Mechanisms influencing competition between hatchery and wild juvenile anadromous Pacific salmonids in fresh water and their relative competitive abilities

Christopher P. Tatara · Barry A. Berejikian

Abstract Avoiding negative effects of competition from released hatchery salmonids on wild fish is a primary concern for recovery efforts and fisheries management. Several factors affect competition among juvenile salmonids including: (1) whether competition is intra- or interspecific, (2) duration of freshwater cohabitation of hatchery and wild fish, (3) relative body size, (4) prior residence, (5) environmentally induced developmental differences, and (6) fish density. Intraspecific competition is expected to be greater than interspecific because of greater niche overlap between conspecific hatchery and wild fish. Competition is expected to increase with prolonged freshwater cohabitation. Hatchery smolts are often larger than wild, and larger fish are usually superior competitors. However, wild fish have the advantage of prior residence when defending territories and resources in natural streams. Hatchery-induced developmental differences are variable and can favor both hatchery and wild fish. Although all these factors influence competitive interactions, fish density of the composite population (wild + hatchery fish) in relation to habitat carrying capacity likely exerts the greatest influence. The extent of competition and relative competitive ability of wild and hatchery fish can be determined by additive and substitutive experimental designs, respectively, and the limited body of substitutive experiments suggests that the relative competitive ability of hatchery and wild fish is approximately equal when measured as growth. Conducting substitutive experiments becomes difficult as the spatial and temporal scales increase. Large-scale experiments comparing supplemented and control reaches or streams hold some promise for quantifying the effects of released hatchery fish on wild fish behavior, growth and survival.

Keywords Competition · Hatchery and wild · Pacific salmonids · Freshwater life stage · Relative competitive ability

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Introduction

The production of anadromous Pacific salmonids in hatcheries for both harvest augmentation and, more recently, conservation and rebuilding of depressed populations has created conditions where hatchery and wild populations interact at life stages ranging from parr to spawning adults, and habitats ranging from freshwater tributaries to open oceans. Of all the potential interactions between hatchery and wild salmonids, competition uniquely and regularly occurs at all life stages and associated habitats, thus raising concerns about the impact of hatchery fish on the

management and recovery of wild salmon populations. Competition among juvenile salmonids primarily occurs during the time period spanning emergence until smoltification and seaward migration, and takes place in freshwater habitats ranging from tributaries to higher order rivers.

Competition occurs when multiple organisms exploit a common limited resource and the fitness of at least one is reduced (Birch 1957). Low productivity and loss of freshwater rearing habitat have been identified as factors limiting the recovery of wild salmon populations (McClure et al. 2008; Morita et al. 2009) and as reasons for initiating hatchery salmon populations (Hilborn 1992). The greater relative productivity of ocean habitat compared to freshwater systems is a major evolutionary pressure driving anadromy in salmonids (Gross et al. 1988). Competition in juvenile salmonids occurs through agonistic contests (interference competition) and through depletion of resources (exploitative competition). In freshwater streams, resource limitations coupled with high hatchery fish densities following release suggest competition may strongly affect wild fish during juvenile life stages and constitute an important determinant of lifetime fitness.

Numerous studies have documented effects of competition between hatchery and wild juvenile salmonids. Recent reviews have synthesized much of the existing knowledge of competition between hatchery and wild fish across the entire family Salmonidae (Einum and Fleming 2001; Weber and Fausch 2003; Kostow 2009). Our paper considers only competition that occurs between hatchery and wild anadromous Pacific salmonids from the time the hatchery fish are released until their seaward migration as smolts. The intent is to review evidence for key mechanisms that may influence relative competitive ability of hatchery and wild fish and highlight approaches that show promise to separate the hatchery rearing effects from density-dependent processes.

Indicators of competition for juvenile Pacific salmonids include agonistic behavior (Peery and Bjornn 1996; Riley et al. 2005, 2009a), feeding behavior (Riley et al. 2005, 2009a), growth (Peery and Bjornn 1996; Weber and Fausch 2005; Yamamoto et al. 2008), and survival (Weber and Fausch 2005). Because competition ultimately results in a reduction of fitness for at least one of the competing populations of organisms, it makes sense to select experimental or

assessment endpoints most closely associated with fitness (Fig. 1). The strength of correlation between indicators of competition and fitness impacts varies, and reflects tradeoffs between establishing evidence of competition and its consequences for fitness. Measurements of agonistic behavior or habitat use provide evidence that competition is occurring but may reflect transient effects, making it difficult to extrapolate their fitness consequences. Experiments that demonstrate displacement from energetically profitable stream micro-habitats or differential rates of food consumption should more strongly reflect impacts on fitness. Measured differences in growth rates between competing populations are likely to have a strong correlation with fitness. Finally, demonstrating differential survival between competing populations directly measures fitness consequences of competition, but it may be more difficult to design experiments powerful enough to detect such consequences.

