An Evaluation of the Utility of Snorkel Surveys for Estimating Population Size and Tracking Trends in Relative Abundance of Rainbow Trout in the Lee's Ferry Reach of the Colorado River

FINAL

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January 11, 2006

Abstract

Reliable indices of abundance and estimates of total population size are critical for management of fish resources in the Colorado River in Grand Canyon. Boat electrofishing has been used to enumerate rainbow trout in the Colorado River in Grand Canyon for almost two decades. Boat electrofishing can only be effectively conducted adjacent to the shore and cannot be used to directly measure the apparent density of fish in offshore areas. In addition, the proportion of the fish caught per unit of effort, hereafter referred to as catchability (q), is not known. These weaknesses pose three major problems. First, to index population size from catch per effort (CPE) data, it is necessary to assume that catchability is either constant across all sample periods and habitat types, or a random effect contributing to the overall variance in relative densities. Second, estimates of the total population size, derived solely from the expansion of apparent shoreline densities, are very uncertain as the offshore area in larger rivers constitutes the majority of the total wetted area over which fish are potentially distributed. Finally, even if apparent shoreline densities are only being used to index total population size, it is necessary to assume that the ratio of fish in shoreline to offshore areas is constant or a random effect among sample periods. The relative densities of fish in offshore and shoreline areas may be controlled by the overall population density, physical conditions (velocity and depth, width of the varial zone, food availability, ambient light intensity) driven by dam operations and annual and seasonal changes in hydrology, and seasonal factors influencing behavior (e.g., spawning). These factors may vary systematically over time and therefore have the potential to corrupt trends in relative abundance based on index sampling of shoreline areas only. To address these issues, snorkel surveys were implemented in the Lee's Ferry reach in June 2001, June and October 2002, and April 2003. Diel studies were used to examine changes in the apparent density of fish in shoreline and offshore areas over a 24-hr.+ period. Statistics on apparent fish densities in offshore and shoreline areas from a randomly selected set of sites were used to evaluate the reliability of snorkeling to estimate trends in relative abundance and population size. Apparent shoreline density estimates derived from boat electrofishing and snorkeling were compared.

There were very large differences in the number of fish observed over a 24-hr. cycle during the diel studies, however the extent of these differences varied across seasons. The ratio of the average daytime count to the peak night count was 0.47 at 8-mile in June 2002 and ranged from 0.36 to 0.39 across the 3 sites in October 2002. In contrast, the ratio of the average daytime to peak nighttime count in April 2003, the peak of the spawning season, was much higher, ranging from 0.62 at the 8-mile site to 0.97 at the 3.5-mile site. The general pattern of apparent fish densities that was observed at the diel study sites consisted of: 1) a relatively uniform distribution of fish along the cross-section during daylight hours at high discharges; 2) increased densities at onshore lanes in the early-evening when discharge was still high; and 3) a decline in densities at onshore lanes during the early morning when discharge was low. In many cases, the changes in apparent density in shoreline lanes were accompanied by opposite changes in apparent density in the outer lanes. We consider this reasonable evidence that onshore-offshore movement was at least partially responsible for the changes in apparent density that were observed between 4-hr. survey periods. Changes in the onshore-offshore distribution of fish over a 24-hr. period appeared to depend on ambient light intensity, discharge, and spawning behavior.

Apparent shoreline fish densities estimated by snorkel surveys declined noticeable from June 2001 (6.2 fish/100 m^2) through April 2003 (1.9 fish/100 m^2). The apparent density of fish in offshore zones was typically about 50% of the apparent density in shoreline areas but varied considerably among trips. The ratio in October 2002 averaged across habitat types was only 0.17 compared to 0.95 in April 2003. Total population estimates declined from 100,000 to 50,000 fish between June and October 2002 and then increased to about 80,000 fish by April 2003. This unlikely change in population size could have been caused by differences in underwater visibility across sample periods. Expanded apparent density estimates from a limited number of diel study sites suggest a decline in population size from about 100,000 fish in June 2002 to 60,000 fish by April 2003.

Acknowledgements

Grand Canyon Monitoring and Research Center (GCMRC) supported this work through a cooperative agreement with the Arizona Game and Fish Department. Thanks to B. Persons for providing administrative support and a review of an earlier draft of this document. Thanks to J. Sneep, S. Decker, R. Ahrens, R. Longe, S. Martell, S. Hall, A. Mankinster, R. Schmidt, and M. Carone for conducting snorkel surveys. Thanks to C. Fritzinger, D. Foster and S. Davis for providing logistical support. Thanks to A. Robinson and an anonymous external reviewer for providing helpful comments on an earlier draft.

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1.0 Introduction

Reliable indices of abundance and estimates of total population size are critical for management of fish resources in the Colorado River in Grand Canyon. Trends in indices of abundance can be compared to changes in the operation of Glen Canyon Dam (GCD) to determine if these changes are having population-level effects. Estimates of fish densities in the Colorado River can be compared to densities in other rivers and to various bio-standards and targets to determine the status of the population. Estimates of total abundance are also required for bioenergetic calculations used to evaluate hypotheses concerning food limitation and predation impacts.

Boat electrofishing has been used to enumerate rainbow trout in the Colorado River in Grand Canyon for almost two decades. The number of fish caught per minute of boat electrofishing effort (CPE) has been the principal index of the abundance of rainbow trout (*Onchorhynchus mykiss*) in the Lee's Ferry reach and in reaches in Grand Canyon (e.g. Speas et al. 2002). Boat electrofishing can only be effectively conducted adjacent to the shore and cannot be used to directly index the density of fish in offshore areas. In addition, the proportion of the fish caught per unit of effort, hereafter referred to as catchability (q), is not known. These weaknesses pose three major problems. First, to index population size from catch per effort (CPE) data, it is necessary to assume that catchability is either constant across all sample periods and habitat types, or is a random effect contributing to the overall variance in relative densities. Second, estimates of the total population size, derived solely from the expansion of apparent shoreline densities, are very uncertain as the offshore area in larger rivers constitutes the majority of the total wetted area over which fish are potentially distributed. Finally, even if apparent shoreline densities are only being used to index total population size, it is necessary to assume that the ratio of fish in shoreline to offshore areas is constant among sample periods. The relative densities of fish in offshore and shoreline areas may be controlled by the overall population density, physical conditions (velocity and depth, width of the varial zone, food availability, ambient light intensity) driven by dam operations and annual and seasonal changes in hydrology, and seasonal factors influencing behavior (e.g., spawning). These factors may vary systematically over time and therefore have the potential to corrupt trends in relative abundance based on index sampling of shoreline areas only.

Underwater observation has been used extensively in behavioral studies of fish in streams (Keenlyside 1962, Fuasch and White 1981, Campbell an Neuner 1985), but its utility for estimating apparent fish density and population size is not well established (Hagen and Baxter 2005). Snorkel–based estimates of juvenile salmonid apparent densities have been shown to be precise and well correlated with electrofishing densities (Girffith 1981, Hankin and Reeves 1988, Mullner and Hubert 1998, Roni and Fayram 2000). Other studies have shown that the reliability of juvenile fish density estimates from snorkeling is sensitive to the actual fish density (Heggenes et al. 1990), habitat complexity (Cunjack et al. 1988, Heggenes et al. al. 1990), and may vary considerably by species (Griffith 1981, Hillman et al. 1992). Apparent densities estimated by snorkeling have been shown to be very sensitive to ambient light intensity because juvenile fish typically conceal themselves during the day (Campbell and Neuner 1985, Hillman et al. 1992). Much less is known about the utility of snorkeling for estimating the apparent density of adult fish. Northcote and Wilkie (1963) poisoned a stream section after conducting a daytime underwater census to compute a catchability for adult rainbow trout of 0.59. Catchability of rainbow trout and steelhead by snorkeling has been shown to be dependent on water clarity (Hagen and Baxter 2005), water clarity and discharge (Korman et al. 2002), as well as behavioral factors (Korman et al. 2005a).

Preliminary field investigations in 1998 in the Lee's Ferry reach highlighted the potential to use snorkel surveys to enumerate rainbow trout. Snorkel surveys are typically used in relatively small streams with low gradients where depth and water clarity are suitable. The Lee's Ferry reach is a very unique large river environment because it has relatively shallow depths and very high water clarity. Snorkel surveys are less intrusive and harmful to fish compared to boat electrofishing surveys and could be used to evaluate some of the assumptions inherent in the electrofishing population index. In recognition of these issues, the Grand Canyon Monitoring and Research Center (GCMRC) funded the Arizona Game and Fish Department (AGF) to implement a pilot-scale snorkel program beginning in 2001-2002 as a component of their contract to provide stock assessment data for rainbow trout in the

Lee's Ferry reach. AGF in turn sub-contracted the snorkel component of this work to Ecometric Research, who piloted the preliminary snorkel investigations in 1998. This report summarizes the results from snorkel surveys conducted by Ecometric Research in June and October 2002, and April 2003.

Three major study components were initiated as part of the 2002-2003 snorkeling work. Diel studies were used to examine the offshore-onshore apparent abundance of fish over a 24-hr.+ period in responses to changes in physical conditions. The objective of this work was to provide information on changes in catchability for both the electrofishing and snorkel surveys that could result from sampling in shoreline areas at different times of day and night and under different discharges. The second component of the program provided snorkel-derived estimates of apparent trout density in shoreline and offshore areas at randomly selected sample sites to index abundance. Apparent shoreline densities from snorkel surveys were also compared with apparent densities for the same areas derived from boat electrofishing. The third component of the program provided estimates of population size for rainbow trout in the Lee's Ferry reach derived from snorkel-based apparent density estimates supplemented with information from diel studies on catchability.

2.0 Methods

A total of 10 snorkel surveys were conducted in the Lee's Ferry reach between August 1998 and April 2003 (Table 1). Initial investigations were conducted on a limited volunteer basis and were used to develop and evaluate various field techniques. The first significant and standardized survey of shoreline and offshore apparent densities was conducted in June 2001. Additional surveys from October 2001 to March 2002 were conducted by AGF. The technique for counting fish used in the AGF surveys differed from the technique used in the June 2001 and June 2002 - April 2003 surveys conducted by Ecometric Research. Data from the AGF surveys was therefore not used in this analysis but are reported in Speas et al. (2002). In addition, the methodology used to estimate offshore apparent densities (transects) was modified between June 2001 and June 2002. As a result, June 2001 data presented in this report are only used for the comparison of electrofishing and snorkel-based apparent shoreline density estimates.

Table 1. Summary of snorkel surveys conducted in the Lee's Ferry reach on the Colorado River. This report presents analyzes data from the June 2001, June and October 2002, and April 2003 surveys.

Survey #	Date	Results Presented in	Investigator	Comparable Technique	Data Management
1	Aug. '98		Korman/Speas/Foster		AGF
2	Aug. '99		Korman/Speas/Foster		AGF
3	Sep. '00		Speas/Hayden		AGF
4	May '01	Speas et al., 2002	Speas et al.		AGF
5	Jun. '01	Speas et al., 2002*	Korman et al.	X	AGF
6	Oct. '01	Speas et al., 2002	Speas/Rogers		AGF
7	Mar. '02	Speas et al., 2002	Speas et al.		AGF
8	Jun. '02	This Report	Ecometric	X	Ecometric
9	Oct. '02	This Report	Ecometric	X	Ecometric
10	Apr. '03	This Report	Ecometric	X	Ecometric

* Comparison of electrofishing- and snorkel-derived shoreline densities from June 2001 sample provided in this report.

