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Predation by hatchery yearling salmonids on wild subyearling salmonids in the freshwater environment: A review of studies, two case histories, and implications for management

Seth W. Naman · Cameron S. Sharpe

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Abstract We conducted a literature review on predation by hatchery yearling salmonids on wild subyearling salmonids in the western United States. The review included 14 studies from the Pacific Northwest and California. In most instances, predation by hatchery yearling salmonids on wild subyearling salmonids occurred at low levels. However, when multiple factors contributing to the incidence of predation were met, localized areas of heavy predation were noted. Total prey consumed ranged from 456 to 111 000 subyearlings for the few studies in which enough information was gathered to make the estimate. We examined two of these studies in more detail: one detecting relatively low predation in four western Washington rivers and one detecting relatively high predation in the Trinity River in northern California. In the case of the rivers in western Washington, over 70% of wild subyearlings had migrated by the time hatchery steelhead were planted and those remaining had grown large enough to reduce their vulnerability to predation. In the case of the Trinity River, less than 20% of wild subyearlings had migrated by the time hatchery steelhead were planted and most were small enough to remain highly vulnerable to predation. We found that managers can effectively minimize the predation rate of hatchery yearling salmonids by reducing the spatial or temporal overlap of predator and prey. Unknown is the extent to which low predation rates, which likely occur in most places hatchery yearlings are released, might still negatively impact prey populations that are at low abundance because of other anthropogenic factors.

Keywords Hatchery · Salmon · Steelhead · Predation · Piscivore

Introduction

Although several researchers have concluded that predation can influence populations of anadromous salmonids (Mather 1998), little is known about the extent to which hatchery salmonids prey upon wild salmonids in freshwater environments. Nonetheless, millions of hatchery salmonids are released into rivers throughout the western United States annually (Levin et al. 2001). Several researchers have studied competition between hatchery and wild salmonids (e.g.

S. W. Naman (✉)
National Marine Fisheries Service,
1655 Heindon Rd,
Arcata, CA 95521, USA
e-mail: seth.naman@noaa.gov

C. S. Sharpe
Washington Department of Fish and Wildlife,
804 Allen Street Ste #3,
Kelso, WA 98626, USA

Present Address:
C. S. Sharpe
Oregon Department of Fish and Wildlife,
28655 Hwy. 34,
Corvallis, OR 97333, USA

Pollard and Bjornn 1973; McMichael et al. 1997; Kostow and Zhou 2006). Some studies have examined predation by wild yearling salmonids on wild subyearling salmonids (e.g. Ruggerone and Rogers 1992; Beauchamp 1995), and others have investigated smallmouth bass predation on wild subyearling salmonids (e.g. Fritts and Pearsons 2004; Naughton et al. 2004). Only two peer-reviewed studies, one by Hawkins and Tipping (1999) and another by Simpson et al. (2009), addressed predation by hatchery yearling salmonids on wild subyearling salmonids. However, there are a variety of contract reports and technical memoranda on the subject. Most of these studies documented low rates of predation, and those that have attempted to estimate the total number of wild subyearling salmonids consumed have reported relatively low numbers (e.g. Cannamela 1993).

Spatial and temporal overlap of predator and prey can be among the most important factors influencing predation on salmonids (Mather 1998) because they influence the density of predator and prey (Abrams and Ginzburg 2000). The size of prey at the time they are encountered by a predator is another important consideration that influences predation (Lundvall et al. 1999). Abiotic factors like turbidity (Turesson and Brönmark 2007), discharge (Hvidsten and Hansen 1988), and habitat complexity (Anderson 2001) can also have an effect on predation. If measures are employed to minimize or eliminate the factors which lead to or exacerbate predation, excessive loss of wild subyearling salmonids to hatchery yearling salmonids can be limited.

Literature review

We reviewed 14 studies on predation by hatchery yearling salmonids (reared for 1 year before release) on wild subyearling prey (Table 1). Other than the research performed by Hawkins and Tipping (1999) and Simpson et al. (2009), all of the documents were contract reports or other forms of grey literature and had not been published at the time of this review. Two of the studies examined predation by yearling coho salmon (*Oncorhynchus kisutch*), while twelve examined predation by hatchery steelhead (*O. mykiss*).