Mechanisms affecting competition between hatchery and wild salmonids can be loosely categorized as (1) 'population factors' that affect groups of competing individuals, and (2) 'individual factors' that are properties of competing individuals (Fig. 2). Population factors include whether competition occurs between members of the same species (intraspecific competition) or different species (interspecific competition), the duration of cohabitation in a common environment, and the population density. Individual factors include relative body size of competitors, effects of rearing environment (hatcheries) on behavioral development, and the advantage of prior
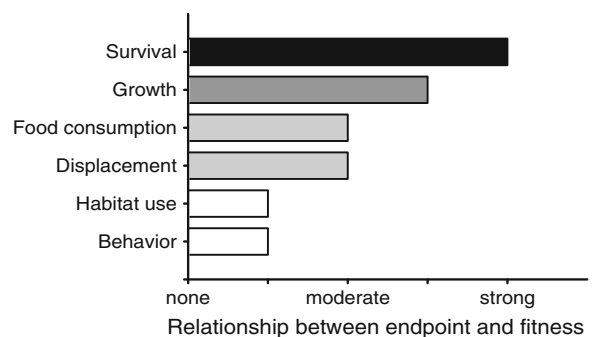
Fig. 1 Relative relationship to fitness of several common experimental endpoints of competition experiments reported for juvenile salmonids. Endpoints with a strong relationship to fitness are preferred over those with weaker relationships

Factors affecting competition
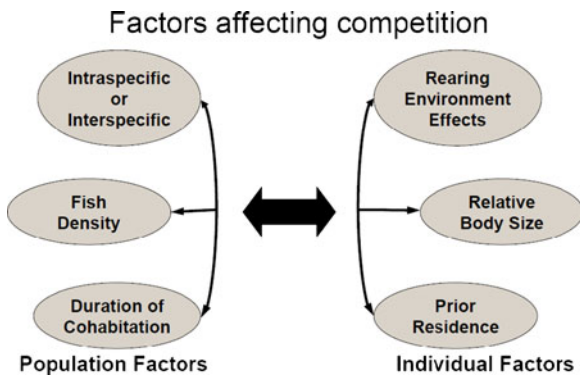
Fig. 2 Six primary factors affecting competition between hatchery and wild juvenile salmonids. Factors labeled as "Population Factors" (left side of figure) affect groups of competing individuals, while those labeled "Individual Factors" (right side of figure) are properties of competing individuals. The arrows indicate that multiple factors within and between groups can interact to influence competition

residence. Although we have categorized the factors, and discuss them singly, it is important to recognize that multiple factors can act simultaneously to affect the outcome of competition.

In this paper, we first discuss six primary factors influencing competition between hatchery and wild juvenile salmon and whether each factor either favors wild or hatchery fish during competition. Next, we discuss different experimental designs for studying competition. Finally, we estimate the relative competitive ability of juvenile hatchery salmon by summarizing results of published substitutive competition experiments. Where competition data is limited for Pacific salmonids our review includes data reported for anadromous salmonids from other regions (e.g., charrs (*Salvelinus spp.*) and Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*).

Population factors influencing competition

Interspecific versus intraspecific competition

Competition between species (interspecific) in native assemblages of anadromous salmonids is minimized because the species occupy somewhat different ecological niches (habitats within a common river system) either spatially or temporally (Hearn 1987; Quinn 2005). Several studies have documented spatial habitat segregation in Pacific salmonids. For example, Bisson

et al. (1988) demonstrated that when juvenile coho salmon (*Oncorhynchus kisutch*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarkii*) co-occur they use habitat differently and that channel hydraulics (flow and depth) and body morphology determine the habitat preferences of each species. Similarly, Yamamoto et al. (2010) found that white spotted charr (*S. leucomaenis*) were found exclusively in upstream reaches while masu salmon (*O. masou*) were found in the middle and downstream sections of the same Japanese stream. The previous studies document niche segregation among species in salmonid populations where the influence of hatchery fish was minimal. In cases where the in-stream location and distribution of wild Chinook salmon (*O. tshawytscha*), coho salmon, steelhead, and cutthroat trout were monitored before and after small-scale releases of hatchery Chinook and coho salmon, few if any changes in wild fish density, group size, microhabitat use, and size were observed (Riley et al. 2004), suggesting the ecological niche of wild fish did not change when hatchery fish were released and low potential for interspecific competition.

