodothyronine (Leloup and Lebel 1993) and sensitizes the interrenal tissue to adrenocorticotropic hormone (ACTH) (Young 1988). Thus, growth hormone acts in combination with cortisol and thyroid hormones to influence smolt development.

Sexual Maturation. Sex hormones secreted by the testes of precocious male parr of juvenile amago, Atlantic, chinook, and masu salmon as well as sea trout are inhibitory to smolt development (Nagahama et al. 1982, Aida et al. 1984, Lundqvist et al. 1986, Thorpe 1987, Dellefors and Faremo 1988, Foote et al. 1991).

Environmental Cues Governing Smolting

Pacific Salmon and Steelhead Trout. Pacific salmon can be divided into two groups according to the environmental cues that guide their development to the smolt stage (Clarke 1992). In the first group are chum, pink, and ocean-type chinook salmon that do not require photoperiod cues for growth and development to the time of seawater entry. These species grow to a specific size which is associated with attainment of the capacity for hypo-osmoregulation in seawater as underyearlings. Their relatively small size at seawater entry and insensitivity to photoperiod makes them more compatible with hatchery propagation. In the second group are coho, stream-type chinook and masu salmon as well as steelhead trout. In the latter group, both growth and smolt development are influenced not only by temperature but also by photoperiod. They normally remain in fresh water for a year or more and their growth in fresh water is highly seasonal. Successful hatchery propagation of these species is more complex than for the first group since it requires the coordinated application of appropriate temperature and photoperiod conditions; it is also more expensive, because of the larger size of the smolts.

Water temperature has a strong effect on growth rate (*see* Chapter 7) and thus influences the time at which juveniles reach the body size required for smolt development. In this way, temperature can determine not only the year but also the season at which smolt development occurs. Kubo (1965) reported that presmolt masu salmon transferred to elevated water temperatures of 9-14°C in early March became smolts earlier than those held at ambient temperatures of 4-6°C. Juvenile coho salmon held in the laboratory at 10°C exhibited maximal levels of gill Na^+,K^+-ATPase one month earlier than those held at 6°C (Zaugg and McLain 1976). Ocean-type chinook juveniles held in the laboratory at 17°C reached maximal hypo-osmoregulatory capacity in seawater about two months earlier than those held at 9°C (Clarke and Shelbourn 1985). This effect of temperature was not strictly a function of body size, because smolts reared at high and low temperature exhibited maximal hypo-osmoregulatory capacity in seawater at different sizes. Seasonal temperature cycles are known to affect smolt development in yearling coho salmon. Accumulated temperature units in a coastal stream during the month of April explained 76% of the variation in median date of migration for wild S1 coho salmon smolts and 80% for S2 smolts (Holtby 1988). Clearcut logging of the watershed increased stream temperatures and advanced the median day of migration by about 10 days. Coho salmon hatcheries in Puget Sound, Washington with a seasonally fluctuating water temperature obtain higher rates of adult returns than do those with a relatively constant temperature during spring (Olson 1978). Similarly, juvenile steelhead trout held on a seasonal temperature cycle of 6.9-18.6°C exhibited greater migratory

behaviour and a more pronounced elevation of gill Na^+,K^+-ATPase activity than those held at a constant temperature of 12°C (Zaugg and Wagner 1973; Wagner 1974).

Temperatures must be sufficient to permit growth of juveniles to smolt size but not so high as to inhibit acclimation to seawater. Usually, temperatures in the 10-14°C range are most beneficial during the season of smolt development and migration. At 20°C, juvenile coho salmon exhibit only a transitory increase in gill Na^+,K^+-ATPase activity (Zaugg and McLean 1976). Acclimation to seawater is impaired at temperatures above 16-17°C.

Photoperiod provides important seasonal information and is the main environmental cue that synchronizes the annual cycle of growth and smolting in species such as coho, masu and stream-type chinook salmon as well as steelhead trout that overwinter in fresh water (Hoar 1976). In nature, fry of these species emerge from the gravel under long spring daylength and then perceive a cycle of long summer days followed by short winter days; lastly, they become smolts in response to increasing daylength in their second year of life. It has been known for some time that exposure of one-summer-old juveniles to long daylength during fall and winter accelerates growth and advances the development of smolt characteristics (Clarke et al. 1978; Zaugg 1981). More recently, it has become apparent that photoperiod conditions during the months immediately following first feeding influence growth and smolting during the first summer (Clarke and Shelbourn 1986). In a hatchery using groundwater or artificially heated water for egg incubation, the time of emergence of fry can be advanced by several months. Under ambient daylight, this has the effect of changing the photoperiod phase at the time of first feeding from long-day to short-day. As a result, growth and smolting may be accelerated (*see* page 537).

Atlantic Salmon. Conventional wisdom says that Atlantic salmon parr transform into smolts in the spring under the influence of photoperiod and temperature (*see* Hoar 1988); river discharge together with temperature influence the time of downstream migration (Jonsson and Rudd-Hansen 1985). The smolting process in Atlantic salmon is completed in the spring, having started some months earlier (*see* Kristinsson et al. 1985; Hoar 1988). In production systems using natural temperature regimes, growth slows or stops in the fall when temperature falls to 3-4°C. By that time, any parr that have reached a threshold size and an accumulation of metabolic reserves make the "decision" to commence smolting (Saunders et al. 1994*b*). The consequence of this decision is a surge in growth resulting in these fish distancing themselves from the other parr that have not made this decision. Fish smaller than the threshold size reduce their growth rate under short-day photoperiod in winter (Skilbrei 1991). A visible result is development of bimodality in length frequency, the upper modal fish being on a developmental path for completion of smolting the following spring; the others will not smolt until a year later (Thorpe 1977). The threshold size has been reported to vary between 75 and 100 mm fork length among various stocks of Atlantic salmon (Kristinsson et al. 1985; Skilbrei 1991).

The surge in growth rate resulting in bimodality is the first manifestation of smolting (Kristinsson et al. 1985; Saunders et al. 1994*b*). This is the basis for indicating that smolting starts some months before the final stages of the process (i.e., silvering, reduced condition factor, development of hypo-osmoregulatory ability, and migratory behaviour) are apparent. Since bimodality develops under a variety of environmental conditions with particular reference to photoperiod and temperature, these environmental factors are probably only permissive. Temperature must be high enough to stimulate feeding and growth. Growth proceeds well under a variety of photoperiod regimes, although a sequence of short and long daylengths is required. Therefore, it appears that there is no specific combination of environmental cues to start the smolting process; it can be initiated under a progression of photoperiod and thermal conditions. Recent work has shown that provision of reasonably high water temperature during the winter allows continued recruitment into the smolting mode (Duston and Saunders 1995*b*) This practice may be used in smolt rearing stations with provisions for elevated temperature in winter.

Temperature and photoperiod serve as important cues for the completion of smolting in the spring and especially for migratory activity. A rising temperature in the 8-10°C range initiates migration of wild smolts (Jonsson and Rudd-Hansen 1985). Increasing daylength in the natural cycle during spring stimulates increases in thyroid hormone activity, hypo-osmoregulatory ability and salinity tolerance (McCormick et al. 1987; Saunders et al. 1989). The two environmental factors work together; increasing daylength alone does not result in development of the smolt characteristics described above unless temperature is suitably high (Virtanen 1988; Duston and Saunders 1995*b*). Similarly, seasonally increasing temperature in the spring may promote growth but with delayed or non-completion of smolting under continuous light conditions (McCormick et al. 1987).

Rainbow Trout and Charrs. Within salmonids there is continuum in the developmental stage and the degree to which smolting may be expressed in a given species (Hoar 1988; McCormick 1994). Although species such as brook trout may be generally regarded as non-smolting, they may share some aspects of salinity tolerance with smolting salmonids. Within a species there is a substantial degree of genetic variation in salinity tolerance and smolt characteristics. Such genetic influences are especially problematic when there are conflicting results from different studies on the same species.

SMOLT PRODUCTION FOR RELEASE

Pacific Salmon and Steelhead Trout

Approximately 75% of the Pacific salmon returning to the Columbia River are derived from hatchery releases. From 1960 to 1990, approximately 40 million yearling

coho smolts were released each year from16 hatcheries along the lower Columbia River (Flagg et al. 1995). Annual releases of yearling stream-type chinook salmon from hatcheries in Washington, Oregon and Idaho totalled about 30 million smolts, while annual releases of underyearling ocean-type chinook were in excess of 100 million smolts.

The Alaska Department of Fish and Game increased its production of coho salmon smolts from 171,000 in 1968 to 930,000 by 1976; similarly, its releases of stream-type chinook salmon smolts increased from 400 in 1964 to 225,000 by 1976 (Wahle and Smith 1979). The number of hatcheries rearing chinook salmon in southeast Alaska increased from one in 1971 to 15 in 1992 . Releases are mainly of yearling smolts because releases of underyearlings have not been cost effective; marine survival rates for juveniles released as underyearlings are usually less than 1% whereas survival of yearling smolts averages about 4% (Heard et al. 1995). In addition to traditional land-based hatcheries, biologists in Alaska have developed floating horizontal and vertical raceways for rearing smolts in fresh or brackish water (Martin and Heard 1987).

The central Gulf of Alaska pink salmon hatchery program has developed into a large ocean-ranching system (*see also* Chapter 14). After hatch, the fry are held in seawater netpens for short periods and then released into near-shore nursery areas at a weight of about 0.3 g. Pink salmon were first released from a hatchery on Kodiak Island, Alaska in 1972. By 1990, there were seven private nonprofit pink salmon hatcheries in the central Gulf of Alaska. In Prince William Sound alone, the number of juveniles released rose from 1 million in 1977 to more than 500 million in 1989, exceeding the number of wild migrants in the area.

Alaskan hatcheries incubate about 100 million sockeye salmon eggs per year. Most of the fry produced are stocked into lakes inaccessible to wild salmon and allowed to develop into smolts under natural conditions. Some hatcheries are testing releases of underyearling sockeye smolts at a size of 4-5 g and others are releasing yearling smolts at sizes of 12-20 g.

