doi:10.7289/V5/TM-SWFSC-555

NOAA Technical Memorandum NMFS

MARCH 2016

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STEELHEAD ABUNDANCE IN SEASONALLY CLOSED ESTUARIES ESTIMATED USING MARK RECAPTURE METHODS

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ABSTRACT

Seasonally-closed estuaries in central California are important rearing habitat for populations of steelhead (*Oncorhynchus mykiss*). During periods of estuary closure, juvenile steelhead recruit to the resulting freshwater lagoons, where they may benefit from enhanced growth conditions afforded by inputs of marine nutrients and subsequent increased marine survival, but also face high predation pressure. Accurate estimation of the number of steelhead rearing in lagoon habitat is, therefore, essential for effective management. We implemented a monthly mark-recapture sampling protocol to estimate abundance of steelhead in the Scott Creek lagoon (Santa Cruz County, California) during three years that experienced different patterns of sandbar closure. Specifically, we conducted paired sampling events in which a marking event and a recapture event were conducted each month during the period of sandbar closure. We used recaptures of steelhead individually marked with passive integrated transponders (PIT tags) to assess performance of three methods of abundance estimation; two methods assuming an open population and one assuming a closed population. Monthly estimates of abundance generated using the open population methods were similar to the closed-population method when recapture rates were ≥10% and the assumption of closure was met. By incorporating each encounter with an individually marked steelhead to inform the estimates of lagoon abundance, the open population methods increased the number of recaptured steelhead in the sampled population, thereby increasing the precision of our abundance estimates relative to the closed-population method. Thus, the open population methods allowed us to more precisely estimate the lagoon population during months when recaptures were very low (0-4%) or the closure assumption was not met. Further, our paired, two-day mark-recapture sampling program provided a consistent sampling routine that could be applied across years with different lagoon closure and population closure dynamics, while minimizing sampling effort and disturbance to the lagoon. Our methods may be broadly applied to bar-built estuary systems throughout central California and will offer valuable insights into ecology and population biology of Central Coast steelhead, which can be applied directly to management of this threatened Distinct Population Segment.

INTRODUCTION

Estuaries provide important nursery habitat for many species of marine and freshwater fishes (Sogard 1992). For anadromous Pacific salmonids (genus *Oncorhynchus*), which exhibit a multi-phase life cycle dependent on both freshwater and marine environments, estuaries serve as important links between these two disparate habitats (Iwata and Komatsu 1984). Timing and extent of estuary use, however, varies considerably with estuary characteristics and within and among salmonid species (Thorpe 1994, Hayes et al. 2004).

Estuaries in central California exhibit a seasonally dynamic hydrographical regime that influences availability of estuarine habitat for salmonids. Rainfall occurs predominantly during winter in central California. During dry summer months, deposition of beach sand coupled with reduced stream flow causes the formation of sandbars across many creek mouths and the subsequent development of a freshwater lagoon in the lowermost portion of the basin (Shapovalov and Taft 1954, Smith 1990). Sandbar formation generally occurs between June and September and creeks become reconnected to the Pacific Ocean following the first heavy rainfall of the year (typically in autumn). Salmonids originating in these seasonally-closed watersheds have a life cycle tied to the seasonal dynamics of sandbar formation. Salmonid smolts can access the ocean and adults may enter spawning habitat only when the estuary is connected to the ocean, whereas nursery habitat exists when the estuary is in the lagoon state.

Downstream migration of juvenile steelhead in this region occurs during winter and spring, with greatest movement occurring between March and June (Shapovalov and Taft 1954, Hayes et al. 2011). In systems with seasonal lagoons, individuals may migrate to sea after rearing for one to several years in upper watershed habitats, or they may exhibit a “cyclical” rearing strategy. Steelhead exhibiting this cyclical strategy rear for a variable period of time in the upper watershed, then migrate to the lagoon where they spend several months before migrating back upstream, ultimately to repeat their downstream migration and enter the ocean a year later (Hayes et al. 2011). Duration of estuarine rearing may vary among individuals and among years, dependent upon fish age/size and the timing of lagoon formation and sandbar breakage (Shapovalov and Taft 1954, Bond et al. 2008, Hayes et al. 2008).

Studies of seasonal lagoon use by steelhead have provided valuable information regarding the ecology and life history of Central California Coast steelhead, including habitat use, growth, survival, and the contribution of lagoon reared individuals to the adult population. Bond et al. (2008) demonstrated that steelhead using seasonal lagoon habitat exhibited considerably greater growth rates than steelhead rearing in the oligotrophic upper watershed. These enhanced growth rates allowed steelhead to reach larger sizes associated with greater marine survival in a shorter period of time than if they had reared exclusively in the upper watershed (Bond et al. 2008, Hayes et al. 2008, 2011). Additional studies indicate that although lagoons represent high reward habitat for steelhead, they may also be high-risk habitats where individuals are exposed to high rates of predation by avian species (Satterthwaite et al. 2012, Frechette at al. 2013). Finally, changes in weather patterns in recent years have led to increasingly variable timing of sandbar formation and breakage (S. Hayes, Unpublished Data), which affects the duration and availability of lagoon habitat, with unknown consequences for salmonid population dynamics and viability.

Given the importance of lagoons as rearing habitat for steelhead, the ability to accurately estimate fish abundance in these habitats is central to the conservation and management of California's coastal steelhead populations. Since 2002, steelhead abundance has been estimated in the lagoon at Scott Creek (37° 2' N, 122° 13' W), a small (75 km^2) coastal watershed in central California that is typical of seasonally closed bar-built estuary systems. Steelhead in Scott Creek are part of the Central Coast Distinct Population Segment of steelhead, which is listed as threatened under the United States Endangered Species Act (ESA; Good et al. 2005). Abundance was estimated using standard capture-mark-recapture methods. Steelhead were captured in the lagoon using a beach seine net, marked with individually identifiable passive integrated transponder (PIT) tags, and released back into the lagoon. During the initial years of lagoon sampling (2003-2008), abundance estimates were generated using the Ricker modification of the Peterson mark-recapture method (Ricker 1975). Tagged individuals were recaptured one month after release to estimate steelhead abundance in the lagoon (hereafter the "lagoon population"). Estimates were averaged to produce a yearly estimate of the lagoon population for 2003-2006 (Hayes et al. 2008), whereas monthly estimates of the lagoon population were generated for 2007 and 2008 (Satterthwaite et al. 2012).

To better understand fluctuations in the lagoon population over the course of the bar-closure period, we began sampling the lagoon twice per month during 2009. We calculated monthly abundance estimates from PIT-tagged steelhead recaptured between one and seven days after release (Satterthwaite et al. 2012). We again employed the closed population Ricker modification of the Peterson method (Ricker 1975) to estimate abundance. The rationale for using the closed-population model was (1) to enable comparison of lagoon abundance estimates with estimates of abundance and survival for steelhead rearing in the upper watershed, where it was necessary to assume a closed population (Satterthwaite et al. 2012) and (2) because movement of steelhead out of the lagoon during the closure period was thought to be minimal, based on detection of PIT-tagged steelhead by instream PIT antennas located upstream of the lagoon in the upper watershed (see Figure 1 in Hayes et al. 2011 for locations of upstream PIT tag antennas).

Our seining efforts, however, were only concentrated in a portion of the total lagoon habitat. It was not possible to seine the upstream portion of the lagoon because of dense vegetation, specifically willow trees (*Salix* sp.), therefore, seining was restricted to the area of the lagoon downstream of the willows (Bond et al. 2008). Detections of PIT-tagged steelhead by an instream PIT tag antenna located in the estuary at the start of the willow-dominated habitat (Figure 1) indicated that PIT-tagged steelhead may move in and out of the sampled area of the lagoon with regularity. Thus, steelhead using the lagoon habitat seem to exhibit movement at two different scales: (1) downstream migration and recruitment to lagoon habitat in the spring with upstream migration back to the upper watershed in the autumn, as described by Hayes et al. (2011); and (2) movement within the lagoon itself (into and out of the sampled area) during the closure period. Migration to and from the lagoon in spring and autumn would not affect monthly estimates of the lagoon population during the closure period. Movement of steelhead out of the sampled area into the willow-dominated habitat during the closure period, however, would influence estimates by invalidating the assumption of a closed population, upon which the

Peterson method is based. Further, the lagoon habitat has become increasingly dynamic in recent years, with periods of bar closure interspersed with periods when the estuary is connected to the ocean. When the estuary is connected to the sea, it may exist either in a lagoon state (which can be sampled via seining) or in a channelized “stream” configuration with no lagoon habitat (which cannot be sampled via seining). Thus, movement of steelhead out of the sampled area of the lagoon, either upstream into willow-dominated habitat or to the ocean would result in biased estimates of the lagoon population, necessitating alternative methods of abundance estimation.

