ANALYSES OF ROTARY SCREW TRAP SAMPLING OF MIGRATING JUVENILE CHINOOK SALMON IN THE STANISLAUS RIVER, 1996-2005

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EXECUTIVE SUMMARY

Rotary screw traps have been used at two locations in the Stanislaus River since 1996 to annually monitor the outmigration of age-0 juvenile chinook salmon (e.g., Demko et al. 2000). Goals of the sampling programs were to provide new information about Chinook salmon production and migration in the Stanislaus River and how these factors may be influenced by changes in flow, temperature, turbidity and other environmental factors. Target species included fall Chinook salmon and rainbow trout/steelhead. To study the characteristics of juvenile migration, screw traps were used to fish the mainstem of the Stanislaus River at two sites: Oakdale (64.5 Rkm) and Caswell (13.8 Rkm). The Oakdale site was located just downstream of the primary spawning and rearing area for fall Chinook salmon. The Caswell site was selected as the farthest location downstream with adequate access to install and monitor two traps.

In this report, we completed extensive exploratory analyses of ten years (1996-2005) of screw-trap sampling data across both trap sites on the Stanislaus River to assess abundance of juvenile fall Chinook salmon and potential factors influencing their survival and body size. The specific objectives of these analyses were as follows:

- Use trap-efficiency models to estimate abundance of migrating juveniles by life stage;
- Quantify relationships between annual survival of migrating juveniles and environmental conditions;
- Quantify relationships between size of juveniles and environmental conditions

A wide range of environmental conditions and Chinook spawner abundances were experienced over the years of study, and these in turn produced substantial variation between years in juvenile abundance, survival, body size and migration timing. Flow, a variable of critical interest to resource users, had a strong positive relationship with migration survival of fry, though associations between flow and survival measures (abundance ratios) for parr and smolts were weak. The annual time step used here to estimate effects of flow on survival is too broad for immediate application to management decisions. However, information gained from data collection and analyses to date indicate that new analysis pathways hold promise for estimating survival on shorter and more useful time scales.

Summary of findings

Abundance and survival

Estimates of the total abundance of juvenile Chinook salmon passing a given trap site varied widely across years. Total passage estimates at Oakdale ranged from a low of 279 thousand in 1996 to a high of 5.4 million in 1999 (Table 1). At Caswell, total passage ranged from 67 thousand in 1996 to 2.1 million in 2000. In most years, fry comprised the majority of juveniles passing Oakdale. The lowest proportion of fry was 27% in 1996, followed by 55% in 2002. In all other years, the proportion of fry ranged from 75% to 91% of the total juveniles. Fry comprised a lower proportion of the total passage at Caswell, particularly in years with sustained low flows during the fry migration period (2001-2005).

Total abundance estimates were used to compute the annual survival rates of juveniles migrating between the trap sites (Table 1). These survival-rate estimates ranged from lows of 8% in 2002 and 2003 to a high of 95% in 1998.

Table 1. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites, and the estimate of survival rate between the trap sites.

	Total Passage Estimate		Survival Rate
Year	Oakdale	Caswell	
1996	279,144	67,513	24%
1997	--	89,160[a]	--
1998	1,259,251	1,193,848	95%
1999	5,433,580	1,543,866	28%
2000	4,214,270	2,140,075	51%
2001	1,154,287	164,922	14%
2002	1,299,477	102,535	8%
2003	1,701,422	131,575[b]	8%
2004	2,438,065	412,051	17%
2005	1,333,744	260,061	19%

[a] The 1997 estimate for Caswell is incomplete because sampling began late in the season (March 19) and missed most of the potential fry and early parr migration.

We found a significant ($P < 0.05$) relationship between flows at OBB and the annual survival-rate estimates, whereby higher flow was associated with higher survival. However, this relationship was highly influenced by the fry component of the migration. A high fraction (28% to 81%) of the fry passing Oakdale were also estimated to have passed Caswell in years with moderate flows during fry migration (1998-2000), but only 1% to 13% of migrating fry were estimated to have passed Caswell in years with lower flows (2001-2005). In contrast to fry, abundance ratios for parr and smolts were more consistent across years, and were only weakly correlated with flows. This suggests that variations in flow or other conditions experienced by these life stages are less critical to parr and smolt survival than for fry. However, we did not test such hypotheses explicitly because abundance ratios for parr and smolts are potentially confounded as measures of survival rate if juveniles rear extensively between the trap sites.

We also found a significant, positive relationship between turbidity and overall survival rates. Mean turbidity levels were correlated with mean flows across years, so it is difficult to determine the relative importance of these variables from a statistical perspective. Nevertheless, the observed variations in annual flows undoubtedly have stronger effects on passage conditions and overall survival rates than the observed ranges in mean turbidity. Rather, it appears that turbidity can greatly enhance fry migration success to Caswell during periodic freshets when turbidity levels spike (e.g., > 20 NTU). Such conditions were more likely to occur during the fry migration period under sustained low flows (e.g., 2004 and 2005). Survival rates did not appear to be strongly related to variations in temperature across years.

Body size

There were obvious differences across years in mean lengths of juveniles. Juveniles migrating in 1996 were clearly larger than those of other years, and were roughly 12 mm above average for juveniles sampled at Oakdale (February 26 – May 20). The smallest juveniles sampled at Oakdale occurred in 1999; these fish were roughly 6 mm below average length. Lengths were also clearly above average in 1998 and below average in years such as 2001, 2004, and 2005.

We found moderately strong associations between mean lengths at Oakdale and annual measures of flow and juvenile abundance. The only significant relationship, however, was between mean length and log-transformed values of total passage at Oakdale. This relationship implied a strong density-dependent effect on body size, suggesting that juveniles experienced higher growth rates (reduced competition) when abundances were low. The relationship was largely driven by the data for 1996, for which juveniles were especially large and total passage at

Oakdale was the lowest on record. Variations in juvenile length did not appear to be strongly related to either temperature or turbidity conditions.

There were also obvious differences in mean lengths between the Oakdale and Caswell sites. Juveniles migrating past Caswell (February 26 – May 20) were found to significantly larger than those at Oakdale in all years. Differences ranged from just 0.8 mm in 1998 to 13.4 mm in 2005. These differences between Caswell and Oakdale lengths were most prominent in years with low flow, such as during March and April of 2002, and throughout most of the parr and smolt migration in 2003 and 2005. These results suggests that juveniles may rear extensively between the trap sites, especially in low flow years. Alternatively, such patterns could also arise if predation of juveniles is strongly size dependent, such that smaller individuals suffer much higher mortality rates.

Juvenile Rearing

We found additional evidence that juveniles rear extensively between the trap sites. We examined ratios of Caswell versus Oakdale passage abundance computed across weekly intervals and across discrete length groups (5 mm intervals). A high abundance ratio implies a large number of fish at Caswell relative to Oakdale. In many years, the weekly abundance ratios were quite low during fry migration (January - February), but then increased rapidly and often peaked above one during parr migration (March - April) before declining again during late parr and smolt migration (May). These patterns strongly suggest that juveniles rearing between the trap sites provided additional contributions to the passage at Caswell, often for numerous weeks during parr migration, for example. Similarly, there were several years for which the length-based abundance ratios were very high (e.g., > 1) across several length groups (predominantly within the parr size class). Clear examples of this evidence of juvenile rearing were found for years with moderate to high flows (e.g., 1998 and 2000) as well as low flows (e.g., 2004 and 2005).

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INTRODUCTION

Effective management of salmon *Oncorhynchus spp.* populations often requires a detailed understanding of the mechanisms determining growth and survival of juvenile salmon during freshwater and early marine life. In recent decades, numerous salmon populations along the west coast of North America have been identified as threatened or endangered, yet in many cases the causal factors underlying declines in abundance remain unclear (Nehlsen et al. 1991; Slaney et al. 1996; McClure et al. 2003; NMFS 2003). Much of this uncertainty exists because population data are often limited to abundances indices for adult spawners (e.g., McClure et al. 2003). However, to distinguish between alternative hypotheses of decline such as the effects of habitat degradation, regulated flow, passage barriers or poor ocean conditions, reliable and cost-effective methods are required for monitoring juvenile abundance and survival during key lifestages.

This need for juvenile salmon data is a pressing issue for the Stanislaus River, California. Adult returns of chinook salmon *O. tshawytscha* to the Stanislaus River have declined from roughly 30 thousand during the 1960's to between 2 and 7 thousand in recent years. Currently, numerous efforts are underway to improve Chinook production in the river system through habitat restoration and flow management. However, little is known about the roles that freshwater, estuary, and marine conditions play in regulating the abundance of Chinook salmon in the Stanislaus River.

To address some of these uncertainties, rotary screw traps have been used at two locations in the Stanislaus River since 1996 to annually monitor the outmigration of age-0 juvenile chinook salmon (e.g., Demko et al. 2000). Goals of the sampling programs were to provide new information about Chinook salmon production and migration in the Stanislaus River and how these factors may be influenced by changes in flow, temperature, turbidity and other environmental factors. Target species included fall Chinook salmon and rainbow trout/steelhead.

In this report, we conducted preliminary analyses of ten years (1996-2005) of screw-trap sampling data across the two trap sites on the Stanislaus River as assess juvenile abundance of fall Chinook salmon and potential factor influencing their survival and body size. The specific objectives of these analyses were as follows:

- Use trap-efficiency models to estimate abundance of migrating juveniles by life stage;
- Quantify relationships between annual survival of migrating juveniles and environmental conditions;
- Quantify relationships between size of juveniles and environmental conditions.

Study site

The Stanislaus River (drainage area: 240,000 ha) begins on the western slopes of the Sierra Nevada Mountains and flows southwest to its confluence with the San Joaquin River at the south end of the Sacramento-San Joaquin Delta in central California (Figure 1). The Stanislaus River supports a natural population of ocean-type (fall-run) chinook salmon that spawn from October through December. Several dams control flows in the Stanislaus River for flood protection, power generation, and water supply. Goodwin Dam at river km (Rkm) 94 is the upstream limit for adult spawner migration (Figure 1). Spawning has been observed as far downstream as Riverbank (Rkm 53.1), but most spawning occurs in the 29 km reach below Goodwin Dam. Juveniles usually begin to emerge from gravels in early January, and migrate downstream of the spawning area as age-0 fry (predominantly in February), parr (March and April) and smolts (May).

To study the characteristics of juvenile migration, we fished rotary screw traps (2.43 m in diameter) in the mainstem of the Stanislaus River at two sites: Oakdale (64.5 Rkm) and Caswell (13.8 Rkm) (Figure 1). The Oakdale site was located just downstream of the primary spawning and rearing area. A single trap was operated in the thalweg of the main (north) channel approximately 2-3 m from the north bank. The channel at this site is about 30-37 m wide and 1.5-4.3 m deep, depending on flow. Lateral placement of the trap depended on the position of the thalweg, and slight adjustments were occasionally made as the thalweg shifted with changes in flow. During 1997, flooding scoured an adjacent side-channel causing a decrease in the proportion of river flow passing through the main channel in subsequent years.

The Caswell site was selected as the farthest location downstream with adequate access to install and monitor two traps. Two traps were fished side-by-side at this site to increase catch rates, which were found to be low in pilot studies. The river at this location is about 24-30 m wide and 1.5-4.6 m deep, depending on flow. Just upstream of the traps, we installed a sandbag wall extending roughly 2 m perpendicular from the north bank to divert flow into the traps and thereby increase catch rates. Depending on flow conditions, the first (north) trap was located 2-3 m downstream of this wall and 2-4 m from the north bank. The second (south) trap was fished directly alongside the first trap. Both traps were placed in an area where water velocity was highest.

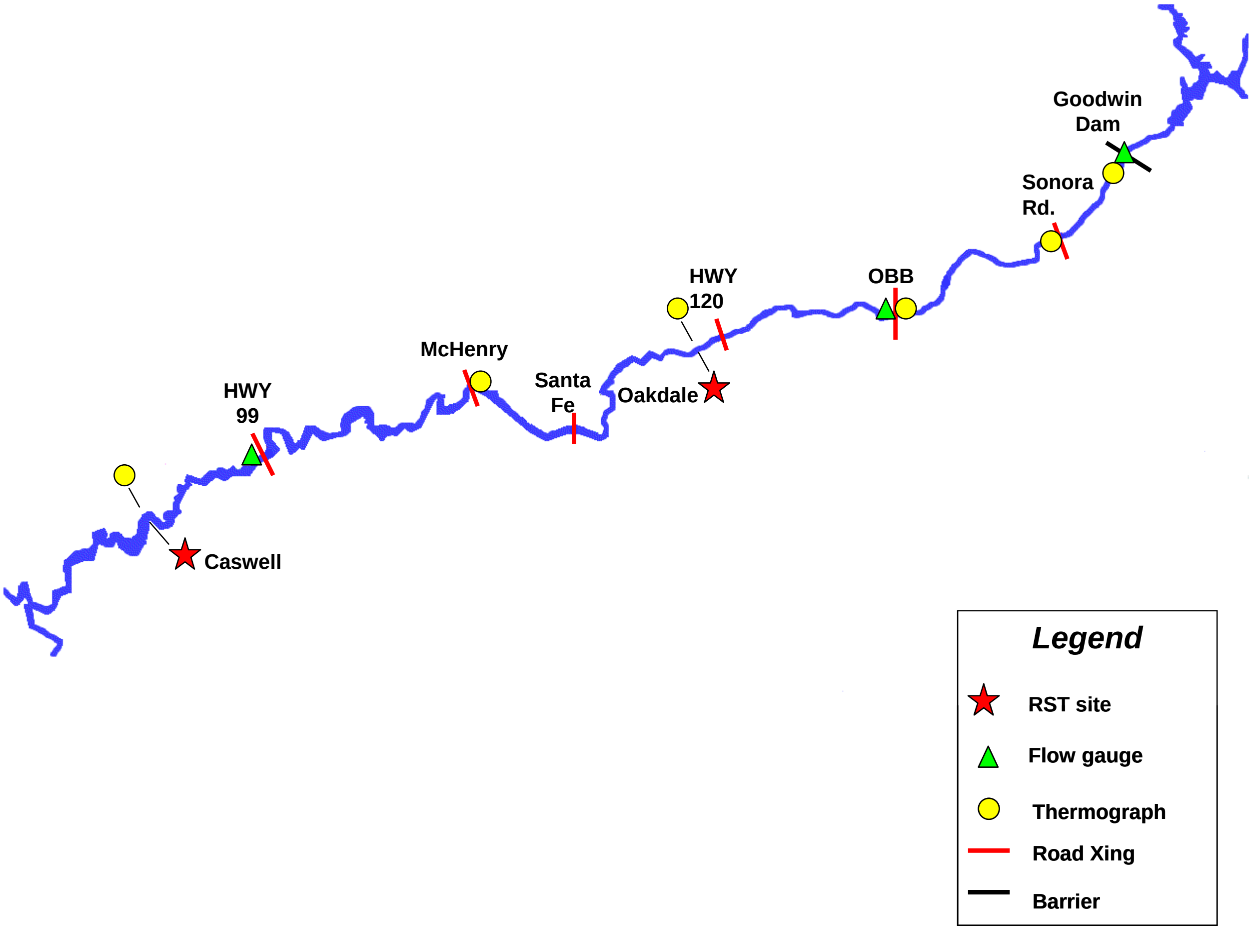


Figure 1. Location of Caswell and Oakdale rotary screw traps and temperature monitoring stations from Goodwin Dam to the mouth of the Stanislaus River. Fall-run Chinook spawning occurs from Goodwin Dam down to Riverbank.

METHODS

Daily captures of juvenile Chinook salmon in the Oakdale and Caswell screw traps provide useful information regarding the size and relative abundance of migrating juveniles. However, because the traps only sample a portion of the water column, reliable estimates of trap efficiency (i.e., the proportion of migrating juveniles caught by a trap) are required to compute indices of total abundance at a given trap site. In turn, estimates of total abundance can then be used to estimate the survival rate of juveniles between the Oakdale and Caswell locations. Thus, the estimation of trap efficiency (also referred to as "catch rates") is a critical first step to analyzing abundance and the factors affecting survival and migration timing of juveniles.

In previous analyses, we developed models for predicting trap efficiency based on numerous mark-recapture experiments. Given that this analytical framework provides the foundation for estimating the passage abundances and survival rates analyzed here, we included much of this material as well additional modifications in this report.

In the following sections, we describe the methods we used in four sets of analyses to: (i) develop models for predicting catch rates (trap efficiency) at each trap location, (ii) estimate abundance, survival, and factors influencing survival, (iii) analyze trends in juvenile body size, and (iv) examine migration timing of juveniles.

Analysis of catch rates (trap efficiency)

From 1996 through 2005, we conducted a total of 356 mark-recapture experiments at the Oakdale and Caswell trap locations to estimate catch rates (trap efficiency) (Table 2). The number of releases varied widely among years. At Oakdale, the number ranged from 9 in 1996 to 39 in 2004, with none in 1997. At Caswell, releases were made in all years, ranging from 5 in 1997 to 39 in 2003 (Table 2). Releases consisted of two basic types: 1) natural fish that had been recently caught at a respective trap site, and 2) juveniles obtained from the Merced River Hatchery. The latter "hatchery" releases accounted for 102 of the 356 releases (Table 2). Efforts were made to conduct releases over a broad range of conditions, though release dates were often constrained by availability of fish. In general, annual releases were spread across several months for each trap site; coverage across years extended from early January to late June. Additional data summaries of release conditions are provided in the Results section.

Table 2. Summary of nighttime mark-recapture releases at the Oakdale and Caswell trap locations. "Days" indicates the number of distinct days for which releases were made, and "R" is the average release size.

	Oakdale					Caswell				
	Total	**Hatchery**	**Natural**	**Days**	**R**	**Total**	**Hatchery**	**Natural**	**Days**	**R**
1996	9	5	4	8	549	15	13	2	8	2720
1997	0					5	4	1	2	3391
1998	10	2	8	8	415	21	17	4	7	2714
1999	17	2	15	16	385	9	4	5	8	1964
2000	12	3	9	12	744	15	5	10	15	1011
2001	26	7	19	16	1037	14	11	3	12	1085
2002	22	0	22	14	526	16	0	16	11	800
2003	38	5	33	31	295	39	4	35	35	109
2004	39	20	19	26	663	8	0	8	8	255
2005	25	0	25	25	383	16	0	16	16	238
Total	198	44	154	156		158	58	100	122	

Mark-recapture procedures

The methods used to conduct releases (mark-recapture experiments) at each site were generally consistent across years. In the case of "natural" release groups, juveniles that had been captured in a trap were held either near the trap or at the upstream release site in net pens for up to four days prior to marking and one day post marking. Fish held near the trap were transported to the upstream release site in insulated coolers on the morning of the release day and placed in holding pens, or were transported just prior to release. For "hatchery" releases, fish were either marked at MRH up to one week prior to release, or were marked onsite one to three days before release. All fish marked at MRH were transported to the release site on the day of release. These fish were placed into net pens and allowed to recover several hours before release. Hatchery groups marked near the release site were transported from MRH at least one day prior to the release day.

Most release groups were marked using photonic dye inoculation because of the high quality of marks and the ability to use the marking equipment in rapid succession. However, some groups were marked with cold-brands or Madajets. We anesthetized all fish with MS-222 before a given mark was applied (Schoettger and Steucke 1970). Only one mark was applied to each fish, and all fish in a release group received the same mark. The mark color and/or location varied between groups so each group could be uniquely identified. Fork lengths were measured and mark retention was evaluated for a random sample of at least 50 marked fish. If mark retention was less than 100%, the group was either sorted to ensure that a known number of marked fish was released, or the proportion of fish found to have clear marks was used to estimate the actual number of marked fish released (i.e., number released = proportion marked * number in group).

All releases were conducted under cover of darkness and at the same location for each trap site, roughly 0.4 km upstream of the trap. Fish were released within a few hours of dusk because previous studies had shown that most juveniles migrate downstream during darkness, with peak catches occurring soon after dark or just prior to dawn (Cramer and Demko 1993; Demko and Cramer 1995). Release times for each group typically ranged from 15 to 60 minutes. During releases, about 50 fish per minute were removed from their net pens using a dip net. This gradual release was intended to prevent fish from behaving as a single school. Although the time and frequency of trap checks following release varied, traps were generally checked on an hourly basis for the first few hours after release and again the following morning. All recaptures were counted and fork lengths were measured for at least the first 50 individuals recovered. Recaptured fish were subsequently released well downstream of the trap to avoid repeat captures.

Physical variables

We obtained daily measurements for several physical variables reflecting conditions that may influence catch rates. First, we measured instantaneous water velocity each day by taking depth-velocity profiles in front of the trap using a Global Flow Probe (manufactured by Global Water, Fair Oaks, California). Instantaneous turbidity was also measured daily at each trap site in Nephelometric Turbidity Units (NTU) using a LaMotte turbidity meter, Model 2008. Daily instantaneous water temperature at each trap site was measured with a mercury thermometer. We also recorded hourly temperatures using Onset StowAway recording thermometers at six sites including the Oakdale screw trap site (Figure 1) Daily average water temperatures were derived by averaging the 24-hourly measurements in a calendar day. In addition, we obtained average daily flow data measured at three USGS gaging stations from the California Data Exchange Center including Orange Blossom Bridge (OBB; 75.5 Rkm), Ripon (RIP; Rkm 25.4), and Goodwin Dam (GDW; Rkm 94).

Logistic regression

We used logistic regression to develop models for predicting catch rates as a function of environmental conditions. In brief, logistic regression is a form of generalized linear model that is applicable to binomial data (McCullach and Nelder 1989; Dobson 2002). Here, the binomial probability of interest is the observed catch rate (q):

$$(1) \qquad q = \frac{c}{R} \ ,$$

where c is number of observed recaptures (a binomial variable) of a given release group of size R. The logistic model with n explanatory variables (x) can be expressed in linear form as:

$$(2) \qquad y = \beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n \ ,$$

where y is the "logit" transform of the observed catch rate (q):

$$(3) \qquad y = \text{logit}(q) = \log\left(\frac{q}{1-q}\right) \ .$$

The coefficients (β), which are estimated via maximum likelihood, provide predicted values of catch rate via the following back-transformation of the logit function:

$$(4) \qquad \hat{q} = \frac{\exp(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \ldots + \hat{\beta}_n x_n)}{1 + \exp(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \ldots + \hat{\beta}_n x_n)} \ .$$

The statistical significance of explanatory variables was tested using analysis of deviance (McCullach and Nelder 1989; Venables and Ripley 1999). The "deviance" of a fitted model is twice the log-likelihood ratio statistic of the fitted model versus the so-called "saturated" model, for which all observed catch rates (q) are treated as free parameters. Under the binomial assumption, a logistic model that adequately explains variability in catch rates will have a deviance roughly equal to the residual degrees of freedom. In all our analyses, however, model deviances were much greater than that expected due to binomial sampling error alone. Such extra-binomial variation, which may arise from either over-dispersion or inadequate model structure (i.e., when key processes affecting catch rates are missing from the model), must be accounted for when testing variables and estimating confidence intervals. Extra-binomial variation is represented by a dispersion parameter, ϕ, which is a scalar of the assumed binomial variance. A value of ϕ close to one implies little or no over-dispersion, whereas a value of 4, for example, indicates considerable over-dispersion. The dispersion parameter is easily estimated from the fit of a logistic regression and does not affect point estimates of coefficients (Venables and Ripley 1999). However, the variance-covariance matrix for coefficients must be multiplied by the estimate of ϕ when conducting statistical tests and computing confidence intervals.

Hatchery versus natural releases

Across years, paired releases of hatchery and natural fish were conducted on eight different days at the Caswell site, and on 13 days at the Oakdale site (Table 3). In total, 21 release groups of natural fish were paired with 26 groups of hatchery fish (Table 3). Differences in catch rates between hatchery and natural fish were examined using logistic regression with two categorical variables (*day* and *source*). The variable *day* accounted for differences in catch rates among all days with paired releases, while *source* tested for differences in catch rates between hatchery and natural releases. Regressions were fit separately to paired releases for the Oakdale and Caswell sites.

Table 3. Summary of paired mark-recapture releases of natural and hatchery fish at the Caswell and Oakdale trap locations. R = number released, c = number recaptured, and q = observed catch rate (=c/R).

			Natural				Hatchery		
Site	**Date**	**Groups**	**R**	**C**	**Q**	**Groups**	**R**	**c**	**q**
Caswell	3/14/1998	1	2149	101	0.047	2	2082	80	0.038
	3/25/1998	1	877	43	0.049	2	2382	66	0.028
	5/18/1998	1	1102	15	0.014	1	1020	31	0.030
	2/19/2003	1	18	0	0.000	1	144	26	0.181
	2/20/2003	1	25	4	0.160	1	121	15	0.124
	2/21/2003	1	28	3	0.107	1	125	18	0.144
	2/22/2003	1	28	3	0.107	1	123	23	0.187
Oakdale	5/30/1998	1	250	19	0.076	1	267	23	0.086
	6/13/1998	1	146	7	0.048	1	175	12	0.069
	1/6/2001	1	262	49	0.187	1	757	107	0.141
	2/19/2003	2	741	50	0.067	2	1301	86	0.066
	2/20/2003	1	196	15	0.077	1	223	6	0.027
	2/22/2003	1	219	7	0.032	1	246	11	0.045
	4/8/2004	1	233	55	0.236	1	655	177	0.270
	4/14/2004	1	26	2	0.077	2	968	119	0.123
	4/15/2004	1	72	3	0.042	2	1107	117	0.106
	4/28/2004	1	27	0	0.000	2	1026	2	0.002
	5/6/2004	1	108	14	0.130	1	548	56	0.102
	5/12/2004	1	42	0	0.000	1	510	13	0.025
	5/13/2004	1	54	2	0.037	1	489	8	0.016
Total		21	6603	392		26	14269	996	

Environmental effects on catch rates

Next, we used logistic regression to examine the potential effects of environmental variables and fish length on catch rates of the Caswell and Oakdale screw traps. In these analyses, we used only night releases and pooled data across releases that were conducted during the same evening. That is, if three distinctly marked groups were released in the same evening, these data were summed (pooled) to provide single values for the total number released (*R*) and recaptured (*c*) (equation 1). This provided a total of 154 day-specific releases for the Oakdale site and 122 releases for the Caswell site (Table 2, "Day" columns).