The Salmonid Enhancement Program was established in 1977 by the Department of Fisheries and Oceans with the aim of restoring catches of Pacific salmon on the west coast of Canada. Many hatcheries were constructed in British Columbia. These used either concrete raceways of the type developed in the Pacific Northwest states (*see* Chapter 6) or earthen channels for rearing of smolts. Hatcheries adjacent to the Strait of Georgia, which separates Vancouver Island from mainland British Columbia, released mainly coho and chinook salmon smolts in support of sport and commercial fisheries. During the 1970s and 1980s, releases of 15- to 25-g yearling coho salmon smolts into the Strait of Georgia increased from about half a million to 7-10 million per year. Marine survival rates ranged from 6 to 20%. Ocean-type chinook smolts were released as underyearlings at a size of 5-7 g; production increased from just over 400 thousand in the early 1970s to 36 million smolts in the late 1980s. Marine survival rates for chinook salmon were highly variable, ranging from 0.3% to 5% (Perry 1995). Hatcheries

constructed on the upper Fraser River and its tributaries experimented with release of stream-type chinook salmon as underyearlings at a size of 2.5-5 g but marine survival rates were very low (Cross et al. 1991; Winton and Hilborn 1994). There are no hatcheries producing sockeye salmon smolts in British Columbia; enhancement of sockeye production has been by means of spawning channels and fertilization of sockeye nursery lakes (McDonald and Hume 1984; Hyatt and Stockner 1985; Stockner 1987; West and Mason 1987).

Twenty-two hatcheries now operate on the Pacific coast of Russia, 17 of which are on Sakhalin Island (Dushkina 1994). These hatcheries release mainly pink salmon (450 million) and chum salmon (200 million): the combined production of coho, chinook and sockeye salmon fry totals only 2.8 million.

Hatchery steelhead trout are commonly grown to a size of about 160 mm fork length before release as yearlings. Hatcheries in North America released 30 million steelhead smolts in 1987. Two-thirds of this production was from facilities in the Columbia River basin (Burgner et al. 1992).

Atlantic Salmon

Atlantic salmon pose a special problem in production systems because of their relatively slow growth rate and large smolt size. These factors result in high cost of production. Water temperature and the length of the growing season control growth rate and attainment of the threshold size or energy content to commence smolting (Figure 1). Under culture conditions, it is relatively easy to produce S1 smolts provided water temperature is sufficiently high and the growing season long enough. The optimum temperature for growth is in the 16-18°C range (Siginivich 1967; Peterson and Martin-Robichaud 1989). Failure to provide such temperatures early in the summer and to maintain them for some months results in slower growth than needed to attain the threshold conditions necessary to commence smolting. The result is a low percentage of S1 smolts and the necessity to hold the fish for another year to produce S2 smolts.

Before the development of Atlantic salmon aquaculture in eastern Canada, production from most rearing stations in eastern North America was mainly S2 smolts because the water supplies were mainly from rivers in which water is usually very cold during winter and too warm in summer to promote rapid growth. Some hatcheries had water supplies from stratified lakes which gave an opportunity to regulate temperature in the favourable range; these led the way in S1 smolt production. In Sweden, where the technology for large-scale smolt production was developed during the 1940s and 1950s to compensate for salmon production lost to hydroelectric power development (Carlin 1959), most smolts were S2 because of temperature constraints. Production of S1 smolts in Atlantic Canada and Maine began after the thermal requirements of juvenile salmon were better understood. When the salmon aquaculture industry started in New

ATLANTIC SALMON - *SALMO SALAR*

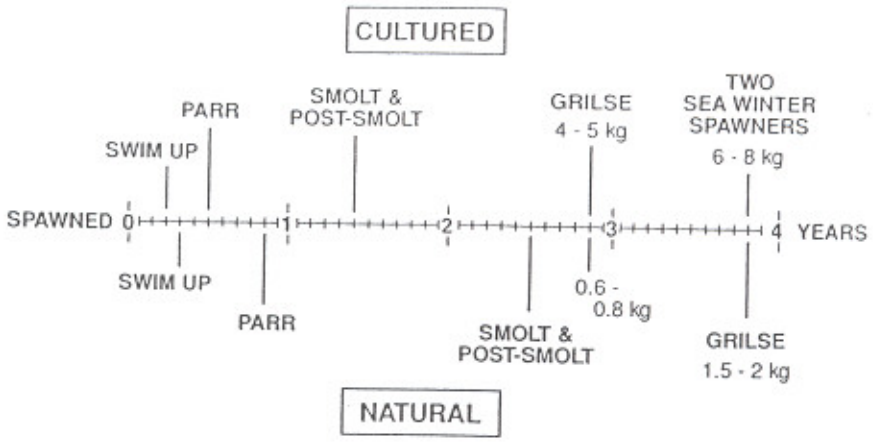

FIGURE 1. Comparison between developmental rates of cultured and naturally produced Atlantic salmon to various life stages. Smolts produced in rearing stations are usually S1 but wild smolts are most commonly S2. Wild smolts in northern rivers are frequently 3-5 years old.

Brunswick in 1978, there were no commercial hatchery-rearing stations, but only government stations for salmon enhancement programs. Smolts supplied to the developing aquaculture industry were a mixture of 1 and 2+, the latter being most common. Now a number of facilities produce smolts for the aquaculture industry. These operators maximize production of S1 smolts to minimize production cost and to optimize use of facilities (Figure 1).

Most smolt production hatcheries use elevated temperature to speed incubation, advance the time of first feeding, and optimize feeding and growth during the summer. For example, the Mactaquac Fish Culture Station of the Canada Department of Fisheries and Oceans uses an accelerated rearing facility with heated water for first feeding and early fry development (Farmer et al. 1990). This approach results in greatly increased S1 smolt production. Cooling water from the bearings at the Mactaquac hydroelectric plant is supplied to a greenhouse facility to which eyed eggs from the Mactaquac Hatchery-Rearing Station are moved about mid-January to begin their accelerated rearing regime. The fry are moved back to the Mactaquac facility in mid-June at a size of about 2 g. Following grading in autumn, about 50% of the fish that are too small to become smolts the next spring are released as fall fingerlings; the remainder are retained as

presumptive smolts. By the following April, these fish exceed 60 g and >90% are classified as smolts (G.J. Farmer, pers. comm.)

Research on Success of Smolt Releases

Effect of Time and Size at Release from Hatcheries on Marine Survival. Historically, hatchery releases were timed to imitate the downstream migration of wild salmon. Hatcheries also emphasized numbers of fish released. Frequently, more eggs were collected than could be reared to smolt size; the excess were released as fish grew.

Returns of tagged smolts demonstrated that the release period during which maximum return rate can be expected may be as brief as a week (Peterson 1973). In some situations, releases delayed from the normal smolt migration time, either from hatcheries or from netpens near the coast produce a dramatic increase in adult returns (Iioka 1979; Novotny 1980; Eriksson 1991). The increased returns from delayed releases may result at least in part from changes in migratory behaviour that allow salmon to escape fishing mortality or predation (*see also* Chapter 14).

Releases of tagged coho and chinook smolts beginning in the 1960s indicated that larger smolts had better marine survival. For hatcheries in the Pacific Northwest states in 1960, the average release weight for ocean-type chinook salmon was 2.3 g and that for coho and stream-type chinook salmon was 14 g; by 1976, the average weight at the time of release had increased to 7.7 g for ocean-type chinook, 41.2 g for stream-type chinook and 26.7 g for coho salmon (Wahle and Smith 1979). Marine survival of ocean-type chinook salmon was highly correlated with size at release from the Big Qualicum River on Vancouver Island, British Columbia, ranging from 1.9% for 6-g smolts to 9.6% for 12-g smolts (Bilton 1984).

Although general trends in survival could be obtained from analysis of return rates from releases made at different sizes and dates over several years, it was not possible to discern the combined effects of smolt size and release date because of annual variability in the rate of marine survival. This difficulty was overcome by means of experiments examining the simultaneous effects of size and time of release on marine survival. A detailed study of coho salmon involved the release of three size groups on four dates from a research hatchery on the east coast of Vancouver Island, British Columbia (Bilton et al. 1982). Returns of adults and "jacks" (males which become sexually mature in the same year that they enter the sea) to the hatchery and to the commercial and sport fisheries were enumerated. The maximum return of adult coho salmon to the hatchery and to the fisheries was estimated to occur from a release of 25-g smolts on June 22 (Bilton et al. 1982). Releases of larger smolts at earlier dates maximized returns of jacks at the expense of adult returns. Subsequently, similar experiments were performed at a production hatchery on the Quinsam River, Vancouver Island in two years. Analysis of the returns indicated that the effect of release date at this hatchery was much greater

than that of smolt size. The maximum returns of adult coho salmon were estimated to occur from a release of 20-30-g smolts on June 5 (Morley et al. 1988). Based on an analysis of several experiments conducted with juveniles released from hatcheries on the Columbia River, Mahnken et al. (1982) recommended that the minimum release size of coho salmon be 130 mm fork length (23 g) in early May or 125 mm fork length (20 g) in early June. They suggested that reversion to parr by fish that were too small at release may be a delayed and unrecognized source of marine mortality in juveniles released from hatcheries.

The effect of size on marine survival of juvenile pink salmon after release was examined at an experimental hatchery on southeast Baranof Island, Alaska (Martin et al. 1981). After hatch, the emerged fry were divided into four groups; one was marked and released unfed into the estuary while the other three were transferred to floating vertical raceways and fed for 30, 60, or 90 days before release. Marine survival of the unfed group (release size 0.23 g) was 3.1%; after feeding for 30 days, mean weight increased to 0.27 g and survival was 4.6% (Martin et al. 1981). Release size increased markedly after 60 and 90 days (0.55 g and 1.95 g, respectively) but survival rates increased only slightly to 5.2% for the 60-day group and then decreased to 4.3% for the 90-day group. When mortality during rearing was taken into consideration, the maximum number of adult returns resulted from the group which was fed for 30 days prior to release (Martin et al. 1981). A similar experiment examined the effect of weight at release on survival of yearling stream-type chinook salmon (Martin and Wertheimer 1989). Differential feeding rates were used to produce large (28-32 g) and small (10 g) smolts after 13.5 months of rearing in floating vertical raceways. Adult return rates (excluding returns of precocious male jacks) were 2.2 - 3% for the large smolts compared with 0.74 - 1.4% for the small smolts (Martin and Wertheimer 1989).