In this paper we use three years of mark-recapture data from the Scott Creek lagoon to examine the consequences of assuming a closed population when estimating steelhead abundance. We identified known violations of the closure assumption based on: (1) movements of PIT-tagged individuals through an instream PIT-tag antenna placed upstream of the lagoon sampling area; and (2) lagoon state (i.e., whether it is closed by sandbar formation or open and connected to the ocean). We apply open-population mark-recapture methods to estimate abundance in the Scott Creek lagoon and compare these with estimates generated previously using the closed-population techniques employed in previous studies (Hayes et al. 2008, Satterthwaite et al. 2012, Frechette et al. 2013). Finally, we identify a sampling method that is robust to changes in population and habitat dynamics, which facilitates application across years with very different lagoon conditions, and we illustrate how these methods may be applied to estimating abundance and exploring steelhead life history in other bar-built estuary systems.

METHODS

The Scott Creek estuary extends approximately 0.8 km upstream of where the creek enters the Pacific Ocean. The estuary can exist in one of three general states: 1) connected and stream-like (no lagoon present); 2) connected to the ocean with a lagoon present (open/lagoon); or 3) closed with a lagoon present (closed/lagoon). When present, the lagoon can be partitioned into three reaches longitudinally. The lowest section of the lagoon extends across the beach to abut the sandbar, and has a substrate composed primarily of sand (Figure 1, lower lagoon). The middle lagoon begins immediately upstream of the Highway 1 bridge and is surrounded by a bulrush (*Scirpus californicus*) dominated marsh. Substrate in the middle lagoon reach is comprised of mixed sand, gravel, and cobble. The upper lagoon is approximately 200 m long and is surrounded by willow (*Salix* sp.) with gravel and cobble substrate. An instream PIT tag antenna is located in the upper lagoon reach and is used to assess the movement of steelhead between the upper lagoon and the middle/lower lagoon. Lagoon depth and surface area vary throughout the lagoon closure period, but previous measurements indicate that depths of 2.1 m (maximum depth) and 0.72 m (mean depth) and surface area of 18,435 m^2 are typical (Hayes et al. 2008).

As introduced previously, we sampled (Figure 2) the Scott Creek estuary when the lagoon was present (open/lagoon or closed/lagoon) using the two-day mark-recapture sampling design described by Satterthwaite et al. (2012), between July and November in 2009, 2010, and 2011. Following the terminology of White and Burnham (1999), we conducted two encounter occasions each month; the first encounter occasion (hereafter referred to as Day 1), was the marking event, in which steelhead were captured, marked with PIT tags, and released back into the lagoon. The second encounter occasion (hereafter referred to as Day 2) was the recapture event, in which all steelhead captured were counted and scanned for the presence of PIT tags. We use the term "paired event" to refer to the marking event (Day 1) and the recapture event (Day 2) within a given month.

Sampling was conducted using a nylon beach seine (30 m × 2 m) following the methods described by Bond et al. (2008). As described previously, dense willow growth prevented seining in the upper lagoon (Figure 1), thus the sampling area was restricted to the lower and middle lagoon. We seined the lagoon sampling area in approximately 50 m sections and ensured that the same area was sampled on each encounter occasion, to ensure that effort was consistent among paired events. During the marking event (Day 1), we deployed PIT tags in a random subset of approximately 100 untagged steelhead and recorded the identity of all steelhead PIT-tagged during previous encounter occasions (hereafter referred to as recaptured steelhead). Although our aim was to tag 100 steelhead per month, this goal was not met for some marking events due to a shortage of PIT tags, failure to capture sufficient numbers of untagged steelhead, or because of adverse weather conditions. Steelhead were handled according to protocols outlined by Hayes et al. (2004) and no steelhead were PIT-tagged during recapture events (Day 2).

To test the hypothesis that the population of steelhead in the lagoon was closed, we examined detections of PIT-tagged steelhead by the instream PIT tag antenna located in the upper lagoon. If a large number of PIT-tagged steelhead were detected moving upstream through the antenna, we would conclude that the population was open, whereas, if no or only a few fish were detected, and the lagoon mouth was closed to the ocean, we would conclude that the population was adequately described by a closed model, conditioned on the assumption that mortality and immigration of unmarked fish was minimal during the relevant time period. To determine whether the lagoon population was effectively closed during a paired event, we calculated the number of steelhead PIT-tagged on Day 1 that were detected by the instream antenna between release on Day 1 and the onset of seining on Day 2. We defined the lagoon population as effectively closed if $< 5\%$ of steelhead PIT-tagged on Day 1 were detected by the PIT tag antenna before seining on Day 2 of a paired event. To determine whether the lagoon population was effectively closed throughout the entire lagoon sampling period (July to November), we calculated the number of PIT-tagged steelhead that were detected by the lagoon antenna between Day 1 of each paired event and 30 November, and were either: (1) subsequently recaptured in the lagoon, or (2) never recaptured in the lagoon after sandbar closure. We examined detections of steelhead tagged in the lagoon in July (newly PIT-tagged steelhead) and steelhead PIT-tagged in the upper watershed before lagoon closure (recaptured individuals). For all other months, we only examined detections of newly PIT-tagged steelhead to avoid double-counting.

We estimated N_i, the abundance of steelhead in the lagoon at time i using two open-population methods and one closed-population method during the periods when the lagoon was present during 2009, 2010, and 2011. First, we used the POPAN (Schwarz and Arnason 1996) formulation of the Jolly-Seber mark-recapture model for open populations (Jolly 1965, Seber 1965). Steelhead that were released unmarked (i.e., without PIT tags) were included in the model as losses on capture (Schwarz and Arnason 1996). Estimates of N_i obtained using the POPAN method will hereafter be referred to as N_P.

Second, we used capture probabilities estimated from a Cormack-Jolly-Seber (CJS) model for open populations (Lebreton et al. 1992) to estimate abundance (N_C) on each sampling occasion using Equation 1 (Equation 4 from Loery et al. 1997), hereafter referred to as the "capture probability method". We present detailed methods for the estimation of N_P and N_C, including the assumptions of the POPAN and CJS models, in Appendix 1.

Equation 1.

$$N_C = \frac{n_i}{p_i}$$

where: n_i = the number of steelhead in the sample at time *i*
p_i = capture probability (from CJS) at time *i*

Finally, we used the closed population Ricker modification of the Peterson method (Equation 3.7 from Ricker 1975) to estimate monthly lagoon abundance, hereafter referred to as N_R. Estimates of N_R and 95% confidence intervals were generated with the mrClosed script in the FSA package for R (Ogle 2011) as described by Satterthwaite et al (2012). Estimates of N_R for 2009 were previously presented by Satterthwaite et al. (2012), and an estimate for August 2010 was presented by Frechette et al. (2013); all other estimates of N_R for 2010 and 2011 are presented for the first time here.

RESULTS

Sandbar dynamics varied considerably among the three years of sampling (Figure 3). The lagoon was present but open to the sea when we sampled in October 2009 and July and November 2010, however, the sandbar was sufficiently formed as to allow lagoon conditions to exist in the absence of a fully closed bar. It must be noted, however, that steelhead could exit the estuary in both directions (upstream and to sea) during months when the lagoon was open during 2009 and 2010. During 2011, the lagoon did not form until November because of abnormally elevated summer stream flows caused by a late rainfall event in June of that year. Thus, lagoon habitat (and consequently sampling) only occurred during November of 2011.

