



ASSESSING THE POTENTIAL FOR PREDATION ON WILD SALMONID FRY BY HATCHERY-REARED SALMONIDS IN WASHINGTON⁶¹

Juvenile salmonids are subject to predation by a variety of avian, mammalian, and piscine predators, and predation has been implicated as an important source of mortality in a number of salmon populations (Fresh 1997; Mather 1998). Recently, concern has been expressed about the potential for hatchery-reared salmon and steelhead to prey on wild juvenile Pacific salmonids (*Oncorhynchus spp.*) and the impact that this predation may have on threatened or endangered salmonid populations (Lichatowich 1999; Levin et al. 2001).

The potential for predation of wild salmonids by hatchery-reared smolts will depend on the sizes, numbers, and spatial distribution of predators and prey, the functional and numerical responses of the predators, and the amount of time that predators and prey are in proximity. Here we review the evidence for predation on wild salmonids by hatchery-reared fish and propose a strategy to estimate risks to wild salmonid populations from predation by hatchery-reared salmonids.

Evidence for Intrageneric Predation by *Oncorhynchus* Spp.

Freshwater

Predation on wild salmonid fry by salmonids is probably most likely in the freshwater environment, where potential salmonid predators are concentrated and exposed to large numbers of prey in a relatively small area. There is abundant evidence that salmonid smolts may prey on wild Pacific salmon fry in streams. Ricker (1941) reported that coho salmon were an important predator of sockeye fry in Cultus Lake, British Columbia (BC). Hunter (1959) reported that coho salmon smolts preyed on chum and pink salmon fry in Hooknose Creek, BC, and used his and other data from BC to estimate that each coho smolt might have consumed 1.5–2.0 fry per day. McCart (1967) reported that coho salmon smolts, rainbow trout, and cutthroat trout were important predators of sockeye salmon fry in the Babine River, BC, with coho smolts consuming an estimated mean of 3.7 sockeye per fish. Parker (1971) suggested that the primary source of mortality of chum and pink salmon fry was predation by coho salmon, but presented no data to support this. Fresh and Schroder (1987) reported that coho salmon consumed a large number of chum salmon fry in Big Beef Creek, Washington (WA), as did resident rainbow and cutthroat trout. Hargreaves and LeBrasseur (1986) found that coho salmon smolts selectively preyed on 48–50 mm chum salmon fry. Ruggerone and Rogers (1992) estimated that 59% of the sockeye fry population in the Chignik Lakes, Alaska (AK), was consumed by juvenile coho. Seiler et al.

⁶¹ This paper was drafted for the HSRG by Stephen C. Riley, Julie A. Scheurer, and Conrad V. W. Mahnken, NOAA Fisheries, Northwest Fisheries Science Center, Manchester Research Station, PO Box 130, Manchester, WA 98353; and H. Lee Blankenship, Northwest Marine Technology, 955 Malin Lane SW, Suite B, Tumwater, WA 98501; March 2003.



(2002) found salmonid prey in the stomachs of juvenile steelhead, coho, Chinook and cutthroat trout that were captured in a screw trap on the Green River, WA.

There are several studies that have reported predation by hatchery salmonids on wild salmonid fry. Sholes and Hallock (1979) estimated that millions of wild Chinook were consumed by hatchery-reared Chinook and steelhead in the Feather River, California (CA), and Cannamela (1993) estimated that hatchery-reared steelhead smolts consumed up to 24,000 wild Chinook fry in the Salmon River, Idaho (ID), over the course of 50 days; these estimates were based on extrapolation from small sample sizes. Menchen (1981) found that steelhead smolts released into Battle Creek, CA, were significant predators on naturally-produced Chinook fry. Beauchamp (1995) reported that wild steelhead smolts were the primary predator of sockeye salmon fry in the Cedar River, although hatchery-reared steelhead smolts, which were released during the latter half of the sockeye migration, did not appear to prey on sockeye fry. Hawkins and Tipping (1999) observed a small proportion of hatchery reared coho, steelhead, and cutthroat smolts preying on wild Chinook smolts. Beauchamp (1990) found that rainbow trout stocked into Lake Washington did not become primarily piscivorous until they reached approximately 250 mm, and did not consume many salmonids at any size, although sockeye salmon fry were available in the lake.

Because hatchery-reared salmonids may not feed as well as wild conspecifics (Sosiak et al. 1979; Bachman 1984; Olla et al. 1998), one might expect that they would be less efficient as predators, although wild and hatchery-reared brown trout in a Norwegian reservoir were observed to have similar rates of piscivory (L'Abée-Lund et al. 2002). Moreover, any reduced feeding might be offset by the generally larger size of hatchery-reared smolts. Although there is evidence that predation of salmonid fry by migrating smolts may be common in streams, the estimation of risk to wild salmonid fry from predation by hatchery-reared smolts in WA streams is hindered by a lack of published data on the comparative feeding habits of hatchery and wild smolts. Recent sampling by the Washington Department of Fish and Wildlife (WDFW) indicates that migrating smolts of hatchery and wild coho and steelhead may prey on chum salmon fry in Washington rivers (H. J. Fuss, WDFW, Olympia, personal communication).

The high potential for encounters between hatchery-reared predators and wild salmonid prey in freshwater environments may be tempered by the fact that hatchery-reared smolts generally spend very little time in rivers before migrating to sea. Although we are unaware of any published data on residence times of hatchery-reared smolts in freshwater, it is widely believed that the majority of these fish migrate out of rivers very quickly. Recent work in Willapa Bay tributaries suggests that over 95% of steelhead, coho and Chinook smolts leave the immediate area of release within several hours (Riley et al. 2001; 2002).