Note that we pooled same-day releases because they are essentially "pseudo-replicates" with respect to those environmental variables for which we had only daily measures (flow, turbidity, etc.). For example, suppose ten groups were released sequentially in one evening with a corresponding set of environmental measures (one flow value, one turbidity value, etc.).

Clearly, no inferences can be made regarding the relationship between a single measure of flow, for example, and the ten observations of catch rate. Consequently, if ten groups were released on another evening under a different set of environmental conditions, it would incorrect to treat the combined data as 20 replicates because environmental conditions were only replicated twice. In some cases, data were pooled across both hatchery and natural releases that were conducted in the same evening. This might be a questionable treatment if hatchery and natural releases had different catch rates; however, as discussed below, there was no evidence that their catch rates differed appreciably.

For both the Oakdale and Caswell data sets, we included the following variables as potential determinants of catch rates: *flow*, *velocity*, *turbidity*, *temperature*, and *size* (average fish length at release). Initial inspection of the data suggested that linear relationships (equation 2) between these variables and y (=logit(q)) appeared reasonable, except in the case of *flow*. We therefore included the natural logarithm of flow, denoted *log(flow)*, as an alternative form for the relationship between catch rates and flow. We also considered two categorical variables: *year* and *type*. The variable *year* tested for potential differences in mean catch rates among years that might arise due to annual changes in channel morphology, bank vegetation, predator abundance, trap placement, etc. The variable *type* tested for potential differences among catch rates of hatchery and natural fish. Note that a pooled release group that contained both hatchery and natural fish was categorized as “hatchery” when more than 50% of the release was comprised of hatchery fish; otherwise, it was categorized as “natural.”

Our approach was to fit logistic models using all years of available data. This approach assumes that relationships between catch rates and an explanatory variable (e.g., flow) will have a similar form across years. An alternative would be to fit models separately to each year of data, but this potentially allows relationships to differ appreciably among years (e.g., a positive effect of flow in one year, but a negative effect in a different year). Such differences would likely have little biological support and would be considered spurious. In contrast, modeling all years simultaneously provides fewer models and more data, which reduces the chance of finding spurious relationships and increases the statistical power to detect relationships that have a consistent basis across years.

We used a stepwise regression procedure to determine which variables to include in a given logistic model. In the first step, a model was fit with an intercept (βo), and then each explanatory variable was entered one at a time. The variable with the greatest explanatory power was then included in the model, and the remaining variables were again entered one at a time. The procedure was terminated when none of the remaining variables had a statically significant effect on survival at the $\alpha = 0.05$ significance level. An alternative approach to model selection was also examined. In this approach, the "best" model was determined using the Akaike Information Criterion (AIC), adjusted for over-dispersion (Burnham and Anderson 2002). However, the stepwise regression and AIC procedures provided the same "best" model in all analyses.

Analysis of abundance and survival

The daily passage abundance (n) of migrating juvenile Chinook salmon was estimated for each trap location during 1996 to 2005 as follows:

$$n = \frac{c}{q} \,, \tag{5}$$

where c was observed daily count and q was the estimated catch rate (trap efficiency) for that day based on the "preferred" logistic model for a given trap site (discussed below). Annual passage was estimated by summing the daily abundance estimates. Standard errors (SE) and confidence intervals for measures of cumulative daily abundance and total annual abundance were computed using methods described in Demko et al. (2000).

Periods of sampling differed across years, and there often many days within those periods when traps were not fished (Table 4). Note that the Oakdale trap was not operated in 1997 (Table 4). To estimate a missing value of daily count (c) within a sampling period, we used the weighted average of all observed counts for the five days before and five days after the missing value (Demko et al. 2000). The weights were equal to one through five, where values that were directly adjacent to the missing day were weighted as five, values that were two days before and after the missing day were weighted as four, and so on. This weighted average was reasonably effective at capturing the temporal trends in daily counts observed across years at each trap site. We also investigated a Kalman filter algorithm (Harvey 1989) that explicitly modeled an annual time series of daily counts and provided estimates of missing values. However, both approaches provided similar estimates, and given the computational complexity of the Kalman filter procedure, we limit our results here to the weighted average approach.

Table 4. Summary of sampling periods for rotary screw trapping on the Stanislaus River at Oakdale and Caswell, 1996-2005.

	Oakdale			Caswell		
Year	Start	End	Days Missed	Start	End	Days Missed
1996	2-Feb	9-Jun	13	6-Feb	2-Jul	5
1997	--	--	--	19-Mar	24-Jun	0
1998	27-Jan	16-Jul	25	8-Jan[a]	16-Jul	19
1999	18-Jan	30-Jun	11	18-Jan	30-Jun	12
2000	16-Dec	1-Jul	16	16-Dec	1-Jul	19
2001	12-Dec	29-Jun	14	22-Dec	28-Jun	10
2002	12-Dec	7-Jun	47	16-Jan	7-Jun	61
2003	20-Dec	5-Jun	31	18-Jan	5-Jun	38
2004	3-Jan	5-Jun	21	10-Jan	5-Jun	45
2005	4-Jan	17-Jun	24	6-Jan	17-Jun	44

[a] Traps were operated briefly on Jan 8-9 and Jan 11-12 with a total estimated passage of 95 fry, followed by a period of 16 days in which traps were not fished. Continuous sampling began on Jan 29.

To examine passage abundance as a function of fish size and life stage, we computed total annual passage by length class (1 mm intervals). We first computed length frequency tables on a weekly basis by pooling all daily length measurements (see section "Analysis of body size" below) for each Julian week. Daily abundance estimates were then multiplied by the length frequency tables and summed to provide annual abundance estimates by length class. In addition, for each trap site and year, we computed annual abundance estimates for three general life-stage categories based on length (e.g., Demko et al. 2000): (1) fry (< 45 mm); (2) parr (45 mm to 80 mm); and smolts (> 80 mm). Across sites and years, there were only three Julian weeks for which length data were not available. In these cases, we combined the length frequency tables from the week before and the week after to compute abundance by length class for the missing week.

Survival rates

Annual survival rates of migrating juvenile Chinook salmon between the Oakdale and Caswell locations were estimated as:

Annual survival rate = (Abundance passing Caswell) / (Abundance passing Oakdale).

To examine potential measures of survival rate over more discrete time periods, we computed weekly ratios of the abundance that passed Caswell versus passage at Oakdale (i.e., *Abundance ratio* = [*Caswell passage*] / [*Oakdale passage*]). There is clear evidence in the daily passage estimates and previous survival studies (e.g., Demko et al. 2000) that fish passing Oakdale can arrive at Caswell as few as one or two days later. We therefore computed abundance ratios across Julian weeks with the days used for Caswell lagged either one or two days ahead of those used for Oakdale. Both ratio estimates provided very similar results across weeks and years, so we only report abundance ratios based on one-day lags.

Similarly, we computed annual abundance ratios for Caswell versus Oakdale across various length groups and for each life stage (fry, parr, and smolt) using the length-class estimates of abundance discussed above. For length groups, we binned lengths using 5 mm intervals (< 35 mm, 35-39 mm, 40-44 mm, …, 105-109 mm).

Relationships between annual survival rate estimates and environmental conditions (flow, temperature, and turbidity) were examined using regression models. Two annual measures for each environmental variable were examined: (1) the average value across the sampling period; and (2) the median value across the sampling period. In addition, three forms of regression model were analyzed. First, models with survival rate as a linear function of each environmental variable were fit using weighted least squares (Neter et al. 1990), where weights were proportional to the inverse of the variances of the survival-rate estimates. Second, for comparison, standard (non-weighted) linear regressions were used. Last, survival rates were fit as a linear function of log-transformed values of each environmental variable using weighted least squares. This latter approach implies a non-linear relationships between survival rates and environmental variables.

Analysis of body size

Across days in each sampling season, the lengths of juvenile Chinook salmon captured by the screw traps were regularly sampled and measured to the nearest mm. Daily sample sizes varied depending on the number of juveniles captured; however, across each sampling season, total sample sizes were large and highly representative of the full sampling period. For example, total sample sizes at Oakdale ranged from 2,442 in 1996 to 10,881 in 2001, while for Caswell, total samples ranged from 1,693 in 1996 to 9,625 in 2000.

We computed daily and weekly summaries of length to examine differences in juvenile body size across years and trap sites. Annual trends in length were characterized by fitting smoothing splines (Venables and Ripley 1999) to the daily length data. Mean lengths by week were graphically compared across years for each trap site as well as between trap sites. For each trap site, differences in mean lengths among years were examined using the following analysis of variance (ANOVA) model (Neter et al. 1990):

$$length_{ijk} = year_i + week_j + e_{ijk}\ , \tag{6}$$

where *length* denotes the length measurement for fish *k* in week *j* of year *i*, *year* and *week* are categorical variables denoting the year and Julian week of migration, and *e* denotes normally distributed variations in individual lengths. For each year, we examined differences in mean lengths between the Caswell and Oakdale trap sites using the following ANOVA model:

$$length_{ijk} = site_i + week_j + e_{ijk}\ . \tag{7}$$

In this case, *site* is a categorical variable denoting the trap location (either Caswell and Oakdale).

Relationships between annual measures of length and environmental conditions were examined using linear regressions. For these analyses, a single index representing between-year differences in length was used. For a given year and trap site, this index was the difference in mean length (across weeks) compared to the across-year mean as estimated by the ANOVA model (i.e., from the coefficients for $year_i$ in equation 6). We then used linear regressions to examine associations between the annual length indices and measures of juvenile abundance, water temperature, and flow. Similarly, we examined relationships between environmental conditions and the annual length differences measured between the Caswell and Oakdale sites. In this case, the length index for each year was the difference in coefficients for $site_i$ in equation 7. Additional details are provided in the "Results" section below.

Analysis of passage timing

We examined general relationships between patterns of daily migration and environmental conditions by plotting daily passage estimates and overlaying plots of a given environmental variable. Specifically, daily passage estimates at Oakdale were compared with average daily flows at OBB, daily measurements of temperature and turbidity taken at the Oakdale trap site, and daily precipitation recorded at New Melones. Daily passage at Caswell was compared with flows at Ripon, temperature and turbidity at Caswell, and daily precipitation at New Melones.

RESULTS

Catch rates (trap efficiency)

Hatchery versus Natural Releases

There was little evidence based on paired-release data that catch rates of hatchery and natural fish differed at either the Caswell or Oakdale site. Although there was a tendency toward higher catch rates for hatchery releases, the observed differences were highly variable (Table 3, Figure 2). Across the eight sets of paired releases at Caswell, hatchery catch rates were estimated to be 1.10 times greater than natural catch rates (95% CI: 0.79 to 1.55), but this difference was not significant (F = 0.33, P = 0.58) and the 95% confidence interval included a broad range of values less than one (i.e., values indicating that hatchery catch rates were less than those of natural fish). Similarly, across the 13 sets of paired releases at Oakdale, there was no apparent difference between natural and hatchery catch rates (F = 0.01, P = 0.93, hatchery/natural = 1.01, 95% CI: 0.82 to 1.25). Furthermore, in the analyses discussed below, in which catch rates were modeled as a function of several environmental variables, the variable *type* (representing hatchery versus natural releases) was not significant for either the Oakdale or Caswell data.

The lack of notable differences between catch rates of natural and hatchery fish is reassuring. The use of large releases of hatchery juveniles across years allowed for the estimation of catch rates during periods when daily captures of natural fish were limited. However, these findings differ from those of Roper and Scarnecchia (1996), who used series of paired-release experiments in the South Umpqua River, Oregon, to determine that hatchery juvenile chinook salmon had significantly lower screw-trap catch rates than wild juveniles. Roper and Scarnecchia (1996) conducted their releases in daylight, and observed that hatchery juveniles tended to move rapidly downstream whereas wild juveniles appeared to migrate almost exclusively at night. Consequently, it appeared that many hatchery juveniles were able to avoid capture in lower-velocity water during daylight when visibility was high. In contrast, the paired releases analyzed here were nighttime releases, which presumably limited potential behavioral differences between hatchery and natural juveniles such as those observed by Roper and Scarnecchia (1996).

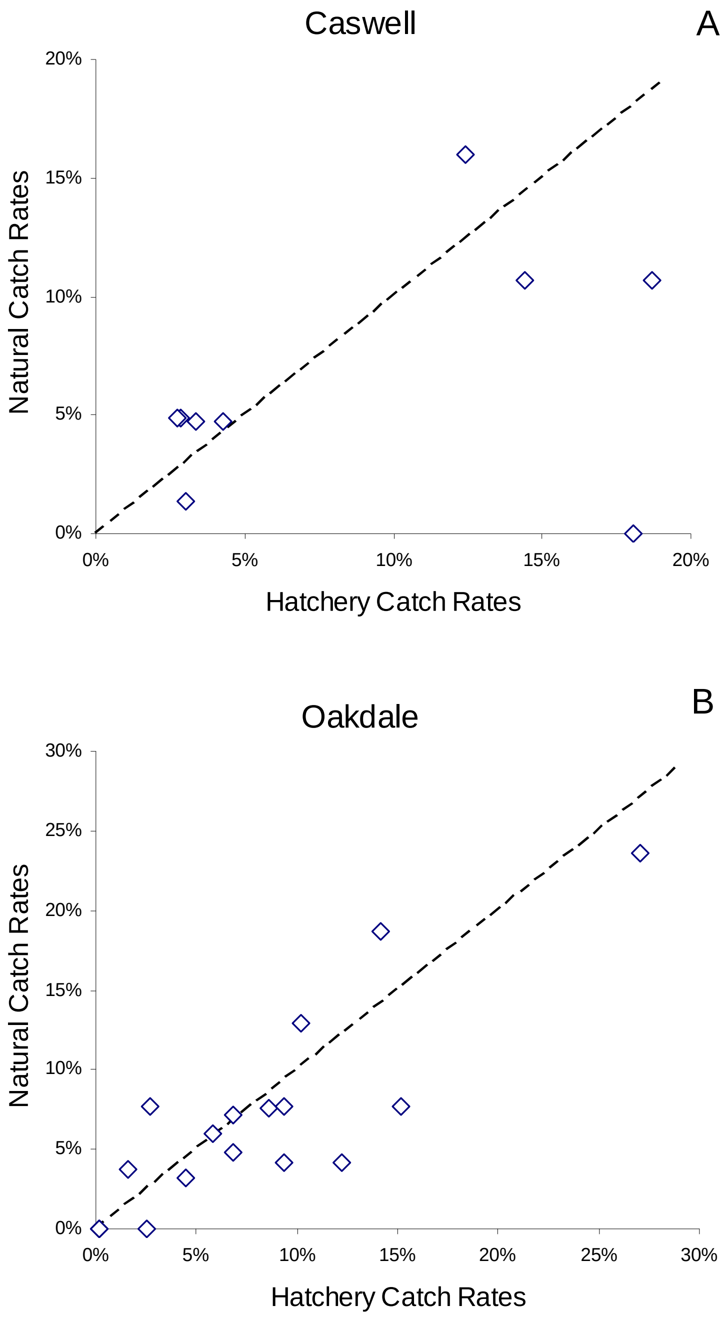


Figure 2. Comparison of catch rates between paired releases of hatchery and natural fish for (A) **the Caswell trap site, and** (B) **the Oakdale trap site. Data shown in Table 4. Dashed lines are 1:1 lines.**

Environmental effects on catch rate: Oakdale trap location

For the Oakdale trap, catch rates and environmental conditions of mark-recapture releases varied widely across years (Figure 3). Median catch rates were generally lower in years with predominantly high flows during release (e.g., 1998-2000, Figure 3). In most years, releases were conducted from February through May (e.g., Julian days 30 – 120), and consequently, used a broad range of fish lengths (e.g., 40 – 80 mm) (Figure 3). In contrast, conditions for flow, turbidity, and velocity varied little in some years (Figure 3).

Across years, catch rates at Oakdale appeared to decline rapidly as flow increased, and to a lesser extent, as fish length increased (Figure 4). Initial inspection of the data also suggested that catch rates were not strongly related to either turbidity or velocity (Figure 4).

Logistic regressions indicated that, among environmental variables, flow had by far the strongest effect on catch rates at the Oakdale site. The “best” regression model based on either step-wise regression or AIC model-selection included the variables *log(flow*), *year*, *turbidity* and *temperature*. Summaries of the regression coefficients and analysis of deviance for this model are provided in Table 5 and Table 6. Plots of the partial effects of each variable on logit(catch rate) are shown in Figure 5. The effect of *log(flow)* accounted for 54% of the total deviance (Table 6) and implied that catch rates declined rapidly as flows increased (Figure 5). The variable *year* accounted for 24% of the total deviance, and indicated that after accounting for other variables, catch rates tended to be much higher in 1996 and 1998 in comparison to later years (Table 5; Figure 5). In contrast, *turbidity* and *temperature* had comparatively weak relationships with catch rates, accounting for only 1.0% and 0.8% of the total deviance, respectively (Table 6). Increases in either *turbidity* or *temperature* were associated with slight declines in catch rates (Figure 5). Adding the variables *length*, *velocity*, or *type* (hatchery versus natural) to the preferred model did not improve the fit (P > 0.3 in all cases). In sum, the “best” model accounted for 80.0% of the total deviance, yielding an estimate of the dispersion parameter of $\hat{\phi}$ = 14.3. No obvious problems were evident among standard diagnostics of residuals.

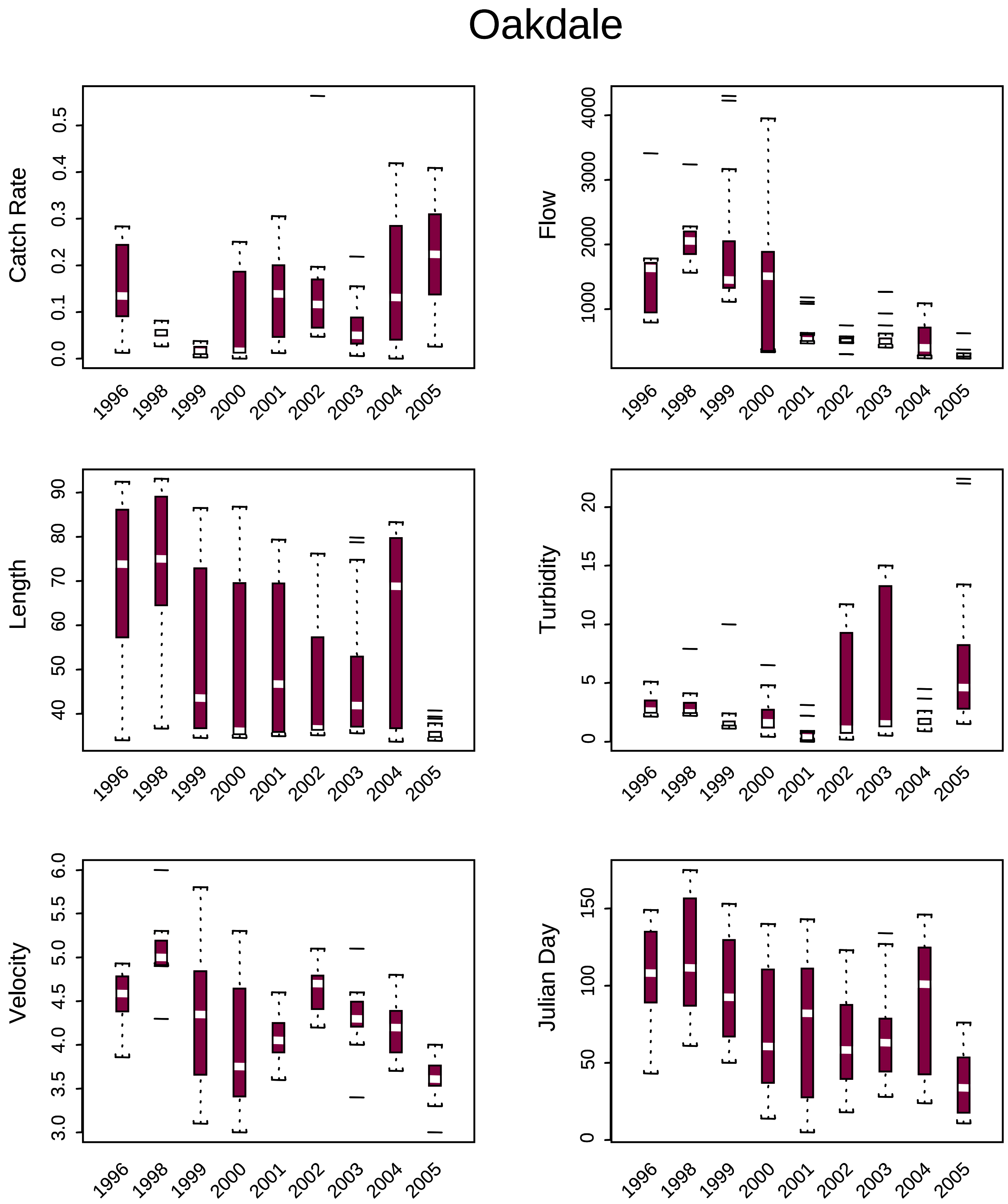


Figure 3. Box plots by year of catch rates and environmental conditions corresponding to the 154 day-specific mark-recapture releases at the Oakdale trap location.

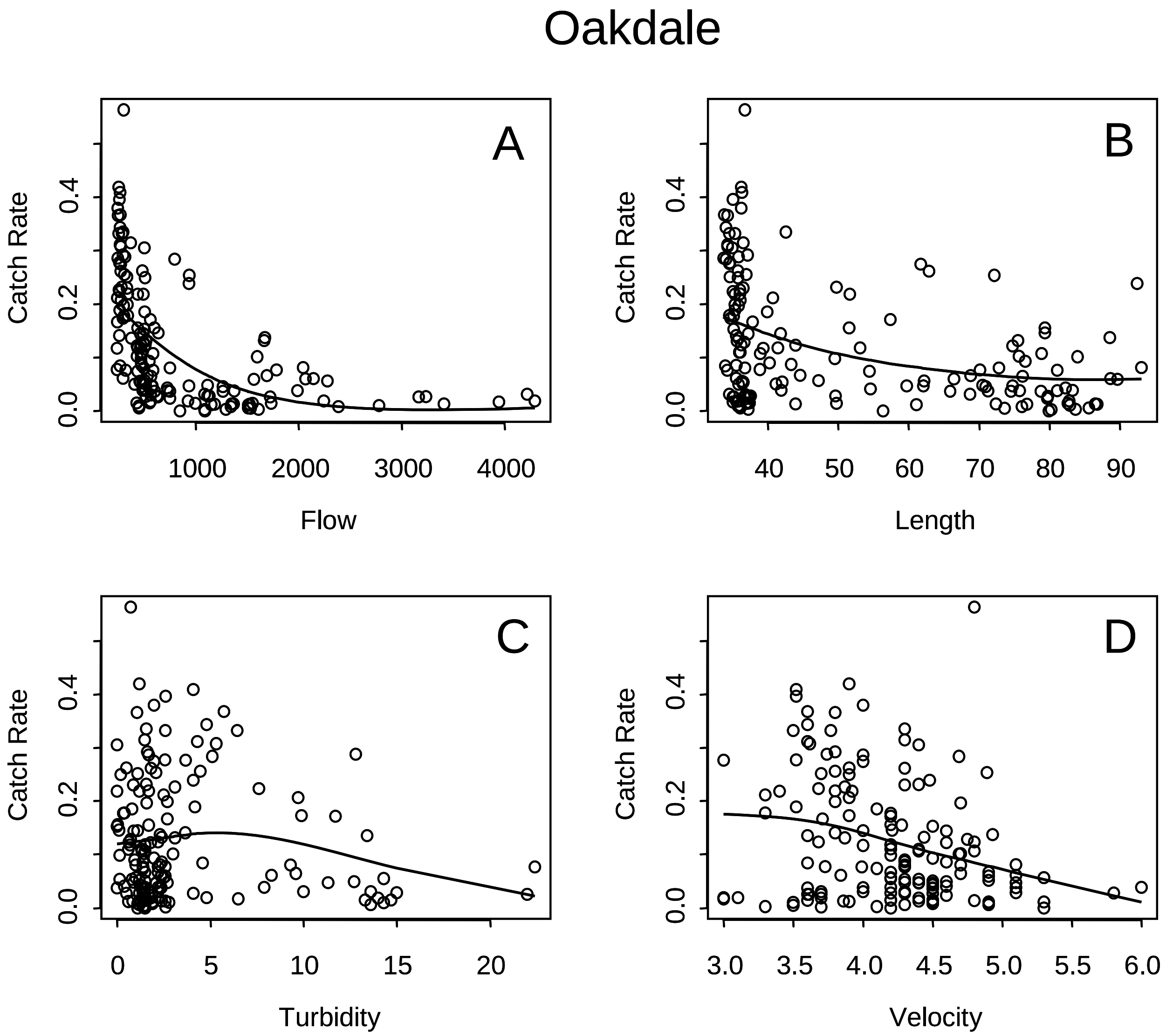


Figure 4. Catch rates as a function of flow, fish length, turbidity and velocity for the 154 day-specific mark-recapture releases at the Oakdale trap location. Solid lines are exploratory fits of smoothing splines.

