Environmental Variables Influencing Downstream Migration of Juvenile Coho Salmon *(Oncorhynchus kisutch)* in Three Northern California Streams

by

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ENVIRONMENTAL VARIABLES INFLUENCING DOWNSTREAM MIGRATION OF JUVENILE COHO SALMON (ONCORHYNCHUS KISUTCH) IN THREE NORTHERN CALIFORNIA STREAMS

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ABSTRACT

Environmental Variables Influencing Downstream Migration of Juvenile Coho Salmon *(Oncorhynchus kisutch)* in Three Northern California Streams

Jennifer Feola

The primary objective of this study was to study the migration of coho salmon (*Oncorhynchus kisutch*) smolts in three coastal streams to determine if the probability of migration was correlated with environmental variables. Streams studied were Boyes, Streelow and Prairie Creeks, all located in Redwood National and State Parks, Humboldt County, California during 1999-2003. Smolt migration data consisted of daily catches from fyke net traps operated from 2 March to 6 June each year. Environmental variables included in models included: year, day of year, water temperature, change in water temperature, cumulative degree-days, discharge, change in discharge, lunar cycle, and the interactions of these variables. A partial logistic model using linear stepwise regression was used for analysis of environmental variables affecting coho salmon smolt movement. Akaike's Information Criterion and Bayes statistics were used to select the best models.

In Boyes Creek, the significant ($p < 0.05$) variables included within the best model were: year, day of year, day of year^2, discharge, change in discharge, the interaction of day of year and discharge, the interaction of day of year and change in discharge and the interaction of water temperature and discharge. In Streelow Creek, the significant ($p < 0.05$) variables included within the best model were day of year and the interaction of day of year and water temperature. In Prairie Creek, the significant (p <

0.05) variables included within the best model were: day of year, discharge, water temperature, degree-days and the interaction of day of year and discharge.

Another objective of this study was to evaluate the use of PIT (passive integrated transponder) tag antennae in measuring downstream migration of coho salmon smolts during the 2003 smolt migration. The pit tag antennae detected 96% of the pit tagged fish that moved past the antennae into live boxes. Seventy-eight percent of the tagged fish moved between the hours of 20:00 and 07:59.

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INTRODUCTION

Few studies have been conducted to determine factors that effect the within- and between-year variation in the probability of migration of salmon smolts. Bohlin et al. (1993) studied variation of the probability of migration of sea-run brown trout (*Salmo trutta*), but all of the variables considered were expressed as an interaction with degree-days. Dorn (1989) used a logistic regression model to determine what environmental variables affected downstream movement of Pacific (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*), however, his model did not consider environmental conditions before the migration period.

Spence (1995) used a logistic regression model to investigate within- and between-year variation of migration timing of coho salmon smolts (*Oncorhynchus kisutch*). Separate models were developed for each creek. The variables investigated included: day of year, water temperature (daily mean water temperature, change in water temperature, cumulative degree-days), discharge (daily mean discharge and change in discharge) and lunar phase and interactions between these variables. Few studies have investigated the influence of time, interacting with environmental conditions, on smolt migration. If time has been considered, it was usually as a single date, either the date of peak migration or median date of migration.

The main objective of my study was to use logistic regression modeling to investigate the effects of year, day of year, cumulative degree-days, daily average water temperature, change in daily average water temperature, daily average discharge, change in daily average discharge, lunar cyle and the interactions of these variables with each other on the probability of migration of coho salmon smolts in three coastal streams in northern California within Redwood National and State Parks, located in Humboldt County. The logistic regression model in my study took into account the temporal dimension of smolt migration. The degree-day variable allowed investigation of the influence of water temperature prior to the migration season on physiological readiness of fish to migrate. Water temperature and discharge have often been cited as variables affecting smolt migration, but there have been few studies that take into account the effects of the change of water temperature and discharge as this study did. My study also investigated the interaction of the variables included within the logistic models.

Coho salmon spend eighteen months or more at sea before migrating to their natal streams to spawn. Adult females deposit their eggs in gravel and after spawning, both adult males and females die. Eggs incubate in the gravel during the winter, and in the spring free-swimming fry emerge from the gravel. The fry live in the stream for a year or more, then migrate downstream to the ocean as smolts and begin growing rapidly in the ocean (Sandercock 1991).

There have been many studies to determine the environmental variables the affect the downstream migration of smolts. Hoar (1965) suggested that an endogenous clock, modified by photoperiod, induces physiological changes favoring life in the marine environment during spring and summer and favoring freshwater existence during autumn and winter. Groot (1981) also claimed that there is a strong internal component involved in triggering changes during the parr-smolt transformation and that this endogenous rhythm only becomes functional when fish reach a certain size. He found that the increase of daily photoperiod was the parameter most important for initiating smolt transformation, while water temperature also influenced the onset of smolting through growth. Wagner (1974) and Wedemeyer et al. (1980) found that photoperiod during spring was the major environmental variable influencing the transformation from stream-dwelling parr to seaward-migrating smolts. Grau (1981) suggested that lunar cycle and photoperiod, affected by temperature and acting through the thyroid, plays an important role in smoltification and onset of migration.

Many physiological changes occur during the parr-smolt transformation of anadromous fish which include increased body silvering, hypoosmotic regulatory capability, salinity tolerance and preference, growth rate, oxygen consumption, ammonia production, blood glucose, endocrine activity, gill Na^+, K^+-ATPase activity, buoyancy and migratory behavior. There is also decreased condition factor, body total lipid content and liver glycogen (Wedemeyer et al. 1980). Most of these changes prepare the fish physically for survival in seawater and reflective silvering is thought to be an adaptation for predator avoidance (McCormick et al. 1998).

Solomon (1978) emphasized the importance of determining the difference between the physiological development of migratory readiness and the actual onset of migration. Physiological alterations along with morphological and behavioral changes take place over an extended period, regulated in part by photoperiod and affected by temperature. When fish attain the proper state of readiness, an environmental stimulus can trigger migration. Spence (1995) noted that at the beginning of the smolting season, few individuals had reached the physiological state necessary to respond to triggering stimuli. As more individuals reached the appropriate physiological state, the fraction of fish moving downstream in response to short-term events became larger. The slight decrease in migration probability near the end of the migration season likely reflected a decrease in thyroxine and other neuro-endocrine factors as conditions became unfavorable for migration or ocean entry.

One group of variables dominated by photoperiod and temperature prior to the smolt run regulated the development and smoltification of Atlantic salmon in western Ireland (Byrne et al. 2003). A second group of variables dominated by total light and water level influenced daily smolt migration. Many other studies have noted the influence of discharge on downstream migration (Berry 1933, White 1939, Allen 1944, Andrews 1959, Solomon 1978, McMahon and Hartman 1989, Bohlin et al. 1993, Ashe et al. 1995, Hvidsten et al. 1995, Spence 1995, Erkinaro et al. 1998, Veselov et al. 1998, Whalen et al. 1999, Antonsson and Gudjonsson 2002, Byrne et al. 2003) along with water temperature (Berry 1933, Andrews 1959, Bjornn 1971, Jonsson and Ruud-Hansen 1985, Holtby et al. 1989, Jonsson et al. 1989, Zafft 1992, Bohlin et al. 1993, Hvidsten et al. 1995, Spence 1995, Erkinaro et al. 1998, Veselov et al. 1998, Roper and Scarnecchia 1999, Whalen et al. 1999, Antonsson and Gudjonsson 2002, Zydlewski et al. 2005), photoperiod (Grau 1981, Seelbach 1985, Zafft 1992) and time (Spence 1995). Another factor found to influence salmonid movement is the lunar cycle (Youngson et al. 1983, Thorpe et al. 1988, Hvidsten et al. 1995, Spence 1995).

Another objective of this study was to evaluate the use of PIT (passive integrated transponder) tag antennae in detecting downstream migration of pit tagged coho salmon smolts during the 2003 smolt migration. Once smolts are primed to migrate and triggered by an environmental stimulus, they are known to travel at night and during periods with low light intensity (Hvidsten et al. 1995, Carlsen et al. 2004). The majority of coho salmon smolts in the Taku River, Alaska (Meehan and Siniff 1962), Chehalis River, Washington (Moser et al. 1991) and Deep Creek, Alaska (Eskelin 2004) migrated downstream during the night. Moore et al. (1998) and Thorpe et al. (1988) found that Atlantic salmon smolts migrated mostly at night and juvenile steelhead (*Oncorhynchus mykiss*) were caught only during darkness in Steamboat Creek Basin, Oregon (Dambacher 1991). In another Oregon study, steelhead smolt movement was observed mostly just after sunset and before sunrise (Andrews 1959). Most sockeye salmon (*Oncorhynchus nerka*) smolts migrated down the rivers entering Barkley Sound, Vancouver Island during twilight or darkness (Wood et al. 1993). Aarestrup et al. (2002) observed nocturnal movement of Atlantic salmon and brown trout in the Danish River Lilleaa.

METHODS AND MATERIALS

Study Area

Boyes Creek, a tributary of Prairie Creek, located in Redwood National and State Parks, Humboldt County, California, is a third order creek that drains a 4.4 km^2 watershed. The study reach was a 2.3 km section beginning at the mouth of the creek. Although the watershed contains some old growth redwood (*Sequoia sempervirens*), portions of this creek were clear-cut in the past. Boyes Creek is dominated with second growth redwood, mixed with big leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), California-laurel (*Umbellularia californica*), and western hemlock (*Tsuga heterophylla*) (Sparkman 2004). In addition to coho salmon, the study reach contained Chinook salmon (*Oncorhynchus tshawytscha*), steelhead, coastal cutthroat trout (*Oncorhynchus clarki clarki*), threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), coast range sculpin (*Cottus aleuticus*) and Pacific lamprey (*Lampetra tridentata*) (Bell et al. 2001).

Streelow Creek is a third order stream and a tributary to Prairie Creek that drains a 5.7 km^2 watershed. The study reach was a 2.2 km section beginning at the mouth of the stream. This creek was extensively clear cut logged in the 1950 -1960's for old growth redwood, and is considered to be in a recovering state. The watershed is forested with second growth redwood, mixed primarily with red alder (Sparkman 2004).

Prairie Creek is a third order tributary to Redwood Creek (Figure 1). The watershed supports old growth redwood, Sitka spruce (*Picea sitchensis*), and Douglas fir

(*Pseudotsuga menziesii*). Understory is dominated by black huckleberry (*Vacinium ovatum*), red huckleberry, (*V. parvifolium*), and ferns (*Polystichum* spp.). Riparian vegetation is predominately red alder, big leaf maple, and salmonberry (*Rubus spectabilis*). Weather in the region is characterized by wet, mild winters, with rainfall between 135 and 200 cm, and relatively dry summers (Bell et al. 2001).

The study reach on Prairie Creek began at Brown's Creek and continued for 6.3 km. There were no barriers to fish movement within the study reach. Fish species were similar to those in Boyes and Streelow Creeks. The reach is nearly pristine. Drainage area above the study reach is 10 km^2. Floods resulting from rainstorms frequently occur between October and March (Bell et al. 2001).

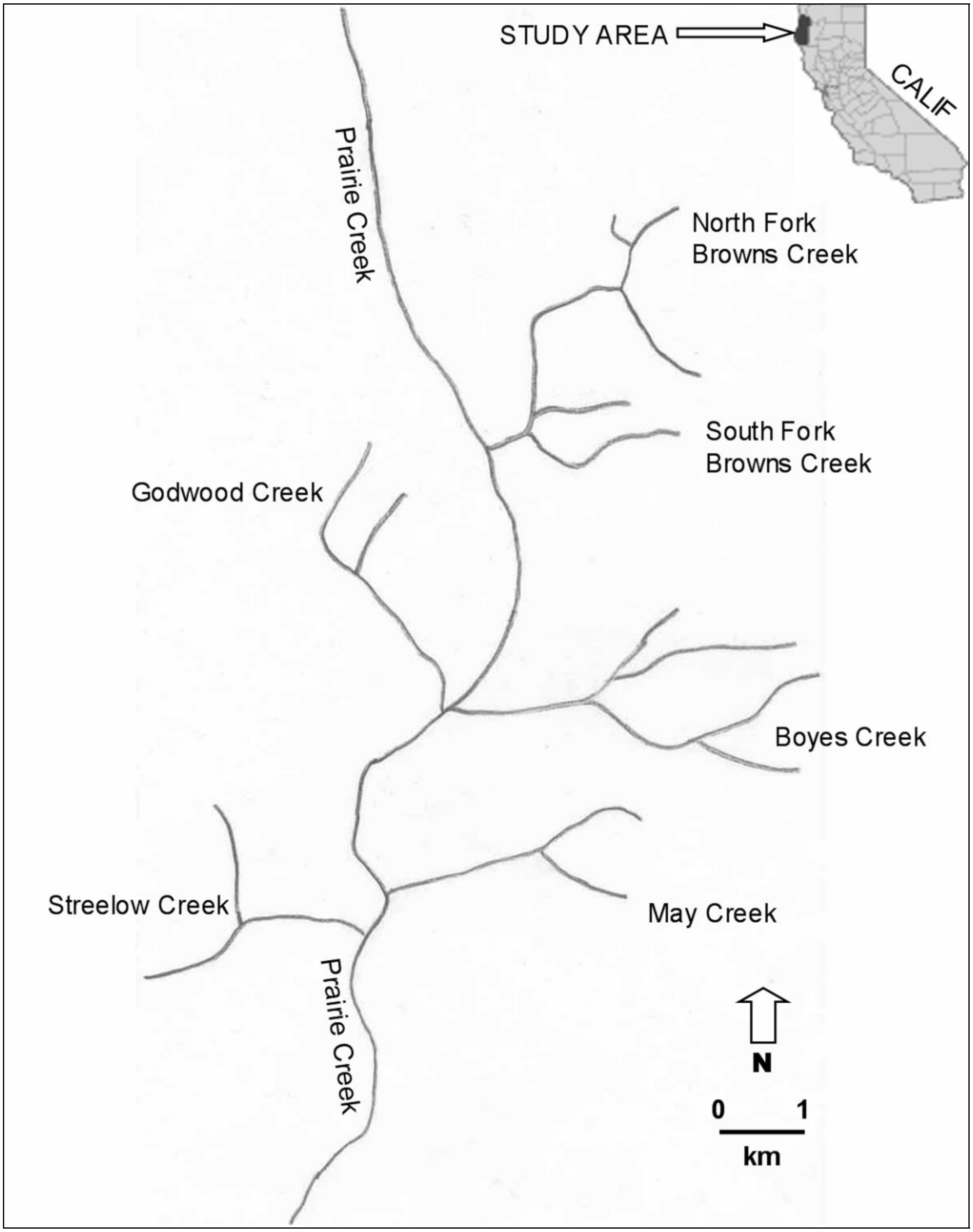


Figure 1. Prairie Creek watershed, Humboldt County, California (from Sparkman 2004).

Field Methods

During July and October 2002, juvenile coho salmon were collected from randomly selected habitat units distributed throughout the study reaches of each stream using a backpack electrofisher (Humboldt State University IACUC protocol 02 03 F.35). Individuals greater than 59 mm fork length (FL) were PIT tagged during this sampling. Additional PIT tags were implanted during November 2002 and March 2003. All fish were anesthetized with MS-222 before handling. After anesthetization, the length (fork length, mm), wet weight (nearest 0.01 g) and location (habitat unit) of each fish was recorded, an 11.5 mm PIT tag was then inserted into the body cavity posterior to the tips of the pectoral fins. The insertion was in the abdomen of the fish to the right or left of the mid-ventral line and between the tips of the pleural ribs. A 12- gauge hypodermic needle was used to insert PIT tags. The needle was directed toward the posterior of the fish and the tag was injected away from the heart or other vital organs. Next, the adipose fin was clipped and the entry site of the PIT tag was treated with sterile Vetbond adhesive glue. A total of 1,273 fish were PIT tagged, 327 in Boyes Creek, 457 in Streelow Creek and 489 in Prairie Creek.

