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Abstract

We conducted a literature review on predation by juvenile hatchery salmonids on naturally-produced salmonid fry in the western United States. The review included 12 studies from the Pacific Northwest and California. In most instances, predation by hatchery fish on naturally-produced fry 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 110,659 fry 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 fry 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 fry had migrated by the time hatchery steelhead were planted and most were small enough to remain highly vulnerable to predation. Unknown is the extent to which low predation rates, which likely occur in most places hatchery steelhead are released, might still negatively impact prey populations that are at low abundance because of other anthropogenic factors.

Predation by juvenile hatchery salmonids on naturally produced salmonids in the freshwater environment: A review of studies, two case histories, and implications for management

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Introduction

Although several researchers have concluded that predation can influence the populations of anadromous salmonids (Mather 1998), little is known about the extent to which hatchery salmonids prey upon naturally produced salmonids. 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 naturally produced salmonids (e.g. Pollard and Bjornn 1973, McMichael et al. 1997, Kostow and Zhou 2006), but predation by hatchery salmonids on naturally produced salmonids remains virtually undocumented in the peer-reviewed literature. Several studies have examined predation by naturally produced salmonids on naturally produced salmonids (e.g. Ruggerone and Rogers 1992, Beauchamp 1995), and others have investigated smallmouth bass predation on salmonids (e.g. Fritts and Pearsons 2004, Naughton et al. 2004). A single study on the Lewis River in western Washington by Hawkins and Tipping (1999) addressed predation by hatchery salmonids on naturally produced 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 fry consumed have reported relatively low numbers (e.g. Cannamela 1993).

This paper will focus on predation by yearling hatchery salmonids on wild salmonid prey in the freshwater environment. Virtually nothing is known about the extent to which hatchery salmonids prey upon wild salmonids in the ocean. Although few studies have examined predation by hatchery adult salmonids on wild fry, if large numbers of hatchery adult steelhead congregate in areas of high wild fry concentrations, it is conceivable that a substantial number of fry could be consumed. However we consider this possibility to be rare and limited to a few specific cases. Vander Haegen et al. (1998) found that 1,041 hatchery adult steelhead consumed 4 salmonid fry (0.004 fry/hatchery fish). This low predation rate is similar to the low predation rates we found in many of the studies on juvenile hatchery salmonid predation that we reviewed. However, because numbers of returning adult steelhead are generally one or two orders of magnitude lower than the number of juveniles released, the amount of fry consumed by adult hatchery steelhead is likely, in most cases, to be negligible in terms of the overall impact to the wild population.

Spatial and temporal overlap of predator and prey can be among the most important factors influencing predation on salmonids (Mather 1998). Predator density and prey density are also important controls on predation (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. It is important for natural resource managers to understand the ecological context in which a particular hatchery operates, and the factors that influence the amount of predation by yearling hatchery salmonids on wild salmonid fry. If measures are employed to minimize or eliminate the factors which lead to or exacerbate predation, releases of hatchery yearlings should not, in most cases, cause excessive loss of wild salmonid fry.

Literature review

We reviewed 12 studies on predation by anadromous hatchery salmonids on wild anadromous prey (Table 1). Other than the research performed by Hawkins and Tipping (1999), all of the documents were contract reports or other forms of grey literature and had not been published at the time of this review. All of the studies examined predation by yearling hatchery steelhead except the study by McConnaughey (1999), which examined predation by yearling coho salmon on wild salmonid fry.

Most of the studies documented at least a low level of predation (≥ 0.001 fry/hatchery fish). The studies that reported no predation by hatchery fish had much smaller sample sizes 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 fry/hatchery fish) in virtually all river systems in which yearling salmonids are released. Very large sample sizes (in the thousands) are 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 authors 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 fry 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 fry/hatchery fish) by Sharpe et al. (2008), and one with a relatively high level of predation (0.539 fry/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 fry were known to be offspring of adults, hatchery and wild, that spawned naturally in a river system because no sub-yearling 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 available as prey were all of natural origin in the Coweeman and Kalama rivers but included both hatchery- and natural-origin fry in the Deschutes and Green rivers.