Table 5. Regression coefficients and standard errors (SE) for the "best" logistic model fit to catch rates of 154 mark-recapture releases at the Oakdale trap site. Note that the coefficient for 1996 is taken to be zero, whereas coefficients for 1998-2005 represent differences in logit(catch rate) relative to 1996.

Variable	Coefficient	SE
Intercept	14.55	1.08
log(flow)	-2.04	0.15
Year = 1998	-0.11	0.35
1999	-2.15	0.41
2000	-2.38	0.29
2001	-1.79	0.21
2002	-2.37	0.25
2003	-2.84	0.26
2004	-2.41	0.25
2005	-2.49	0.28
Turbidity	-0.05	0.02
Temperature	-0.03	0.01

Table 6. Analysis of deviance for the "best" logistic model fit to catch rates of 154 mark-recapture releases at the Oakdale trap site. Df = degrees of freedom.

Variable	Df	Deviance	Residual df	Residual deviance	F Value	P-value
Intercept			155	9611.8		
log(flow)	1	5160.0	154	4451.8	361.4	<0.001
Year	8	2350.8	146	2100.9	20.6	<0.001
Turbidity	1	92.3	145	2008.7	6.5	0.012
Temperature	1	77.2	144	1931.5	5.4	0.021
Total	11	7680.3		1931.5		

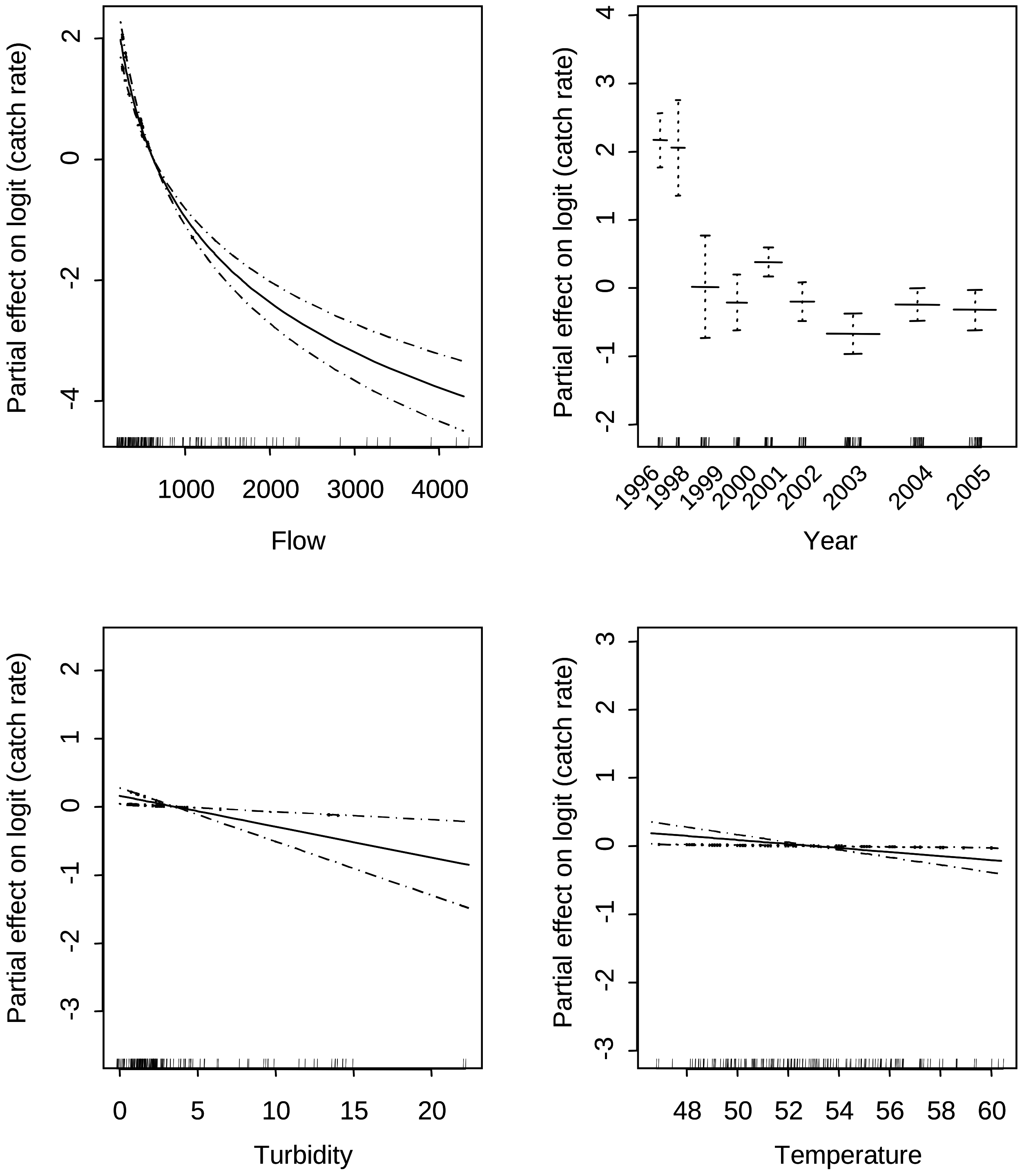


Figure 5. Partial effects of log(*flow*), *year*, *turbidity*, and *temperature* on deviance residuals of logit(catch rate) for the Oakdale trap site. Each plot has the same scale for the Y-axis so that the relative effect of each variable can be compared. Dashed lines indicate approximate 95% pointwise confidence intervals. Tick marks on the X-axis show locations of survival-rate estimates for a given variable.

Caswell trap location

Similar to the Oakdale site, catch rates and environmental conditions for mark-recapture releases at Caswell varied widely across years (Figure 6). Median catch rates for 2001-2005 were much greater than those for 1996-2000. The most obvious difference in environmental conditions between these periods was that flows were considerably lower during years with high catch rates (2001-2005) (Figure 6). Indeed, there was a strong negative trend between flows and catch rates across years (Figure 7). Correlations between catch rates and length, turbidity, and water velocity were less clear (Figure 7).

The “best” logistic model for the Caswell data included *log(flow*), *length*, and *year* (Table 7 and Table 8; Figure 8). Again, the dominant explanatory variable was *log(flow),* accounting for 67.6% of the total deviance (Table 7). Fish length at release, which accounted for 5.2% of the deviance, appeared to have a moderate negative effect on catch rates. For Caswell, the variable *year* (6.6% of deviance) indicated that catch rates during 1997-2000 were lower on average, but higher in 2003 (Table 7; Figure 8). In all cases, adding another variable to the preferred model (with or without the variable *year*) did not improve the model fit. Overall, the preferred model accounted for 79.4% of the total deviance, yielding an estimate of $\hat{\phi} = 8.45$. Again, no obvious problems were evident among diagnostics of residuals.

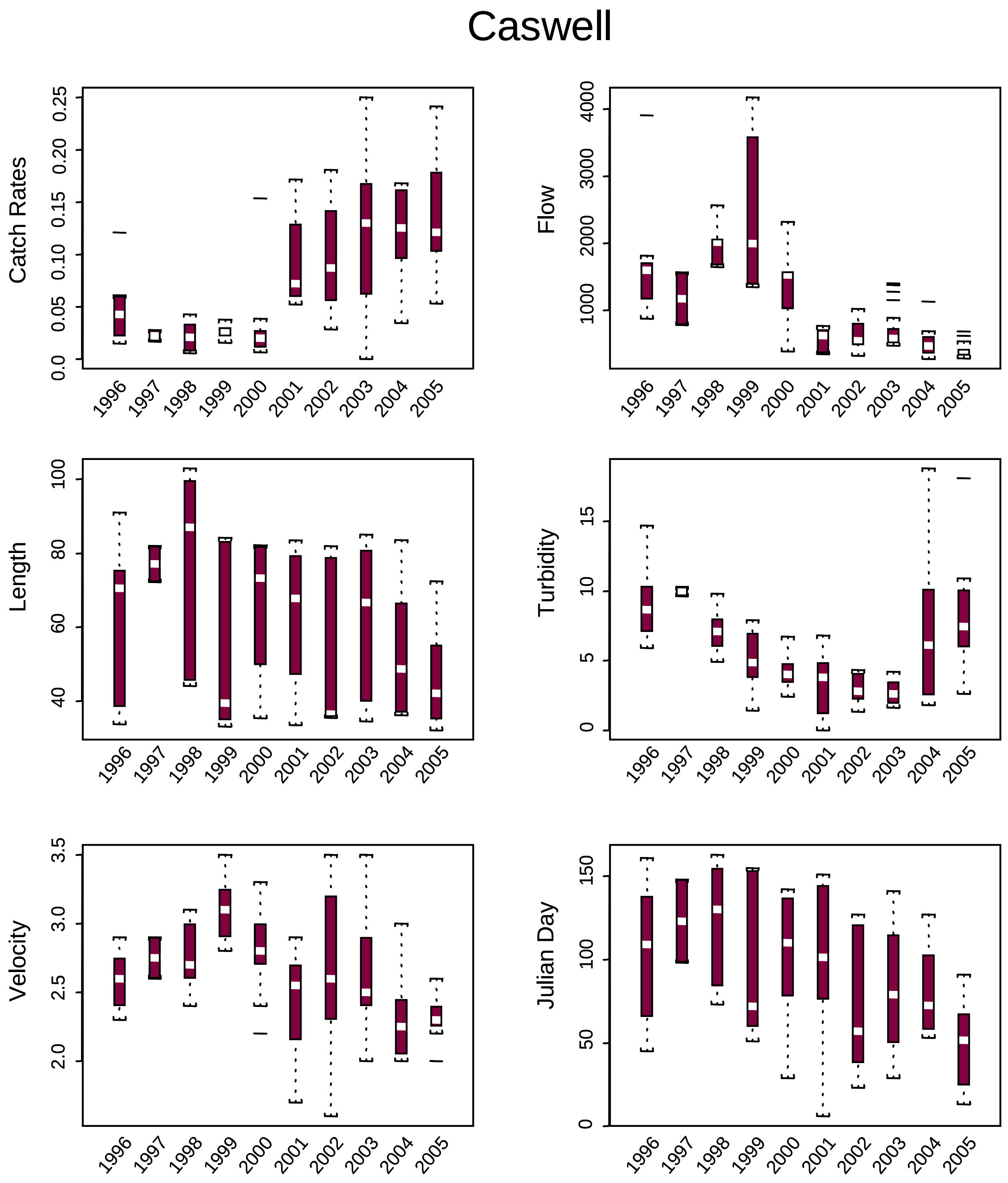


Figure 6. Box plots by year of catch rates and environmental conditions corresponding to the 122 day-specific mark-recapture releases at the Caswell trap location.

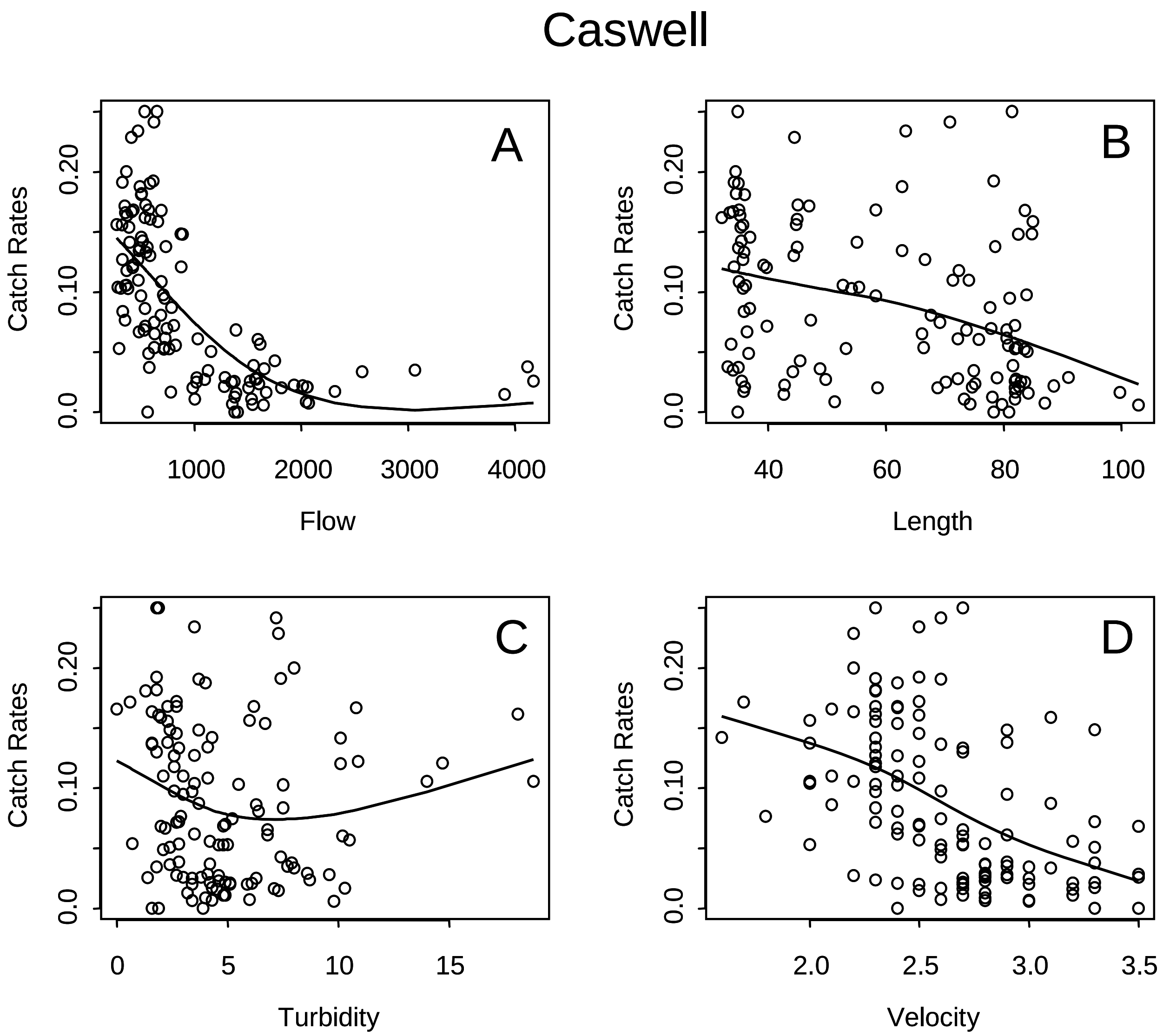


Figure 7. Catch rates as a function of flow, fish length, turbidity and velocity for the 122 day-specific mark-recapture releases at the Caswell trap location. Solid lines are exploratory fits of smoothing splines.

Table 7. **Regression coefficients and standard errors (SE) for the preferred logistic model fit to catch rates of 122 mark-recapture releases at the Caswell trap site. Note that the coefficient for 1996 is taken to be zero, whereas coefficients for 1997-2005 represent differences in logit(catch rate) relative to 1996.**

Variable	Coefficient	SE
Intercept	2.82	0.89
log(flow)	-0.68	0.13
Length	-0.01	0.00
Year=1997	-0.42	0.24
1998	-0.41	0.17
1999	-0.43	0.18
2000	-0.63	0.17
2001	0.03	0.18
2002	-0.11	0.19
2003	0.41	0.19
2004	-0.05	0.26
2005	-0.07	0.23

Table 8. **Analysis of deviance for the logistic model fit to catch rates of 122 mark-recapture releases at the Caswell trap site. Df = degrees of freedom.**

Variable	Df	Deviance	Residual df	Residual deviance	F Value	P-value
Intercept			121	4305.0		
log(flow)	1	2909.7	120	1395.3	344.3	<0.001
Length	1	225.9	119	1169.4	26.7	<0.001
Year	9	282.1	110	887.3	3.7	<0.001
Total	11	3417.7		887.3		

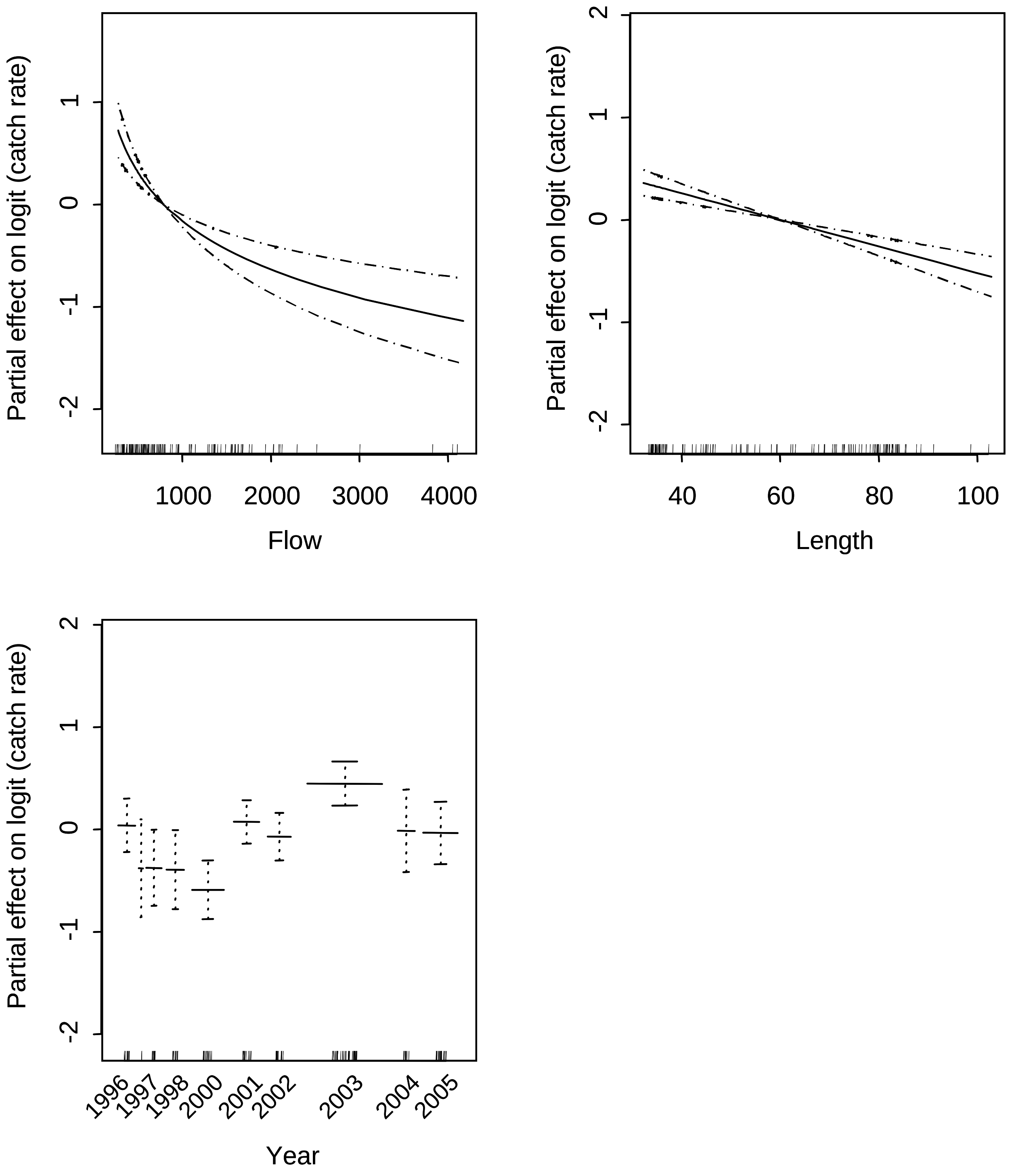


Figure 8. Partial effects of log(*flow*), *length*, and *year* on deviance residuals of logit(catch rate) for the Caswell trap site. Each plot has the same scale for the Y-axis so that the relative effect of each variable can be compared. Dashed lines indicate approximate 95% pointwise confidence intervals. Tick marks on the X-axis show locations of survival-rate estimates for a given variable.

Summary

Flow was the dominant variable affecting catch rates of juvenile Chinook salmon at both trap locations. Flow influences the proportion of the total water volume sampled by a trap, the proportion of the water column sampled below the trap (i.e., water depth), as well as the position of the trap relative to the gradient of water velocities and current patterns across the river channel. The logistic regressions strongly supported linear relationships between logit(q) and log(*flow*), which implies via equation (3) that catch rates were roughly proportional to the inverse of flow (i.e., $q \propto 1/(1+flow)$). This relationship is consistent with the simple mechanism that catch rates are proportional to the fraction of total water volume (V) sampled, that is, $q \propto 1/V$. Assuming roughly constant water velocities (changes in velocity were small in comparison to flow; e.g., Figure 4 and Figure 7), flow is a reasonable indicator of volume, in which case $q \propto 1/flow$. This does not necessarily imply that fish were randomly distributed throughout the cross section of the river channel or that catch rates were equivalent to the fraction of water volume sampled. Rather, the relationships simply indicate that as flows increased, catch rates declined in a manner consistent with anticipated declines in the fraction of water volume sampled by the traps. Raymond (1979) found similar relationships between river flow and recovery rates of marked juvenile salmon at Ice Harbor Dam on the Snake River.

The effects of other physical variables and fish length were minor in comparison to flow. The relationship for fish length at the Caswell site suggests that larger juveniles had lower catch rates because they were either distributed differently than smaller fish or could better avoid capture, though no such relationship was evident for the Oakdale trap. However, the significant relationships found for turbidity and temperature at Oakdale do not have clear interpretations. We expected catch rates to increase as turbidity increased, which would presumably reduce visibility and trap avoidance. Yet the opposite relationship was found, and given that it was relatively weak, we consider there to be a high likelihood that this turbidity relationship is spurious. The weak relationship for temperature, whereby catch rates declined as temperature increased, may reflect temperature effects on juvenile distribution in the water column, for example. Of course, this relationship may also be spurious. As discussed in the next section, we selected an alternative "preferred" model for the Oakdale site because of concern that the turbidity and temperature relationships were likely spurious.

There were two important sources of variability that were unrelated to the environmental variables we examined. First, there was significant between-year variability in mean catch rates at both trap sites. As noted earlier, such variability could arise from annual changes in channel morphology, bank vegetation, predator abundance, trap placement, and so on. The second type of variability was extra-binomial variation, which was quantified by the variance-scalar estimates of the "best" logistic models ($\hat{\phi}$ = 14.3 for Oakdale and $\hat{\phi}$ = 8.45 for Caswell). These values suggest that the residual deviance in catch rates was roughly 14 and 8 times greater for the Oakdale and Caswell sites, respectively, than expected due to binomial sampling error alone. This indicates that key explanatory variables were missing from the model (or were inadequately measured), or that juveniles do not behave according to the binomial model, which assumes each fish in a release group is independent and has the same probability of capture, q. Both possibilities likely hold. For example, measurements of flow taken at much finer spatial and temporal scales would likely improve predictions of catch rates. However, it is also likely that subtleties of movement behaviors (e.g., schooling) will consistently violate the assumption of independence even when physical conditions are essentially constant. Given the large sample sizes and high contrast in explanatory variables used in the analyses, the high levels of extra-binomial variation did not preclude reliable inferences of factors affecting catch rates. However, it is important that extra-binomial variation be accounted for when computing variances of abundance estimates of migrating juveniles; otherwise, variances may be grossly underestimated.

Preferred models

As noted above, the relationships found for turbidity and temperature at Oakdale do not have clear interpretations. The direction of the estimated effect of turbidity on catch rates is inconsistent with our prior expectations and previous findings (Demko et al. 2000). We therefore removed turbidity and re-fit the logistic model for Oakdale. For the new model, the effect of temperature was marginally significant (P = 0.048), and explained only 0.6% of the deviance (compared to 54% for *log(flow)* and 24% for *year*). We therefore considered the effect of temperature to be inconsequential if not spurious, and removed it from the model as well. Thus, the final "preferred" model for Oakdale included only *log(flow)* and *year*. The parameter estimates for this model are shown in Table 9.

The “preferred” model for Caswell was the “best” model described above. The preferred model for each site was used to estimate catch rates (trap efficiencies) in each year (equation 4), which were then used to compute the daily passage estimates (equation 5) discussed below. Estimates of daily trap efficiencies from the preferred models are shown for Oakdale (Figure 9) and Caswell (Figure 10) for 1996-2005. For comparison, trap efficiencies are also shown for models without the variable *year* (i.e., models for which the same flow or flow/size relationship is assumed to exist across all years).

Table 9. Regression coefficients and standard errors (SE) for the “preferred” logistic model fit to catch rates of 154 mark-recapture releases at the Oakdale trap site. Note that the coefficient for 1996 is taken to be zero, whereas coefficients for 1998-2005 represent differences in logit(catch rate) relative to 1996.