The smolt trap season was defined as 2 March to 6 June because those were the dates on which all traps were fishing for all creeks each year. Smolt trapping was accomplished using fyke nets installed facing upstream in the thalweg. Single traps were installed in Boyes and Streelow Creeks near the mouths of each stream and in Prairie Creek approximately 200 meters upstream of Brown’s Creek (Figure 2). Traps were checked for fish and cleared of debris daily. A 15.24 cm diameter PVC pipe was attached to the end of each net which connected to a live box, a 17.78 cm diameter ring antenna (FS2001F-ISO, Destron-Fearing Corporation, South St. Paul, Minnesota) was attached to the outside of the PVC pipe (Figure 3). This portable transceiver system recorded time, date and unique PIT tag number as fish implanted with PIT tags swam from the fyke net, through or near the pipe to the live box. Each data logger and antenna was powered by a sealed, deep cycle 12 volt, 75 ampere-hour battery. Batteries were changed and data loggers were downloaded every five or six days.

All migrating coho salmon smolts captured in the live box were anesthetized with MS-222, their length (fork length, mm) and wet weight (nearest 0.01 g) recorded and checked for the presence of the adipose fin. Coho salmon without an adipose fin were scanned with a handheld PIT tag pocket reader to record the PIT tag number.

During 2003, water temperature data was collected by installing data loggers (HOBO, Onset Computer Corporation, Bourne, Massachusetts) in each stream mid-depth in a pool near the center of the study reach. Data loggers were programmed to record every hour and were downloaded each month. Stage height in Boyes and Streelow Creeks was recorded with a water level logger (WL15, Global Water Instrumentation, Inc., Sacramento, California). Data loggers were programmed to record every 15 minutes and were downloaded every month with a laptop computer.

Figure 2. Fyke net and live box in Prairie Creek, Redwood National and State Parks, Humboldt County, California (Spring 2003).

Figure 3. PIT tag recorder and PIT tag ring antenna.

Stream flow measurements were made during various stage heights with an electronic flow meter (Flow Mate 2000, Marsh-McBirney Inc., Frederick, Maryland). Measurements covered the full range of stream flow conditions for the sampling period. Discharge data for Prairie Creek was provided by Redwood National Park. Lunar data was obtained online from the Astronomical Applications Department of the U.S. Naval Observatory at http://aa.usno.navy.mil.

During 1999-2002, migrant traps were operated the same and environmental variables were collected in the same manner as 2003. However, PIT tag antennae were not used in any creek and stage height was not recorded in Boyes and Streelow Creeks.

Data Analysis

Probability of capture curves were created using an exponential decline and constant relationship of probability of capture and discharge (Figure 4). These curves were applied to the discharge data for each creek during each trap season to calculate the daily probability of capture. Darroch Analysis with Rank-Reduction (DARR) was used to estimate weekly probability of capture. DARR is a method for analysis of stratified mark-recapture data from small populations, with application to estimating abundance of smolts from outmigrant trap data (Bjorkstedt 2000). Rating curves for stage versus discharge were developed for Boyes and Streelow Creeks (Excel, Microsoft Inc., Seattle, Washington).

Tukey's 'Honest Significant Difference' method was used to analyze any differences in size of coho salmon smolts among creeks for each sample year (R Version 2.3.1, 2006). This procedure creates a set of confidence intervals on the differences between the means of the levels of a factor with the specified family-wise probability of coverage. The intervals are based on the Studentized range statistic, Tukey's 'Honest

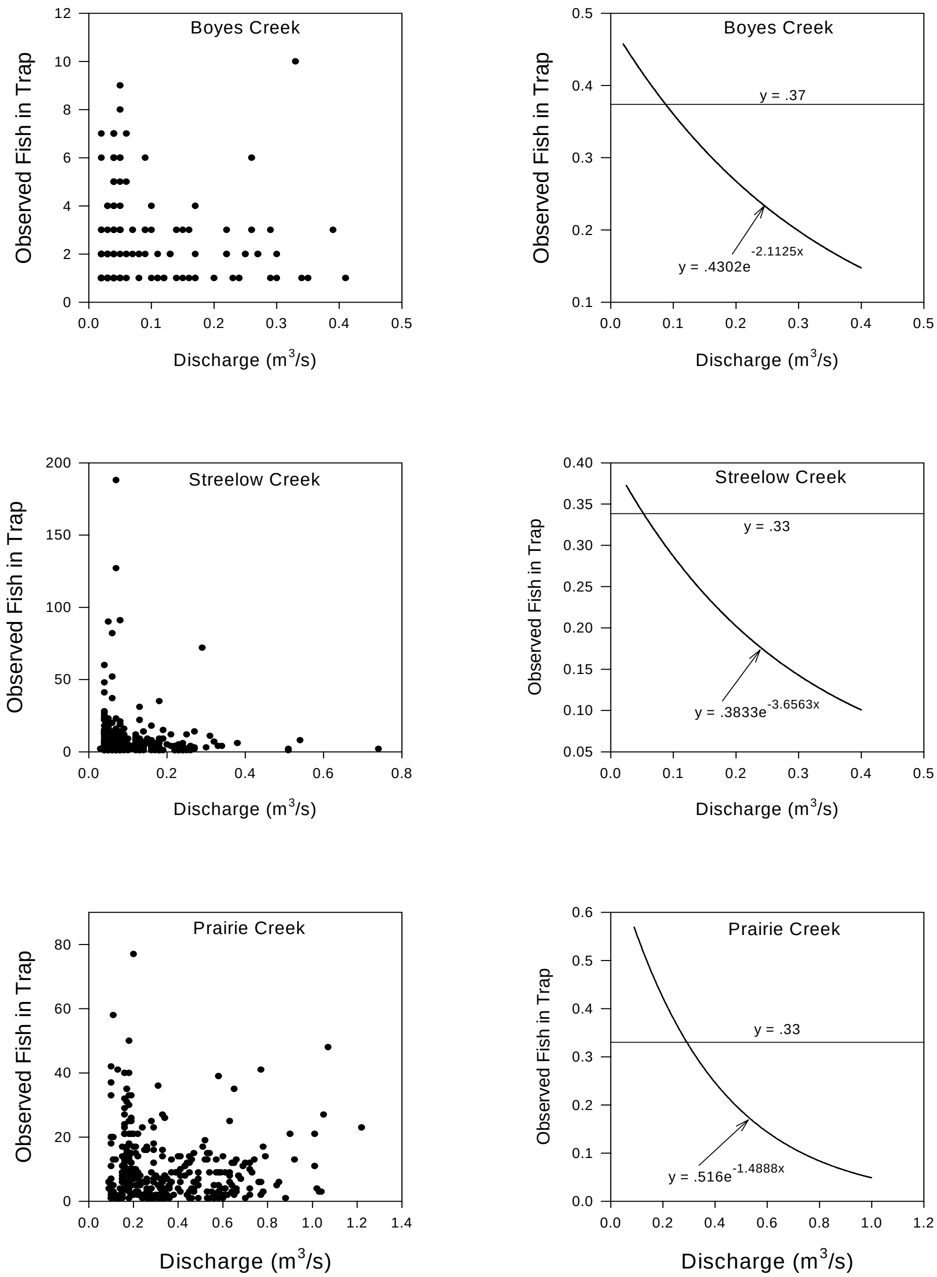


Figure 4. Number of coho salmon smolts observed in traps relative to discharge and constant and exponential decline discharge-capture probability relationships for Boyes and Streelow Creeks during 2000-2002 and Prairie Creek during 1999-2003, Redwood National and State Parks, Humboldt County, California.

Significant Difference' method. All size data were log transformed before being analyzed for differences.

Modeling

The observed number of coho salmon smolts was expanded to predicted total daily number of fish based on binomial expansion, using the exponential decline and constant discharge to capture probability relationships.

The binomial distribution consists of:

$$L(k) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}$$

Where k=daily number of coho salmon smolts captured, n=total daily number of coho salmon smolts passing trap and p=daily probability of capture from the discharge relationship.

Since we know k and have specified a given p from the discharge relationship, n is calculated by:

$$\hat{n} = \frac{Sum(L(k \mid n) * n)}{Sum(L(k \mid n))}$$

Where $\hat{n}$=weighted mean of the n considered as possible true n yielding the observed k. For each day, L(k) was calculated for the specified p for a range of n=[1,1000], with L(k|n)=likelihood of observing k given n and the specified p for the day.

A partial logistic model using linear stepwise regression (SPLUS, Professional Edition, 2000, Seattle, Washington) was fit to the binomial expansion results and used for analysis of environmental variables affecting coho salmon smolt movement. The time period during which 5%-95% of the total smolt run reached the trap was modeled.

In the logistic regression model, λ_i is the logit link function and is used to relate the independent linear variables to the response variable

$$\lambda_i = x_i \beta$$

where

$$\lambda_i = \ln[(\pi_i/(1-\pi_i)]$$

The dependent variable, λ_i , or logs-odd ratio, is the natural logarithm of the probability of migration, relative to the probability of remaining upstream during the $_i$th interval. The vector of variables is x_i and β is the vector of regression coefficients

Discrete time intervals are used in the model, where y_i is the number of positive responses (migrants) and x_i is the vector of environmental variables measured during the $_i$th interval. An assumption of the model is that during interval $_i$, the number of migrants, y_i that pass downstream out of a potential pool of n_i fish is binomially distributed (Bi):

$$y_i = \mathrm{Bi}(n_{i,} \pi_i)$$

where π_i is a parameter for migration rate, prob(fish migrate | fish did not migrate prior to interval $_i$). The analysis relates the probability of migration π_i , to the vector x_i of explanatory variables. The predicted probability of a positive response π_i is calculated as

$$P(\pi_i) = e^{\lambda i}/(1+ e^{\lambda i})$$
$$= e^{xi\,\beta}/(1+e^{xi\,\beta})$$

predicted number of migrants during interval $_i$ of a given year is

$$P(y_i) = n_i\pi_i$$
$$= n_i[e^{xi\,\beta}/(1+e^{xi\,\beta})]$$

Nine independent variables and eight interactions were included in the models (Table 1). Akaike's Information Criterion (AIC) was used as a means of selecting the best models (Burnham and Anderson 2002). The AIC was defined as:

$$AIC = -2 * \log(L_i) + 2 * K_i$$

where L_i is the sample log likelihood for the i^{th} of i alternative models, and K_i is the number of independent parameter estimates for the i^{th} model. The term $2 * K_i$ may be viewed as a penalty for using too many parameters. In application, one computes AIC for each candidate model and selects the model with the smallest AIC and this model is estimated to be the "closest" to the unknown reality. However, it is not the absolute size of the AIC value, but the differences between the AIC values that are important.

After calculating AIC values, delta (Δ_i), likelihoods (L_i) and Akaike weights (w_i) were calculated. Delta was defined as:

$$\Delta_i = AIC_i - AIC_{min}$$

where AIC_i was the AIC value for the i^{th} model and AIC_{min} was the lowest AIC value from among all models. Such Δ_i values allow a quick comparison and ranking of candidate models. Models with Δ_i values within zero to two of the best model also have substantial strength.

The likelihood represents the relative strength of evidence for each model. L_i was defined as:

$$L_i = \exp^{(-\Delta i/2)}$$

Table 1. Main effect and interaction terms included in logistic regression models tested to analyze environmental variables affecting coho smolt movement in Boyes, Streelow and Prairie Creeks, Redwood National and State Parks, Humboldt County, California.

Main effect terms	Variables in model
Yr	Year
D	Day of year
D^2	Day of year squared
DD	Cumulative degree-days from 1 Jan to 1 Mar (beginning of trap season)
W	Daily average water temperature on day y
W2	Change in daily average water temperature from two days prior
Q	Daily average discharge on day y
Q2	Change in daily average discharge from two days prior
L	Lunar cycle
Interaction terms	
$D{:}D^2$	Day of year x day of year squared
D:W	Day of year x daily average water temperature on day y
D:W2	Day of year x change in daily average water temperature from two days prior
D:Q	Day of year x daily average discharge on day y
D:Q2	Day of year x change in daily average discharge from two days prior
D:L	Day of year x lunar cycle
W:W2	Daily average water temperature on day y x change in daily average water temperature from two days prior
Q:Q2	Daily average discharge on day y x change in daily average discharge from two days prior
L:Q2	Lunar cycle x daily average discharge from two days prior
W:Q	Daily average water temperature on day y x daily average discharge on day y

It is more convenient to normalize these quantities so that they equal one, which is accomplished by calculating Akaike weights (w_i) as:

$$w_i = \frac{\exp^{(-\Delta_i/2)}}{\sum_{r=1}^{R} \exp^{(-\Delta r/2)}}$$

Akaike weights are interpreted as the weight of evidence in favor of model *i* being the best model given that one of the models must be the best model of the given set of models. Credible intervals were developed by adding up the Akaike weight values from largest to smallest values. A credible interval is interpreted as the probability that the right models are present within the interval.

RESULTS

Discharge and Probability of Capture

Probability of capture forecasted from the exponential decline relative to discharge, the constant efficiency and the DARR estimates were dissimilar (Figures 5, 6). In some streams and years, each method of estimating efficiency produced similar patterns relative to discharge, such as Boyes Creek during 2001. More often, the probability of capture forecasted from the exponential decline relative to discharge and the constant efficiency were somewhat similar to each other, but both differed from DARR estimates. Sometimes all three methods of estimating efficiency differed.

Size

Size frequency distributions were adequate to separate coho salmon fry from smolts during 1999-2003 (Figures 7, 8). The separation of fry from smolts appeared to be at about 50 mm each year. Coho salmon ranged in size between 25 mm and 138 mm, with most fry between 30-39 mm. This size category accounted for an average of 25.4% of the fish that entered the trap.

The size distribution of coho salmon smolts captured approximated a normal curve. Forty-nine percent of smolts captured were between 80 and 109 mm FL. The largest percentage of smolts caught in any 10 mm size group, 19.2%, was in the 90-99 mm group. At the tail ends of the distribution, smolts 50-59 mm and greater than 130 mm FL represented less than 1% of the total number caught.

The range in size of smolts reflected growth during the spring. During the first month of trapping, the average size of coho salmon smolts in Boyes Creek was 79.1 mm in 2000, 80.2 mm in 2001 and 76.9 mm in 2002. During the last month of trapping, the average size of coho salmon smolts was 90.6 mm in 2000, 106.5 mm in 2001 and 103.1 in 2002. During the first month of trapping in Streelow Creek, the average coho salmon smolt size was 90.0 mm in 2000, 89.4 mm in 2001 and 87.9 mm in 2002. During the last month of trapping, average coho salmon smolt size was 101.8 mm in 2000, 103.6 mm in 2001 and 112.0 mm in 2002. During 1999, the average coho salmon smolt size was 77.3 mm during the first month of trapping and 95.7 mm during the last month in Prairie Creek. During 2000, the average size ranged from 75.4- 97.6 mm. The average size ranged from 78.5-102.1 mm in 2001, 85.7-109.5 mm in 2002 and 73.7-98.8 mm in 2003.

