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ARTICLE

Linking individual size and wild and hatchery ancestry to survival and predation risk of threatened steelhead (*Oncorhynchus mykiss*)

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Abstract: We examined the role of individual size and origin (wild versus hatchery) to predation risk and marine survival for threatened juvenile steelhead (*Oncorhynchus mykiss*) in a coastal California watershed. In this study, we found that individual size and origin were strongly associated with increased predation risk of steelhead by a generalist avian predator (western gull, *Larus occidentalis*) and associated with survival to reproduction by tracking the fate of juvenile steelhead tagged with passive integrated transponder (PIT) tags. Across six cohorts (2005–2010), larger steelhead (>170 mm fork length (FL)) experienced marine survival rates at least 60 times higher than the smallest individuals. Predation risk by western gulls was highest for intermediate-sized fish (145–190 mm FL), which was at least ten times higher than the predation risk of the smallest individuals and four times higher than the predation risk of the largest individuals. Wild steelhead experienced both higher predation risk and higher survival rates than hatchery fish of the same size. Although gulls disproportionately remove intermediate-sized wild steelhead from the population, they also remove large wild individuals that may otherwise experience the highest adult return rates. Instead of focusing on population size alone, conservation measures could also be guided towards the recovery of larger and wild individuals, whose survival is paramount for population recovery.

Résumé : Nous avons examiné le lien entre la taille et l'origine (sauvage ou d'écloserie) des individus, d'une part, et le risque de prédation et la survie en mer, d'autre part, pour des truites arc-en-ciel (*Oncorhynchus mykiss*) juvéniles menacées dans un bassin versant de la côte californienne. En suivant des truites arc-en-ciel juvéniles dotées de radioétiquettes passives intégrées (PIT), nous avons constaté que la taille et l'origine des individus étaient fortement associées à un risque de prédation accru des truites arc-en-ciel par un prédateur aviaire généraliste (le goéland d'Audubon, *Larus occidentalis*) et étaient associées à la survie jusqu'à la reproduction. À l'échelle de six cohortes (2005–2010), les plus grandes truites (longueur à la fourche (LF) >170 mm) présentaient des taux de survie en mer au moins 60 fois plus élevés que les truites les plus petites. Le risque de prédation par des goélands d'Audubon était le plus élevé pour les individus de taille intermédiaire (LF de 145–190 mm), ce risque étant au moins 10 fois plus élevé que pour les individus les plus petits et quatre fois plus élevé que pour les individus les plus grands. Les truites arc-en-ciel sauvages présentaient un risque de prédation et des taux de survie plus élevés que les poissons issus d'écloserie de même taille. Si les goélands extraient une quantité disproportionnée de truites arc-en-ciel sauvages de taille intermédiaire de la population, ils en retirent également de grands individus sauvages qui, autrement, pourraient présenter les taux de retour d'adultes les plus élevés. Plutôt que d'être axées exclusivement sur la taille de la population, les mesures de conservation pourraient également viser le rétablissement d'individus plus grands et sauvages dont la survie est primordiale pour le rétablissement des populations. [Traduit par la Rédaction]

Introduction

Individual traits influence ecological parameters such as population dynamics and survival (Palkovacs and Hendry 2010; Bolnick et al. 2011), which necessitates the incorporation of phenotypic variability into fisheries management (Fraser 2013). For most species of fishes, the greatest mortality rates occur during early life stages, and only a few individuals survive to reproduction (type III survivorship curve; Deevey 1947). In declining populations of Pacific salmon (*Oncorhynchus* spp.), where <0.1% of eggs survive to maturity (Shapovalov and Taft 1954), the few survivors may bear traits influential in shaping ecology and population dynamics. This likely explains the tremendous individual variation in traits across Pacific salmon, including morphology (Roni and Quinn

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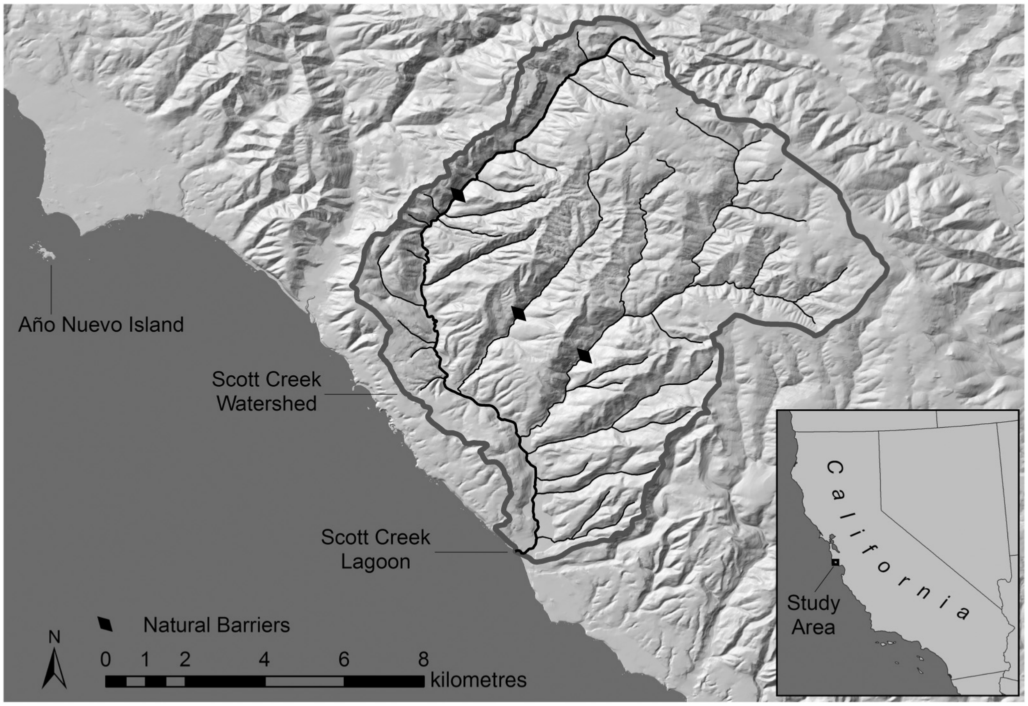
Fig. 1. Map of the study location, including the Scott Creek watershed (California, USA) and Año Nuevo Island.



1995), physiology (Hinch and Rand 1998), and life history strategies (Thorpe 2007).

Early ocean mortality may be the most critical life stage in determining salmon population dynamics (Kareiva et al. 2000). Individual traits such as size (Ward et al. 1989; Sogard 1997), estuarine residence time (Magnusson and Hilborn 2003; Bond et al. 2008), and origin (wild or hatchery; Jonsson et al. 2003; Beamish et al. 2012) are commonly associated with marine survival, but the relationship among these traits may differ across systems or species. For example, size at outmigration is not always associated with increased marine survival (Ward 2000). Therefore, identifying individual characteristics that influence marine survival continues to be an important research direction and critical for managing imperiled populations.