During 2009 we conducted 4 paired events, and captured an average of 616 ± 303 (mean ± 1standard deviation) steelhead on Day 1 and 339 ± 254 steelhead on Day 2 of sampling, with averages taken across all encounter occasions each year. During 2010 we conducted 5 paired events and captured an average of 519 ± 422 steelhead on Day 1 and 199 ± 157 steelhead on Day 2 of sampling. During November 2011, we captured 171 steelhead on Day 1 and 62 on Day 2 of the lone paired event. We PIT-tagged between 50 and 133 steelhead on Day 1 of sampling each month (all years). When combined with previously PIT-tagged steelhead, the number of "marked" individuals released back into the lagoon at the end of Day 1 of each paired event was between 117 and 219 PIT-tagged steelhead. Marked steelhead were recaptured between zero and five times in a given sampling year (Table 1).

We observed considerable movement of steelhead between the sampling area and the upper lagoon throughout the summer and fall lagoon rearing period (Figure 4). During 2009, 256 uniquely PIT-tagged steelhead were detected by the lagoon antenna, of which 41% (105/256) were recaptured during at least one subsequent encounter occasion. During 2010, 377 uniquely PIT-tagged steelhead were detected by the lagoon antenna, of which 49% (184/377) were recaptured during at least one subsequent encounter occasion. This movement is deemed evidence that steelhead in the Scott Creek lagoon should not be considered a closed population for the entirety of the lagoon rearing period (July to November during 2009 and 2010).

During 2009, very few steelhead moved out of the sampling area between Day 1 and Day 2 (<1.5 %; Table 2) of each paired event. The lone exception to this occurred in October when 62% of PIT-tagged steelhead moved upstream immediately after capture and tagging on Day 1. Only 9% (10/113) of PIT tags detected by the antenna between the two encounter occasions in October were recaptured in the lower or middle lagoon on Day 2. Given the lack of emigration from the sampling area during most sample events in 2009, we concluded that the steelhead population in the lagoon was effectively closed between Day 1 and Day 2 for all months except October (Table 2). During 2010, the population of steelhead in the sampling area was effectively closed between Day 1 and Day 2 for July and August only; during these months fewer than 3% of PIT-tagged steelhead moved out of the lagoon sampling area between Day 1 and Day 2 (Table 2). During September, October, and November, 15% to 32% of all PIT-tagged steelhead were detected moving out of the lagoon sampling area between Day 1 and Day 2, indicating an open population (Table 2). No steelhead detected by the lagoon antenna between Day 1 and Day 2 of sampling during 2010 (all months) were subsequently recaptured on Day 2. Thus, individuals that moved out of the lagoon immediately following an initial mark event on Day 1 likely did not return to the sampling area before seining on Day 2, providing support for the presence of an open population. It is important to note that the antenna is not 100% effective at detecting fish due to various factors. In addition to inherent detection inefficiency, the antenna does not sample either the entire width of the channel or the full depth of the water column at some water stages. Thus, it is possible that movement of fish in and out of the sampled area of the lagoon was greater than presented here by some unquantifiable amount. Unfortunately, the lagoon PIT tag antenna malfunctioned in August 2011 and remained off-line until the following year, so we were unable to assess population closure assumptions for the November 2011 sampling events.

Lagoon abundance estimates generated using the three alternative methods (POPAN with losses on capture, N_P; probability of capture, N_C; and the Ricker modification of the Peterson estimator, N_R) for 2009 and 2010 are presented in Figure 5. Since only a single paired event was conducted in 2011 (November; see Figure 3), we were only able to use open population methods to estimate lagoon abundance for 2009 and 2010. Application of the closed population Ricker modification of the Peterson estimator (N_R) to the paired event conducted in November 2011 resulted in an abundance estimate of 473 (95% CI = 330 to 712) steelhead.

To estimate abundance using the POPAN method with losses on capture (N_P), a minimum of three encounter occasions (including the initial marking event) is required. We estimated N_P

from the POPAN model that received the lowest Akaike Information Criterion (corrected for sample size, AICc) score, indicating that the model possessed the optimal balance between parsimony and fit (see Appendix 1 for a description of the alternative model formulations that we compared). The model that received the lowest AICc score (for both 2009 and 2010) had constant survival (Φ_i), and time dependent capture (p_i) and entry (b_i) parameters (Table 3, model 9.A; Table 4, model 10.A). For the 2009 data, model fit was deemed adequate (Program RELEASE; χ^2 = 13.33, df = 19, P = 0.82), therefore no variance inflation factor was applied to the resulting model set (Lebreton et al. 1992). For the 2010 data, however, we observed slight lack of model fit (Program RELEASE; χ^2 = 39.65, df = 26, P = 0.04). It was not possible to determine whether lack of model fit was from excess variation in the data (but correct model structure) or from use of a model that could not account for the underlying structure within the data. The variance inflation factor for the model was 1.5, however, suggesting that model fit was adequate (Lebreton et al. 1992). We applied the variance inflation factor of 1.5 to the resulting model set to account for any overdispersion and used quasi-Akaike's information criterion adjusted for small sample size (QAICc) for model comparison (Lebreton et al. 1992). After application of the variance inflation factor, the best-supported model received nearly all the model support, based on comparison of the resulting QAICc weights (Table 4).

Estimates of survival and capture probabilities (with SE and 95% CI) derived from the optimal POPAN model for 2009 and 2010 are presented in Appendix 2. Estimated survival (Φ) was 0.9888 during 2009 and 0.9955 during 2010. Estimated capture probabilities (p_i) were between 0.0270 (September_1; 2010) and 0.6861 (October_1; 2009). Because capture was time-dependent, abundance on the first sampling occasion was not estimable (Schwarz and Arnason 1996; Arnason and Schwarz 2002). Resulting estimates of N_P for 2009 and 2010 are presented in Figures 5 and 6.

We used estimates of capture probability (p_i) derived using the CJS method to estimate N_C from Equation 1 for sampling occasions in 2009 (Figure 5) and 2010 (Figure 6). A minimum of three capture occasions was required to estimate p_i using CJS, so we could not estimate N_C for 2011. The capture probabilities we used were derived from the CJS model that received the lowest AICc or QAICc score (as appropriate), and thus achieved the optimal balance of parsimony and model fit.

For 2009, the CJS model that received the lowest AICc score was fully time dependent, therefore, the first and last estimates of survival and capture parameters were confounded (Table 3, Model 9.E) and we were not able to estimate abundance (N_C) for these occasions (Appendix 1). Estimated capture probabilities (p_i) that we applied to estimate abundance during 2009 (using Equation 1) were between 0.2593 and 0.5880 (Table 5). Model fit was deemed adequate (Program RELEASE; χ^2 = 13.33, df = 19, P = 0.82), therefore no variance inflation factor was applied (Lebreton et al. 1992).

For the 2010 data, we observed slight lack-of-model fit (Program RELEASE; χ^2 = 9.65, df = 26, P = 0.04), therefore we applied a variance inflation factor ($\hat{c} = \chi^2$/df) of 1.5 to the model set. The CJS model that received the lowest QAICc score had constant survival (Φ_i) and time dependent capture (p_i) probabilities (Table 4, Model 10.E). Estimated survival was 0.9960 (95% CI: 0.9901 to 0.9984). Estimated capture probabilities (p_i) applied to estimate abundance using Equation 1 were between 0.0229 and 0.4330 (Table 5).

DISCUSSION

Here we present a sampling program for assessing abundance of steelhead in California coastal lagoon systems, which is robust to the dynamic nature of these habitats and corresponding fish behavior. The paired, two-day mark-recapture sampling program provides a consistent sampling routine that can be applied across years with different lagoon closure and population closure dynamics. The appropriate method of abundance estimation can then be applied to the mark-recapture events in a given year, based on whether the assumption of a closed population is met. This is particularly important when habitat and population dynamics can change quickly and unpredictably and differentially affect the assumptions on which open and closed population mark-recapture estimators depend. The sampling design we employed might have been analyzed using the robust design model with each month being analogous to the primary periods, between which the population is assumed to be open, and each paired event analogous to the secondary samples, during which the population is assumed to be closed (Kendall et al. 1995). As we demonstrated however, the assumption of a closed population between Day 1 and Day 2 of a paired sampling event was routinely violated, therefore, the robust design model was not considered appropriate for estimating steelhead abundance in the Scott Creek estuary. Of the three approaches we employed to estimate steelhead abundance in the Scott Creek lagoon, the POPAN model produced the narrowest confidence intervals, thus the most precise estimates of abundance during 2009 and 2010. The Ricker modification of the Peterson method produced the widest confidence intervals (i.e., the least precise estimates), however, estimates were nonetheless precise when the closure assumption was met, validating use of this method when requirements of the open population methods (i.e., minimum of three capture occasions) were not met.