Although most hatchery-reared smolts may migrate out of rivers relatively quickly, some steelhead smolts released from hatcheries have been observed to remain in rivers for months or years after release; these fish are known as 'residual' steelhead. Recent snorkeling in WA coastal streams has reported counts of residual steelhead between 1.25–37.7 fish per km several months after release, and stomach sampling on one stream revealed that five of 44 (11%) residual steelhead sampled contained salmonid remains, and a further 11% contained unidentifiable fish remains (Riley et al. 2001). McMichael and Pearsons (2001) found that residual hatchery-reared steelhead migrated up to 12.8 km upstream of their release point and outnumbered wild salmonid



yearlings in several stream reaches. Martin et al. (1993) reported that residual hatchery-reared steelhead preyed on wild Chinook fry in the Tucannon River. Predation by residual steelhead on wild salmonids may represent an important impact on wild salmon populations and deserves further study.

Estuarine and Nearshore Marine Environments

Juvenile salmon and steelhead may spend considerable time in estuaries and nearshore environments before moving into offshore marine habitats (Healey 1980; Simenstad et al. 1982; McCabe et al. 1986; Percy 1992). The amount of time spent in estuaries by different salmonid species varies from several days to several months among estuaries and among years, and is probably related to environmental conditions (e.g., temperature, prey availability, stream flow) and the physical characteristics of individual estuaries (Simenstad et al. 1982). There is evidence that all five species of Pacific salmon may co-occur in habitats within the Campbell River estuary, BC (Korman et al. 1997), indicating that the potential for intrageneric predation exists in these habitats, although Macdonald et al. (1987) found that larger fish tended to occupy deeper water in these habitats.

Compared to freshwater studies, there is little evidence that wild salmonids are preyed on by other salmonids in estuarine or nearshore environments. Diets of juvenile Pacific salmon in the nearshore marine environment are often dominated by invertebrates (Manzer 1969; Feller and Kaczynski 1973; Craddock et al. 1976; Kjelson et al. 1982; Shreffler et al. 1992; Simenstad et al. 1992; Perry et al. 1996; Miller and Simenstad 1997; Moulton 1997; Gray et al. 2002), but may contain fish after the fish grow larger and move offshore (Healey 1991b; Tadokoro et al. 1996; Landingham et al. 1998), although salmonids have rarely been identified as prey. Emmett (1997) and Simenstad et al. (1992) suggested that the primary fish predators of juvenile salmon in estuaries were cutthroat trout and steelhead smolts, but did not cite any data to support this, and McCabe et al. (1983) suggest that intrageneric predation on salmonids was rare in the Columbia River estuary. Durkin (1982) reported that the diet of coho salmon smolts (128–138 mm) in the Columbia River estuary was composed almost entirely of invertebrates, and found no evidence that salmonids were utilized as prey. Murphy et al. (1988) found no evidence that coho salmon smolts preyed on chum or pink fry in a southeast AK estuary. Macdonald et al. (1987) did not report any salmonids in the diets of coho or Chinook smolts in the Campbell River estuary. Similarly, no salmonids were identified in the stomachs of juvenile Chinook salmon captured in nearshore habitats in Puget Sound (Miller et al. 1977; Fresh and Schroder 1984; Buckley 1999). Recent sampling in Puget Sound, however, has revealed that cutthroat trout may be significant predators of wild salmonid fry in nearshore areas (D. Beauchamp, UW, personal communication).

The results of numerous investigations suggest that intrageneric predation of wild juvenile salmonids is not common in estuarine or nearshore marine environments, but this may reflect difficulties in sampling and the relative paucity of work that has been conducted in these environments compared to freshwater. Because predation of juvenile salmonids by marine fishes may be significant in these environments (e.g., Beamish et al. 1992), the relative risk of predation by hatchery-reared salmonids may be low. However, we are not aware of any studies that have been specifically designed to look for predation by hatchery-reared salmonids in estuarine or



nearshore habitats. Hatchery-reared Chinook salmon smolts may spend less time (Levings et al. 1986) and use different habitats (Levings et al. 1986; Macdonald et al. 1987) in the Campbell River estuary than wild smolts, which may affect their predation potential compared to wild fish. More research on the feeding habits of hatchery-reared salmonids in nearshore and estuarine environments is necessary if predation risk to wild salmonids is to be estimated.

Offshore Marine Environment

There is little evidence of intrageneric predation among salmonid species in the offshore marine environment. Although fish may make up a significant component of the diets of juvenile Chinook and coho in offshore marine environments, salmonid remains have rarely been identified as prey (Manzer 1969; Peterson et al. 1982; Brodeur 1989; Brodeur and Percy 1990; Percy et al. 1990; Brodeur et al. 1992; Landingham et al. 1998; Buckley 1999; Hunt et al. 1999). In a sample of stomach contents collected between 1996 and 2002 from 86,266 ocean age-0 salmon (12,005 of which were hatchery-origin) from Puget Sound and the waters off Vancouver Island, only one fish was observed to have salmonid remains in its stomach (Ruston Sweeting, Canadian Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC, unpublished data). Although many of these studies used small sample sizes and were not designed to look for evidence of intrageneric predation, the fact that virtually all of the data collected indicate that salmonids do not feed on other salmonids offshore indicates that offshore predation by salmonids is probably not an important source of mortality to Washington salmon and steelhead stocks.

Offshore predation on wild salmonids by hatchery-reared smolts may be rare because encounter rates between the two may be low. Larger fish may move offshore earlier than smaller fish (Percy 1992), and the two may not co-occur in the marine environment when wild fry are small enough to be preyed upon by hatchery smolts. Future studies of salmonid diets in the offshore environment should estimate the density of potential predators and prey to evaluate how likely they are to encounter each other.