Three studies documented no predation, five studies detected low predation levels (0.001≤ subyearlings/hatchery fish <0.011) and six studies documented higher levels of predation (≥ 0.011 subyearlings/hatchery fish). The studies that reported no predation by hatchery fish had much smaller sample sizes (less than 100 samples) than those that did (Table 1). Therefore, we feel that it is likely that there is at least a low level of predation (≥ 0.001 subyearlings/hatchery fish) in virtually all river systems in which yearling salmonids are released. Very large sample sizes (in the thousands) are

Table 1 Sample size, number of subyearlings ingested, and the predation rate (subyearlings ingested/hatchery fish examined) for studies on predation by yearling hatchery salmonids on wild subyearling salmonids in the freshwater environment. Studies are ordered by the average amount of subyearling salmonids consumed per hatchery fish examined

Citation	Sample size	Subyearlings ingested (n)	Subyearlings per hatchery fish	Study examined smolts or residuals
Beauchamp 1995	18	0	0.000	Smolts
Harper 1999	59	0	0.000	Residuals
Pearsons et al. 1994	55	0	0.000	Residuals
Canamella 1993	6762	10	0.001	Smolts
Sharpe et al. 2008	6029	10	0.002	Smolts
Martin et al. 1993	1713	3	0.002	Residuals
McConnaughey 1999 (coho salmon)	11 127	25	0.002	Smolts
Jonasson et al. 1994	358	1	0.003	Residuals
Jonasson et al. 1995	175	2	0.011	Residuals
Whitesel et al. 1993	611	8	0.013	Residuals
Hawkins and Tipping 1999 (coho salmon)	1656	109	0.066	Smolts
Simpson et al. 2009	447	69	0.154	Smolts
Hawkins and Tipping 1999 (steelhead)	232	57	0.246	Smolts
Naman 2008	1636	882	0.539	Smolts

required in order to detect predation when it occurs at these low levels. Because it is unlikely that the predation rate can ever be reduced to zero, managers should focus on taking steps to minimize the predation rate to the extent deemed necessary to achieve legal requirements or ecological goals. None of the studies we reviewed tested if the predation mortality caused by hatchery fish was additive or compensatory. That is, it is difficult to know if all of the subyearlings consumed by hatchery fish would have died anyway by other means, or if some would have survived and returned as adults.

We examined two studies in more detail; one with a relatively low level of predation (0.002 subyearlings/hatchery fish) by Sharpe et al. (2008), and one with a relatively high level of predation (0.539 subyearlings/hatchery fish) by Naman (2008). Picking two studies with results that differed strongly (more than two orders of magnitude) allowed for a good comparison of the factors that led to both relatively low and relatively high levels of predation, highlighting potential differences in the river systems and hatchery practices.

Case histories

Naman (2008) used hook and line, seine, and electrofishing to capture hatchery steelhead from the study reach located on the Trinity River in northern California. All consumed subyearlings were known to be offspring of adults, hatchery and wild, that spawned naturally in the river system because no subyearling hatchery fish were released prior to the end of the study period. Sharpe et al. (2008) used rotary screw traps in western Washington to capture hatchery steelhead. Methods were employed to segregate hatchery steelhead and potential prey once trapped. Chinook salmon (*O. tshawytscha*) available as prey were all of natural origin in the Coweeman and Kalama rivers but included both hatchery- and natural-origin subyearlings in the Deschutes and Green rivers.