Among-species diversity in traits such as spawn timing and outmigration timing can act to temporally segregate salmonid species within the same river. A classic example of temporal separation within a river is the spawning and juvenile residence patterns of Pacific salmon (Chinook) species in the fall, and steelhead spawning in the winter and spring (Brannon et al. 2004). When the ecological niches of different salmonid species overlap, intrinsic differences in competitive ability among species may influence the outcome of competition as demonstrated with experimental pairwise contests among four species of wild salmonids (Hasegawa et al. 2004). Most experiments using pairwise comparisons of salmonid species are conducted using introduced and native species, but the same type of experiments could be conducted using the species comprising native anadromous salmonid assemblages. Because both species and effects of hatchery rearing can influence interspecific competition among hatchery and wild salmonids, it is difficult to generalize whether hatchery or wild fish would be favored.

Hatchery salmonids released into streams commonly share habitat preferences with wild conspecifics, and consequently have greater potential for niche overlap than would be seen for heterospecifics. Hatchery steelhead parr released into replicated fenced stream

sections exhibited similar habitat preference as natural fish (Tatara et al. 2009), held similarly sized territories, exhibited similar relationships between body size and territory size, and similar rates of aggression, feeding, and growth (Tatara et al. 2008, 2009). In another experiment, hatchery steelhead that residualized (failed to migrate) were found in the same habitats as similar sized wild fish in three supplemented Hood Canal (Washington) rivers (Berejikian et al. 2011). In an in-stream enclosure experiment residual hatchery steelhead significantly reduced the growth of wild rainbow trout (*O. mykiss*), but not the growth of Chinook salmon, suggesting greater intensity of intraspecific competition (McMichael et al. 1997). Finally, Hill et al. (2006) found that hatchery and wild steelhead smolts in Abernathy Creek (Washington) exhibited similar microhabitat use, but did not displace wild fish. Collectively, these studies indicate that the effects of intraspecific competition are greater than those of interspecific and are likely attributable to niche overlap. Whether hatchery or wild fish are favored during intraspecific competition depends on fish density and habitat carrying capacity, relative body size, hatchery effects on behavioral development, and prior residence.

Duration of freshwater cohabitation

The intensity and frequency of competition between hatchery and wild anadromous salmonids is expected to increase with the duration of freshwater cohabitation. This is especially relevant as hatchery stocking usually occurs after natural juvenile salmonid populations have completed a "critical period" (Elliott 1989, 1990) where their numbers have been reduced through competition. Stocking after the "critical period" could effectively reset the clock for density-dependent mortality. The two factors that determine the duration of cohabitation are species-specific differences in age of seaward migration (Randall et al. 1987; Kato 1991; Fig. 3), and the life stage at which hatchery fish are released. The freshwater life history stages of several species of Pacific salmon [Chinook, coho, sockeye (*O. nerka*), and masu] and steelhead can last up to several years, but is most commonly less than two years for salmon and three years for steelhead trout. Pink (*O. gorbushca*) and chum (*O. keta*) salmon freshwater residence is limited to incubation, emergence, and nearly immediate

seaward migration. Wild fish of species with prolonged freshwater life histories are at greater risk for competition with hatchery fish because multiple cohorts of wild fish will likely be present when hatchery fish are released (Fig. 3).

Almost all species of hatchery-reared anadromous Pacific salmonids are grown at an accelerated rate and released as yearling smolts, with the intent for most smolts to quickly migrate to the ocean soon after release, minimizing the duration that hatchery and wild fish would cohabitate in freshwater. However, some hatchery programs for sockeye (Hebdon et al. 2004), coho (Theriault et al. 2010), and steelhead (Hume and Parkinson 1987; Close and Anderson 1992) release hatchery fish at the parr stage in part to avoid possible developmental deficits attributed to hatchery environments. Hatchery programs for pink (Boldt and Haldorson 2004) and chum salmon (Reese et al. 2009; Small et al. 2009) almost exclusively release juveniles at the parr life history stage. Additionally, juvenile steelhead and Chinook salmon released from some hatchery programs as yearlings may residualize in freshwater and either mature precociously (Chinook salmon), or undergo smoltification and migrate a year later (steelhead: Viola and Schuck 1995; see Berejikian et al. 2011, for the role of residualism on ecological interactions). Hatchery parr and smolts that residualize will likely extend the duration of freshwater cohabitation and potential for competitive effects on wild fish.

