The Behavior and Ecology of Pacific Salmon and Trout

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Introduction

As with most fields of knowledge, there is a certain amount of terminology associated with the life cycles of salmon, trout, and char (collectively termed *salmonids*). I do not wish to dwell on semantics but some common usage is needed for ease of understanding. The term *egg* refers to the unfertilized ovum, produced by the female. Once fertilized by a sperm cell (mixed with fluids from the male, collectively called *milt*), the egg becomes an embryo, the cell divisions begin, and development proceeds. The embryo is immediately buried by the female in a gravel nest, termed a *redd*, in a stream or lake beach. The redd is composed of several pockets of eggs, deposited and buried by the female in a sequence of spawning events. The embryo develops within the egg membrane for several months and, at an appropriate stage of development, it hatches. The hatchling is termed an *alevin*, with a large, external yolk sac for nourishment. As the alevin grows, the yolk is metabolized until it is fully or largely gone and the young salmon can feed on its own. It then wriggles up through the gravel and emerges into the stream or lake as a fry. Depending on the species, the fry might migrate directly to sea (chum, pink, and some sockeye and chinook), migrate to a lake (sockeye), or remain in the stream (most salmonid species). Those staying in freshwater tend to have vertical brown-green bars on their sides that provide camouflage. These bars are known as *parr* marks and the fish are called parr. There is no set stage when fry become parr (though some people restrict the term fry to fish in their first year of life), and the term *fingerling* also refers to little salmonids.

After some period in freshwater (days, months, or years, depending on species and population), the salmon migrate to sea. To accomplish this transition, they must alter many aspects of their bodies, including color, shape, osmoregulatory (salt balance) physiology, energy storage, patterns of drinking, urination, and behavior. The fish in this transitional stage are termed *smolts*. Smolts can be found in freshwater readying themselves for migration, migrating in freshwater, and in the nearshore marine environment. Because it is a transitional stage, there are no sharp distinctions between smolts and non-smolts. However, the term is not used to describe salmon that have been feeding for long at sea; salmon at sea are generally just termed immature.

There is also a bit of jargon associated with nonanadromous salmonids. Populations are called residents if they spend their entire lives in the stream where they were spawned. In contrast, fluvial populations rear for some time in the natal stream, then migrate to a larger river to grow, and return to the small stream to spawn. Adfluvial populations rear in the natal stream, migrate to a lake for further growth, then return to the stream to spawn. These migrations can be short but in some cases cover several hundred kilometers.

At some point the salmon at sea begin a complex set of physiological processes that will lead them to migrate back to freshwater, spawn, and die. Salmon that have made this "decision" are referred to as maturing fish. They include males and females, of course, and also what are termed *jacks* in many species and populations. Jacks are sexually mature male salmon representing an age group younger than the youngest females in the population. For example, female coho salmon (and most males of the species) spend one full year and a summer at sea, so jacks are males that spend only one summer at sea before maturing. Most sockeye salmon spend two or three years at sea, so those spending only one full year would be jacks. There are only very rare instances of *jills* (females of such young age), for reasons discussed later. Jacks are not to be confused with grilse, a term used by Atlantic salmon biologists to refer to salmon spending one full year at sea. Both males and females can be grilse, and some populations are largely or entirely composed of grilse. In the case of the "traditional" species of salmon (coho, chinook, chum, pink, and sockeye), all individuals die after spawning. However, in rainbow and cutthroat trout, some individuals survive after spawning and are known as *kelts* during their downstream migration.

Several terms associated with fishing so pervade the scientific literature that they too must be explained. The salmon run is the total number of adults surviving the natural mortality agents and heading back to freshwater to spawn. Some are caught (the catch) and the others that evade the fishing gear and spawn are called the escapement. Depending on the dynamics of the population and the management regime, the ratio of catch to escapement can vary greatly. Fishery is a term referring to a type of gear operating on one or several species in a particular area. For example, one might speak of the gillnet fishery for sockeye salmon in Bristol Bay, Alaska, and the troll fishery for coho and chinook salmon off the Oregon coast.

Key themes in the biology of salmon, trout, and char

This book is about one genus of fishes, *Oncorhynchus*, within the family Salmonidae. This family has two other main genera, *Salmo* and *Salvelinus*. Later in this chapter I introduce these genera and their primary species in North America. However, it is possible to get quickly lost in the diversity of life-history patterns among the species within these genera, and then to become even more baffled by the myriad population-specific variants. It is therefore important to understand that there are three key themes in the biology of this family. Each theme is broadly distributed among salmonids but each has interesting and important exceptions.