The effect of rearing density in hatchery ponds on smolt quality and rate of adult return is not reviewed in this chapter (*see* Chapters 6 and 7; Fagerlund et al. 1981; Martin and Wertheimer 1989; Banks 1992, 1994; Ewing and Ewing 1995).

Long-Term Survival Trends in the Pacific. The introduction of the Oregon Moist Pellet in the early 1960s enabled the release of larger, healthier smolts from hatcheries in the Pacific northwest states. As production of smolts increased markedly during the 1960s and early 1970s, adult returns increased correspondingly. However, returns of adult salmon began to decline noticeably in the late 1970s and early 1980s.

The Little White Salmon National Fish Hatchery was built on the lower Columbia River in 1896 for release of juvenile ocean-type chinook salmon. The hatchery released only unfed fry until 1908 and thereafter increasing numbers were held and fed prior to release at a larger size. Following completion of the Bonneville Dam in 1938, adult returns declined substantially (Nelson and Bodle 1990). Because of low adult returns from 1965 to 1985, the number of eggs transplanted from other rivers exceeded the number of eggs taken from adults returning to the hatchery in 11 out of 21 years (Nelson and

Bodle 1990). Because of low returns and low contribution to the sport and commercial fisheries, the Little White Salmon Hatchery discontinued production of ocean-type chinook salmon. The demise of this stock of chinook salmon cannot be attributed to any single cause, but the construction of the Bonneville Dam and the transplanting of eggs from other stocks are thought to be major factors (Nelson and Bodle 1990).

Coho salmon smolts originating from the Columbia River and coastal streams in Oregon migrate into coastal waters from central California to Washington; this region represents the southernmost production area for coho salmon in the northeast Pacific Ocean. Smolt releases into this area increased from fewer than 1 million in the 1950s to more than 30 million by 1970. However, between 1967 and 1976, catch and escapement of hatchery coho salmon began to fluctuate and then it declined markedly after 1977 (Nickelson 1986). This decline was attributed to a decline in ocean upwelling. Analysis of return rates indicated that survival of smolts released during strong upwelling years was more than twice that of smolts released in poor upwelling years.

These fluctuating ocean conditions affected the survival not just of hatchery smolts but also of wild coho smolts migrating from streams on the west coast of Vancouver Island, British Columbia (Holtby et al. 1990) and of marine populations such as the northern anchovy (*Engraulis mordax*) (Nickelson 1986). Other long-term trends in catches of salmon (including both wild and hatchery-produced) in the north Pacific Ocean have been correlated with changes in the intensity of the Aleutian low pressure system which has a strong influence on oceanographic conditions (Beamish and Bouillon 1993).

Marine survival of coho and chinook smolts produced in British Columbia hatcheries has also varied significantly and tended to decrease since the late 1970s. The average survival rate for coho smolts declined from 14% for 1979 releases to 8% for 1989 releases. For ocean-type chinook salmon over the same period, it ranged from 1.5% down to 0.5%. There was no overall trend for chum salmon; survival of fed fry ranged from 0.6 to 2.4% and for unfed fry from 0.2 to 1.2% for releases between 1979 and 1987. Marine survival of fed pink salmon fry increased from 3.4% in 1980 to 12.4% in 1989; for unfed fry it ranged from 0.7 to 9.9%.

Returns of adult pink salmon to the Prince William Sound area in Alaska increased considerably from the late 1970s to 1990 in parallel with the increase in hatchery releases (Eggers et al. 1996). Marine survival was approximately 3-5%, being higher in years of warmer temperatures during seaward migration than in cooler years.

Virtually all of the Japanese production of chum and pink salmon is supported by hatcheries. The number of returning chum salmon increased from 5 million in the 1960s to 50 million in the 1980s; over the same period, the returns of pink salmon increased from 1.2 million to 3.8 million. These increased returns resulted both from increased hatchery releases and from improved rates of marine survival. Prior to the introduction of manufactured dry diets in the 1965 brood year, marine survival rates for hatcheries in

Hokkaido averaged about 1%; since then they have been 2-3% (Kaeriyama 1996). The marine survival of pink salmon fry released from hatcheries on Sakhalin Island, Russia, is approximately 1-3% and for chum fry, is 2% (Dushkina 1994).

Atlantic Salmon Programs in Eastern North America and Europe. Most Atlantic salmon-producing countries adopted the technology developed mainly by Sweden for production and release of smolts in place of the long-practiced release of earlier life stages, i.e., fry and parr (Carlin 1959). Larsson (1980) and Lindroth and Larsson (1985) documented the development of Swedish smolt rearing and release programs and their importance to the Baltic salmon fishery. The Carlin smolt tag provided an effective marking system and allowed meaningful evaluation of smolt releases (Carlin 1955). The tag is small enough to apply to a 10-cm fish. It is retained reasonably well, has an expansion sector to prevent overgrowth during rapid marine growth of the salmon and, therefore, remains visible. Some of its disadvantages were overcome in various modifications by groups using it (Saunders 1968). More recent developments include the magnetic coded wire nose tag (Jefferts et al. 1963) and visual implant tag. The coded wire tag was a major breakthrough because, unlike the external Carlin tag, it does not cause permanent lesions resulting in damage to the fish and increased likelihood of tag loss. The highly visible Carlin tag may attract predators whereas the nose tag is not visible externally. Moreover, the coded wire tag is less expensive and easier to apply. However, both types of tag are still in use, the coded wire tag because it is easy to identify great numbers of fish and the Carlin tag and its modifications where external visibility is important.

The great success with the Swedish smolt release program in the Baltic Sea during the 1950s and 1960s led most salmon-producing countries to attempt similar programs. Tag returns in the Baltic reached 30-40%, largely because Baltic (Atlantic) salmon remain in that sea where there is an intense fishery. Releases of tagged smolts from the west coast of Sweden and from many of the salmon rivers in other parts of Europe and North America gave much lower, highly variable tag returns, owing to more extensive migration patterns, an unexplained higher rate of natural mortality, and exposure to a plethora of distant and local commercial fisheries. In the 1960s, the extensive use of the visible Carlin tag was indispensable in developing knowledge of the growing high seas Atlantic salmon fishery off west Greenland. Saunders et al. (1965) learned that at least some stocks of European and North American salmon feed in those waters during late summer and autumn.

There has been some interest in taking advantage of the homing behaviour of salmon and the smolt production-release technology to develop commercial sea ranching (Thorpe 1980). Most efforts to do this with Atlantic salmon have failed owing to unpredictable and usually low rates of return, and the political problems caused by private versus public ownership and interception in foreign waters. Return rates in some parts of Iceland are high enough to allow commercial sea ranching but this industry is subject to unpredictably low rates of return (*see* Chapter 14).

Smolt-release programs in most countries are aimed at enhancement or re-establishment of wild stocks. Tagged smolts have greatly increased the understanding of salmon migrations and are an important management tool. Declining or lost stocks of salmon have been at least partially restored through smolt release. Much has been learned about the importance of smolt quality, stock origin, and timing and methods of release, which have led to the moderate success of this activity.

PRODUCTION OF SMOLTS FOR COMMERCIAL CULTURE

Coho and Chinook Salmon

Early commercial salmon farms in Washington State and British Columbia concentrated mainly on coho and to a lesser extent, chinook salmon, which were harvested at a size of 250-350 g (Novotny 1975). Coho and chinook salmon were preferred over pink, chum and sockeye salmon because rearing trials indicated that these latter species were less amenable to netpen rearing because of their greater susceptibility to disease and algal blooms (Brett et al. 1978).

The coho salmon was chosen for its rapid growth, hardiness and availability of surplus eggs from public hatchery facilities. Because most private hatcheries were of limited size and capacity, the managers attempted to make most efficient use of their facilities. This was achieved by producing underyearling smolts. Ground water with a temperature between 7 and 10°C was used to accelerate egg incubation, but at these temperatures many juvenile coho salmon failed to become underyearling smolts in the absence of photoperiod manipulation. Following transfer to seawater netpens at sizes as small as 7 g, these coho salmon frequently became "stunts" and were lost from production (Clarke and Nagahama 1977; Folmar et al. 1982; Nishioka et al. 1982).

As the production strategy shifted to harvest at a larger size, farms in British Columbia began to prefer chinook over coho salmon because its later age at maturity permitted a longer growout period and more flexibility for harvest time. The chinook salmon stocks were mostly of the ocean-type stock, which could be more successfully transferred to seawater at a weight of 7 g. Alternate freshwater rearing methods for chinook salmon were developed to produce larger smolts and thereby reduce the time required for seawater growout. One schedule involved transfer to seawater in October at a weight of 35 g; another involved transfer in March - April at a weight of 50-80 g. These later transfers of larger fish succeeded to shorten the period required for growout in seawater and to bring salmon to market size over a wider season. By 1994, 40% of the chinook smolts transfered to seawater for growout were yearlings. There was also an increase in production time for coho smolts: by 1994, 60% of smolts produced for salmon farms in British Columbia were yearlings.

The annual harvest of coho salmon from Chilean farms is about 30,000 tonnes. Initially, salmon farms in Chile were dependent upon imported eggs. Because of the 6-month phase difference in seasons between the northern and southern hemispheres, commercial smolt suppliers were able to produce 20-30-g coho smolts after nine months without photoperiod manipulation. At present, Chilean farmers produce most of their smolts from their own broodstocks. Elevated temperatures are used in hatcheries to accelerate growth of fry which are then moved to netpens in lakes for rearing to smolt size and transport to the seawater cages as yearlings.