Western Washington Rivers

Between 2003 and 2005 Sharpe et al. (2008) studied juvenile steelhead predation on Chinook salmon fry using stomach content analysis. Juvenile 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. Salmonid fry or parts thereof in the gut were identified to species. Of 6,029 hatchery steelhead examined, 10 fall Chinook salmon fry had recently been consumed (0.002 fry/stomach). The range of observed predation across the various release groups of hatchery steelhead was 0 and 0.01 fry/steelhead stomach with considerable variation in the incidence of predation between streams and years. On average, the work suggested that 0.6% of total juvenile 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 fry had emigrated (Figure 1) and after fry had grown large enough reduce or eliminate their susceptibility to predation. The average size of Chinook salmon fry 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 with negligible predation by migrating hatchery steelhead on fall Chinook salmon fry.

Insert Figure 1

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 2,302 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, unpublished 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, unpublished 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, unpublished 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). Of 1,636 hatchery steelhead examined, 882 had recently consumed salmonid fry. Naman (2008) estimated that approximately 111,000 Chinook salmon and coho salmon fry 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 fry produced in the study reach. However, additional fry would have been consumed before and after the study period, and by the juvenile 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 fry had emigrated (Figure 2) and before fry had grown large enough reduce or eliminate their susceptibility to predation. The average size of Chinook salmon and coho salmon fry 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 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.

Insert Figure 2

Predation mechanisms

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

$$\hat{F} = \hat{N} \cdot \hat{p} \cdot \frac{\hat{h}}{\hat{t}}, \qquad (1)$$

where $\hat{N}$ is the estimated population of hatchery juveniles, $\hat{p}$ is the estimated predation rate of the hatchery juveniles (number of fry consumed/number of hatchery juveniles), $\hat{h}$ is the estimated number of feeding hours in a day (using 24 assumes continual feeding throughout the day and night), and $\hat{t}$ 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 fry consumed during a certain period of study.

Figure 3 depicts the number of fry consumed by juvenile hatchery salmonids for different release numbers and predation rates. Assumptions in Figure 3 were; 15 hours of feeding time ($\hat{h}$); and a water temperature of 10°C with the gastric evacuation equation $\hat{t} = 56.2e^{-0.073T}$ for 95% evacuation of salmonid prey from brown trout developed by He and Wurtsbaugh (1991) 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 3,000 consumed fry in a single day. Fewer and fewer fry would be consumed in successive days as the number of hatchery juveniles decreases as they emigrate or perish. However, large numbers of fry can be consumed in a single day when moderately high predation rates (≥ 0.05 fry/hatchery fish) are combined with the release of large numbers of hatchery fish (≥ 0.2 M; Figure 3). For example, using the assumptions of temperature and gastric evacuation mentioned above, a predation rate of 0.05 fry/hatchery fish and a release of 0.5 M hatchery fish would result in 13,846 fry being consumed in a single day.

Insert Fig. 3

The term $\frac{\hat{h}}{\hat{t}}$ 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 1991; 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 $\hat{N}$ and $\hat{p}$ as the means by which managers can alter the number of fry 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 fry 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.

Managing the predator population

Clearly, decreasing $\hat{N}$, the estimated population of hatchery juveniles, will decrease the estimated number of fry consumed for a given predation rate (Figure 3). This is a very effective means to reduce the number of fry 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.

Although Naman (2008) found no difference in the estimated predation rate of smolting and non-smolting steelhead, releasing hatchery fish that are ready to smolt upon release can reduce the number of fry consumed. This will effectively reduce $\hat{N}$ 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, $\hat{p}$, in equation 1 is an effective means to reduce the number of fry consumed by hatchery juveniles. The means by which managers can reduce the predation rate is to reduce the degree of spatial *or* temporal overlap of predator and prey. For a hatchery salmonid to prey upon a wild salmonid fry, predator and prey must overlap in *both* time and space. For example, a hatchery that releases fish near redd sites may seem to be at risk of having a high predation rate based on release location, but if the date of release of hatchery fish occurs after most wild juveniles have emigrated, the predation rate will be low. There are several factors influencing the predation rate that can change with release timing and release location, including the contact rate of predator and prey, size differential between predator and prey, and the difference in mobility (swimming speed) of 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. However, in river systems where wild fish occur at very low abundances, even low predation rates (< 0.01) when combined with the release of large numbers of hatchery yearlings (> 250,000) can result in the loss of a high proportion of the number of wild fry produced.

Because yearling hatchery salmonids can consume salmonid prey up to approximately 45% of their body length (Pearsons and Fritts 1999), virtually all wild fry and subyearling juveniles are susceptible to predation by yearling juvenile 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). Using the reasoning outlined above, we feel that releases of sub-yearling hatchery fish, such as subyearling Chinook salmon, are not likely to be at risk of having a high predation rate, if any, because salmonid fry would be far from the optimum prey size, if the sub-yearling hatchery fish were not completely limited by gape size (Gill 2003).