Variable	Coefficient	SE
Intercept	13.76	1.05
log(flow)	-2.17	0.15
Year = 1998	-0.01	0.36
1999	-1.96	0.42
2000	-2.37	0.30
2001	-1.72	0.21
2002	-2.36	0.26
2003	-3.02	0.27
2004	-2.51	0.25
2005	-2.73	0.28

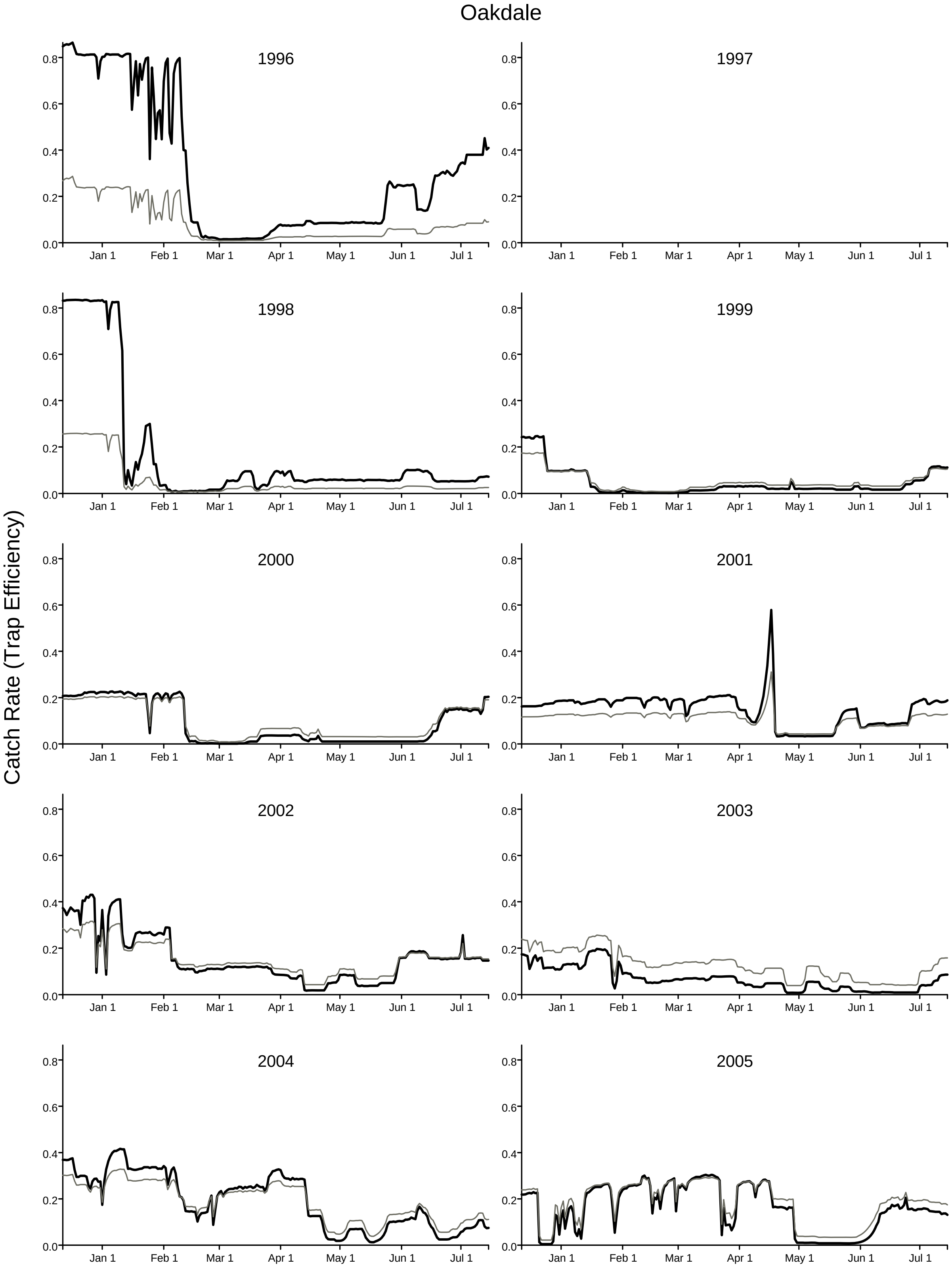


Figure 9. Estimates of trap efficiency for the Oakdale trap site based on the "preferred" logistic model (bold line) and the model without *year* or year-specific effects (gray line).

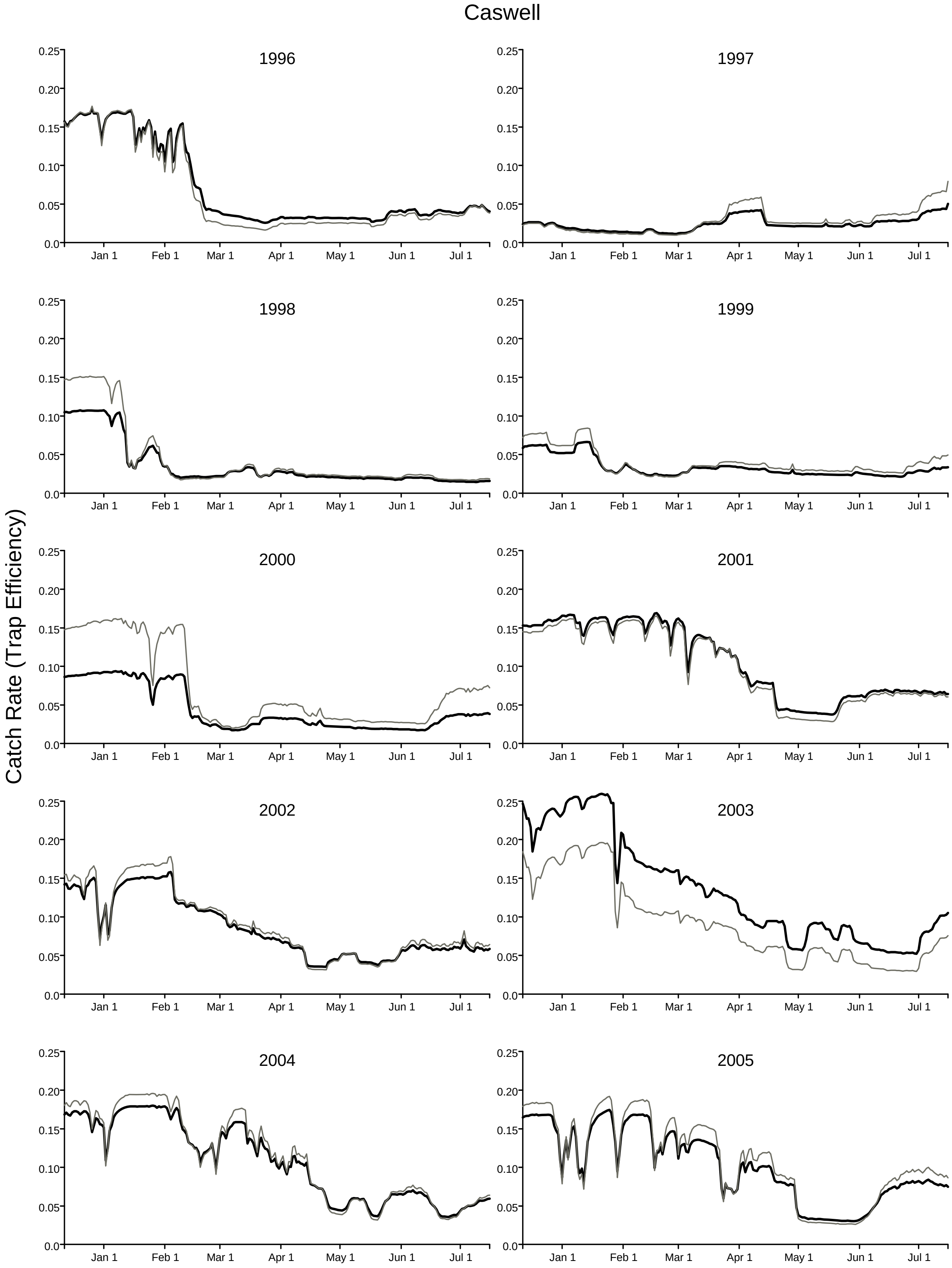


Figure 10. Estimates of trap efficiency for the Caswell trap site based on the "preferred" logistic model (bold line) and the model without *year* or year-specific effects (gray line).

Abundance

Estimates of the total abundance of juvenile Chinook salmon passing the Oakdale and Caswell trap sites varied widely across years (Table 10; Figure 11). For Oakdale, total passage estimates ranged from a low of 279,444 in 1996 to a high of 5,433,580 in 1999 (Table 10). For all other years, passage estimates at Oakdale ranged from roughly 1.1 million to 4.2 million juvenile Chinook salmon. At Caswell, total passage estimates ranged from 67,513 in 1996 to 2,140,075 in 2000. Note that the passage estimate for 1997 is incomplete; sampling at Caswell in 1997 did not begin until March 19 (Table 4), and thus most of the potential fry and early parr migration was missed. As expected, the estimated passage at Caswell was less than at Oakdale in all years. However, the Caswell and Oakdale estimates were very similar in 1998 (Table 10), which may indicate that one or both estimates were considerably biased for that year (discussed below).

The estimated precision (an indicator of reliability) of the passage estimates also varied across years (Table 10; Figure 11). Estimates of standard error (SE) provide an absolute measure of precision, while coefficients of variation (CV = SE / Passage Estimate) provide a relative measure of precision. In general, standard errors were roughly proportional to the passage estimates at a given site, and hence, estimates of CV were roughly constant across years (Table 10). As a result, large passage estimates had much wider confidence intervals than low passage estimates (Figure 11). In addition, estimates for Caswell were more precise than those for Oakdale. The CV of Caswell estimates ranged from 12% to 17%, whereas the CV of Oakdale estimates ranged from 18% to 26% (Table 10). Caswell estimates were more precise because the logistic model for catch rates (trap efficiencies) at Caswell provided a better fit to the mark-recapture data than for Oakdale. Given the logistic difficulties and relatively low cost of these sampling programs, we consider the precision of Caswell estimates as excellent and those for Oakdale as quite good.

Table 10. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites. SE = standard error of the estimate. CV = coefficient of variation of the estimate, where % CV = (SE / Total Passage) * 100.

	Oakdale			Caswell		
Year	Total Passage	SE	CV	Total Passage	SE	CV
1996	279,144	51,386	18%	67,513	7,835	12%
1997	--	--	--	89,160[a]	10,753	12%
1998	1,259,251	325,990	26%	1,193,848	198,309	17%
1999	5,433,580	1,318,235	24%	1,543,866	251,520	16%
2000	4,214,270	797,072	19%	2,140,075	251,097	12%
2001	1,154,287	211,855	18%	164,922	17,632	11%
2002	1,299,477	249,942	19%	102,535	12,361	12%
2003	1,701,422	332,330	20%	131,575[b]	22,807	17%
2004	2,438,065	525,285	22%	412,051	71,337	17%
2005	1,333,744	287,191	22%	260,061	38,679	15%

[a] The 1997 estimate for Caswell is incomplete because sampling began late in the season (March 19) and missed most of the potential fry and early parr migration.

[b] Estimates of missing counts were not made for Caswell between Jan 22-28, 2003. Such estimates would be unrealistically high due to a large pulse flow event and corresponding large outmigration that occurred on Jan 29-30.

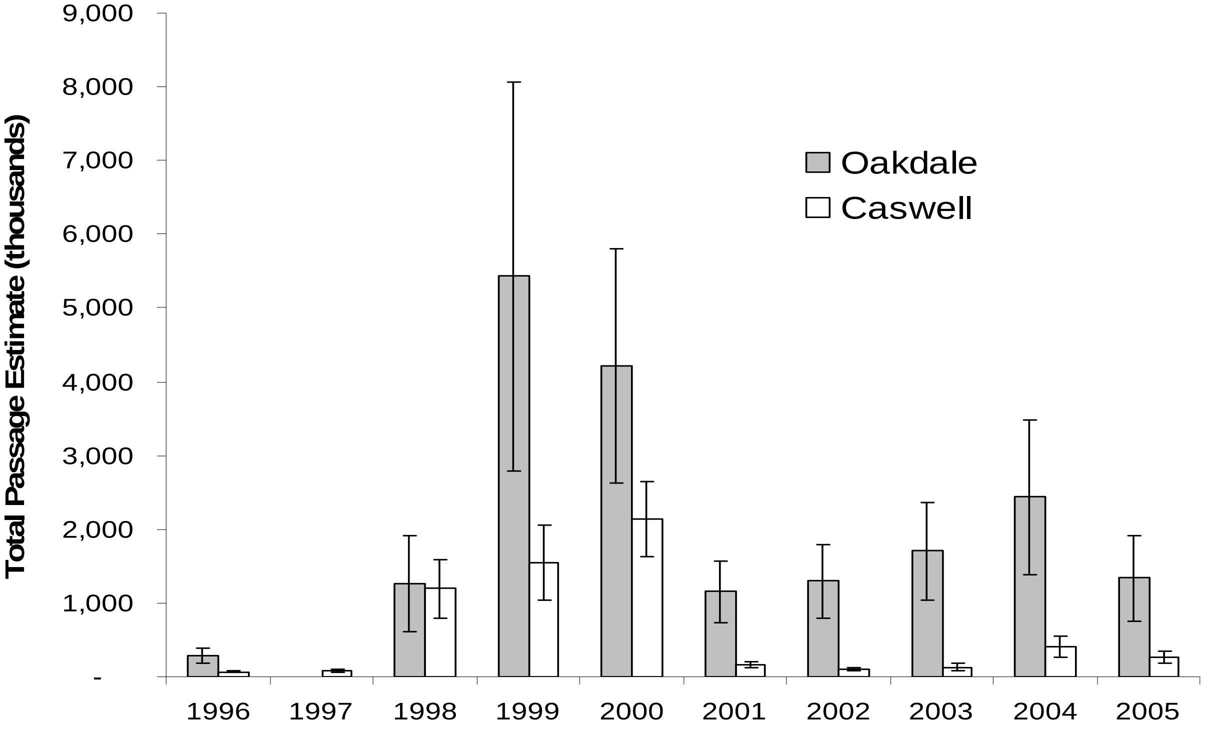


Figure 11. Total passage estimates by year at the Oakdale and Caswell trap sites. Error bars denote approximate 95% confidence intervals. No trapping occurred at Oakdale in 1997.

Cumulative abundance

Patterns of cumulative daily abundance of juvenile Chinook salmon passing the Oakdale and Caswell sites showed marked differences across years and between sites. Dates for percentiles of cumulative passage are presented in Table 11, and cumulative trends are compared across years in Figure 12. Trends by year with 95% confidence intervals are shown for Oakdale and Caswell in Figure 13 and Figure 14, respectively.

At Oakdale, the predominant pattern featured a rapid and large migration of fry during late January and/or through February, followed by a protracted (lengthy) migration of lower abundances of parr and smolt from March though May (Figure 12 and Figure 13). Clear examples of this pattern included years with relatively high flows during fry migration (e.g., 1998 and 1999) as well as years with predominantly low flows (e.g., 2004 and 2005). Consequently, for 1998-2005, the mid-points (50th percentile) of cumulative passage occurred early, ranging from January 29 in 2005 to February 26 in 2002 (Table 11). In fact, an estimated 90% of the total abundance passed Oakdale by mid-March in four of these years (1999, 2000, 2004 and 2005) (Table 11). In contrast, migration at Oakdale appeared to be much more delayed in 1996 (Figure 12). The mid-point of migration in 1996 was estimated to occur on April 19, roughly two months later than in the other years (Table 11).

Table 11. Cumulative percentiles of total estimated passage of juvenile Chinook salmon in the Stanislaus River at the Oakdale and Caswell trap sites, 1996-2005. Duration indicates the number of days between the 10th and 90th percentiles.

	Oakdale				Caswell			
Year	10%	50%	90%	Duration	10%	50%	90%	Duration
1996	13-Feb	19-Apr	10-May	86	22-Feb	1-May	22-May	89
1997	--	--	--	--	26-Mar[a]	26-Apr[a]	26-May[a]	61[a]
1998	2-Feb	11-Feb	22-Apr	79	5-Feb	15-Feb	1-May	85
1999	28-Jan	16-Feb	9-Mar	40	25-Jan	12-Feb	14-Mar	48
2000	25-Jan	15-Feb	2-Mar	36	14-Feb	16-Feb	31-Mar	45
2001	27-Jan	13-Feb	4-May	97	2-Apr	1-May	19-May	47
2002	4-Feb	26-Feb	17-May	102	23-Mar	1-May	19-May	57
2003	28-Jan	8-Feb	8-Apr	70	29-Jan	24-Mar	9-May	100
2004	5-Feb	19-Feb	27-Feb	22	27-Feb	3-Mar	19-Apr	51
2005	13-Jan	29-Jan	1-Mar	47	30-Jan	21-Feb	4-May	94

[a] The 1997 estimate for Caswell is not comparable with other years because sampling began late in the season (March 19) and missed most of the potential fry and early parr migration.

Patterns of cumulative abundance for Caswell showed greater variety across years (Figure 12). Similar to Oakdale, passage at Caswell featured rapid and large migrations of fry followed by protracted and lower migrations of parr and smolt in 1998 and 1999 (years with moderate flow during fry migration) as well as 2004 and 2005 (low-flow years) (Figure 12 and Figure 14). In contrast to Oakdale, fry abundances passing Caswell in 2001 and 2002 were very limited, and hence, cumulative abundances in these years increased slowly through February and March before increasing rapidly in April and early May. As discussed below, this implies that fry survival was extremely low in 2001 and 2002, although some extended rearing of fry may have also occurred between the trap sites.

The patterns of cumulative abundance were quite consistent in showing later juvenile migrations at Caswell than at Oakdale (Table 11). For example, in all years, the 90th percentile of cumulative migration at Caswell occurred after the 90th percentile at Oakdale. Similarly, the estimated 10th and 50th percentiles at Caswell occurred after those at Oakdale in all years except 1999, for which the Caswell estimates preceded the Oakdale estimates by a few days (Table 11). This general consistency is reassuring because it suggests that daily estimates of passage abundance at each trap site are reasonably reflective of actual passages. Of course, these estimates contain considerable measurement error (Figure 13 and Figure 14), but much of this error relates to the absolute value of the passage estimates. In contrast, comparisons of relative passage estimates across days for a given year and trap site are subject to much less error.

The general durations of juvenile migration also showed interesting patterns across years (Table 11). Here, we used the number of days between the 10th and 90th percentiles of cumulative passage as an index of duration. For years 1996-2000, which had moderate to high flows throughout the migration period, the Oakdale and Caswell cumulative distributions were similar, with slightly longer migration durations (three to 11 days) at Caswell than at Oakdale (Table 11). However, two patterns were evident for 2001-2005, which had generally low flows during the migration period. For 2001 and 2002, Caswell durations were roughly 50 days shorter than for Oakdale (Table 11) because of the lack of significant fry passage at Caswell (Figure 14). In contrast, in 2003-2005 the durations at Caswell were roughly 30 days longer than at Oakdale. As discussed later, numerous fry passed Caswell in these years, but subsequent migrations of parr and smolt contributed more greatly to the cumulative abundance at Caswell than at Oakdale.

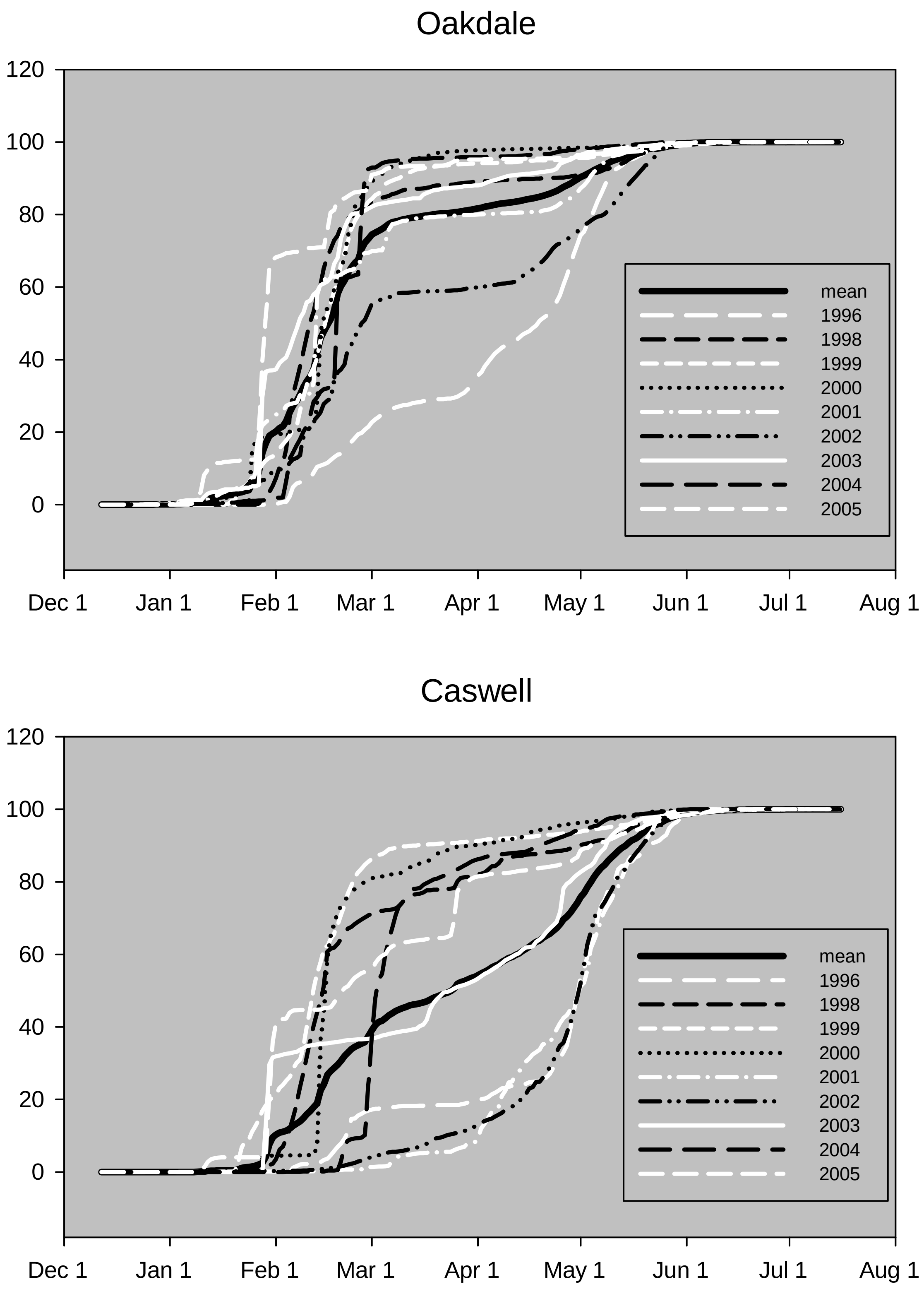


Figure 12. Cumulative percentage of the estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites, 1996-2005. Data for 1997 were excluded because no trapping occurred at Oakdale and trapping at Caswell began late in the season.

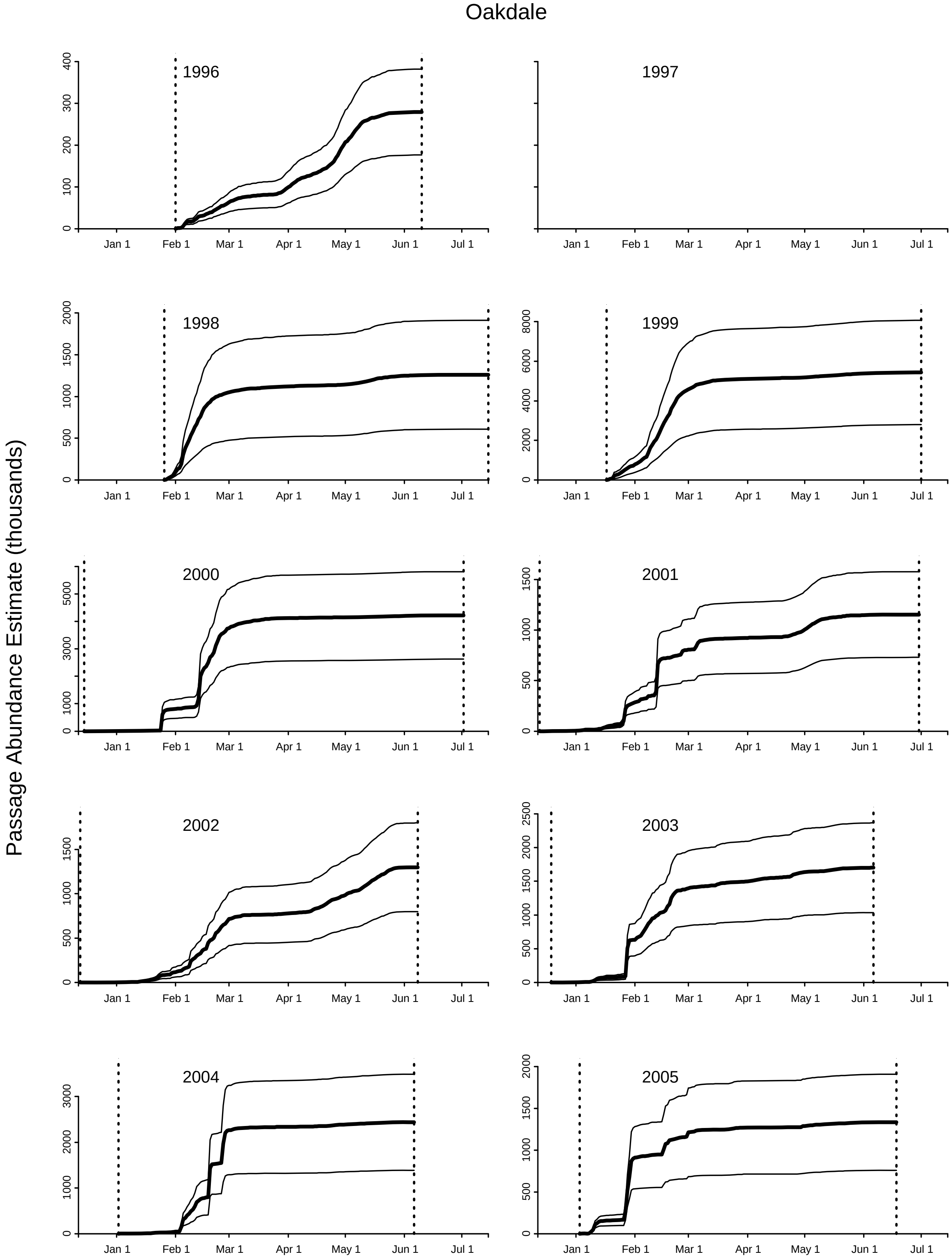


Figure 13. Cumulative passage estimates (bold line) by year at the Oakdale trap site. Thin lines denote approximate 95% confidence intervals. Dashed vertical lines indicate start and end dates for trapping.