Atlantic Salmon

Farming of Atlantic salmon commenced in Norway in the 1960s and had become a well-established industry by the early 1970s. It grew from 287 farms producing 171 tonnes of Atlantic salmon in 1973 to 791 farms producing 118,000 tonnes of salmon by 1989 (Tilseth et al. 1991). Over this period, the number of commercial smolt producers increased from 17 to 657. Although there has been a consolidation in the industry since 1989, production has continued to expand and about 85 million smolts were transferred to seawater in 1995 (Torrissen et al. 1995). The growth of the Norwegian salmon farming industry was favoured by a long, protected coastline with suitable growing conditions and assisted by government support. Atlantic salmon farming has also developed in Scotland, Ireland, Canada, U.S., Chile and Australia.

The salmon aquaculture industry in eastern Canada started before there was production of smolts specifically for this purpose. Smolts for the first successful commercial venture in New Brunswick were provided from those produced for salmon enhancement and research. Fortuitously, the first smolts used in a commercial venture were from the Saint John River stock (Sutterlin et. al. 1981). In nature these fish usually mature as grilse (after one winter at sea) and as multi-sea-winter salmon in a ratio of about 1:1. Under conditions of cage culture in the southern Bay of Fundy, the incidence of grilse in that first group, harvested in 1979, was insignificant. Subsequently, the incidence of grilse has sometimes been higher but rarely over 10-15%. This low incidence of grilse has been a boon to the local industry. But in other countries and other parts of Canada, the industry has been plagued by early maturity as grilse, a problem since these are smaller and less desirable (and profitable) than multi-sea-winter salmon. Other local stocks of salmon were more likely to mature as grilse and the people in the fledgling industry quickly learned that these should not be used for cage culture.

After the marine aquaculture industry was established in Canada, several private companies began to produce smolts because government facilities could not meet the growing demand. Moreover, the government facilities were mandated to produce smolts for the public, not the private-sector. The private sector smolt producers used a combination of technology already in use by government producers and that transferred from Norway and Scotland where Atlantic salmon aquaculture was already well

developed. At first, production of S1 smolts was rarely over 50%, many fish having to be reared a second year as S2 smolts. Modification of the imported technology to take account of the lower water temperature, which restricted growth to incipient smolt size by the end of the first growing season, better husbandry, and improved facilities led to improved S1 smolt production. Meanwhile, research was showing how environmental manipulation and attention to the requirements for smolt development could be used to enhance production of S1 smolts.

MODIFICATION OF SMOLT AGE AND SEASON

Acceleration Using Photoperiod and Temperature

Pacific Salmon. As mentioned earlier, early attempts by salmon farmers to accelerate smolting of coho salmon using elevated temperatures produced variable results. This variability was due to a lack of understanding of the effect of photoperiod (Clarke 1992). Photoperiod exposure during the months after first feeding regulates growth and smolting during the first summer. This was first demonstrated experimentally using photoperiod cycles phased at 1-month intervals (Clarke and Shelbourn 1986). Coho fry were exposed from the time of first feeding to simulated natural photoperiod cycles with phases beginning with either December, January or February daylengths at temperatures of 8, 11 or 14°C. After 6 months of rearing, the coho salmon started on the February photoperiod at 14°C had separated into two distinct size modes. The upper mode had an average weight of 72 g and were able to regulate plasma sodium concentrations to 165 mmol/l after a 24-h seawater challenge. The lower mode had an average weight of 18.9 g and plasma sodium level was elevated to 179 mmol/l after seawater challenge. In contrast, the groups started under December or January daylength had unimodal size distributions and adapted well to seawater. There were corresponding differences in the ability of coho salmon from the three photoperiod phases to grow in seawater; those from the December and January groups grew about five times as fast as did those started under the February photoperiod phase.

The effect of photoperiod phase on smolting of coho salmon is a function of initial daylength. Clarke et. al. (1989) reared coho fry from the time of first feeding under constant 9.5 h (short-day) or 14.5 h (long-day) photoperiod for 2 months and then under simulated natural photoperiod (14.5 h increasing to 17 h) for 4 months. The fry given the initial short-day treatment grew more rapidly and more uniformly in both fresh and salt water than did those given an initial long-day photoperiod. Stream-type chinook salmon respond to photoperiod in the same manner as coho salmon so that the same sequence of short- and long-day photoperiods can be used to produce underyearling smolts (Clarke et al. 1989, 1992, 1994*b*). Masu salmon respond in a similar fashion (Okumoto et al. 1989). It should be noted that this protocol is not effective for Atlantic salmon. The latter species is not responsive to the short-day photoperiod during the first

3 months from start feeding (Clarke 1994). Short-day treatment of juvenile Atlantic salmon is applied only after they have exceeded the threshold size of 7-12 cm fork length (*see* page 539).

Juvenile coho salmon measure daylength not by the accumulated hours of daylight, but by the time during the day when light is experienced. This was demonstrated by Thorarensen and Clarke (1989) using a skeleton photoperiod. Coho fry were divided into nine groups and held under three initial photoperiods (6L:18D, 10L:14D, 14L:10D) for 2 months and subsequently under 3 final photoperiods (16L:8D, 9L:6D:1L:8D, 10L:14D) for three months in a factorial design. Fish exposed first to short-day photoperiods (6L:18D and 10L:14D) and then to a long-day photoperiod (16L:8D) grew faster and had a greater hypo-osmoregulatory capacity in a 24-h seawater challenge test than did any of the other groups. Coho salmon first given short-day photoperiods and then held under the skeleton photoperiod (9L:6D:1L:8D) grew slightly less than those on the complete long-day final photoperiod but substantially better than those kept on the short-day final photoperiod. Coho salmon exposed initially to long-day photoperiod displayed greatly reduced growth and impaired hypo-osmoregulatory capacity in seawater on all subsequent photoperiods, indicating that responsiveness to inductive photoperiods depends on prior photoperiod experience. The effect of the sequence of short-day followed by long-day photoperiods is to change the developmental path taken by underyearling salmon from the parr to the smolt phase of the life cycle. The difference in growth rate between fish on the normal versus accelerated paths is not detectable until about a month after completion of the initial 2-month priming photoperiod.

Light must be excluded completely at night during the period of short-day treatment. Failure to do so will impair growth and smolting. Thorarensen et al. (1989) exposed coho fry to light intensities of 0.0001 - 0.05 lux at night during the initial short-day period. After subsequent exposure to inductive long-day photoperiods, all groups receiving low levels of night illumination had a lower growth rate and poorer hypo-osmoregulatory capacity in a 24-h seawater challenge test than did the control group kept in total darkness at night during the short-day period.

The daylength that must be exceeded to obtain a long-day response is termed the critical daylength (Bünning 1973). For coho salmon fry, the critical daylength during the 2-month priming period is between 11.5 and 12 h (Clarke 1991). Thus, for production of accelerated smolts, the hours of daylight should be kept below this critical daylength for 2 months from first feeding. Ten hours is suggested, but shorter daylengths can be used. Growth of fry will be slightly slower on a 6-h day than on a 10-h day during the priming period.

The effectiveness of a constant short-day photoperiod means that simple light control systems can be used to produce the initial priming photoperiod in a hatchery. At the end of the priming period, the fish can be returned to natural daylength. Short-day conditions can be produced in outdoor tanks by using light-tight covers which are

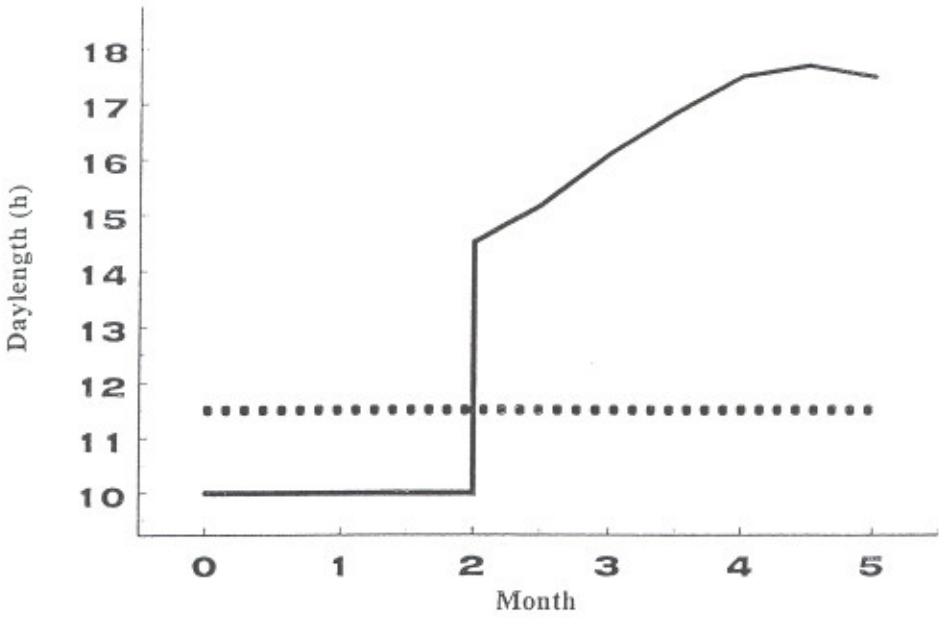

FIGURE 2. A photoperiod schedule for producing underyearling coho salmon smolts. Fry are held under a constant daylength of 10 h during a 2-month priming period in late winter and spring followed by exposure to natural increasing daylength during late spring and summer. The horizontal dotted line indicates the daylength during the priming period below which a short-day response is obtained.

removed and replaced according to a regular schedule each day. Figure 2 illustrates the use of a constant 10-h photoperiod followed by natural increasing spring daylength. Although photoperiod manipulation enables production of underyearling smolts at temperatures as low as 8°C, much larger and more uniform coho salmon smolts are produced at temperatures between 10 and 15°C (Clarke and Shelbourn 1989).

Atlantic Salmon. Smolt production, whether for stock enhancement or aquaculture, is best done in the shortest possible time in order to minimize cost and make the most efficient use of facilities. Notwithstanding the usual requirement of two or more years of juvenile growth to reach the smolt stage in nature, artificial production has achieved increasing incidence of S1 smolts by optimizing conditions for rapid growth, notably by maximizing the period with favourable temperature, provision of adequate amounts of high energy feed and practicing good husbandry (Figure 1). Research on the effects of photoperiod on growth and smolting has elucidated the role of daylength controlling the endogenous rhythm of smolting. Moreover, photoperiod affects seasonal patterns of endocrinological activity which in turn, affect growth, development of hypo-osmoregulatory activity and salinity tolerance, and migratory activity (Duston and

Saunders 1990; Saunders et al. 1994*b*). With this knowledge, technology has developed for using photoperiod manipulation to speed growth and thereby increase the number of parr reaching the threshold size or energy level for smolting after one summer's growth (Saunders and Duston 1992). This, together with improved husbandry, has resulted in much improved production of S1 smolts.