Anadromy

All salmonids spawn in freshwater and some spend their entire lives there. However, many migrate to sea to grow to their final size and then return to freshwater to spawn. This life-history pattern, known as *anadromy*, leads to rapid growth and high density of salmon relative to nonanadromous salmonids. All Pacific salmon species are anadromous, but some species (notably sockeye and masu salmon, and rainbow and cutthroat trout) have nonanadromous populations and there may be nonanadromous individuals (typically males) in masu and some chinook salmon populations.

In a thoughtful review, Rounsefell (1958) pointed out that anadromy is not an all-or nothing matter; rather, there are degrees of anadromy and closely related life-history traits. He proposed six criteria to assess the extent of anadromy: the spatial extent of migration at sea; the duration of residence at sea in relation to the duration in freshwater; the state of maturity attained at sea; spawning habits and habitats (e.g., use of intertidal areas); postspawning mortality; and the occurrence of nonanadromous forms of the species. Integrating information on these aspects of life history and behavior, he classified pink, chum, and chinook salmon as "obligatory anadromous" species (though chinook less so than the others), and coho and sockeye were termed "adaptively anadromous." He used the term "optionally anadromous" for rainbow and cutthroat trout, Atlantic salmon, brown trout, Dolly Varden, brook trout, and Arctic char.

Hoar (1976) reinforced these themes and showed that seaward migration and the transition from parr to smolt stages is part of a complex set of behavioral and physiological adaptations that vary among species. More recently, Hutchison and Iwata (1997) assessed the extent of aggressive behavior by juvenile salmonids from nine species. They found that the more aggressive species were those that spend more time in freshwater prior to migration, so anadromy is truly connected to the entire life cycle of the species, not just to migration.

Anadromy is a subset of a broader category of migratory life-history patterns termed *diadromy* (McDowall 1988). Diadromous fishes have regular migrations between breeding grounds in freshwater or the ocean and feeding grounds in the other environment. These fishes are scarce in proportion to the fishes that spend their entire lives in freshwater or at sea. They are distinguished from euryhaline fishes that are tolerant of a broad range of salinities and often reside in estuaries but are not specifically migratory. Among the diadromous fishes, about half are anadromous, including not only salmonids but clupeids (including American shad, *Alosa sapidissima*), striped bass (*Morone saxatilis*), lampreys (Petromyzontidae), sturgeons (Acipenseridae), smelt (Osmeridae), and others.

The opposite pattern from anadromy is *catadromy*: species that spawn at sea and rear in freshwater. The most famous catadromous fishes are the anguillid eels but there are other examples as well. Finally, some fishes display *amphidromy*; they spawn in freshwater, migrate to sea as larvae and feed there for a while, and then return to freshwater for further growth before spawning. Examples include the galaxiids of the Southern Hemisphere. There are about 20,000 species of fishes, and according to McDowall (1988), only 160 (0.8%) of them are diadromous. Of the diadromous fishes, about 87 (54%) are anadromous, 41 (25%) are catadromous, and 34 (21%) are amphidromous.

Gross (1987) theorized that animals migrate when the benefits of being in some new habitat exceed the benefits of the present habitat, minus the cost of moving. We may infer that migration between salt- and freshwater, regardless of the direction, is very costly because so few fishes do it. Diadromy requires physiological adaptations for ion regulation in freshwater and at sea. Survival in both environments may also require changes in body plan and behavior, in addition to a shape suited to migratory performance. There are thus many reasons not to migrate. Among diadromous fishes, anadromy is more common at higher latitudes and catadromy more common at lower latitudes (McDowall 1988). Northcote (1978) and Gross et al. (1988) pointed out that at higher latitudes productivity (hence growing opportunities) tend to be greater at sea than in freshwater, and the more rapid growth of salmon at sea than in streams and lakes supports this. At low latitudes, freshwater environments are often more productive than marine ones, and this may explain the tendency for diadromous fishes to spawn at sea and rear in freshwater in these regions.