The snorkeling program developed in the Lee's Ferry reach consisted of three different types of surveys:

1. 'Shoreline surveys' provided an index of the number of fish adjacent to the shoreline.
2. 'Transect surveys' along a series of cross-sections perpendicular to the longitudinal axis of the river (i.e., cross-sections) at each shoreline sample site were used to provide an index of the density of fish in offshore areas relative to shoreline areas.
3. 'Diel surveys', conducted at 4-hr. intervals over a 24-hr. period at a limited number of sites were used to evaluate changes in shoreline catchability and potential offshore-onshore movement of fish.

The number of shoreline, transect, and diel study sites sampled during the surveys analyzed in this report is provided in Table 2.

Table 2. Sampling intensity for snorkel surveys by sampling trip. The 'EF' vs. Shoreline Sites' column refers to the number of common sites where both electrofishing and snorkel-based shoreline surveys were completed.

Sample Period	Shoreline Sites	Snorkel Sites with Transects (Total # Transects)	Diel Sites	EF vs. Shoreline Sites
Jun. '01	?	?	0	23
Jun. '02	30	28 (144)	1	29
Oct. '02	36	36 (218)	3	36
Apr. 03	30	30 (182)	2	28

2.1 Diel Surveys

Sites were divided into 5-6 lanes running parallel to the longitudinal axis of the river. The boundary of each lane was identified by a series of buoys marked with glow sticks to make the lanes visible during nighttime swims. The number of fish in each lane was enumerated by drifting from the upstream to downstream end of the site in the center of each lane and scanning from side to side. Lane width was set at 12 m, approximately twice the horizontal visibility. Horizontal visibility was quantified by measuring the maximum horizontal distance that a diver could distinguish the outline of another divers leg during the day or the boundary of a white object illuminated with a dive light during the night. Using a lane width twice the horizontal visibility ensured that divers would not count fish in adjacent lanes if they maintained their position in the center of their lane. UK-100 dive lights (25 Watts) were used during nighttime surveys. Surveys were conducted at approximately 4-hr. intervals for a minimum of a 24 hr. period. Counts of all fish observed in each lane were replicated 3 times for each 4-hr. time interval that was sampled. 3 divers could perform 18 counts per time invertal (6 lanes * 3 replicates) in about one hour. The interval between replicate swims in a lane was ca. 15 minutes. Horizontal visibility was measured at the end of each 4 hr. session. Terrestrial light intensity was measured with a Licor cosine-corrected quantum sensor (LI-190SA). Underwater light intensity was measured using an Onset Hobo light meter submerged to ca. 1 m depth. To estimate the discharge at each site for each sample period, we routed the relevant portions of the Glen Canyon Dam discharge record to the upstream limit of the sample sites using a one-dimensional model of diurnal discharge wave propagation (Wiele and Griffin, 1997).

Diel sites were selected based on morphology, apparent fish densities, and logistical considerations. The sites needed to have a sufficient apparent density of fish to reduce the error associated with counting very low numbers of fish where missing a few fish could lead to a large difference in the ratio of apparent densities across lanes or time periods. Sites also needed to be shallow enough so that the bottom could be seen at the outer lanes during peak discharge. Sites were also selected based on their proximity to camping areas and to minimize navigation hazards. We sampled 8-mile bar in June and October 2002 and April 2003. We sampled an area on river-right at 3.5-mile in October 2002 and April 2003, and an area just upstream of the 9-mile campground on river right in October 2002. The sites were approximately 70 m in width and over 200 m in length (Table 3).

Table 3. Size characteristics of diel sample sites.

Site	# of Lanes	Lane Width (m)	Total Width (m)	Site Length (m)	Total Area (m^2)
3.5-mile	6	12	72	180	12,960
8-mile	6	12	72	250	18,000
9-mile	5	12	60	210	12,600

Comparison of fish counts among lanes over survey periods can be used to make inferences about onshore-offshore fish movement and the distribution of fish along a cross-section. However, these inferences are dependent how the proportion of fish counted in a lane relative to the total number that are present varies over lanes and survey periods. Four alternate models regarding changes in catchability can be used to interpret the data:

Q1 Catchability is constant across lanes and survey periods. Under this model the total number of fish summed across all lanes would be constant across 4-hr. survey periods under the assumption that the number of fish migrating in or out of the site is negligible (i.e., a closed population). Differences in apparent densities among lanes over time would represent real changes in density due to offshore-onshore movement. The observed spatial pattern in apparent density in any survey period would reflect the true spatial distribution of fish.

Q2 Catchability is constant across lanes within a survey period, but is variable across periods. Under this model, the total number of fish counted across lanes would not be constant over time because of temporal changes in catchability. As for model Q1, differences in apparent density among lanes within a survey period would represent real differences in density. However, differences in apparent density in a lane across survey periods could be due to changes in density or catchability.

Q3 Catchability is not constant across lanes or over survey periods, but the relative differences in catchability among lanes is constant over survey periods. Under this model, changes in the ratio of fish counts from two lanes over time represent real changes in densities due to offshore-onshore movement. Unlike Q2, the data cannot be used to make inferences about offshore-onshore fish distribution within a survey period.

Q4 Catchability is not constant across lanes or over survey periods and the relative differences in catchability among lanes is not constant over survey periods. Under this model, changes in the ratio of fish counts from two lanes over time could be due to changes in densities or catchability. Differences in apparent fish density across lanes within a survey period, or within a lane across survey periods, could be due to changes in catchability or movement.

Model Q1 has the most restrictive set of assumptions and allows us to make the most definitive statements concerning onshore-offshore movement. At the other end of the spectrum, model Q4 makes no assumptions about catchability over space or time and does not allow us to make any inferences concerning fish movement in and out of shoreline areas.

2.2 Shoreline and Transect Surveys

We compared estimates of apparent density of fish based on electrofishing in shoreline areas with those derived from shoreline snorkel surveys. As electrofishing surveys are conducted at night while shoreline snorkel surveys in this study were conducted during the day, differences in apparent density estimates between methods reflect the effects of differences in catchability due to the sampling gear as well differences in catchability between daytime and nighttime due to behavior and offshore-onshore movement of fish. Shoreline and transect sample sites were selected based on a random-stratified design supplemented with repeated-measure (fixed-site) locations. The GIS department of GCMRC (S. Mietz, GCMRC, Flagstaff, AZ.) created a shoreline-habitat coverage for the Lee's Ferry reach consisting of 360 sample units. The river was divided into left and right sections using a GIS-centerline.

Each side was then further subdivided into the sample units based on shoreline type (Talus, Cobble Bar, Cliff, Sand Bars, Debris Fan) identified by air photographs. Previous investigations have shown that trout density based on boat electrofishing is higher in talus/cobble bar/debris fan habitats compared to habitats dominated by cliffs and sand bars (Speas et al. 2002). Longitudinal position has also been shown to effect trout density with higher densities occurring in the upper and lower sections of the Lee's Ferry reach and lower densities in the middle. A total of 27 sites were randomly selected from 6 strata (two habitat types * 3 longitudinal areas). The number of sites selected from each strata were proportional to the total sample units in the strata. A different set of random sites was selected for each trip. In addition to the 27 random sites, 9 sites that have been repeatedly sampled by AGF since the early 1990's were selected for each survey.

AGF personnel identified the upstream and downstream shoreline boundaries of the random and repeated-measure sites with orange flagging tape and glow-in-the-dark markers prior to the commencement of the snorkel surveys. Shoreline boundaries were identified by a combination of air-photographs and GPS coordinates. Snorkel surveys were conducted one or two weeks prior to the electrofishing surveys. We assumed that fish densities remained relatively constant between the dates of the snorkel surveys to the dates of electrofishing at each site. Due to logistic and time constraints, it was not always possible to survey all the random and repeated measure sites on each snorkel trip (Table 2), however a minimum of 30 sites were sampled per trip. The methodology for the electrofishing surveys is reported by Speas et al. (2002).

Shoreline and transect surveys were conducted by a 3 person crew consisting of two divers and one boat operator. After arriving at a site, buoys were deployed at the upstream and downstream shoreline and centerline corners. A series of three to four buoys were deployed along the longitudinal axis of the site at a distance from the shore equal to sum of the horizontal visible distance and the width of the varial zone. The varial zone was defined as the width of shoreline between the waters edge at the time of the survey and the edge of the periphyton and macrophyte community. Exploratory sampling during early surveys revealed that few fish utilize the varial zone, probably due to an absence of food and cover. All Buoy locations were recorded with a Garmin-12 GPS receiver. A shoreline count consisted of a diver swimming along the buoy line and scanning the volume directly beneath him and in a shoreline direction only. Fish observed outside of the buoy line or less than 150 mm in length were not enumerated. Three shoreline counts were completed at each site. The interval between shoreline replicate counts at a site was approximately 10 minutes. Following the shoreline counts, a single diver performed a series of transect counts by swimming in a cross-stream direction and enumerating the number of fish in the shoreline (shore to buoy line) and offshore (buoy line to centerline boundary) sections of the sample unit. A gas-powered 'aqua-scooter' was used as a mechanical assist to propel the diver and help maintain his position along the cross-section. Upon completing the first transect at the upstream end of the site, the diver would move downstream and repeat the procedure. Six transects were evenly distributed along the longitudinal axis of each site.

The apparent density of fish in the shoreline area was computed by averaging number of fish counted across three passes and dividing by the shoreline area. Shoreline area was computed as the product of the site length derived from the GIS coverage and the horizontal visibility. The offshore area was computed by subtracting the shoreline area from the total area of the sample unit provided in the GIS coverage. The average number of fish counted in the shoreline and offshore areas across the six transects was computed and divided by the shoreline and offshore area to derive apparent offshore and onshore densities, respectively.

2.3 Population Estimates

Rainbow trout population estimates for the Lee's Ferry reach were computed based on habitat-stratified estimates of shoreline and offshore apparent densities and catchability. Total population size (TotalPop) was computed from,

$$TotalPop = \sum_{i} \sum_{h} \frac{ObsPop_{i,h}}{q}, \qquad (1)$$

where ObsPop is the observed population in zone 'i' ('i'=s for shoreline areas, 'i'=o for offshore areas) and habitat type 'h' ('h'="CB/TA/DF" for cobble bar, talus, or debris fan shoreline types; 'h'="SB/CL" for sand bar and cliff shoreline types), and q is the catchability. While q should really be computed as the total number of fish counted relative to the total number present at-a-site, we estimated it as the ratio of the average total count of fish at a diel site across swims conducted during daylight, relative to the peak count at night. This method assumes that the peak nighttime count represents the total number of fish present at the site. For any trip, site-specific estimates of q were averaged to derive a single catchability value for the trip, thus we assume that q does not vary by habitat type or between offshore and onshore areas.