According to Ricker (1975), statistical bias in the estimate of N_R is low when MC is greater than 4N, where N is the true population abundance, M is the number of individuals marked in the first sample, and C is the number of individuals captured in the second sample (Ricker 1975). During 2009, MC was much greater than $4N_R$ for all sampling occasions (Appendix 3), suggesting that statistical bias was low (Ricker 1975). Further, recapture rates were fairly high during 2009 (15.5% to 51.8%), suggesting that sampling error was low. During 2010, MR was less than $4N_R$ in September, indicating appreciable statistical bias during that month (Ricker 1975). Recapture rates were very low in 2010 (less than 4%, with the exception of August, when it was 15.5%; Appendix 3). Although we could not directly assess the closure assumption for November 2011, MC was much greater than $4N_R$, indicating that statistical bias was negligible, and the recapture rate was also high (27%). We observed that statistical bias was negligible for all months when the lagoon population was effectively “closed” between within-month sampling events. Thus, the Ricker modification of the Peterson method was appropriate for estimating lagoon abundance when the assumption of a closed population was met and recapture rates were high (≥ 10%).

The open population methods we used employ encounter histories of uniquely PIT-tagged individuals to estimate model parameters, N_P in the case of the POPAN model, and capture probability for CJS. Each encounter with an individually marked steelhead, therefore, informed the estimates of lagoon abundance, thereby increasing the number of recaptured steelhead in the sampled population. Increasing the number of recaptures increased the precision of our abundance estimates relative to the Ricker method, and also allowed us to estimate the lagoon population during months when recaptures were extremely low. The precision of the estimates from the capture probability method depended on the precision of the estimates of probability of capture (p_i) derived from the CJS model. The capture probability method improved precision of estimates relative to the Ricker method, however, capture probabilities (p) used to estimate abundance in 2010 were low, generating estimates that had low precision (Wood et al. 1998) relative to abundance estimates generated using the POPAN method. The POPAN method produced the most precise abundance estimates and was the most appropriate method for estimating abundance regardless of whether the lagoon population was considered open or closed and the number of capture occasions was greater than three.

The two-day sampling design described here has several benefits. First, it requires minimal effort (in terms of personnel and time) to obtain monthly population estimates, and is relatively non-invasive since steelhead and habitat are disturbed only two days per month. Minimizing disturbance to the lagoon is important to protect steelhead and other aquatic biota from exposure to anoxic sediments that may be released from the substrate during seining and from any increased susceptibility to avian predation that may occur after capture. Second, the open population POPAN and CJS models can be applied even when the sandbar is not fully closed and steelhead can potentially emigrate to the ocean. Third, the two-day sampling design allows for the estimation of abundance and survival for all months. Had only one sampling event occurred per month it would not have been possible to use the CJS model to estimate abundance for the first (July) and last (November) months of 2009 because of confounding that results from a fully time-dependent model. That is, when a model is fully time-dependent, as was the case for the best-fit CJS model in 2009, the final abundance and capture probability will be confounded; the initial abundance and capture probability will be likewise confounded (Arnason and Schwarz 2002; Schwarz and Arnason 1996). Finally, we demonstrated that when recapture rates were high and the closure-assumption was met between Day 1 and Day 2 of a paired event, the closed-population method performed nearly as well as the open population methods for estimating lagoon abundance. However, the POPAN and capture probability methods require at least three sampling occasions to estimate survival and abundance. In years when the lagoon forms for a short period of time, the two-day sampling design still allowed reliable estimation of lagoon abundance using the Ricker modification of the Peterson method as long as recapture rates were high and the sampling area was effectively closed between Day 1 and Day 2 of sampling, as we observed in 2011 when the Scott Creek lagoon formed only for a brief period during November.

Application of open-population methods allowed us to observe biological processes that went unnoticed using the closed-population Ricker method. For example, during 2009 sandbar breakage occurred on 15 October during a multi-day rainstorm that elevated stream flows and necessitated that the mark and recapture events be conducted seven days apart, instead of on consecutive days. Due to this extended lapse between mark and recapture events in October, the Ricker method only allowed us to document a decrease in the lagoon population that occurred between August and October 2009. The open population methods allowed us to estimate the lagoon population immediately before and after bar-breakage, enabling us to identify the timing of large-scale movement of steelhead out of the lagoon immediately following bar-breakage. This large-scale movement of steelhead out of the lagoon during October 2009 likely represents movement into the upper watershed, rather than movement to sea. Of 181 PIT-tagged steelhead present in the lagoon on 12 October, 63% (113 individuals) were detected moving upstream past the lagoon antenna, of which 25 individuals were also detected by a second antenna array located approximately 0.2 km upstream of the estuary, consistent with migration into the upper watershed.

Identification of an open population between most sampling intervals in 2010 offers further insight into lagoon population dynamics. Steelhead abundance in the lagoon was greater in 2010 than in 2009, a pattern that would have been obscured by the large confidence intervals surrounding estimates generated using the closed population Ricker method. The open population was the result of steelhead moving upstream between encounter occasions (as indicated by PIT tag antenna detections) and may have been related to the greater lagoon abundance during 2010. Hayes et al. (2008) reported density-dependence in growth rates for steelhead rearing in the Scott Creek lagoon and Satterthwaite et al. (2012) predicted that steelhead move out of the lagoon when growth opportunities become reduced. Thus, the increased movement that we observed between the lagoon sampling area and the upper lagoon during 2010 may have been steelhead responding to decreased growth opportunities in the lagoon caused by density-dependent interactions. Alternatively, risk of predation in the lagoon by species of freshwater birds, for example common mergansers (*Mergus merganser*) and belted kingfishers (*Ceryle alcyon*) is thought to be high (Frechette et al. 2013, Hayes et al. 2011). Freshwater pisciverous birds were more prevalent in the lagoon during summer/autumn 2010 than during 2009 (Frechette et al. 2013). The upper lagoon is characterized by considerable cover in the form of overhanging vegetation and roots, so increased movements between this habitat and the lagoon sampling area could have been in response to increased predation pressure in 2010 relative to 2009. Finally, although mortality rates of steelhead due to PIT-tagging are thought to be relatively low (< 2% of individuals one month post-tagging; Sogard et al. 2009), it is possible that effects of handling and habitat disturbance may be magnified at greater population sizes, resulting in the increased movement out of the sampling area between encounter occasions during 2010.

Management Implications

The dynamics of bar-built estuaries, specifically the timing and duration of sandbar closure, are tied to stream flow, sand availability, and wave dynamics, which in turn are driven by rainfall and storm surges (Shapavaolv and Taft 1954, Smith 1990). In recent years, the timing and strength of storms has shifted, and the sandbar at the mouth of Scott Creek has formed earlier and opened later in the season (A. Osterback, personal observation). As such changes in sandbar dynamics alter availability of lagoon habitat, we expect that steelhead population dynamics also may change.

Further, like many estuaries worldwide, those in central California have been heavily impacted by human use (Heady et al. 2015). Many have been channelized through urban areas or to permit bridge construction, effectively reducing available lagoon habitat. Habitat may also become shallower (agraded), which reduces predator refuge and increases summer water temperatures. Intentional breaching of sandbars during the closure period by urban managers or the public may eliminate lagoon habitat altogether (Smith 1990, Heady et al. 2015). Previous work in Scott Creek has demonstrated the importance of lagoon-reared steelhead to the persistence of populations in this region and underscored the importance of maintaining this critical habitat (Bond et al. 2008, Hayes et al. 2008, 2011). The degree of population openness that we observed in the Scott Creek lagoon further highlights the importance of maintaining connectivity (Hayes et al. 2011), particularly during years of high population abundance, when steelhead may need to move between habitats more frequently to compensate for reduced growth opportunities or increased predation risk in the lagoon.