A further improvement is production of underyearling (S0) smolts. Research has drawn on the understanding of the role the environmental variables, photoperiod and temperature, to speed juvenile development through the stages leading to smolting. The timetable of development has been advanced wherever possible, i.e., maturation of spawners, incubation of the eggs, development through the alevin stage, first feeding, and fry and parr growth. Spawning is advanced by subjecting the spawners to an artificially advanced regime of decreasing daylength. Incubation is conducted under temperatures higher than those in nature but which have been found compatible with production of reasonably large, viable alevins (Peterson et al. 1977). Similarly, the process of yolk utilization and first feeding is accelerated at elevated temperatures up to 16°C. Early growth through the fry stage is also maximized at temperatures up to 16 °C (Peterson and Martin-Robichaud 1989). Extended daylength from the time of first feeding, which can be as early as January, has been used to speed growth and provide the background for further photoperiod manipulation believed necessary to initiate the smolting process (Saunders et al. 1990). By mid-summer when the parr have reached the threshold size for smolting of about 10 cm, the photoperiod is abruptly reduced to a constant level of about 7 h and held at this level for about 2 months before restoration of a simulated natural or constant long photoperiod (Duston and Saunders 1995*a*). Thereafter, the fish develop smolt characteristics and can be transferred to seawater in November.

Although this system appears to produce viable Atlantic salmon smolts, it is most beneficial in areas where seawater temperatures remain favourable for growth during winter. For salmon farms with low winter temperatures, there is little advantage in putting smolts in seawater that is cooling rapidly to levels at which feeding and growth are minimal. S0 smolts transferred to sea cages in New Brunswick have reached market size somewhat earlier than if they had been reared to smolts and transferred to seawater at the usual times (Duston and Saunders 1995*a*). Continuing research is leading to earlier smolt development and transfer to sea cages to take advantage of favourable temperatures in autumn. A reduction in the time spent in the smolt-rearing station will lead to more efficient use of facilities and lower cost of production. Another objective in production of S0 and other off-season smolts is to achieve a more even annual production of market-sized fish. Duston and Saunders (1995*a*) succeeded in producing underyearling (0+) smolts in 10 months by subjecting fry to a long photoperiod (17L:7D) followed by one or two months of short photoperiod (7L:17D) and a return to long photoperiod. There is convincing evidence that salmonids perceive a long or short photoperiod in relation to previous photoperiod history; days must be longer or shorter than the previous daylength (Randall et al. 1991; Berge et al. 1995; Duston and Saunders

1995*a*; Sigholt et al. 1995). Further research should lead to reducing the seasonal fluctuations in production or directing production to periods of peak market demand

Studies on Performance of Smolts Produced for Commercial Farms

Pacific Salmon. Because growth and survival of salmon held in netpens is more readily observed than that of smolts released to the ocean, it is much easier to determine the reasons for success or failure of a particular batch of smolts. Thus, the development of salmon farming led to a considerable increase in knowledge about smolting and acclimation to seawater. Pioneering studies were conducted by the U.S. National Marine Fisheries Service at a marine experimental facility in Puget Sound, Washington. Survival and growth of groups of underyearling and yearling coho salmon transferred to seawater netpens was monitored for 6 months (Mahnken et al. 1982). Some fish which had the appearance of silvery parr at the time of transfer in April began to regain parr marks after the summer solstice. Unlike the rapidly growing post-smolts, the stunted and parr-revertant coho salmon did not increase in size, so that a bimodal size frequency distribution was apparent by October (Folmar et al. 1982; Mahnken et al. 1982). The size of the largest fish with parr marks at any given time in seawater was found to be a good indicator of the minimum size for survival and growth in seawater; this critical size increased from the summer to winter solstice and then decreased again as the normal smolting time approached in spring. Mortality of the stunts and parr-revertants increased during autumn and winter although a few parr-revertants survived to become smolts the following spring. Similar experiments conducted in France obtained best survival following seawater transfers in September and October for underyearling coho salmon and in April for yearlings; transfers during June and July led to significant mortality due to high water temperatures (Harache et al. 1980; *see also* page 544).

Clarke and Shelbourn (1989) performed a factorial experiment in the laboratory to determine the simultaneous effects of freshwater temperature, seawater temperature, and time of transfer to seawater on growth and hypo-osmoregulatory performance of underyearling coho smolts. A delayed photoperiod was used to ensure synchronous development of underyearling smolts and groups were transferred to seawater at intervals from May 8 to August 28 at mean weights ranging from 4.7 g to 49.6 g. Hypo-osmoregulatory capacity in a 24-h seawater challenge test reached a maximum first at higher freshwater rearing temperatures, ranging from July 5 at 15°C to July 12 at 11°C and July 24 at 8°C. Growth in seawater relative to that in fresh water was fastest when fish were transferred to temperatures higher than their freshwater rearing temperature. The transfer date for maximal growth rate in seawater relative to that in fresh water was not affected by seawater temperatures in the range of 8.9 to 15.8°C. At the end of the experiment in mid-October, the mean weight was greatest for groups reared in 14-15°C fresh water and transferred to seawater in May. Growth was also more uniform in coho salmon reared at higher freshwater temperatures. The coefficient of variation for final weight was much less for coho salmon that had been reared in fresh water at

temperatures of 11-15°C compared with those reared at temperatures of 7-8°C (Clarke and Shelbourn 1989).

A similar factorial experiment examined the performance of underyearling ocean-type chinook salmon transferred from fresh water (7-17°C) to seawater (9.5-14.5°C) at intervals from April to June (Clarke and Shelbourn 1985). The optimum hypo-osmoregulatory performance measured in a 24-h seawater challenge test was estimated to occur after transfer of 5.6-g chinook salmon from 13.8°C fresh water to 10.2°C seawater. Maximal growth in seawater relative to that in fresh water occurred with transfer of 6-g fish from 9.7°C fresh water to 14.1°C seawater (Clarke and Shelbourn 1985). Relative growth in seawater declined sharply at temperatures above 14°C. There was considerable mortality during the first month in seawater in groups reared in 16°C fresh water; this was associated with extensive descaling which started in fresh water and persisted after transfer to seawater. This tendency for descaling of larger ocean-type chinook salmon is a concern for hatcheries producing large smolts for offseason transfer. If ocean-type chinook salmon stocks are used, the rearing density must be lowered for fish larger than 10 g. An alternative is to use stream-type chinook or their hybrids, both of which have a much greater resistance to descaling (Clarke et al. 1994*b*).

Betaine has been known as an osmolyte in plants and microbes for some time but is now used to facilitate entry of smolts to seawater. Based on experiments with Atlantic salmon and rainbow trout (*see* below), many commercial salmon farms prepare their smolts for seawater transfer by feeding a betaine/amino acid mixture for 6 weeks before and after the transfer. An experiment conducted with yearling ocean-type chinook salmon confirmed that this dietary supplement produced a significantly greater growth rate and lower plasma sodium concentration after transfer to seawater netpens (Clarke et al. 1994*a*). Individually tagged yearling chinook salmon were fed either a control diet or one containing 1% betaine for 6 weeks in fresh water and an additional 8 weeks following entry into seawater in early April. Hypo-osmoregulatory performance in 24-h seawater challenge tests was not significantly affected by feeding betaine for 5, 47, or 70 days. However, the plasma sodium concentration was significantly lower in the betaine-fed group after 8 weeks in seawater. Growth after transfer to seawater was significantly greater in the group receiving betaine. Examination of individual growth rates revealed that the effect of betaine was to reduce the number of fish growing poorly (i.e., <0.5% body weight · day^{-1}); if these poor performers were removed from the analysis, there was no longer a significant effect of betaine on growth rate.

Atlantic Salmon. Based on experience with transferring of New Brunswick stocks of smolts to sea cages in the Bay of Fundy, temporal and thermal constraints strongly affect survival and growth performance. The spring-time "window" for smolt transfer in the Fundy area is from approximately mid-April to late May. It became apparent during the early development of the industry that smolts should not experience freshwater temperatures above 12°C in the spring before transfer. Temperatures of 13-16°C result in a loss of gill Na^+,K^+-ATPase activity and salinity tolerance. Because surface water

supplies to smolt rearing stations warm quickly in May, there is a very narrow window for successful smolt transfer; this period was the month of May in the early years of the industry, and in some cases only the first half of May for rearing stations with warmer water. This necessitated moving smolts in late April when sea temperature is as low as 5°C. This was found not to be a constraint and many producers were forced to transfer many of their smolts in April when both fresh and seawater temperatures were 5°C or lower. The consequences of such early transfer were usually favourable, in contrast with those done later after freshwater temperatures had risen to 15°C or higher. Seawater temperatures in the Fundy region rise from about 5°C in mid April to 8-10°C in late June.

Smolt size is of great importance for initial survival after transfer to seawater and for long-term growth performance. Although smaller smolts sometimes survive and grow well, it is preferable to stock out smolts of 16 cm or larger. Smaller individuals are likely to be non-smolts or previously mature males, both of which may not survive and grow well. Some smolt producers mistakenly hold their fish in fresh water as long as possible in the spring, hoping to have them reach smolt size before the latest acceptable time of transfer to seawater. Such fish have not made the earlier "decision" to become smolts and will not do so that season in spite of having reached smolt size in the spring. For the Saint John River stock used extensively in the Bay of Fundy, large smolts (>20 cm) are more likely to mature as grilse than are smaller individuals. Therefore, large S2 smolts and similarly large S1s are more likely to mature as grilse than their smaller (<18 cm) siblings. For the Saint John stock reared in the Bay of Fundy, the optimum smolt is an S1 from 18 to 20 cm because large smolt size is positively correlated with large size at harvest (O'Flynn et al. 1995).