The observed or apparent population within a zone and habitat type was computed from,

$$ObsPop_{i,h} = Area_{i,h} * Den_{i,h} , \quad (2)$$

where, Area is the total area for a zone-habitat type combination and Den is the observed (apparent) fish density. For the shoreline zone, Area was computed as the product of the length of shoreline from the GIS coverage and the average horizontal visibility (HV) for the trip,

$$Area_{s,h} = Length_h * HV , \quad (3)$$

In the offshore zone, Area was computed as the difference between the total area of all sample units within a habitat strata from the GIS coverage ($Area_{t,h}$) and the area of the shoreline zone for that strata,

$$Area_{o,h} = Area_{t,h} - Area_{s,h} , \quad (4)$$

Apparent fish density in the shoreline zone was simply the average apparent density across sites (j=1 to N sites) within the habitat strata,

$$Den_{s,h} = \frac{\sum_{j=1}^{Nsites} Den_{j,h}}{Nsites}, \qquad (5)$$

Apparent fish density in the offshore zone was the product of the apparent density for the shoreline zone and the average ratio of the offshore-to-shoreline apparent densities ($TranDen_{i,h}$) across sites derived from the transect surveys,

$$Den_{o,h} = Den_{s,h} * \frac{TranDen_{o,h}}{TranDen_{s,h}}, \qquad (6)$$

This computation of offshore density is equivalent to averaging the offshore apparent densities among sites within habitat strata. We preferred to use eqn. 6 as the ratio of offshore-to-shoreline apparent density is an informative statistic that reflects the proportion of fish potentially vulnerable to sampling in shoreline areas.

3.0 Results

3.1 Diel Surveys

There were large differences in the number of fish observed over a 24-hr. period, however the extent of these differences varied across seasons (Fig. 1). During June and October 2002 sample periods, counts were much lower during daytime than nighttime swims at all sites. The ratio of the average daytime count to the peak night count was 0.47 at 8-mile in June 2002 and ranged from 0.36 to 0.39 across the 3 sites in October 2002 (Table 4). In contrast, the ratio of the average daytime to peak nighttime counts in April 2003 was much higher, ranging from 0.62 at the 8-mile site to 0.97 at the 3.5-mile site. The April survey was coincident with the peak of spawning (Korman et al. 2005b), and many fish were observed holding over redds and exhibiting other spawning behavior at the 3.5-mile site. We suspect that spawning and staging behaviors improve the likelihood of observing a fish during daylight hours, thereby increasing the daytime/nighttime count ratio. With the exception of the April survey at the 3.5-mile site, the total number of fish counted at a site was not constant over 4-hr. survey periods. Given the large area of the sites and the fact that the outer lanes extended well into the river thalweg where apparent fish densities were quite low, it seems improbable that the large differences in daytime vs. nighttime counts was due to fish moving in and out of the site. Thus, catchability was not constant across 4-hr. survey periods and model Q1 must be rejected.

The apparent density of fish in shoreline and offshore areas at diel study sites changed over a 24-hr. period. In October 2002, these changes were relatively consistent among sites (Fig. 2). During daylight hours, observed densities were fairly similar across lanes while at night densities in the onshore lanes (1-3) increased relative to offshore lanes. At the 3.5-mile site, the increased nighttime apparent shoreline densities were not accompanied by decreased apparent densities in offshore lanes. This pattern suggests that catchability in shorelines lanes increased at night to a greater extent than in offshore lanes (model Q4) that limits inferences about onshore-offshore movement. At the 8-mile site, the very high apparent density seen in shoreline lanes at night was accompanied by a substantial decrease in densities in lane 5. During early morning (3:45) when discharge was at minimum levels (Table 5), apparent fish density declined at the innermost wetted lane and increased in the outer lanes. These patterns suggest that offshore-onshore movement was at least partially responsible for the observed changes in apparent density. The pattern at the 9-mile site in October 2002 was similar to the pattern seen at 8-mile. The elevated apparent densities of fish in shoreline lanes during the first two nighttime swims (20:15 and 23:45) was at least partially caused by an onshore movement of fish as the apparent density in lane 3 declined. The early morning (4:00) decline in onshore apparent densities was accompanied by an increase in apparent densities in the outer lanes, again evidence for fish movement. Changes in apparent density at the 8-mile site in June 2002 also suggest that a nighttime onshore movement of fish was at least partially responsible for the observed patterns in apparent density. Onshore apparent densities were highest during the earliest nighttime swims when discharge was still high (Fig. 2, Table 5). At the lower discharge associated with the early morning night swims (3:45) apparent densities of fish in the innermost lane decreased while those in the outer lanes increased.

Table 4. Average daytime and peak night counts at diel sampling sites used to compute the seasonal estimates of catchability (q) for total population estimates. The product of the apparent density of fish at each site (based on the peak nighttime count) and the total wetted area for the Lee's Ferry reach are also shown as alternate estimates of total population size.

Sample Period	Site	Average Daytime Count	Peak Nighttime Count	Day-to-Night Ratio (q)	Seasonal q	Apparent Density Nighttime (#/100 m^2)	Expanded Lee's Ferry Population
Jun. '02	8 Mile	296	632	0.47	0.47	3.5	120,000
Oct. '02	3.5 Mile	89	227	0.39		1.7	60,000
Oct. '02	8 Mile	180	494	0.36		2.7	94,000
Oct. '02	9 Mile	72	187	0.39	0.38	1.5	52,000
Apr. '03	3.5 Mile	146	151	0.97		1.4	50,000
Apr. '03	8 Mile	222	357	0.62	0.79	2.0	70,000
Grand Average q				0.53			

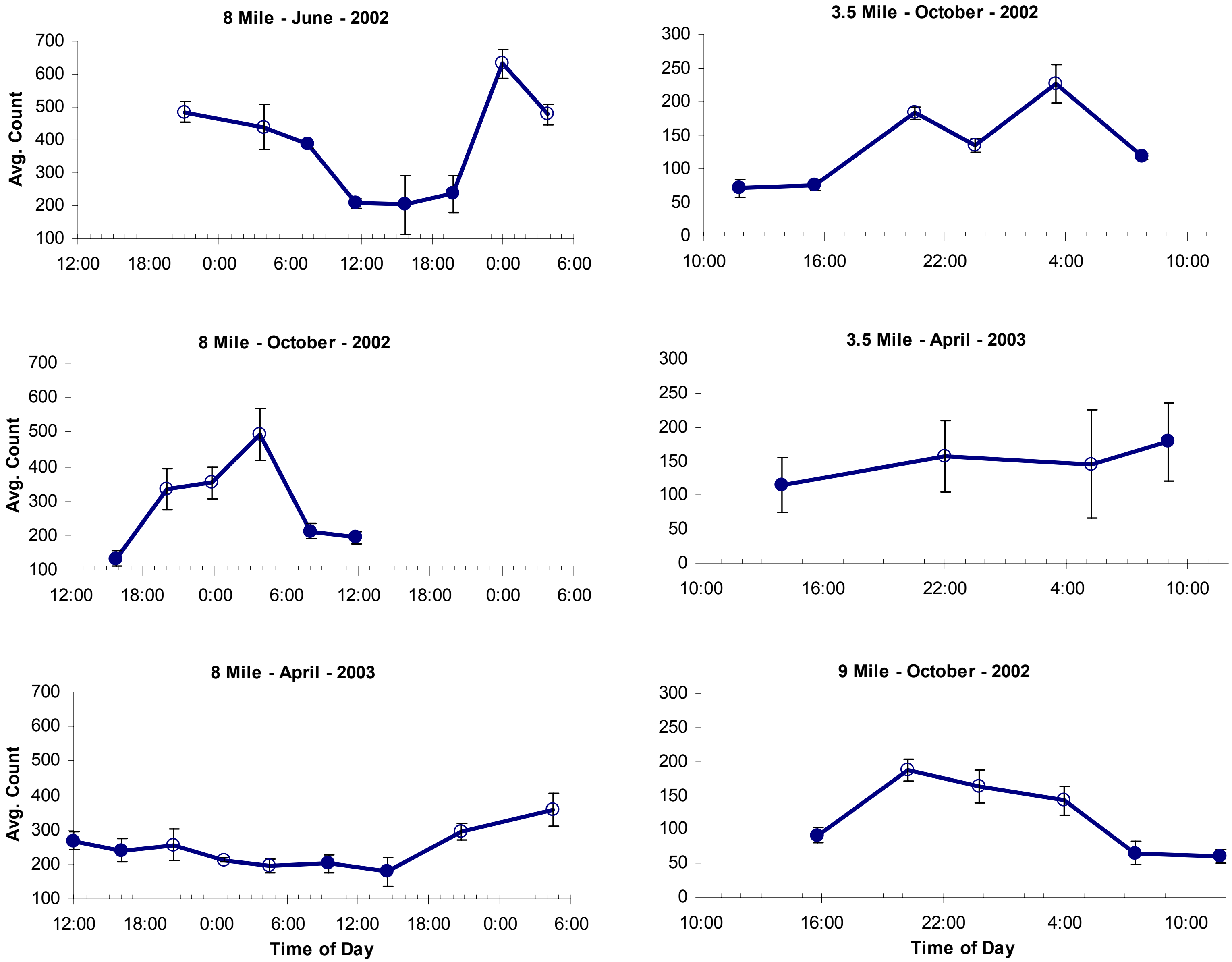

Figure 1. The total number of fish counted at approximately every 4 hrs. at 3 study sites on 3 sampling trips. Points and error bars denote the average and 95% confidence limits based on 3 replicate counts. Closed and open circles denote daylight and nighttime sample periods, respectively.