Western Washington Rivers

Between 2003 and 2005 Sharpe et al. (2008) studied yearling steelhead predation on Chinook salmon subyearlings using stomach content analysis. Yearling hatchery-origin steelhead trout were released in the Deschutes, Green, Coweeman and Kalama rivers upstream of and within known fall Chinook salmon rearing areas in western Washington. In all years, actively migrating steelhead smolts were captured in rotary screw traps and stomach contents were checked by gastric lavage or dissection. In 2003 and 2004, non-migratory steelhead were captured by angling and electrofishing in the Deschutes River and gut contents were inspected. Subyearling salmonids or parts thereof in the gut were identified to species. Of 6029 hatchery steelhead examined, 10 fall Chinook salmon subyearlings had recently been consumed (0.002 subyearlings/stomach). The range of observed predation across the various release groups of hatchery steelhead was 0 and 0.013 subyearlings/steelhead stomach with considerable variation in the incidence of predation between streams and years. On average, the work suggested that 0.6% of total subyearling Chinook salmon production might be consumed annually by migrating hatchery steelhead.

The low incidence of predation observed was likely a result of the timing of hatchery steelhead releases, which occurred after more than 70% of subyearlings had emigrated (Fig. 1) and after subyearlings had grown large enough to reduce or eliminate their susceptibility to predation. The average size of Chinook salmon subyearlings at the time hatchery steelhead were planted across all years and rivers in the western Washington study ranged from 59 mm to 78 mm and averaged 66 mm. Sharpe et al. (2008) concluded that steelhead release protocols used widely in the Pacific Northwest were associated

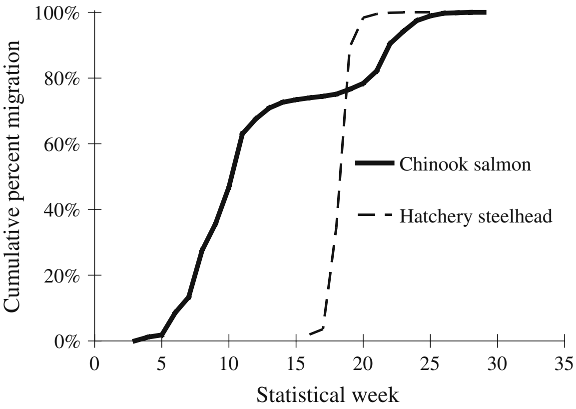

Fig. 1 Timing of typical cumulative percent migration of wild Chinook salmon and hatchery steelhead in Western Washington rivers (modified from Sharpe et al. 2008)

with negligible predation by migrating hatchery steelhead on fall Chinook salmon subyearlings.

Trinity River, California

The study performed by Naman (2008) occurred on the upper Trinity River in Northern California. Important characteristics of the study area include a dam located at the terminus of anadromous fish migration, a hatchery located at the base of the dam, and 2302 coho salmon and Chinook salmon redds (from both hatchery and wild spawners) located within 3.2 km of the hatchery in the fall and winter preceding the study (U.S. Fish and Wildlife Service, unpubl. data). The hatchery has a mitigation goal of 800 000 yearling steelhead, and hatchery records indicate an average release of 806 800 from 2005 to 2009 (California Department of Fish and Game, unpubl. data). The release date is 15 March of every year, with a volitional release period lasting between 10 and 14 days (California Department of Fish and Game, unpubl. data).

The Trinity River study documented the highest predation rate of any study that we reviewed, orders of magnitude greater than most others (Table 1). In total, 1636 hatchery steelhead were examined, yielding 882 recently consumed subyearling salmonids. Naman (2008) estimated that approximately 111 000 Chinook salmon and coho salmon subyearlings were consumed during the 30 day period of study by about half of the total number of steelhead released in 2007 (see Naman 2008 for details). It was estimated that this was approximately 6% of the Chinook salmon and coho salmon subyearlings produced in the study reach. However, additional subyearlings would have been consumed before and after the study period, and by the hatchery steelhead that were not included in the calculations.

The high incidence of predation observed was likely a result of the timing of hatchery steelhead releases, which occurred when less than 20% of subyearlings had emigrated (Fig. 2) and before subyearlings had grown large enough to reduce or eliminate their susceptibility to predation. The average size of Chinook salmon and coho salmon subyearlings at the time hatchery steelhead were released was 44 mm and 34 mm, respectively. Naman (2008) concluded that the early release date of 15 March, combined with a release location that was directly adjacent to several thousand salmonid redds, resulted in the prey being relatively vulnerable and occurring at relatively high densities at the time of release. That is, both spatial and temporal overlap of predator and prey were met, resulting in a high predation rate. In addition, abiotic conditions in the river, including constant discharge of 8.5 m^3s^{-1} and turbidity of ≤2 nephelometric turbidity units, resulted in advantageous conditions for predators, likely contributing to the high predation rate.