Population density of competitors

Arguably, the most important factor determining the effects of both intra- and interspecific competition between wild and hatchery Pacific salmonids is the density of the composite population (wild plus hatchery fish) in relation to the carrying capacity of the habitat. Size of emergent salmonid fry populations varies to some degree with the number of successfully reproducing adults and may exceed the carrying capacity of rearing habitat, resulting in survival rates that are negatively density-dependent during the months immediately after hatching (Elliott 1989, 1990). After this initial critical period a process referred to as "self-thinning", where average fish size increases as population density decreases, frequently describes population dynamics of stream living salmonids (Armstrong 1997; Dunham and Vinyard

Fig. 3 Ages of seaward migration and potential for competition during the juvenile life history stage for several wild anadromous Pacific salmonid species. The most common ages of seaward migration are denoted with black shading, and less common ages with grey shading. Data on age of seaward migration adapted from Randall et al. (1987) and Kato (1991). Hatcheries frequently compress the age of seaward migration to one year

Species	Age at seaward migration					Potential for competition
	0	1	2	3	4	
Pink	■					Low
Chum	■					Low
Chinook	■	■	▨			High
Coho	▨	■	■	▨		High
Sockeye	▨	■	■	▨		High
Masu		■	■	▨		High
Steelhead		▨	■	■	▨	High

1997; Keeley 2003). Self-thinning can be driven by several underlying mechanisms including space limitations, metabolic rate, or food consumption, but distinguishing which factor(s) drives the process in any one particular situation is difficult, even in experimental situations (Keeley 2003).

Released hatchery fish may increase density-dependent mortality of wild fish by increasing total salmonid density above stream carrying capacity during food- or habitat-limited periods (e.g., in summer, after the initial critical period). Effects of elevated temperature and low flow on growth and mortality have been demonstrated for stream dwelling salmonids which typically occur during the late summer (Ovidio et al. 2008; Riley et al. 2009b; Xu et al. 2010). A review of growth in stream-dwelling salmonids (including several Pacific salmonid populations) found evidence of density dependence in fifteen of nineteen populations (Grant and Imre 2005). Ten of the populations displayed reductions in growth rate at fish densities <1 fish/m^2, where space limitations of the habitat were unlikely, suggesting exploitative competition for limited food resources and not interference competition (Grant and Imre 2005; but see Ward et al. 2007). Strong evidence for intraspecific competition comes from studies manipulating stocking densities of juvenile sockeye salmon in Alaskan lakes (Koenings and Burkett 1987). The smolt biomass and average smolt size of age-1 and age-2 smolts decreased as stocking density increased. Fish density has also been shown to affect interspecific competition. Harvey and Nakamoto (1996) stocked enclosures in two California creeks with juvenile coho salmon and either no juvenile steelhead (control), steelhead at their natural density, and steelhead at twice the natural density, and found that weight loss of juvenile coho increased as the density of juvenile steelhead increased. Determining how stocking density favors either wild or hatchery fish during competition would depend on whether carrying capacity was exceeded and the proportion of each type of fish in the composite population.

Individual factors influencing competition

Relative body size of competitors

The effect of body size on competitive ability has been investigated for both intraspecific (Abbott et al. 1985; Pettersson et al. 1996) and interspecific (Sabo and Pauley 1997; Young 2004) competition in Pacific salmonid species. Generally, larger fish dominate intraspecific agonistic pairwise contests (Abbott et al. 1985; Rhodes and Quinn 1998), with size differences of approximately five percent (body weight) sufficient to ensure dominance in the larger fish. However, as the group size of competing individuals increases, the competitive advantage of large body size in establishing dominance declines (Pettersson et al. 1996), suggesting that body size differences between hatchery and wild fish may become a less important factor governing competition as the stocking density of hatchery fish increases. Most hatchery programs grow large smolts to maximize their post-release survival (Holtby et al. 1990; Henderson and

Cass 1991; Tipping 1997; Miyakoshi et al. 2001), resulting in hatchery fish size that are nearly always larger than wild fish (Miyakoshi et al. 1998; Hill et al. 2006; Larsen et al. 2006; Kostow 2009). Thus, the larger size of hatchery fish likely provides a significant competitive advantage over wild fish in dyadic contests for territories throughout streams in the Pacific Northwestern United States, especially for hatchery fish released as parr, or for hatchery smolts that residualize (i.e., fail to migrate).

Determining the effects of body size on interspecific agonistic contests is complicated by interspecific differences in competitive ability (Hasegawa et al. 2004). Natural size differences between competing species can influence niche partitioning (Young 2004) and competitive ability (Sabo and Pauley 1997). However, size is not an absolute determinant of dominance in interspecific contests; brown trout (*Salmo trutta*) and rainbow trout were superior competitors to native white-spotted charr even when they were smaller than the charr (Hasegawa et al. 2004). Similarly, interactions between relative body size and species specific aggression have been demonstrated for cutthroat trout and coho salmon (Sabo and Pauley 1997). Young (2004) conducted an experiment manipulating both size differences between coho salmon and steelhead and stocking density. When these two species occur together, the coho salmon are often larger than steelhead and competitively superior. Maintaining this natural size advantage resulted in habitat selection by both species that was primarily dependent on coho density. Removing the size advantage of coho reduced the per capita effect on steelhead by half and produced habitat selection patterns affected similarly by intra- and interspecific competition. It is difficult to generalize how relative body size affects interspecific competition between hatchery and wild salmonids, even when the hatchery species is larger than the wild. Regardless, both intra- and interspecific competition between hatchery and wild salmonids could be minimized by releasing hatchery fish grown to a size that matches that wild population's size distribution.

