

# ***A review of the characteristics, habitat requirements, and ecology of the Anadromous Steelhead Trout (*Oncorhynchus mykiss*) in the Skeena Basin***

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## **INTRODUCTION**

Six species of anadromous salmonids (*Oncorhynchus spp.*) spawn in the Skeena River basin of northwestern British Columbia. One of the most impressive runs occurs between July and August when the summer-run steelhead enter the Skeena to prepare for spawning. This significant migration of wild steelhead (*Oncorhynchus mykiss*) is among the most productive and natural runs in the world. Population estimates by the Joint Northern Boundary Technical Committee (JNBTC) in 1991 indicate that more than 32,000 steelhead travel through the Skeena River annually to utilize its glacial tributaries for spawning. Despite the stocking of fry between the years of 1985 and 1988, the Skeena's run of steelhead sustains itself without the aid of hatcheries (JNBTC 1991). Although they are stable, the populations of steelhead in the Skeena Basin are influenced by habitat availability, access to spawning grounds, and the survival of the oceanic and freshwater life-stages. The importance of steelhead as a sport-fish and indicator of environmental health justifies a full understanding of this unique natural resource. The extreme variation in the life history of steelhead however, makes this species challenging to study and manage. This paper intends to outline the major factors influencing steelhead populations in the Skeena River and its tributaries by reviewing the characteristics, habitat requirements, and ecology of *Oncorhynchus mykiss*.

## **LIFE HISTORY**

Rainbow trout and steelhead represent two divergent ecotypes that are genetically identical but separated by life history strategies (Heath 2001). Steelhead are the anadromous form of *Oncorhynchus mykiss* and rainbow trout are the resident form that stay in streams and reservoirs year-round. The common name rainbow trout refers to the ecotype that completes its entire lifecycle in freshwater. Resident forms can make annual spawning migrations into the tributaries of major river and lake systems, but never enter the ocean. The presence of an

anadromous life-cycle delineates steelhead from the common rainbow trout. Steelhead utilize oceanic and freshwater habitats and show high variation in each of their life stages. Anadromy allows steelhead and other pacific salmon to feed in productive oceanic environments and then enter river systems to deposit eggs in streams that are more conducive for juvenile growth. Steelhead can be found in the rivers of central California to the streams of Alaska's Bristol Bay and often inhabit the same watersheds as the resident rainbow trout. Recent evidence has shown that steelhead and rainbow trout produce viable offspring of either the anadromous or resident form when interbred (Bryant 1999). Although it is possible that significant gene transfer can occur between these two eco-types, little information is available on the frequency of this event.

### **Physical Characteristics**

Steelhead and rainbow trout share some common physical characteristics. Each have short heads, elongate and moderately compressed bodies that are indicative of the subfamily Salmoninae. Steelhead differ physically from rainbow trout by their size at maturity. Rainbow trout weigh approximately 4 pounds after 4 years of growth in freshwater, while a mature steelhead averages 9 pounds upon leaving the oceanic environment. Differences between rainbow trout and steelhead can also be seen by comparing fecundity. Anadromous species like steelhead produce nearly three times as many eggs: up to 11,000 eggs for a female of length 80 cm (Stolz 1991). Increased size and fecundity in steelhead is a result of anadromy; fish can invest greater amounts of energy into reproductive and somatic tissues. While rainbow trout appear similar throughout their life-cycle, steelhead can show large variation in appearance between life stages. In the ocean steelhead will appear silver to light blue with spots located on dorsal edges. Although often mistaken for other pacific Salmonids, steelhead differ in that they lack the hyoid teeth that indicate a Coho (*O. kisutch*) or King Salmon (*O. tshawytscha*) (Pollard 1997). In adult steelhead, sexual dimorphism is reduced, but spawning males often take on much darker red and green hues compared to females. The presence of a "kype" or hook on the bottom jaw and dark red opercula also distinguishes mature males from females (figure 1). As the time in freshwater increases for spawning steelhead, most will take on the coloration in Figure 1, but some may never lose their bluish oceanic coloration (Combs 1971). Young steelhead in the freshwater environment are either silvery (smolts) or appear identical to rainbow trout (parr). These shared physical characteristics between resident rainbow trout and juvenile steelhead

make it hard to differentiate between the two eco-types. Mark and recapture experiments allow managers to determine the numbers of steelhead in a given watershed. Information on the proportion of resident and anadromous forms of *Oncorhynchus mykiss* in the Skeena Basin is unavailable and would play a key role in management decisions.