Homing

Not only do surviving salmon return from ocean feeding areas to streams for spawning but they almost invariably return to the site where they were spawned. This trait, known as *homing*, leads to reproductive isolation of salmon populations (i.e., little interbreeding between salmon from one river and another). These isolated populations, exposed to different physical factors such as temperature, flow, and gravel size, and biotic factors such as predators, prey, competitors, and pathogens, evolve specializations to improve survival in their home river. In addition to such genetic adaptations, the populations may also vary in abundance at carrying capacity and in productivity (number of offspring produced per spawning female at low density). These differences in population dynamics necessitate that they be managed and conserved as discrete populations rather than as species, and this greatly complicates fisheries management. It must be noted, however, that if all salmon homed, new habitat would never be colonized. Much of the present range of salmon was glaciated within the last 10,000 to 15,000 years, so colonization (straying) was also an essential element in the evolution and present distribution of salmon. Such straying continues to provide gene flow among existing populations and allows for colonization after natural disasters extirpate populations.

Semelparity

Not only do salmon migrate to sea and come back to their natal stream to spawn but death inevitably follows reproduction in many Pacific salmon species. This life-history pattern, termed *semelparity*, transfers millions of kilograms of salmon flesh from the ocean to nutrient-poor freshwater ecosystems, reversing the gravity-driven tendency for water and nutrients to flow seaward. However, the trout species often survive spawning, and their life-history pattern is termed *iteroparity* (as in iterative reproduction). Semelparity is not unique to salmon, as some other fishes (e.g., lamprey) and many insects and other invertebrates are semelparous. However, there may be no other group of semelparous animals that are as large as salmon and whose synchronized death contributes as much to the local ecology. Semelparity probably evolved in response to increased adult mortality from the rigors of anadromy and long-distance migration. The adults expend all their energy during migration and reproduction rather than retaining some to assure their own survival. In females, this extra energy for reproduction is put into producing especially large eggs (Crespi and Teo 2002) and guarding the nest after spawning.

Are salmonids typical fishes?

These three key themes provide an important introduction to salmon behavior and ecology. However, a bit more information may be helpful before we consider species-specific details. There are several notable life-history traits common to Pacific salmon in particular and salmonids in general. Taken together, they make salmon quite different from other fishes spawning and rearing with them in freshwater. Some of these differences stem from the anadromous life history or at least are most exaggerated in the anadromous forms, and many of the traits are interrelated. Within salmonids, the species are arrayed along continua related to body size and longevity, dependence on freshwater rearing, extent of anadromy and iteroparity, and breeding season. Wootton (1984) reviewed the life-history patterns of Canadian freshwater fishes (Scott and Crossman 1973) and his summary makes a very useful basis for comparing salmonids to other sympatric species (see also Winemiller and Rose 1992 for further comparisons of fish life-history patterns).

Salmonids grow rapidly but do not live long. The marine waters occupied by salmonids provide superior growing conditions compared to freshwater habitats, and salmonids have high metabolic rates, allowing rapid growth if food is available. Growth facilitates survival and reproductive potential (fecundity and egg size in females, and competitive ability in males). However, salmonids (especially Pacific salmon) have rather short life spans. They are much larger for their age than other freshwater fishes but sacrifice longevity for growth rate (fig. 1-1). Some char and nonanadromous trout, however, can live 10 years or more.

FIGURE 1-1. The relationship between age at first maturity and adult body size of freshwater fish species from Canada (from Wootton 1984; salmonid data updated by Quinn).

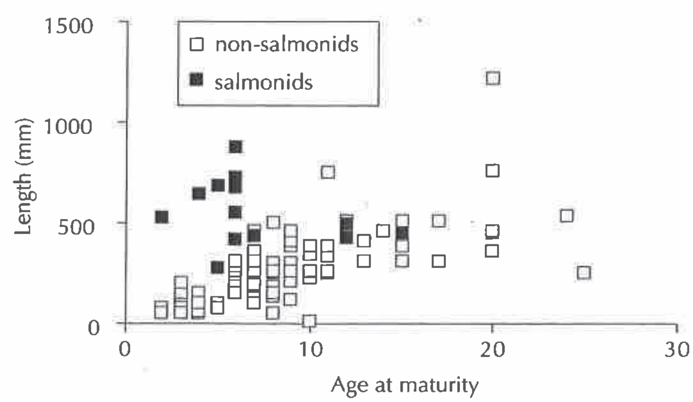


FIGURE 1-2. Modal month of spawning by freshwater fishes in Canada (from Wootton 1984).