Effects of rearing environment on behavioral development

In the absence of body size, prior residence, and stock differences, hatchery rearing environment can affect behavioral development and competitive ability of juvenile anadromous salmonids. Both genetic (e.g., intentional and unintentional domestication selection) and environmental (artificial hatchery rearing conditions) factors can cause hatchery populations to differ from natural populations (see reviews by Einum and Fleming 2001; Weber and Fausch 2003; Kostow 2009). Behavioral differences can initially be attributed to phenotypic responses to the unnatural abiotic and biotic environmental conditions in hatcheries, and over generations of culture may involve genetic responses as well (Einum and Fleming 2001). Levels of aggressive behavior were generally found to be greater (but not always, Kostow 2009) in hatchery fish and attributed to both environmental (high density, Weber and Fausch 2003) and genetic differences, while differences in feeding behavior were predominantly caused by the hatchery rearing environment, and resulted in poorer growth of hatchery fish upon release (Einum and Fleming 2001). Increased aggressiveness may impart a temporary competitive advantage to released hatchery fish, but may also be maladaptive because it increases the visibility of predator-naïve hatchery fish. The combined behavioral attributes of elevated aggressiveness and inefficient feeding may ultimately result in poor smolt-to adult survival of hatchery fish (Kostow 2009). These reviews are not limited to anadromous Pacific salmonids, and while they provide strong evidence that the hatchery environment can alter the behavior of hatchery fish, it is difficult to generalize whether the differences confer a competitive advantage to hatchery or wild fish because differences in behavior are not consistent among species or hatchery populations within a species, and may depend on the testing environment (laboratory versus stream, see Einum and Fleming 2001; Riley et al. 2005; Tatara et al. 2009). In short, hatchery fish have been shown to be both more and less competitive than natural-origin cohorts and competitive asymmetries may favor either hatchery or wild fish.

Advantage of prior residence

Animals that arrive first at a specific area gain a competitive advantage over later arriving individuals known as the "prior residence effect" (Archer 1987; Krebs and Davies 1987), and this holds true for juvenile salmonids with established territories.

The phenomenon of prior residence has been best described for Atlantic salmon (Huntingford and deLeaniz 1997; Metcalfe et al. 2003) and non-anadromous brown trout (Deverill et al. 1999), but has been demonstrated in Pacific salmon as well (coho salmon, Rhodes and Quinn 1998). The advantages of prior residence may derive from familiarity with the habitat, reflect cost-benefits of defending an acquired territory versus finding a new territory, or reflect dominance in prior agonistic contests (Rhodes and Quinn 1998; Huntingford and deLeaniz 1997). The benefit of prior residence can be moderated by body size, effects of rearing environment (hatchery versus wild intruder), domestication, and prior winning experience (Rhodes and Quinn 1998; Metcalfe et al. 2003). Although fish with prior residence do not always win territorial contests, prior residence will likely confer a competitive advantage to wild fish in contests with released hatchery fish because the wild fish generally occupy the habitat prior to the hatchery releases.

Experimental designs for determining relative competitive ability

A major question for the recovery and management of Pacific salmon is whether hatchery fish impart greater competitive impacts on wild fish because of their origin and rearing history that go beyond the density-dependent effects of stocking. The answer to this question is elusive despite the extensive study of competition between hatchery and wild fish, largely because of experimental design issues. Most studies of direct competition in juvenile salmonids have employed additive designs (whether explicitly stated or not) where hatchery fish are stocked with wild fish, and compared to controls without hatchery fish (Weber and Fausch 2003; Fig. 4). A distinguishing feature of additive designs is that stocking treatment densities exceed control density, thus any results reflect the combined effects of the hatchery fish properties and increased density. Additive designs answer important questions about the *effect* of stocking hatchery fish at certain fish densities in relation to a specific habitat and its carrying capacity (Fausch 1988, 1998), but they do not resolve whether or not hatchery fish, in general, are weaker, superior, or equivalent competitors as

wild fish. Alternative, substitutive experimental designs test for the relative competitive ability (RCA) of hatchery fish by disentangling hatchery fish properties from the effects of density. In substitutive experiments, the density of the control group (all wild fish) equals the density of the hatchery stocking treatment (wild and hatchery fish; Fig. 4). Interpretation of substitutive competition experiments involves making comparisons between the wild fish stocked alone (control) to wild fish stocked with hatchery fish at the same density as the control (Fig. 5). Weber and Fausch (2003) provide additional discussion on the use of additive and substitutive designs to study both intra- and inter-specific competition among salmonids.