**Figure 1.** The presence of a kype and dark red opercula on males (left) clearly distinguishes them from spawning females (right) (Whitney 1979).

### **Behavioral Characteristics**

Steelhead share similar behavior with rainbow trout and other anadromous salmonids. Homing behavior, a phenomenon where fish migrate to the exact stream and location where they were born, is present in steelhead. During the freshwater rearing period steelhead imprint a chemical marker that is specific to their natal stream (NRC 1996). This chemical marker records the concentrations of solutes and the chemical profile of a stream to an amazing accuracy. After feeding in the ocean for 1-4 years steelhead enter freshwater and use the position of the sun and magnetic north to navigate towards spawning grounds. When close to their natal stream, steelhead and other salmonids rely on the chemical imprint to locate the exact area where they were hatched. Steelhead in the Skeena basin exhibit homing behavior, and frequently return to their natal stream with high fidelity. Interestingly, homing creates genetically different sub-populations that differ by basin, stream, and even location within a stream (Altukhov 2000). Using DNA microsatellite technology, Heath (2001) found significant genetic variation on the individual, tributary, and watershed level within the Nass and Skeena river basins. This indicates that each sub-population of steelhead is uniquely adapted to its environment, and that they are reasonably isolated from fish that spawn in different areas. These sub-populations may differ by the timing of runs, size of fish, and even behavior patterns. Heath (2001) also found that genetic relatedness between populations is correlated with distance. Sub-populations that are farther

apart share fewer microsatellite combinations. These findings support Slatkin's 1993 isolation-by-distance model and may help to reconstruct and explain the dispersal of steelhead and other fish populations in northwestern British Columbia. It is likely that dispersal was aided by the glacial history and geology of the region. [for more information on the geology and glacial history of the Skeena Region, see Slotnick in this volume]

## Life Stages

The steelhead life-cycle can be divided into five parts: the egg, fry, smolt, adult, and spawning stages (figure 2). It is important to note that the length of each stage is highly variable and controlled by biotic and abiotic factors. The following sections describe the stages, habitat requirements, and factors affecting survival in the steelhead life-cycle. The information presented intends to illuminate the remarkable and complex ecology of *O. mykiss* in the Skeena River system. Withler (1966) reported that the time spent rearing in freshwater increases from North to South along the Pacific Coast of North America. This may be an effect of shortened growing seasons in northern latitudes that require young to stay in freshwater streams for longer periods of time before they are capable of surviving in the ocean. A recent but still in press publication by Titus et al reports that no such latitudinal correlation exists between California and British Columbia steelhead populations. This conflicting information is representative of the complex and highly variable systems that steelhead inhabit. It is important then, to manage each sub-population of steelhead in a way that tailors to their specific life history strategies and challenges.