Predation is an important source of mortality for many species (Sih et al. 1985); therefore, traits that influence vulnerability to predation can impact prey population dynamics (Pettorelli et al. 2011). The influence of predation will be substantially higher if predators target prey with characteristics associated with high rates of survival compared with prey with characteristics already susceptible to other sources of mortality (Griffin et al. 2011). Avian predators may have a particularly large impact on salmonid prey population dynamics because birds typically prefer larger individuals as prey, and salmonid size is positively associated with survival (Sogard 1997). For juvenile salmon in the Columbia River, some avian predators select for larger and hatchery-raised individuals (Collis et al. 2001; Ryan et al. 2003), and variable vulnerability of specific stocks to avian predation may affect salmonid population dynamics in this system (Roby et al. 2003). The impact of avian predation on prey population dynamics in other systems remains less understood. Previously, we estimated that western gulls (*Larus occidentalis*) may consume approximately 30% of outmigrating juvenile steelhead (*Oncorhynchus mykiss*) in a small California watershed (Osterback et al. 2013). However, it is unknown whether these predators select individuals with traits that are positively associated with survival to reproduction or whether they only eat individuals that will inevitably die from other sources of mortality before reproducing.

Here we compare the individual size, origin, and outmigration year of Endangered Species Act (ESA)-listed (threatened) juvenile steelhead that were consumed by a generalist predator (western gull) or survived to return as a spawning adult. We ask several questions: (*i*) Are size, origin, and outmigration year associated with predation risk by western gulls? (*ii*) Are size, origin, and outmigration year associated with survival to maturity? (*iii*) Do these characteristics overlap, such that the effects of size, origin, and outmigration year are similar for both predation risk and survival to maturity? By comparing the characteristics of juveniles that are consumed with those that survive to maturity, we can better understand whether predators are removing individuals from the population that otherwise tend to have high marine survival and are likely to contribute to the productivity of these imperiled populations.

Materials and methods

Study system

The study area includes Scott Creek, a small (~70 km²), central California coastal watershed, and Año Nuevo Island (ANI), a small coastal island (10 ha), which hosts the third largest western gull breeding colony in central California (Capitolo et al. 2009) and is located ~12 km north from the mouth of Scott Creek (Fig. 1). Scott Creek supports wild populations of threatened central California coast steelhead (Federal Register 2006) and represents the putative southern range of endangered coho salmon (*Oncorhynchus kisutch*; Federal Register 2005). A conservation hatchery on Scott Creek (Monterey Bay Salmon and Trout Project, MBSTP) releases a few thousand age-1+ hatchery steelhead and coho salmon into Scott Creek each winter or spring, where individuals are progeny of wild adults captured in Scott Creek and are at least one generation removed from the hatchery (Hayes et al. 2004).

Scott Creek is a dynamic system; the creek mouth is closed during part of the year, which influences patterns of juvenile steelhead outmigration and predation by western gulls. In the late summer and fall, the combination of low stream flow and sand deposition from oceanic wave action results in a sand bar that separates the creek from the ocean and creates a freshwater lagoon (Hayes et al. 2008; Bond et al. 2008). Thus, the seasonal formation of the sand bar limits timing of juvenile salmonid outmigration to the winter and spring when connectivity between the creek and ocean exists (typically December through June). Concurrent with salmonid outmigration, western gulls gather at the shallow mouth of Scott Creek to drink, bathe, and opportunistically prey on items traveling downstream, including outmigrating juvenile salmonids (Frechette et al. 2012). Recovery of prey tags from the western gull breeding areas on ANI in combination with a tag transportation experiment revealed that gull predation may account for approximately 30% of the tagged wild juvenile steelhead population in Scott Creek during some years (Osterback et al. 2013). Individual factors such as individual size, wild ancestry, and lagoon residence have all been associated with emigration patterns and survival of steelhead in Scott Creek (Bond et al. 2008; Satterthwaite et al. 2012; Phillis et al. 2014), whereas relatively less is known about individual traits that contribute to predation risk by western gulls, except that lagoon-reared individuals represent the majority of fish consumed (Frechette et al. 2012). To our knowledge, individual characteristics such as size, origin, and outmigration year associated with predation risk and survival in Scott Creek or any other system have not been explicitly compared to date.

Individual characteristics of juvenile steelhead

To identify individual size, origin, and outmigration year of juvenile steelhead in Scott Creek, we and the National Marine Fisheries Service Southwest Fisheries Science Center captured juvenile steelhead between 2005 and 2010. We captured wild juvenile steelhead through a combination of downstream migrant trapping, lagoon seining, and backpack electrofishing. We captured age-1+ hatchery individuals at the MBSTP hatchery prior to their release in Scott Creek and clipped adipose fins to identify hatchery origin in the field. We handled all steelhead according to the methods described by Hayes et al (2004) and recorded size (fork length, FL), origin (wild or hatchery-raised), date, and location for each individual. All steelhead were PIT (passive integrated transponder)-tagged to provide a unique identification for each tagged individual. PIT tags have high tag retention rates (>95%; Sogard et al. 2009) and contain no battery, so they can last beyond the lifespan of a tagged individual. As a result, PIT tags can provide unique information on an individual many years after the initial tagging event (i.e., recaptured as an adult 1–3+ years after tagged as a juvenile) and even beyond an individual's lifespan (i.e., recaptured after deposition on ANI).

For this study, we only included wild and hatchery juvenile steelhead that were present in western gull foraging areas during lagoon residence or outmigration. Therefore, all wild steelhead included in the analysis were tagged or recaptured during seining events in the Scott Creek lagoon, which typically occurred in the late summer and fall when the lagoon was separated from the ocean. We excluded wild steelhead that were never directly observed using lagoon habitat because many of these individuals were likely a younger age class that may not have initiated downstream migration towards the lagoon or ocean (Hayes et al. 2008). For hatchery juveniles, we restricted our analyses to individuals that were tagged at the MBSTP hatchery in late winter or early spring as age-1+ juveniles. In Scott Creek, the vast majority of hatchery steelhead migrate out to the ocean soon after release (Hayes et al. 2004), and typically only a small percentage of hatchery males in Scott Creek mature in the freshwater environment (2.3%; Phillis et al. 2014). It is unknown whether stream-maturing males will remain as resident trout or eventually outmigrate to the ocean (Hayes et al. 2004). We excluded any hatchery individuals that were recaptured as residents and therefore did not outmigrate the same year as their release.

By restricting our analysis to wild steelhead caught in the lagoon and hatchery steelhead that were not observed as residents following their release, we can assign a likely outmigration year to these individuals to account for variation in outmigration timing. Outmigration year was the same as calendar year for hatchery juveniles because they typically migrate to the ocean soon after release (Hayes et al. 2004). For wild individuals captured in the lagoon, we assigned the outmigration year for the following year (calendar year + 1), because wild steelhead that rear in the lagoon typically outmigrate the following winter after the lagoon opens, and the creek is no longer separated from the ocean (see Hayes et al. 2008 for more details on outmigration timing of juvenile salmonids in Scott Creek).