Relative Size of Predators and Prey

There is evidence that salmonids are capable of preying on fish that are up to approximately 50% of their body length, but the majority of prey is probably much smaller. Keeley and Grant (2001) provide linear regression relationships for salmonid body size and prey size based on a variety of salmonid diet studies. Their results for salmonids feeding on fish in streams suggest that the mean prey size for 100–200 mm salmonids is between 13–15% of predator body size. There was very little variability among salmonid species in these predator/prey size relationships. Damsgard (1995) developed a maximum prey size relationship for salmonids (based on mouth size) which suggests that salmonids are physically capable of consuming prey that are 49–51% of their body length.

In a laboratory experiment, Pearsons and Fritts (1999) found that hatchery-reared coho salmon consumed Chinook salmon that were up to 46% of their body length. Several other studies suggest that small juvenile salmonids will prey on fish up to about 40–45% of their body length (Martin et al. 1993; McConnaughey 1998), although Hargreaves and LeBrasseur (1986) found that yearling



coho salmon very occasionally preyed on juvenile chum that were up to 75% of their body length. A recent study of Arctic char feeding on conspecifics suggests that the maximum relative prey size was approximately 47% of predator length (Finstad et al. 2001). It is therefore reasonable to assume that salmonid predators are capable of consuming prey up to approximately 50% of their body length.

The relative sizes of downstream-migrating smolts or fry of different species of salmonids in Washington suggest that several possible predator/prey combinations are likely to occur. Virtually all *Oncorhynchus* species could be potential prey for larger salmonids in freshwater when they are small, but those that migrate to sea at a small size are probably most vulnerable because they become concentrated in the downstream reaches of rivers. The relative vulnerability of wild juvenile salmonids to predation in freshwater depends on the release location of hatchery fish; if fish are released near the mouth of the river, then migrating fry are probably most vulnerable to predation. Hatchery fish that are released further upstream may encounter concentrations of all species of salmonid fry that occur in a given river.

Pink and chum salmon typically migrate at the smallest size of all species of Pacific salmonids (Heard 1991; Salo 1991; Hard et al. 1996; Johnson et al. 1997), often less than 50 mm in length. Ocean-type Chinook migrate as fry or smolts at sizes ranging from 30–100 mm (Myers et al. 1998, Healey 1991a). Smolts from WA sockeye salmon populations usually migrate to sea as 90–150 mm yearlings, but fry may be vulnerable to predation during earlier migrations to lake habitat and within lakes (Gustafson et al. 1997). These species are probably most likely to be preyed upon by hatchery-reared salmonids in WA.

Hatchery-reared chum, pink, sockeye, and ocean-type (underyearling) Chinook are unlikely to prey on wild salmonids due to their relatively small size at release and their non-piscivorous feeding habits. Yearling coho, Chinook, and steelhead smolts are typically released from WA hatcheries at sizes ranging from 115–140, 150–180, and 180–240 mm, respectively (H. Fuss, WDFW, personal communication); these species have the greatest likelihood of preying on wild salmonid fry due to their large size. Although some hatchery-reared smolts, particularly steelhead, are large enough to feed on wild yearling salmonids, it is less likely that they would do so because yearlings would be far less abundant than fry. Hatchery-reared steelhead might be expected to prey on the largest size-range of prey due to their larger size; at 50% of body size, coho, Chinook and steelhead smolts could consume prey up to 70, 90 and 120 mm in length, respectively (Figure 1). Hatchery-reared coho, however, are probably the most likely species to have significant effects on wild salmonid populations in WA due to the large numbers released: WDFW released approximately 32.7 million coho in 2000, compared with 10 million steelhead and 3.5 million yearling Chinook (H. Fuss, WDFW, personal communication).