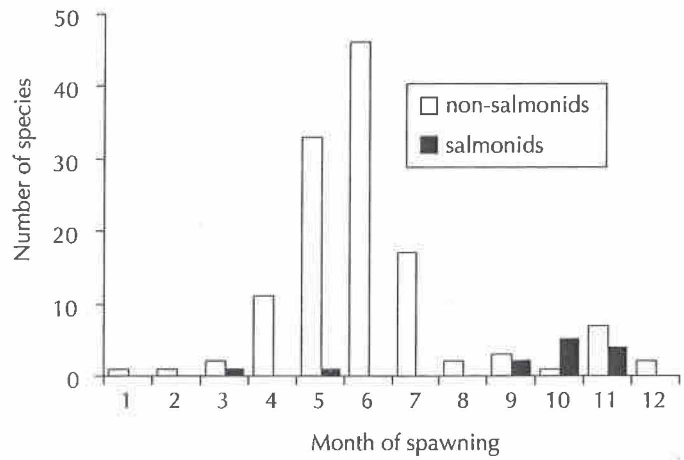
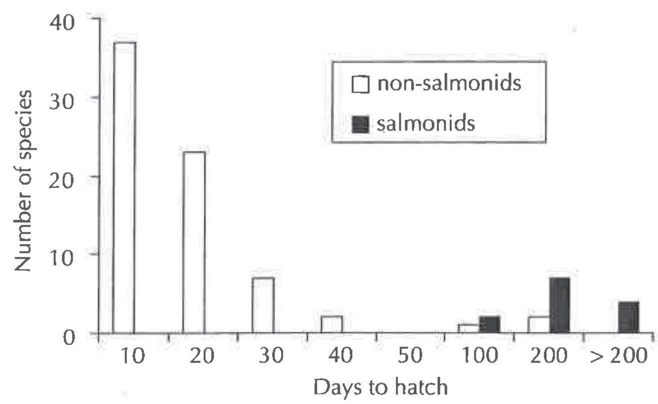


FIGURE 1-3. Number of days from fertilization to reliance on external food sources (hatching, or emergence for salmonids) for Canadian freshwater fish species (from Wootton 1984).



Pacific salmon spawn in the fall. This is quite unusual; most freshwater fishes in the north temperate region spawn in the spring (especially May and June; fig. 1-2). The definition of fall, with respect to spawning season, does vary. Spawning may be as early as July for sockeye in Alaska and as late as February for chum and coho salmon in Washington. Rainbow and cutthroat trout spawn in spring but again, the seasons are defined with respect to local conditions and the actual months can vary. Other than salmonids, the other main group of fall-spawning fishes is the family Coregonidae or whitefish, and they are related to salmonids. Salmonid eggs, spawned in the fall, develop slowly so the juveniles begin feeding in spring when the long days and intense sunlight melt the ice, warm the water, and food (e.g., insects and zooplankton) becomes more abundant. The eggs of spring-spawning fishes develop more rapidly than salmon (fig. 1-3), so the larval fish can also take advantage of warm temperatures and abundant primary and secondary production for rapid growth.

FIGURE 1-4. Distribution of egg sizes among freshwater fishes in Canada (from Wootton 1984).

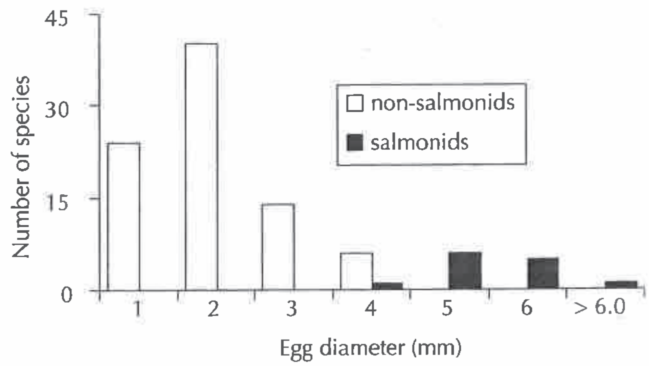
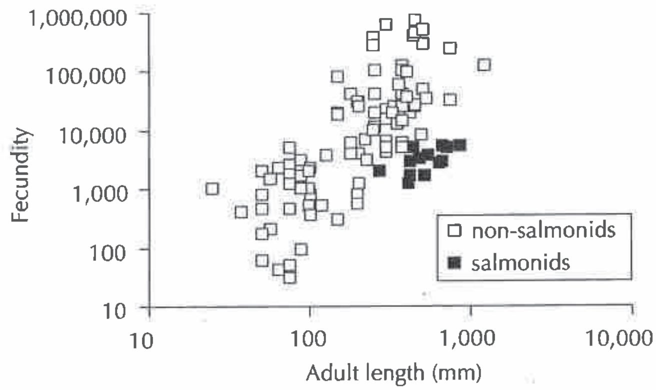


FIGURE 1-5. Relationship between fecundity and mean body length among freshwater fishes in Canada (from Wootton 1984; salmonids updated by Quinn).