**Figure 2.** Depiction of Steelhead Life-Cycle (GSRP 2004).

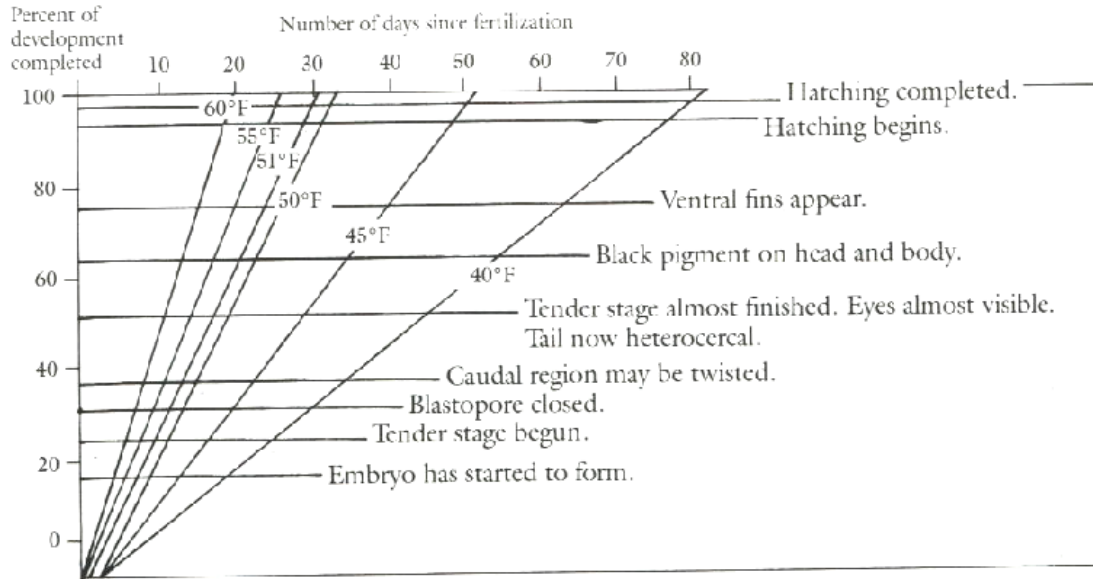
*The Egg and Alevin*

Steelhead lay their eggs in “redds” or depressions in the river bottom. Females select and dig redd sites and then cover the opaque red eggs after fertilization (figure 3). By covering the redds with loose and coarse sediments, females create a well-protected habitat for egg development. The size of the clasts is important, because larger gravels allow for the percolation of water and oxygen across egg membranes. Female selection of quality redd sites influences the survival of eggs and will be discussed in subsequent sections. After being covered, eggs will reside in the interstitial spaces of coarse gravels for 20 to 80 days, and their survival is closely interconnected with water quality and temperature (Combs 1971).



**Figure 3.** Alevin (left) and eggs (right) in gravel. (Stolz 1991)

Eggs depend on stream conditions to supply high dissolved oxygen concentrations (DO) and cool water temperatures for growth and metabolism. Without adequate supplies of oxygen, aerobic processes in the egg are limited, producing deformed juveniles that are incapable of survival. DO concentrations below 5 ppm will extend incubation times and increase the probability of mortality. Subsequently, if DO concentrations fall below 2 ppm, most eggs will die of anoxia (Stolz 1991). Water temperature is another physical aspect of egg habitat that influences survival and growth. At 15.4 °C (60 °F) steelhead eggs will hatch within 20 days, but as water temperatures decrease, the time of incubation lengthens (figure 4). The graph indicates a linear relationship between water temperature and egg development, however it does not show the effect of temperatures greater than 16°C. Mortality rates dramatically increase as temperatures rise above 16°C, and most eggs die if temperatures reach 21°C (Stolz 1991).



**Figure 4.** Diagram representing incubation time and temperature relation in steelhead trout. (Stolz 1991)

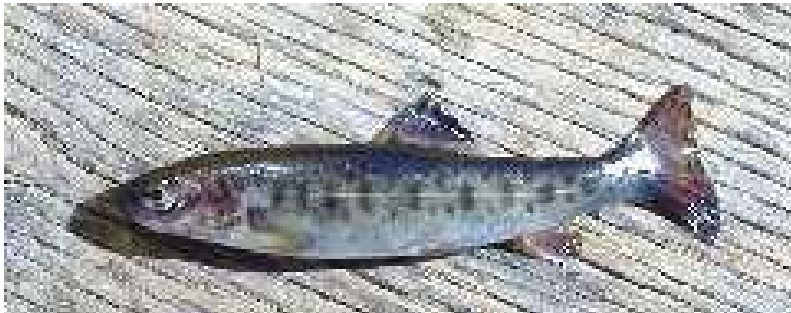
Organic material and fine sediments reduce the amount of available oxygen for eggs in the riverine environment. Fine sands and clays inhibit the movement of oxygenated water through the bed load and reduce available rearing habitat for eggs. The presence of decaying organic material further decrease DO concentrations by using oxygen in oxidative reactions. Land uses such as logging, mining, and road building influence the amount of organic and fine sediments that river systems receive (Murphy 1995). Logging and mining activities in the Skeena Basin are reduced, so clean gravels and exceptional egg rearing habitat should be prevalent. Predation will likely affect the survival of eggs to a greater degree than habitat availability in the Skeena Basin. Resident fish, birds, and even juvenile steelhead feed on eggs that get separated from the substrate.