Finally, increased growth opportunities afforded by estuarine rearing have been directly linked to increased adult escapement for central California steelhead (Bond et al. 2008, Hayes et al. 2008). Although smaller parr (<150 mm) constitute a greater proportion of the spring downstream migrant population, these parr typically recruit to the lagoon and migrate to sea as smolts in subsequent years following lagoon rearing. These lagoon-reared smolts are disproportionately represented in the population of adult steelhead returning to spawn (Bond et al. 2008, Osterback et al. 2014). Thus, we recommend the exploration of lagoon abundance estimates as a means of forecasting returns of adults to natal rivers, which could directly inform recovery plans. A program to monitor lagoon abundance, such as we described here for Scott Creek, can be applied to assess outcomes of management strategies designed to enhance lagoon rearing habitat in this and other bar-built estuary systems.

The sampling program that we have implemented in Scott Creek permits reliable estimation of lagoon steelhead abundance given habitat and population dynamics that are unpredictable and change quickly with climatic events. Scott Creek is typical of central California watersheds, therefore, this sampling design is readily applicable to other bar-built coastal estuaries in California. By minimizing effort to two days of sampling per month, one team could effectively conduct sampling across many central California watersheds, providing valuable information that can be built into management and recovery plans for this threatened species. In addition to monitoring changes in abundance with changing climate or as a result of management actions, these studies can further enhance our understating of how key biological processes operate across Central California Coast steelhead populations. Implementing studies of lagoon populations throughout central California bar-built estuaries would offer further insights into recruitment, growth and density dependence, predation and survival rates, and the relative contribution of lagoon rearing to the persistence of the Central Coast steelhead Distinct Population Segment as a whole.

ACKNOWLEDGEMENTS

This project was funded by the California Department of Fish and Wildlife Fisheries Restoration Grant Program. Big Creek Lumber, CalPoly Swanton Pacific Ranch, and the County of Santa Cruz provided site access and project support. S. Auten, B. Dietterick, and J. Webb were especially helpful. We thank C. Schwarz for modeling advice. We thank J. Kiernan, S. Lindley, H. McRae Tabisola, and S. Sogard for their helpful revisions of this manuscript. An army of volunteers from the NOAA's Fisheries Ecology Division, Moss Landing Marine Laboratories, and the University of California Santa Cruz helped pull the seine net and sort, count, and tag fish during monthly lagoon sampling. Although too many to name, their excellent attitudes and hard work are greatly appreciated. We would especially like to thank M. Beakes, J. Harding, C. Kern, J. Moore, N. Parker, J. Perez, C. Phyllis,N. Retford, A. Soberij, and S. Sogard.

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FIGURES

Figure 1. Diagram of the Scott Creek estuary during sandbar closure showing the location of lower, middle, and upper reaches. The California Highway 1 bridge crosses Scott Creek, and was used to arbitrarily deliniate the lower and middle lagoon sampling areas. The lower limit of the upper lagoon was defined by the start of streambank vegetation predominantly comprised of willow (*Salix* sp.). The lagoon PIT tag antenna was situated approximatly 200 m upstream of the start of the upper lagoon.

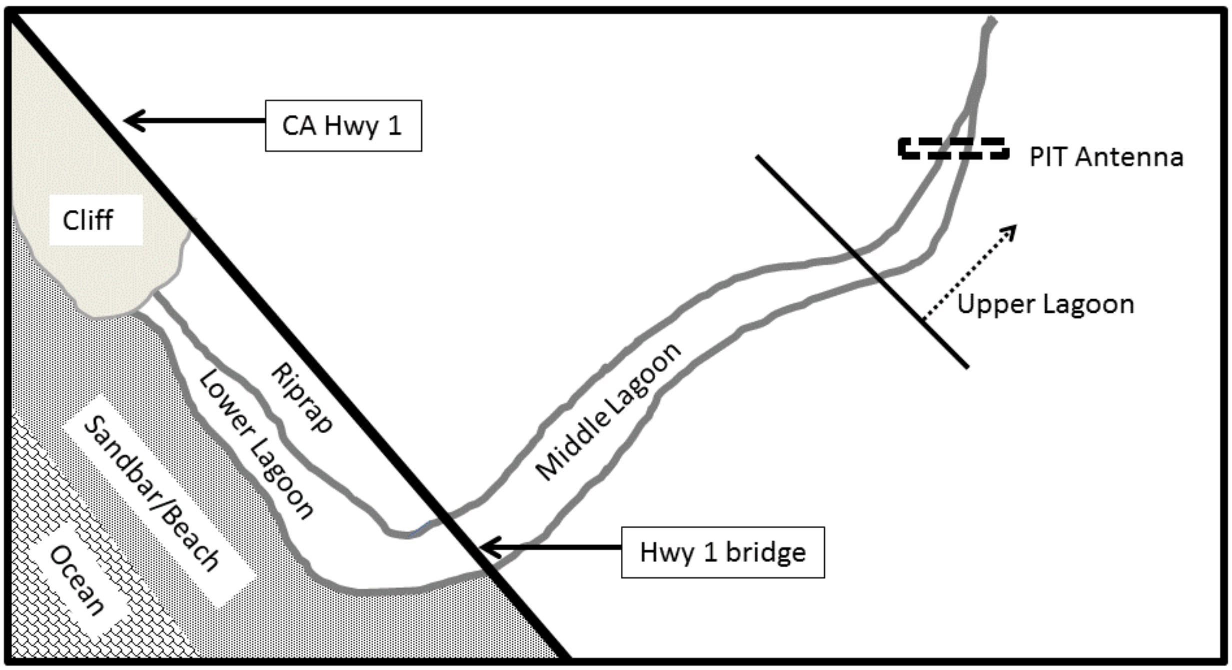


Figure 2. Seining the Scott Creek middle lagoon. The white dashed line indicates the upper limit of the middle lagoon; beyond the line, willow (*Salix* sp.) are evident along the streambank.

Figure 3. Sandbar and population dynamics in the Scott Creek estuary, 2009-2011. Sampling occasions are abbreviated by the first letter of the month with the number 1 indicating Day 1 of sampling and 2 indicating Day 2 of sampling each month (J = July; A = August; S = September; O = October). The state of the estuary, either closed with a lagoon present (C), or open (O) is indicated for each sampling occasion. The state of the population (O = open; C = closed) was assigned based on detections of PIT-tagged steelhead by the instream PIT antenna located in the upper lagoon. Utility of each estimation method (N_P = POPAN with losses on capture; N_C = probability of capture; N_R = Ricker modification of the Peterson estimator) is presented for each sampling occasion as applicable (dark gray box) or not applicable (light gray box with double asterisks) given sandbar and population dynamics. Months when sampling was not conducted is indicated by NS.

	Occasion	J-1	J-2	A-1	A-2	S-1	S-2	O-1	O-2	N-1	N-2
2009	Lagoon State	**C**	**C**	**C**	**C**	**C**	**C**	**C**	**O**	**C**	**C**
	Population State	**C**	**C**	**C**	**C**	**NS**	**NS**	**C**	**O**	**C**	**C**
Estimation Method	N_P	**				**NS**	**NS**				
	N_C	**				**NS**	**NS**				**
	N_R	**		**		**NS**	**NS**	**		**	
2010	Lagoon State	**O**	**O**	**C**	**C**	**C**	**C**	**C**	**C**	**O**	**O**
	Population State	**O**	**O**	**C**	**C**	**C**	**C**	**C**	**C**	**O**	**O**
Estimation Method	N_P	**									**
	N_C	**									**
	N_R	**		**		**		**		**	**
2011	Lagoon State	**O**	**O**	**O**	**O**	**O**	**O**	**O**	**O**	**C**	**C**
	Population State	**NS**	**NS**	**NS**	**NS**	**NS**	**NS**	**NS**	**NS**	**C**	**C**
Estimation Method	N_P	**	**	**	**	**	**	**	**	**	**
	N_C	**	**	**	**	**	**	**	**	**	**
	N_R	**	**	**	**	**	**	**	**	**	

Figure 4. Number of steelhead marked each month in the Scott Creek lagoon (all tagged fish in July, only newly tagged fish in all other months) during 2009 (left panel) and 2010 (right panel) that were PIT-tagged each month and subsequently detected by the lagoon antenna (Tagged/Detected, grey shading) or not detected (Tagged/ND, black shading).