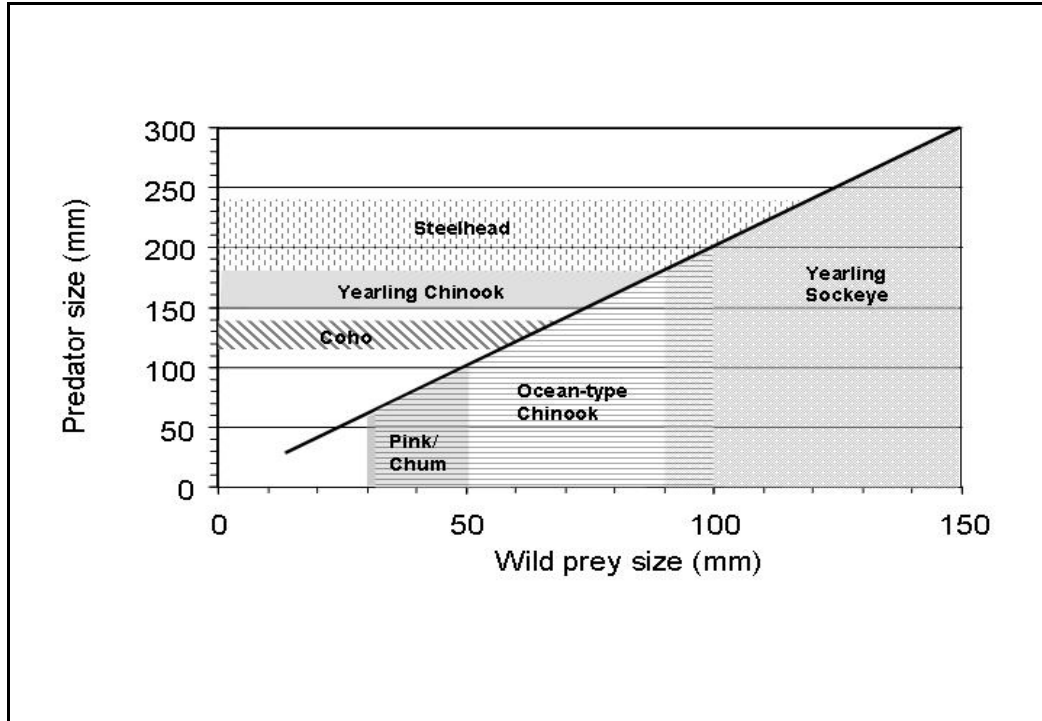


Figure 1. Relative sizes of hatchery-reared salmonid predators (at release) and their potential migratory salmonid prey in Washington, assuming that predators may consume fish up to 50% of their body size.

Spatial and Temporal Overlap of Potential Predators and Prey

Predators and prey must show significant overlap in time and space in order for predation to have an impact on prey populations. Estimation of the risk to wild salmonid populations in WA from hatchery-reared salmonid predation is complicated because both predators and prey may be migratory and the spatial and temporal overlap between predators and potential prey may vary among locations and years. The likelihood that hatchery-released juvenile salmonids will prey on wild salmonids will depend on, among other factors, the spatial and temporal distribution of wild salmonids relative to hatchery-reared predators.

Spatial Overlap

Hatchery-reared yearling coho, Chinook and steelhead are released from a number of hatcheries throughout WA. For example, yearling Chinook are released from hatcheries on 15 rivers in coastal (Sol Duc, Dungeness), Puget Sound (Skagit, Nooksack, Skykomish, Green, Deschutes), and Columbia River (Cowlitz, Kalama, Lewis, Klickitat, Tucannon, Yakima, Wenatchee, Methow) regions (H. Fuss, WDFW, personal communication). The distribution of potential wild



salmonid prey within WA varies widely by species. For example, sockeye salmon populations occur in only six drainages in WA (Gustafson et al. 1997), pink salmon occur in eleven (Hard et al. 1996), while coho occur in most drainages capable of supporting salmon. An initial step that should be taken, as we suggest below, is to tabulate the distribution of hatchery-reared yearling salmonid smolts and their potential salmonid prey to identify basins where predation by hatchery-reared fish might be expected to be most important.

The previous section suggests that predation on wild salmonid fry by hatchery-reared salmon and steelhead is most likely to occur in freshwater, although the potential for predation in estuarine and nearshore environments deserves more study. Relatively little is known about the distribution and habitat use of wild and hatchery-reared salmonids in estuarine and nearshore environments, which makes it difficult to determine the potential for spatial overlap of hatchery predators and wild prey. For example, the likelihood that hatchery-reared salmonids might migrate within the nearshore environment (e.g., among estuaries) is unknown. Further research on salmonid use of nearshore and estuarine environments is necessary to determine the potential for predation of wild salmonids by hatchery-reared fish.

Temporal Overlap

Chum salmon fry emerge from the gravel between late-January and June and usually begin migrating downstream immediately after emergence (Johnson et al. 1997), although some reside in freshwater for up to one month before migrating (Simenstad et al. 1982). Peak chum migrations usually occur between March and April in WA streams (Healey 1982). In WA, juvenile migrations are usually short, ranging from just a few hours to a few days, because chum salmon generally spawn in the lower reaches of rivers. Simenstad et al. (1982) found that the average residence time per estuary was ten weeks and 24.5 days for individuals. Chum salmon juveniles spend more time rearing in estuaries than most other anadromous salmonid species.

Pink salmon have the shortest freshwater residence phase of all *Oncorhynchus* species. Most adult returns occur in odd years in WA (except for an even-year run in the Snohomish River), so juveniles are primarily present in freshwater in even years (Hard et al. 1996). Juvenile pink salmon begin migrating immediately upon emerging from the gravel (Simenstad et al. 1992). Emergence and migration typically occur between March and April in WA, but may extend into May. The duration of residence in the estuary ranges from a few days to three months, but is generally short (Healey 1982). Later emerging fry tend to move directly into salt water without pausing long in the estuary (Hurley and Woodall 1968).

During the period of emergence and migration to the nursery lake, sockeye fry are highly vulnerable to predation by other fish and birds (Gustafson et al. 1997). Fry emerge in the Cedar River, WA between January and early June, with peak emergence from early-March through mid-May (Stober and Hämäläinen 1979, 1980; Seiler and Kishimoto 1996). Most sockeye in WA smolt and migrate seaward after one year of lake residence (Gustafson et al. 1997).

Ocean-type Chinook salmon migrate seaward as subyearlings during one of three distinct phases, here referred to as immediate, fry, and fingerling migrants. The immediate phase fish migrate soon after yolk resorption (Lister et al. 1971, Healey 1991a). Most Chinook salmon migrate as fry



between March and June after rearing for 60-150 days in freshwater. Fingerling migrants stay in the river until late summer of their first year (Myers et al. 1998). Juvenile fall Chinook salmon are therefore likely to be present in freshwater anytime between emergence in late-January or February through September. Ocean-type Chinook juveniles make greater use of estuaries for rearing than their spring-type counterparts, and earlier migrating smolts spend proportionately more time rearing in the estuary environment. Levings et al. (1986) reported that individual wild Chinook fry resided in the Campbell River, BC estuary for 40 to 60 days. Estuary residence times in southern BC (e.g. Campbell River estuary) may be shorter than elsewhere due to the abundant sheltered coastal habitat available in that region. Simenstad et al. (1992) found individuals residing in large WA estuaries for up to 189 days. McCabe et al. (1986) reported subyearling Chinook present in the Columbia River estuary year-round, but most numerous from May through September. Fall Chinook are present in the estuary environment throughout the spring, summer and fall (Healey 1982).