Alevins, the yolk-sac dependent young which emerge from eggs, inhabit the interstices of gravel and are often washed downstream if the substrate is mobilized. They can subsist on yolk-sac reserves for up to five weeks depending on water temperature and quality, but generally utilize all of their reserves in 3 to 7 days (Pauley 1986). Alevins grow best in water around 10°C (45°F), and lower temperatures increase the length of this stage. Like eggs, alevins that are exposed to excessive temperatures (>21°C) usually die (Stolz 1991). Poor water quality, specifically low concentrations of oxygen, can also influence development of alevins by

inhibiting oxygen dependent growth processes. So like eggs, alevins need cool temperatures and clean gravels that are relatively free of decaying organic matter and fine sediments. Alevins are also reliant on the inter-gravel habitat for protection from predators. Birds and both resident and anadromous fishes will prey upon these newly emerged juveniles if they cannot seek shelter in the substrate. As alevins consume the remaining yolk reserves, they become independent swimmers and start to rely directly on external food sources such as zooplankton and small invertebrates.

### *Fry*

The change from yolk-dependency to self sustenance in the riverine environment marks the transition from alevin to fry. In this stage juvenile steelhead can grow quite rapidly (fingerling size within a year) as they enter the water column and feed on aquatic insects, terrestrial insects, and zooplankton (Willers 1991). This stage can last from 2-5 years and is highly variable between populations of steelhead. Within the Skeena Basin, steelhead rear in freshwater environments for 4-5 years before they emigrate to sea (Whately 1975). Fry can reach a size of over 120 mm while in the freshwater environment and rely heavily on habitat for optimal growth and survival. Lateral parr marks camouflage fry in freshwater habitats (figure 5).



**Figure 5.** Lateral parr marks on steelhead fry serve to camouflage juvenile fish in the river environment. (Stolz 1991)

While in the freshwater environment, steelhead fry are found in clear, low velocity, and low gradient streams where they can utilize their highly adapted vision to search for prey and avoid predators. In streams with high flows, fry will often revert to nocturnal feeding, but where river velocities are low, fry have been documented utilizing daylight hours for feeding (Bradford

2001). As juvenile steelhead mature, the probability for nocturnal feeding increases and fish spend the majority of the day concealed in the substrate. This high variability is likely because fry must balance the trade-off between risky but rewarding daytime feeding and less efficient but safer night feeding (Bradford 2001). Quality habitat allows fry to feed, seek shelter from increasing flows, and hide from predators. River systems with logs, overhanging banks, roots, and woody debris are prime habitat locations (Pauley 1986). Tributaries to the Skeena River will likely have prime habitat for freshwater rearing, and hold large numbers of juvenile steelhead.

Biotic factors that influence fry survival include predation from both resident and anadromous fish, and competition for feeding areas among cohorts. Individuals who can establish territories for feeding are more likely to survive. Predation from other salmonids, otters, and birds can greatly reduce the numbers of surviving individuals. Abiotic factors affecting survival include the availability of habitat, and the clarity and temperature of water. In other Pacific Northwest streams logging, damming, and road construction has greatly reduced habitat. As humans remove trees from forests and alter flow regimes with dams, the amount of woody debris in streams is greatly reduced. The tributaries of the Skeena are relatively untouched by anthropogenic forces. Log jams, debris, and undercut banks will likely support numerous species of salmonids. The amount of food in river systems also influences fry survival. Bilby (1998) conducted an experiment to determine how carcasses of spent and decaying *Oncorhynchus spp* affect the survival of juvenile steelhead. Results from this southeastern Washington stream indicated that consumption of salmon carcasses and eggs can significantly improve the health and survival of fry. In addition, most steelhead feed on the multitude of insects that inhabit river and riparian environments including various species of mayfly (Ephemeroptera), caddisfly (Trichoptera), and stonefly (Plecoptera).