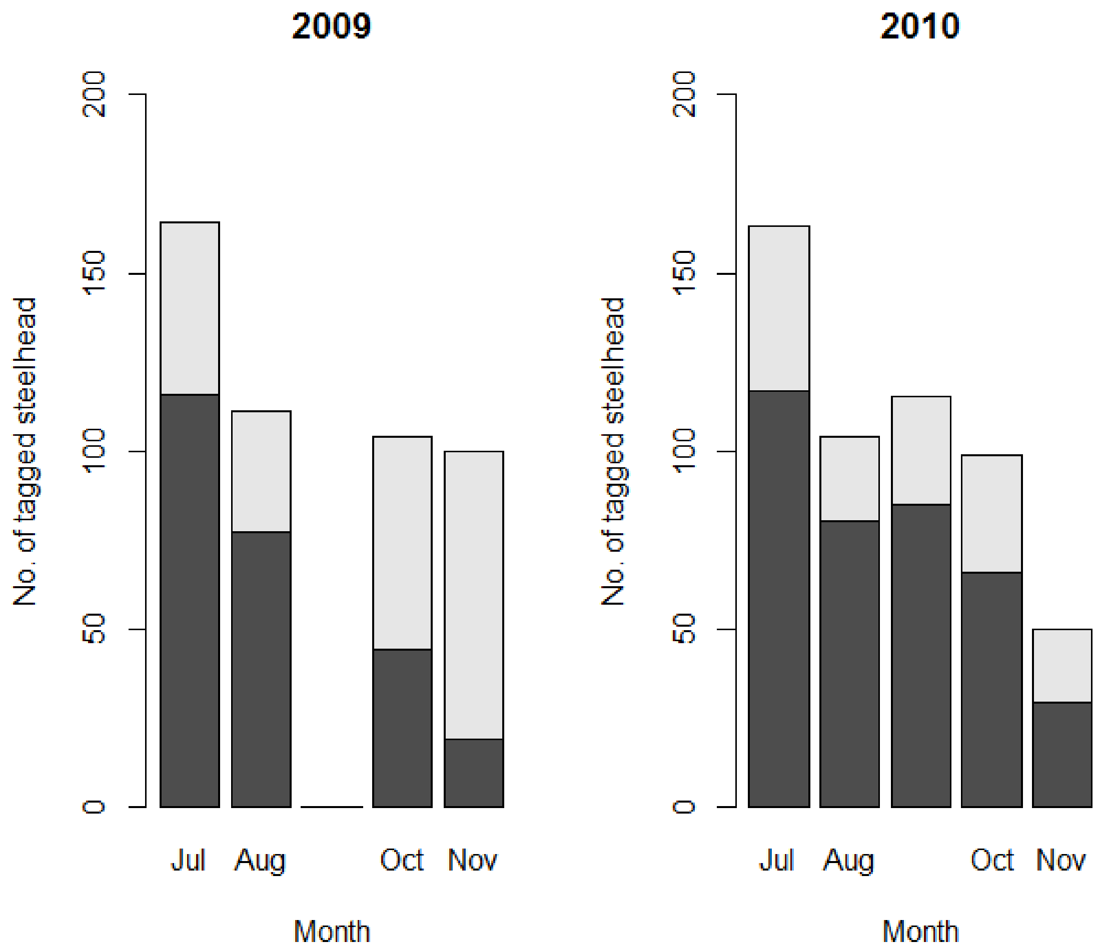


Figure 5. Estimates of steelhead abundance (with 95% CI) in the Scott Creek lagoon during 2009. POPAN abundance (N_P) was derived from the best-supported POPAN model [Φ(.)p(t)β(t)], where (t) = time dependent and (.) = constant. CJS abundance (N_C) was derived from the best-supported CJS model [Φ(t)p(t)] by dividing the number of steelhead in the sample at time *i* by the capture probability (from CJS) at time *i*. Ricker abundance (N_R) was estimated using the Ricker modification of the Peterson estimate for closed-populations. The x-axis indicates the sampling period by month (J = July; A = August; S = September, O = October, N = November) and occasion (1 = 1st sampling occasion per month; 2 = 2nd sampling occasion per month).

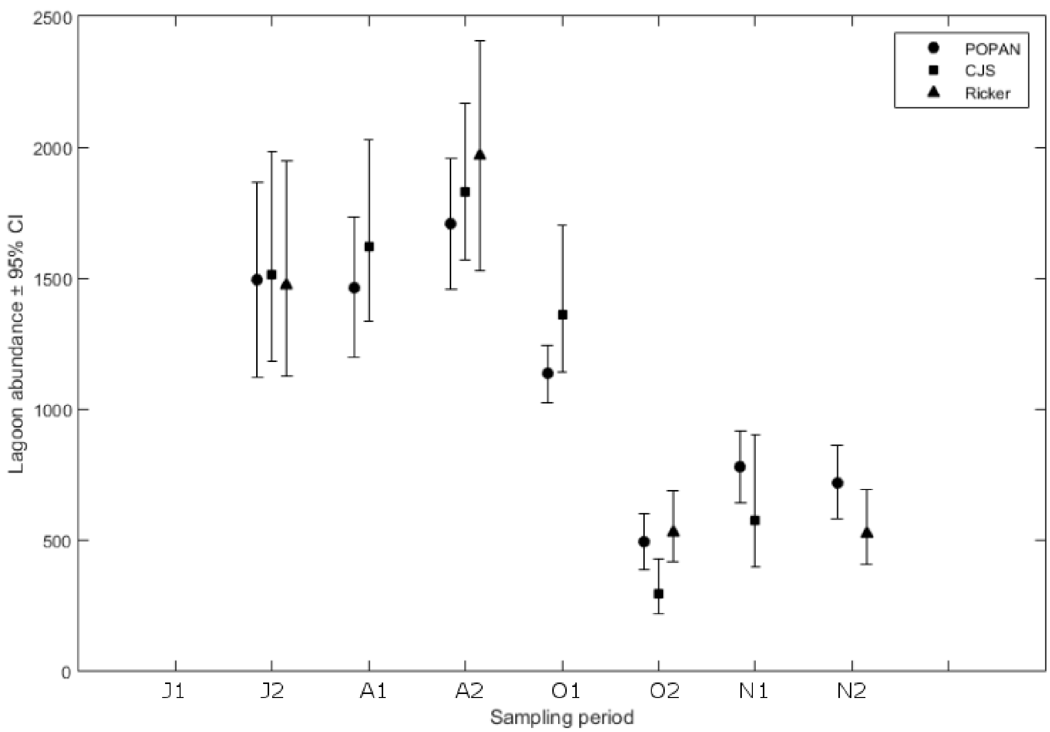
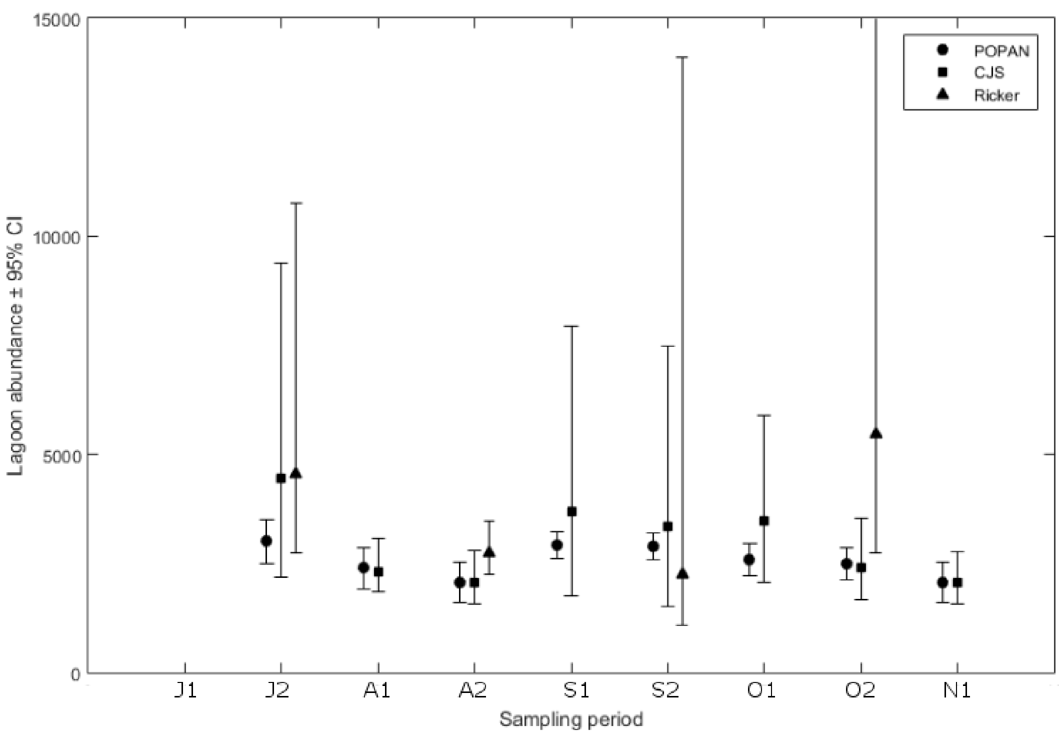