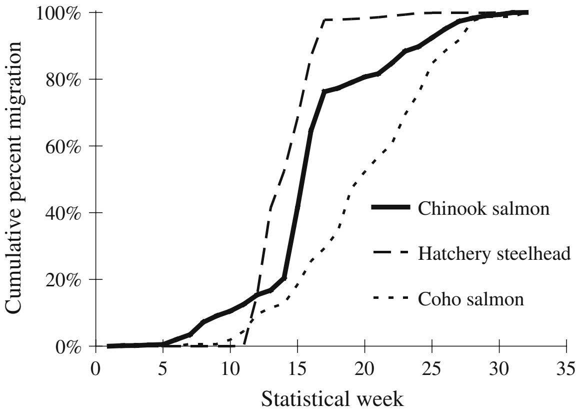

Fig. 2 Timing of cumulative percent migration of wild Chinook salmon and coho salmon and hatchery steelhead in the upper Trinity River, CA, 2007 (unpublished data provided by Hoopa Valley Tribal Fisheries)

Predation mechanisms

One simple expression of the estimated number of subyearlings consumed on any given day, $\widehat{F}$, is given by

$$\widehat{F} = \widehat{N} \cdot \widehat{p} \cdot \frac{\widehat{h}}{\widehat{t}}, \tag{1}$$

where $\widehat{N}$ is the estimated population of hatchery yearlings, $\widehat{p}$ is the estimated predation rate of the hatchery yearlings (number of subyearlings consumed/ number of hatchery yearlings examined) $\widehat{h}$ is the estimated number of feeding hours in a day (using 24 assumes continual feeding throughout the day and night), and $\widehat{t}$ is the estimated time in hours for a specified level of gastric evacuation at a specified water temperature. Results of this equation would be summed over a number of days to estimate the number of subyearlings consumed during a certain period of study.

Figure 3 depicts the daily number of subyearlings consumed by yearling hatchery salmonids for different release numbers and predation rates using Eq. 1. Assumptions in Fig. 3 were; 15 h of feeding time ($\widehat{h}$); and a water temperature of 10°C with the gastric evacuation equation $\widehat{t} = 56.2e^{-0.073T}$ for 95% evacuation of salmonid prey from brown trout developed by He and Wurtsbaugh (1993) where T is water temperature in degrees Celsius. For predation rates that were common in the studies we reviewed (≤ 0.01), the release numbers modeled resulted in less than 3000 subyearlings consumed in a single day. Fewer and fewer subyearling salmonids would be consumed in successive days as the number of hatchery yearlings decreases as they emigrate or perish. However, large numbers of subyearling salmonids can be consumed in a single day when moderately high predation rates (≥ 0.05 subyearlings/hatchery fish) are combined with the release of large numbers of hatchery fish (≥ 0.2 M; Fig. 3). For example, using the assumptions of temperature and gastric evacuation mentioned above, a predation rate of 0.05 subyearlings/hatchery fish and a release of 0.5 M hatchery fish would result in 13 846 subyearlings being consumed in a single day.

The term $\widehat{h}/\widehat{t}$ in this model is largely out of the control of natural resource managers. The biology and ecological setting of piscivorous hatchery fish dictates the number of feeding hours in a day. The gastric evacuation rate is mainly a function of water temperature (He and Wurtsbaugh 1993; Finstad 2005), which generally cannot be altered by natural resource managers in order to slow the metabolism of piscivorous hatchery fish. That leaves the terms $\widehat{N}$ and $\widehat{p}$ as the means by which managers can alter the number of subyearlings consumed by hatchery fish. For management purposes, it may useful to think of these terms as independent (prey dependent; Abrams and Ginzburg 2000) and to take management actions that address the predation rate and the potential predator population separately. However, in some extreme or rare cases the two terms may not be completely independent. An example would be when the amount of subyearlings consumed is great enough to reduce prey density (predator dependent or ratio dependent; Abrams and Ginzburg 2000) to the extent that the encounter rate of predator and prey is reduced, causing a decline in the predation rate.