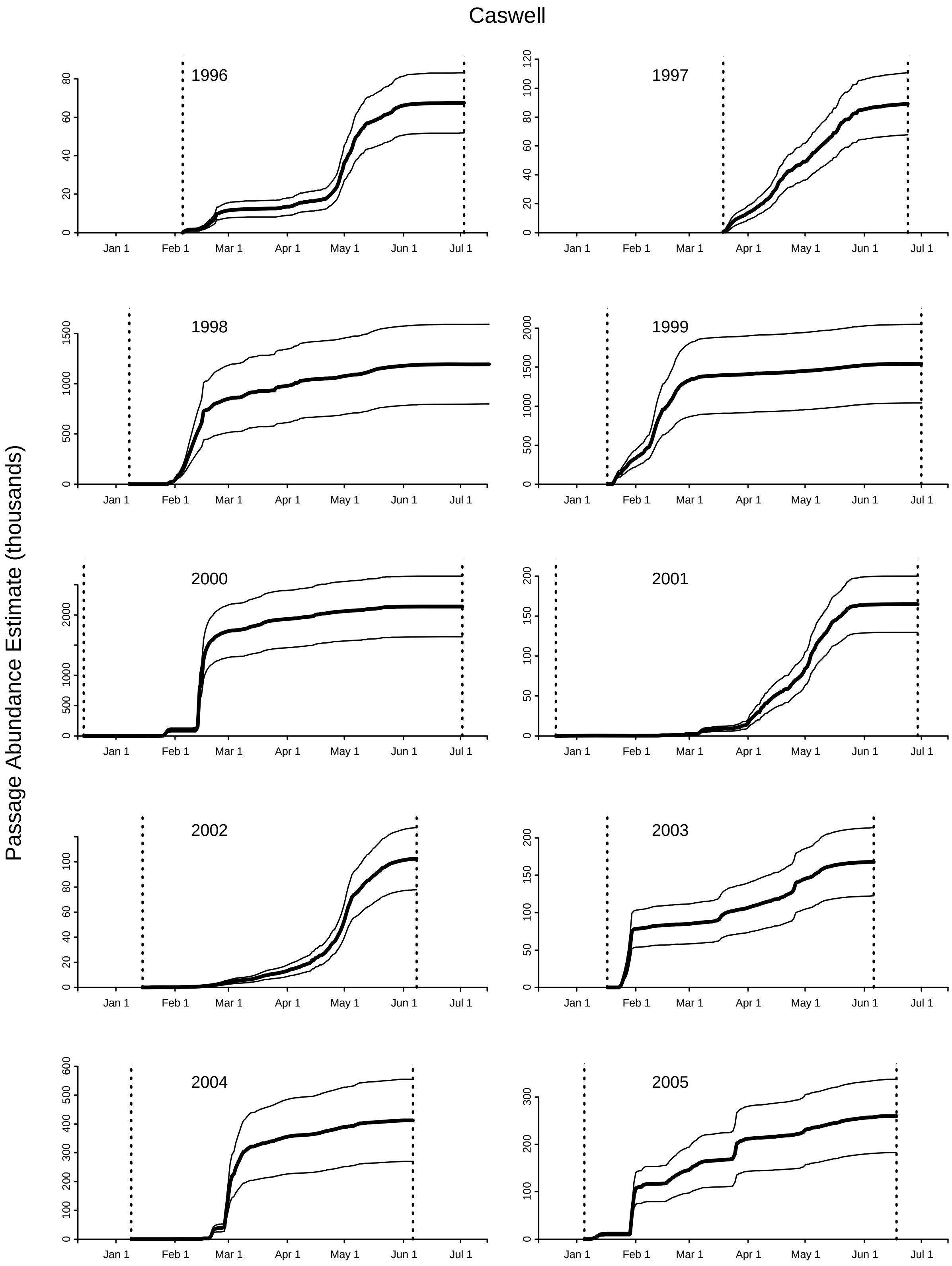


Figure 14. Cumulative passage estimates (bold line) by year at the Caswell trap site. Thin lines denote approximate 95% confidence intervals. Dashed vertical lines indicate start and end dates for trapping.

Abundance by life stage and length class

Estimates of total abundance by life stage show that in most years juveniles passing Oakdale are predominantly fry (Table 12). Estimates of fry (< 45 mm) passage ranged from a low of 76 thousand in 1996 to a high of 4.9 million in 1999 (Table 12). Abundances of parr (45-80 mm) and smolt (> 80 mm) were much less variable. Parr estimates ranged from 44 thousand in 1996 to 405 thousand in 1999, while smolt estimates ranged from 28 thousand in 2004 to 222 thousand in 2002. In 1996, fry comprised 27% of all juveniles passing Oakdale, which was by far the lowest fry percentage across years (Table 12; Figure 15). The next lowest fry percentage was 55.4% in 2002. Across the remaining seven years, fry comprised between 75.4% and 91.2% of the total passage at Oakdale (Table 12; Figure 15). By comparison, percentages of parr at Oakdale ranged from 6.2% in 2005 to 27.5% in 2002, while smolt percentages ranged from just 1.1% in 2004 to 57.1% in 1996.

In all years, lower proportions of fry were observed at Caswell than at Oakdale (Table 13; Figure 15). Reductions in fry percentages were most notable for 2001 and 2002. Estimates of fry passage at Caswell for 2001 and 2002 were only eight thousand and five thousand, respectively, comprising just 4.6% and 5.3% of the total passage at Caswell (Table 13). Fry percentages at Caswell were also much lower than at Oakdale in 2003 and 2004, and to a lesser extent, in 2005 (e.g., Figure 15). In contrast, the proportion of fry at Caswell remained high (e.g., > 70%) in years that had moderate to high flows during early migration (e.g., 1998-2000) (Figure 15).

Table 12. Passage estimates (in thousands) for juvenile Chinook salmon by life stage at the Oakdale trap site.

	Passage Estimate (thousands)			Percent (%) of Total		
Year	Fry	Parr	Smolt	Fry	Parr	Smolt
1996	76	44	159	27.2	15.7	57.1
1997	--	--	--	--	--	--
1998	1,046	113	100	83.1	9.0	7.9
1999	4,917	405	112	90.5	7.5	2.1
2000	3,756	399	59	89.1	9.5	1.4
2001	870	229	55	75.4	19.9	4.8
2002	720	358	222	55.4	27.5	17.1
2003	1,399	251	52	82.2	14.7	3.1
2004	2,164	246	28	88.8	10.1	1.1
2005	1,217	83	34	91.2	6.2	2.6

Table 13. Passage estimates (in thousands) for juvenile Chinook salmon by life stage at the Caswell trap site.

	Passage Estimate (thousands)			Percent (%) of Total		
Year	**Fry**	**Parr**	**Smolt**	**Fry**	**Parr**	**Smolt**
1996	12	4	51	18.1	6.5	75.4
1997	0.2[a]	26	63	0.2[a]	29.6	70.2
1998	848	219	127	71.0	18.3	10.6
1999	1,376	96	73	89.1	6.2	4.7
2000	1,655	421	64	77.4	19.7	3.0
2001	8	122	35	4.6	74.2	21.2
2002	5	52	45	5.3	51.0	43.8
2003	48	47	36	36.5	35.9	27.6
2004	272	121	18	66.1	29.4	4.5
2005	126	95	39	48.3	36.6	15.1

[a] Sampling at Caswell in 1997 began late in the season and hence most fry and early parr were not sampled.

As discussed below, the reductions in fry percentages imply that fry experience higher mortality rates than parr and smolts while migrating between the Oakdale and Caswell sites. A similar relationship might be expected between parr and smolts, with fewer parr at Caswell either due to higher mortality or extensive rearing and growth of parr prior to reaching Caswell. Indeed, there a substantially greater smolt to parr ratio at Caswell in some years. For example, in 1996, the smolt-to-parr ratio at Oakdale was 3.6 (= 159 thousand / 44 thousand) (Table 12). However, the smolt-to-parr ratio at Caswell was 11.6, a more than 3-fold increase in abundance of smolts relative to parr. Similar increases occurred in 1999 and 2003. In most other years, the increase in smolt versus parr abundance at Caswell was modest (up to 1.4 times that at Oakdale), while in 1998 the smolt-to-parr ratio at Caswell was roughly one-third lower than at Oakdale.

More detailed summaries of passage estimates by length class are provided for all life stages in Figure 16 and Figure 17, and for only parr and smolts in Figure 18 and Figure 19. Note the consistent pattern of fry predominance at Oakdale (Figure 16), but the distinct lack of fry at Caswell in 2001 and 2002 (Figure 17). For parr and smolt, large differences in the relative abundances of length classes were evident across years. For example, compared to years 1996, 2001, and 2002, much higher proportions of small and medium-sized parr passed both Oakdale and Caswell in 1998, 2000, 2004, and 2005 (Figure 18; Figure 19). Also, relative abundances of small and medium-sized parr were much lower at Caswell than at Oakdale in 1999 and 2003, which is consistent with the increasing smolt-to-parr ratios noted above.

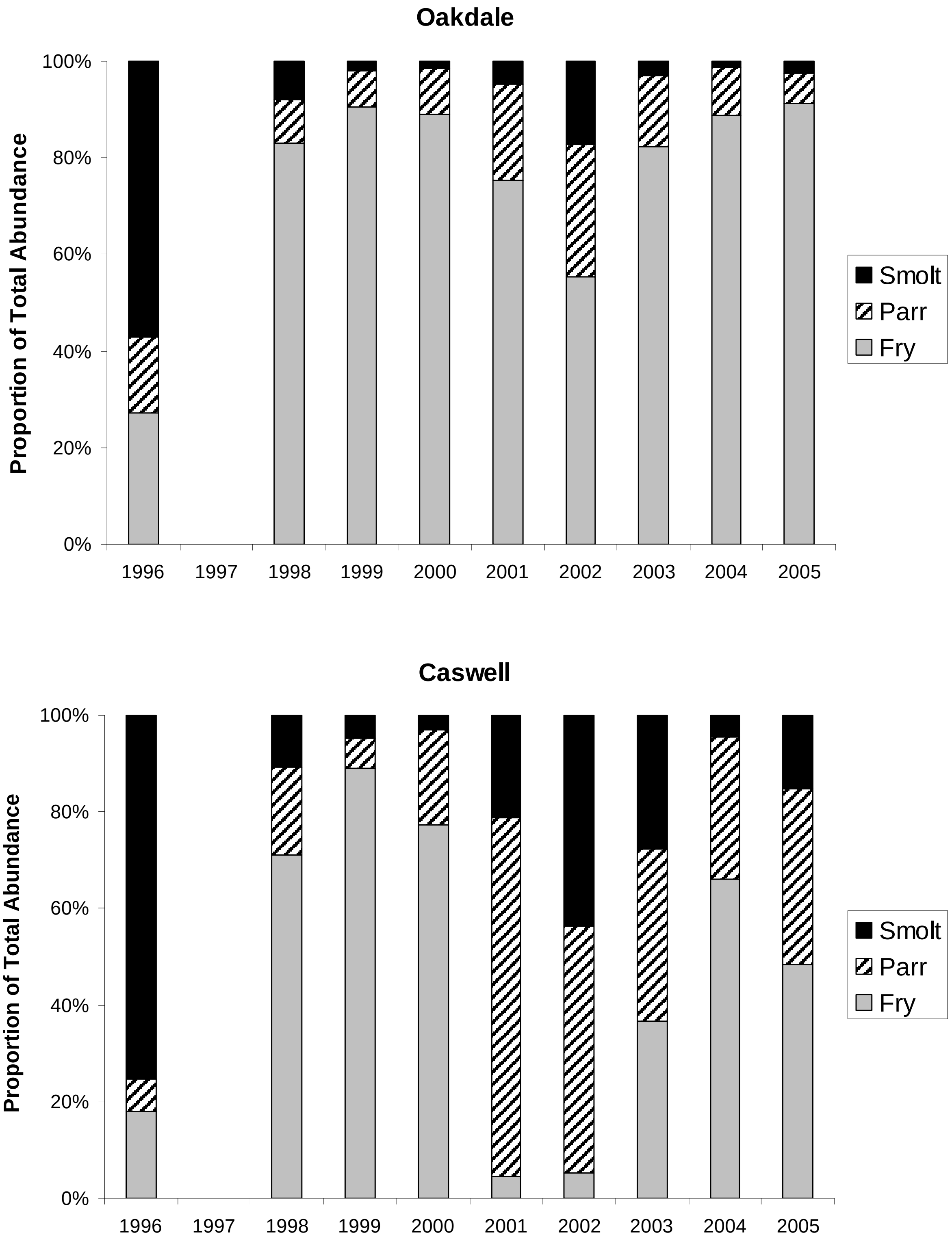


Figure 15. Estimated proportions (%) of total annual passage comprised of fry, parr, and smolt at the Oakdale trap site (top panel) and Caswell trap site (bottom panel). Data for 1997 were excluded because no trapping occurred at Oakdale and trapping at Caswell began late in the season.

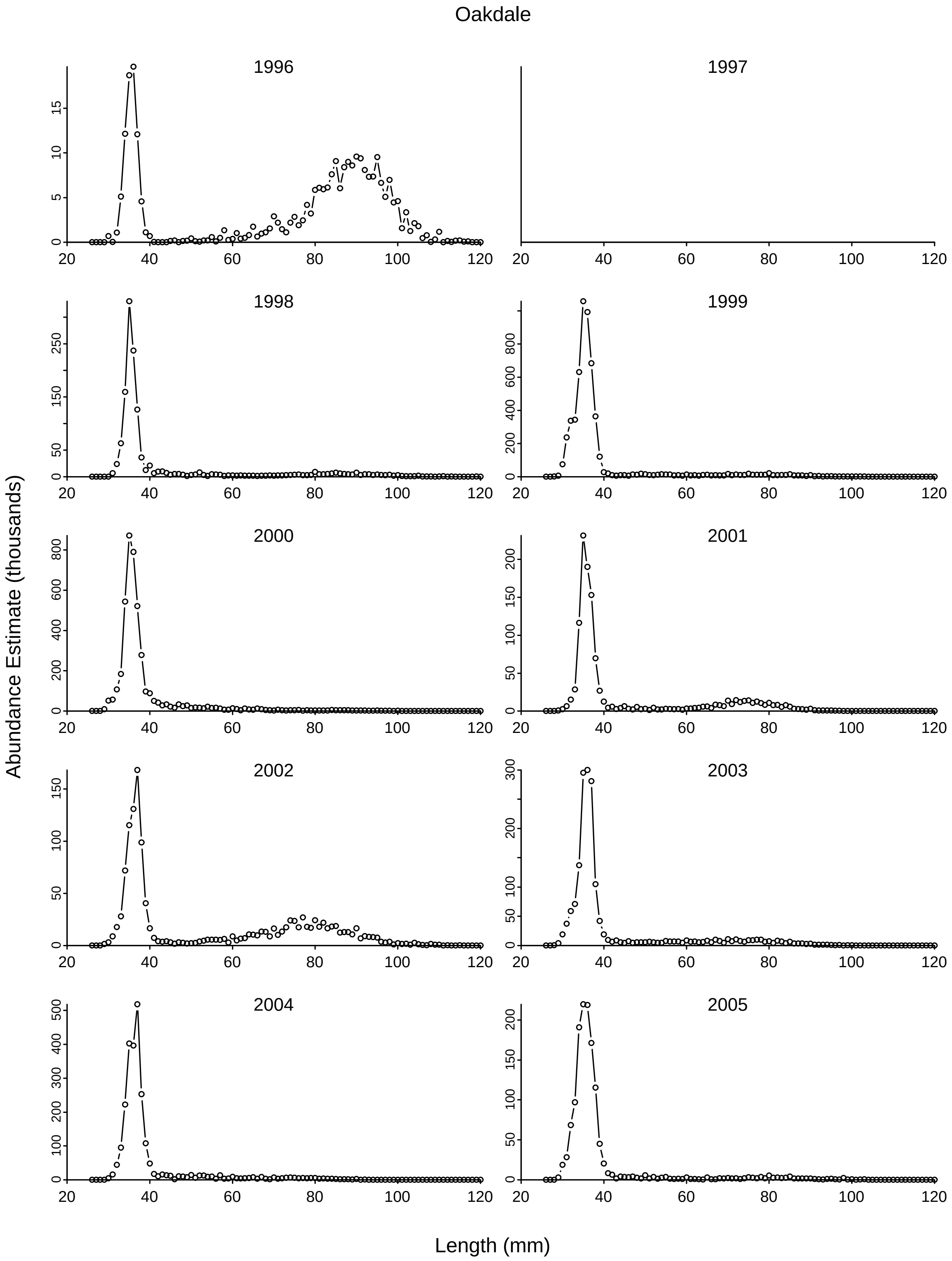


Figure 16. Total abundance estimates by length class (mm) of juvenile Chinook salmon passing the Oakdale trap site. No trapping occurred at Oakdale in 1997.

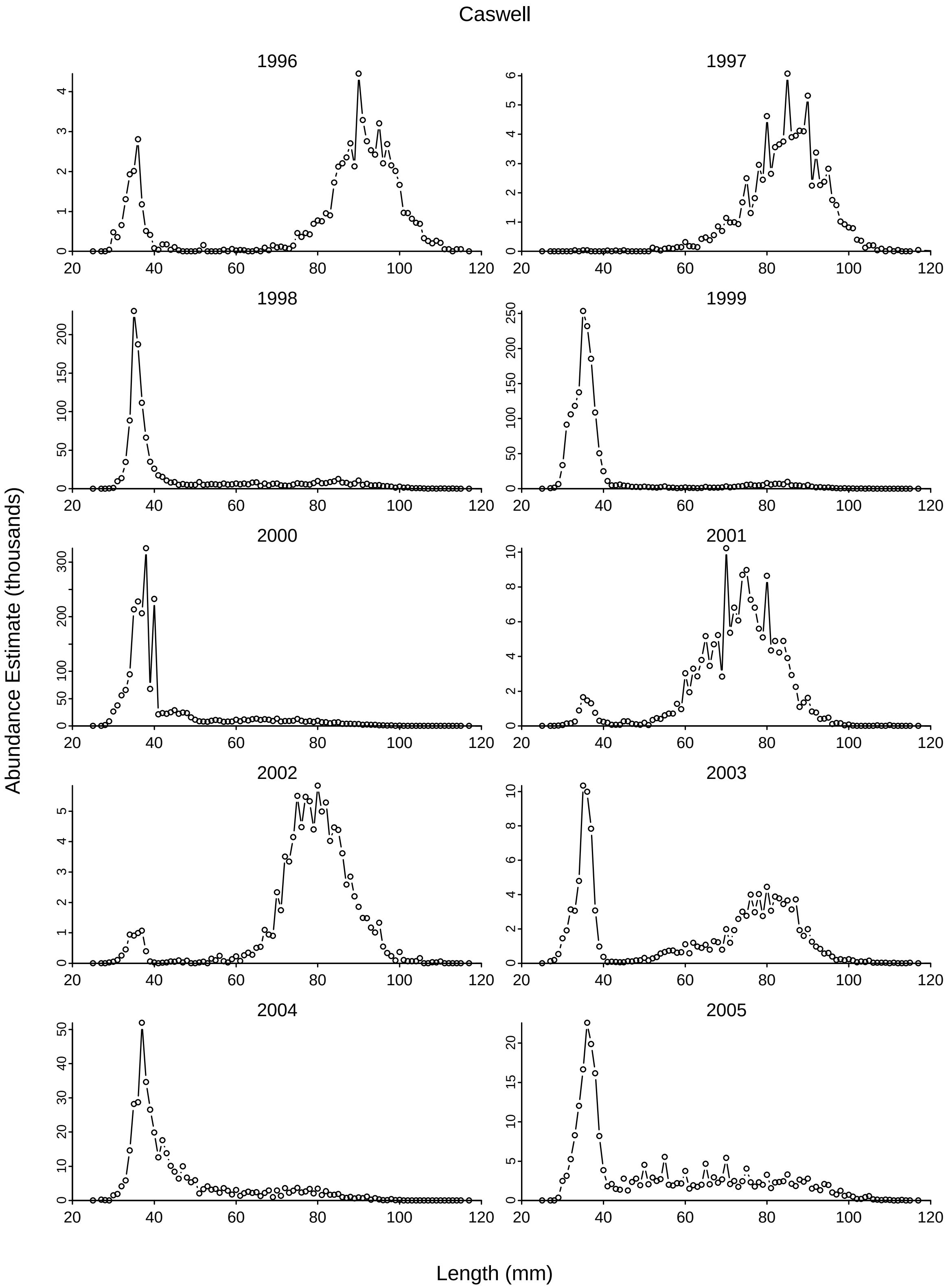


Figure 17. Total abundance estimates by length class (mm) of juvenile Chinook salmon passing the Caswell trap site. Trapping began late in 1997, missing the fry and early parr migration.

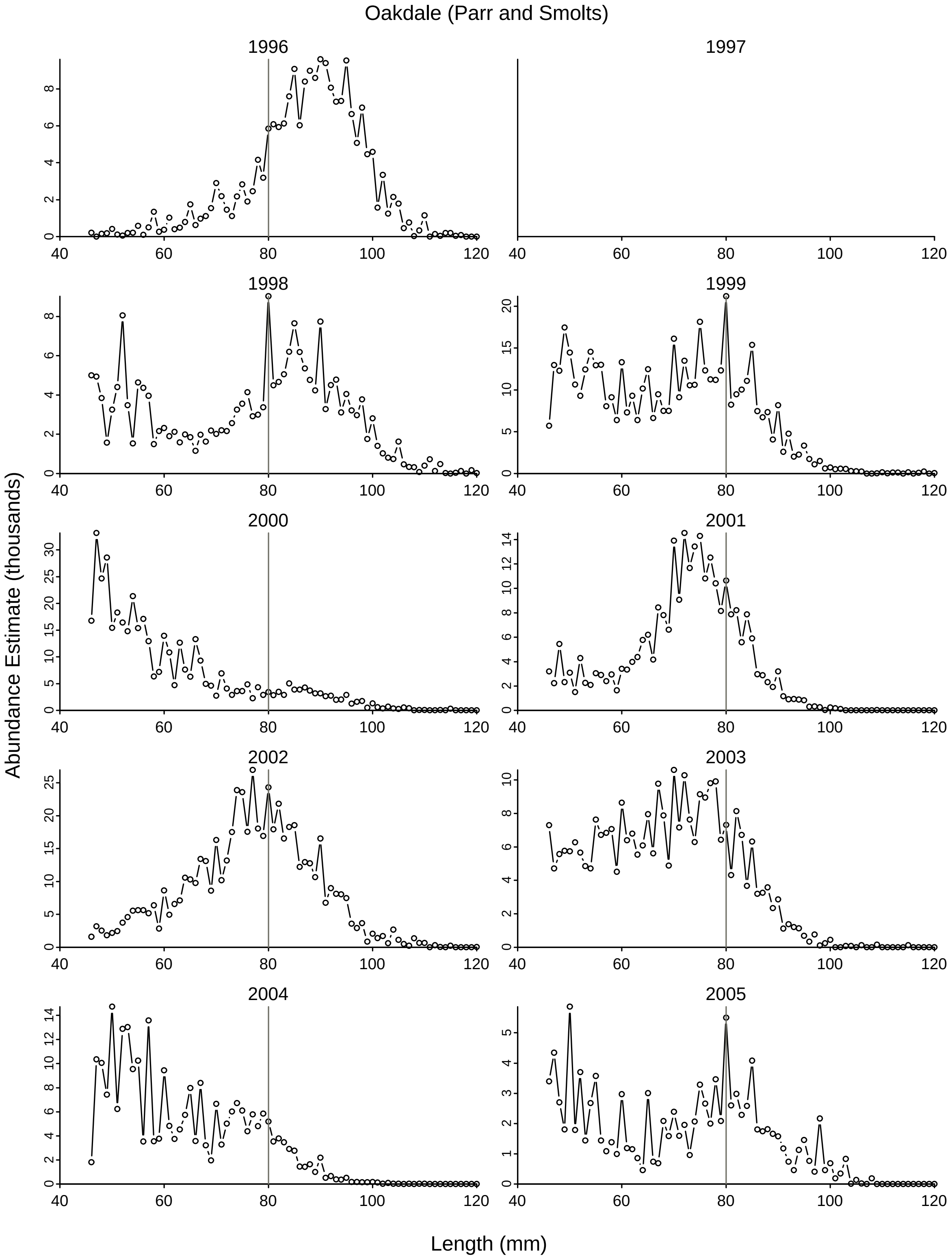


Figure 18. Total abundance estimates by length class (mm) of parr and smolts (> 80 mm; vertical line) passing the Oakdale trap site. No trapping occurred at Oakdale in 1997.