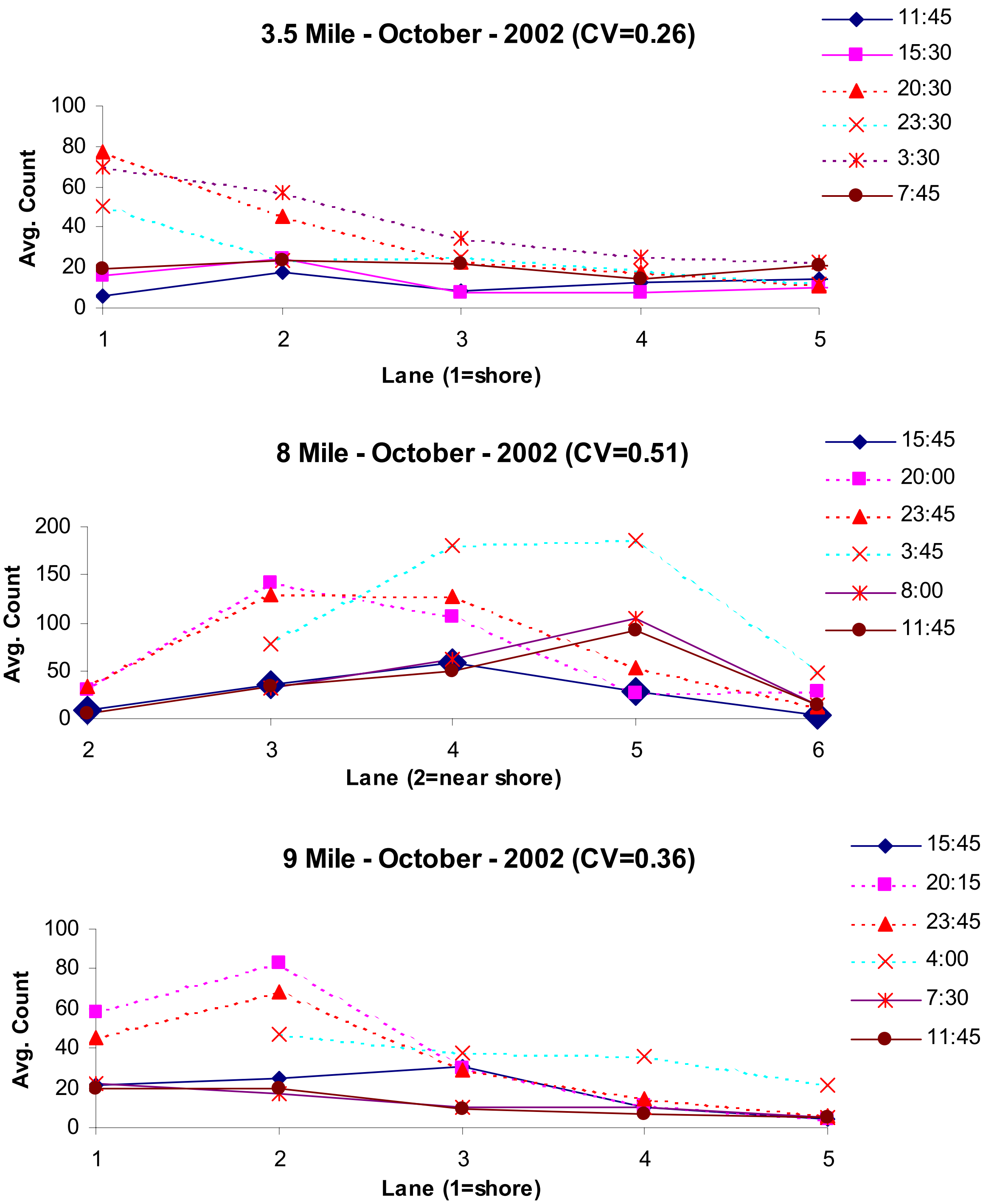

Figure 2. Average count of fish by swim lane over a 24-hr.+ diel cycle. Lane number increases from shoreline to thalweg. Dashed lines denote swims conducted at night, while solid lines denote daytime swims. The coefficient of variation (CV), determined across 3 passes in each lane, averaged across all lanes and time periods, are shown in the titles.

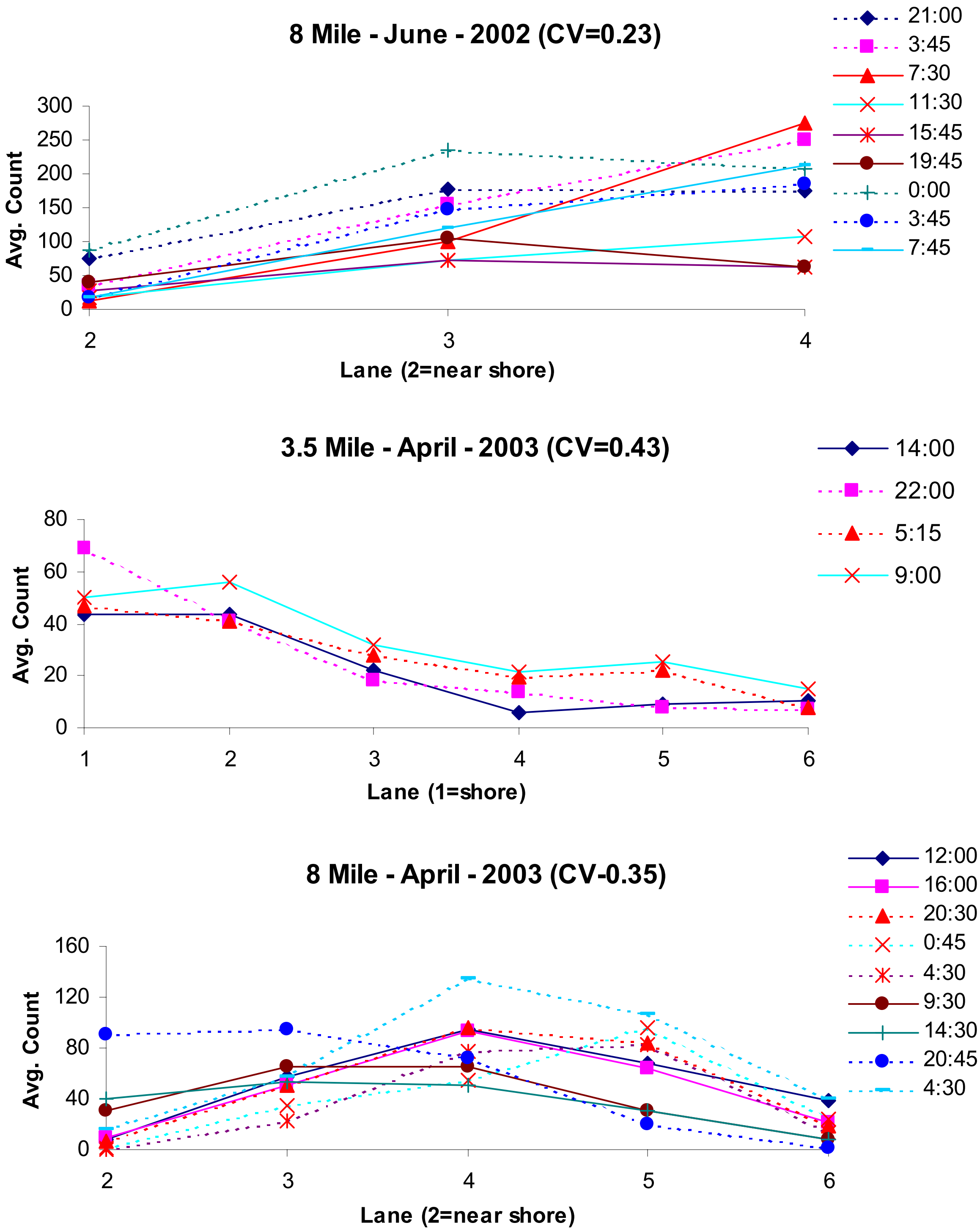

Figure 2. Con't.

Table 5. Physical conditions during the sample periods at diel study sites.

Date	Site	Day	Time	Swim Type	Horizontal Visibility (m) Leg	White	Light Intensity (Lumens / ft^2)	(Quanta)	Discharge (cfs)
Jun. '02	8 Mile	19	21:00	Night		7.6			15,582
		20	3:45	Night		7.6			9,634
		20	7:30	Day	7.6				10,156
		20	11:30	Day	7.2				13,661
		20	15:45	Day	7.0				15,700
		20	19:45	Day	7.5	8.2			15,766
		21	0:00	Night		7.2			12,750
		21	3:45	Night		7.3			9,664
		21	7:45	Day	9.7				10,581
Oct. '03	8 Mile	7	15:45	Day			16		9.984
		7	20:00	Night	4.2	6.5	0		10,127
		7	0:00	Night	3.0	5.0	0		8,303
		8	3:45	Night	5.1	5.8	0		5,230
		8	8:00	Day	5.2		18		7,623
		8	11:45	Day	4.8		240		9,508
	9 Mile	8	15:45	Day	5.5		48		10,115
		8	20:15	Night		6.9	0		10,216
		8	0:00	Night	5.0	6.2	0		7,870
		9	4:00	Night		4.2	0		5,226
		9	7:30	Day	5.8		7		9,037
		9	11:45	Day	7.0		314		9,673
	3.5 Mile	10	11:45	Day	4.0		116		9,065
		10	15:30	Day	4.8		48		9,302
		10	20:30	Night	4.7	5.7	0		10,023
		10	23:30	Night	5.5		0		9,642
		11	3:30	Night	2.5	5.2	0		5,833
		11	7:45	Day	3.7		21		6,326
Apr. '03	8 Mile	13	12:00	Day	6.2		728	1,598	7,857
		13	16:00	Day	5.3		84	1,073	7,920
		13	20:30	Night	3.8	5.9	0	0	7,932
		14	0:45	Night	3.4	5.5	0	0	7,060
		14	4:30	Night	3.9	5.4	0	0	6,457
		14	9:30	Day	5.3		185	831	10,264
		14	14:30	Day	6.3		136	988	12,229
		14	20:45	Night	4.1	6.9	0	0	12,319
		15	4:30	Night	3.5	5.6	0	0	6,382
	3.5 Mile	15	14:00	Day	5.2		176	766	11,904
		15	22:00	Night	4.4	7.4	0	0	12,493
		16	5:15	Night	5.3		0	0	6,555
		16	9:00	Day	6.3		29	95	8,729

The April 2003 movement patterns were quite distinct from those observed during other sampling periods (Fig. 2). At the 3.5-mile site the onshore-offshore distribution was very consistent over time with the innermost lanes having the highest apparent densities of fish. This pattern was very different from the one seen in October at the same site, where higher inshore apparent densities were only seen at night. The 3.5-mile site was an active spawning location at the time of the April survey and we suspect that fish holding over redds resulted in the relatively stationary movement pattern that was observed.

The April 2003 movement pattern at 8-mile (Fig. 2) was particularly informative because the sampling occurred between Sunday and Monday when 24-hr. discharge trends were very different. This was helpful in untangling the effects of changes in light intensity and discharge on potential offshore-onshore movement. The first half of the survey (12:00 – 4:30) occurred Sunday afternoon and early Monday morning when discharge was low and steady at 6.5-8 kcfs (Table 5). The latter half of the sampling period occurred under a typical weekday daily discharge pattern where flow rose during the morning to a peak of over 12 kcfs by mid-day and began declining by late evening reaching a minimum discharge by early morning. During the steady discharge on Sunday, the onshore-offshore distribution was relatively constant among 4-hr. samples although a slight offshore movement was observed during the 4:30 sample when discharge reached a minimum level. As discharge rose on Monday (9:30 and 14:30) the apparent distribution of fish across the lanes became more uniform than the daytime distribution observed on Sunday at lower flows at the same time of day. At peak discharge during darkness (20:45) the apparent density of fish in the innermost lanes (2-3) were substantially greater than during any other survey period including the 20:30 sample during Sunday low flows. This is good evidence that high discharge during the evening results in an onshore movement of fish. As flows dropped during early morning (4:30) near the end of the survey, the apparent densities in the innermost lanes decreased and were accompanied by peak apparent densities in mid-to-outer lanes (4-5).

3.2 Shoreline and Transect Surveys

Average shoreline apparent densities were highest in cobble bar-, talus-, and debris fan-dominated shorelines relative to those dominated by sand bars and cliffs in all sample periods (Tables 6 and 7). Apparent shoreline fish densities estimated by snorkel surveys declined noticeable from June 2001 through April 2003 in both habitat types. The average apparent density across habitat types in June 2001 was approximately 3-fold higher than the average apparent density in April 2003. Apparent shoreline densities based on electrofishing did not show a declining trend over the sampling periods. Apparent densities of trout tended to be higher at sites in the upper half of the Lee's Ferry reach and lowest at sites within the first few miles from Lee's Ferry (Fig. 3).