Studies using additive experimental designs dominate the literature on competition for juvenile anadromous salmonids, making empirical estimations of the relative competitive ability of juvenile hatchery salmonids difficult. A review of competition (Weber and Fausch 2003) found only two published studies employing substitutive designs, and an additional six substitutive studies of competition have been published since then (Table 1). All eight studies were conducted on anadromous salmonids, but only five of the eight studies were conducted on salmonids native to the Pacific Rim. Here, we use the results of all eight studies to calculate the RCA of juvenile hatchery salmonids presented below.

Relative competitive ability of hatchery fish

Methods

Substitutive competition experiments of juvenile salmonids report endpoints ranging from behavior to growth, and survival (Table 1). A common metric is needed to compare studies of different species using different endpoints. We chose to compare the studies by calculating the relative competitive ability of hatchery fish with the following formulas depending on the way the authors reported the data. Mean values of competition metrics were obtained directly from published figures and tables within manuscripts with the exception of Riley et al. (2005, 2009a), which were calculated from the data files used to construct the figures. When the responses for wild fish alone
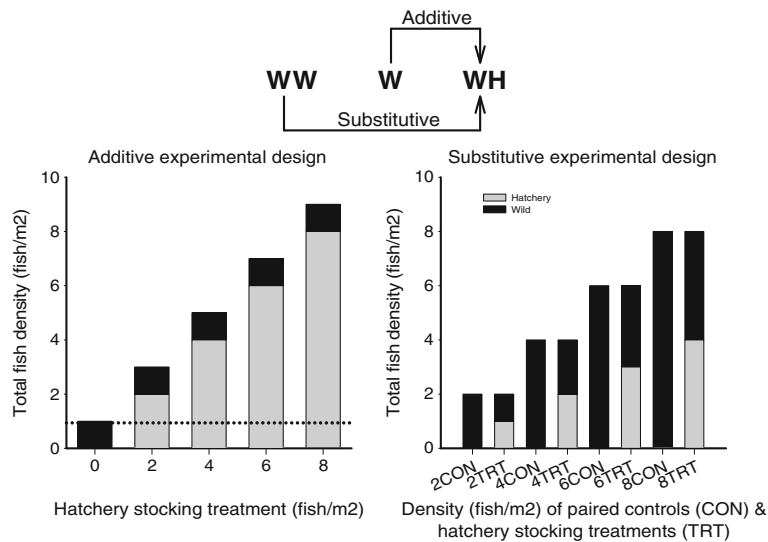
Fig. 4 Three treatments can be used to construct additive and substitutive designs (adapted from Weber and Fausch 2003). Each capital letter represents the same number of fish, with "W" and "H" denoting wild and hatchery fish, respectively. Hatchery fish could be of the same species as the wild (intraspecific) or of a different salmonid species (interspecific). If treatment "W" is compared to treatment "WH" an additive design is used. If treatment "WW" is compared to treatment "WH" a substitutive design is used. Additive designs are confounded with density as indicated by the bar graph on the left; the control (represented by hatchery stocking treatment "0" and the dotted reference line) density is always less than that of the hatchery stocking treatments. Substitutive designs are not confounded by density because each level of density tested has its own control consisting entirely of wild fish as shown by the bar graph on the right

and wild fish stocked with hatchery fish were reported, we used formula 1. When only the responses for wild fish and hatchery fish were reported, we used formula 2. When several trials
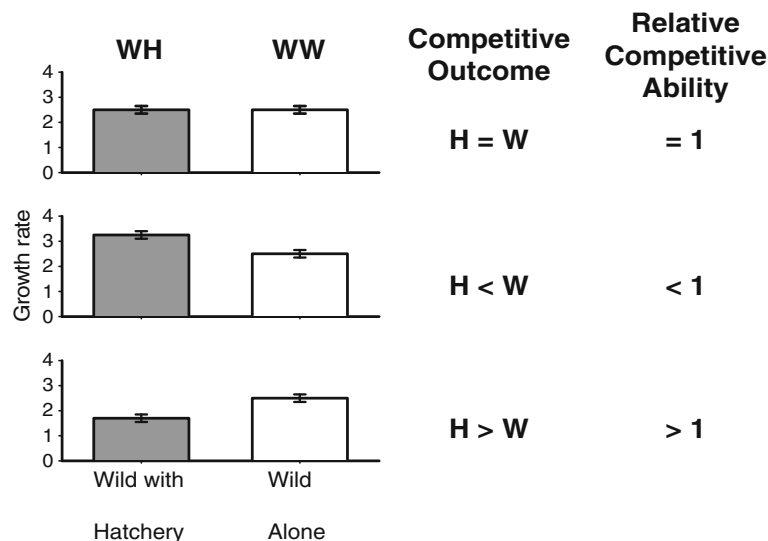
Fig. 5 Interpretation of results from substitutive experimental designs involves comparing the value of the experimental endpoint of wild fish alone (control = WW, white bars) to that of the wild fish stocked with hatchery fish (treatment = WH, grey bars). Hypothetical growth data is shown with three possible outcomes. Competitive outcome indicates whether hatchery or wild fish are superior competitors. The relative competitive ability (RCA) of hatchery fish is calculated by dividing the response (in this case growth rate) for wild fish alone by the response for wild fish stocked with hatchery fish (RCA = WW / WH)