Effects of size, origin, and outmigration year on predation risk

Based on avian preference for larger prey (Sogard 1997) and possible preference for lagoon-reared wild steelhead as western gull prey (Frechette et al. 2012), we hypothesized that gulls selectively consumed large wild-reared steelhead; thus, predation risk would be higher for steelhead with characteristics that we also hypothesized would be associated with high marine survival. To test this hypothesis, we compared the individual size and origin of PIT-tagged juvenile steelhead in Scott Creek with those steelhead whose PIT tags were deposited on ANI by western gull predators (Osterback et al. 2013). To identify interannual variation in other biotic and abiotic factors, year was included as a factor to allow for comparisons between fish among outmigration years.

We identified which juvenile steelhead were consumed by gulls by scanning ANI annually from 2006 through 2013 to recapture PIT tags from steelhead that had been consumed and deposited by western gulls. Scans of ANI include traversing the island with a portable PIT antenna and GPS to document the location and unique identification code of each deposited tag (for more details, see Frechette et al. 2012). Mobile PIT antenna specifications are described in Bond et al. (2007). Previous research identified that the majority of PIT tags originating from fish in Scott Creek that were eaten by gull predators were deposited on ANI during the winter or spring, suggesting predation occurs primarily during emigration to the ocean or immediately after ocean entry (Frechette 2010). We directly observed gulls prey on outmigrating juvenile salmonids (Frechette 2010) and thus assume they primarily prey on live fish; however, we cannot rule out that gulls also may consume juvenile steelhead that were already dead. It is important to note that the recapture of PIT tags addresses relative predation risk and does not quantify overall predation rates. Overall predation rates are much higher than the recapture rates reported in this study because the majority of consumed tags are deposited off-colony (Osterback et al. 2013).

We quantified factors associated with predation risk of juvenile steelhead in Scott Creek with a generalized linear model (GLM) with a logit transformation, where the binary response variable was "recaptured on ANI" (1) or "not recaptured on ANI" (0). "Recaptured on ANI" individuals were juveniles whose PIT tags were detected on ANI after presumably being consumed and defecated by western gull predators. For "not recaptured on ANI" individuals, we have no evidence they were consumed by gulls. Because recapture probabilities were high for detecting PIT tags on ANI (~64%; Frechette et al. 2012), there is a low probability that individuals of unknown fate were deposited on ANI and went undetected. Instead, individuals of unknown fate likely were eaten by gulls, and tags were deposited off-colony or were not eaten by gulls. The following factors were included as possible predictors in the candidate models: FL (mm), FL^2 (mm^2), origin (hatchery versus wild), and outmigration year. We included the quadratic term FL^2 to determine if intermediate-sized fish experienced different predation or survival rates when compared with small and large individuals. We also included outmigration year as a factor to account for interannual variation and assess whether predation risk varied among years. Owing to the limited years of data ($N = 6$), we were unable to assess specific factors that drive year-to-year variation. We did not include interactions as possible predictors for candidate models because we did not have an a priori hypothesis regarding interactions, and post hoc analyses showed the inclusion of interactions did not improve model fit.

We used a multimodel inference approach to identify parameters that best support the data (Burnham and Anderson 2002; Grueber et al. 2011). With the MuMIn package in R (R Development Core Team 2013), we used the dredge function to evaluate the set of all possible candidate models and used Akaike's information criterion for small sample sizes (AIC_c) to compare model fit between candidate models. We conducted model-averaging, which is recommended when the weight of the top model is less than 0.9 and multiple candidate models are within two ΔAIC_c units of the best approximating model (Grueber et al. 2011). We used the natural average method of estimating parameter weights because all parameters are of interest, and some may have relatively weak effects when compared with other factors (Grueber et al. 2011).

To estimate the relative effects of each parameter within the averaged models, we standardized the input variables by subtracting the mean and dividing by two times its standard deviation to allow comparisons of all parameters on a similar scale (Gelman 2008). Data standardization was conducted using the arm package in R (R Development Core Team 2013), where FL and FL^2 were modeled as continuous parameters, and the other parameters of origin and outmigration year were modeled as binary and dummy variables, respectively. Effect sizes of each parameter were then compared with a reference state to determine how changes in a given parameter would affect the response variable. We included 95% confidence intervals (CIs) for each estimate of effect sizes, such that effect sizes are strong predictors and significantly different from the reference state if 95% CIs do not overlap with zero. The reference state for all analyses was a wild steelhead with a mean FL in outmigration year 2010.

The above modeling approach assumed that FL at last capture was indicative of an individual's size when exposed to gull predators; however, it is possible that the majority of gull predation does not occur in the greater lagoon area but instead occurs upon outmigration in the winter or spring during the last several metres of the lagoon just before it enters the ocean (Frechette 2010). For hatchery steelhead, the vast majority of individuals are known to outmigrate to the ocean soon upon release into Scott Creek (Hayes et al. 2004), so individual measurements taken at the hatchery before their release are likely relatively equivalent to their size during exposure to gull predation. However, the size of wild lagoon-reared steelhead may have been recorded from 1 day to several months before outmigration; therefore, if gull predation happens upon outmigration, their recorded size may be substantially smaller than their size upon outmigration. To address this potential bias, we used the same modeling approach as described above, except we replaced the observed FL with an adjusted FL for wild lagoon-reared individuals. The adjusted FL is the estimated size of a wild lagoon-reared individual upon outmigration and is based on (*i*) the estuarine specific growth rate equation in Hayes et al. (2008), which incorporates year-specific, density-dependent effects of the lagoon population size, and (*ii*) the number of days between when an individual was last captured in the lagoon and the first date the lagoon opened for that given outmigration year. Comparisons between this model and the previous model will reveal whether the effect of FL on predation risk changes depending on when predation may occur. Note the adjusted FL analysis assumes individuals outmigrate on the first day of sandbar breakage and thus only represents one of many potential delayed outmigration scenarios.

Effects of size, origin, and outmigration year on survival

We hypothesized that survival will be highest for large wild steelhead when compared with smaller individuals or individuals of hatchery origin. To identify size, origin, and outmigration years associated with survival, we compared the characteristics of PIT-tagged juveniles with those individuals that survived the marine ecosystem and returned to Scott Creek 1–3+ years after ocean entry as mature adults. Size, origin, and outmigration year of the juveniles that survived to spawn were then compared with the characteristics of all tagged juveniles. We cannot rule out the possibility that smaller fish may have delayed ocean entry such that reduced survival may reflect a combination of mortality incurred in freshwater habitat before ocean entry and mortality following ocean entry.