The apparent offshore-to-shoreline ratio varied considerably among trips (Table 8). The ratio in October 2002 averaged across habitat types was only 0.17 compared to 0.47 in June 2002 and 0.95 in April 2003. The increase in apparent densities of fish in offshore areas estimated through transect surveys was consistent with the pattern seen at diel sites. The relatively higher offshore-onshore ratio was likely caused by differences due to spawning and staging behavior, which resulted in fish holding positions away from the shoreline in higher velocities where redds were located. Of particular interest was the very low offshore to onshore ratio in cobble bar and talus shorelines observed in October 2002 (0.1). We completed the most transects in October relative to the other sample periods (218) yet saw the fewest number of fish in offshore areas (257). Reduced visibility in October due to lower ambient light intensity and reduced water clarity could have resulted in the low proportion of fish observed offshore (Table 8).

Table 6. Sample sites from shoreline and transect snorkel surveys. "CB", "TA", "SB", and "CL" denote shorelines dominated by cobble bars, talus, sand bars, or cliffs, respectively.

	Jun. '02			Oct. '02			Apr. '03		
Site #	Site	River Mile	Habitat	Site	River Mile	Habitat	Site	River Mile	Habitat
1	26.85R	0.8	CB	25.65R	0.7	SB	25.55L	0	TA
2	26.65R	0.7	CB	24.05R	-0.9	TA	25.1L	-0.2	SB
3	26.25L	0.5	TA	G15	-1.25	SB	24.75L	-0.4	SB
4	24.95L	-0.3	SB	23.0R	-1.5	SB	G12	-3.95	CB
5	23.9R	-1	TA	21.9L	-2.2	SB	18.75R	-4.2	TA
6	23.75R	-1.1	TA	21.9R	-2.2	SB	18.2R	-4.5	CL
7	G15	-1.25	SB	20.75L	-2.9	TA	16.55L	-5.5	SB
8	21.65L	-2.4	DB	G13	-2.9	TA	G10	-5.7	TA
9	G13	-2.9	TA	19.65R	-3.6	CB	15.5R	-6.2	SB
10	G12	-3.95	CB	19.7L	-3.6	CL	15.2R	-6.4	SB
11	17.7L	-4.8	TA	19.25R	-3.9	CB	G9	-7	SB
12	17.2L	-5.2	TA	G12	-3.95	CB	12.55L	-8	TA
13	16.85R	-5.3	CB	17.7R	-4.8	SB	11.1R	-8.9	CL
14	16.75L	-5.4	SB	G10	-5.7	TA	10.65R	-9.2	CB
15	G10	-5.7	TA	16.0R	-5.9	SB	10.2L	-9.4	TA
16	G9	-7	SB	14.7L	-6.7	CL	10.3R	-9.4	CB
17	13.15L	-7.6	SB	G9	-7	SB	9.4R	-9.9	TA
18	12.85L	-7.8	TA	13.7R	-7.3	TA	G6	-10.15	TA
19	12.85R	-7.8	TA	13.0R	-7.7	SB	8.9R	-10.2	TA
20	12.4R	-8.1	TA	12.85L	-7.8	TA	8.0L	-10.8	CB
21	12.25R	-8.2	TA	11.85R	-8.4	SB	G5	-11.9	CB
22	11.55R	-8.6	CB	11.75L	-8.5	TA	5.75R	-12.2	CL
23	9.65L	-9.8	SB	9.35L	-10	SB	5.15R	-12.6	SB
24	G6	-10.15	TA	G6	-10.15	TA	4.75L	-12.8	TA
25	8.15R	-10.7	SB	8.15L	-10.7	TA	3.1R	-13.8	CL
26	8.0L	-10.8	CB	7.75L	-10.9	SB	G4	-13.9	TA
27	7.9L	-10.85	SB	6.7L	-11.6	CB	1.85L	-14.5	TA
28	G3	-14.55	TA	6.15R	-11.9	CB	G3	-14.55	TA
29	1.05L	-15.1	TA	G5	-11.9	CB	1.6R	-14.8	CL
30	0.9L	-15.2	TA	3.4R	-13.6	CL	1.05L	-15.1	TA
31				G4	-13.9	TA			
32				2.75R	-14	SB			
33				2.2L	-14.4	TA			
34				G3	-14.55	TA			
35				1.2L	-15	TA			
36				1.2R	-15	CB			

Table 7. Statistics on the apparent density of rainbow trout based on daytime shoreline snorkel surveys and nighttime boat electrofishing surveys stratified by habitat type and sampling periods. "CB/TA" and "SB/CL" denote shorelines dominated by cobble bars and talus or sand bars and cliffs, respectively.

Snorkeling (fish/100 m^2)				Electrofishing (Fish/100 m)			
	CB/TA	**SB/CL**	**All**		**CB/TA**	**SB/CL**	**All**
Average				Average			
Jun. 01			6.2	Jun. 01			16.1
Jun. 02	3.6	2.5	3.3	Jun. 02	16.1	10.2	14.3
Oct. 02	3.2	1.4	2.4	Oct. 02	21.9	10.8	17.0
Apr. 03	2.4	1.2	1.9	Apr. 03	21.2	10.5	16.6
Standard Deviation				Standard Deviation			
Jun. 01			4.8	Jun. 01			10.9
Jun. 02	3.0	3.1	3.0	Jun. 02	11.5	7.2	10.6
Oct. 02	2.8	1.6	2.5	Oct. 02	15.2	6.3	13.2
Apr. 03	1.6	2.2	1.9	Apr. 03	12.3	6.3	11.4
# of Sites				# of Sites			
Jun. 01			22	Jun. 01			23
Jun. 02	22	8	30	Jun. 02	20	9	29
Oct. 02	20	16	36	Oct. 02	20	16	36
Apr. 03	18	12	30	Apr. 03	16	12	28

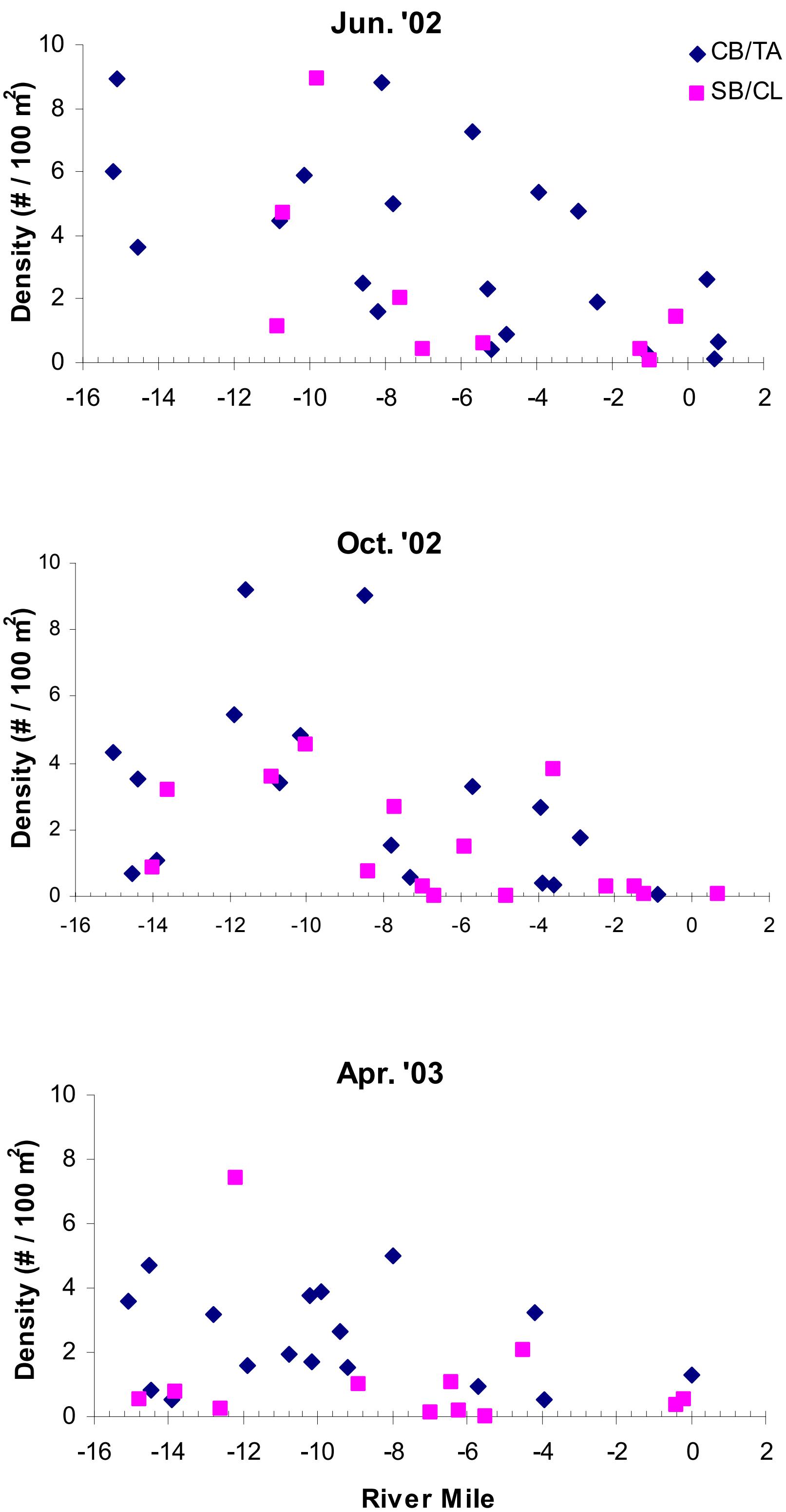

Figure 3. Average apparent densities of rainbow trout by river mile based on daytime shoreline snorkel surveys stratified by cobble bar/talus (CB/TA) and sand bar/cliff shoreline habitats. Glen Canyon Dam is located at river mile –15.6 and Lee's Ferry is located at river mile 0.

Table 8. Summary statistics for transect surveys. "CB/TA" and "SB/CL" denote shorelines dominated by cobble bars and talus or sand bars and cliffs, respectively.

Ratio of Offshore Density/Shoreline Density				
Average	Jun. 02	Oct. 02	Apr. 03	Average
CB/TA	0.44	0.10	0.75	0.43
SB/CL	0.21	0.26	1.48	0.59
Average	0.40	0.17	0.95	0.48
Standard Deviation				
CB/TA	0.47	0.11	1.21	0.76
SB/CL	0.16	0.51	2.68	1.50
Average	0.44	0.34	1.72	1.03
Horizontal Visibility (m)				
Average	6.6	4.9	5.5	5.7
Total number of Fish Counted on Transects				
	Jun. 02	Oct. 02	Apr. 03	Total
Shoreline Zone	348	231	165	744
Offshore Zone	585	257	576	1418
Total	933	488	741	2162
Number of Transects	144	218	182	
Fish/Transect	6.48	2.24	4.07	

Estimates of the apparent density of fish in offshore zones relative to shoreline zones are an important component of our population computation (eqn. 6). The 'transect technique' where a diver is propelled by a motorized aquascooter perpendicular to the longitudinal axis of the river is likely less precise at defining the onshore-offshore distribution of fish relative to swimming in lanes at increasing distance from shore as was done in the diel studies. Fewer fish would be counted using the transect technique relative to the lane method where a greater area is sampled, leading to increased sampling error. In addition, error in the divers estimate of the lane he is in when counting fish via the transect technique would also decrease precision. We used the transect technique to estimate offshore-onshore distribution because it was much quicker to implement relative to the lane method and allowed us to estimate apparent offshore densities at all snorkel sites. To assess the relative precision of the two methods, we counted the number of fish in each lane at the 8-mile diel site following daytime swims in June 2002 using the transect method, and compared the proportion of fish in each lane relative to the proportions derived from the lane method (Fig. 4). The correlation in the offshore-onshore proportions between the two methods was very strong, suggesting that the transect method does provide an accurate characterization of fish distribution.