Size of coho salmon smolts differed among streams most years. Smolt trap years 1999 and 2003 were not analyzed because of low sample sizes in Boyes and Streelow Creeks. For trap year 2000, significant differences were found between Boyes Creek and Prairie Creek and Boyes Creek and Streelow Creek. (Table 2). The mean size for Boyes Creek was 87.0 mm, while it was 93.8 mm for Streelow Creek and 93.2 mm for Prairie Creek. Significant differences were detected between Streelow Creek and Boyes Creek and Streelow Creek and Prairie Creek during 2001. The mean fork length was 98.1 mm in Streelow Creek, 89.0 mm in Boyes Creek and 91.4 mm in Prairie Creek. Significant differences were detected between all streams during trap year 2002. The average size of

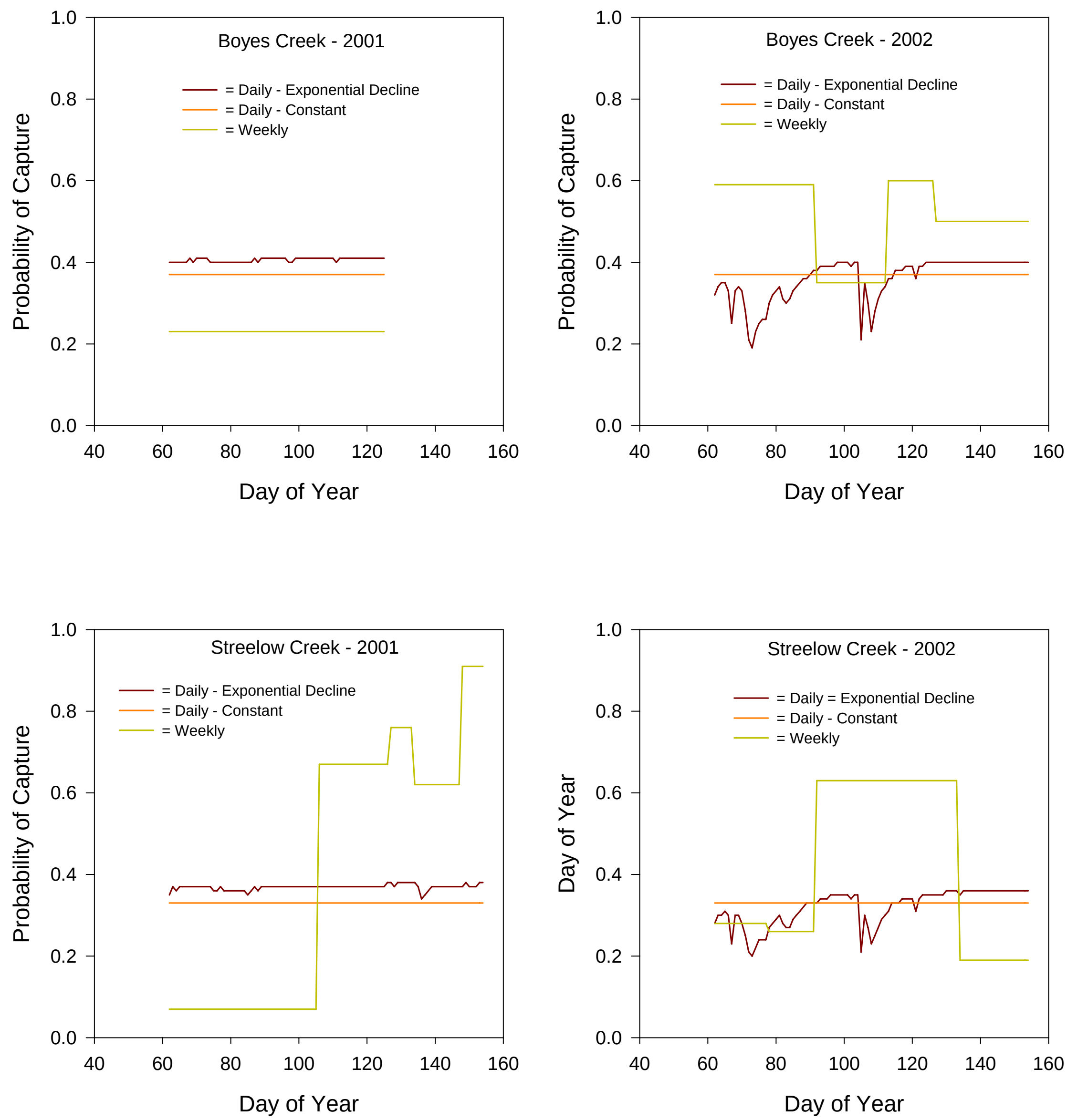


Figure 5. Daily and weekly estimated probability of capture of coho salmon smolts at Boyes and Streelow Creeks during the 2001 and 2002 trap season, Redwood National and State Parks, Humboldt County, California. Daily probability of capture was based on an exponential decline and constant relationship.

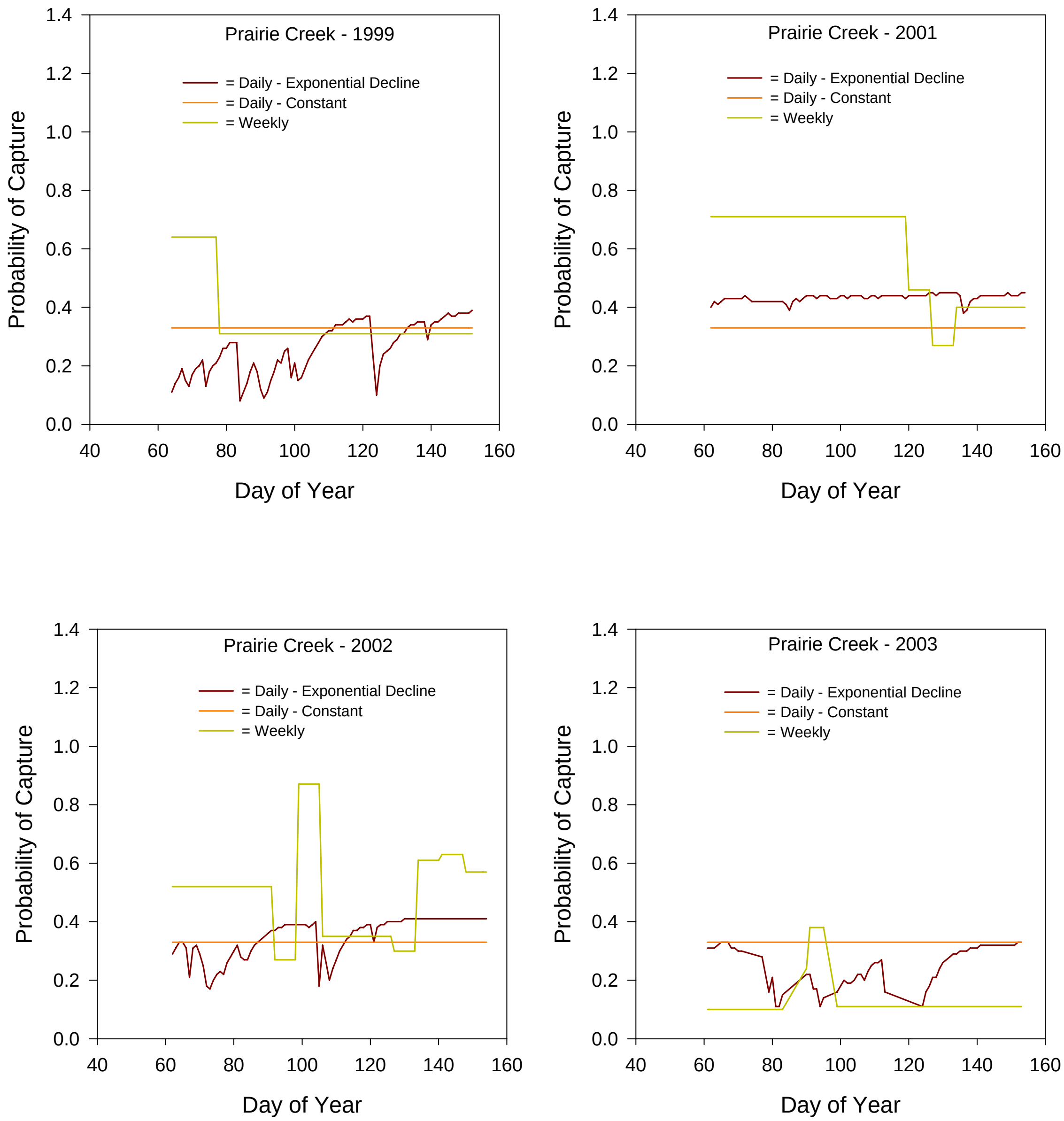


Figure 6. Daily and weekly estimated probability of capture of coho salmon smolts during 1999 and 2001-2003 trap season in Prairie Creek, Redwood National and State Parks, Humboldt County, California. Daily probability of capture was based on an exponential decline and constant relationship.

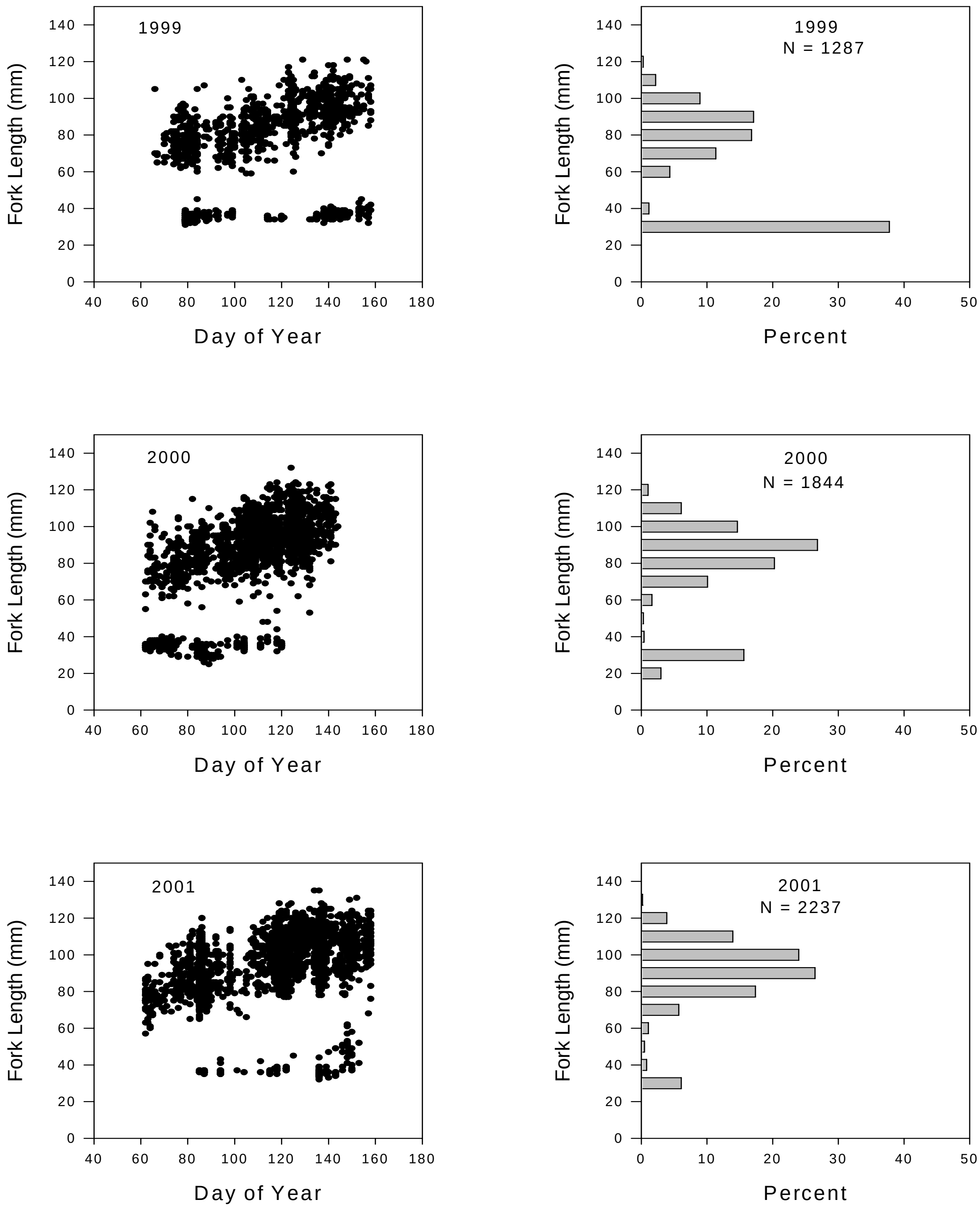


Figure 7. Size frequency distribution of fork length of coho salmon in traps at Boyes, Streelow and Prairie Creeks, Redwood National and State Parks, Humboldt County, California, during trap years 1999-2001.

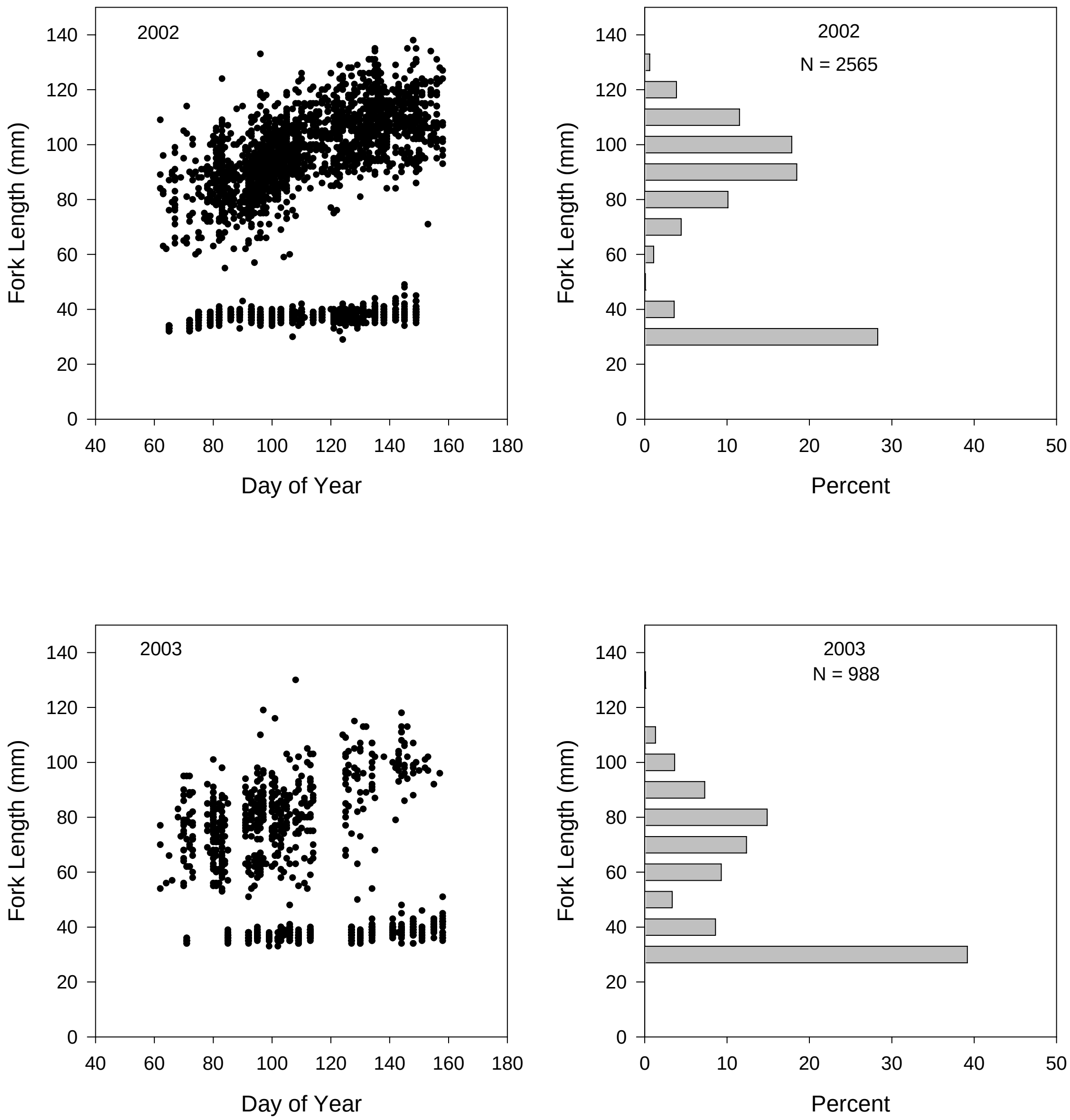


Figure 8. Size frequency distribution of fork length of coho salmon in traps at Boyes, Streelow and Prairie Creeks, Redwood National and State Parks, Humboldt County, during trap years 2002-2003.

Table 2. Length differences of coho salmon smolts in Boyes, Streelow and Prairie Creeks during trap years 2000-2002, Redwood National and State Parks, Humboldt County, California.