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 (≥ 60mm), or emigrate; for salmonids that emerge from gravels in the winter and early spring, this generally means releasing hatchery fish after May 1. For potential prey species like steelhead that emerge from spawning gravels in April and May, reducing the temporal overlap of predator and prey may not be feasible. Therefore, providing spatial segregation of predator and prey by releasing hatchery steelhead downstream from areas of high fry concentration is likely to be a more effective way to reduce the predation rate.

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, salmonid fry 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). In order to maintain a low 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 fry 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.

Abiotic Factors

Turbidity is one of the foremost abiotic factors that can influence the predation rate of piscivores (Gregory and Levings 1998; Robertis et al. 2003; Turesson and Brönmark 2007). Increased levels of turbidity reduce prey detection distance and thereby search efficiency, leading to a lower prey encounter rate and a lower predation rate (Turesson and Brönmark 2007). Hatchery programs that release yearlings in river systems with low turbidity (≤ 6 nephelometric turbidity units; Gregory and Levings 1998;

Robertis et al. 2003) are expected to have a significantly greater predation rate, other factors being similar, than those that release fish in very turbid river systems (≥ 27 nephelometric turbidity units; Gregory and Levings 1998). Turbidity is generally not a factor that can be manipulated by fisheries managers, but understanding how turbidity effects the predation rate of hatchery yearlings on wild fry can help managers assess the risks posed by a given hatchery program. If release of hatchery yearlings can occur during a time of high spring discharge when turbidity is higher than normal, this should aid in minimizing the predation rate.

Another important abiotic factor that can influence the predation rate of hatchery salmonids on wild salmonids is habitat complexity and the amount of escape cover available to prey (Crowder and Cooper 1982; Lundvall et al. 1999; Anderson 2001). Hatcheries often release fish into river systems with compromised habitat conditions because hatcheries are meant to serve as replacement for reduce salmonid production due to lost or diminished habitat quality (NRC 1996). Reductions in habitat quantity or quality are expected to exacerbate the problem of predation by hatchery juveniles by reducing the quantity of prey refuges, thereby increasing the success rate of predator attacks or increasing the encounter rate of predator and prey, either of which can increase the predation rate.

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 fry/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 fish, substantial numbers of salmonid fry 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 fry produced. The major difference between two studies we examined was the timing of release (Figures 1 and 2). 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 fry 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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Tables

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

Citation	Sample size	Fry ingested (n)	Fry/hatchery fish
Beauchamp 1995	18	0	0.000
Harper 1999	59	0	0.000
Pearsons et al. 1994	55	0	0.000
Canamella 1993	6,762	10	0.001
Sharpe et al. 2008	6,029	10	0.002
Martin et al. 1993	1,713	3	0.002
McConnaughey 1999	11,127	25	0.002
Jonasson et al. 1994	358	1	0.003
Jonasson et al. 1995	175	2	0.011
Whitesel et al. 1993	611	8	0.013
Hawkins and Tipping	232	57	0.246
Naman 2008	1,636	882	0.539

Figure captions

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)

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)

Fig. 3 Fry consumed by juvenile hatchery salmonids for different release numbers and predation rates in one day. Assumptions for this model were; 15 hours of feeding time (H); a water temperature of 10°C; and the gastric evacuation model $\hat{t} = 56.2e^{-0.073T}$ for 95% evacuation of salmonid prey from brown trout developed by He and Wurtsbaugh (1991) where T is water temperature in degrees Celsius.