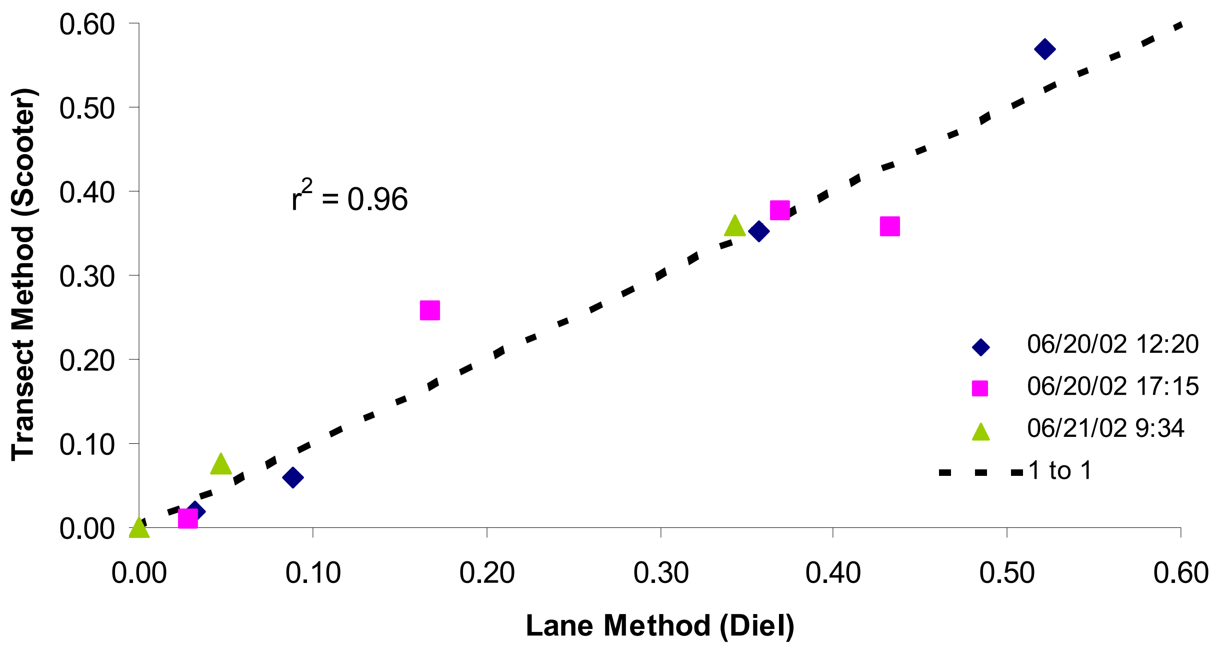

Figure 4. Comparison of estimates of the proportion of fish in different lanes at increasing distance from the shoreline based on two different field techniques. The 'Transect Method' consists of making multiple passes in a cross-stream direction counting the number of fish in each lane. The diver moves perpendicular to the longitudinal axis of the river and maintains his position using a motorized aquascooter. The 'Lane Method' consists of making multiple passes within each lane by floating in downstream direction (see methods for diel surveys).

3.2.1 Pass and Observer Effects

We used a variety of statistics to evaluate variation and potential biases associated with counting fish during the shoreline and transect surveys and diel studies. Within-site variation of shoreline counts, resulting from differences in counts among passes and divers at-a-site was generally quite low with an average coefficient of variation (CV) of 25% for sites with more than 10 fish (Fig. 5). CV increased dramatically for sites with low counts, as seeing or missing a few fish could result in a large proportional difference in counts. Within-site variation in counts at low-density sites would have little effect on the precision of average density or population estimates, as this variation is determined by the absolute error (i.e. the standard deviation), which is low at sites with few fish.

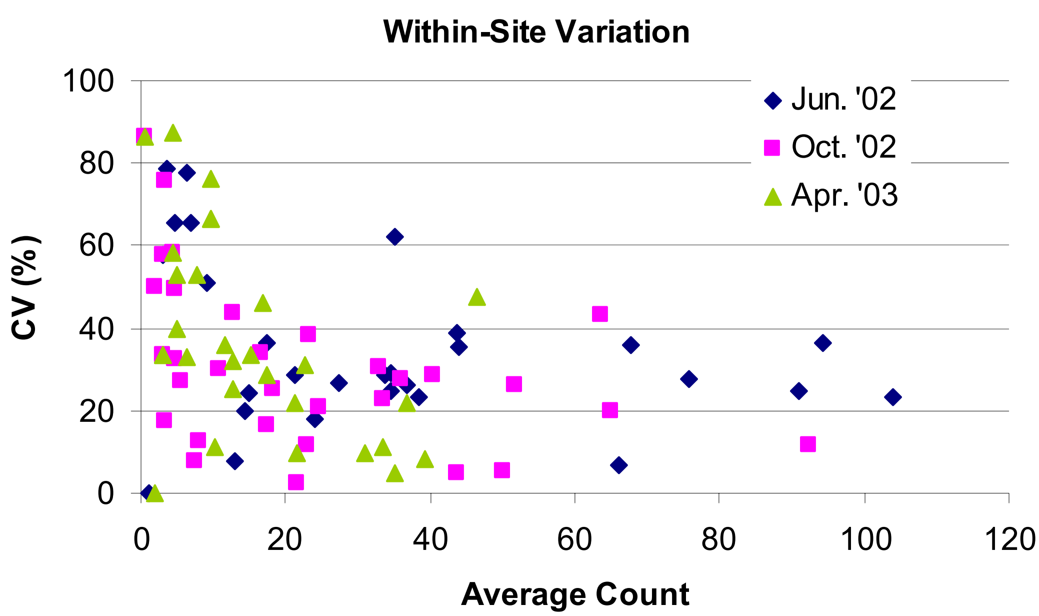

Figure 5. Within-site variation (expressed as the coefficient of variation in %) as a function of the average total count of fish at each shoreline snorkel site. The within-site variation is the result of differences in counts among divers and passes at-a-site.

Repeated passes at a site over a short time-frame as conducted during shoreline and diel surveys has the potential to lead to decreases in fish counts over successive passes if fish exhibit a flight response to divers and move out of the sample area. There was no evidence of this dynamic in the shoreline or diel data. The average ratio of fish counted on the second or third pass relative to the number counted on the first pass was generally very close to 1 for the shoreline surveys (Table 9). A similar ratio was observed for the counts at diel sites.

Table 9. Statistics of the ratio of the average number of fish counted on pass 2 or 3 relative to the average number counted on pass 1 during shoreline surveys.

	Jun. 02	Oct. 02	Apr. 03
Average			
Pass2/Pass1	1.13	0.87	1.07
Pass3/Pass1	1.06	0.99	1.15
Standard Deviation			
Pass2/Pass1	1.10	0.51	0.76
Pass3/Pass1	0.84	0.44	0.47

Diver experience did affect shoreline and diel counts. Divers with limited experience typically had shoreline counts that were 60-70% of the average count for the site (Table 10). There was less difference among counts from experienced divers, but some of these divers (SM, JS, RA) did see 10-20% more fish than others (JK, SH).

Table 10. Statistics of the ratio of individual diver counts to the average count among divers at-a-site.

			Ratio of Diver Count to Avg. Count Across Divers	
Sample Period	Diver Code	Diver Experience	Average	Standard Deviation
Jun. '02	JK	High	0.9	0.3
	MY	Low	0.6	0.1
	RA	High	1.1	0.4
	RL	High	1.0	0.4
Oct. '02	SM	High	1.1	0.5
	AM	Low	0.7	0.5
	JS	High	1.0	0.2
Apr. '03	JS	High	1.1	0.3
	SH	High	0.8	0.3

3.3 Population Estimates

Total habitat area derived from the GCMRC GIS coverage for Lee's Ferry shoreline types and apparent density estimates derived from shoreline and transect snorkel surveys were used to compute rainbow trout population estimates for the Lee's Ferry reach (Table 11). Observed (apparent) population estimates were ca. 47,000, 18,000, and 63,000 fish in June 2002, October 2002, and April 2003 respectively (eqn. 2). Decreases in apparent shoreline densities between the June and October sample periods was part of the reason for the apparent population decline, but the dominant factor was the change in offshore-onshore apparent density ratio observed in cobble bar and talus habitat types (Table 8). The ratio of offshore to onshore apparent densities in this habitat type declined from 0.44 in June 2002 to 0.10 in October 2002. This in turn led to a large decline in the apparent offshore density that was applied to the large habitat area of the offshore zone. It is quite unlikely that sampling error in transect surveys could have caused this anomalously low ratio. Sampling intensity in October was very high (218 transects), yet we observed less than half the number of fish in offshore areas relative to other sampling periods where the total number of transects was less (Table 8). It is more likely that reduced light intensity and water clarity during the October sample period led to an underestimate of the true offshore density.

The observed population in April 2003 was about 34% of the June 2002 estimate and 260% of the October 2002 estimate. The total population estimates, which correct for changes in catchability (Table 4) were less variable across sample periods. The total population declined from about 100,000 to 50,000 fish between June and October 2002 and then increased to about 80,000 fish by April 2003. The trend in population estimates (observed or total) does not match the trend in apparent shoreline densities, which showed a fairly steady decline from the first to last sample period (Table 7). The difference between population and apparent shoreline density trends was driven by the anomalously low offshore-shoreline apparent density in October 2002.

Table 11. Population estimates for rainbow trout in the Lee's Ferry Reach for 3 sample periods.

Habitat Area				Apparent Density of Fish			Number of Fish		
	Shoreline Length (m)	Total Wetted Area (m^2)							
CB/TA/DF	32,814	1,956,966							
SB/CL	24,434	1,536,479							
Total	57,248	3,493,445							
	Jun. 02	Oct. 02	Apr. 03	Jun. 02	Oct. 02	Apr. 03	Jun. 02	Oct. 02	Apr. 03
Horizontal Visibility (m)	6.5	4.9	5.5						
Shoreline Area (m^2)				Shoreline Density (# /100 m^2)					
CB/TA/DF	214,274	162,100	179,819	3.74	3.19	2.42	8,017	5,168	4,348
SB/CL	159,554	120,704	133,899	2.19	1.39	1.19	3,499	1,673	1,590
Total	373,828	282,804	313,718	2.97	2.29	1.80	11,516	6,841	5,938
Offshore Area (m^2)				Offshore Density (# /100 m^2)					
CB/TA/DF	1,742,692	1,794,866	1,777,147	1.67	0.33	1.80	29,085	5,844	32,037
SB/CL	1,376,924	1,415,775	1,402,580	0.45	0.37	1.76	6,242	5,181	24,742
Total	3,119,616	3,210,641	3,179,727	1.06	0.35	1.78	35,326	11,025	56,779
					Observed Population		46,842	17,865	62,718
Total Wetted Area (m^2)									
CB/TA/DF	1,956,966	1,956,966	1,956,966		q (avg. day vs. peak night)		0.47	0.38	0.79
SB/CL	1,536,479	1,536,479	1,536,479						
Total	3,493,445	3,493,445	3,493,445		**Total Population**		**99,665**	**47,014**	**79,389**

As an alternate means of computing the total population size of rainbow trout in the Lee's Ferry reach, we divided the peak nighttime count for each diel survey by the total area of each diel study site to derive an apparent density (Table 4) and then multiplied by the total wetted area of the Lee's Ferry reach derived from the GCMRC GIS coverage ($3.49 * 10^6$ m^2). Population estimates ranged from a minimum of 50,000 based on the lowest apparent density case (3.5-mile in April 2003) to 120,000 based on the highest apparent density (8-mile in June 2002). The most defensible estimate, based on the average apparent density across 3 diel sites in October 2002, was 70,000 fish. This value was considerably higher than the October estimate from the random sites (Table 11) and could reflect the possibility that the densities at diel sites are higher than the average density over the reach.