The Norwegian Research Council initiated a program to improve smolt quality in their salmon farming industry in 1990. Staff of companies producing smolts for sale to salmon farms have been trained in the determination of smolt quality (*see* page 545). During the past few years, this increased focus on smolt quality has helped Norwegian salmon farms to reduce considerably the mortality of smolts after transfer to seawater netpens. Another component of the program developed photoperiod treatments for production of underyearling smolts (*see* page 540). Minimizing handling stress, for example by using water-to-water transfers, can greatly reduce mortality associated with entry to seawater (Flagg and Harrell 1990).

Supplementation of the diet with a betaine/amino acid mixuture before and after transfer to seawater can facilitate hypo-osmoregulation by Atlantic salmon smolts, as discussed earlier for Pacific salmon. Yearling Atlantic salmon fed 1.5% betaine in the diet for 2 months in fresh water had an improved hypo-osmoregulatory performance in a 48-h seawater challenge at a salinity of 39‰, elevated gill Na^+,K^+-ATPase, and an elevated plasma thyroxine concentration compared with those fed a control diet (Virtanen et al. 1989). Subsequent studies with different levels of betaine supplementation indicated that 1% betaine supplementation in smolt diets, starting 6-8 weeks before

transfer to seawater and for 3 weeks afterward will reduce weight loss and hasten the recovery of appetite (Virtanen et al. 1994). However, Duston (1993) reported that feeding Atlantic salmon parr in fresh water for 25 days with 1.5% betaine did not influence growth, gill Na^+,K^+ ATPase activity, or plasma osmolality after transfer to seawater during autumn.

Offseason Transfers

The highly seasonal nature of the smolting process under natural conditions can be an impediment to salmon farming. One problem for salmon farms is the seasonal fluctuation in salmon harvest associated with the normal life cycle. It is desirable to spread harvests across seasons to minimize seasonal variation and provide a more constant amount of salmon for market throughout the year. In some regions, unfavourable conditions in the ocean due to seasonal temperature extremes or algae blooms need to be avoided. Therefore, techniques for offseason transfers of smolts have been developed to meet the requirements of industry.

Coho Salmon. Harache et al. (1980) demonstrated that one-summer-old (S0) coho salmon could be transferred successfully to 35‰ seawater in Brittany, France, after temperatures dropped below 16-17°C. The fish had to be larger than 170 mm fork length by September or 210 mm by late December in order to avoid growth stunting. Japanese salmon farms transfer underyearling coho salmon to seawater netpens at a minimum size of 120 g from mid October to early December when seawater temperatures drop below 17-18°C (Iwata and Clarke 1987).

Atlantic Salmon. Considering the progress made in reducing the time to produce smolts and success with transferring them to seawater at off-season times, it is likely that smolts can eventually be produced throughout the year by using environmental manipulation. The practicality of doing so will depend largely on local environmental conditions. In regions with little variation in sea temperature during the year there may be greater practicality in off-season smolt production and transfer to seawater than in regions with wider extremes in sea temperature. Frantsi and Justason (1988) noted that off-season transfer of yearling Atlantic salmon could be used to increase hatchery efficiency and expand the harvest season in New Brunswick salmon farms. Research in Norway has been directed at autumn transfer of underyearling Atlantic salmon. This practice has developed considerably in recent years and by 1995, 25% of all smolts transferred to netpens on Norwegian salmon farms were underyearlings transferred in autumn (T. Hansen, Matre Aquaculture Station, Matredal Norway, pers. comm.).

TECHNIQUES FOR ASSESSING SMOLT READINESS AND QUALITY

Salinity Tolerance Test

One of the prime requirements of a smolt is that it must be able to tolerate abrupt transfer from fresh water to seawater and continue growing there. A simple test has been developed in which presumptive smolts are transferred directly from fresh water to hypersaline water (salinity 37-40‰) and observed for 96 h (Adams et al. 1975; Komourdjian et al. 1976; Saunders et al. 1985). Those surviving for this time are capable of direct transfer to normal salinities (30-32‰). It has usually been observed that salmon with such high salinity tolerance also have elevated gill Na^+,K^+ ATPase activity. The salinity tolerance test is an easy and a reliable way of determining whether or not a given lot of smolts is ready for transfer to seawater. Hypersaline water must be used for the test because tolerance of 30‰ seawater is not an adequate criterion to identify smolts; large parr may survive indefinitely but fail to grow adequately (Clarke and Nagahama 1977; Harache et al. 1980; Folmar et al. 1982).

The salinity tolerance test is conducted in temperature-controlled tanks (usually 100-200 l) filled with water made up to a salinity of 37.5‰ by mixing appropriate amounts of a salt mixture (Instant Ocean® or measured amounts of the principal salts in natural seawater). Temperature is usually maintained at the same level as that to which the fish have been acclimated in their rearing tanks. Temperatures higher or lower than those during recent experience may be used to learn how smolts may respond after transfer to sea cages where temperature may be far different from that recently experienced by the smolts. The fish are fasted for 24 h prior to being transferred from their freshwater holding tanks directly to the salinity baths. Feed is not offered during the 96-h test. Dead fish, if any, are removed daily. The results are expressed as percent survival after 96 h.

Johnsson and Clarke (1988) suggested that the period of the test be extended to 144 h from 96 h at low temperatures and when the fish are larger than 50 g in order to increase the test's sensitivity. In order to determine the seasonal development of salinity tolerance and analyze the results statistically, it is possible to perform a series of tolerance tests at different salinities. As mortality rises quickly with increasing salinity, it is advisable to use five salinities in increments of 1 or 2‰ in order to obtain at least two or three concentrations giving mortalities in the range between 2 and 98% (Blackburn and Clarke 1987; Johnsson and Clarke 1988). This enables a calculation of the 96-h median lethal salinity with confidence limits by means of probit analysis. The 96-h LC50 test has been used with juvenile rainbow and steelhead trout (Johnsson and Clarke 1988), chinook, coho and chum salmon (Clarke et al. 1989) and pink salmon (Varnavsky et al. 1991). Table 1 summarizes LC50 salinities measured for various species as they grow.

The 96-h LC50 test can use 100 juveniles (20 fish at each of five salinities) or more. When limited numbers of larger fish are available, the 24-h seawater challenge

TABLE 1.

The 96-h LC50 salinity measured for various species in relation to size.

Species	Weight or fork length	Temperature °C	LC50 salinity	Source
Rainbow trout	9.5 g	11	29.4	1
	33.0 g	11	35.1	1
	95.0 g	11	35.8	1
Steelhead trout	4.0 g	11	28.9	1
	10.4 g	11	31.4	1
	24.6 g	11	35.1	1
	46.9 g	11	37.4	1
	80.6 g	11	39.4	1
Chum salmon	42 mm	10	42	2
	54 mm	10	46	2
	71.2 mm	10	50.0[1]	2
Coho salmon [2]	34.5 mm	10	26.5	2
	46.1 mm	10	32.1	2
	53.1 mm	10	34.2	2
	62.7 mm	10	35.4	2
	95.7 mm	10	40.8	2
Chinook salmon [3]	37.6 mm	10	25	2
	45.0 mm	10	28.2	2
	56.4 mm	10	34.5	2
	70.4 mm	10	36.2	2
	100.7 mm	10	41.4	2
Pink salmon	0.2 g	7	39.2- 40.4	3
	0.5 g	7	38.9 - 39.2	3

Sources: 1-Johnsson and Clarke (1988); 2-Clarke et al. (1989); 3-Varnavsky et al. (1991).

[1] Extrapolated value

[2] Accelerated photoperiod applied to produce underyearling smolts

[3] Ocean-type stock

plasma sodium test can be used as an alternative (*see* below). The latter test is also has the benefit that it does not usually cause death of the fish. In view of increasing regard for animal welfare, the use of the salinity tolerance test rather than alternate procedures that cause less distress and mortality may have to be justified.

Seawater Challenge Hypo-osmoregulatory Test

The seawater challenge hypo-osmoregulatory test measures the ability of salmonids to regulate plasma ion concentrations shortly after their abrupt transfer to seawater. The seawater challenge test was developed initially to measure the readiness of accelerated underyearling coho salmon for transfer to seawater netpens for growout (Clarke and Blackburn 1977). This test was chosen as an indicator because it demonstrated a regular developmental pattern even at the elevated temperatures used for growth acceleration, unlike other indicators such as lipid content and condition factor (Clarke et al. 1978; Clarke 1982). Furthermore, this test is simpler and cheaper to perform than assays for gill Na^+,K^+-ATPase or plasma thyroxine. However, for species such as chum and pink salmon that may be too small from which to collect a blood sample, the salinity tolerance test can be used as an alternative.

The seawater challenge test involves transfer of a sample of fish to seawater at their acclimation temperature; after 24 h, the fish are anesthetized and a blood sample is collected. Plasma is separated from the blood cells by centrifugation and then diluted for measurement of sodium concentration using a flame photometer, atomic absorption spectrophotometer or sodium ion analyzer (Blackburn and Clarke 1987). Alternatively, osmolality can be measured in undiluted plasma using an osmometer (Grau et al. 1985); this practice has been adopted in hatcheries operated by the Department of Fisheries and Oceans in British Columbia. A third option is to measure plasma chloride concentration using a chloride titrator (Sigholt et al. 1989). Many commercial hatcheries in Norway and Canada now use plasma chloride concentration as an indicator of performance in the seawater challenge test, the advantage being that a chloridometer is relatively inexpensive and easy to use. Expected plasma sodium concentration in smolts after a 24-h challenge is approximately 160-165 mmol/l. For plasma osmolality, the corresponding value is 330-340 mosmol/l and for plasma chloride 140-150 mmol/l. Mortality in the test indicates very poor hypo-osmoregulatory capacity and may be indicative of gill damage or significant health problems in the smolts.