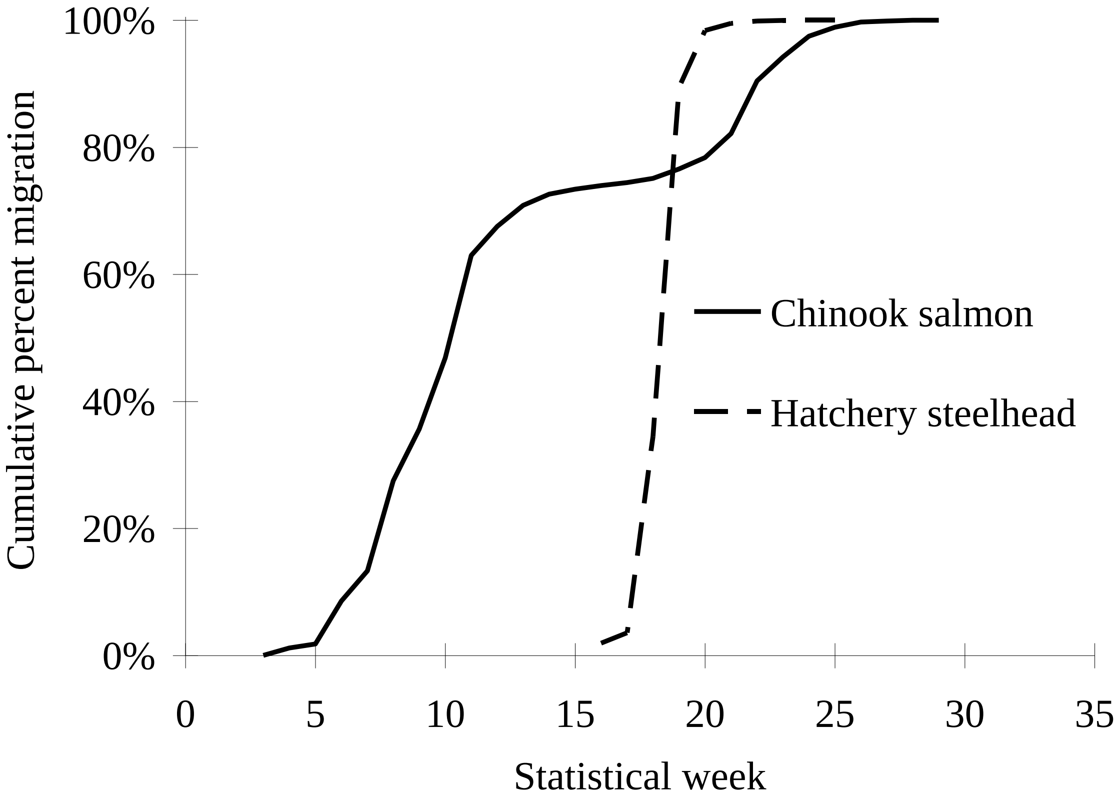
100%
80%
60%
40%
20%
0%
Cumulative percent migration
0
5
10
15
20
25
30
35
Statistical week
Chinook salmon
Hatchery steelhead

Fig. 1

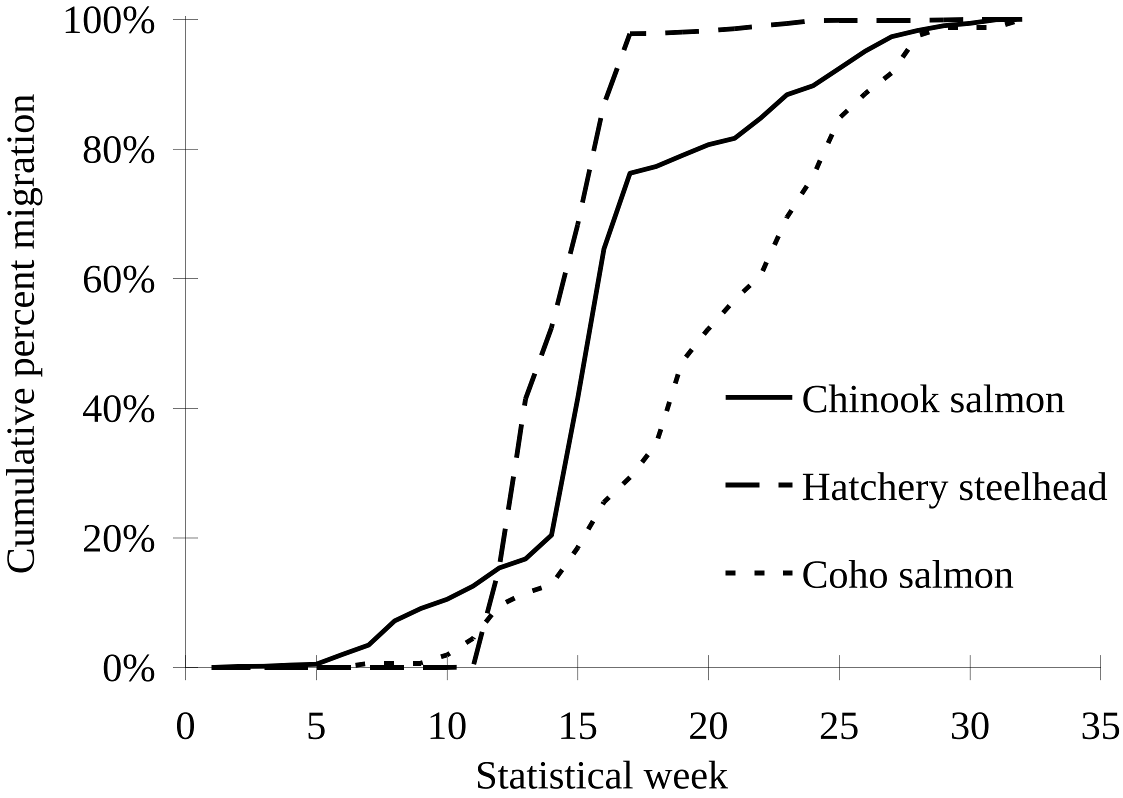
100%
80%
60%
40%
20%
0%
Cumulative percent migration
0
5
10
15
20
25
30
35
Statistical week
Chinook salmon
Hatchery steelhead
Coho salmon