Stream comparison			Year	Difference (mm)	p value
Prairie Creek	vs.	Boyes Creek	2000	6.1	< 0.0001
Prairie Creek	vs.	Streelow Creek	2000	0.7	0.5504
Streelow Creek	vs.	Boyes Creek	2000	6.8	< 0.0001
Prairie Creek	vs.	Boyes Creek	2001	2.4	0.3790
Prairie Creek	vs.	Streelow Creek	2001	6.7	< 0.0001
Streelow Creek	vs.	Boyes Creek	2001	9.1	< 0.0001
Prairie Creek	vs.	Boyes Creek	2002	12.1	< 0.0001
Prairie Creek	vs.	Streelow Creek	2002	2.9	< 0.0001
Streelow Creek	vs.	Boyes Creek	2002	9.2	< 0.0001

a coho salmon smolt was 90.0 mm in Boyes Creek, 99.2 mm in Streelow Creek and 102.1 mm in Prairie Creek. For all years investigated, the smallest fish were found in Boyes Creek. The largest fish were found in Streelow Creek in 2000 and 2001, while the largest fish in 2002 were found in Prairie Creek.

Environmental Variables

Rating curves were developed for Boyes and Streelow Creeks in 2003 (Figure 9) and correlated with discharge in Prairie Creek.   Stage height explained most of the variation in average daily discharge in both Boyes Creek (R^2 = 0.9553) and Streelow Creek (R^2 = 0.9830). Average daily discharge in Prairie Creek also explained most of the variation in average daily discharge in both Boyes Creek (R^2 = 0.9330) and Streelow Creek (R^2 = 0.8204). Average daily discharge varied among years, but seasonal patterns were similar in each stream (Figure 10). Greatest average daily discharge was recorded before the migrant trapping season, except in 2003.   In 2003, high discharge events were recorded through April in all three streams. The highest daily average discharge occurred during the trapping season in Boyes Creek. Among years, the range in daily average

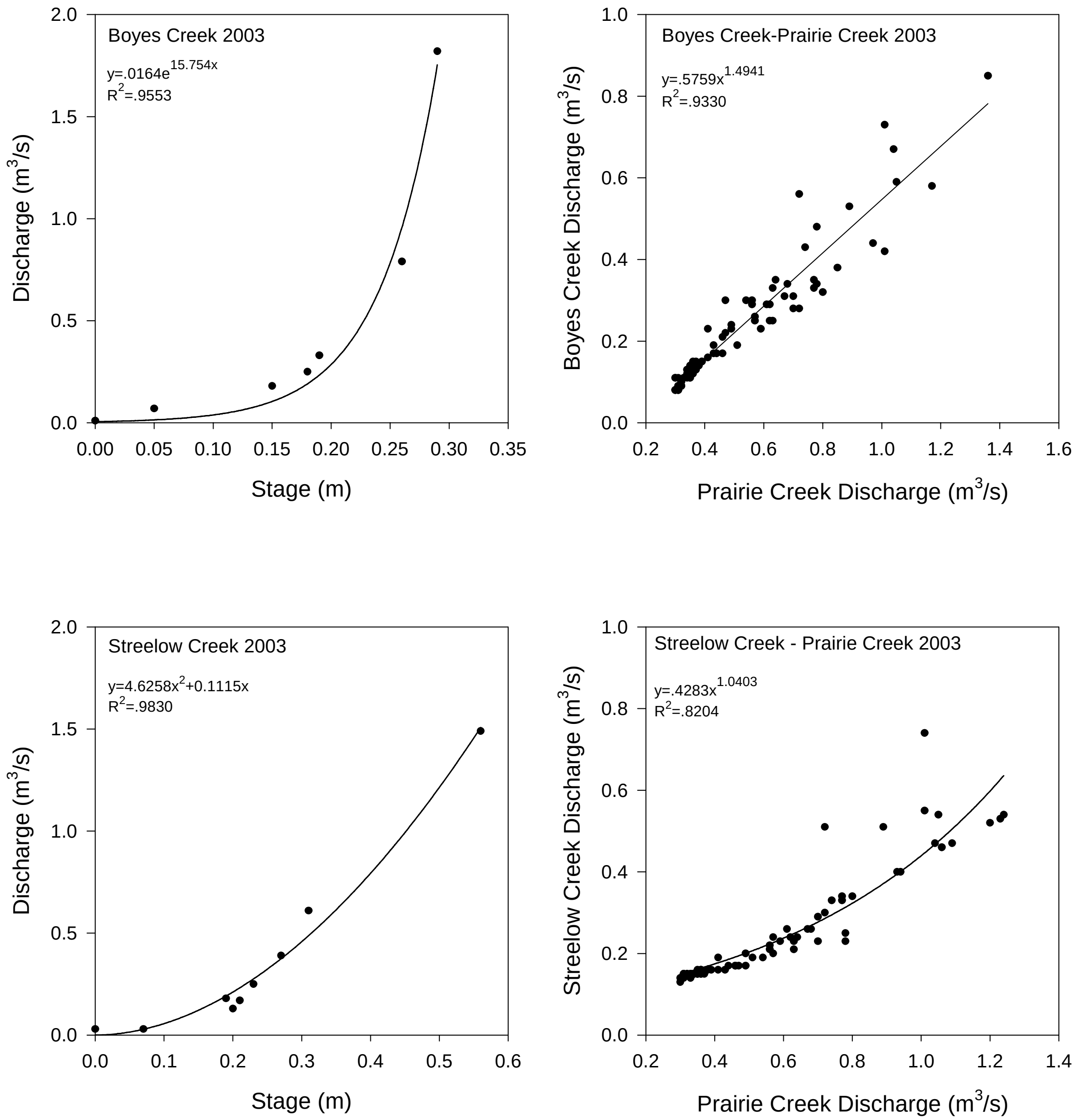


Figure 9. Rating curve and regression rating curve for Boyes and Streelow Creeks constructed from data collected for Boyes, Streelow and Prairie Creeks during trap year 2003, Redwood National and State Parks, Humboldt County, California.

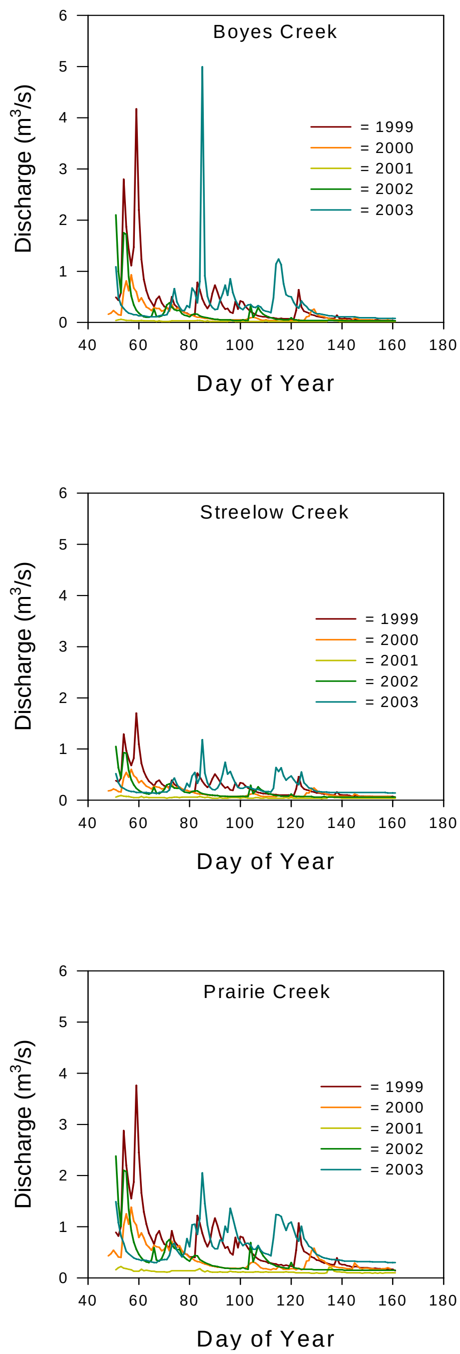


Figure 10. Average daily discharge data for 1999-2003 at Boyes, Streelow and Prairie Creeks, Redwood National and State Parks, Humboldt County, California. Trapping season included days of year 62–158 (1999, 2001-2003) and 61–157 (2000).

discharge was greatest in 2003 and lowest in 2001 (Table 3). It is noteworthy that the single greatest daily average discharge recorded during the period, 4.99 m^3/s on 26 March 2003, occurred in Boyes Creek which has the smallest watershed of the three streams studied.

Daily average water temperature increased each year in each stream during the period of smolt migration (Figure 11). Although water temperature varied daily in each stream, degree-days accumulated in each stream during the smolt trapping period were similar (Figure 12). Water temperature data was unavailable from May 2, 2001 to June 2, 2001 due to failure of dataloggers. I assumed that water temperature increased gradually during this period and applied a constant increase in water temperature per day during this period.

Number of moon phases was nearly equal during the 1999-2003 migrant trapping seasons. During this period there were 17 first, full and last quarter moon phases and 18 new moon phases. Each moon phase occurred three or four times within each trapping season.

Movement

Dates on which 5%, 50% and 95% of the total coho salmon smolts were caught during the 2000-2002 trap seasons revealed similar patterns of smolt movement from each stream (Figure 13). Movement from Boyes Creek preceded movement from the other two streams in 2001. In 2000 and 2002, however, the dates on which 5% and 95% of smolts had been captured were similar in each stream.

Table 3. Range of average daily discharge during 1999-2003 trap seasons in Boyes, Streelow and Prairie Creeks, Redwood National and State Parks, Humboldt County, California.

Year	Boyes Creek (m^3/s)	Streelow Creek (m^3/s)	Prairie Creek (m^3/s)
1999	0.04-1.23	0.07-0.72	0.16-1.66
2000	0.04-0.60	0.06-0.44	0.16-1.03
2001	0.02-0.06	0.03-0.08	0.09-0.21
2002	0.03-0.38	0.06-0.32	0.15-0.75
2003	0.08-4.99	0.13-1.18	0.30-2.05

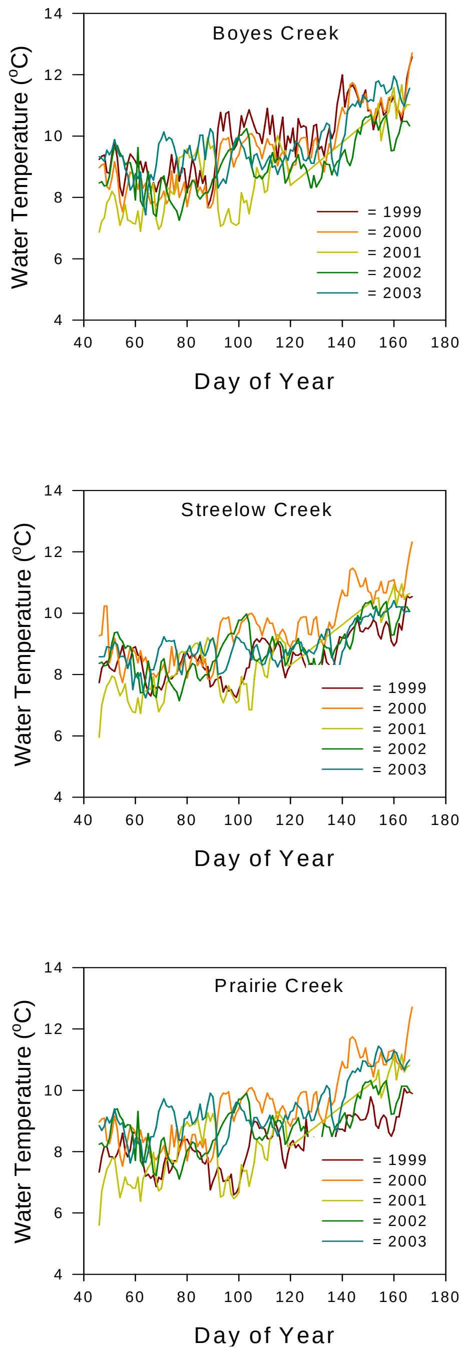


Figure 11. Average daily water temperature data for 1999-2003 at Boyes, Streelow and Prairie Creeks, Redwood National and State Parks, Humboldt County, California. Trapping season included days of year 62–158 (1999, 2001-2003) and 61–157 (2000).

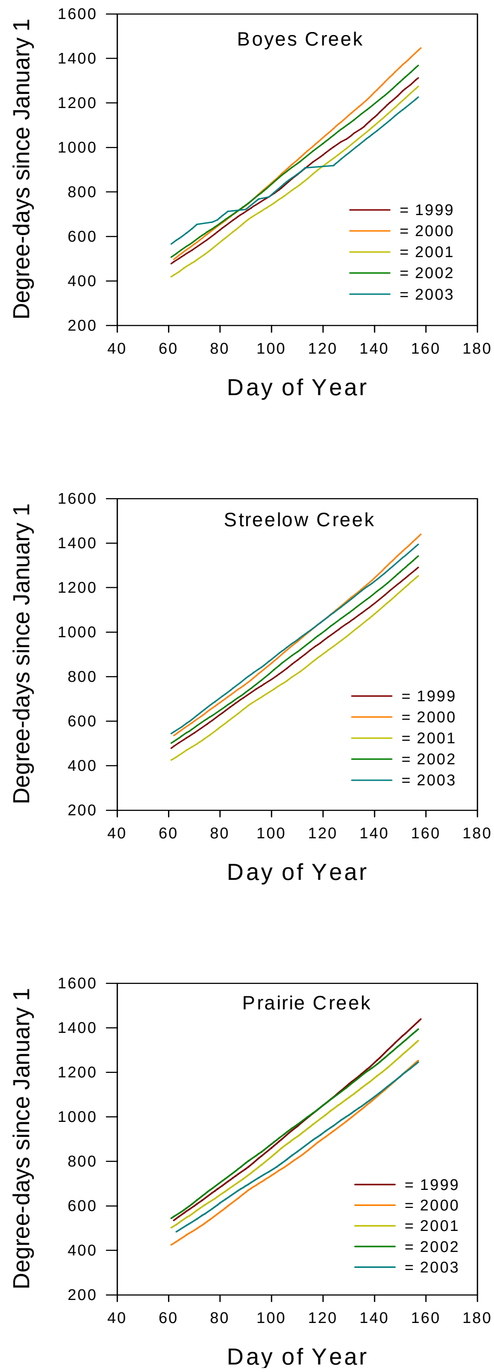


Figure 12. Cumulative degree-days since January 1 for 1999-2003 at Boyes, Streelow and Prairie Creeks, Redwood National and State Parks, Humboldt County, California. Trapping season included days of year 62–158 (1999, 2001-2003) and 61–157 (2000).