Figure 6. Estimates of steelhead abundance (with 95% CI) in the Scott Creek lagoon during 2010. POPAN abundance (N_P) was derived from the best-supported POPAN model [Φ(.)p(t)β(t)], where (t) = time dependent, (.) = constant. CJS abundance (N_C) was derived from the best-supported CJS model [Φ(.)p(t)] by dividing the number of steelhead in the sample at time *i* by the capture probability (from CJS) at time *i*. Ricker abundance (N_R) was estimated using the Ricker modification of the Peterson estimate for closed-populations. The x-axis indicates the sampling period by month (J = July; A = August; S = September, O = October, N = November) and occasion (1 = 1st sampling occasion per month; 2 = 2nd sampling occasion per month). Note the different y-axes. The upper 95% confidence limit for O_2 was 24,390 and is not shown to maintain legibility of the figure.



TABLES

Table 1. Percentage of individual PIT-tagged steelhead that were recaptured between zero and five times in the Scott Creek lagoon during 2009 and 2010. No individual steelhead were recaptured more than 5 times.

Number of recapture events	% of individuals	
	2009	2010
0	41.2	57.9
1	32.9	28.8
2	15.9	10.4
3	7.3	2.1
4	2.5	0.8
5	0.2	0

Table 2. PIT-tagged steelhead released on Day 1 of sampling and subsequently detected by the lagoon antenna before sampling on Day 2, and either not recaptured or recaptured on Day 2 of sampling.

Year	Month	Marked	Fish detected/ not recaptured (Day 2)		Fish detected/ recaptured (Day 2)	
			n	%	n	%
2009	July	164	2	1.22	0	0
	August	197	0	0	0	0
	October	181	113	62.43	10	8.85
	November	116	0	0.00	0	0
2010	July	163	5	3.07	0	0
	August	219	5	2.28	0	0
	September	127	40	31.50	0	0
	October	124	19	15.32	0	0
	November	220	36	16.36	0	0

Table 3. Comparison of candidate POPAN and CJS models used to estimate abundance of steelhead in the Scott Creek lagoon during 2009. Abundance estimates (N_P) were generated by the POPAN method with losses on capture from the model with the lowest AICc. The CJS model with the lowest AICc value was used to derive estimates of capture probability, which we used as an input for Equation 1 to estimate abundance (N_C). AICc = Akaike's Information Criterion adjusted for small sample sizes, Delta AICc = difference in AICc between the AICc for a given model and the AICc for the best-supported model, AICc Weight = Akaike weight indicating the relative support for a model, based on AICc, Φ_i = probability of survival, p_i = probability of capture, b_i = probability of entry, (t) = time dependent, (.) = constant.

Method	Model ID	Model	AICc	ΔAICc	AICc weights
POPAN	9.A	Φ(.)p(t)b(t)	2147.391	0.000	1.000
	9.B	Φ(t)p(t)b(t)	2195.845	48.454	0.000
	9.C	Φ(t)p(.)b(t)	2236.327	88.936	0.000
	9.D	Φ(.)p(.)b(t)	2542.880	395.488	0.000
CJS	9.E	Φ(t)p(t)	2047.649	0.000	0.995
	9.F	Φ(.)p(t)	2058.357	10.709	0.005
	9.G	Φ(t)p(.)	2062.707	15.059	0.001
	9.H	Φ(.)p(.)	2146.841	99.193	0.000

Table 4. Comparison of candidate POPAN and CJS models used to estimate abundance of steelhead in the Scott Creek lagoon during 2010. Abundance estimates (N_P) were generated by the POPAN method with losses on capture from the model with the lowest AICc. The CJS model with the lowest AICc value was used to derive estimates of capture probability, which we used as an input for Equation 1 to estimate abundance (N_C). QAICc = quasi-Akaike's Information Criterion adjusted for small sample sizes, Delta qAICc = difference in QAICc between the QAICc for a given model and the QAICc for the best-supported model, QAICc Weight = quasi-Akaike weight indicating the relative support for a model, based on QAICc, Φ_i = probability of survival, p_i = probability of capture, b_i = probability of entry, (t) = time dependent, (.) = constant.

Method	Model ID	Model	QAICc	ΔQAICc	QAICc weights
POPAN	10.A	Φ(.)p(t)b(t)	1355.839	0.000	0.999
	10.B	Φ(t)p(t)b(t)	1369.691	13.851	0.001
	10.C	Φ(t)p(.)b(t)	1697.837	341.998	0.000
	10.D	Φ(.)p(.)b(t)	2135.521	779.682	0.000
CJS	10.E	Φ(.)p(t)	1287.418	0.000	0.991
	10.F	Φ(t)p(t)	1296.918	9.500	0.009
	10.G	Φ(t)p(.)	1477.457	190.039	0.000
	10.H	Φ(.)p(.)	1492.327	204.909	0.000

Table 5. Estimates of probability of capture from the best fit CJS models for 2009 [Φ(t)p(t)] and 2010 [Φ(.)p(t)] used to estimate abundance (N_C) using Equation 1. Estimates of the survival parameters (Φ) are also presented. Estimates for each parameter are presented with associated standard errors (SE) and upper and lower 95% confidence intervals (CI).

Year	Parameter	Parameter Estimate	SE	Lower 95% CI	Upper 95% CI
2009	p (Jul_2)	0.262	0.035	0.200	0.335
	p (Aug_1)	0.472	0.045	0.385	0.559
	p (Aug_2)	0.391	0.031	0.333	0.452
	p (Oct_1)	0.686	0.034	0.617	0.748
	p (Oct_2)	0.226	0.029	0.173	0.289
	p (Nov_1)	0.215	0.024	0.171	0.266
	p (Nov_2)	0.248	0.029	0.196	0.308
	Φ_1 (Jul_1 to Jul_2)		Confounded		
	Φ_2 (Jul_2 to Aug_1)	0.992	0.003	0.985	0.995
	Φ_3 (Aug_1 to Aug_2)	1.000	0.000	1.000	1.000
	Φ_4 (Aug_2 to Oct_1)	0.990	0.002	0.984	0.993
	Φ_5 (Oct_1 to Oct_2)	0.919	0.020	0.869	0.951
	Φ_6 (Oct_2 to Nov_1)	0.984	0.009	0.950	0.995
	Φ_6 (Nov_1 to Nov_2)		Confounded		
2010	p (Jul_2)	0.062	0.023	0.029	0.127
	p (Aug_1)	0.433	0.056	0.329	0.544
	p (Aug_2)	0.196	0.029	0.146	0.258
	p ($Sept_1$)	0.035	0.013	0.016	0.073
	p ($Sept_2$)	0.023	0.009	0.010	0.050
	p (Oct_1)	0.060	0.016	0.035	0.100
	p (Oct_2)	0.090	0.017	0.061	0.131
	p (Nov_1)	0.356	0.051	0.264	0.461
	Φ	0.996	0.002	0.990	0.998

APPENDICES

Appendix 1.