In summary, chum and Chinook salmon have the longest estuary residencies whereas pink and sockeye typically spend less time rearing in this environment (Healey 1982; Simenstad et al. 1992). Pink and chum salmon typically migrate to the estuary soon after emergence, whereas Chinook and sockeye spend a few months to a year rearing in freshwater before migration. The active rather than passive migration, nocturnal movement, and schooling behaviors of pink, sockeye and to a lesser extent chum salmon are behavioral adaptations to reduce predation risk during migration (Burgner 1991).

We have identified hatchery-reared yearling coho, fall and spring Chinook, and steelhead smolts as potential predators of wild salmonid fry, and a comparison of their release dates with the stream and estuary residencies of wild fry may identify periods when intrageneric predation could occur. In Puget Sound, hatchery-reared yearling coho smolts are released from late-April through June (Fuss and Ashbrook 1995). Yearling fall Chinook are released between March and May; yearling spring Chinook are released in April and May. Yearling summer Chinook smolts are released from late-March through early-April. Hatchery steelhead generally smolt after one year and are released from April through June. As we suggest below, determining the potential temporal overlap between hatchery-reared smolts and their potential prey in rivers where hatchery smolts are released is an important first step in determining the likelihood of predation by hatchery-reared smolts.

Predator Functional and Numerical Responses

The functional response of a predator is the relationship between the consumption rate of a predator and the abundance of prey. For example, predator consumption may be limited unless sufficient numbers of prey are available, and predators may be 'swamped' at high prey densities. There is relatively little information on the functional response of salmonid predators to congeneric prey, although Fresh and Schroder (1987) found that consumption of chum fry by fish predators (primarily rainbow trout and coho) leveled off at higher densities of prey, suggesting that relative predator consumption was limited at higher prey densities. Peterman and Gatto (1996), however, suggested that predators on salmonid fry were not likely to be swamped by all but the largest prey populations.



The functional response of hatchery-reared salmonids may depend on a number of factors, including prey behavior (e.g., schooling, sheltering), habitat use of predators and prey, physiological condition of predators (e.g., smolt status), habitat availability, temperature, discharge, and turbidity. For example, chum salmon do not form tight schools and typically migrate at night (Mason 1974; Salo 1991), while pink salmon fry migrate in tight schools near the water surface. This may mean that chum fry may be more widely dispersed than pinks, which may make them less vulnerable to predation by larger fishes.

The numerical response describes how predators respond in terms of numbers to prey abundance. For example, some predators have been shown to aggregate in areas where salmonid prey are abundant (Larsson 1985; Beamish et al. 1992). We are aware of no published studies that describe the migratory behavior of hatchery-reared salmonids with respect to the abundance of potential prey. For example, if hatchery-reared smolts delay migration in order to feed on wild fry in freshwater or estuarine environments, the impact of predation on wild salmon populations might be greater.

A Strategy to Estimate Risks to Wild Salmon and Steelhead Populations from Hatchery-Reared Salmonid Predation

1. Describe Spatial and Temporal Overlap of Predators and Prey

Based on WDFW and other agency stocking programs, the spatial distribution, migration timing, and size of yearling hatchery-reared salmonids should be tabulated for freshwater, estuarine, and offshore habitat. The spatial distribution, migration timing and size of potential prey in basins where hatchery predators are present should similarly be tabulated. This information will allow the identification of areas where predation on wild fry by hatchery-reared fish is likely to be important.

2. Conduct Research to Estimate Predation Rates on Wild Salmonids

Within areas identified in step 1, field research should be conducted to determine the importance of predation by hatchery-reared salmonids on wild salmonid fry in freshwater and estuarine environments. The data collected should include, but not be limited to, predation rates by hatchery fish, density and habitat use of hatchery and wild fish, residence time of wild and hatchery-reared fish in freshwater and estuarine environments, the proportion of wild fry consumed by predators, and the relative importance of predation by hatchery fish versus other predators.

Laboratory research could be combined with field work to examine questions about how predator and prey behavior and habitat use may affect predation rates, how environmental factors (temperature, flow, turbidity) may affect predation, and the functional response of predators to multiple prey types. The ultimate goal of this research would be to obtain estimates of predation



rates of hatchery-reared fish on wild salmonid fry and to determine how these are likely to vary in order to develop models to estimate risk to wild salmonid populations from predation by hatchery fish.

3. Develop Models to Estimate the Risk of Predation by Hatchery-Reared Smolts.

The risk to wild salmon and steelhead populations associated with predation by hatchery-reared fish should be estimated by developing models based on data collected from specific locations where predation is determined to be likely. These models could then be applied to other areas to determine the likelihood that predation by hatchery-reared smolts effects wild salmonid populations throughout the state.

Models have previously been developed to estimate the impacts of predators on migrating salmonids (e.g., Petersen and DeAngelis 1992). Recent research indicates that the scale at which modeling is conducted may have significant effects on results, and that modeling should be undertaken at the smallest temporal and spatial scales that are relevant (Petersen and DeAngelis 2000; DeAngelis and Petersen 2001). The type of models that are to be developed should be determined before data collection begins in order to ensure that data are collected at the appropriate scale to provide relevant results.