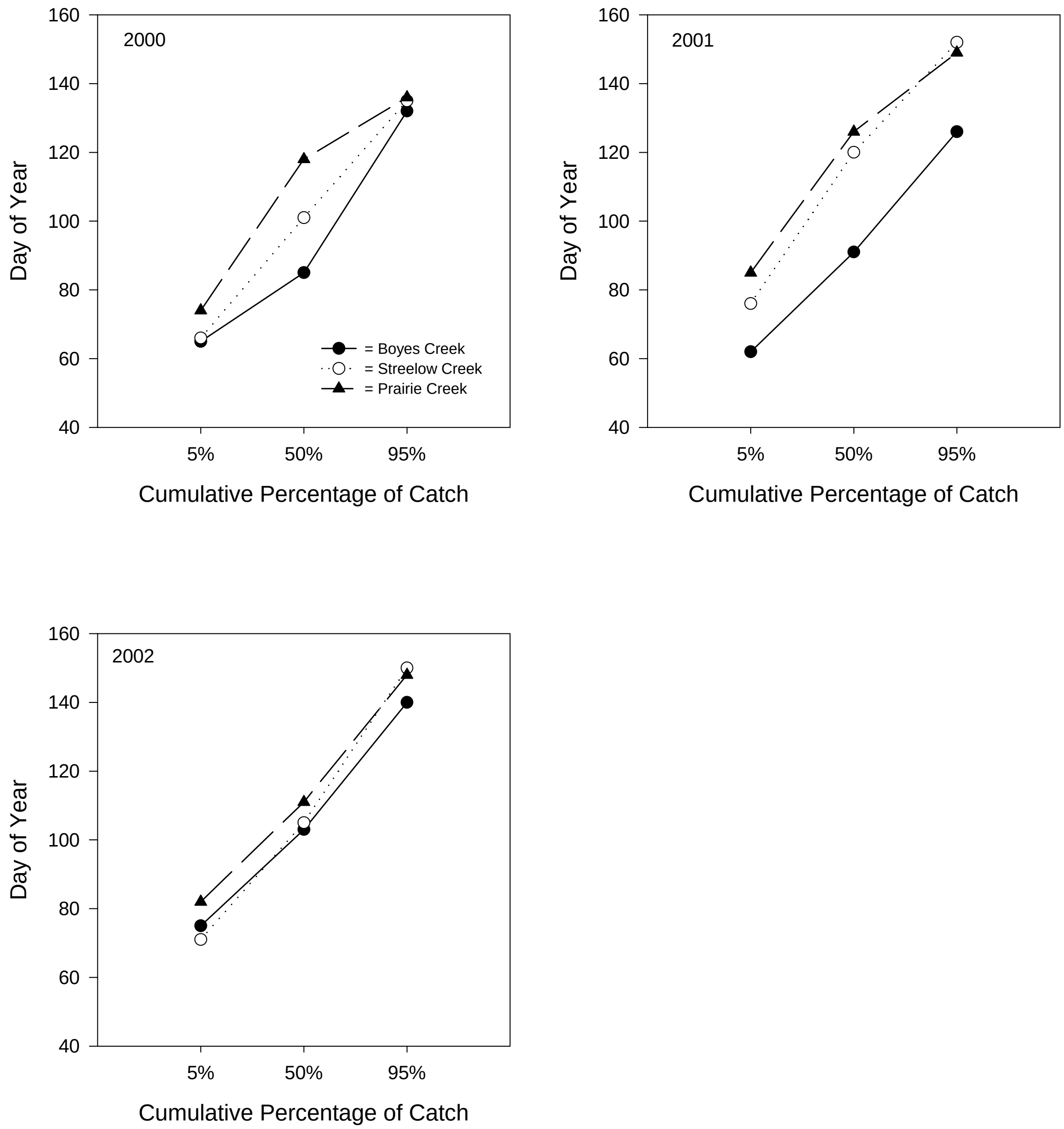


Figure 13. Day of year on which 5%, 50% and 95% of total coho salmon smolt run was caught at downstream migrant trap in Boyes, Streelow and Prairie Creeks during 2000-2002, Redwood National and State Parks, Humboldt County, California.

In Boyes Creek, the date on which 5% of the total smolts were caught ranged from March 3, 2001 to March 11, 2002. The 95% threshold dates ranged from 22 May during 2000 and 2002 to May 26, 2001. In Streelow Creek, the earliest date on which 5% of the total coho salmon smolts were caught was on March 5, 2000 and the latest date was March 15, 2001. The date on which 95% of the total coho salmon smolts were caught ranged from May 18, 2000 to May 31, 2001. In Prairie Creek, the earliest date on which 5% of the total coho smolts were caught was on March 10, 2000 and the latest date was March 18, 2002. May 15, 2000 was the earliest date on which 95% of the total smolts were caught and 28 May was the latest date which occurred during 2001 and 2002

A total of 100 PIT tagged juvenile coho salmon were captured in or detected passing the three traps during 2003. Ninety-six PIT tagged fish were recorded by the remote antennae in 2003, and four were not recorded by antenna. The distance tagged fish moved before reaching smolt traps was calculated for Prairie Creek during trap years 2000-2003 (Figure 14). Sampling records for previous electrofishing efforts were examined to see where the pit tagged fish were last located before they were trapped. Distance smolts moved in 1999 could not be calculated because there were no electrofishing records for 1998. In 2004, the number of trapped coho salmon that could be traced to previous electrofishing efforts was small.

In all creeks, seventy-eight percent of tagged fish captured in 2003 moved between the hours of 20:00 and 07:59 (Figure 15). Peaks of movement occurred during 06:00-07:59 hr, 20:00-21:59 hr and 22:00-23:59 hr. Together, 52.6% of the coho salmon smolts moved during these three time intervals.

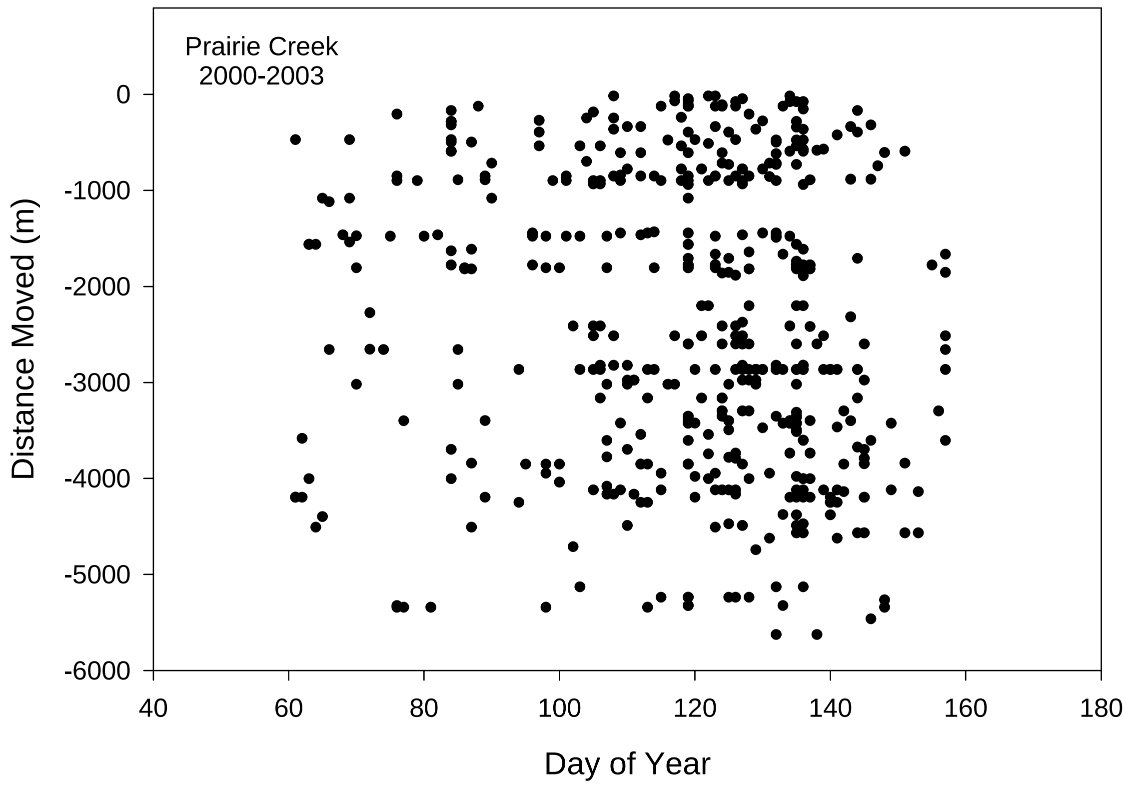


Figure 14. Distance coho salmon smolts moved from last detection site to Prairie Creek trap during 2000-2003, Redwood National and State Parks, Humboldt County, California.

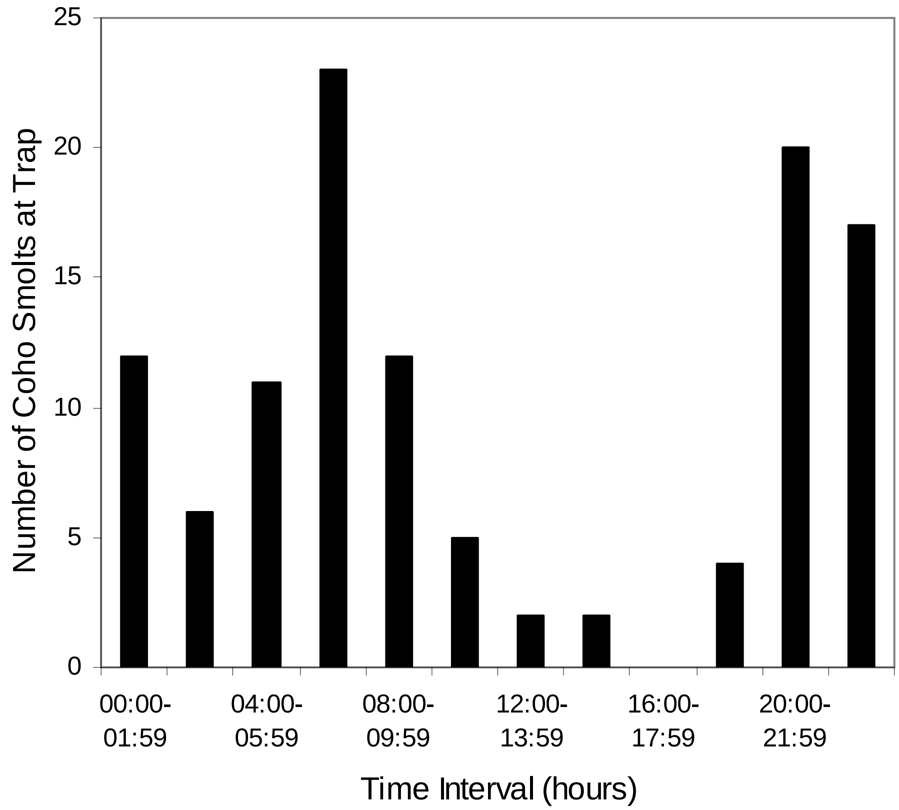
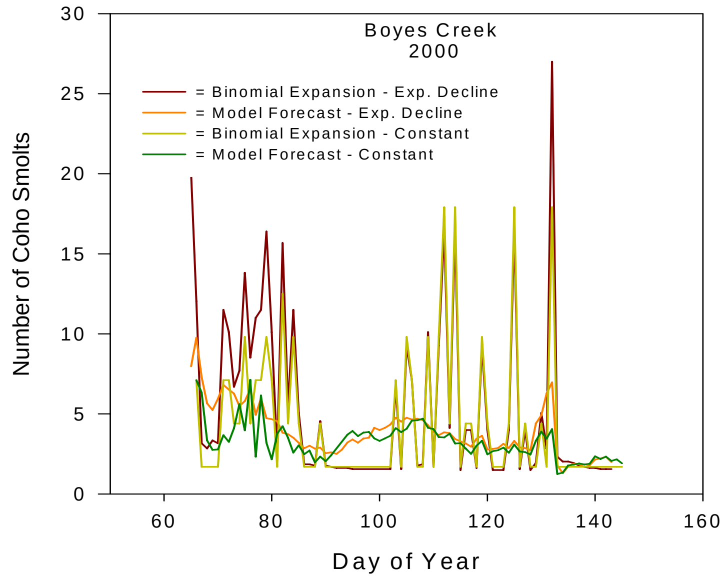


Figure 15. Time of movement of pit tagged coho salmon smolts in Boyes, Streelow and Prairie Creeks, Redwood National and State Parks, Humboldt County, California, during 2003.

Modeling

The daily number of coho salmon smolts to have migrated was predicted based on binomial expansion using the exponential decline and constant discharge to capture probability relationships. The daily number of migrating coho salmon smolts was then predicted based on logistic models being fit to the binomial expansion results. All model selection results and Bayes statistics are based on the exponential decline discharge to capture probability relationship. Five environmental variables were common to the best model for each of the three streams: day of year, discharge, change in discharge, water temperature and interaction of day of year with discharge. Day of year was significant ($p < 0.05$) for all models (Appendices A-I). Differences among models in Akaike's Information Criterion (AIC) suggested from three to five models were worthy of consideration for each stream.

The predicted number of coho salmon smolts migrating from Boyes Creek using the partial logistic model was consistently lower and less variable than estimates derived from the binomial expansion (Figures 16, 17). The best model for Boyes Creek included six variables in addition to the above variables: year, day of year^2, change in water temperature, lunar cycle and the interactions of day of year with change in discharge and water temperature with discharge (Tables 4, 5). All variables included in the best model were significant ($p < 0.05$), except for lunar cycle ($p = 0.1345$), change in water temperature ($p = 0.0646$) and water temperature ($p=0.3448$). However, water temperature was included within a significant interaction.



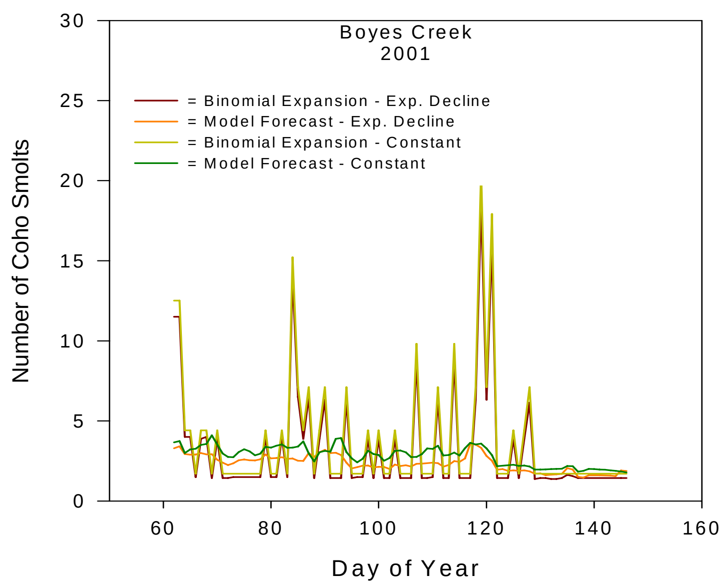


Figure 16. Daily number of coho salmon smolts predicted to have migrated based on binomial expansion (using exponential decline and constant discharge to capture probability relationships) and number predicted based on logistic model being fit to the binomial expansion results in Boyes Creek during 2000-2001, Redwood National and State Parks, Humboldt County, California.

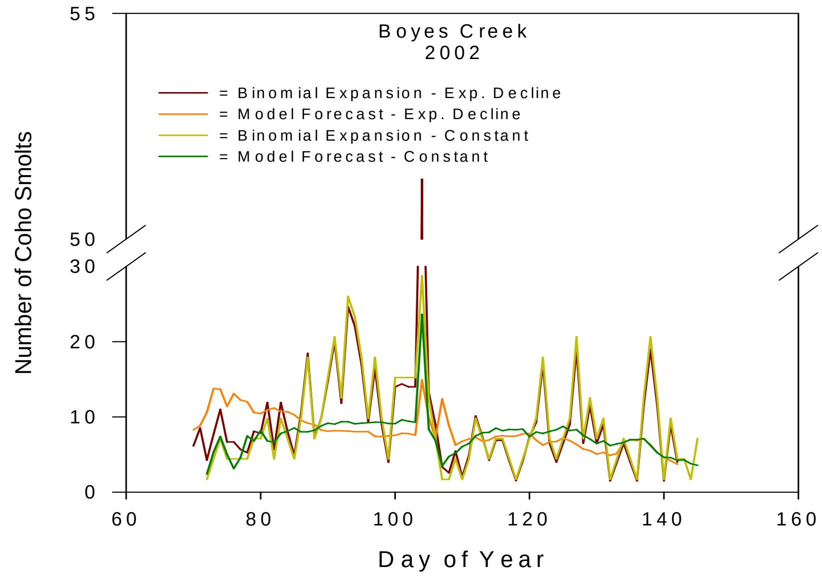


Figure 17. Daily number of coho salmon smolts predicted to have migrated based on binomial expansion (using exponential decline and constant discharge to capture probability relationships) and number predicted based on logistic model being fit to the binomial expansion results in Boyes Creek during 2002, Redwood National and State Parks, Humboldt County, California.