Salmonids have very large eggs compared to other bony fishes (fig. 1-4). The large eggs produce large fry, with higher survival rates than smaller fry. The tradeoff, however, is that the female can only devote about 20% of her weight to gonads. The investment in reproduction must balance number against size of eggs to maximize the number of surviving progeny. Thus salmonids also have fewer eggs, for their size, than other freshwater fishes (fig. 1-5). These eggs provide the embryos and alevins with enough yolk to survive the long winter.

Salmonids display female parental care, in the form of egg burial. Both of these features are atypical in fishes. Parental care is shown in only about 21% of the families of bony fishes (Gross and Sargent 1985), though it is more common among freshwater than marine fishes. Among the fishes with parental care, the provider is more often the male rather than the female (61% vs. 39% of families). The evolution of parental care is a complex matter and beyond my scope, but the benefits and drawbacks are obvious in a general way. Care increases the odds of survival of the offspring in the present generation but is costly to the parent (in depleted energy, risk of predation, lost feeding opportunities, etc.), and so reduces survival and future reproductive opportunities.

Female salmon provide care by preparing a depression in the gravel, winnowing out fine gravel by turning on their side and rapidly sweeping the tail up and down. When the eggs have been fertilized the female buries them and (in the semelparous species) guards them from disturbance by other females until she dies. Egg burial is a very unusual form of parental care. Some fishes such as grunions, *Leuresthes tenuis*, bury their eggs in the upper intertidal region of sandy beaches, and larval emergence is synchronized to the next spring tide series. This seems risky enough, but burying embryos in stream gravel for many months seems like a poor form of care because sediment transport and scour commonly occur. The large size of fall spawning salmonids may enable them to bury their eggs deep enough to avoid the effects of winter floods (Montgomery et al. 1996).

Salmonids are generalists. Juveniles use the whole range of freshwater habitats available to them, and many species commonly occupy both streams and lakes. They are opportunistic feeders; small salmonids eat primarily insects and zooplankton and larger individuals eat fishes and invertebrates. Salmonids also have a generalized body shape suited to mobility, lacking some of the specialized features such as the armor and spines of sticklebacks (Gasterosteidae) and large mouth of sculpins (Cottidae).

Salmonid life at sea is spent in the epipelagic (near-surface) coastal and offshore waters, where they feed on a diverse diet of zooplankton, macro-invertebrates (e.g., krill, squid), and small, schooling fishes such as herring, eulachon, and sand lance. In the region occupied by salmon, the salmon themselves are among the most abundant fishes. They are preyed upon by various fishes when they are small and by sharks and marine mammals when they are adults.

Finally, *salmon populations tend to be very productive.* This term does not mean that they are abundant or that they occur at high density, though they may have these attributes too. Rather, it means that when the population is below its carrying capacity, each salmon produces many surviving offspring. Thus salmon can support higher fishing rates than most species. Consider the fact that most fish and game–management regulations are designed to make sure that all or most individuals of the regulated species have a chance to breed at least once before they are subjected to exploitation (e.g., size limits for recreational fishing, mesh sizes for commercial fishing, hunting regulations, etc.). However, all salmon caught are virgins, and sustainable fisheries often catch at least 50% of the run. Thus in the absence of fishing, competition (for spawning habitat by adults or food and space by juveniles) would exert stronger control over the abundance of salmon than we see today.

The stage: The physical environment occupied by salmon

Before introducing the characters in the play, we might briefly set the stage. Salmon and trout are products of their environment, and they spawn and rear in bodies of water ranging from tiny creeks above waterfalls in the mountains, or streams discharging straight into saltwater, to large rivers; and from small beaver ponds and ephemeral wetlands to the largest lakes of the region. Their native range is from northern Mexico to the Arctic Ocean on one side of the Pacific, and from Taiwan, southern Japan, and Korea to the Arctic Ocean on the other side (fig. 1-6), though salmon are present only as scattered populations in the Arctic. They are found in a number of large rivers (table 1-1) as

FIGURE 1-6. Map of the North Pacific Ocean, showing the coastal extent of spawning by Pacific salmon and trout (shaded) and some of the major rivers and other geographical features.