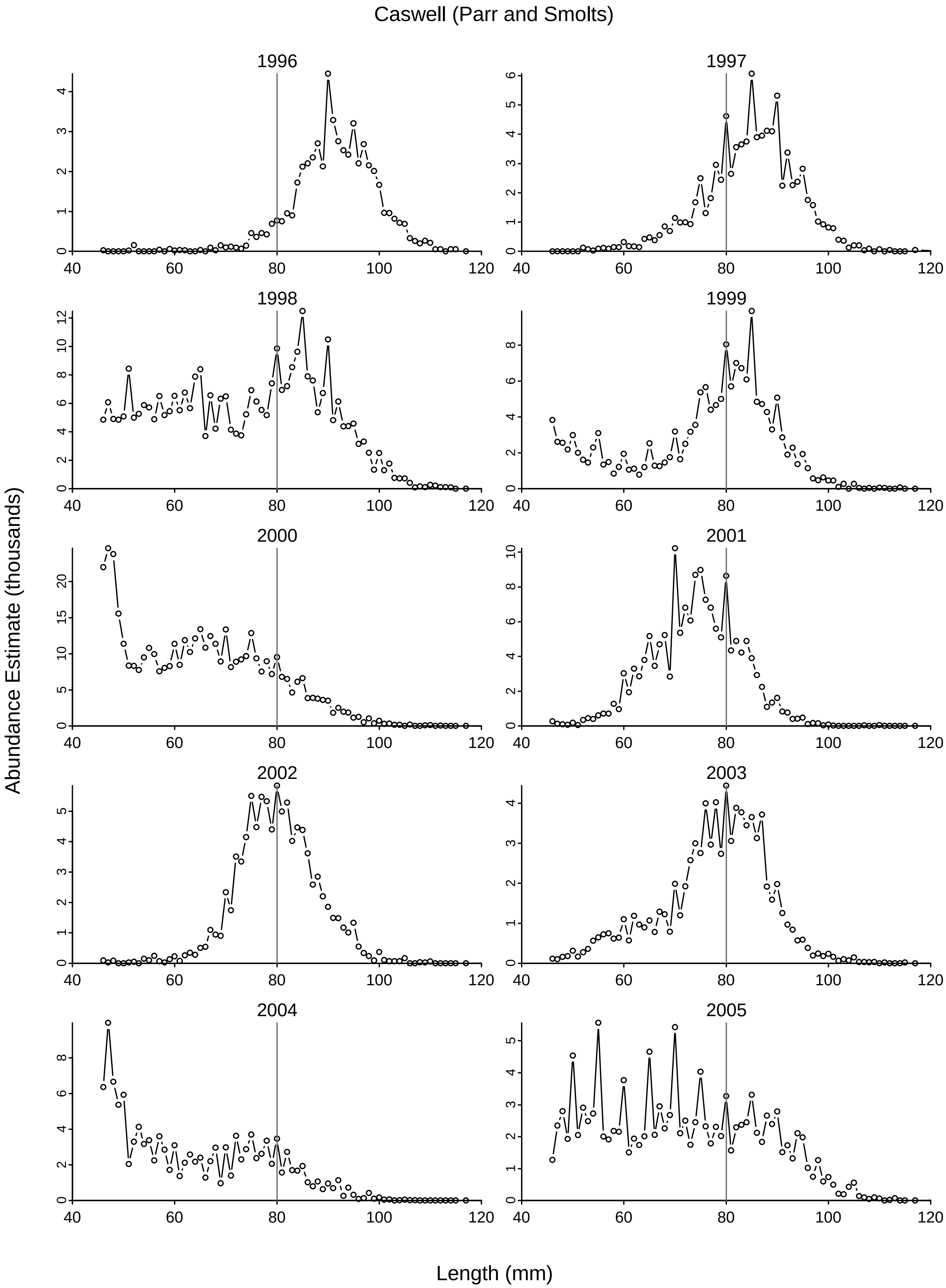


Figure 19. Total abundance estimates by length class (mm) of parr and smolts (> 80 mm; vertical line) passing the Caswell trap site. Trapping began late in 1997, missing the fry and early parr migration.

Survival

Estimates of annual survival rates for all juvenile Chinook salmon migrating between the Oakdale and Caswell trap sites ranged from lows of 0.08 (8% survival) in 2002 and 2003 to a high of 0.95 (95% survival) in 1998 (Table 14; Figure 20). Standard errors (SE) were roughly proportional to the magnitude of the survival-rate estimates, so confidence intervals increased dramatically as estimates increased (Figure 20). For example, the 95% confidence interval for the 1998 survival estimate (0.95) was 0.38 to 1.52. Clearly, survival cannot be greater than one, but this illustrates the high uncertainty associated with high estimates of survival. Survival estimates were less than 0.2 in years that had generally low flows during early migration (2001-2005), but ranged from 0.28 to 0.95 for years with moderate to high flows (1996-2000) (Table 14).

Table 14. Annual survival-rate estimates of all juvenile Chinook salmon migrating between the Oakdale and Caswell trap sites. Also shown are abundance ratios by life stage of juveniles passing Caswell versus Oakdale. SE = standard error of the survival estimate.

	Total Survival		Abundance Ratio		
Year	Estimate	SE	Fry	Parr	Smolt
1996	0.24	0.05	0.16	0.10	0.32
1997	--	--	--	--	--
1998	0.95	0.29	0.81	1.93	1.27
1999	0.28	0.08	0.28	0.24	0.65
2000	0.51	0.11	0.44	1.05	1.09
2001	0.14	0.03	0.01	0.53	0.64
2002	0.08	0.02	0.01	0.15	0.20
2003	0.08	0.02	0.03	0.19	0.69
2004	0.17	0.05	0.13	0.49	0.66
2005	0.19	0.05	0.10	1.15	1.14

Patterns in abundance ratios by life stage (Table 14) were consistent with hypotheses that smaller juveniles experience higher mortality rates, but may also rear and grow extensively between the trap sites. Note that these abundance ratios are analogous but not equivalent to survival rates. If all juveniles passing the Oakdale trap migrated rapidly to the Caswell site (e.g., passing Caswell a few days after Oakdale), then they would have roughly the same size and life-stage category at each site. In this case, the ratio of Caswell:Oadkale abundance would be a reasonable estimate of survival. However, if numerous fry and parr rear extensively between the trap sites and thereby reach parr or smolt size classes before passing Caswell, we would expect

Caswell:Oadkale abundance ratios to increase for parr and smolts, and possibly approach or exceed values of one.

Evidence of poor fry survival was observed in 2001-2005, for which fry abundance ratios ranged from 0.01 to 0.13 (Table 14; Figure 21). For 1996-2000, fry abundance ratios ranged from 0.16 to 0.81, implying moderate to high fry survival. Differences in parr and smolt ratios were less pronounced across years (Figure 21). The lowest ratios for both parr and smolts were observed in 1996 (0.10 for parr and 0.32 for smolts) and 2002 (0.15 for parr and 0.20 for smolts). A key difference between these years, however, was that 2002 had a much higher proportion of fry passing Oakdale. As a result, the overall survival rate was considerably lower in 2002 than in 1996 (Table 14). For most other years, parr and smolt abundance ratios were moderate to high. Values for both life stages exceeded one in 1998, 2000, and 2005 (Figure 21). Such high ratios suggest that numerous juveniles may have reared between trap sites in these years.

We attempted to gain further insight into relative survival and rearing between the trap sites by examining abundance ratios across more discrete length groups (Figure 22) and time periods (Figure 23). In most years, the Caswell:Oakdale abundance ratios generally increased as the length of migrating juveniles increased (Figure 22). This was especially evident in 1996 and 2001-2005. Such patterns indicate that larger juveniles have higher survival rates. However, there were also several years for which abundance ratios were very high for intermediate length groups. For example, in 2000, ratios peaked for the 70 mm (i.e, 70-74 mm fish) and 75 mm length groups, and were greater than one for all groups ranging from 60 mm to 85 mm (Figure 22). A similar pattern was observed in 2005 for 55-75 mm groups and 85-95 mm groups. These patterns strongly suggest that considerable juvenile rearing occurred between trap sites, which resulted in additional contributions of larger parr and possibly smolts at the Caswell site. This premise was also strongly supported by patterns in abundance ratios across Julian weeks (Figure 23). In most years, ratios were quite low during fry migration (January - February), and then increased rapidly and often peaked above one during parr migration (March - April) before declining again during late parr and smolt migration (May).

As expected, periods with exceptionally high abundance ratios (Figure 23) generally corresponded to those length groups with high abundance ratios (Figure 22). For year 2000, the high ratios during April and early May corresponded with the passage timing of 60-85 mm juveniles at Caswell. Similarly, the high ratios for late March and April in 2005 corresponded with the passage of 55-75 mm groups. As another example, in 2004 it appeared that juvenile rearing contributed to the passage of additional large fry and small parr at Caswell. Ratios for the 40-45 mm length groups (i.e., fish ranging from 40-49 mm) were relatively high in 2004 (Figure 22), corresponding to the high abundance ratios in March, which were considerably greater than one (Figure 23).

Patterns for 1996 were distinct. In that year, abundance ratios for length groups increased slowly and reached moderate levels across smolt size classes (> 80 mm) (Figure 22). Ratios by week rose quickly toward values of one during late May (Figure 23). In contrast to other years, there was limited juvenile passage at Oakdale throughout much of the fry and parr migration period (February to early April) in 1996 (Figure 13), and passage at Caswell surged as smolts outmigrated during late April and early May (Figure 14). Thus, the patterns in abundance ratios appear to reflect steadily increasing survival of parr and smolts as a function of length, as well as a potentially strong contribution of rearing smolts to the Caswell passage late in the migration.

Another anomalous year was 1998. The abundance ratios for this year were extremely high across life stages, length groups, and Julian weeks (Figure 21 - Figure 23). This is not surprising given that the overall survival rate of juveniles passing between Oakdale and Caswell was estimated at 95% (Table 14). This survival-rate estimate was highly uncertain (Figure 20), and is undoubtedly an overestimate of the true survival rate for 1998. Consequently, all abundance ratios are likely overestimates as well. Ratios by length group provide clear evidence of this; it is highly unlikely that ratios of all length groups from 40-90 mm could be greater than one (Figure 22). Nevertheless, the *relative* patterns in abundance ratios across life stages, length groups, and weeks should be generally reflective of the actual *relative* patterns for 1998. This is because biases in abundance estimates for 1998 would most likely arise from a systematic bias in trap-efficiency estimates for one or both trap sites, which would bias all daily abundance estimates in a similar manner. Indeed, relative patterns in abundance ratios for 1998 are similar to those for 2000, another year with apparent high survival (Figure 22; Figure 23).

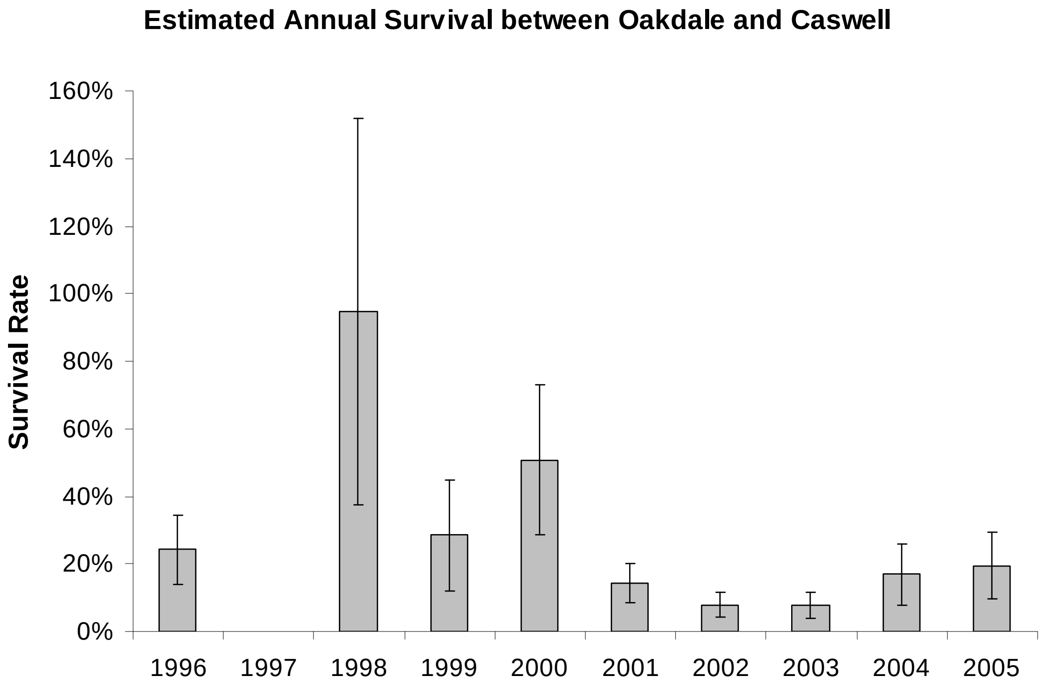


Figure 20. Annual survival-rate estimates of all juvenile Chinook salmon migrating between the Oakdale and Caswell trap sites. Error bars indicate approximate 95% confidence intervals.

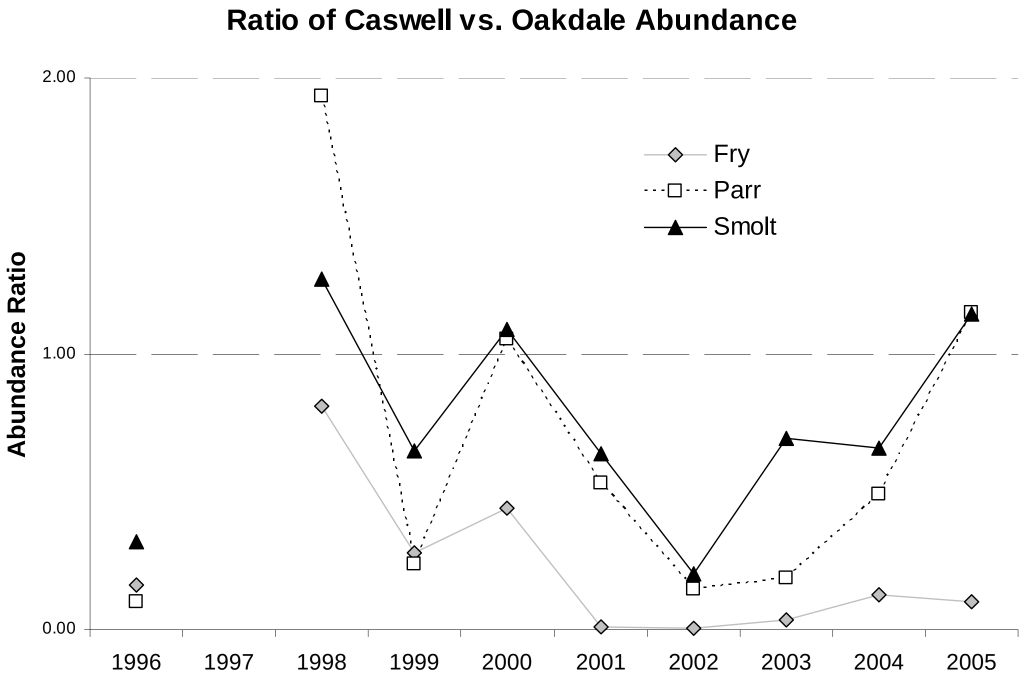


Figure 21. Abundance ratios by life stage of juvenile Chinook salmon migrating past the Caswell trap site versus the Oakdale site. A ratio greater than one indicates that more juveniles were estimated to have passed Caswell than Oakdale.

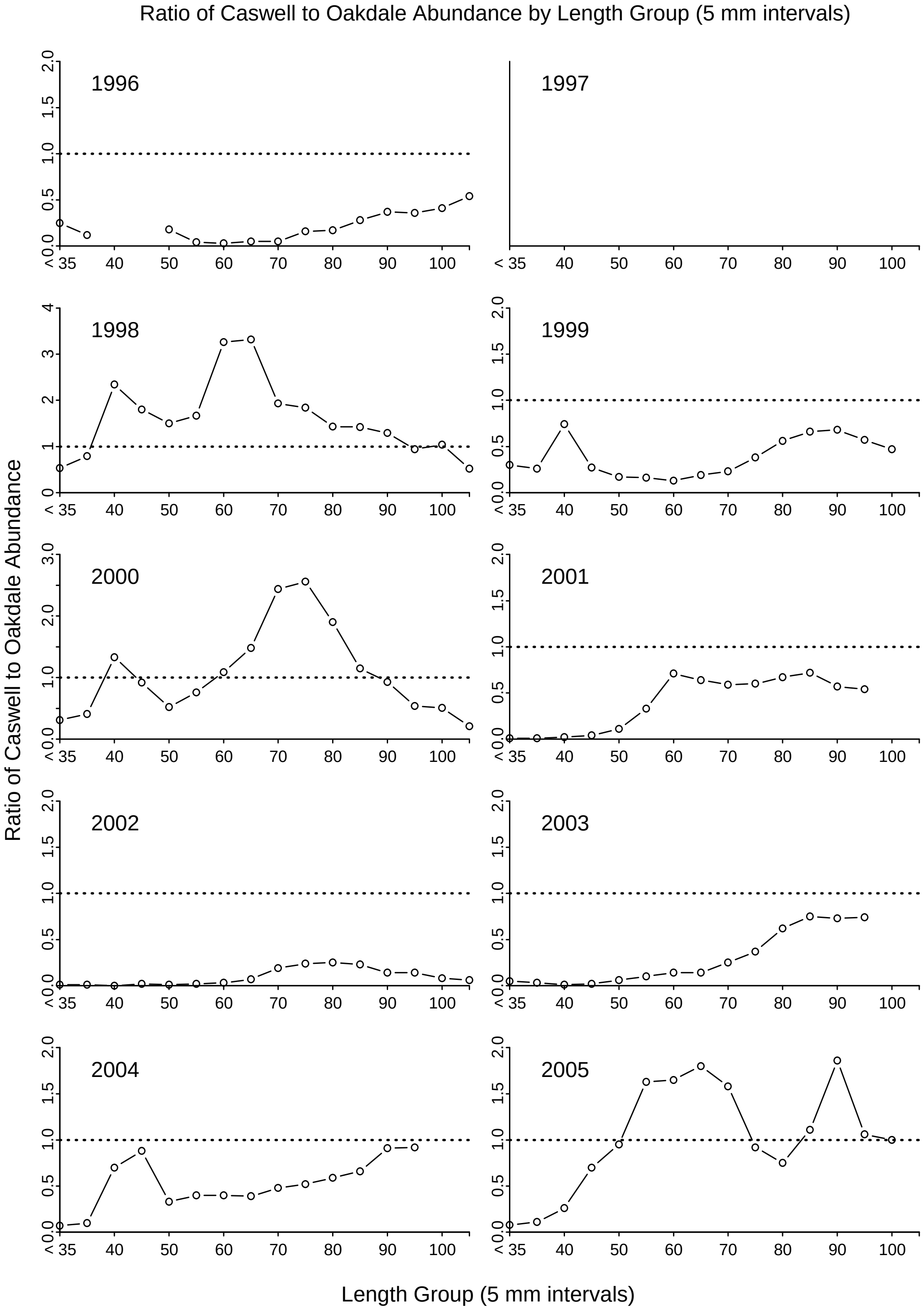


Figure 22. Abundance ratios by length group (5 mm intervals) of juvenile Chinook salmon migrating past the Caswell trap site versus the abundance at the Oakdale site. A ratio greater than one (dashed line) indicates that more juveniles were estimated to have passed Caswell than Oakdale.

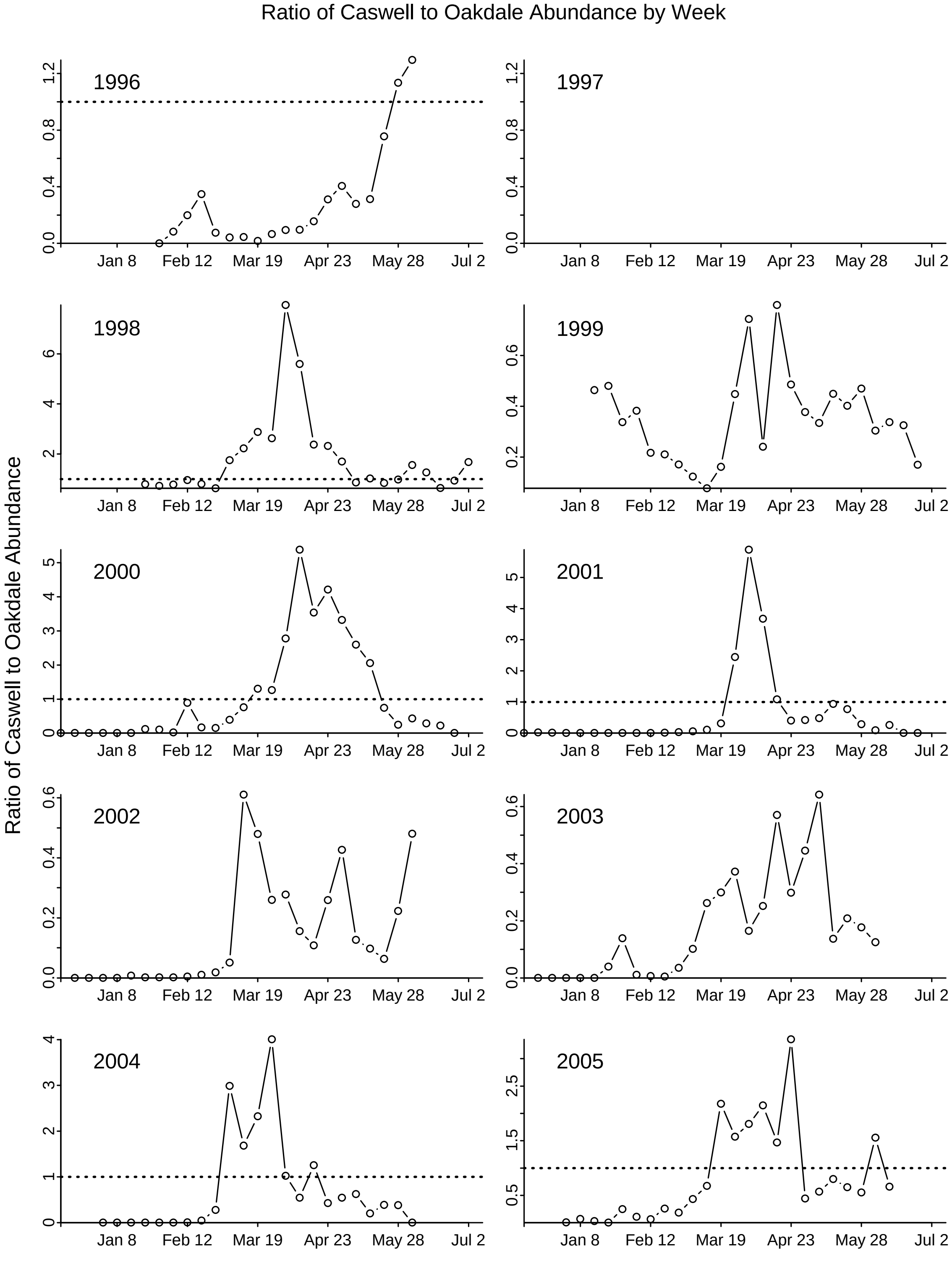


Figure 23. **Abundance ratios by week of juvenile Chinook salmon migrating past the Caswell trap site versus the abundance at the Oakdale site (Caswell data lagged one day ahead). A ratio greater than one (dashed line) indicates that more juveniles were estimated to have passed Caswell than Oakdale.**

Factors affecting survival

Across years, there was considerable variation in Stanislaus River flows during the general migration period for juvenile Chinook salmon (January 15 – May 15). Mean flow at Orange Blossom Bridge (OBB) ranged from a low of 405 cfs in 2004 to a high of 2532 cfs in 1998 (Table 15). Median values were somewhat lower, ranging from 266 cfs in 2005 to 2049 in 1998. Values of flow Ripon (RIP) were slightly higher than those at OBB, but showed very similar variations across years (Table 15).

Temperatures were much less variable (Table 15). For example, mean temperatures at the Oakdale site ranged from 10.2 ºC in 1999 to 12.5 ºC in 2004. Across years, temperatures were roughly 1.5 ºC higher on average at Caswell than at Oakdale.

Table 15. Mean and median values for flow, temperature, and turbidity measurements at the Oakdale and Caswell trap sites for the period January 15 through May 15.