3.4 Comparison of Density Estimates Between Boat Electrofishing and Shoreline Snorkel Surveys

The relationships between estimates of apparent shoreline fish density based on snorkel surveys during the day and those based on boat electrofishing at night were weak (Fig. 6). Apparent shoreline densities estimated by electrofishing explained between 20 and 30% of the variance in snorkel-based estimates (Table 12). The scatter plots for the 2002 and 2003 sample periods show a linear relationship between the two methods for most points with a series of positive outliers for sites where apparent snorkel densities were considerably higher than the corresponding electrofishing densities. These points could represent areas where dippers became saturated or areas with deeper or faster water where electrofishing would be less effective compared to snorkeling. The ratio of apparent shoreline densities from snorkeling to electrofishing progressively declined from 2.1 in June 2001 to 0.5 in April 2003 (Fig. 6, Table 12). This occurred because apparent shoreline densities estimated by snorkeling (Table 7) showed a decline over the sample periods (6.2 to 1.9 fish/100 m^2) while those derived by electrofishing did not (14.3-17.0 fish/100 m).

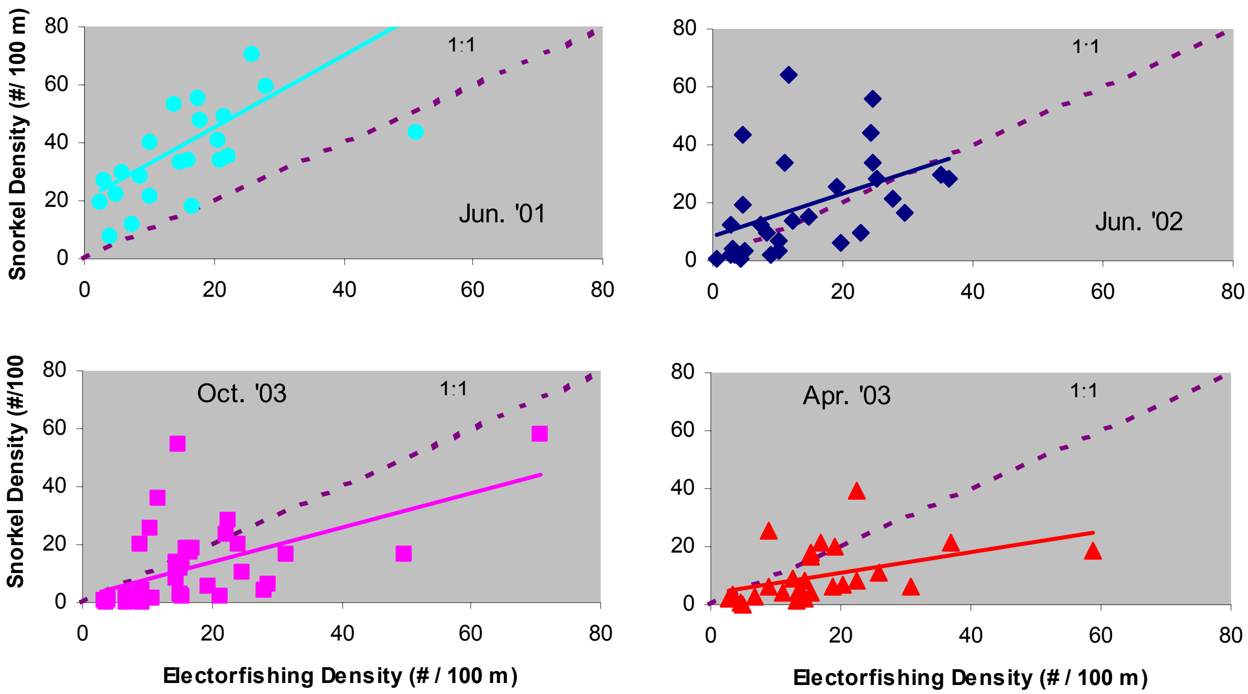

Figure 6. Comparison of apparent shoreline density estimates derived by shoreline snorkel surveys conducted during the day and boat electrofishing surveys conducted at night over four sample periods. Lines represent the best-fit linear regressions for each sample period.

Table 12. Linear regression statistics of the apparent density of rainbow trout in shoreline areas estimated from snorkel shoreline surveys and boat electrofishing. The slope at intercept = 0 is the ratio of snorkel to electrofishing apparent densities.

Sample Period	based on best-ft intercept r^2	n	Slope with intercept=0
Jun. '01	0.24	23	2.1
Jun. '02	0.21	29	1.2
Oct. '02	0.30	36	0.7
Apr. ' 03	0.20	28	0.5

We chose to standardize electrofishing catch by shoreline length rather than by electrofishing time as typically done for Lee's Ferry rainbow trout assessments (e.g. Speas et al., 2002). This departure was based on an exploration of the relationship between space and time indices of effort in relation to apparent fish density. The average ratio of electrofishing time to site length over the sample periods was 3.1. A site with an average length of 160 m was typically electrofished for 500 sec. However, the number of seconds of electrofishing effort was not well correlated with the length of the site (Fig. 7 top). Thus, some sites appear to have been more thoroughly sampled than others. There was a fairly strong relationship between electrofishing CPE standardized by shoreline distance and time (Fig. 7, middle), but variation around the average relationship depended on how thoroughly the site was sampled (i.e., the ratio of seconds shocked to site length). Sites with relatively higher apparent densities of fish based on length-standardized effort (positive outliers) tended to be sampled more thoroughly (Fig. 9, middle and bottom) compared to sites with relatively low length-standardized apparent densities (negative outliers).

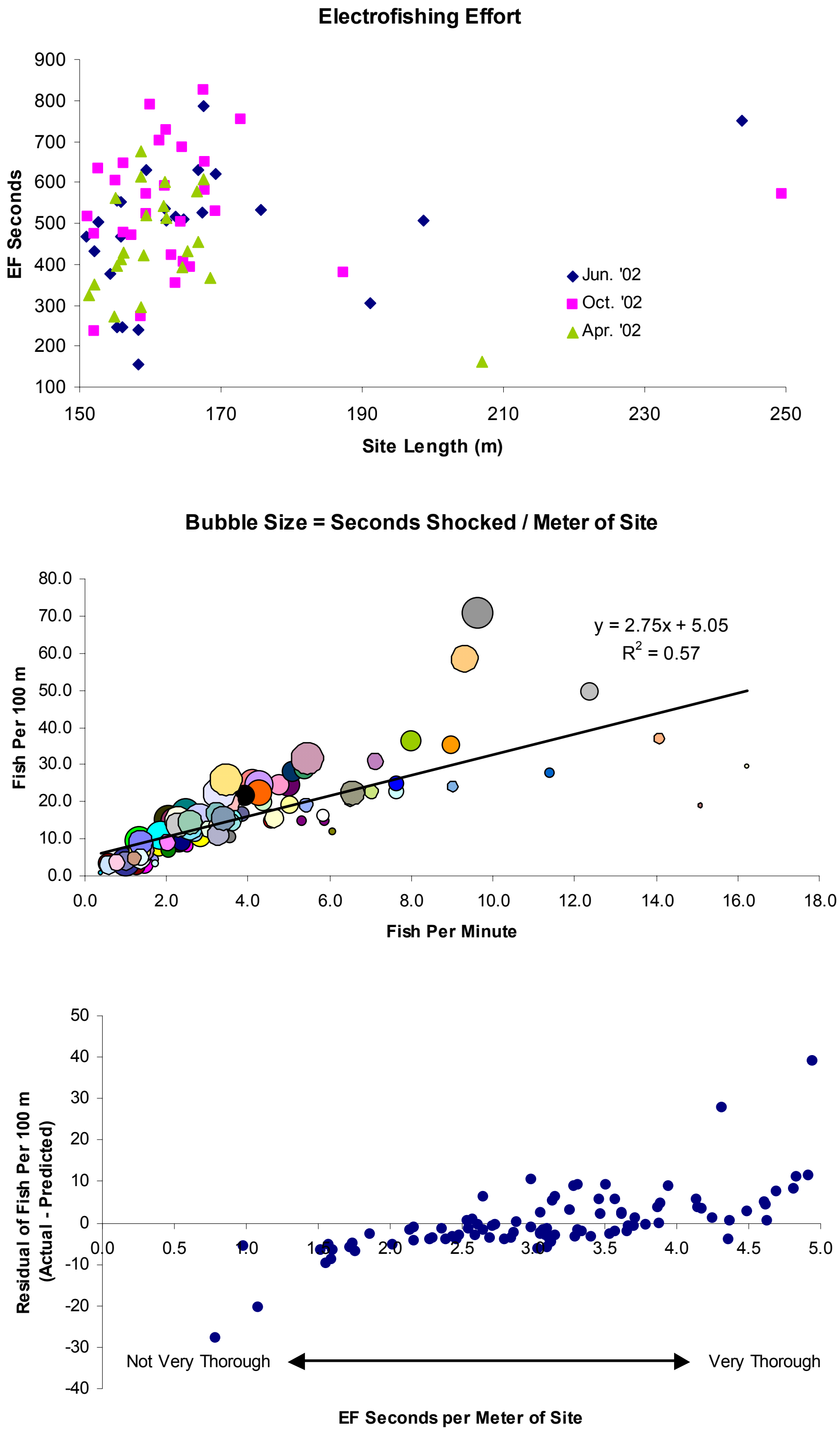

Figure 7. Statistics for boat electrofishing effort over 3 sample periods. The top graph plots the number of seconds of shocking time as a function of site length. The middle graph shows the relationship between electrofishing catch-per-effort (CPE) expressed as fish per distance fished relative to CPE standardized by time fished. Bubble size is an index of how thoroughly a site was fished (seconds shocked per meter of site). The bottom plot is the residuals from this relationship plotted against an index of how thoroughly the site was sampled.