Table 4. Boyes Creek 2000-2002 model selection results for variables best describing coho salmon smolt downstream migration, Redwood National and State Parks, Humboldt County, California.

Model Number	Structure[1]
1	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q
2	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q+W:W2
3	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q+W:W2+D:D^2
4	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q+W:W2+D:D^2+D:W2
5	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q+W:W2+D:D^2+D:W2+Q:Q2
6	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q+W:W2+D:D^2+D:W2+Q:Q2+D:L
7	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q+W:W2+D:D^2+D:W2+Q:Q2+D:L +DD
8	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q+W:W2+D:D^2+D:W2+Q:Q2+D:L +DD+D:W
9	Yr+D+D^2+Q+Q2+W+W2+L+D:Q+D:Q2+W:Q+W:W2+D:D^2+D:W2+Q:Q2+D:L +DD+D:W+L:Q2

[1] Yr= year, D = day of year, D^2 = day of year squared, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, L = lunar cycle, : = interaction among variables.

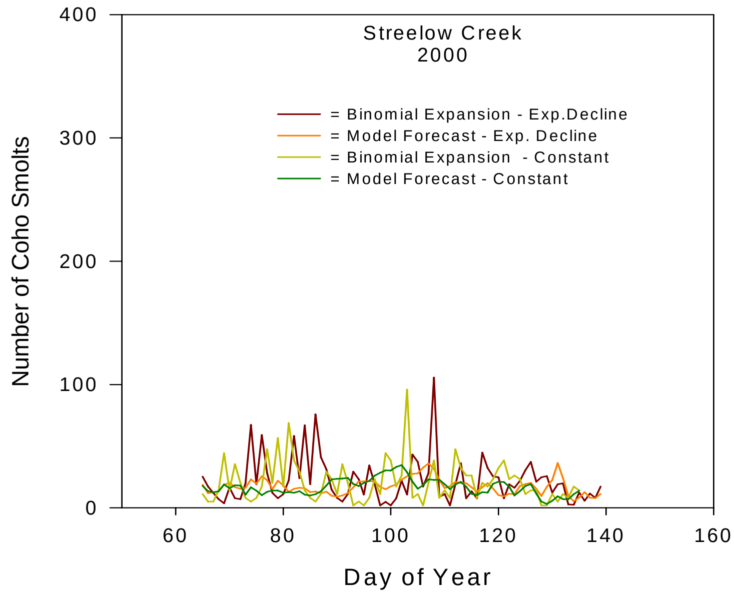
Table 5. Boyes Creek 2000-2002 Bayes statistics results for model selections best describing coho salmon smolt downstream migration, Redwood National and State Parks, Humboldt County, California.

Model	AIC	Delta	W_i	C.I.	P value	R^2
1	123.3059	0.0000	0.2480	0.2480	0.0000	0.4722
2	123.6705	0.3646	0.2066	0.4546	0.0000	0.4752
3	124.0288	0.7229	0.1727	0.6274	0.0000	0.4770
4	124.5338	1.2279	0.1342	0.7616	0.0000	0.4784
5	125.2685	1.9626	0.0929	0.8545	0.0000	0.4819
6	126.0274	2.7215	0.0636	0.9181	0.0000	0.4831
7	126.9140	3.6081	0.0408	0.9589	0.0000	0.4836
8	127.8535	4.5476	0.0255	0.9844	0.0000	0.4839
9	128.8432	5.5373	0.0156	1.0000	0.0000	0.4840

The second best model included all variables within the top model, with the addition of the interaction of water temperature with change in water temperature ($p = 0.2569$). The coefficient sign for change in water temperature changed from a negative to a positive from the best model. The third best model included all of the variables within the second best model in addition to the interaction term of day of year with day of year^2 ($p = 0.3819$). The variables day of year ($p = 0.2235$) and day of year^2 ($p = 0.2570$) became insignificant when compared to the second best model.

The number of predicted coho salmon smolts migrating from Streelow Creek using the partial logistic model was also consistently lower and exhibited less variability than estimates derived from the binomial expansion (Figures 18, 19). The best model for Streelow Creek included the five variables common to all three streams and two additional variables: degree-days and the interaction of day of year with water temperature (Tables 6, 7). Day of year and the interaction of day of year with water temperature were significant variables ($p < 0.05$). Water temperature ($p = 0.1387$) was not a significant variable, but was included within a significant interaction term.

The second best model included the same variables as the best, with the addition of lunar cycle ($p = 0.2916$). The third best model for Streelow Creek included day of year^2 ($p = 0.3494$). The interaction of day of year with water temperature changed from significant to insignificant ($p = 0.0027$ to $p = 0.0781$) when compared to the second best model.



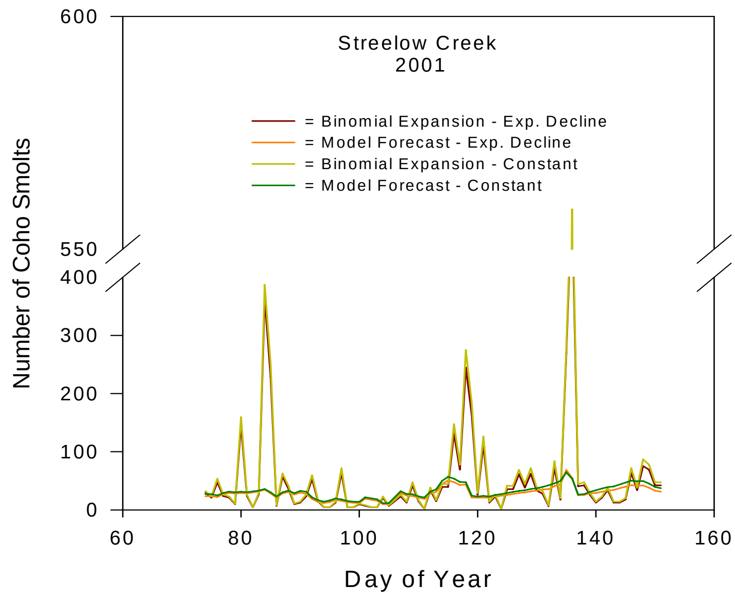


Figure 18. Daily number of coho salmon smolts predicted to have migrated based on binomial expansion (using exponential decline and constant discharge to capture probability relationships) and number predicted based on logistic model being fit to the binomial expansion results in Streelow Creek during 2000-2001, Redwood National and State Parks, Humboldt County, California.

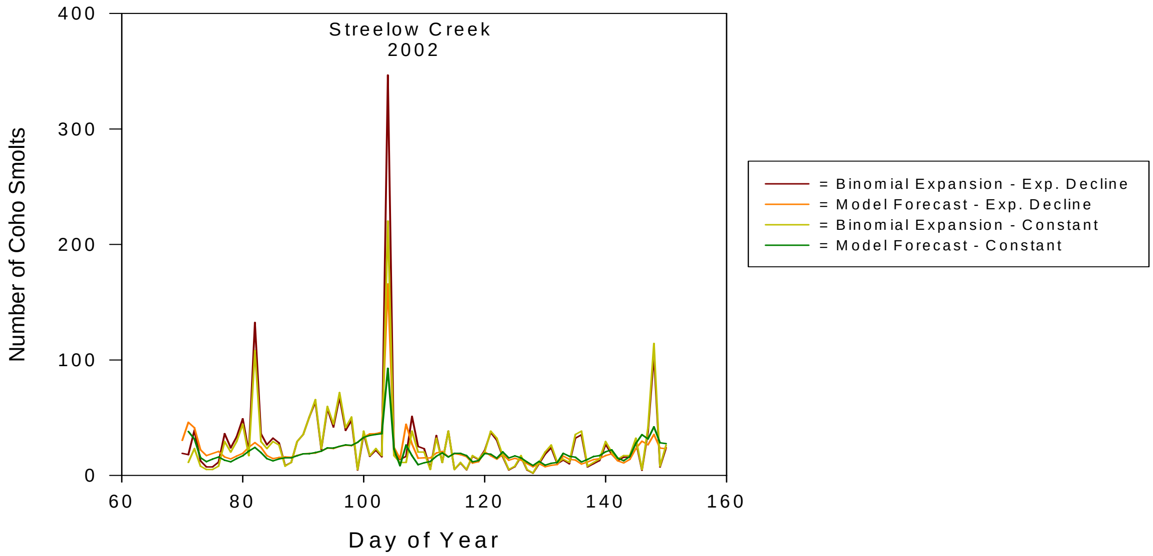


Figure 19. Daily number of coho salmon smolts predicted to have migrated based on binomial expansion (using exponential decline and constant discharge to capture probability relationships) and number predicted based on logistic model being fit to the binomial expansion results in Streelow Creek during 2002, Redwood National and State Parks, Humboldt County, California.

Table 6. Streelow Creek 2000-2002 model selection results for variables best describing coho salmon smolt downstream migration, Redwood National and State Parks, Humboldt County, California.

Model Number	Structure[1]
1	D+Q+Q2+W+DD+D:Q+D:W
2	D+Q+Q2+W+DD+D:Q+D:W+L
3	D+Q+Q2+W+DD+D:Q+D:W+L+D^2
4	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2
5	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2
6	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2+D:W2
7	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2+D:W2+D:Q2
8	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2+D:W2+D:Q2+W:Q
9	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2+D:W2+D:Q2+W:Q+Yr
10	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2+D:W2+D:Q2+W:Q+Yr+Q:Q2
11	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2+D:W2+D:Q2+W:Q+Yr+Q:Q2+L:Q2
12	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2+D:W2+D:Q2+W:Q+Yr+Q:Q2+L:Q2+D:L
13	D+Q+Q2+W+DD+D:Q+D:W+L+D^2+D:D^2+W2+D:W2+D:Q2+W:Q+Yr+Q:Q2+L:Q2+D:L+W:W2

[1] Yr= year, D = day of year, D^2 = day of year squared, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, L = lunar cycle, : = interaction among variables.

Table 7. Streelow Creek 2000-2002 Bayes statistics results for model selections best describing coho salmon smolt downstream migration, Redwood National and State Parks, Humboldt County, California.

Model	AIC	Delta	W_i	C.I.	P value	R^2
1	199.9422	0.0000	0.3818	0.3818	0.0000	0.5072
2	200.7227	0.7805	0.2584	0.6402	0.0000	0.5096
3	201.6990	1.7568	0.1586	0.7988	0.0000	0.5115
4	202.6448	2.7026	0.0988	0.8976	0.0000	0.5135
5	204.2139	4.2717	0.0451	0.9427	0.0000	0.5139
6	205.2555	5.3133	0.0268	0.9695	0.0000	0.5156
7	206.1507	6.2085	0.0171	0.9866	0.0000	0.5177
8	207.8003	7.8581	0.0075	0.9941	0.0000	0.5179
9	209.4054	9.4632	0.0034	0.9975	0.0000	0.5181
10	211.0719	11.1297	0.0015	0.9990	0.0000	0.5182
11	212.7380	12.7958	0.0006	0.9996	0.0000	0.5183
12	214.3945	14.4523	0.0003	0.9999	0.0000	0.5184
13	216.0613	16.1191	0.0001	1.0000	0.0000	0.5185

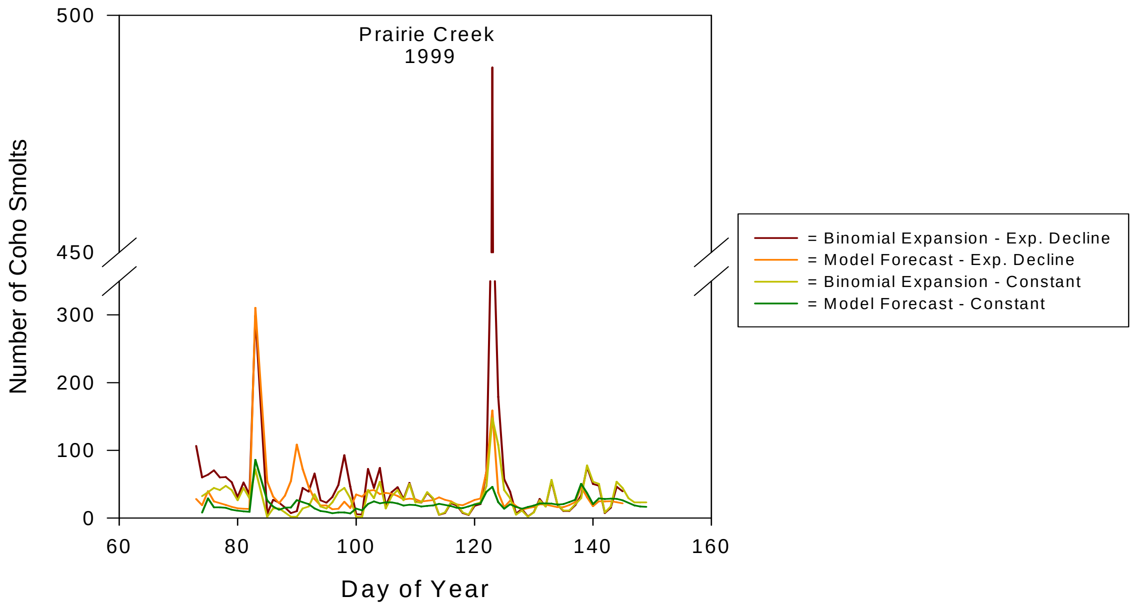
The number of predicted coho salmon migrating from Prairie Creek using the partial logistic model was also consistently lower and exhibited less variability than estimates derived from the binomial expansion. However, logistic model estimates for peaks of migration in Prairie Creek were similar to estimates derived from the binomial expansion in 1999, 2002 and 2003 (Figures 20-22). The best model for Prairie Creek included the five variables common to all three streams and four additional variables: degree-days ($p = 0.0024$), lunar cycle ($p = 0.3764$) and interactions of day of year with change in discharge ($p = 0.1264$), and lunar cycle with change in discharge ($p = 0.0709$) (Tables 8, 9). The variables day of year, discharge, water temperature, degree-days and the interaction of day of year with discharge were significant ($p < 0.05$).

The second best model for Prairie Creek included variables within the best model with the addition of change in water temperature ($p = 0.1604$). The third best model included the interaction of water temperature with change in water temperature ($p = 0.1816$). The coefficient sign changed from negative to positive for change in water temperature in the third best model when compared to the second best model.

The coefficients of the variables in the best models were compared for each creek (Table 10). In Boyes Creek, the significant variables ($p < 0.05$) included day of year, discharge, change in discharge and the interaction of day of year with discharge, all with negative coefficients. The following variables were significant, with a positive coefficient: year, day of year^2 and the interactions of water temperature with discharge and day of year with change in discharge. Water temperature was not a significant variable within the top model, but was included within a significant interaction (negative coefficient).

In Streelow Creek, the significant variables within the best model included day of year (negative coefficient) and interaction of day of year with water temperature (positive coefficient). Water temperature was not a significant variable within the top model, but was included within a significant interaction (negative coefficient).

In Prairie Creek, the following were significant variables within the best model with positive coefficients: day of year, discharge, water temperature and degree-days. The interaction of day of year with discharge was a significant variable within the best model, with a negative coefficient.