	Flow at OBB (cfs)		Temperature [C]		Turbidity (NTU)	
Year	**Mean**	**Median**	**Mean**	**Median**	**Mean**	**Median**
1996	1912	1679	11.0	11.0	3.1	2.8
1997						
1998	2532	2049	11.0	10.8	4.7	4.3
1999	2062	1428	10.2	9.8	2.9	1.9
2000	1426	1275	11.7	11.4	3.5	2.0
2001	655	503	11.7	12.2	1.4	0.6
2002	573	497	11.5	11.8	0.9	0.7
2003	549	503	11.9	11.9	1.7	1.5
2004	405	299	12.5	13.3	2.1	1.6
2005	436	266	12.3	12.6	4.9	3.4
Caswell Trap Location						
	Flow at RIP (cfs)		**Temperature [C]**		**Turbidity (NTU)**	
Year	**Mean**	**Median**	**Mean**	**Median**	**Mean**	**Median**
1996	1916	1620	12.4	12.2	7.7	7.0
1997						
1998	2561	2080	11.7	11.4	9.6	7.9
1999	2206	1766	11.7	11.0	5.4	4.4
2000	1449	1408	12.8	12.2	6.1	4.6
2001	671	398	13.1	13.3	4.4	3.4
2002	647	517	12.7	13.2	3.2	3.0
2003	612	573	13.1	13.3	3.0	2.9
2004	475	378	14.1	15.5	6.5	3.9
2005	506	334	13.8	13.9	7.8	5.3

Similar to flow, turbidity levels were quite variable across years (Table 15). Mean turbidity (NTU) at Oakdale ranged from 0.9 in 2002 to 4.9 in 2005. Turbidity levels at Caswell were roughly double those at Oakdale. At Caswell, turbidity measures were lowest in 2003 and highest in 1998. In all cases, mean turbidity was greater than the median value, reflecting periodic events of high turbidity.

We found strong associations between annual survival-rate estimates (Table 14) and measures of flow and turbidity (Table 15). In these analyses, we found very similar results for mean and median measures of environmental conditions. We therefore limit our results to comparisons that used mean values, which better reflect the contributions of periodic extreme conditions (e.g., high flow or turbidity events) that may enhance passage survival. Correlations between survival rates and mean conditions at Oakdale were 0.77 for flow, -0.35 for temperature, and 0.72 for turbidity (Table 16). Similar correlations were found for conditions at Caswell. The large, positive correlations for flow and turbidity suggest that increases in flow and turbidity are associated with higher survival rates.

Table 16. Correlations between annual means for flow, temperature, and turbidity at Oakdale (Table 15) and annual survival-rate estimates of juvenile Chinook salmon migrating between the Oakdale and Caswell trap sites (Table 14). Also shown are correlations for annual abundance ratios by life stage of juveniles passing Caswell versus Oakdale (Table 14).

	Flow at OBB	Temperature	Turbidity
Annual Survival Rate	0.77	-0.35	0.72
Fry Abundance Ratio	0.80	-0.40	0.71
Parr Abundance Ratio	0.36	0.09	0.72
Smolt Abundance Ratio	0.25	0.17	0.66

Using linear regression analyses, we found statistically significant relationships between survival rates and measures of flow and turbidity. A summary of results for 18 regression models is shown in Table 17. For models fit to survival rates using weighted least squares, significant associations were found for OOB flow (P = 0.049; Model 1, Table 17) and turbidity at Caswell (P = 0.016; Model 12). These variables explained 45% and 59% of the variation in survival rates, respectively. Similar relationships existed for RIP flow (Model 10) and Oakdale turbidity (Model 3), but these fits were slightly worse and had P-values slightly greater than 0.05.

The estimated effect of temperature on survival at either site was minimal and not significant (Models 2 and 11).

The regression for OBB flow had an estimated slope of 0.00013 (Model 1, Table 17). Thus, the model predicts that a 1,000 cfs increase in flow would result in an increase in survival rate of 0.13 (Figure 24A). Likewise, the slope estimate for turbidity at Caswell was 0.035, indicating an increase in survival of 0.035 for each one NTU increase in turbidity (Figure 25A).

We consider weighted least squares to be most appropriate method for fitting these regressions. This approach accounts for the vastly different variances (= SE^2) among the annual survival-rate estimates (see Table 14 and Figure 20). Consequently, high survival estimates like those for 1998 and 2000 receive less weight in the fitted regression because these estimates are quite uncertain. The effect is quite evident in the fitted regression (Figure 24A), with the regression line tending toward the survival-rate estimates for 1996 and 1999 (i.e., years with moderate flows but more precise survival estimates).

For comparison, we fit “standard” least-squares regressions, which assume that all survival estimates have roughly equal variances. The key difference was that the estimated slopes of the flow and turbidity models roughly doubled in comparison to the weighted least squares estimates (Table 17). For example, the slope of the standard regression for OBB flow was 0.00026 (Model 4) compared to 0.00013 (Model 1), suggesting a much stronger effect of flow on survival (Figure 24B). A similar increase occurred for the Caswell turbidity regression (Figure 25B). Obviously, in the standard regressions the high survival estimates for 1998 and 2000 have greater weight and the regression lines are pulled toward those values. Although it is tempting to have greater confidence in the standard regressions because they provide better “visual” fits to the data (Figure 24 and Figure 25), from a statistical perspective, the weighted least squares regressions will tend to provide more accurate and reliable estimates.

Using log-transformed values of environmental conditions did not appreciably improve the (weighted) regressions (Table 17). These models were considered because they can describe potential non-linear relationships whereby survival rates increase toward an asymptote as a given variable increases. Such relationships have been documented between survival rates of juvenile salmonids and flows in Yakima River (Pyper and Smith 2005) and Sacramento River (Newman and Rice 2002). However, regression fits worsened for log(flow) for both OBB and RIP flow data (Models 7 and 16), and the implied form of relationship between survival and flow appeared inappropriate (Figure 24C). Regressions for log(turbidity) were very similar to those for turbidity, but with slightly nonlinear relationship with survival (e.g., Figure 25C). Again, associations between temperature and survival were weak.

Table 17. Summary of linear regression models for survival rates as a function of either flow, temperature, or turbidity. Regressions were fit using three different methods: weighted least squares (LS); standard least squares (Standard); and using log-transformed data for the environmental variable (Log) with weighted LS. SE = standard error of the slope estimate. P-value = P-value for the null hypothesis that the slope equals zero. R-square is the proportion (in %) of variation in survival rates accounted for by the variable.

	Oakdale Environmental Conditions						
Model	**Method**	**Variable**	**Intercept**	**Slope**	**SE**	**P-value**	**R-square**
1	Weighted LS	Flow (OBB)	0.027	0.00013	0.00006	0.049	45%
2	Weighted LS	Temperature	0.451	-0.029	0.069	0.689	2%
3	Weighted LS	Turbidity	0.037	0.048	0.021	0.057	43%
4	Standard	Flow (OBB)	-0.012	0.00026	0.00008	0.016	59%
5	Standard	Temperature	1.841	-0.134	0.137	0.359	12%
6	Standard	Turbidity	-0.070	0.130	0.056	0.053	44%
7	Log	Flow (OBB)	-0.703	0.127	0.063	0.083	37%
8	Log	Temperature	1.026	-0.371	0.792	0.654	3%
9	Log	Turbidity	0.081	0.095	0.043	0.065	41%

	Caswell Environmental Conditions						
Model	**Method**	**Variable**	**Intercept**	**Slope**	**SE**	**P-value**	**R-square**
10	Weighted LS	Flow (RIP)	0.019	0.00013	0.00006	0.055	43%
11	Weighted LS	Temperature	0.184	-0.005	0.062	0.934	0%
12	Weighted LS	Turbidity	-0.025	0.035	0.011	0.016	59%
13	Standard	Flow (RIP)	-0.022	0.00026	0.00008	0.018	57%
14	Standard	Temperature	2.720	-0.189	0.104	0.113	32%
15	Standard	Turbidity	-0.240	0.089	0.033	0.029	52%
16	Log	Flow (RIP)	-0.787	0.138	0.069	0.086	36%
17	Log	Temperature	0.396	-0.110	0.813	0.897	0%
18	Log	Turbidity	-0.114	0.173	0.053	0.014	60%

In summary, there were significant, positive relationships between survival rates and measures of flow and turbidity. However, flow and turbidity were moderately correlated across years. For example, the correlation between OBB flow and Oakdale turbidity was 0.49, and the correlation between RIP flow and Caswell turbidity was 0.56. It is therefore difficult to determine the relative importance of these variables from a statistical perspective because they are somewhat confounded. From a biological perspective, the variations in annual flows would likely have stronger effects on passage conditions than the observed ranges in turbidity conditions. As discussed below, patterns in daily passage estimates suggest that flow is a critical factor governing the migration of fry, though extreme turbidity events appear important as well.

Finally, it is interesting to note that the annual abundance ratios for fry, parr, and smolts had quite different correlations with flow. For example, correlations between annual means in OBB flow and the fry, parr, and smolt abundance ratios were 0.80, 0.36, and 0.22, respectively (Table 16). Correlations were similar for RIP flows. The strong correlation for fry is not surprising; fry were the predominant life stage in most years and their abundances at Caswell largely determined the overall survival rate. However, the weak correlations for parr and especially smolts suggest that the relative survival of these life stages may be much less dependent on flow conditions. In contrast, correlations with turbidity were much stronger for parr and smolts (Table 16). Of course, these correlations must be interpreted cautiously. There are only nine years of data, and the abundance ratios by life stage are not true measures of survival rate because they are potentially confounded by juvenile rearing between the trap sites.

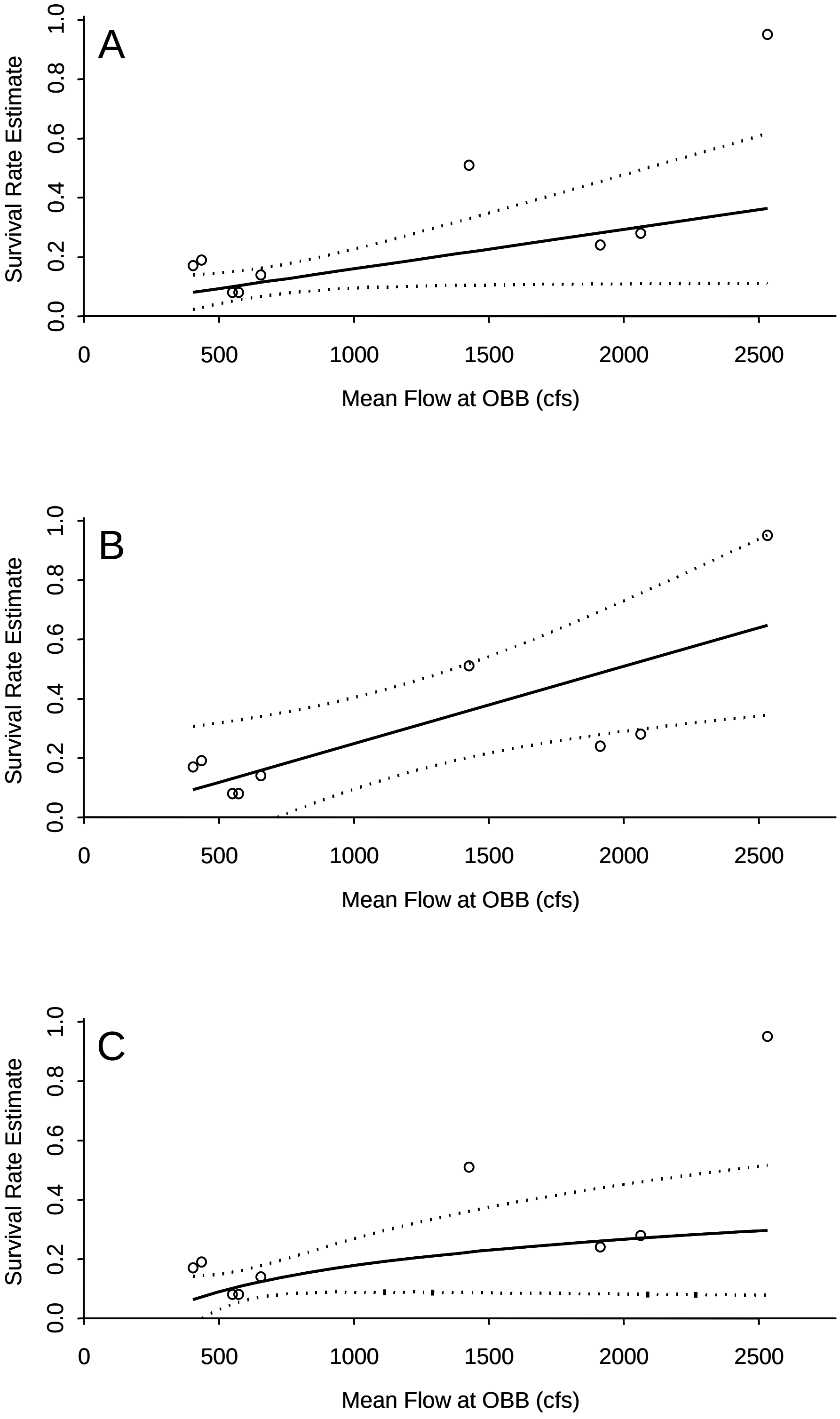


Figure 24. Linear regressions of annual survival rate as a function of mean flow at OBB fit using (A) weighted least squares, (B) standard least squares, and (C) weighted least squares with survival as a function of log-transformed flow values. Dashed line indicate the 95% confidence interval for the regression line.

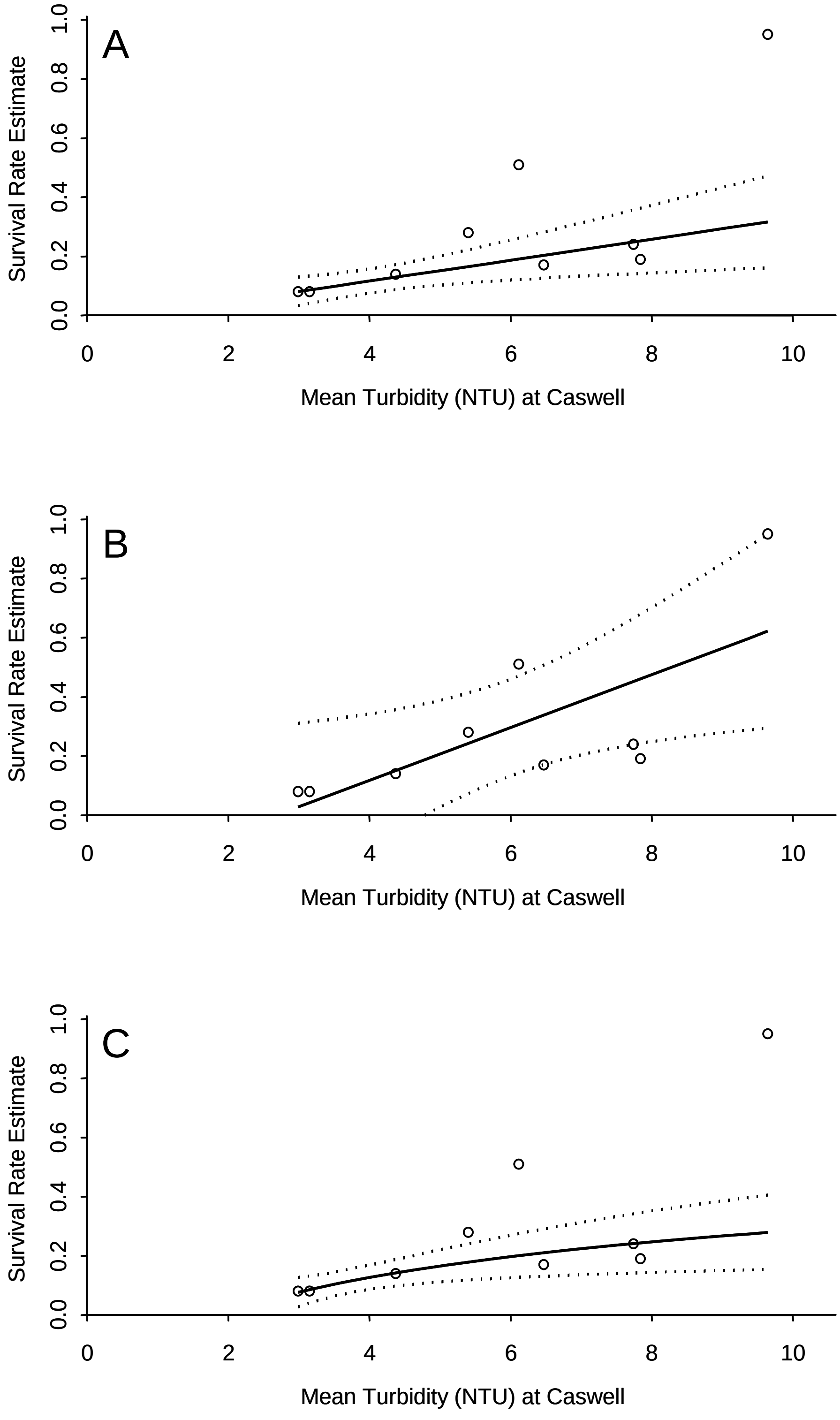


Figure 25. Linear regressions of annual survival rate as a function of mean turbidity at Caswell fit using (A) weighted least squares, (B) standard least squares, and (C) weighted least squares with survival as a function of log-transformed turbidity values. Dashed line indicate the 95% confidence interval for the regression line.

Body Size

Samples of juvenile length provided an extensive data set that allowed for high statistical power in analyses of body sizes across years and between trap sites. Mean lengths of juveniles by Julian week are shown for Oakdale in Table 18 and for Caswell in Table 19. Annual sample sizes were large (bottom rows of Table 18 and Table 19), and sampling coverage across days within each season was extensive (Figure 26 and Figure 27).

At Oakdale, trends in mean lengths of juveniles during fry migration were consistent across years (Table 18). Mean lengths approached roughly 40 mm by late February or early March (Julian weeks 9 or 10), and surpassed 45 mm by mid-March (Julian week 12). Obvious differences across years in length trajectories began in early March with the onset of parr migration (Table 18). For example, mean lengths in 1996 increased rapidly during March and early April, reaching the smolt size class (80 mm) two to seven weeks earlier than in other years.

The year-to-year differences in mean lengths at Oakdale are clearly depicted in Figure 28. Lengths in 1996 were obviously the highest among years, and were roughly 10 mm above average from late March through May (Figure 28). Above average lengths were also evident in 1998 throughout the parr and smolts migration periods. In contrast, the smallest juveniles were recorded in 1999, followed by 2001 (Table 18; Figure 28).

Interestingly, somewhat different patterns in mean lengths were observed at the Caswell trap site (Table 19; Figure 29). Again, mean lengths were consistently above average throughout most of the parr and smolt migration in 1996, and also in 1997, a year without Oakdale data (Figure 29). However, mean lengths at Caswell were also clearly above average during early parr migrations (e.g., March) in 2002 and 2003, and from March through May in 2005 (Figure 29). Below average lengths were evident for most weeks in 1999, 2001, and 2004.

There were also obvious differences in mean lengths between the Oakdale and Caswell sites. For example, daily trends in mean lengths (i.e., smoothing splines fit to the daily data in Figure 26 and Figure 27) show that juveniles migrating past Caswell were often much larger than those at Oakdale (Figure 30). Differences were most prominent during March and April of 2002, and throughout most of the parr and smolt migration in 2003 and 2005 (Figure 30).

Table 18. Mean fork length (mm) by Julian week of juvenile Chinook salmon captured at the Oakdale trap site, 1996-2005. The fry (< 45 mm), parr (45-80 mm), and smolt (> 80 mm) life stages are represented in white, light gray, and dark gray, respectively.

Julian week	Start date	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	Mean
50	12/10	--	--	--	--	33.9	34.8	--	--	--	--	34.3
51	12/17	--	--	--	--	35.3	34.7	33.0	34.5	--	--	34.4
52	12/24	--	--	--	--	34.8	34.0	35.4	--	--	--	34.7
1	1/1	--	--	--	--	34.7	35.0	35.6	34.0	33.5	34.6	34.6
2	1/8	--	--	--	--	35.2	36.1	34.8	35.0	35.0	35.0	35.2
3	1/15	--	--	--	34.7	35.8	35.9	36.7	34.7	35.2	34.2	35.3
4	1/22	--	--	35.6	35.2	36.8	36.4	37.0	35.6	35.4	35.1	35.9
5	1/29	35.6	--	35.5	35.1	38.0	36.4	37.0	36.5	35.4	36.8	36.3
6	2/5	36.4	--	--	35.2	36.5	36.5	36.3	36.4	37.0	34.6	36.1
7	2/12	35.4	--	36.2	35.3	36.5	36.1	37.0	36.8	36.8	35.2	36.2
8	2/19	36.2	--	36.7	35.7	36.7	36.0	38.0	36.5	36.3	37.1	36.6
9	2/26	36.5	--	38.7	36.3	37.6	37.2	40.1	40.1	39.6	36.6	38.1
10	3/5	42.0	--	46.3	40.2	41.5	40.7	40.7	42.6	42.0	39.5	41.7
11	3/12	48.3	--	51.0	43.7	50.6	44.9	45.3	49.3	40.7	41.7	46.2
12	3/19	63.0	--	53.9	46.1	57.1	45.8	52.9	55.2	50.5	52.2	53.0
13	3/26	77.1	--	65.6	53.3	61.9	55.2	59.6	60.0	57.6	55.6	60.7
14	4/2	79.4	--	68.4	59.5	65.3	62.7	61.0	63.5	67.0	64.6	65.7
15	4/9	83.7	--	75.1	60.6	67.6	66.9	66.8	67.8	68.0	69.8	69.6
16	4/16	86.4	--	78.5	62.9	69.8	71.3	71.6	72.4	71.2	76.0	73.4
17	4/23	89.6	--	84.2	70.6	74.7	72.0	78.2	72.9	73.4	76.8	76.9
18	4/30	91.2	--	83.0	75.0	78.2	73.9	78.7	75.9	75.9	78.1	78.9
19	5/7	--	--	85.4	75.2	80.4	77.8	79.7	78.0	77.1	80.4	79.2
20	5/14	95.4	--	87.2	76.9	85.0	78.5	82.1	81.1	79.5	86.3	83.6
21	5/21	94.4	--	87.7	79.0	85.8	78.8	87.0	83.3	83.6	89.4	85.4
22	5/28	95.5	--	89.6	81.3	89.6	80.4	87.0	85.9	85.0	93.1	87.5
23	6/4	96.7	--	91.3	83.5	94.6	85.0	86.9	86.6	85.1	90.7	88.9
24	6/11	--	--	94.4	86.9	95.4	86.3	--	--	--	90.1	90.6
25	6/18	--	--	96.9	90.3	94.0	88.0	--	--	--	--	92.3
26	6/25	--	--	97.0	91.7	84.3	88.3	--	--	--	--	90.3
27	7/2	--	--	99.0	--	--	--	--	--	--	--	99.0
Sample	**size**	2,442		6,025	7,705	7,060	10,881	9,021	7,940	7,408	6,035	64,517

Table 19. Mean fork length (mm) by Julian week of juvenile Chinook salmon captured at the Caswell trap site, 1996-2005. The fry (< 45 mm), parr (45-80 mm), and smolt (> 80 mm) life stages are represented in white, light gray, and dark gray, respectively.