4.0 Discussion

We generally observed at least twice as many fish during nighttime surveys at diel study sites relative to the number of fish seen during the day. We consider it quite unlikely that the nighttime increase was due to fish moving into the sites given their large area and coverage into the thalweg where apparent fish densities were very low. In support of this assumption, Pert and Erman (1994) observed little movement of rainbow trout out of a very short study reach (20 m) in the Stanislaus River where the daily minimum and maximum flows varied from 1.5 to 5 m^3/s. In the Lee's Ferry reach, fish were more likely to be seen by divers at night because their body coloring was not an effective camouflage when illuminated by powerful dive lights. In addition, it may have been easier to see fish at night when concealment behaviour is typically much reduced (see review by Hagen and Baxter 2005). In support of this latter hypothesis, we saw little difference in daytime and nighttime counts during the spawning season at a site where active redds were observed (3.5-mile in April 2003). It was likely that spawning and staging behavior overrode typical daytime hiding behavior/flight responses in this case.

The general pattern of apparent fish densities that was observed at the diel study sties consisted of:

1. a relatively uniform distribution of fish along the cross-section during daylight hours at high discharges;
2. increased apparent densities in onshore lanes under darkness when discharge was still high; and
3. a decline in apparent densities in onshore lanes during the early morning when discharge was low.

In many cases, the changes in apparent density in shoreline lanes were accompanied by opposite changes in apparent density in the outer lanes. We consider this reasonable evidence that onshore-offshore movement was at least partially responsible for the changes in density that were observed between 4-hr. survey periods. Increased apparent shoreline densities at night were not accompanied by decreased apparent densities in offshore lanes at the 3.5-mile site in October 2002 and suggest that increases in catchability during nighttime surveys were greater in onshore lanes compared to offshore ones. This differential catchability is not surprising as the effectiveness of the dive lights for illuminating fish was likely much higher in the shallow depths of the shoreline lanes relative to offshore lanes with greater depth.

The relative importance of onshore-offshore movement vs. differential catchability in explaining the patterns in apparent density we observed in the diel surveys cannot be unequivocally determined from our data. What is relatively certain is that the apparent fish density in shoreline areas that are shallow enough to be sampled by boat electrofishing are generally highest during the first half of the night when electrofishing is typically conducted. Population estimates based on nighttime electrofishing catches that assume equal offshore and onshore densities at the time of sampling likely considerably overestimate total population size. It is important to note that our diel sampling sites were not selected randomly and are therefore potentially not representative of a typical site in the Lee's Ferry reach. We picked sites that had relatively high apparent fish densities to reduce sampling error, and based on logistic and safety considerations. It is possible that fish density potentially influences the extent of onshore and offshore movement and differences in catchability between night and day. We feel our site selection was rationale given the challenges of the intensive sampling approach, but caution should be used when extrapolating the results to sites in the Lee's Ferry reach with lower apparent fish densities.

Activity patterns of stream-dwelling fish can be viewed in the context of individuals making decisions about the trade-off between foraging and the risk of predation (Bradford and Higgins 2001). A useful construct is the "minimize u/g" rule (Metcalfe et al. 1999), which suggests that fish should occupy habitats that minimize the ratio of mortality risk (u) to growth (g). This construct provides a feasible explanation for the onshore-offshore movement patterns we observed at the diel sites. Shoreline habitats provide reduced velocities and likely higher food availability, that is, increased growth opportunities, relative to offshore habitats. Predation risk from visual predators is likely higher in shoreline habitats because of reduced depth, but only during the day when visual predators are active. The u/g construct therefore predicts an onshore movement into shoreline habitats that maximize growth during periods of low light intensity and high discharge as was observed. Low discharge during the early morning forces fish away from the innermost lanes as reduced depth become physically limiting. Pert and Erman (1994) evaluated the movement of fish and habitat selection in the Stanislaus River where there is a threefold difference in discharge between minimum and maximum daily flows. Two types of individuals were identified on the basis of habitat use under a range of discharges. Pattern-1 individuals displayed strong site fidelity and used higher focal point velocities at higher discharges. Pattern-2 individuals were generally more mobile and showed no relationship between discharge and focal point velocity. Onshore-offshore movement caused by changing discharge is a complex process, dependent on both the extent of changes in habitat conditions along the cross-section, and behavioral tendencies to remain in established territories or move to areas with better conditions.

Snorkel surveys provide an alternate means to boat electrofishing for indexing rainbow trout abundance in the Lee's Ferry reach. Boat electrofishing has a number of advantages including the availability of a lengthy historical time series and the ability to capture fish to estimate growth, population age structure, and other biological characteristics. Snorkel surveys likely have lower sampling error as counts are replicated at-a-site and more sites can be sampled per day (ca. 10 sites per 3 person crew vs. 5 sights for an electrofishing crew). More importantly, snorkel surveys provide a means of assessing the apparent density in offshore areas, a factor that varied noticeably among sample periods. Offshore areas may represent sub-optimal habitats because of reduced cover and higher velocities relative to shoreline areas. These sub-optimal habitats may be the first areas to show differences in abundance as population levels change. Indexing shoreline areas alone may result in a hyperstable index if the offshore-onshore distribution is density dependent.

We consider the snorkel-based population estimates of rainbow trout for the Lee's Ferry reach to be quite uncertain. Our catchability estimates, which were used to expand the observed densities, were not directly measured but instead calculated based on the ratio of average counts over daytime swims to peak counts at night. The implicit assumption is that all fish are seen during the peak count at night. It is possible that more fish were present, and that we have therefore overestimated the overall catchabilities and underestimated the true population sizes. We also had to assume that there was no variation in catchability across habitat types within a sample period. As there was a maximum of 3 sites for which our estimate of catchability could be computed, this was the only reasonable approach. However, it should be recognized that there could be considerable error in the overall population estimate due to site-to-site variation in catchability. McKinney et al. (1999) used mark recapture to estimate the population size of fish >= 150 mm in a small area (5,667) in Aug. 1998, and then expanded the estimate to the Lee's Ferry reach (783,935). Speas et al. (2002) estimated a mean population size in June 2001 of 91,000 based on apparent nearshore electrofishing densities and a multiple pass depletion estimate of catchability of 0.47. The June 2001 estimate is reasonably close to the snorkel-based estimate of 100,000 for June 2002 (Table 11). The April 2003 snorkel-derived population estimate suggests that population size between June 2002 and April 2003 dropped by 20%. The electrofishing index of abundance shows no change over this period.

The changes in snorkel-based total population estimates derived from the random and fixed sites may be partly caused by changes in the catchability of fish in offshore areas that were not accounted for in our assessment. It is very unlikely that the population was reduced to half of its abundance over a four-month period between June 2002 and October 2002, and then increased by over 50% by April 2003 (Table 11). The major factor causing this bizarre pattern was the reduction in the estimate of the number of fish in offshore areas in cobble bar-, talus- and debris fan-dominated shoreline habitats in October. Reduced underwater visibility during the October sample session could have resulted in an underestimate of the offshore population size relative to other sample periods. Sampling during the peak of the spawning period in April when fish were more visible to divers could have resulted in a positive bias in the offshore population size relative to other months. If snorkeling is to be used to index or estimate population size it will be important to conduct surveys when ambient light intensity and water clarity are similar and when differences in catchability due to behavioral effects are minimized, or to develop calibration relationships as in Hagen and Baxter (2005) and Korman et al. (2002 and 2005a).

The relationship between apparent shoreline densities obtained by electrofishing and snorkeling was relatively weak (Fig. 6). The weak correlation is not surprising considering that sampling occurred during day vs. night and under different discharges, all factors that effect offshore-onshore fish distribution and catchability. The weak correlation does not invalidate either method and we feel there is little value in continuing the electrofishing-snorkel survey comparison as currently designed. A more useful approach would be to conduct snorkel surveys in offshore and shoreline areas immediately before and after a site is electrofished. These data could be used to estimate the electrofishing catchability within the shoreline area and the proportion of the population in the sampling unit represented in the shoreline area that is sampled by electrofishing. The utility of this approach is debatable as it assumes that the snorkel counts provide a good estimate of the total number of fish present in both onshore and offshore environments.

The snorkel-to-electrofishing density ratio declined 4-fold from June 2001 to April 2003 (2.1 to 0.5, Fig. 6, Table 12). This occurred because apparent shoreline densities from snorkel surveys declined by 3-fold (6.2 to 1.9 fish/100m^2), while electrofishing densities increased slightly (Table 7). The systematic change in the ratio of apparent shoreline densities based on snorkeling vs. electrofishing surveys is potentially indicative of a real change in the population not picked up by the electrofishing index due to hyperstability; or alternately, biases in snorkel-based densities due to differences in catchability. We have no data to evaluate biases in catchability although changes in water clarity, light availability, and behaviour certainly could have created problems. There are two possible mechanisms explaining why electrofishing indices could be hyperstable relative to those derived by snorkelling. It is quicker to count a fish than it is to dip it and put it in a holding tank, so it is logical to assume that dippers likely saturate at lower fish densities than divers. Thus at higher fish densities, we would expect the snorkel-to-electrofishing ratio to be higher than at lower fish densities. An alternate explanation is that onshore-offshore movement is density-dependent. If shoreline low-velocity areas were preferred during the night (as predicted by the u/g construct) when electrofishing surveys were conducted, a higher proportion of fish would use this habitat at lower densities. Hence, under declining densities over the sample periods, shoreline densities estimated from electrofishing at night would remain relatively constant, while snorkel densities obtained during the day would decline, leading to a reduction in the snorkel-to-electrofishing density ratio.

Speas et al. (2004) estimated catchability for rainbow trout in Grand Canyon from electrofishing through depletion experiments and found no relationship between catchability and apparent trout density, implying no hyperstability in the electrofishing-based index of abundance. Their results should be viewed with caution as the depletions did not occur in enclosed areas and sampling was only conducted in shoreline areas. The interpretation of their catchability estimates depends on what is assumed about the exchange of fish between onshore areas that were sampled, and offshore areas that were not. If there was little exchange, then the catchability they measured simply reflects the efficiency of the gear at removing fish in onshore areas, not the overall catchability, which also includes the proportion of fish that are not present in the sample area.

Bayley and Austen (2002) make a strong argument why boat electrofishing effort should be standardized by site area or length rather than by time as currently used for Grand Canyon indices.

"The frequently debated issue of rating effort in terms of space or time should be considered in terms of the interpretation of catch per effort as a fraction (catchability) of the number of fish caught in a determined area. If fish retrieval or navigation around snags reduces mean boat speed, CPE with effort measured as time fished is inherently biased….. In all cases, effort should be measured as the length of the shoreline fished."

Our analysis showed considerable variation in the ratio of electrofishing time to site length, or thoroughness (Fig. 7, top). Less time electrofished per unit length sampled at some sites may be the result of higher velocities that push the boat through the site faster. Alternatively, more electrofishing effort may be applied at sites with high fish densities if the boat operator is circling back or reducing speed to increase the number of fish retained by dippers. A time-standardized CPE index will be affected if the change in electrofishing time resulting from the latter behavior is not proportional to the additional number of fish caught. The fact that the ratio of catch standardized by length to catch standardized by time tends to be higher when a site is fished more thoroughly (Fig. 7), suggests that changes in effort are not proportional to the number of fish caught at a site. We recommend that the ratio of electrofishing time to site length ratio be held as constant as possible in future surveys. Site length should be measured directly in the field using a survey tape and electrofishing catches should be standardized by site length as recommended by Bayley and Austen (2002).

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