Fig. 2

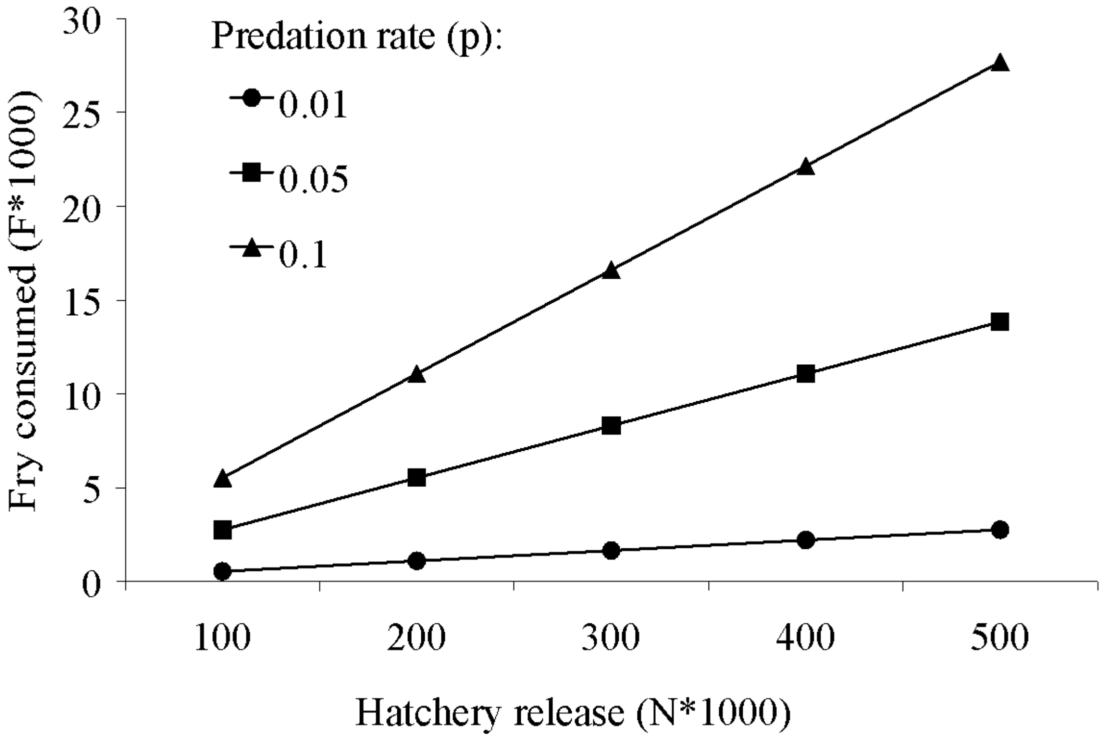
Predation rate (p):
0.01
0.05
0.1
Fry consumed (F*1000)
0
5
10
15
20
25
30
100
200
300
400
500
Hatchery release (N*1000)

Fig. 3

Seth Naman
EBFI2156R1
Response to reviewer

All of the requested changes to the organization of the document have been made. The section on "Abiotic factors" was kept in the "Predation mechanisms" section which was moved in its entirety to the end of the document. We tried putting the "Abiotic factors" section into the Introduction as requested, but it seemed out of place and was moved back. Additional text was added to the introduction section to bolster it.