To identify PIT-tagged juveniles that survived to become spawning adults, we captured adults returning to Scott Creek during the spawning season (typically December through June) between 2005 and 2013 through a combination of snorkel surveys and daily operation of a floating resistance panel weir (Bond et al. 2008). All returning adults were scanned for PIT tags and cross-referenced with juvenile PIT tag data to identify the juvenile size and origin of each returning adult from juvenile outmigration years 2005 through 2010.

To identify individual size, origin, and outmigration year associated with survival, we used the same analysis as the predation risk analysis, including a GLM with a logit transformation, a multimodel inference approach, and data standardization for effect sizes to identify factors that inform the response variables. For the survival analysis, the binary response variables included "survived to spawn" (1) and "did not survive to spawn" (0). "Survived to spawn" represented fish that were tagged as juveniles and then were subsequently captured in Scott Creek as an adult and therefore survival was confirmed. Individuals defined as "did not survive to spawn" included the remaining juvenile tagged steelhead that did not return as adults, for which we have no evidence they survived to spawn. Capture efficiency of adult spawners is high in this system (~73%; Hayes et al. 2013), suggesting individuals that were not detected returning to spawn likely died. The same four factors assessed in the predation risk analysis were included as possible predictors for the survival analysis: FL (mm), FL^2 (mm^2), origin (hatchery versus wild), and outmigration year. Similar to the predation risk analysis, we re-ran the model using the adjusted FL to assess whether the effect of size on survival for wild individuals is sensitive to the timing of predation (i.e., in the lagoon versus upon outmigration).

Results

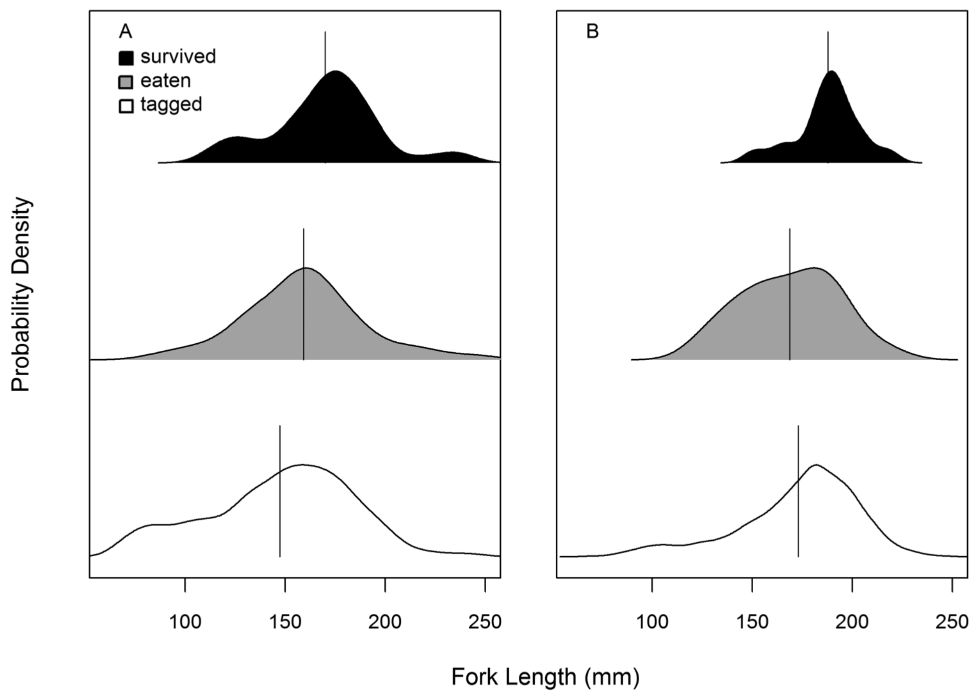
Between outmigration years 2005 and 2010, we PIT-tagged 7523 hatchery and wild lagoon-reared juvenile steelhead in Scott Creek (Table 1). Tagged individuals represent ~25% of the total hatchery production and ~15% of the initial lagoon population size (Hayes et al. 2013) and ranged in size from 65 to 250 mm FL with a mean size of 167.8 mm FL (Fig. 2). Of the tagged juveniles, 93 were subsequently recaptured on ANI after presumably being consumed by a western gull, 61 were recaptured as adults in Scott Creek, and 7369 individuals had an unknown fate (Table 1). For wild steelhead, the mean size (147.4 mm FL) of tagged juveniles was smaller than both the individuals recaptured on ANI (159.2 mm FL) and the individuals that returned as adults (170.0 mm FL; Fig. 2). For hatchery steelhead, the mean size (173.1 mm FL) of all the tagged individuals was slightly larger than the individuals recaptured on ANI (168.8 mm FL) and smaller than the individuals that returned as adults (187.8 mm FL; Fig. 2). Mean recapture rates of PIT tags on ANI were 3.2% for wild lagoon-reared steelhead and 0.7% for hatchery juveniles (Table 1). Mean survival rates were 2.9% for wild lagoon-reared steelhead and 0.3% for hatchery juveniles (Table 1). The high mortality rates inferred by our study match previous

Table 1. Sample sizes for the predation risk and the survival analysis for Scott Creek steelhead in outmigration years 2005 through 2010.

Origin, location		No. of individuals 2005	2006	2007	2008	2009	2010	Total
Wild, lagoon	Tagged*	170	261	57	192	393	465	1538
	Recaptured on ANI†	1	8	5	3	16	16	49
	Returned as adult‡	6	17	1	4	1	15	44
Hatchery	Tagged*	499	534	474	961	2955	562	5985
	Recaptured on ANI†	6	19	2	6	7	4	44
	Returned as adult‡	4	0	0	8	3	2	17

*Total number of tagged steelhead.
†Number of tagged individuals subsequently recaptured on Año Nuevo Island (ANI) after presumably being eaten by a western gull.
‡Number of tagged individuals that survived to return as an adult.

Fig. 2. Probability densities for fork length (FL) of wild (A) and hatchery (B) steelhead included in this study, including all tagged individuals (white), all individuals recaptured on Año Nuevo Island after being eaten by a gull (grey), and all individuals that survived to return as adults (black). Data are represented as bean plots that show the full distribution of probability densities for FL, where vertical lines indicate mean FL.



observations of typical very low smolt to adult survival for Scott Creek steelhead (~1.6%; Hayes et al. 2013).

Effects of size, origin, and outmigration year on predation risk

Predation risk was influenced by the individual characteristics of steelhead in Scott Creek. Origin, FL^2, and outmigration year were the strongest predictors of predation risk, as demonstrated by their inclusion in all of the best-approximating models, whereas FL had a relatively weak effect (Table 2; Fig. 3A). For a given FL, wild steelhead were consistently more susceptible to predation than were hatchery-raised individuals (Fig. 3A), where predation risk was over four times higher for wild individuals when compared with individuals that were reared at the hatchery (Fig. 4A). In contrast with our predictions, FL was a weak predictor of predation risk (Fig. 3A); however, FL^2 was a strong predictor of predation risk. Intermediate-sized steelhead (145–190 mm FL) experienced over 10 times the predation risk than the smallest individuals (65 mm FL) and over four times the predation risk than the largest individuals (250 mm FL; Fig. 4A), regardless of origin. Predation risk was 2.7 times higher for juvenile steelhead that outmigrated in 2006 (Fig. 3A) when compared with individuals that outmigrated during the reference year (2010), which had similar predation risk as the other 4 years of the study (Fig. 3A).