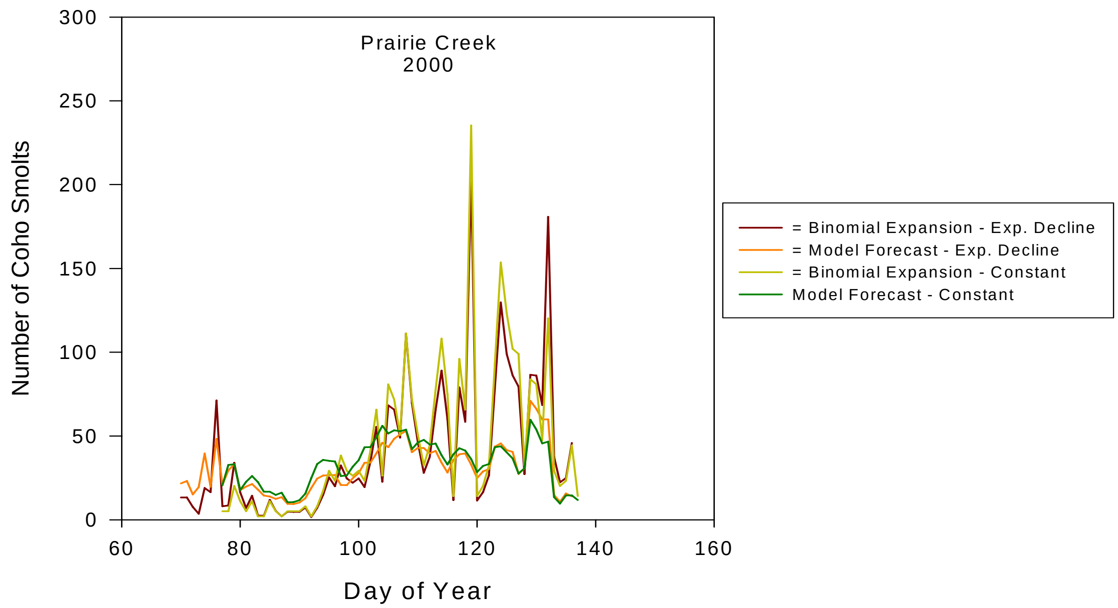
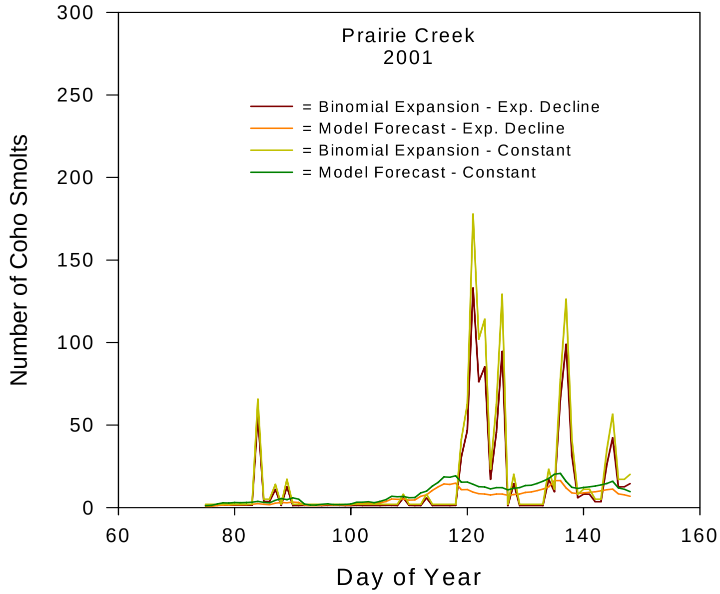


Figure 20. Daily number of coho salmon smolts predicted to have migrated based on binomial expansion (using exponential decline and constant discharge to capture probability relationships) and number predicted based on logistic model being fit to the binomial expansion results in Prairie Creek during 1999-2000, Redwood National and State Parks, Humboldt County, California.



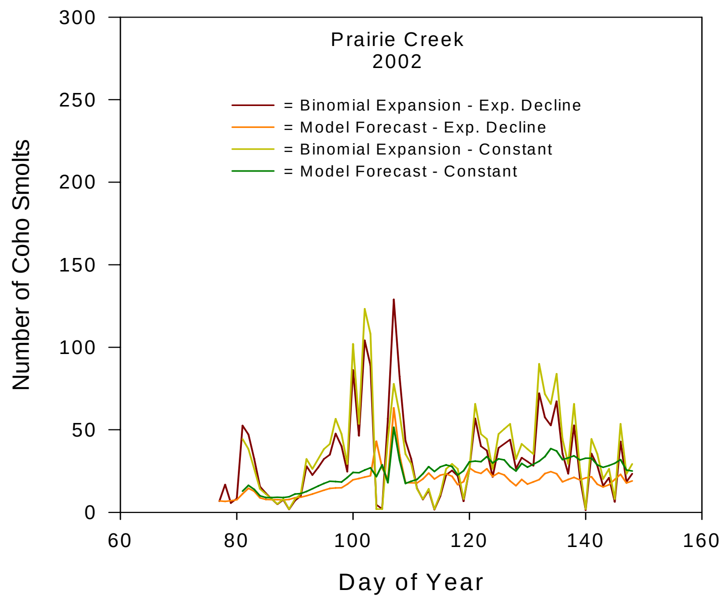


Figure 21. Daily number of coho salmon smolts predicted to have migrated based on binomial expansion (using exponential decline and constant discharge to capture probability relationships) and number predicted based on logistic model being fit to the binomial expansion results in Prairie Creek during 2001-2002, Redwood National and State Parks, Humboldt County, California.

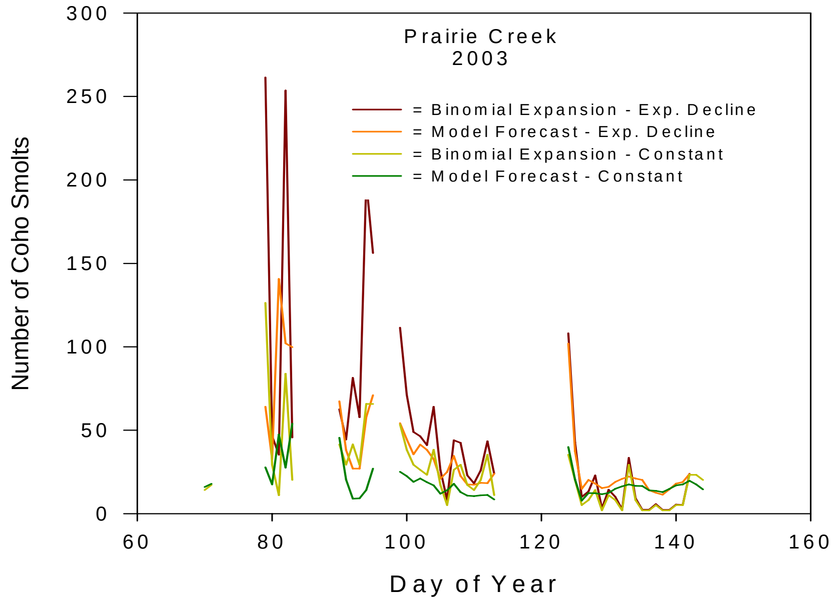


Figure 22. Daily number of coho salmon smolts predicted to have migrated based on binomial expansion (using exponential decline and constant discharge to capture probability relationships) and number predicted based on logistic model being fit to the binomial expansion results in Prairie Creek during 2003, Redwood National and State Parks, Humboldt County, California.

Table 8. Prairie Creek 1999-2003 model selection results for variables best describing coho salmon smolt downstream migration, Redwood National and State Parks, Humboldt County, California.

Model Number	Structure[1]
1	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2
2	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2
3	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2
4	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2+D:L
5	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2+D:L+D^2
6	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2+D:L+D^2+D:W
7	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2+D:L+D^2+D:W+Q:Q2
8	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2+D:L+D^2+D:W+Q:Q2+D:W2
9	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2+D:L+D^2+D:W+Q:Q2+D:W2+W:Q
10	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2+D:L+D^2+D:W+Q:Q2+D:W2+W:Q +Yr
11	D+Q+Q2+W+DD+L+D:Q+D:Q2+L:Q2+W2+W:W2+D:L+D^2+D:W+Q:Q2+D:W2+W:Q +Yr+D:D^2

[1] Yr= year, D = day of year, D^2 = day of year squared, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, L = lunar cycle, : = interaction among variables.

Table 9. Prairie Creek 1999-2003 Bayes statistics results for model selections best describing coho salmon smolt downstream migration, Redwood National and State Parks, Humboldt County, California.

Model	AIC	Delta	W_i	C.I.	P value	R^2
1	395.2551	0.0000	0.2410	0.2410	0.0000	0.5682
2	395.2994	0.0443	0.2357	0.4768	0.0000	0.5708
3	395.5648	0.3097	0.2065	0.6832	0.0000	0.5732
4	396.1552	0.9001	0.1537	0.8369	0.0000	0.5753
5	397.2577	2.0026	0.0886	0.9255	0.0000	0.5767
6	398.6359	3.3808	0.0445	0.9699	0.0000	0.5778
7	400.3240	5.0689	0.0191	0.9890	0.0000	0.5785
8	402.1952	6.9401	0.0075	0.9965	0.0000	0.5791
9	404.4393	9.1842	0.0024	0.9990	0.0000	0.5792
10	406.7276	11.4725	0.0008	0.9998	0.0000	0.5792
11	409.0513	13.7962	0.0002	1.0000	0.0000	0.5792

Table 10. Comparison of coefficients of best models for Boyes, Streelow and Prairie Creeks, Redwood State Park, Humboldt County, California. + or – indicates sign of coefficients, NS indicates that variable coefficients were not significant at α = 0.05, but were included in the model, NI indicates that coefficients were not significant at α = 0.05, but were included in the model because of significant interactions.

Variable[1]	Boyes Creek	Streelow Creek	Prairie Creek
D	-	-	+
Q	-	- (NS)	+
Q2	-	+ (NS)	- (NS)
W	- (NI)	- (NI)	+
D:Q	-	+ (NS)	-
L	- (NS)		- (NS)
D:Q2	+		+ (NS)
DD		+ (NS)	+
Yr	+		
D^2	+		
W2	- (NS)		
W:Q	+		
D:W		+	
L:Q2			- (NS)

[1] Yr= year, D = day of year, D^2 = day of year squared, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average discharge, DD = degree-days from 1 Jan to 1 Mar, L = lunar cycle, : = interaction among variables.

DISCUSSION

The binomial expansion using the exponential decline relationship of discharge to capture probability was more sensitive to discharge, tracking peaks of movement better. Overall, models based on the exponential decline relationship seemed to mimic the binomial expansions more. However, peaks were not as high because the models took into account other variables besides discharge. The number of coho salmon smolts observed in traps relative to discharge and a literature search on this subject also indicate that the exponential decline relationship is more appropriate than the constant relationship for model predictions. This indicates that discharge affects the capture probability, and to a lesser extent, migration.

The exponential decline probability of capture to discharge relationship was observed in a study of spring migration of wild and hatchery Chinook salmon and steelhead trout in the Imnaha River, Oregon, where trap efficiency rates were lowest when flows were highest (Ashe et al. 1995). Unwin (1986) also found a decline in catch efficiency with increased discharge while trapping juvenile Chinook salmon in a tributary of the Rakaia River, New Zealand. Rawson (1984) stated that the decline of trap efficiency for sockeye salmon smolts over time was perhaps due to increasing discharge in the Kasilof River, Alaska. Murphy et al. (1991) also found that trap efficiency was inversely related to discharge for juvenile salmon smolts in the Taku River, Alaska.

A preliminary analysis was conducted using a global model, including the environmental variables from all years and all creeks to determine the variation in probability of migration of coho salmon smolts as a function of environmental variables. The variable stream had a significant affect on smolt movement in initial modeling, therefore streams were modeled separately.

The day of year variable represented the change in migration tendency as the migration season progressed, while other variables explained deviations from this normal pattern. Water temperature, change in water temperature, discharge, change in discharge and lunar cycle were included to explain any deviations from the normal pattern. Degree-days was constant for any given year and was an additive term used to assess whether the number of degree-days experienced by fish before the trapping seasons influenced daily migration probabilities. The interactions between time and the main effect variables were included to assess whether the influence of a particular factor increased or decreased as the migration season progressed. The other interaction terms were included to examine whether the importance of one factor varied with the level of a second factor (Spence 1995). The modeling demonstrated differences among environmental variables that were correlated with smolt movement for each creek.

Year was a significant variable influencing migration probability in Boyes Creek. There was no indication of year to year differences in Prairie and Streelow Creeks. There was an increased probability of migration as the season progressed in Prairie Creek indicated by a positive coefficient for day of year. The smolt migration of coho salmon and Chinook salmon in a tributary of northern Lake Michigan was most strongly influenced by photoperiod (Seelbach 1985). Time is a substitute variable for photoperiod because the relationship between the two variables is almost linear.

Photoperiod and water temperature prior to the Atlantic salmon smolt run regulated the smoltification process during a 30 year study in western Ireland (Byrne et al. 2003). Spence (1995) noted that time variables explained the most variation in probability of migration for coho salmon smolts. He found that with increased day length, there was an increased migration probability. He also stated that at the beginning of the season, few fish had reached the physiological state needed to respond to stimuli that would trigger migration. As more fish reached the physiological state needed for migration, the number of fish moving downstream in response to short-term events became larger. Near the end of the season, the number of fish migrating was smaller but represented a larger proportion of the remaining total and the probability of migration remained high.

Modeling results indicated that the coho salmon smolts in Boyes and Streelow Creeks experienced a decrease in probability of migration as the season progressed, which was not expected. There was no obvious pattern of large numbers of smolts migrating from these streams early in the season.

Migration probability was positively associated with daily mean water temperature in Prairie Creek, revealing an increased migration probability at higher temperatures. This finding is supported by Holtby et al. (1989) who found that variability in stream temperatures in spring accounted for 60% of the variability in the median date of coho smolt migration. Solomon (1978) found that downstream migration was closely correlated with water temperature with only small numbers of fish moving below a threshold temperature, and increasing numbers with increasing water temperatures.

Antonsson and Gudjonsson (2002) found that the timing of migration of Atlantic smolts in Icelandic rivers appeared to be dependent on water temperature. Jonsson and Ruud-Hansen (1985) reported that water temperature and smolt descent were highly correlated. Their results indicated that the timing of smolt migration was controlled by a combination of actual water temperatures and water temperature increases. Daily mean water temperature was retained in the best models for Boyes and Streelow Creeks because water temperature was a part of a significant interaction term.

The influence of water temperature on probability of migration increased as the season progressed and was indicated by a positive coefficient for Streelow Creek for the interaction of day of year with water temperature. The interaction between water temperature and time on the physiology and behavior of smolts indicated that these two variables regulated smolting in a study of Atlantic salmon smolts (Zydlewski et al. 2005).

The change of water temperature from two days prior was not a significant variable in the best model for any of the streams. Other studies have found this variable to have an influence on probability of migration. In the River Orkla, Norway, changes in water temperature influenced the downstream migration of smolts (Hvidsten et al. 1995). Bohlin et al. (1993) also found that timing of seaward migration of sea-run brown trout (*Salmo trutta trutta*) was positively associated with water temperature change in a small stream in southwestern Sweden. Spence (1995) reported a greater tendency for coho salmon smolts to migrate on days when water temperatures were increasing instead of decreasing.

The importance of the variable water temperature increased as discharge increased in Boyes Creek. This was indicated by the positive coefficient for the interaction of water temperature with discharge. Spence (1995) found the opposite effect, with a negative coefficient for the interaction term.

There was a decrease in probability of migration with increases in daily mean discharge for Boyes Creek. Spence (1995) supported this finding, as he noted a lower probability of coho salmon smolt migration at higher discharge. The opposite results occurred in Prairie Creek, with an increase in the probability of migration with increases in daily mean discharge. Many studies have found the same results. Byrne et al. (2003) reported that two groups of environmental variables had a significant influence on daily catch of Atlantic salmon smolts in western Ireland. One group of variables was dominated by photoperiod and water temperature and operated prior to the smolt run, regulating smolt development. The second group of variables was dominated by total light and discharge and was considered to control daily smolt migration.

Whalen et al. (1999) stated that many smolts may migrate during peaks in discharge occurring after water temperature thresholds have been met until smolt physiological readiness declines. Bohlin et al. (1993) found that the daily variation of the smolt run of brown trout was positively associated with discharge. They stated that possible reasons were that high or increasing flow facilitates traversing obstacles and that turbidity from higher discharge may reduce predation risks.

A decrease in migration probability was related to the two day change in discharge for Boyes Creek. Spence (1995) found that as short-term discharge increased, probability of migration of coho salmon smolts generally increased. He suggested that freshets trigger downstream movement, but that migration probability increases over the season as flow decreases in the spring.