### *Smolt*

After steelhead rear in the Skeena Basin for 4-5 years, they are large enough (14 to 18 cm) to enter the ocean (Pauley 1986). During this stage juveniles undergo physiological changes that ready them for the salt-water environment. In freshwater juvenile steelhead are hypertonic and must excrete water and dilute urine to counteract salt loss. Smolts must develop a physiological process to deal with hypotonicity in the ocean and the water loss that results. As with many other ocean fish, steelhead swallow large amounts of water and excrete concentrated



salts in their feces to maintain equilibrium. Smolts also undergo physical changes on their way downstream. They progressively lose lateral parr marks and develop small silvery scales that will function as counter-shading in the ocean environment (figure 6). Smolts will utilize the same habitat as fry on their migration to the ocean and will continue to feed on aquatic insects, other Salmonids, and fish eggs. Ocean-ward migration for steelhead in northern British Columbia usually occurs in the spring when melting snow and glaciers increase water flows (Mckinnel 1997).

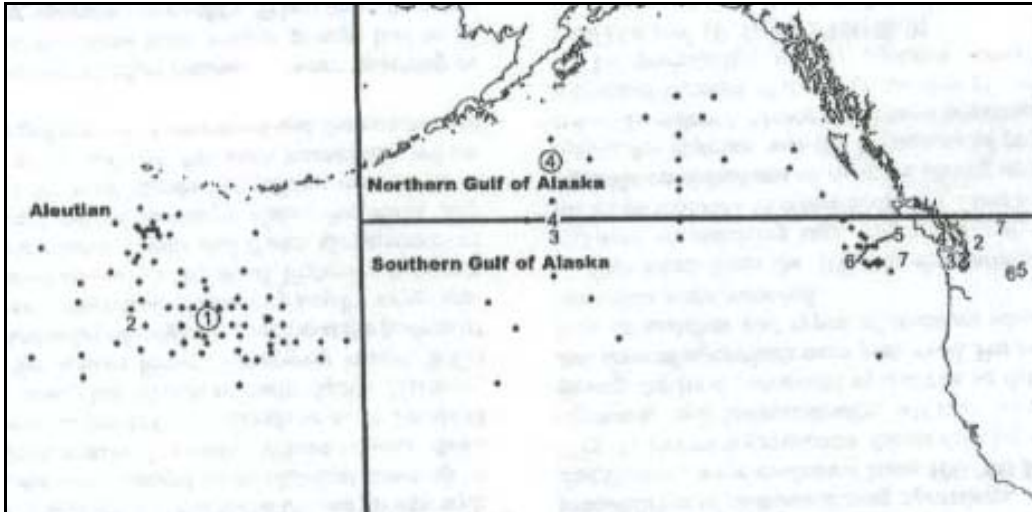


**Figure 6.** Rainbow trout (bottom) and steelhead (top) undergoing smoltification. Note presence of silver-like scales on steelhead and loss of definitive parr marks. (Stolz 1991)

### *Adults*

Once steelhead enter the ocean environment, their behavior changes dramatically as they become carnivorous. In the ocean steelhead are known to eat squid, greenling, and amphipods, but are largely opportunistic feeders (Combs 1971). In this life stage steelhead will attain their maximum growth rate, much like other Pacific Salmonids who are the top predators in the North Pacific Ocean. The distribution of steelhead in the Pacific Ocean varies depending on latitude and often follows sea surface temperature patterns. Steelhead are generally found in waters of 48°F to 53° F. California populations usually migrate north-south along the continental shelf, while more northern populations congregate in the open ocean (NRC 1996); however, the

distribution of steelhead in the ocean is extremely variable (figure 7). Fishing industries have reported that steelhead do not school like salmon and usually stay within the upper 40 feet of water (NRC 1996).