Using adjusted FL for wild lagoon-reared individuals had little effect on the model, suggesting that regardless of predation timing, FL^2 remained a strong predictor of predation risk. The model using adjusted FL (Fig. 5A) had similar results to the original model (Fig. 3A), where predation risk was highest for wild steelhead (Fig. 5A). The year effects were also similar between the original model and the model using adjusted FL, where predation risk was highest in 2006. These results suggest the influence of size on predation risk is similar whether using observed length at capture or predicted length at outmigration.

Effects of size, origin, and outmigration year on survival

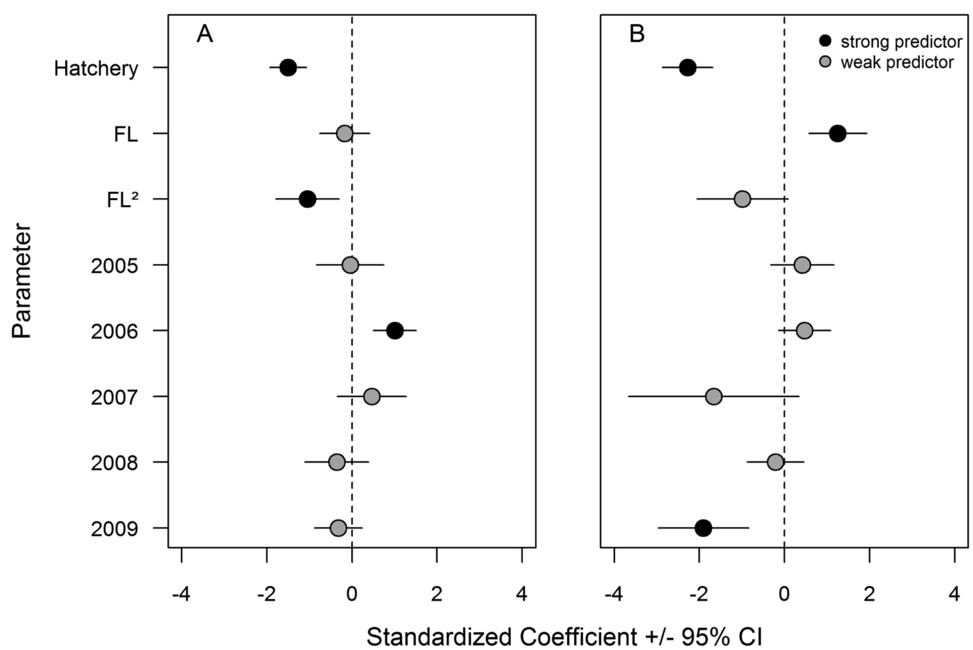
Individual characteristics of juvenile steelhead strongly influenced the probability an individual survived to return as a spawning adult. Consistent with our predictions, survival was best predicted by origin, FL, and outmigration year, whereas FL^2 had a relatively weak effect (Table 2; Fig. 3B). Origin had a significant effect on survival rates; for a given FL, wild individuals experienced over nine times the survival rate of hatchery fish (Fig. 4B). The most influential factor was FL; larger individuals (>170 mm FL)

Table 2. Best approximating models for the predation risk and survival analysis.

Response variable	Independent variables	AIC_c	ΔAIC_c	w_i
Eaten (recaptured on ANI)	Origin + FL^2 + 2006	934.4	0.00	0.111
	Origin + FL^2 + 2006 + 2007	935.0	0.67	0.079
	Origin + FL^2 + 2006 + 2009	935.1	0.76	0.076
	Origin + FL^2 + 2006 + 2008 + 2009	935.6	1.25	0.059
	Origin + FL^2 + 2006 + 2008	935.8	1.45	0.054
	Origin + FL + FL^2 + 2006	936.0	1.67	0.048
	Origin + FL^2 + 2006 + 2007 + 2009	936.3	1.96	0.042
	Origin + FL^2 + 2005 + 2006	936.4	1.99	0.041
Survived (returned as adult)	Origin + FL + FL^2 + 2007 + 2009	592.3	0.00	0.127
	Origin + FL + FL^2 + 2006 + 2007 + 2009	592.4	0.11	0.120
	Origin + FL + FL^2 + 2005 + 2006 + 2007 + 2009	592.8	0.56	0.096
	Origin + FL + FL^2 + 2005 + 2007 + 2009	593.5	1.23	0.069
	Origin + FL + FL^2 + 2007 + 2008 + 2009	593.9	1.61	0.057
	Origin + FL + 2007 + 2009	594.2	1.95	0.048

Note: All models within <2 ΔAIC_c of the best-approximating model are shown and were incorporated into an averaged model for each analysis, which is recommended when no single candidate model contains more than 0.90 of the model weights (w_i), as discussed in Grueber et al. (2011). Origin (hatchery versus wild), fork length (FL, mm), FL^2, and outmigration year (2005–2009) were included as possible predictors in comparison with the reference year (2010).

Fig. 3. Model-averaged parameter estimates for both the predation risk (A) and the survival (B) analyses. Effect sizes were standardized by subtracting the mean and dividing by two times its standard deviation, as recommended by Gelman (2008). Effect sizes of each parameter were then compared with a reference state (dashed line with coefficient = 0) to determine how changes in a given parameter would affect the response variable. The reference state for both the predation risk and survival analysis was a wild steelhead with a mean fork length (FL) in outmigration year 2010. All points are coefficient estimates of the averaged model, with 95% confidence intervals.



were over 60 times more likely to survive than the smallest individuals (65 mmFL; Fig. 6). The relatively small number of recaptured individuals (Table 1), especially at the higher size classes (Fig. 2), likely contributed to increased uncertainty in our estimates of survival for large individuals (Fig. 4B). Steelhead that outmigrated in 2009 experienced less than one-sixth the survival rate as individuals that outmigrated during the reference year (2010), which was similar to the other years of the study (Fig. 3B). The results from the survival analysis support our hypothesis that large wild steelhead experience the highest survival rates.

The influence of size, origin, and year on survival did not change significantly when using the model with predicted FL at outmigration (Fig. 5B) when compared with the original model that included the observed FL at last capture (Fig. 3B). In the adjusted model (Fig. 5B), survival remained highest for large wild individuals, and those migrating in 2009 experienced the lowest survival.