References

- Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Trans. Am. Fish. Soc.* 113:1-32.
- Beamish, J.R., B.L. Thomson, and G.A. McFarlane. 1992. Spiny dogfish predation on Chinook and coho salmon and the potential effects on hatchery-produced salmon. *Trans. Am. Fish. Soc.* 121:444-455.
- Beauchamp, D. A. 1990. Seasonal and diel food habitats of rainbow trout stocked as juveniles in Lake Washington. *Trans. Am. Fish. Soc.* 119:475-482.
- Beauchamp, D. A. 1995. Riverine predation on sockeye salmon fry migrating to Lake Washington. *N. Am. J. Fish. Manage.* 15:358-365.
- Brodeur, R. D. 1989. Neustonic feeding by juvenile salmonids in coastal waters of the Northeast Pacific. *Can. J. Zool.* 67:1995-2007.
- Brodeur, R. D., and W. G. Percy. 1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. *Fish. Bull.* 88:617-636.
- Brodeur, R. D., R. C. Francis, and W. G. Percy. 1992. Food consumption of juvenile coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) on the continental shelf off Washington and Oregon. *Can. J. Fish. Aquat. Sci.* 49: 1670-1685.



- Buckley, R. M. 1999. Incidence of cannibalism and intra-generic predation by Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Washington Department of Fish and Wildlife, Resource Assessment Division, Olympia, WA. 22 p.
- Burgner, R. L. 1991. Life history of the sockeye salmon (*Oncorhynchus nerka*). In: C. Groot and L Margolis (editors), Pacific salmon life histories, p. 3-117. Univ. British Columbia Press, Vancouver.
- Cannamela, D. A. 1993. Hatchery steelhead smolt predation of wild and natural juvenile Chinook salmon fry in the upper Salmon River, Idaho. Idaho Department of Fish and Game unpublished report, Boise, ID.
- Craddock, D.R., T.H. Blahm, and W.D. Parente. 1976. Occurrence and utilization of zooplankton by juvenile Chinook salmon in the lower Columbia River. Trans. Am. Fish. Soc. 105:72-76.
- Damsgard, B. 1995. Arctic charr, *Salvelinus alpinus* (L.), as prey for piscivorous fish – a model to predict prey vulnerabilities and prey size refuges. Nordic J. Freshw. Res. 71: 190-196.
- DeAngelis, D. L., and J. H. Petersen. 2001. Importance of the predator's ecological neighborhood in modeling predation on migrating prey. Oikos 94:315-325.
- Durkin, J. T. 1982. Migration characteristics of coho salmon (*Oncorhynchus kisutch*) smolts in the Columbia River and its estuary. In: V. S. Kennedy (editor), Estuarine comparisons, p. 343-364. Academic Press, New York.
- Emmett, R.L. 1997. Estuarine survival of salmonids: the importance of interspecific and intraspecific predation and competition. In: Emmett, R.L., and M.H. Schiewe (editors). Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWFSC-29, 313 p.
- Feller, R. J., and V. W. Kaczynski. 1973. Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. J. Fish. Res. Bd. Can. 32: 1419-1429.
- Finstad, A.G., P. A. Jansen, and A. Langeland. 2001. Production and predation rates in a cannibalistic Arctic char (*Salvelinus alpinus* L.) population. Ecol. Freshw. Fish 10: 220-226.
- Fresh, K. L. 1997. The role of competition and predation in the decline of Pacific salmon and steelhead. In D. J. Stouder, P. A. Bisson, and R. J Naiman (editors) Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.
- Fresh, K. L. and S. L. Schroder. 1984. Salmon-herring predator/competitor interactions project – Phase 111. Washington Department of Fish and Wildlife unpublished report, Olympia, WA.



- Fresh, K.L., and S.L. Schroder. 1987. Influence of abundance, size, and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. *Can. J. Fish. Aquat. Sci.* 44: 236-243.
- Fuss, H. J., and C. Ashbrook. 1995. Hatchery operation plans and performance summaries. Vol. 1, No. 2-Puget Sound, Washington Department of Fish and Wildlife unpublished report, WDFW, Olympia, WA.
- Gray, A., C. A. Simenstad, D. L. Bottom, and T. J. Cornell. 2002. Contrasting functional performance of juvenile salmon habitat in recovering wetlands of the Salmon River, Oregon, USA. *Restor. Ecol.* 10:514-526.
- Gustafson, R. G., T. C. Wainwright, G. A. Winans, F. W. Waknitz, L. T. Parker, and R. S. Waples. 1997. Status review of sockeye salmon from Washington and Oregon. U. S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-33, 282 p.
- Hard, J. J., R. G. Kope, W. S. Grant, F. W. Waknitz, L. T. Parker, and R. S. Waples. 1996. Status review of pink salmon from Washington, Oregon, and California. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWFSC-25, 131 p.
- Hargreaves, N. B., and R.J. LeBrasseur. 1986. Size selectivity of coho (*Oncorhynchus kisutch*) preying on juvenile chum salmon (*O. keta*). *Can. J. Fish. Aquat. Sci.* 43: 581-586.
- Hawkins, S.W., and J.M. Tipping. 1999. Predation by juvenile hatchery salmonids on wild fall Chinook salmon fry in the Lewis River, Washington. *Cal. Fish and Game* 85: 124-129.
- Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon, *Oncorhynchus tshawytscha*. *Fish. Bull.* 77:653-668.
- Healey, M. C. 1982. Juvenile Pacific salmon in estuaries: the life support system. *In: V. S. Kennedy (editor), Estuarine Comparisons*, p. 315-341. Academic Press, New York.
- Healey, M. C. 1991a. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). *In: C. Groot and L Margolis (editors), Pacific salmon life histories*, p. 311-393. Univ. British Columbia Press, Vancouver.
- Healey, M. C. 1991b. Diets and feeding rates of juvenile pink, chum, and sockeye salmon in Hecate Strait, British Columbia. *Trans. Am. Fish. Soc.* 120:303-318.
- Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). *In: C. Groot and L Margolis (editors), Pacific salmon life histories*, p. 121-230. Univ. British Columbia Press, Vancouver.
- Hunt, S. L., T. J. Mulligan, and K. Komori. 1999. Oceanic feeding habits of Chinook salmon, *Oncorhynchus tshawytscha*, off northern California. *Fish. Bull.* 97:717-721.



- Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. *J. Fish. Res. Bd. Can.* 16:835-886.
- Hurley, D. A., and W. L. Woodall. 1968. Responses of young pink salmon to vertical temperature and salinity gradients. *Int. Pac. Salmon Fish. Comm. Prog. Rep.* 19:80 p.
- Johnson, O. W., W. S. Grant, R. G. Kope, K. Neely, F. W. Waknitz, and R. S. Waples. 1997. Status review of chum salmon from Washington, Oregon, and California. U. S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-32, 280 p.
- Keeley, E.R, and J.W.A. Grant. 2001. Prey size of salmonids fishes in streams, lakes, and oceans. *Can. J. Fish. Aquat. Sci.* 58: 1122-1132.
- Kjelson, M.A., P.F. Raquel, and F.W. Fisher. 1982. Life history of fall-run juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary, California. In V. S. Kennedy, editor. *Estuarine Comparisons*, p. 393-411. Academic Press, New York, New York.
- Korman, J., B. Bravender, and C. D. Levings. 1997. Utilization of the Campbell River estuary by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in 1994. *Can. Tech. Rep. Fish. Aquat. Sci.* 2169.
- L'Abée-Lund, J. H., P. Aass, and H. Sægrov. 2002. Long-term variation in piscivory in a brown trout population: effect of changes in available prey organisms. *Ecol. Freshw. Fish* 11:260-269.
- Landingham, J. H, M. V. Sturdevant, and R. D. Brodeur. 1998. Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia. *Fish. Bull.* 96:285-302.
- Larsson, P. O. 1985. Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar*, populations. *J. Fish. Biol.* 26:391-397.
- Levin, P. S., R. W. Zabel, and J. G. Williams. 2001. The road to extinction is paved with good intentions: negative associations of fish hatcheries with threatened salmon. *Proc. Royal Soc. London B, Series B* 268:1-6.
- Levings, C. D., C. D. McAllister, and B. D. Chang. 1986. Differential use of the Campbell River estuary by wild and hatchery-reared juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 43: 1386-1397.
- Lichatowich, J. 1999. *Salmon without rivers*. Island Press, Washington, D.C.
- Lister, D. B., C. E. Walker, and M. A. Giles. 1971. Cowichan River Chinook salmon escapements and juvenile production 1965-1967. *Can. Fish. Serv.* 1971-3, 8 p.



- Macdonald, J. S., I. K. Birtwell, and G. M. Kruzynski. 1987. Food and habitat utilization by juvenile salmonids in the Campbell River estuary. *Can J. Fish. Aquat. Sci.* 44:1233-1246.
- Manzer, J. I. 1969. Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. *J. Fish. Res. Bd. Can.* 26: 2219-2223.
- Martin, S.W., A.E. Viola, and M.L. Schuck. 1993. Investigations of the interactions among hatchery reared summer steelhead, rainbow trout, and wild spring Chinook salmon in southeast Washington. WDFW, Report 93-4, Olympia.
- Mason, J. C. 1974. Behavioral ecology of chum salmon fry (*Oncorhynchus keta*) in a small estuary. *J. Fish. Res. Bd. Can.* 31:83-92.
- Mather, M. E. 1998. The role of context-specific predation in understanding patterns exhibited by anadromous salmon. *Can. J. Fish. Aquat. Sci.* 55(Suppl. 1):232-246.
- McCabe, G. T., W. D. Muir, R. L. Emmett, and J. T. Durkin. 1983. Interrelationships between juvenile salmonids and nonsalmonid fish in the Columbia River estuary. *Fish. Bull.* 81:815-826.
- McCabe, G. T., R. L. Emmett, W. D. Muir, and T. H. Blahm. 1986. Utilization of the Columbia River estuary by subyearling Chinook salmon. *Northwest Science* 60:113-124.
- McCart, P. 1967. Behaviour and ecology of sockeye salmon fry in the Babine River. *J. Fish. Res. Bd. Can.* 24:375-428.
- McConnaughey, J. 1998. Predation by coho salmon smolts (*Oncorhynchus kistutch*) in the Yakima and Klickitat Rivers. Yakama Indian Nation report, Toppenish, WA.
- McMichael, G. A., and T. N. Pearsons. 2001. Upstream movement of residual hatchery steelhead into areas containing bull trout and cutthroat trout. *N. Am. J. Fish. Manage.* 21: 943-946.
- Menchen, R. S. 1981. Predation by yearling steelhead *Salmo gairdneri* released from Coleman National Fish Hatchery on naturally produced Chinook salmon *Oncorhynchus tshawytscha* fry and eggs in Battle Creek, 1975. California Department of Fish and Game unpublished report.
- Miller, B. S., C. A. Simenstad, L. L. Moulton, K. L. Fresh, F. C. Funk, W. A. Carp, and S. F. Borton. 1977. Puget Sound baseline program nearshore fish survey. *Fish Res. Inst. Univ. Wash.* FRI-UW-7710.
- Miller, J.A., and C.A. Simenstad. 1997. A comparative assessment of a natural and created estuarine slough as rearing habitat for juvenile Chinook and coho salmon. *Estuaries* 20:792-806.