Table 1 Summary of eight published substitutive competition experiments used to calculate the relative competitive ability of juvenile hatchery anadromous salmonids. Salmonids native to the Pacific Rim occupy the first five entries in the table.

Competition metrics are presented in an order that represents increasingly stronger relationships to fitness (as in Fig. 1, from top to bottom)

Species	Competition metric	Experimental setting	Fish density (various units)	Comparison method[c]	Number of trials	Relative Competitive Ability (RCA)	Reference
Steelhead	Aggression Feeding	Laboratory flume	1.8 to 7.1 fish/m^2	W v H	6 6	0.54 1.39	Riley et al. 2005
Steelhead	Aggression Feeding	Laboratory flume	0.9 to 1.8 fish/m^2	W v H	4 4	1.39 1.13	Riley et al. 2009a
Chinook	Aggression Growth	Laboratory artificial stream	4.5 to 9 fish/m^2	W v H WW v WH	4 6	4.95 1.76	Peery and Bjornn 1996
Chinook	Growth Survival	Field enclosure	10 fish/m2	WW v WH	2 2	0.97 0.99	Weber and Fausch 2005
White-spotted charr	Growth[a,*] Growth[b]	Field enclosure	4 fish/m^2	WW v WH	1 1	0.88 1.28	Yamamoto et al. 2008
Brown trout	Growth*	Field stream section	0.55 to 2 fish / linear m stream length	W v H	1	0.84	Sundstrom et al. 2004
Brown trout	Growth*	Field enclosure	4.7 fish/m^2	WW v WH	1	2.67	Vehanen et al. 2009
Brown trout	Growth	Field stream section	Doubling of natural biomass	WW v WH	1	1.09	Bohlin et al. 2002

[a] Hatchery fish were size matched with wild fish

[b] Hatchery fish were 10% larger than wild fish

[c] W v H indicates that hatchery fish were compared directly to wild fish to calculate RCA, while WW v WH indicates that wild fish alone were compared to wild fish with hatchery fish

*Study reported a significant effect of competition at $\alpha \leq 0.05$

were reported in the same study, we calculated RCA separately for each trial and then reported the average RCA for all trials.

$$RCA = WW/WH \qquad (1)$$

Or

$$RCA = H/W \qquad (2)$$

where, RCA = relative competitive ability of hatchery fish; WW = average response of wild fish alone (control); WH = average response of wild fish with hatchery fish (treatment); W = average response of wild fish; and, H = average response of hatchery fish.

There are three possible interpretations of the calculated RCA value. When the RCA<1 hatchery fish are inferior competitors than wild fish. If the RCA=1, then the hatchery fish are equal competitors to wild fish. Finally, if the RCA>1, then the

hatchery fish are superior competitors than wild fish (Fig. 5).

Results

The calculated RCAs and summaries of the substitutive competition experiments are presented in Table 1; all of the studies investigated intraspecific competition between hatchery and wild fish. Statistical analysis of the calculated RCAs was restricted (i.e., very low power) by the small sample size. The RCAs for the behavioral metrics of competition (feeding and agonistic behavior) were more variable (ranging from 0.54 to 4.95) than the RCAs for growth (ranging from 0.84 to 2.67). Based on behavior, hatchery fish were more often superior competitors when compared to wild fish (i.e., 4 of 5 RCAs were >1). When competition was measured using growth metrics, the RCAs were not significantly different than 1 (non-parametric 2-sided sign test, $n=7$, $p=1.00$), suggest-

ing that hatchery fish are on average equal competitors with wild fish (small sample size noted). Three of the seven growth RCAs were less than one, and four of the seven were greater than one. The only study that reported survival indicated that hatchery and wild Chinook salmon were approximately equal competitors (RCA=0.99). When RCAs for all competition metrics were combined, they were still not significantly different than 1 (nonparametric 2-sided sign test, $n=13$, $p=0.58$).