**Figure 7.** Ocean distribution of tagged and recovered steelhead in study by Mckinnel (1997)

Steelhead in the Skeena Basin stay in the ocean for 1-3 years (Smith 2000). Although they are considered the top predators in the ocean environment, the survival of steelhead in the oceanic environment is influenced by biotic and abiotic interactions. The greatest threat of predation in the ocean comes from seals, orcas, and humans. Steelhead are not targeted by commercial fishing operations, but many are caught as wasteful by-catch in the Pacific's billion dollar salmon fishing industry. Predation in the ocean environment can take a significant toll on steelhead populations, but recent studies have focused on the abiotic factors that can influence all salmonid populations. Mantua (1997) showed that steelhead and other anadromous Pacific Salmonids face abiotic challenges that are correlated to climatic shifts and the movement of the Aleutian low. During strong climatic shifts ocean productivity drops in the Pacific Ocean. Welch (2000) reported that the correlation between ocean productivity and salmonid numbers has a geographical structure. Northern stocks of steelhead, like those in the Nass and Skeena Basins, fared better than southern regions like the Washington and Oregon coasts when the last major climatic shift occurred in 1990 (Welch, 2000). It is now widely recognized that climatic shifts

can affect ocean productivity and thus the oceanic survival of steelhead and other Salmonid species. [for more information of climate effects on salmonids, see Khanna in this volume].

### *Spawning*

Willers (1991) stated that the timing of steelhead spawning migrations is possibly regulated by seasonal cycles, circadian rhythms, temperature, and precipitation. Models that attempt to correlate migration with environmental conditions such as tides, weather, and ocean temperatures however, are challenging to support because steelhead have been documented moving upstream in every month of the year (Combs 1971). In northwest British Columbia steelhead generally move out of the ocean and into river systems in two distinct runs. The first, or summer run, begins in May and tails off in early October. These fish will reside in river systems for up to eight months before spawning. The second, or winter run, takes place between November and December. The greatest number of steelhead enter the Skeena system in the summer months. Once in river systems, steelhead undergo hormonal changes that induce the complete maturation of gametes, but steelhead that spawn within coastal regions often enter the mouths of rivers fully matured (Smith 2000). Those destined for interior regions usually reach full sexual maturity before arrival at their natal stream (Stolz 1991).

Unlike many anadromous Pacific Salmonids, steelhead can spawn more than once. Post-spawning behavior varies greatly with respect to sex. Of those who survive the rigors of spawning, males are more prone to stay in river systems for an extended period of time, while females often migrate back to the ocean after depositing their eggs (Combs 1971). The proportion of steelhead returning for a second, third, or even fourth spawning episode is different for each river basin (Withler 1966). Females returning for multiple spawnings are capable of producing up to 12,000 eggs. In more northern regions first year spawners frequently dominate river systems and produce between 4,000 and 7,000 eggs (Combs 1971). Information on the proportion of repeat spawners in the Skeena River is limited, but general trends can be used to estimate this important component of steelhead populations. The proportion of repeat spawners decreases as latitude increases along the Pacific Coast which suggests that spawning in the Skeena will be dominated by first year fish (Withler 1966).

The availability of quality spawning habitat is an integral part of steelhead ecology. Steelhead frequently spawn at the head and tail of riffles in depths of 10 to 138 cm (Stolz 1991).

These areas have a constant flow of water that rushes through the interstices of the substrate and oxygenates the deposited eggs. The velocity of water within a reach is an important component of spawning habitat. Steelhead generally spawn in velocities of 0.6 to 1.5 m/s with larger females selecting sites in the upper end of this spectrum (Stolz 1991). Excessive velocities may uncover eggs and pose a significant challenge to courting fish. The size and quality of gravels is perhaps the most important aspect of spawning habitat. Gravels that are loaded with sediment and organic matter are not hospitable environments for developing eggs. Clean and coarse gravels are necessary for greater spawning success. The temperature of water can also influence spawning steelhead. When temperatures drop below 4°C most steelhead will discontinue spawning, and when temperatures exceed 16°C spawning success is greatly reduced (Stolz 1991).