- Moulton, L. L. 1997. Early marine residence, growth, and feeding by juvenile salmon in northern Cook Inlet, Alaska. *Alask. Fish. Res. Bull.* 4:154-177.
- Murphy, M. L., J. F. Thedinga, and K. V. Koski. 1988. Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in southeastern Alaska. *Fish. Bull.* 86:213-222.
- Myers, J. M., R. G. Kope, G. J. Bryant, D. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. T. Lindley, and R. S. Waples. 1998. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. U. S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-35, 443 p.
- Olla, B. L., M. W. Davis, and C. H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. *Bull. Mar. Sci.* 62:531-550.
- Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *J. Fish. Res. Bd. Can.* 28: 1503-1510.
- Pearcy, W. G., R. D. Brodeur, and J. P. Fisher. 1990. Distribution and biology of juvenile cutthroat trout *Oncorhynchus clarki clarki* and steelhead *O. mykiss* in coastal waters off Oregon and Washington. *Fish. Bull.* 88:697-711.
- Pearcy, W. G. 1992. Ocean ecology of north Pacific salmonids. University of Washington Press, Seattle.
- Pearsons, T.N., and A.L. Fritts. 1999. Maximum size of Chinook salmon consumed by juvenile coho salmon. *N. Am. J. Fish. Manage.* 19: 165-170.
- Perry, R. I., N. B. Hargreaves, B. J. Waddell, and D. L. Mackas. 1996. Spatial variation in feeding and condition of juvenile pink and chum salmon off Vancouver Island, British Columbia. *Fish. Oceanogr.* 5: 73-88.
- Peterman, R. M., and M. Gatto. 1976. Estimation of functional responses of predators on juvenile salmon. *J. Fish. Res. Bd. Can.* 35:797-808.
- Petersen, J. H., and D. L. DeAngelis. 1992. Functional response and capture timing in an individual-based model: predation by northern squawfish (*Ptychocheilus oregonensis*) on juveniles salmonids in the Columbia River. *Can J. Fish. Aquat. Sci.* 49:2551-2565.
- Petersen, J. H., and D. L. DeAngelis. 2000. Dynamics of prey moving through a predator field: a model of migrating juvenile salmon. *Mathematical Biosciences* 165:97-114.
- Peterson, W. T., R. D. Brodeur, and W. G. Pearcy. 1982. Food habits of juvenile salmon in the Oregon coastal zone, June 1979. *Fish. Bull.* 80:841-851.



- Ricker, W. E. 1941. The consumption of young sockeye salmon by predacious fish. J. Fish. Res. Bd. Can. 5: 293-313.
- Riley, S. C., H. J. Fuss, and L. L. LeClair. 2001. Development of field methods to determine the effects of hatchery releases on wild juvenile salmonids. Report to the Hatchery Scientific Review Group of the Interagency Committee for Outdoor Recreation, Olympia, WA.
- Riley, S. C., H. J. Fuss, and L. L. LeClair. 2002. Development of field methods to determine the effects of hatchery releases on wild juvenile salmonids. Report to the Hatchery Scientific Review Group of the Interagency Committee for Outdoor Recreation, Olympia, WA.
- Ruggerone, G.T., and D.E. Rogers. 1992. Predation on sockeye salmon fry by juvenile coho salmon in the Chignik lakes, Alaska: implications for salmon management. N. Am. J. Fish. Manage. 12: 87-102.
- Salo, E.O. 1991. Life history of chum salmon, *Oncorhynchus keta*. In: C. Groot and L Margolis (editors), Pacific salmon life histories, p. 231-309. Univ. British Columbia Press, Vancouver.
- Seiler, D., and L. E. Kishimoto. 1996. Annual report 1995 Cedar River sockeye salmon fry production evaluation program. WDFW report. 9 p., Olympia, WA.
- Seiler, D., G. Volkhardt, L. Kishimoto, and P. Topping. 2002. 2000 Green River juvenile salmonid production evaluation. Washington Department of Fish and Wildlife Report #FPT 02-03.
- Sholes, W. H., and R. J. Hallock. 1979. An evaluation of rearing fall-run Chinook salmon, *Oncorhynchus tshawytscha*, to yearlings at Feather River Hatchery with a comparison of returns from hatchery and downstream releases. Cal. Fish Game 65:239-255.
- Shreffler, D.K., C.A. Simenstad, and R.M. Thom. 1992. Temporary residence by juvenile salmon in a restored estuarine wetland. Can. J. Fish. Aquat. Sci. 47:2079-2084.
- Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. In: V. S. Kennedy (editor), Estuarine comparisons, p. 343-364. Academic Press, New York.
- Sosiak, A. J., R. G. Randall, and J. A. McKenzie. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in a stream. J. Fish. Res. Bd. Can. 36:1408-1412.
- Stober, Q. J., and A. H. Hämäläinen. 1979. Cedar River sockeye salmon production. Univ. Wash. Fish. Res. Inst. FRI-UW-7917. 52 p., Seattle, WA.
- Stober, Q. J., and A. H. Hämäläinen. 1980. Cedar River sockeye salmon production. Univ. Wash. Fish. Res. Inst. FRI-UW-8016. 59 p., Seattle, WA.



Tadokoro, K., Y. Ishida, N. Davis, S. Ueyangagi, and T. Sugimoto. 1996. Change in chum salmon (*Oncorhynchus keta*) stomach contents associated with fluctuation of pink salmon (*O. gorbuscha*) abundance in the central sub arctic Pacific and Bering Sea. *Fish. Oceanogr.* 5:89-99.