The 24-h interval for the challenge test was chosen by Blackburn and Clarke (1987) for coho salmon at 10°C because plasma sodium concentrations were maximal at that time. However, the maximum may occur earlier or later than this in relation to temperature and species used. The maximum rise in levels of sodium ion in juvenile chum (Iwata et al. 1982) and pink salmon (Varnavsky et al. 1991) occurred after 12 h in seawater. Virtanen and Oikari (1984) reported that plasma sodium was higher at 48 h than at 24 h after transfer of juvenile Atlantic salmon to seawater at 1.5°C.

Clarke and Blackburn (1977) used a salinity of 30‰ for the challenge test because it was readily available. More recently, a salinity of 35‰ has been produced by adding salts to natural seawater (Berge et al. 1995; Sigholt et al. 1995). Although more time and effort is required to make this higher salinity, its use improves the ability of the test to detect smolts with a fully developed ability to osmoregulate in seawater, particularly when the fish are larger than 80 g. The use of 35‰ seawater is now a common practice for testing of Atlantic salmon smolts produced in commerical hatcheries in Norway.

A balanced salt mixture *must* be used to make artificial seawater because single ion solutions are toxic (Hoar 1966; Blackburn and Clarke 1987). Addition of a precise weight of salt might not produce the calculated salinity because of variable amounts of moisture absorbed during storage. Therefore, it is advisable to measure the salinity after dissolving the salt and make adjustments as necessary to achieve the intended concentration. It is important that salinity be accurate to within 1‰ for results to be comparable among tests. Salinity can be measured using a hydrometer, refractometer or conductivity meter; if a chloride titrator is used, salinity can also be calculated from the chloride concentration according to the following equation:

$$\text{salinity (‰)} = 0.03 + [1.805 \cdot \text{chloride (mmol/l)} \cdot 0.035453] \quad (1)$$

The salt should be added to the water at least a day before the test to ensure that it is dissolved thoroughly. Spurious mortality may be observed when using freshly made artificial seawater. Fewer toxicity problems are observed when salt is added to ordinary seawater to bring the salinity up to the desired concentration.

A single test will not indicate whether hypo-osmoregulatory capacity is increasing or decreasing. Therefore, it is worthwhile to perform the test at regular intervals during the last 2 to 3 months before seawater entry. This allows the development of the smolts to be examined so that the optimum time for seawater entry can be estimated well in advance. Other factors that can influence the results obtained from the seawater challenge test include seawater temperature, density of the fish in the test tank, contamination of the blood samples with seawater, and descaling of the smolts. Temperature in the test tanks should be close to the acclimation temperature for the smolts. The risk of contamination can be minimized by rinsing the smolts in fresh water and blotting them dry before taking a blood sample.

In addition to Pacific and Atlantic salmon, the seawater challenge test has been used for rainbow and steelhead trout, sea (brown) trout, Arctic charr, Dolly Varden charr (*Salvelinus malma*) and coastal cutthroat trout (*Oncorhynchus clarki*) (Hogstrand and Haux 1985; Blackburn and Clarke 1987; Johnson and Heifetz 1988; Yeoh et al. 1991; Arnesen et al. 1992; Johnsson et al. 1994).

Gill Na^+,K^+-ATPase Activity

Gill Na^+,K^+-ATPase is an ion-translocating enzyme involved in salt secretion of fish in seawater (Silva et al. 1977). In smolts there is generally a strong correlation between seasonal increases in salinity tolerance and gill Na^+,K^+-ATPase activity, and this enzyme has been widely used as a 'marker' for the parr-smolt transformation (McCormick and Saunders 1987; Hoar 1988). There are several useful techniques for measurement of gill Na^+,K^+-ATPase activity of teleosts (Johnson et al. 1977; Zaugg 1982; Mayer-Gostan and Lemaire 1991), including a "microassay" suitable for non-lethal biopsies and organ culture (McCormick 1993; Schrock et al. 1994). Measurement of Na^+,K^+-ATPase is most frequently accomplished by measurement of V_{max} in a microsomal preparation or crude homogenate and expressed as activity per unit wet weight of protein. A higher specific activity is obtained when using microsomal preparations compared with crude homogenates, but smolt-related increases are comparable with both methods. The breakdown of adenosine triphosphate (ATP) is detected (most often by measuring inorganic phosphate or adenosine diphosphate, ADP) in the presence and absence of ouabain, a specific inhibitor of Na^+,K^+-ATPase. Such biochemical measurements are, by their nature, method-dependent, and efforts should be made to validate and optimize assay conditions for expression of enzyme activity, including tissue preparation and amount, ion concentrations, pH, ouabain, detergent and temperature. As with salinity challenge tests, a time series is necessary to determine smolt status accurately.

Hormone Assays

Measurement of hormones involved in smolting can be useful for following smolt development and effects of husbandry processes on growth and salinity tolerance. Thyroid hormones, cortisol, growth hormone, insulin-like growth factor I and prolactin have all been implicated in regulating the osmoregulatory changes that occur during smolting (Hoar 1988; McCormick 1994). These hormones, pancreatic peptides and others may also be involved in growth and metabolic changes during smolting (Hoar 1988). Radioimmunoassays applicable to measurement of hormones in salmonid plasma have been developed for thyroid hormones (Dickhoff et al. 1978), cortisol (Redding et al. 1984), growth hormone (Bolton et al. 1986; Le Bail et al. 1991), insulin-like growth factor I (Moriyama et al. 1994) and prolactin (Hirano et al. 1985). It should be noted that these assays can be relatively expensive and require both technical and interpretive expertise. Non-radioactive enzyme immunoassays (e.g., enzyme-linked immunosorbant assay or ELISA) have been developed for measurement of plasma cortisol in salmonids (Barry et al. 1993; McCormick, unpubl. data). Although commercial assays for thyroid hormones and cortisol developed for use in mammals may be applied to fish, their validity requires careful evaluation

Other Tests: Weight Changes, Enzymes, Silvering

Silvering. Although smolts are usually silvery in colour, this criterion is not universally reliable as an indicator of smolt status in reared Atlantic or Pacific salmon (Wedemeyer et al. 1980). Feed components and perhaps tank colour can result in parr becoming silvery. Such fish, particularly those reared under inappropriate photoperiod or temperature regimes often fail to develop or do not maintain salinity tolerance or elevated gill Na^+,K^+-ATPase activity in spite of having large size (McCormick et al. 1987; Duston et al. 1991). Duston (1995) has developed a light reflectance meter to measure silvering of smolts.

Metabolic Enzymes. The concentration of liver mitochondria and the activities of the respiratory chain enzyme, cytochrome c oxidase and another mitochondrial enzyme, citrate synthase, are higher in smolts than in parr (Blake et al. 1984; McCormick et. al. 1989).

Condition Factor and Morphology. The smolting process is characterized by changes in the dynamics of growth. This is often reflected in the relation between length and weight. Condition factor provides a measure of weight per unit length. It is calculated as $[\text{weight} \cdot 100 \cdot \text{length}^{-3}]$ where weight is measured in grams and fork length is measured in centimetres (*see also* Chapter 2). Smolts reared under natural conditions have a lower condition factor than parr due to faster growth in length (particularly in the tail region) than in weight (Winans and Nishioka 1987; Beeman et al. 1994). Condition factor varies among species and is influenced by temperature and feeding rate. Juveniles which are accelerated by rearing at high temperature and on a high energy ration may exhibit little or no decline in condition factor during smolting. For this reason, condition factor is perhaps best used as a simple measure of body shape of fish produced in a particular hatchery over time. Variation in condition factor among groups of smolts produced at hatcheries with distinct rearing environments are not readily interpreted as differences in smolt quality.

More detailed morphometric measurements can be made using a digitizing board attached to a computer. A large number of morphological traits can be examined using principal components analysis. Winans and Nishioka (1987) first used this procedure to describe changes in body shape of hatchery-reared coho salmon during smolting. The technique has also been applied to stream-type chinook salmon and steelhead trout smolts (Beeman et al. 1994, 1995). An advantage of this method is that it is suited to assessment of smolts when lethal sampling is not possible. The morphometric measurements can be taken from photographs of live smolts. However, it does require a larger sample size than do the more invasive methods.

Weight Change in Seawater. Small but measurable changes in length and weight of juvenile salmonids occur due to dehydration after transfer to seawater. Zaugg and Beckman (1990) found that these decreases in length and weight of juvenile coho salmon

transferred to 31‰ seawater for 24 h were less pronounced during the period when the level of gill Na^+,K^+-ATPase was greatest. They suggested that this phenomenon could be used as a simple test of seawater readiness. Blackburn and Clarke (1987) measured weight loss in juvenile coho salmon, steelhead trout and domesticated rainbow trout in 24-h seawater challenge tests. In five out of six groups, the correlation between weight loss and plasma sodium concentrations was significant. However, the slopes and intercepts were not homogeneous, indicating that the relationship would have to be calibrated separately for each stock being tested. The coefficient of variation for weight loss is much larger than for the seawater challenge blood sodium test, so that larger sample sizes are required to detect differences among groups. Varnavsky et al. (1991) reported that weight loss in juvenile pink salmon was maximal 12 h after transfer to 30‰ seawater.

Cataracts. The formation of ocular cataracts (opacity of the lens) due to osmotic stress has been studied in coho salmon (Iwata et al. 1987). In a series of transfers of yearling coho salmon to seawater at different seasons, increased cataract formation was associated with a decreased ability to acclimate to seawater. Iwata et al. (1987) proposed that the occurrence of cataracts after transfer to seawater may provide a simple method for assessing smolt status. However, this test has not gained wide acceptance.

TRANSFER OF NON-SMOLTING SPECIES TO SALT WATER

Rainbow Trout

As in most salmonids, larger rainbow trout have increased survival following seawater exposure. Jackson (1981) found that mortality and plasma osmolality decreased with increasing size for fish between 11 and 30 g following transfer to 30‰. Rainbow trout smaller than 15 g can survive direct transfer to salinities <22‰ (Landless 1976). Since osmotic perturbations can increase with relatively small increases in salinity and changes in temperature (*see* below), the size necessary for maximum seawater survival will depend on environmental conditions. Weight > 50 g would appear to be a minimum for direct transfers to salinities > 30‰ (Landless 1976; Jackson 1981).