Comparing effects of size, origin, and outmigration year between predation risk and survival

There was overlap in the factors that influenced predation risk and survival. Wild juvenile steelhead experienced both higher predation risk by western gulls and also experienced higher survival when compared with juveniles raised at the hatchery (Fig. 4). Size also had similar effects on predation risk and survival, especially for certain size classes. For example, individuals between 170 and 190 mm FL experienced some of the highest odds of predation risk and survival (Fig. 6). However, the relative increase in survival as a function of individual size is larger than the relative increase in predation risk for all size classes. Therefore, origin

Fig. 4. The probability of (A) predation risk (i.e., tag recapture on Año Nuevo Island) and (B) survival for wild and hatchery steelhead across the range of fork lengths. Estimates are based on juveniles from outmigration year 2010, which was a year with typical predation risk and survival. Estimates are calculated from the model-averaged logistic regression model for both analyses. Shading indicates 95% confidence intervals.

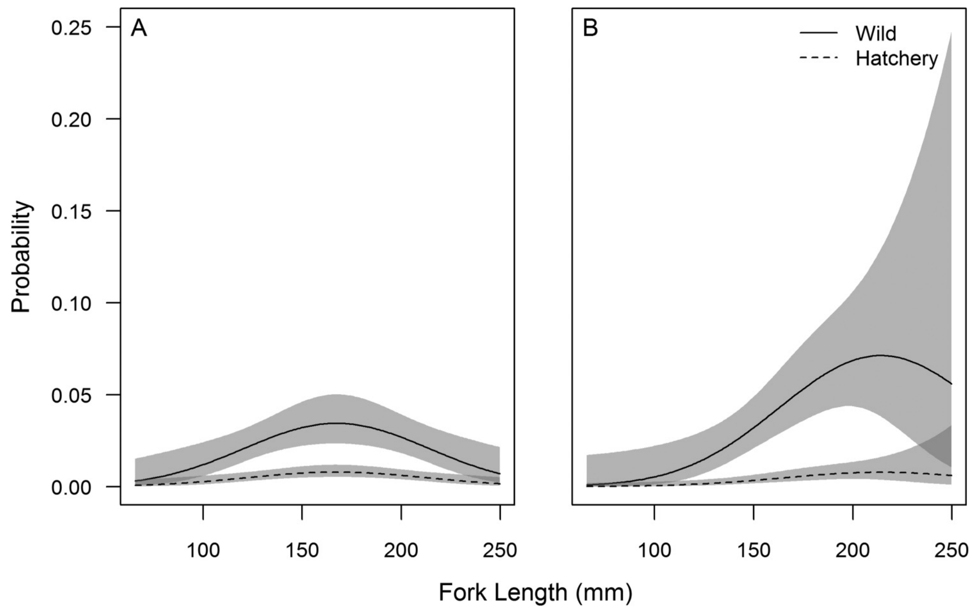
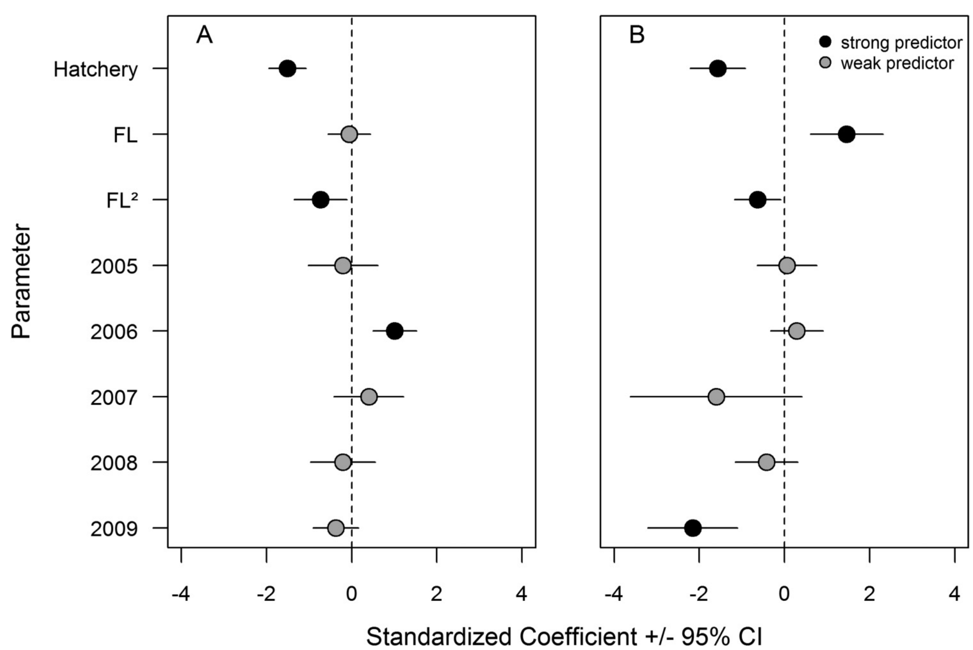


Fig. 5. Model-averaged parameter estimates for both the predation risk (A) and the survival (B) analyses upon outmigration by using the adjusted fork length (FL) for wild lagoon-reared individuals. Effect sizes were standardized by subtracting the mean and dividing by two times its standard deviation, as recommended by Gelman (2008). Effect sizes of each parameter were then compared with a reference state (dashed line with coefficient = 0) to determine how changes in a given parameter would affect the response variable. The reference state for both the predation risk and survival analysis was a wild steelhead with a mean FL in outmigration year 2010. All points are coefficient estimates of the averaged model, with 95% confidence intervals.

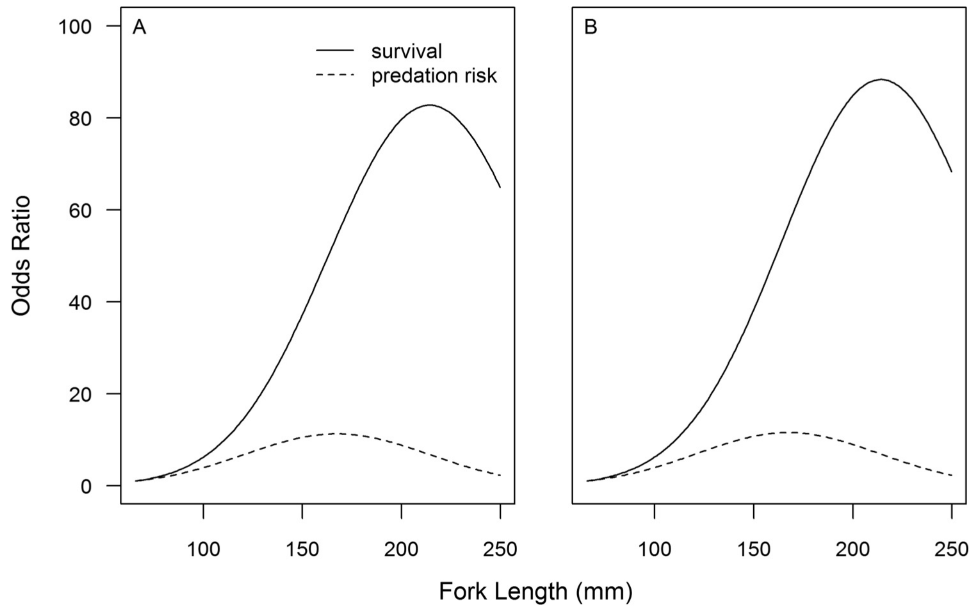


similarly affects an individual's susceptibility to predation and survival, whereas FL may increase an individual's probability of survival substantially more than its probability of predation.