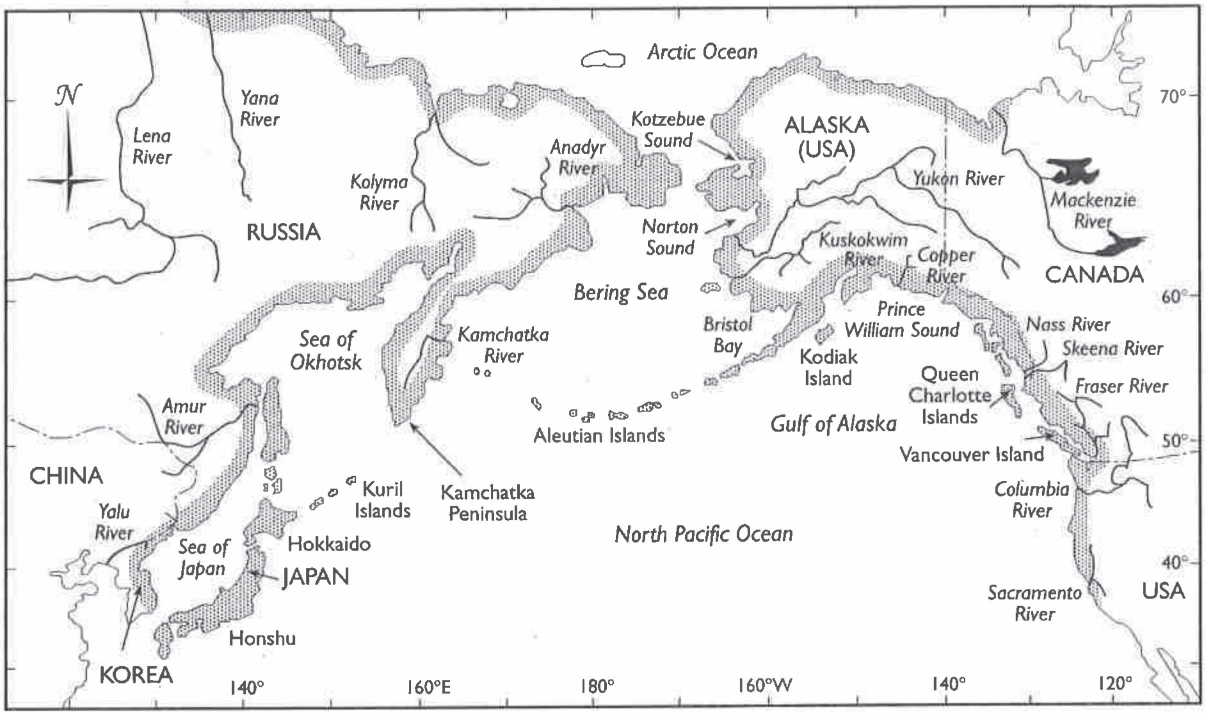


TABLE 1-1. Mean annual discharge (m³/sec) and length (km) of major North American rivers with Pacific salmon (from Favorite et al. 1976 and unpublished public records). For those marked with an asterisk (*), discharge was not recorded at the mouth.

River	*Mean discharge (m³/sec)*	*Length (km)*
Mackenzie	7500	4250
Yukon	7000	3185
Columbia	6650	2250
Fraser	2938	1360
Kuskokwim*	1280	1165
Copper*	1040	462
Skeena*	920	570
Nass*	830	380
Sacramento*	650	607

well as in thousands of smaller streams. Of course, there are also great rivers in Asia that support salmonids. The Lena River flows from just north of Lake Baikal 4270 km to the Arctic Ocean, with a discharge of about 16,400 m³/sec. The Amur River flows 4510 km from Mongolia to the Sea of Okhotsk with a discharge of 12,500 m³/sec. Thus the Lena has roughly twice the discharge of the Mackenzie, and the Amur has nearly twice that of the Yukon, so these are indeed major rivers of the world. The Anadyr (1117 km) and Yalu