Recommendations

Determining the extent and effect of competition between hatchery and wild Pacific salmonids requires answers to fundamental ecological questions such as: does increasing the population size with hatchery fish have the same impact as an equivalent increase caused by natural increases of wild fish to the population? Such answers can be most efficiently provided by substitutive competition experiments and by calculating the RCAs of hatchery fish. An alternative method to substitutive designs exists for calculating RCAs, and involves measuring population growth rate after manipulating the density of the competitor (Laska and Wootton 1998); conducting these experiments in wild and hatchery salmonid populations would be extremely difficult. Knowing the RCA value of hatchery fish could improve hatchery management because it could indicate whether changes in hatchery practices were needed to equalize the competitive ability of hatchery fish. Ideally, hatcheries would want to produce fish with an RCA=1. Hatchery fish with RCAs<1 would likely have lower fitness than wild fish, making supplementation efforts inefficient. Conversely, hatchery fish with RCAs>1 would be more likely to negatively impact fitness of wild fish jeopardizing population viability and/or recovery. If information about the RCA of hatchery fish is unavailable, a prudent approach would be to release hatchery fish so that potential competition with wild fish is minimized.

Although the number of competition experiments using substitutive designs has grown since Weber and Fausch's (2003) review, there are still not enough studies to rigorously test whether the RCAs of hatchery and wild juvenile salmonids are equal.

Closer scrutiny of Table 1 provides insight into deficiencies future studies should address. Future intraspecific substitutive competition experiments should focus on competition endpoints closely associated with biological fitness, and be conducted at densities reflective of conditions where competition will occur in natural systems. Furthermore, there is a need to increase species diversity to be inclusive of all anadromous Pacific salmonid species with hatchery counterparts; currently there are no substitutive studies for coho, sockeye, masu, chum, and pink salmon. Although the effects of intraspecific competition are likely to be greater than those of interspecific competition for juvenile salmon, there is a need to conduct substitutive experiments of interspecific competition where one species is of hatchery origin and the other wild. Substitutive designs have been used for interspecific competition in juvenile salmonids (especially between native and introduced salmonids), but none have tested a native but hatchery-raised species against a different wild species.

One drawback of substitutive competition experiments is that they are nearly impossible to conduct as the spatial scale of the experiment exceeds the size of stream enclosures, and the temporal scale exceeds several weeks. Because competition can occur over temporal and spatial scales greater than what substitutive experiments can handle, additional experimental approaches are needed to gain a fuller understanding of competition between hatchery and wild fish. One approach to extend the temporal scale would be to conduct substitutive experiments at a mesocosm spatial scale in artificial stream channels. Another promising approach to extending both temporal and spatial scales is to conduct field-scale experiments where replicated supplemented (treatment) and unsupplemented (control) reaches or tributaries are monitored before and after hatchery supplementation occurs (sensu Pearsons and Temple 2007, 2010). By monitoring changes in the supplemented and non-target species, the effects of both intra- and interspecific competition can be assessed simultaneously. Comparisons could then be made using a before-after, control-impact (BACI) experimental design to determine the effects of competition. Pursuing both approaches (substitutive and field-scale experiments), while difficult, holds promise for clarifying the competitive impacts of hatchery fish on wild populations.

Conclusions

The expansive body of literature on competition among hatchery and wild juvenile Pacific salmonids provides for some generalization. (1) Hatchery fish are more likely to compete with wild fish of the same species because they share the same ecological niche. (2) Competition increases with the duration of freshwater residence, and this is a function of both species life history and hatchery culture and release practices. Parr (sometimes referred to as "fry") releases will increase the potential for freshwater competition, as do high rates of residualism. (3) Competitive advantages of large body size favor hatchery fish because they are most frequently larger than wild fish at the time of release. (4) The competitive advantage of prior residence favors wild fish because they already occupy habitat before hatchery fish are released. (5) The effects of the hatchery rearing environment are unclear with regard to the competitive advantage of hatchery fish. (6) Both intra- and interspecific competition are density-dependent in relation to habitat carrying capacity. And (7) The current (and limited) body of substitutive experiments suggests that the relative competitive ability of hatchery fish is approximately equivalent to wild fish when measured as growth.

As interest in the ecological interactions between hatchery and wild Pacific salmon grows, scientists and resource biologists are looking for information to improve salmon management and recovery efforts, and to guide system-wide hatchery reform efforts (Mobrand et al. 2005). Of particular importance is how to account and mitigate for the prevalence and effects of competition between hatchery and wild fish for all life history stages. Past studies of competition have successfully described the effects and identified mechanisms of competition, and reviews of competition have identified potential ecological risks of hatchery programs (Einum and Fleming 2001; Kostow 2009). Although risks of competition have been successfully identified, they remain difficult to quantify and extrapolate across species and ecosystems. Additional substitutive competition studies could improve our understanding of the ecological risks of stocking hatchery fish and answer the general question of whether differences in competitive ability exist between hatchery and wild fish across populations and species (Weber and Fausch 2003).

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