Abundance Estimates using POPAN with Losses on Capture (N_P)

We used the POPAN (Schwarz and Arnason 1996) formulation of the Jolly-Seber mark-recapture model for open populations (Jolly 1965, Seber 1965), to estimate steelhead abundance (N_i) in the lagoon on encounter occasion *i*. This estimate of N_i was derived from a set of four fundamental parameters also estimated using POPAN, as implemented within Program MARK v. 5.1 (White and Burnham 1999). The fundamental parameters were: (1) the probability that an individual steelhead survives between occasion *i* and *i* + 1 (Φ_i); (2) probability of capture (p_i) at occasion *i*; (3) super-population size (N), the total number of steelhead that recruit to the estuary and survive to time *i* + 1 (Schwarz and Arnason 1996), and (4) the proportion of individual steelhead from the super-population that entered the lagoon sampling area after time *i* and survived to time *i* +1 (probability of entry, b_i). It must be noted that probability of entry was not of direct interest and is biased due to our treatment of releases of unmarked steelhead as "losses on capture"; however, this should not have biased estimates of N_i, which was the parameter we were interested in estimating (Schwarz and Arnason 1996).

We created a candidate set of four models, in which survival (Φ_i) and probability of capture (p_i) parameters were either held constant (·) or allowed to vary with time (t). Probability of entry (b_i) was always allowed to vary with time. When fitting the candidate models, we used the logit link function for the parameters Φ_i and p_i and the identity link function for the parameter N. The set of b_i parameters must sum to 1, so we used the multinomial logit link function to constrain the b_i parameters to facilitate convergence (Schwarz and Arnason 1996, White and Burnham 1999).

We compared models using Akaike's Information Criterion, adjusted for small sample sizes (AICc). The model obtaining the optimal balance of parsimony and fit received the lowest AICc value, and was used to estimate lagoon abundance (referred to as N_P in the text). We assessed relative support of models in the candidate model set by comparing AICc weights (Burnham and Anderson 2002). We applied a χ^2 goodness of fit test to the fully time-dependent model to assess model fit. Goodness of fit testing was accomplished using Program RELEASE (Burnham et al. 1987), run within Program MARK v. 5.1 (White and Burnham 1999). When lack of fit was detected (see Results), we applied a variance inflation factor ($\hat{c} = \chi^2/\text{df}$, where df = degrees of freedom) to the model set and subsequently used quasi-Akaike's Information Criterion (QAICc) for model comparison (Lebreton et al. 1992).

Key assumptions of the POPAN model are: (1) tags are retained throughout the experiment and are read properly; (2) sampling is instantaneous relative to the study period; (3) probability of capture and survival of marked and unmarked individuals are homogeneous; and (4) the study area did not change in size during the course of the study (Lebreton et al. 1992, Arnason and Schwarz 2002). We assumed that tag loss by steelhead was negligible, as Sogard et al. (2009) reported that PIT tag retention rates for juvenile steelhead were > 95%. We also assumed field personnel correctly read and recorded all PIT tag identities. Seining efforts were considered instantaneous relative to inter-survey intervals (which ranged between 1 and 41 days). We assessed assumption 3 using Program RELEASE (Burnham et al. 1987), run within Program MARK v. 5.1 (White and Burnham 1999). Finally, the area of the lagoon that was seined (the sampling area) was held constant among surveys.

Abundance Estimates using the Capture Probability Method (N_C)

We used the Cormack-Jolly-Seber (CJS) model for open populations (implemented within Program MARK v. 5.1, White and Burnham 1999) to estimate two fundamental parameters: (1) the probability that an individual steelhead survives between sampling occasion *i* and *i* + 1 (Φ_i) and (2) probability of capture (p_i) at sampling occasion *i*. We created a candidate set of four models, in which survival (Φ_i), and probability of capture (p_i) parameters were either held constant (·) or allowed to vary with time (t), and we used the logit link function when fitting the candidate models. As with the POPAN models, we used AICc to select the best supported model and compared AICc weights to assess relative support of models (Burnham and Anderson 2002). The capture probabilities from the model with the lowest AICc score were used in Equation 2 to estimate the abundance of steelhead in the lagoon for each sampling occasion *i*. Abundance estimates generated using this method are referred to as N_C in the text.

The standard assumptions of the CJS model are the same as assumptions one, two, and three, described previously for the POPAN model (Lebreton et al. 1992). As with the POPAN model, we tested the assumptions of homogenous catchability and survival of marked and unmarked individuals using Program RELEASE (Burnham et al. 1987), and applied a variance inflation factor if lack of fit was detected (Lebreton et al. 1992).

Appendix 2.

Estimates of survival (Φ) and capture (p) parameters from the best supported POPAN models for 2009 [Φ(.)p(t)β(t)] and 2010 [Φ(.)p(t)β(t)]. Estimates for each parameter are presented with associated standard errors (SE) and upper and lower 95% confidence intervals (CI).

Year	Parameter	Parameter Estimate	SE	Lower 95% CI	Upper 95% CI
2009	Φ	0.989	0.001	0.986	0.991
	p (Jul_1)	Confounded			
	p (Jul_2)	0.262	0.035	0.200	0.335
	p (Aug_1)	0.472	0.045	0.385	0.559
	p (Aug_2)	0.391	0.031	0.333	0.452
	p (Oct_1)	0.686	0.034	0.617	0.748
	p (Oct_2)	0.226	0.029	0.173	0.289
	p (Nov_1)	0.215	0.024	0.171	0.266
	p (Nov_2)	0.248	0.029	0.196	0.308
2010	Φ	0.996	0.002	0.990	0.998
	p (Jul_1)	Confounded			
	p (Jul_2)	0.092	0.012	0.072	0.117
	p (Aug_1)	0.419	0.053	0.319	0.526
	p (Aug_2)	0.197	0.029	0.147	0.260
	p (Sep_1)	0.044	0.005	0.034	0.056
	p (Sep_2)	0.027	0.004	0.020	0.036
	p (Oct_1)	0.080	0.010	0.063	0.101
	p (Oct_2)	0.087	0.010	0.068	0.110
	p (Nov_1)	0.356	0.051	0.263	0.461

Appendix 3.

Captures of steelhead in the Scott Creek lagoon on the second sampling occasion of each month during the lagoon period, 2009 and 2010. The number of fish marked on occasion 1 (M) are presented with the number recaptured on occasion 2 (R) and the total number of steelhead captured on occasion 2 (C). The ratio of recaptured fish (PIT-tagged on occasion 1) to the total sample on occasion 2 (R:C) is presented as a percentage. The total number of recaptures on occasion 2 (including fish not handled on occasion 1) are presented as a number (Total Recaps) and as a ratio of total fish captured on occasion 2 (Total R:C) expressed as a percentage. Since only one recapture occasion was conducted in 2011, Total Recaps and the Total R:C ratio are not applicable (NA).

Year	Sampling Occasion	M	R	C	R:C (%)	MC	Total Recaps	Total R:C (%)
2009	$July_2$	164	43	392	11.0	64288	61	15.6
	$August_2$	197	67	674	9.9	132778	112	16.6
	$October_2$	181	38	112	33.9	20272	58	51.8
	$November_2$	117	39	177	22.0	20709	67	37.9
2010	$July_2$	163	9	277	3.3	45151	20	7.2
	$August_2$	419	62	408	15.2	170952	73	17.9
	$September_2$	115	3	77	3.9	8855	12	15.6
	$October_2$	124	4	217	1.8	26908	52	24.0
	November2	220	0	16	0.0	3520	170	23.2
2011	November2	133	16	59	27.1	7847	NA	NA