In Boyes and Prairie Creeks, the influence of discharge on probability of migration decreased as the season progressed and was indicated by a negative coefficient for the interaction of day of year with discharge. Spence (1995) found the same result in one of the four streams that he investigated. As the season progressed, there was an increase in migration probability related to change in discharge in Boyes Creek. Spence (1995) found the same results in two of the four streams he studied.

There was a positive correlation between cumulative thermal experience prior to migration season and migration probability in Prairie Creek. This indicated that smolts tended to migrate sooner when experiencing warmer conditions. The timing of seaward migration of sea-run brown trout was positively associated with the number of degree-days in a small stream in southwestern Sweden (Bohlin et al. 1993). These authors suggested that degree-days may affect physiological processes as well as serving as a cue for environmental conditions. They also suggested that the probability of a smolt migrating was increased with time or degree-days in a way that was affected by body size. Spence (1995) reported that coho salmon smolts were found to migrate earlier in years when water temperatures were warmer during the pre-migration period and later when water temperatures were colder in two of five streams studied.

Atlantic salmon smolts in simulated streams that experienced an early increase in water temperature moved downstream earlier. In addition, there was a longer migratory period for smolts that experienced cold spring water temperatures. The water temperature effects were better explained with degree-days because downstream movement began at the same number of degree-days when fish experienced different water temperature regimes. The interaction between water temperature and time, expressed as degree-days, on both the physiology and behavior of smolts indicated these variables regulated the smolt process (Zydlewski et al. 2005).

The following variables were not significant factors in the migration of coho salmon smolts in any of the streams in my study: change in water temperature, lunar cycle, the interaction of day of year with day of year^2, day of year with change in water temperature, day of year with lunar cycle, discharge with change in discharge or lunar cycle with change in discharge.

The variables within the best models do not provide a complete picture of smolt migration. Other factors, not considered in the models, may contribute to explaining variation in the data. One of those factors is the phenomena of fish moving downstream, providing a stimulus for other fish to move. Hansen and Jonsson (1985) discovered that the presence of hatchery smolt shoals can stimulate wild smolts to migrate. Bohlin et al. (1993) suggested that migration in schools may reduce predation risk, with a result of increased temporal variation not explained by body size and environmental factors. Veselov et al. (1998) found that migration of individual Atlantic salmon smolts began at the same time at all riffles in the Varzuga River, with shoals forming that promoted a more rapid migration to the river mouth. Hvidsten et al. (1995) claimed that the shoaling behavior observed in Atlantic and Pacific salmon stocks was important for smolt survival and was probably a major factor influencing smolt runs. Olsen et al. (2004) demonstrated that Atlantic salmon siblings were migrating closer in time than unrelated fish, regardless of whether they had been raised together, suggesting that smolts migrated in family structured groups.

Another factor not incorporated into the modeling was competition. In years where populations are large, some fish may move downstream as fish grow and competition for space increases. This may result in an earlier migration of these fish (Spence 1995). Fish may behave in the same manner if there is enough space, but not enough food.

Size of fish may be another variable that could explain more of the variation of the data if included in the modeling. Bohlin et al. (1996) found that smaller sea-run brown trout tended to migrate later in the season than bigger brown trout. Size affected the probability of migration among previously immature and previously mature male Baltic salmon (*Salmo salar*) (Fangstam et al. 1993). Allen (1944) claimed that there was a close relationship between size and time of migration of Atlantic salmon smolts, but that there was not a critical size at which smolts migrated.

Growth rate may be another factor that influences probability of migration. Okland et al. (1993) observed that fast-growing Atlantic salmon and brown trout parr smolted younger and smaller than slow-growing parr. They suggested that slow growers with a low metabolic rate may osmoregulate less well in salt water than fast growers with a higher metabolic rate at a given size. They also suggested that, given their high metabolic requirements, fast growers may be more limited by food resources in freshwater, which may be a reason why they migrate to the ocean earlier. They concluded that instead of a specific smolt size in a population, selection may favor a growth-specific size at smolting for each fish.

The PIT tag equipment was effective in detecting 96 of the 100 pit tagged fish that were caught in the traps. Of the 10 PIT tags detected by the antenna in Boyes Creek, nine of them were detected adjacent to the trap. This was determined by noting that no fish were found in the trap during the day the antenna detected a PIT tag. Either a PIT tagged fish was swimming outside of the PVC pipe within the read range of the antenna (30.48 cm) or swimming in and out of the PVC pipe within the read range of the antenna and not entering the trap. A solution to the latter problem would be to force more water into the PVC pipe so that the fish has to swim into the trap and cannot escape. This could be accomplished by constricting the flow as it enters the fyke net to increase water velocity. A longer PVC pipe to allow for a larger slope from the bottom of the fyke net to the top of the trap could also be tested. The Streelow Creek antenna detected 71.1% of the PIT tagged fish outside of the trap while the Prairie Creek antenna detected 36.6% of the PIT tagged fish outside of the trap. Although this gives additional information on fish moving near the trap, there is no way to physically measure these fish if needed. Many scientists use PIT tags as a way to track movement and growth and length and weight measurements are crucial for calculating growth. Overall, Prairie Creek had the highest discharge during the study period which may explain the lower numbers of fish detected adjacent to the trap.

Traps were removed for periods of 17-26 days in the 2003 trapping season due to high flows throughout much of the period from 13 March - 3 May. Due to PIT tag equipment malfunctions, there were even fewer days with valid PIT tag recapture information. The internal batteries of the pit tag antennae lost power even when the antennae were powered by external 12-volt batteries. This most likely occurred because of the cold temperatures and taking the PIT tag recorders in from the field and recharging them overnight every month or two resolved this problem. Two ring antennae were replaced during the 2003 trapping season, possibly due to moisture getting into the connection despite sealing that area.

If one was interested only in smolt movement, the equipment used would be a labor saving device because the live box could be removed, therefore traps would not have to be checked daily. Fyke nets would still have to be checked and cleared of debris when necessary and equipment pulled during high flows, but the hours spent checking traps and weighing and measuring fish would be eliminated. This equipment would also eliminate the possibility of trappers missing adipose fin clips which are an indication that a fish is pit tagged. It would be important to make sure that there is always a sufficient velocity of water running through the traps to avoid fish swimming out of the traps, which appeared to occur often during this study.

There was no evidence that fish located farther from the trap reached the trap at later dates. I observed fish arriving at the trap on the same day that were last located far from each other. This supports the findings of Hvidsten et al. (1995) who found the largest catches of Atlantic salmon smolts occurred when smolts coming from different parts of the River Orkla, Norway were caught on the same night. Smolts from upstream areas stimulated migration of smolts located downstream, creating shoals of descending smolts. Allen (1944) stated that active migration only occurs when a suitable stimulus is provided by the environment. The extent of the reaction to the stimulus depends on the degree to which a smolt has become susceptible to such stimuli. He also surmised that the passage of actively migrating smolts stimulated other smolts to move downstream. Hoar (1953) found that parr smolt transformation involved morphological, biochemical and behavioral changes associated with increased endocrine activity. A smolt upstream that is more biologically ready to migrate would move earlier in the season than a fish that is less developed physiologically and located downstream.

The majority of fish movement within this study occurred at night. This finding is supported by a number of Atlantic salmon studies (White 1939, Thorpe et al. 1988, Moore et al. 1998, Antonsson and Gudjonsson 2002, Carlsen et al. 2004) that found that the majority of juvenile salmon moved between dusk and dawn. Coho salmon smolts moved more at night than during the day in the Taku River, Alaska (Meehan and Siniff 1962). A study involving the downstream migration of radio-tagged Atlantic salmon and brown trout found that both species migrated primarily at night. However, daytime migration was obvious on one particular day with a stable low discharge and a large increase in water temperature. This study observed that increased water temperature may result in an increase of the number of daytime smolt migrants. Thorpe et al. (1988) concluded that downstream nocturnal movement of Atlantic salmon in a flume experiment represented displacement which occurred with loss of visual orientation, therefore migration resulted from reduced activity. However, Solomon (1978) stated that migration was an active process in response to a combination of environmental conditions, and not a passive displacement downstream following a hormonally-induced reduction in swimming activity. Hvidsten et al. (1995) suggested that nighttime movement of smolts reduced the risk of predation.

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APPENDICES

Appendix A. Linear regression results of the best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Boyes Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
Yr	0.2518	0.0721	3.4939	0.0006
D	-0.0537	0.0230	-2.3364	0.0204
D^2	0.0004	0.0001	3.7236	0.0002
Q	-34.4974	9.5293	-3.6201	0.0004
Q2	-13.1704	4.6412	-2.8377	0.0050
W	-0.0825	0.0871	-0.9467	0.3448
W2	-0.1630	0.0877	-1.8574	0.0646
L	-0.0655	0.0436	-1.5019	0.1345
D:Q	-0.0949	0.0376	-2.5261	0.0122
D:Q2	0.1224	0.0471	2.5996	0.0100
W:Q	5.0471	1.2295	4.1051	0.0001
Intercept	-2.5314	1.3183	-1.9201	0.0561

[1] Yr= year, D = day of year, D^2 = day of year squared, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average water temperature, L = lunar cycle, : = interaction among variables.

Appendix B. Linear regression results of the second best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Boyes Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
Yr	0.2459	0.0722	3.4061	0.0008
D	-0.0538	0.0230	-2.3428	0.0200
D^2	0.0004	0.0001	3.7270	0.0002
Q	-34.6881	9.5246	-3.6419	0.0003
Q2	-13.2043	4.6383	-2.8468	0.0048
W	-0.0774	0.0872	-0.8885	0.3752
W2	0.5055	0.5946	0.8501	0.3962
L	-0.0676	0.0436	-1.5488	0.1228
D:Q	-0.0950	0.0375	-2.5319	0.0120
D:Q2	0.1214	0.0471	2.5793	0.0105
W:W2	-0.0742	0.0653	-1.1366	0.2569
W:Q	5.0676	1.2288	4.1240	0.0001
Intercept	-2.5282	1.3175	-1.9189	0.0563

[1] Yr= year, D = day of year, D^2 = day of year squared, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average water temperature, L = lunar cycle, : = interaction among variables.

Appendix C. Linear regression results of the third best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Boyes Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
Yr	0.2525	0.0726	3.4765	0.0006
D	-0.1851	0.1517	-1.2207	0.2235
D^2	0.0017	0.0015	1.1363	0.2570
Q	-33.9795	9.5638	-3.5529	0.0005
Q2	-13.0630	4.6435	-2.8132	0.0053
W	-0.0597	0.0895	-0.6663	0.5059
W2	0.4576	0.5974	0.7659	0.4445
L	-0.0697	0.0437	-1.5932	0.1125
$D{:}D^2$	0.0000	0.0000	-0.8762	0.3819
D:Q	-0.0939	0.0376	-2.4976	0.0132
D:Q2	0.1198	0.0471	2.5433	0.0117
W:W2	-0.0691	0.0656	-1.0545	0.2928
W:Q	4.9717	1.2343	4.0279	0.0001
Intercept	1.6223	4.9170	0.3299	0.7418

[1] Yr= year, D = day of year, D^2 = day of year squared, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average water temperature, L = lunar cycle, : = interaction among variables.

Appendix D. Linear regression results of the best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Streelow Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
D	-0.0955	0.0410	-2.3288	0.0208
Q	-2.6109	4.2049	-0.6209	0.5353
Q2	3.4109	1.9768	1.7255	0.0858
W	-0.7304	0.4915	-1.4860	0.1387
DD	0.0029	0.0019	1.5041	0.1339
D:Q	0.0666	0.0457	1.4587	0.1460
D:W	0.0127	0.0044	2.8960	0.0042
Intercept	-1.1558	4.3645	-0.2648	0.7914

[1] D = day of year, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, : = interaction among variables.

Appendix E. Linear regression results of the second best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Streelow Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
D	-0.1025	0.0415	-2.4683	0.0143
Q	-3.2326	4.2447	-0.7616	0.4471
Q2	3.3798	1.9765	1.7100	0.0886
W	-0.8265	0.4997	-1.6538	0.0996
DD	0.0030	0.0535	1.0571	0.2916
L	0.0565	0.0535	1.0571	0.2916
D:Q	0.0739	0.0462	1.6006	0.1109
D:W	0.0134	0.0044	3.0326	0.0027
Intercept	-0.5065	4.4064	-0.1149	0.9086

[1] D = day of year, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, L = lunar cycle, : = interaction among variables.

Appendix F. Linear regression results of the third best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Streelow Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
D	-0.1208	0.0459	-2.6320	0.0091
D^2	0.0002	0.0002	0.9377	0.3494
Q	-5.9213	5.1234	-1.1557	0.2490
Q2	3.5208	1.9827	1.7757	0.0771
W	-0.4898	0.6154	-0.7959	0.4269
DD	0.0034	0.0020	1.7048	0.0896
L	0.0589	0.0535	1.0997	0.2726
D:Q	0.0974	0.0525	1.8536	0.0651
D:W	0.0101	0.0057	1.7698	0.0781
Intercept	-0.9690	4.4351	-0.2185	0.8272

[1] D = day of year, D^2 = day of year squared, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, L = lunar cycle, : = interaction among variables.

Appendix G. Linear regression results of the best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Prairie Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
D	0.0617	0.0057	10.8326	0.0000
Q	7.4772	1.5086	4.9564	0.0000
Q2	-2.0972	2.7559	-0.7610	0.4472
W	0.4723	0.0975	4.8455	0.0000
DD	0.0048	0.0016	3.0563	0.0024
L	-0.0467	0.0527	-0.8859	0.3764
D:Q	-0.0469	0.0149	-3.1432	0.0018
D:Q2	0.0395	0.0258	1.5323	0.1264
L:Q2	-0.7514	0.4147	-1.8121	0.0709
Intercept	-17.9697	1.0181	-17.6507	0.0000

[1] D = day of year, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, L = lunar cycle, : = interaction among variables.

Appendix H. Linear regression results of the second best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Prairie Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
D	0.0613	0.0057	10.7489	0.0000
Q	7.5653	1.5076	5.0181	0.0000
Q2	-2.1077	2.7517	-0.7660	0.4443
W	0.5331	0.1065	5.0060	0.0000
W2	-0.1819	0.1293	-1.4069	0.1604
DD	0.0044	0.0016	2.7592	0.0061
L	-0.0355	0.0532	-0.6674	0.5050
D:Q	-0.0471	0.0149	-3.1655	0.0017
D:Q2	0.0396	0.0258	1.5370	0.1253
L:Q2	-0.7904	0.4150	-1.9048	0.0577
Intercept	-18.2971	1.0428	-17.5457	0.0000

[1] D = day of year, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, L = lunar cycle, : = interaction among variables.

Appendix I. Linear regression results of the third best logistic model, used for analysis of environmental variables affecting coho salmon smolt movement in Prairie Creek, Redwood National and State Parks, Humboldt County, California.

Variable[1]	Coefficient	Std. Error	t value	p-value
D	0.0611	0.0057	10.7339	0.0000
Q	7.5019	1.5065	4.9797	0.0000
Q2	-1.7367	2.7623	-0.6287	0.5300
W	0.5352	0.1064	5.0311	0.0000
W2	1.4177	1.2018	1.1796	0.2390
DD	0.0044	0.0016	2.7659	0.0060
L	-0.0323	0.0532	-0.6074	0.5440
D:Q	-0.0468	0.0149	-3.1465	0.0018
D:Q2	0.0361	0.0259	1.3966	0.1635
W:W2	-0.1901	0.1420	-1.3388	0.1816
L:Q2	-0.7818	0.4145	-1.8861	0.0602
Intercept	-18.2715	1.0417	-17.5398	0.0000

[1] D = day of year, Q = daily average discharge, Q2 = 2 day change in daily average discharge, W = daily average water temperature, W2 = 2 day change in daily average water temperature, DD = degree-days from 1 Jan to 2 Mar, L = lunar cycle, : = interaction among variables.