Discussion

Here we examined individual characteristics such as individual size, origin, and outmigration year that influenced survival and predation risk of threatened steelhead. We found that wild individuals experience more than four times the predation risk and over nine times the survival rates than those reared at the hatchery. Intermediate-sized individuals (145–190 mm FL) experienced the highest increase in predation risk, and larger individuals (>170 mm) experienced greater than 60 times the survival rates than the smallest individuals. Thus, if large wild juveniles can

Fig. 6. The increase in odds of survival or predation risk with fork length for wild (A) and hatchery (B) steelhead. Odds ratios were calculated by dividing the survival or predation risk at a given fork length by the survival or predation risk of a fish at the smallest size (65 mm).



survive the gauntlet of gull predation during their outmigration to the ocean, they will likely experience high survival once in the ocean and contribute to the overall productivity of the population. Although previous work in Scott Creek identified or predicted characteristics such as size and origin that were associated with survival of juvenile salmonids (Bond et al. 2008; Satterthwaite et al. 2012; Sogard et al. 2012) and documented high rates of western gull predation on these same populations (>30%; Osterback et al. 2013), it was unknown whether gulls consumed individuals that would otherwise experience high survival rates. The results from this study provide the first empirical evidence that western gulls are consuming predominately wild steelhead, including many larger wild individuals that are critical to the persistence of the population.

We observed strong evidence that origin influenced predation risk of juvenile steelhead, where wild individuals experienced over four times the predation risk than individuals raised at the hatchery (Fig. 4A). This is contrary to many systems where hatchery-raised individuals experience similar or increased predation rates (Collis et al. 2001; Ryan et al. 2003). There are several mechanisms that may predispose hatchery fish to predation in other systems but do not apply to Scott Creek. For example, hatchery-reared salmonids may be more susceptible to predation risk than wild fish because they feed closer to the surface and are therefore more conspicuous to visual predators (Collis et al. 2001). However, in Scott Creek depth preference may not be a factor if predation is occurring at the creek mouth, since shallow water depths there would force all steelhead to travel near the surface. Hatchery fish typically experience increased predation rates from genetic domestication (Berejikian 1995). However, in Scott Creek, hatchery steelhead may share more characteristics with their wild counterparts when compared with other systems because they are raised in a small conservation hatchery where stock are progeny of wild-reared adults (Hayes et al. 2004). This hypothesis is tempered by other studies that have shown hatchery fish even just one generation removed from the wild can result with maladaptive antipredator responses (Jackson and Brown 2011). One important factor that may lead to higher predation risk on wild fish verses hatchery steelhead is predator satiation, where increased abundance of outmigrating juveniles may reduce the risk of any one fish to predation (Ryan et al. 2003; Hostetter et al. 2012). In Scott Creek, hatchery steelhead are released into the creek as age-1+ juveniles, and most individuals outmigrate to the ocean within 1 month (Hayes et al. 2004). In contrast, wild steelhead outmigrate from Scott Creek in smaller numbers and over a period of several months, which may increase the time exposed to predators and the individual risk of predation. Regardless of the mechanism, the individual risk of being eaten by an avian predator is greater for wild fish compared with hatchery fish.

Interestingly, we found intermediate-sized individuals experience the highest predation risk in Scott Creek, which suggests western gulls are disproportionately removing average-sized individuals from the population. Our results differ from much of the existing literature, where small size of an individual is often directly related to predation risk. For example, small individuals can be more susceptible to predation because they have reduced swimming ability (Taylor and McPhail 1985) or are less likely to survive the physiological challenges associated with transition from fresh to salt water (Beakes et al. 2010). However, avian predators are one of the few predators of teleost fishes that prefer larger individuals as prey (Sogard 1997), as is supported by a study in the Columbia River where Caspian terns (*Hydroprogne caspia*) preferred larger juvenile steelhead to smaller juvenile Chinook salmon (*Oncorhynchus tshawytscha*) (Collis et al. 2001). The removal of intermediate-sized steelhead by western gulls may be driven by at least two possible mechanisms. First, gulls may be selectively removing individuals based on size. While western gulls are generalists and have a flexible diet (Pierotti and Annett 1990), they have also demonstrated individual specialization for specific prey (Annett and Pierotti 1999), including size-selective predation of urchins in the rocky intertidal zone (Snellen et al. 2007) and selection of larger fish prey by larger males when compared with smaller females (Pierotti 1981). Second, if predation does occur primarily upon steelhead outmigration, it is also possible that gulls are not selecting steelhead based on size, and instead the disproportionate predation of intermediate-sized fish reflects the size of individuals that outmigrate to the ocean. For example, smaller steelhead in Scott Creek may be more likely to delay outmigration (Satterthwaite et al. 2012) and thus may experience mortality in the freshwater environment before given the chance to outmigrate. Similarly, larger male steelhead are more likely to mature in the freshwater environment and thus may never attempt to outmigrate (Phillis et al. 2014). Therefore, although western gulls have been documented as size-selective predators in other systems, there are other factors that may explain the removal of intermediate-sized juvenile steelhead by gull predators in this study.

Survival rates were generally low across all years of the study, but survival increased dramatically for large individuals (Fig. 4B). We found that regardless of origin, larger individuals have 60 times the survival rate than the smallest individuals (Fig. 6), which suggests the characteristics of individuals may be just as important, if not more, than the number of individuals for population recovery. Our results support our predictions and are similar to other studies that have shown relative body length is an important predictor of survival within juvenile salmonid populations (Henderson and Cass 1991; Zabel and Achord 2004; but see Welch et al. 2011). Additionally, increased growth rates can be attained by rearing in estuarine habitat (Hayes et al. 2008), which may contribute to higher survival (Levy and Northcote 1982). Previous research in Scott Creek has shown the importance of lagoon habitat, which provides elevated growth opportunities that allow individuals to attain large body sizes and experience higher survival. As a result, lagoon-reared individuals contribute more than 87% of the returning adult steelhead population (Bond et al. 2008). It is important to note the influence of body size on survival can vary because of environmental conditions even within a system. For example, previous studies have shown size-selective survival for juvenile salmonids occurs primarily during periods of increased environmental stress, such as when ocean entry coincides during years or seasons with unfavorable ocean conditions (Holtby et al. 1990; Saloniemi et al. 2004; Jonsson and Jonsson 2014b). In contrast, size-selective survival is no longer observed for steelhead in Keogh River, British Columbia, potentially because of a decline in ocean productivity that results in reduced growth rates for juvenile steelhead (Welch et al. 2000; Ward 2000). We observed strong size-selective survival for six consecutive cohorts of steelhead over a broad range of coastal environmental conditions. Therefore, our finding that large individuals experience higher survival rates is consistent with many other studies and previous research conducted in Scott Creek.