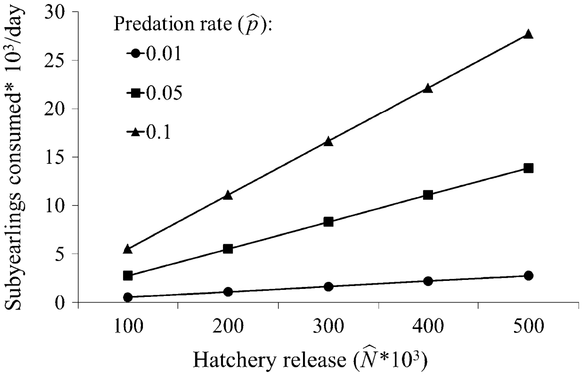

Fig. 3 Subyearling salmonids consumed by yearling hatchery salmonids for different release numbers and predation rates in 1 day. Assumptions for this model were; 15 h of feeding time ($\widehat{h}$); a water temperature of 10°C; and the gastric evacuation model $\widehat{t} = 56.2e^{-0.073T}$ for 95% evacuation of salmonid prey from brown trout developed by He and Wurtsbaugh (1993) where T is water temperature in degrees Celsius

Managing the predator population

Large hatchery releases ($\widehat{N}$) can lead to large estimates of the numbers of subyearling salmonid prey consumed for a given predation rate (Fig. 3; Sholes and Hallock 1979). In river systems where wild fish occur at very low abundances, even low predation rates (< 0.011) when combined with the release of large numbers of hatchery yearlings (> 0.25 M) may result in the loss of a high proportion of the number of wild subyearling salmonids produced. Reducing the number of hatchery fish released can decrease the estimated number of subyearlings consumed for a given predation rate (Fig. 3). This is a very effective means to reduce the number of subyearlings consumed by hatchery fish and requires little change to the current management scheme for a hatchery program, other than releasing fewer fish. This will also reduce costs for a hatchery program.

Residualism of yearling hatchery smolts occurs when the smolts fail to migrate by early or mid-June of the same calendar year in which the smolts were released (Viola and Schuck 1995; Simpson et al. 2009). Releasing hatchery fish that are ready to smolt upon release can reduce the number of subyearlings consumed. This will effectively reduce $\widehat{N}$ on any given day by decreasing the amount of time that potential predators are in the freshwater environment, thereby reducing the duration of ecological interactions between hatchery and wild fish (Kostow 2009). For hatchery steelhead, the preferred size at release is approximately 200 mm with a Fulton's condition factor slightly less than 1.0 (Tipping et al. 1995). At this size, the hatchery steelhead will be large enough to be physiologically capable of smolting (Chrisp and Bjornn 1978), but not so large as to cause higher than normal rates of residualism (Viola and Schuck 1995).

Managing the predation rate

Reducing the estimated predation rate, $\widehat{p}$, in Eq. 1 is an effective means to reduce the number of subyearlings consumed by hatchery yearlings. Managers can reduce the predation rate by altering the degree of spatial and temporal overlap of hatchery yearlings with prospective prey. Such changes can alter the size differential between predator and prey, mobility differences between predator and prey, and contact rate between predator and prey. Mather (1998) concluded that predation has a greater effect on salmonids when prey are of a size that predators can easily consume, and predator and prey overlap in time and space.

Because yearling hatchery salmonids can consume salmonid prey up to approximately 45% of their body length (Pearsons and Fritts 1999), virtually all wild subyearling salmonids are susceptible to predation by yearling hatchery salmonids based on body length. However, as the difference in size between predator and prey decreases, the predation rate will also decrease (Christensen 1996; Lundvall et al. 1999). For a predator that is not limited by gape size, one likely mechanism for this trend is due to a shrinking difference in mobility (as measured by swimming speed) between predator and prey as prey size increases (Christensen 1996). The predation rate will be much greater for 30 mm prey than it will be for 60 mm prey, because the 60 mm prey has a much greater swimming speed than the 30 mm prey, reducing the value of the prey to the predator by increasing the cost of capture and handling (Gill 2003).