The salinity of coastal seawater can vary greatly and is an important consideration for growth and survival of rainbow trout. Johnsson and Clarke (1988) found that 7-15 g rainbow trout grew equally well at 14 and 19‰ but growth was reduced at 24‰. For 30-g fish mortality and osmotic perturbations increase with salinities greater than 15‰, and the rate of increase in plasma osmolality increases more rapidly and to higher levels in 32‰ than in 28‰ (Jackson 1981). Jürss et al. (1986) reported that for 40 to 60-g fish growth rate was lower for fish at 20‰ than at 8‰ or in fresh water. For 51- to 153-g rainbow trout, growth rate decreased with increasing salinity (20-32‰) relative to fish in fresh water and 10‰ (McKay and Gjerde 1985). MacLeod (1977) found that food intake

of 40-g rainbow trout was significantly lower at 32.5‰ than at lower salinities (0, 7.5, 15 and 28‰) and that absorption efficiency decreased with increasing salinity. This study also demonstrated that increases in salinity of 7.5-13‰ resulted in transitory decreases in food intake and growth rate that recovered within 14 days. The findings of the latter study underscore a weakness present in many of the above studies, which are generally short term and may be unable to distinguish an initial decrease in growth caused by salinity acclimation as opposed to long-term growth following acclimation.

Although we know of no published studies with rainbow trout, work with other salmonids suggests that gradual acclimation will increase survival (Boeuf and Harache 1984). In support of this idea, Johnston and Cheverie (1985) reported improved survival, growth and ionoregulation in rainbow trout in an estuary with fluctuating salinity (17-29‰) than one with constant, high salinity (28-29‰). Inclusion of salt in the diet for a period before transfer can also improve the salinity tolerance of small (<40 g) rainbow trout to 36‰ seawater (Salman and Eddy 1990).

Temperature is an important factor in survival and growth of rainbow trout in seawater. Saunders (1975) reported that rainbow trout previously acclimated to 30‰ salinity and that subsequently experienced seasonal decreases in temperature suffered high mortality when temperatures dropped below 0°C. Rainbow trout previously reared in 8°C fresh water experienced much higher mortality, and osmotic and ionic disequilibrium when transferred to 1°C seawater (26‰) than 8°C seawater (Sigholt and Finstad 1990). Johnsson and Clarke (1988) reported that in isothermal transfers of 10- to 90-g fish, salinity tolerance (as judged by a 96-h LC50 test) was greatest at 11°C, lowest at 17°C and intermediate at 5°C. It will be important to consider not only the absolute temperature at the time of transfer, but also the temperature difference from the freshwater rearing conditions. Jürss et al. (1987) found that in 55-g rainbow trout in 20‰, growth was greatest at 11°C, followed in order by that at 6°C, 16°C and 1°C. These studies suggest that the optimal temperatures for seawater growth of rainbow trout are in the 8-14°C range.

Only limited information exists on seasonal changes in salinity tolerance and seawater growth of rainbow trout. The effects of temperature discussed above suggest that in conditions of seasonally changing seawater temperatures, salinity tolerance would be lowest in winter and summer. Johnsson and Clarke (1988) found no effect of photoperiod on salinity tolerance of rainbow trout, whereas increased daylength increased salinity tolerance in steelhead trout. However in another study, spring increases in gill Na^+,K^+-ATPase activity were found in domesticated rainbow trout held at relatively constant temperature (10 - 13°C), suggesting the possibility of temperature-independent seasonal increases in salinity tolerance (Rey et al. 1990). Smith and Thorpe (1976) reported that in spring at high ration levels, rainbow trout had a higher growth rate and nitrogen assimilation efficiency in seawater relative to fish in fresh water; this difference was not detected in autumn even though the tests were conducted at the same temperature. Hybridization with domesticated rainbow trout reduced the seasonal

variation in freshwater growth of anadromous steelhead trout; the seasonal decline in growth rate during winter was more pronounced in steelhead than in half-sib rainbow-steelhead hybrids or in domesticated rainbow trout (Johnsson et al. 1993). Moreover, the hybrid trout had a greater hypo-osmoregulatory capacity than did steelhead trout as shown in 24-h seawater challenge tests during winter whereas the steelhead had a greater hypo-osmoregulatory capacity during the normal smolting season in May (Johnsson et al. 1994).

Brown Trout

Not nearly as much is known of the ontogeny and environmental influences on salinity tolerance of brown trout compared to present knowledge of rainbow trout. Salinity tolerance increases with increasing size (Parry 1958; Boeuf and Harache 1982; Tanguy et al. 1994), although information on a clear size threshold for seawater transfer is lacking and will likely depend on the stock and environmental conditions. Gordon (1959) found that salinity tolerance was lower in summer than from September through April and suggested this was due to high summer temperatures. Boeuf and Harache (1982) found smolt-like physiological changes in an anadromous stock of brown trout (sea trout) and none in a non-anadromous stock of brown trout, but there were no differences in short-term salinity tolerance between the two forms. Tanguy et al. (1994) have found, however, that sea trout had higher long-term survival in seawater than did brown trout.

Arctic Charr

Size, season, and temperature seem to affect salinity tolerance of Arctic charr in a manner similar to that in rainbow trout. Several reports indicate increasing salinity tolerance with increased size of Arctic charr (Arnesen et al. 1992; Delabbio et al. 1990; Staurnes et al. 1992; Dempson 1993). Size thresholds of 60 and 200 g for introduction to seawater were reported by Staurnes et al. (1992) and Delabbio et al. (1990), respectively; differences in criteria (short- and long-term, respectively) and environmental conditions may account for these discrepancies. Those authors also reported substantially greater salinity tolerance in anadromous Arctic charr relative to non-anadromous strains. Anadromous stocks of Arctic charr spend only short periods of the summer in seawater and none are known to overwinter in the sea (Dempson and Kristofferson 1987).

As with other salmonids, increasing salinity results in greater osmotic perturbations and lower survival in Arctic charr (Arnesen et al. 1993; Dempson 1993). Food intake decreases with increasing salinity for the first several days after exposure, but this difference is no longer detectable after 30 days and has no effect on long-term growth rates (Arnesen et al. 1993). Dempson (1993) suggested that gradual acclimation may be particularly important for fish between 12 and 15 cm.

Seasonal changes reported by several authors indicate that salinity tolerance is greatest in spring (even when temperature remains constant), and that this seasonality is found in landlocked populations (Finstad et al. 1989*a*; Arnesen et al. 1992; Schmitz 1992). In Arctic charr previously acclimated to seawater, plasma ions and mortality increase in winter (Wandsvik and Jobling 1982; Staurnes 1993). This may be primarily a temperature effect, as salinity tolerance is much lower at 1°C than at 8°C (Finstad et al. 1989*a*, 1989*b*), though a temperature-independent seasonality is also possible. Transfer of mature male Arctic charr to seawater results in greater mortality and elevations of plasma sodium relative to immature fish (Staurnes et al. 1994).

Brook Trout (Charr)

McCormick and Naiman (1984*a*) found a strong size-dependence of salinity tolerance of brook trout gradually acclimated to 32‰, with 100% survival of immature fish greater than 17 cm. Although gradual acclimation increases survival in seawater (Pelletier and Besner 1992), direct transfer of 19-21-cm brook trout to 25‰ resulted in 85% survival (Besner and Pelletier 1991). No seasonality in salinity tolerance or gill Na^+,K^+-ATPase activity was found in brook trout reared and tested at constant temperature (McCormick and Naiman 1984*a*, 1984*b*). Fish reared under seasonal changes in freshwater temperature and exposed to seasonal changes in seawater temperatures had higher salinity tolerance and gill Na^+,K^+-ATPase activity in May than in late summer (Besner and Pelletier 1991). Salinity tolerance of mature male brook trout is substantially less than that of mature females and immature fish, especially during the spawning season (McCormick and Naiman 1985).

Dolly Varden and Lake Trout

Very little information exists on the salinity tolerance of these charr species. Using the 24-h seawater challenge, Johnson and Heifetz (1988) found that wild, migrating Dolly Varden charr had similar hypo-osmoregulatory capacity as migrating coho salmon smolts. Over a relatively narrow size range (11-15 cm), there was no effect of size on salinity tolerance in this species. No published reports on the salinity tolerance of lake trout (*Salvelinus namaycush*) appear to exist. As anadromous populations of lake trout are rare, it is likely that their salinity tolerance is the lowest among the species discussed here.

AREAS OF CURRENT RESEARCH AND FUTURE RESEARCH NEEDS

One current area of research is the refinement of techniques for producing underyearling and other off-season smolts. This requires additional fundamental research

to learn how photoperiod affects the growth processes leading up to the commencement of smolting. Also, the timing and duration of photoperiod manipulation to optimize production needs refinement. Further research is required to produce underyearling smolts earlier in the autumn while sea temperatures are sufficiently high to promote growth in regions with low winter temperature.

Research is continuing to increase the predictability of performance after transfer of smolts to seawater netpens, particularly to shorten the interval during which food consumption is reduced (Usher et al. 1991; Stradmeyer 1994). Knowledge of the genetic control of smolting is limited for most species. Considerable potential remains for selective breeding to improve smolt yield under intensive culture, particularly as underyearlings (Withler et al. 1995).

Another area offering great promise in future is transgenic technology (*see* Chapter 17). This approach has the potential to shorten the time required to produce smolts as well as being able to produce them off-season. Fast-growing Atlantic and Pacific salmon have been produced using a growth hormone gene construct introduced by microinjection into eggs just before fertilization (Du et al. 1992; Devlin et al. 1994). The fast-growing trait is heritable, having been observed in F1 offspring. Further research in this field will include growth and metabolic studies, smolting biology, response to temperature and photoperiod, and to changes in salinity. A major consideration in the use of transgenic fish, where there is a possibility of escape, is that they must be incapable of interbreeding with normal fish. One method for achieving this is through the production of all-female triploids. Although triploids are used for commercial rainbow trout farming, the technology is still under development for Atlantic and Pacific salmon. One aspect of triploidy requiring further evaluation is its effect on smolting (Boeuf et al. 1994*b*).

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