Consistent with our predictions, we found wild steelhead had significantly higher survival rates than hatchery-raised individuals (Fig. 4B). In a recent review article (Araki et al. 2008), results suggest the reproductive success (e.g., fitness) of salmonids is typically lower for hatchery fish, even if they are progeny of local wild-reared individuals. Decreased fitness of hatchery salmonids is often attributed to relaxed or maladaptive selection for the natural environment (Lynch and O'Hely 2001), because individuals are not exposed to natural selection events at the hatchery that they would have otherwise been exposed to in the wild. However, in Scott Creek, if hatchery individuals survive to adulthood, they can demonstrate similar relative reproductive success as wild adults (G. Charrier, S.A. Hayes, J.C. Garza, and D.E. Pearse, unpublished data). While similar reproductive success between hatchery and wild individuals has also been found in other systems (Dannewitz et al. 2004), this is relatively uncommon (Christie et al. 2012; Jonsson and Jonsson 2014*a*) and is likely due to stochastic variation from the small steelhead population size and strong environmental drivers in Scott Creek (G. Charrier, S.A. Hayes, J.C. Garza, and D.E. Pearse, unpublished data). Therefore, management approaches that focus on increasing wild juvenile survival by addressing avian predation and restoring lost lagoon rearing habitat may result in disproportionately more individuals reaching adulthood than other restoration or management activities.

We found strong overlap among some characteristics associated with predation risk and those associated with increased survival. Consequently, our results suggest that gulls consume primarily intermediate-sized wild steelhead juveniles, and were it not for gull predation many of these individuals (especially those greater than 170 mm FL) may otherwise experience a relatively high probability of survival. This indicates gull predation is an additive source of mortality, similar to modeling work from the Columbia River Basin, which predicted an increase in salmonid population growth with a reduction in Caspian tern predation (Roby et al. 2003). However, gulls are not the only predators that may contribute additive sources of mortality. The relatively stronger relationship between size and survival when compared with size and predation risk (Figs. 3, 4, 6) suggests gulls are not the only source of mortality and that other sources of mortality besides gull predation, such as that by predatory fishes (e.g., Willette 2001), likely drive size-based survival patterns. Our results suggest, therefore, that gulls are removing wild individuals from the population, including the intermediate-sized and large ones that are important for juvenile steelhead population recovery. However, other factors are also contributing to size-dependent survival rates.

Both predation risk and survival rates varied among years; however, the mechanism for interannual variability remains unclear. Predation risk was relatively high in 2006, whereas survival was relatively low for those individuals that outmigrated in 2009 (Fig. 3). Predation risk and survival of salmonids can be affected by many environmental and biological factors, including stream flow (Connor and Tiffan 2012; Hostetter et al. 2012), upwelling (Scheuerell and Williams 2005), and the abundance of prey (type II or III functional response; Holling 1959). Demographic stochasticity can also contribute to variability in mortality rates and contribute to extinction risk, particularly for small populations (Lande 1998). The mechanisms contributing to the interannual variability observed in this study could not be identified with such few years of data ($N = 6$). In addition, small sample sizes of recaptured tags (Table 1) are likely prohibiting robust comparisons of predation risk and survival among years (Fig. 3). Environmental, biological, and demographic factors may contribute to annual fluctuations in survival and predation risk and can contribute to extinction risk or inhibit recovery of salmonid populations.

The effects of individual size and origin on survival and predation risk of juvenile steelhead were based on assumptions about the tagged population and the timing of predation. First, we assumed the tagged population was representative of the hatchery and wild fish that were exposed to gull predation. Although it is possible some hatchery individuals may not have emigrated or may have experienced mortality between release and ocean entry, it is likely that most hatchery individuals emigrated to the ocean because few hatchery steelhead mature and continue to reside in freshwater (2.3%; Phillis et al. 2014), and most individuals emigrate in less than 1 month (Hayes et al. 2004), thereby limiting exposure to sources of mortality in the freshwater environment. We assumed wild lagoon-reared steelhead were susceptible to gull predation because of spatial overlap with gulls; however, previous research suggests gull predation is likely to occur upon emigration to the ocean the following winter (Frechette 2010). Therefore, we compared results between two models that include different assumptions regarding the timing of predation for wild juveniles. The original model (Fig. 3) assumes predation occurs in the lagoon and therefore uses FL at last lagoon capture, whereas the alternative model (Fig. 5) uses an adjusted FL to represent size at outmigration on the first day of sandbar breakage. We found similar results between the two models and therefore demonstrate that potential biases in size assignment for wild lagoon steelhead are not substantial enough to eliminate the relationship between size and predation risk or survival. However, it is important to note that this alternate analysis assumes all wild steelhead in the lagoon survive to emigrate on the first day of sandbar breakage, even though weekly apparent survival probabilities (~0.95; Satterthwaite et al. 2012) document mortality in the Scott Creek lagoon. Therefore, only a subset of tagged individuals included in this study would survive to outmigration, and thus the predation risk estimates reported in this study are conservative. Alternatively, individuals may delay outmigration after sandbar breakage. We cannot determine from the data in this study whether the original model (Fig. 3) or the alternate model (Fig. 5) is more representative of the size and population of wild individuals exposed to predation; however, we can determine that size-based patterns persist through an exploratory analysis using these two scenarios. Regardless, the strong relationship between size and survival has been documented in other studies with wild steelhead in Scott Creek (Bond et al. 2008) and was observed with hatchery individuals in this study (Fig. 6), where size assignment was more robust.

Identifying successful management and conservation measures is a priority for imperiled populations of Pacific salmon. Although conservation efforts often focus on increasing population size by improving habitat or altering hatchery practices (Sharma et al. 2005), the results of this study emphasize that recovery actions should consider individuals whose characteristics contribute disproportionately to population productivity. In Scott Creek, larger (>170 mm FL) wild individuals were less than 6% of the outmigrating steelhead population in this study yet experienced 60 times the survival rate than small wild individuals. Therefore, restoration activities that increase growth and size of steelhead could have dramatic impacts on population size. For instance, future management actions could include efforts to restore the Scott Creek lagoon to its original larger size, which would expand rearing habitat and high growth opportunities that support larger, wild individuals. Although western gulls removed primarily intermediate-sized individuals, they also removed large wild individuals from the population. Therefore, reducing gull predation is a potential management option, especially since western gull populations have increased (Hester et al. 2013), perhaps from increased anthropogenic subsidies (A.-M. Osterback, unpublished data). The results from this study can inform conservation approaches towards the recovery of individuals whose survival is paramount for population recovery.

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