Steelhead and other anadromous fish face both natural and anthropogenic factors that greatly reduce the success of spawning. During their migration and spawning episodes, steelhead are preyed upon by bears, otters, and fisherman. Because most of the steelhead angling on the Skeena is catch and release, bears and otters may comprise the greatest threat. Although these interactions can pose a significant risk to the success of spawning, they are not considered to be as important as water flows, water quality, temperature, and the continuity of streams. In other parts of the Pacific Northwest, humans have severely altered the flow regimes of rivers and tributaries by constructing dams for the retention of water. In the Columbia River system natural steelhead populations have dwindled from their historical highs. Much of the loss is attributed to dams and the loss of spawning habitat and discontinuity that diversions create. Intraspecific interactions can also affect the success of a spawning steelhead. Females who spawn early relative to the rest of the population, may have their eggs exposed by females that are preparing redds (Fukushima 1998). Spawning early however, may be beneficial by giving emerging fry a head-start in establishing feeding territories. This interesting interaction between early and late spawners indicates that steelhead populations are dynamic.

## **DISCUSSION**

For fisheries managers in the Skeena Basin the greatest challenge is correlating environmental conditions with decreasing populations. The utilization of fresh and salt water environments however, makes this task nearly impossible. Bradford (1995) explained that because mortality is integrated over two habitats, pinpointing the cause for declining steelhead

populations becomes problematic. A negative impact in one life stage can be buffered by improving conditions in another stage or compounded by decreased survival in another. The steelhead life-cycle must then be treated as a highly variable and dynamic system that needs conservative management. Within each life-stage there are characteristics, habitat requirements, and factors that affect survival. Changes in factors such as habitat availability, temperatures, and ocean productivity can directly alter survival rates and overall population numbers.

When steelhead are in the freshwater environment, survival is controlled largely by the availability of habitat (Pauley 1986). Tributaries of the Skeena River will likely have large woody debris, undercut banks, and clean gravels that are necessary for the overall survival of the freshwater life-stages. As pressure mounts to exploit logging opportunities in the Skeena watershed, fisheries managers must consider how such land uses will affect habitat availability and population stability. Logging near streams greatly influences salmonid habitat and will likely invoke a change to this dynamic system. If a population of steelhead relies heavily on high spawning success because other life-stages have low survival rates, then logging could potentially illicit a population crash.

A recurring theme in steelhead ecology is that temperature has an overriding importance in sustaining populations. Temperature controls the development of eggs, fry, smolt, and spawning behavior. Steelhead and other anadromous fish in the northwest have evolved enzymes, life-cycles, and behaviors in ancient environments where cold and clean water was prevalent. As humans divert and slow water, the temperatures in these environments are increasing at a rate much greater than evolution can keep up with. The Skeena and its tributaries are unusual in that dams, culverts, and major human influences are limited. This region offers an incredible opportunity to observe and analyze the life-cycle of steelhead in a nearly pristine environment where temperature patterns are not influenced by dams or diversions.

Adult steelhead rely on productive ocean environments that supply abundant food sources such as squid, greenling, and zooplankton. These ocean conditions inevitably fuel spawning migrations by providing the energy that allows fish to move upstream. Climatic shifts that reduce ocean productivity and the growth and survival of adults are part of the overall habitat constraints that steelhead populations face. Oscillations in the North Pacific's Aleutian Low have been hypothesized to be the cause of decreased oceanic survival of adult steelhead (Mantua 1997). Although humans can induce large scale climatic changes (global warming),

there seems little we can do to control them. Fisheries managers can however, amend their actions to account for reduced survival due to patterned oscillations.

## CONCLUSION

Steelhead are an important natural resource throughout their range for both economic and ecological reasons. In the Skeena Basin steelhead produce millions of dollars a year for local communities by attracting fisherman from throughout the world. Due to temperature and habitat requirements of steelhead in each of its life-history stages, this species is a good indicator of the health of both aquatic and oceanic systems in northwestern British Columbia. The presence of a large and stable run of steelhead in the Skeena Basin indicates that environmental conditions in this region of British Columbia must be excellent. If steelhead populations in the Skeena River are to remain stable, then the aquatic and oceanic environments that sustain this population must be managed as a dynamic system. Changes in habitat, temperature, or biotic interactions in any life-stage may illicit an imbalance. It is critically important to understand how and to what degree any changes in land use or management can affect the sustainability of this productive system.

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