Another important factor influencing the predation rate is prey density. Prey density affects the encounter rate of predator and prey (Abrams and Ginzburg 2000; Turesson and Brönmark 2007), thereby influencing the predation rate. In general, subyearling salmonids can be found at highest densities near locations where adults build redds, decreasing in density as distance from redds increases (Richards and Cernera 1989; Beall et al. 1994). Densities of subyearling salmonids also tend to be greater earlier in the spring before they emigrate (March and April) than later in the spring after most have emigrated (May and June). The contact rate of predator and prey can also be influenced by abiotic factors like turbidity (Gregory and Levings 1998; Robertis et al. 2003; Turesson and Brönmark 2007) and habitat complexity (Crowder and Cooper 1982; Lundvall et al. 1999; Anderson 2001), which usually cannot be altered by managers.

An effective means for managers to take advantage of the trend toward a decreasing predation rate with increasing prey size is to release hatchery fish after prey have had time to grow to a larger size (≥ 60 mm) or emigrate; for salmonids that emerge from gravels in the winter and early spring, this generally means releasing hatchery fish after May 1. Simpson et al. (2009) found that hatchery steelhead smolts released in mid-April consumed significantly more subyearling salmonids than those released in May. For potential prey species like wild steelhead that emerge from spawning gravels in April and May, reducing the spatial overlap of predator and prey may be the most effective way to reduce the predation rate. Hatchery programs should avoid releasing fish near areas where adults congregate to build redds (reduces spatial overlap), unless the date of release for hatchery fish occurs after the majority of wild subyearling salmonids have emigrated, resulting in a low prey density (reduces temporal overlap). Either temporal or spatial overlap must be minimized in order to achieve a low predation rate, but not necessarily both.

Conclusion

We believe that there is enough evidence to assume that at least a low level of predation occurs for all yearling hatchery releases (≥ 0.001 subyearlings/hatchery fish). An important consideration for managers is the fact that when low predation rates, which likely occur in virtually any setting, are coupled with large quantities of hatchery yearlings, substantial numbers of wild subyearling salmonids can be consumed. This is especially important to consider when the prey are rare or occur at low abundances because predation by hatchery yearlings could account for a significant proportion of the total number of wild subyearling salmonids produced.

Differences in water temperatures between the Trinity River and the Western Washington rivers, which can affect metabolism of predators, were unlikely to be great enough to have caused the large observed differences in predation rates. Both studies occurred in temperate regions in the spring months when water temperatures are neither excessively cold nor warm. We are not aware of a plentiful and preferred food item in the Western Washington rivers that occurs at high enough densities to make comparison of the subyearling salmonid predation rates between the two studies invalid.

The major difference between the two studies we examined in detail was the timing of release (Figs. 1 and 2). Similarly, Simpson et al. (2009) found a significantly greater predation rate for yearling hatchery steelhead smolts released in mid-April (0.41 subyearlings/hatchery fish) than those released in May (0.03 and 0.07 subyearlings/hatchery fish). Simpson et al. (2009) concluded that the hatchery steelhead released earlier in the study (mid-April) had access to large quantities of small and vulnerable subyearling salmonids. In the Trinity River study where a high predation rate was documented, hatchery steelhead were released on 15 March, roughly 45 d earlier than in the western Washington Rivers where a low predation rate was documented. The early release date on the Trinity River, combined with a release location adjacent to several thousand redds, resulted in hatchery steelhead encountering high densities of small and vulnerable prey. In the study of rivers in western Washington, most subyearlings had emigrated or grown large enough to limit their susceptibility to predation at the time hatchery steelhead were released. We suggest that fisheries managers use segregation of potential predators and prey, through limiting either their spatial or temporal overlap, in order to reduce the predation rate. Where appropriate, managers should also consider reducing the number of potential predators released into river systems, particularly where wild salmonid prey occur in low numbers.

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