Julian week	Start date	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	Mean
50	12/10	--	--	--	--	--	--	--	--	--	--	--
51	12/17	--	--	--	--	--	32.5	--	--	--	--	32.5
52	12/24	--	--	--	--	--	35.0	--	--	--	--	35.0
1	1/1	--	--	--	--	34.0	34.3	--	--	--	35.0	34.4
2	1/8	--	--	35.1	--	34.0	34.0	--	--	--	34.1	34.3
3	1/15	--	--	--	34.6	35.0	35.8	35.6	--	--	34.5	35.1
4	1/22	--	--	--	34.9	35.8	35.3	36.1	38.0	33.7	--	35.6
5	1/29	--	--	36.0	35.0	35.7	35.6	37.0	35.0	--	36.3	35.8
6	2/5	34.6	--	35.7	34.9	37.4	36.3	38.3	35.0	36.6	38.3	36.3
7	2/12	34.8	--	37.1	35.5	37.7	35.6	36.7	37.6	36.7	40.9	37.0
8	2/19	34.9	--	36.5	35.3	36.3	36.3	34.7	39.9	36.8	46.9	37.5
9	2/26	36.5	--	38.6	36.0	41.0	35.2	37.5	51.4	37.8	53.8	40.9
10	3/5	44.0	--	49.9	40.5	49.8	38.2	58.2	57.0	44.8	54.9	48.6
11	3/12	41.8	--	52.8	42.6	55.4	51.2	68.4	62.7	48.4	58.7	53.6
12	3/19	45.0	72.9	60.8	48.1	60.3	64.0	73.2	69.4	56.4	68.8	61.9
13	3/26	79.5	77.2	66.5	56.0	67.2	65.4	78.8	74.2	59.3	68.1	69.2
14	4/2	83.1	81.2	67.3	63.4	69.6	66.5	83.0	78.8	64.1	75.9	73.3
15	4/9	83.9	82.0	72.1	70.4	68.8	67.8	81.6	79.7	72.4	83.5	76.2
16	4/16	89.6	84.2	78.8	74.2	69.3	71.0	76.9	83.5	72.4	85.5	78.5
17	4/23	91.1	85.3	81.1	78.0	72.5	72.5	79.6	81.0	75.7	86.1	80.3
18	4/30	91.8	87.3	83.9	79.2	75.3	75.7	80.2	83.1	79.7	82.7	81.9
19	5/7	91.6	88.1	87.0	79.9	80.9	78.3	79.7	83.0	81.5	86.8	83.7
20	5/14	94.4	89.8	86.3	82.0	83.7	80.2	80.2	83.4	82.0	90.0	85.2
21	5/21	95.0	89.9	86.9	83.9	85.6	81.3	86.1	85.3	88.3	92.7	87.5
22	5/28	94.5	90.3	90.1	85.7	87.7	81.7	87.2	86.7	90.8	93.8	88.8
23	6/4	98.8	89.2	93.5	86.3	91.8	84.5	87.3	90.7	--	94.2	90.7
24	6/11	87.7	89.6	94.6	89.9	89.3	85.2	--	--	--	92.6	89.9
25	6/18	104.0	93.0	99.8	90.2	95.7	--	--	--	--	--	96.5
26	6/25	101.3	--	110.0	94.3	--	--	--	--	--	--	101.9
27	7/2	--	--	100.0	--	--	--	--	--	--	--	100.0
Sample	**size**	1,693	2,325	7,206	8,285	9,625	6,529	3,138	5,446	5,255	5,830	55,332

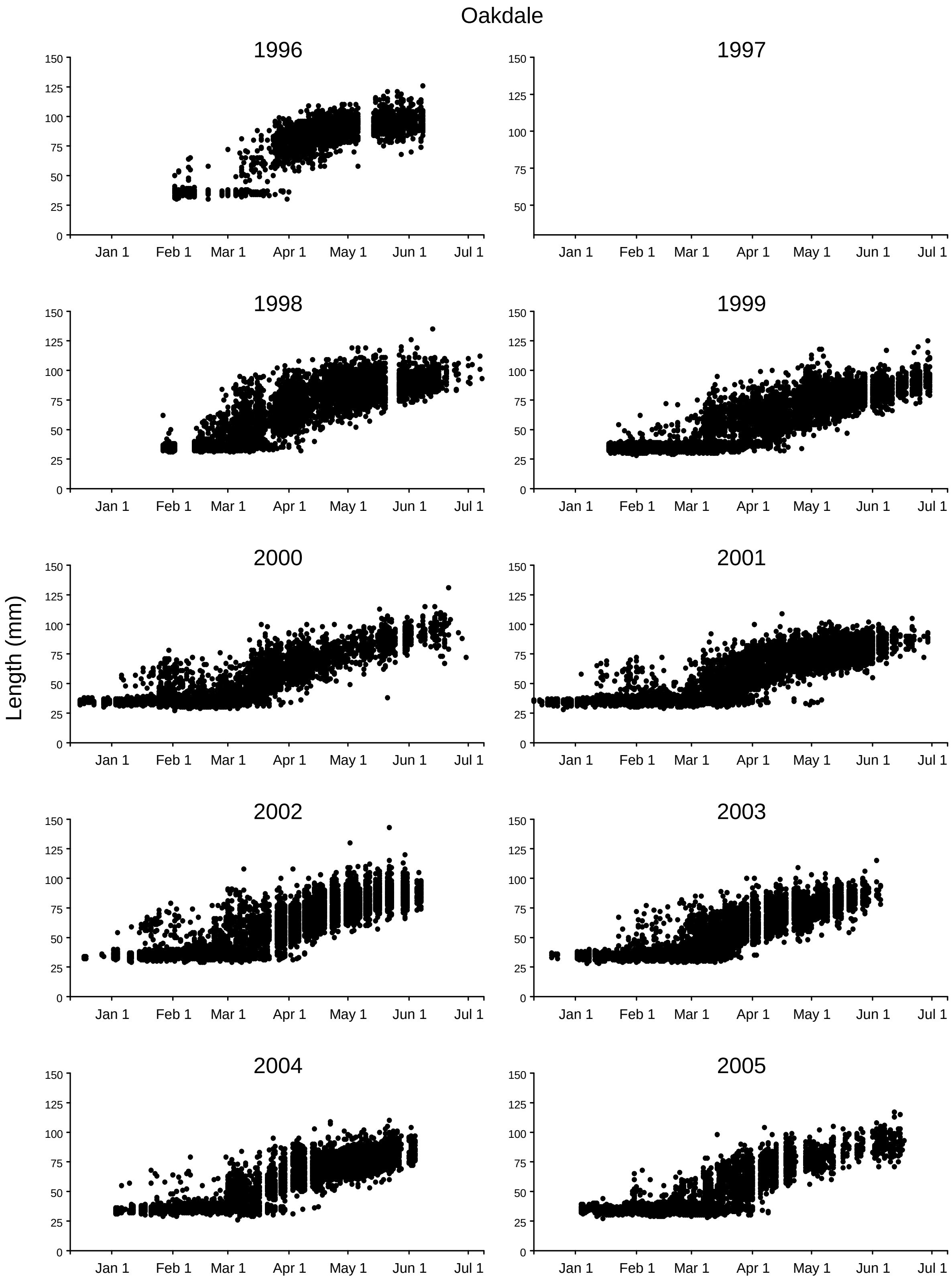


Figure 26. **Lengths of all sampled juvenile Chinook salmon by day at the Oakdale trap site.**

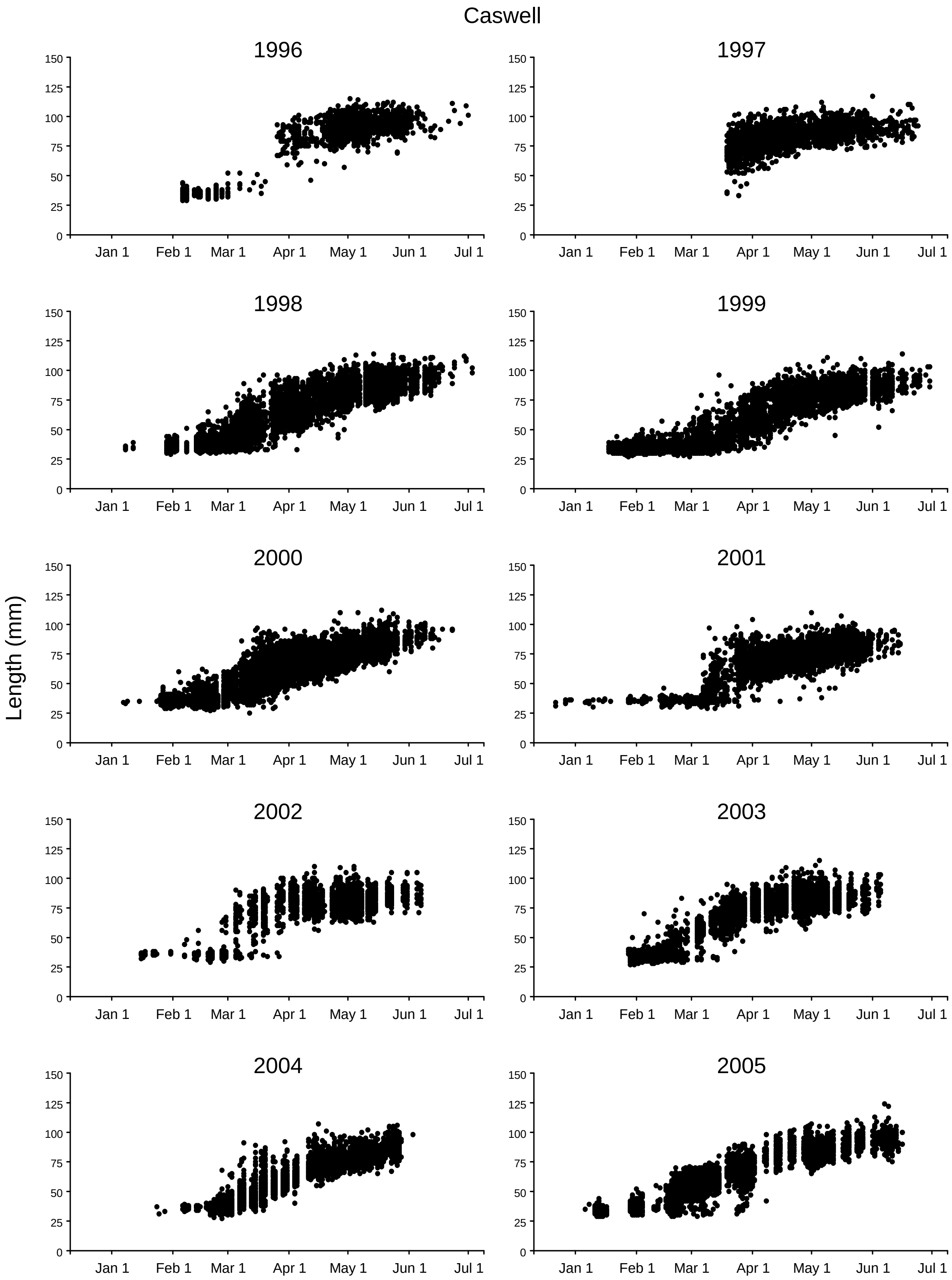


Figure 27. **Lengths of all sampled juvenile Chinook salmon by day at the Caswell trap site.**

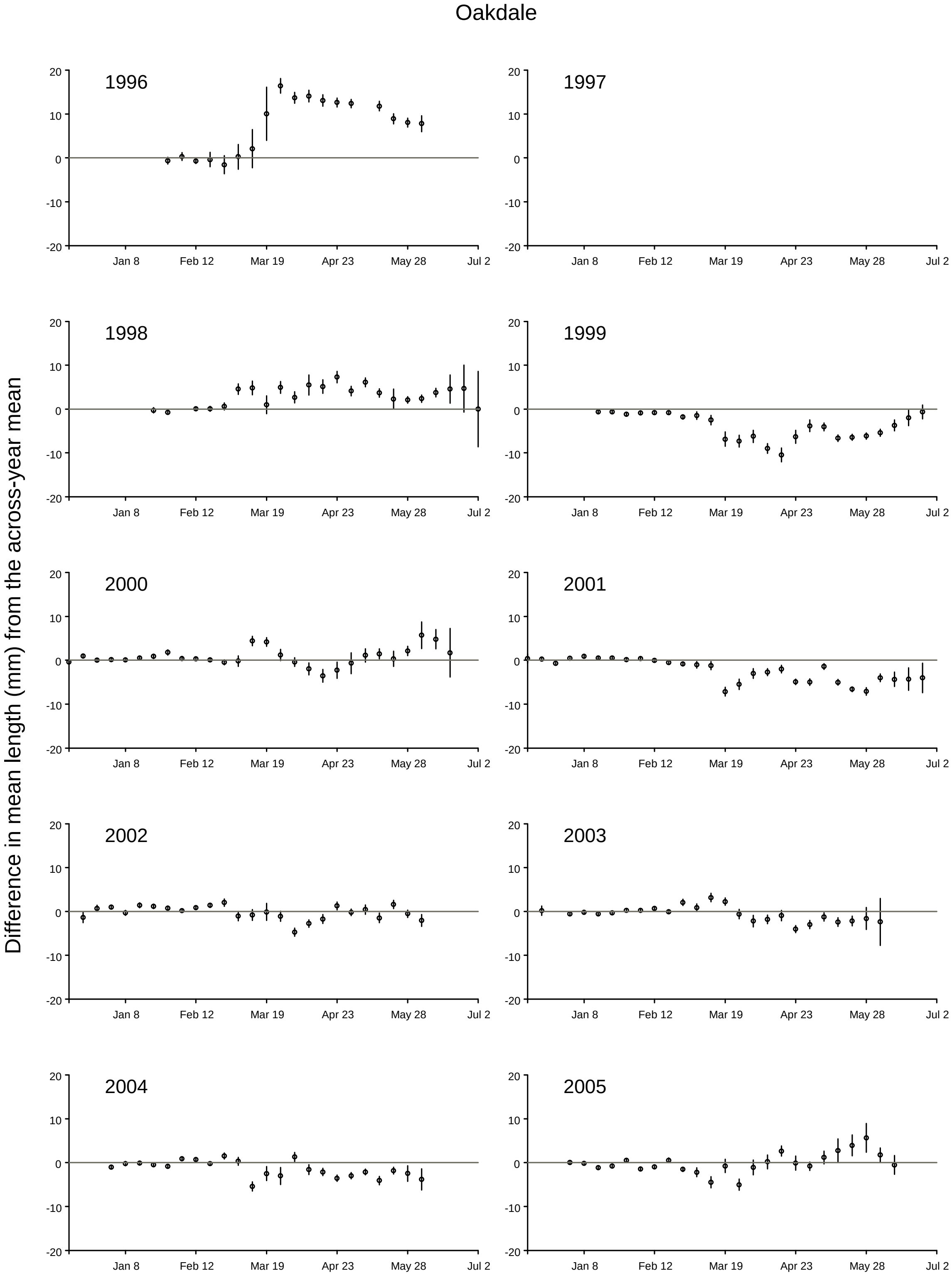


Figure 28. **Differences in mean length by week compared to the across-year weekly means for juvenile Chinook salmon sampled at the Oakdale trap site. Actual means are shown in Table 18. Vertical lines indicate 95% confidence intervals.**

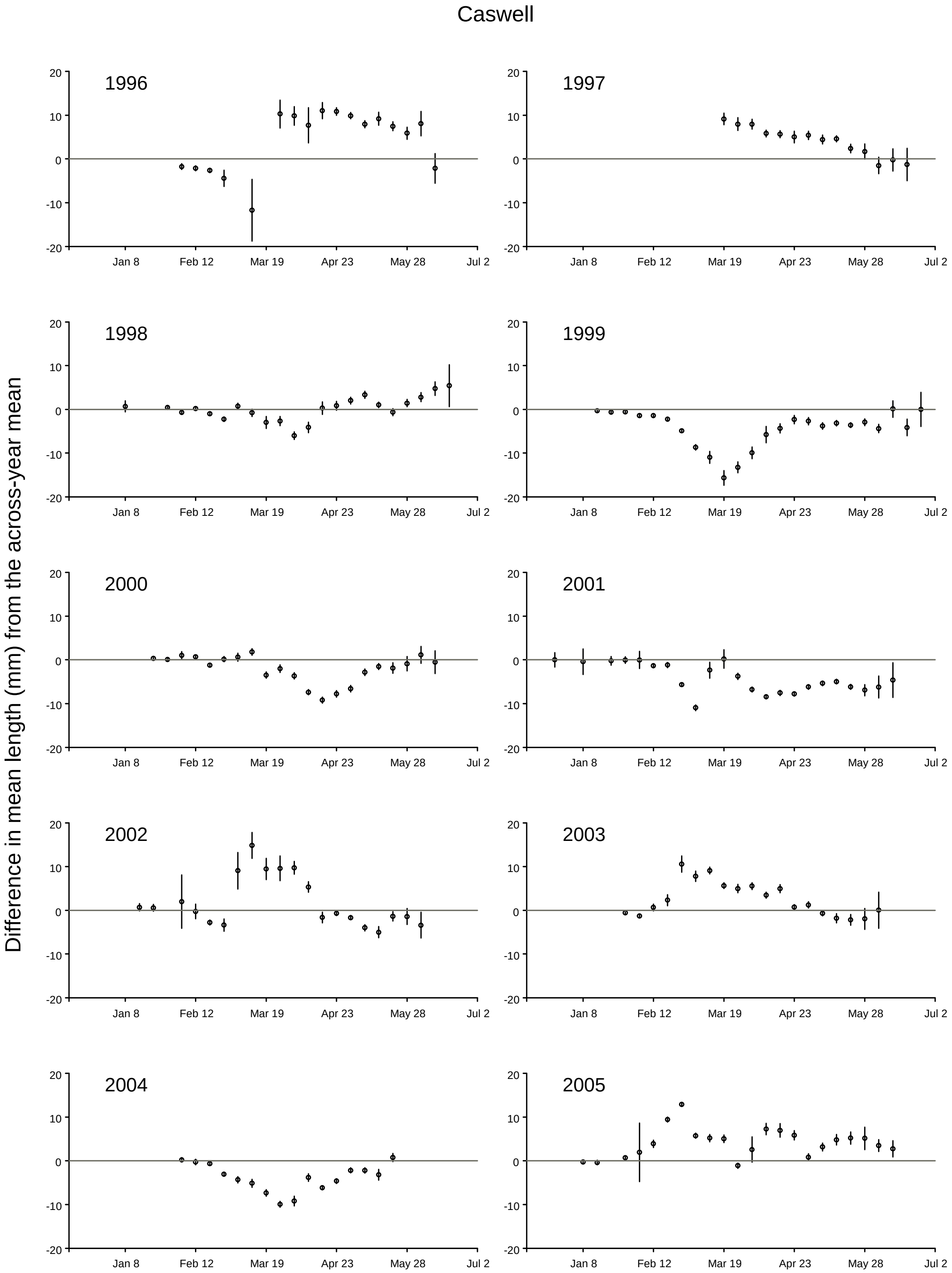


Figure 29. **Differences in mean length by week compared to the across-year weekly means for juvenile Chinook salmon sampled at the Caswell trap site. Actual means are shown in Table 19. Vertical lines indicate 95% confidence intervals.**

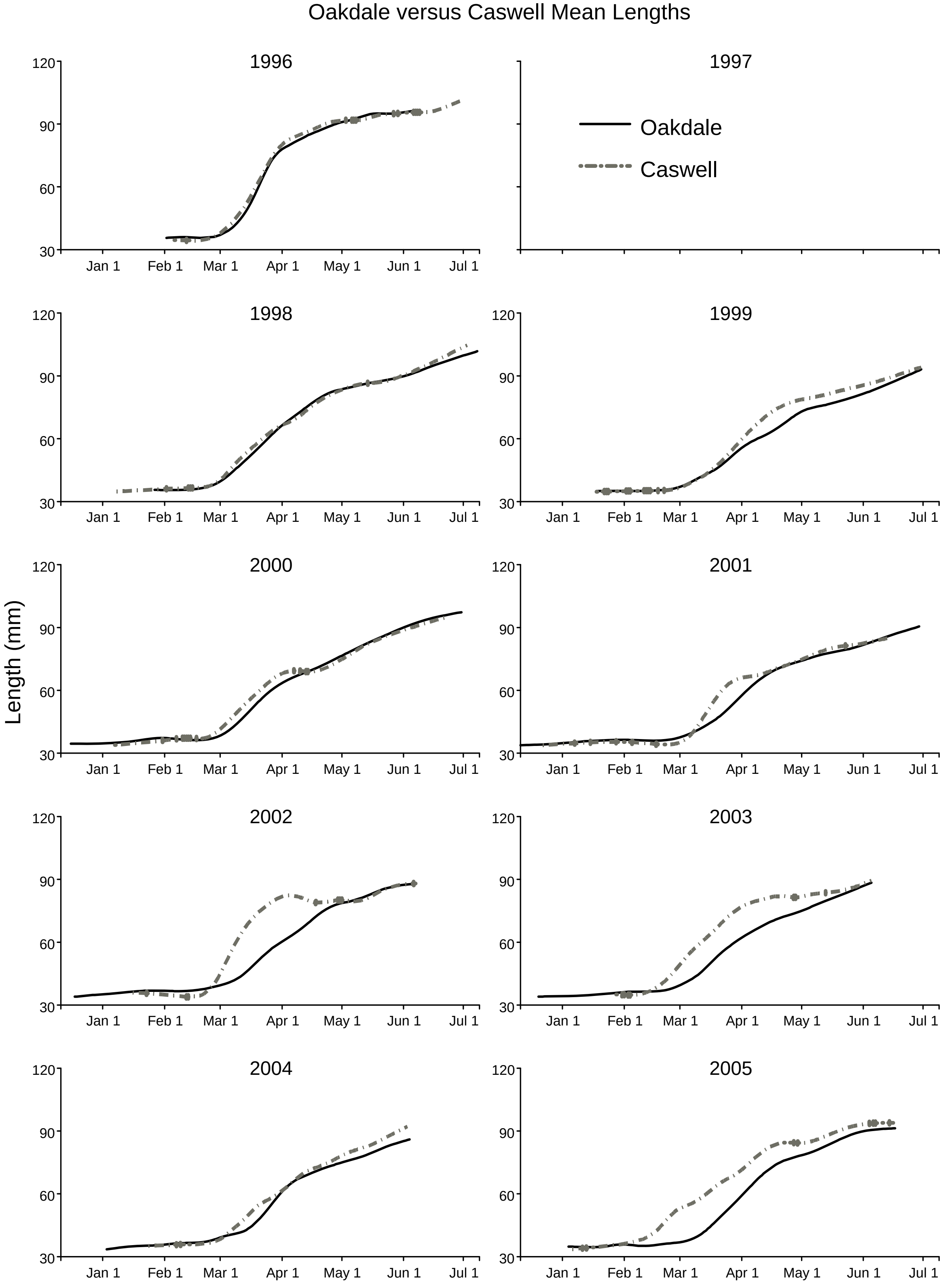


Figure 30. **Trends in daily mean length of juvenile Chinook salmon sampled at the Oakdale trap site (solid line) and Caswell trap site (dashed line).**

Analysis of variance

As described in the Methods section, we quantified annual differences in length using analysis of variance (ANOVA) models. These analyses were limited to data for Julian weeks 9-20 (February 26 – May 20), which covered the general period of early parr to smolt migration when differences in length were evident and sufficient data were available across years. Note that because sample sizes were so large, the ANOVA models we examined were highly significant ($P < 0.001$) and produced extremely precise estimates of the differences of interest.

For Oakdale, the estimated differences (across weeks) in mean length ranged from a low of -5.7 mm in 1999 (i.e., juveniles were 5.7 mm below average compared to all years) to a high of 12.2 mm in 1996 (Table 20; Figure 31). Lengths were also clearly above average in 1998 and below average in years such as 2001, 2004, and 2005. For Caswell, lengths were considerably above average in 1996 and 1997, and well below average in 1999, 2001, and 2004 (Table 20; Figure 31). For comparisons between the trap sites on a year by year basis (i.e., each estimate was derived one year at a time), differences between Caswell and Oakdale ranged from just 0.8 mm (i.e., Caswell juveniles were 0.8 mm larger on average than at Oakdale) to 13.4 mm in 2005 (Table 20; Figure 32). Thus, in terms of week to week differences between the trap sites, juveniles at Caswell were estimated to be larger than those passing Oakdale in all years (all $P < 0.01$), and in years such as 2002, 2003, and 2005, those differences were substantial (Figure 32).

Table 20. Estimated differences in mean length of juvenile Chinook salmon by year compared to the mean across all years. Separate estimates are shown for the Oakdale and Caswell sites. Also shown are the estimated differences for each year in mean length between the Caswell and Oakdale trap sites. In all cases, estimates are based on length data for Julian weeks 9 through 20 (Feb. 26 to May 20). SE = standard error of the estimate.

	Annual length difference (mm) at Oakdale		Annual length difference (mm) at Caswell		Difference between sites (Caswell minus Oakdale)	
Year	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
1996	12.2	0.25	9.5	0.24	1.2	0.39
1997			6.5	0.19		
1998	3.6	0.16	-1.6	0.12	0.8	0.23
1999	-5.7	0.16	-7.2	0.13	3.6	0.22
2000	0.4	0.20	-3.9	0.10	3.0	0.21
2001	-3.8	0.14	-6.5	0.11	2.5	0.16
2002	-1.3	0.15	0.7	0.16	7.1	0.27
2003	-0.7	0.16	3.5	0.14	11.0	0.20
2004	-2.3	0.16	-5.5	0.13	2.6	0.17
2005	-2.4	0.20	4.5	0.14	13.4	0.23

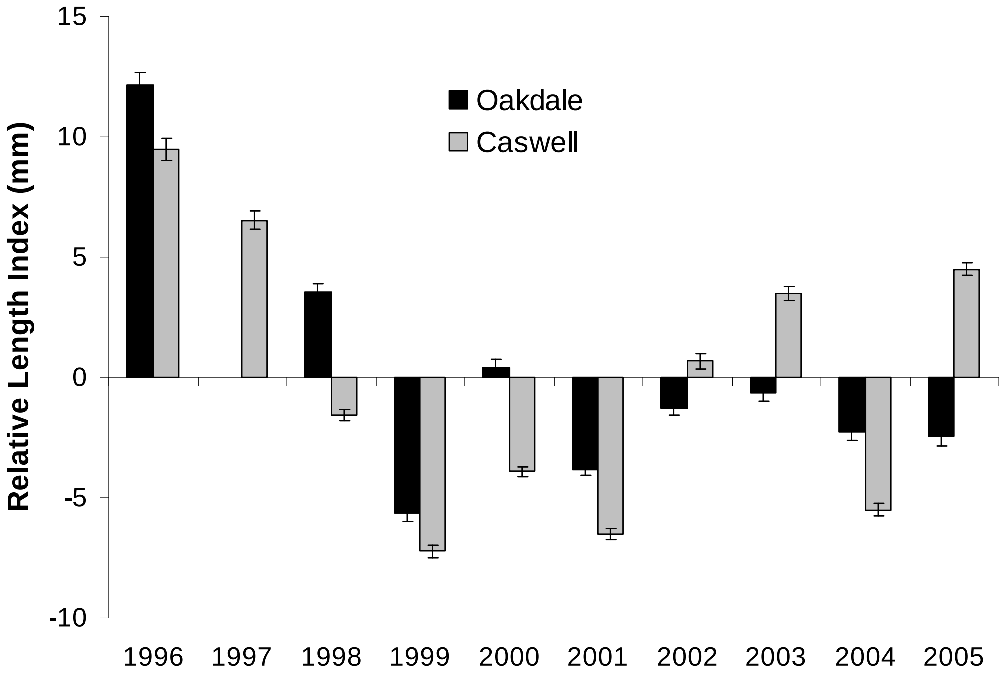


Figure 31. Relative length index by year of juvenile Chinook salmon sampled at the Oakdale and Caswell trap sites. This index is the estimated difference in mean length relative to all other years for Julian weeks 9-20 (Feb 26-May 20). Errors bars denote 95% confidence intervals.

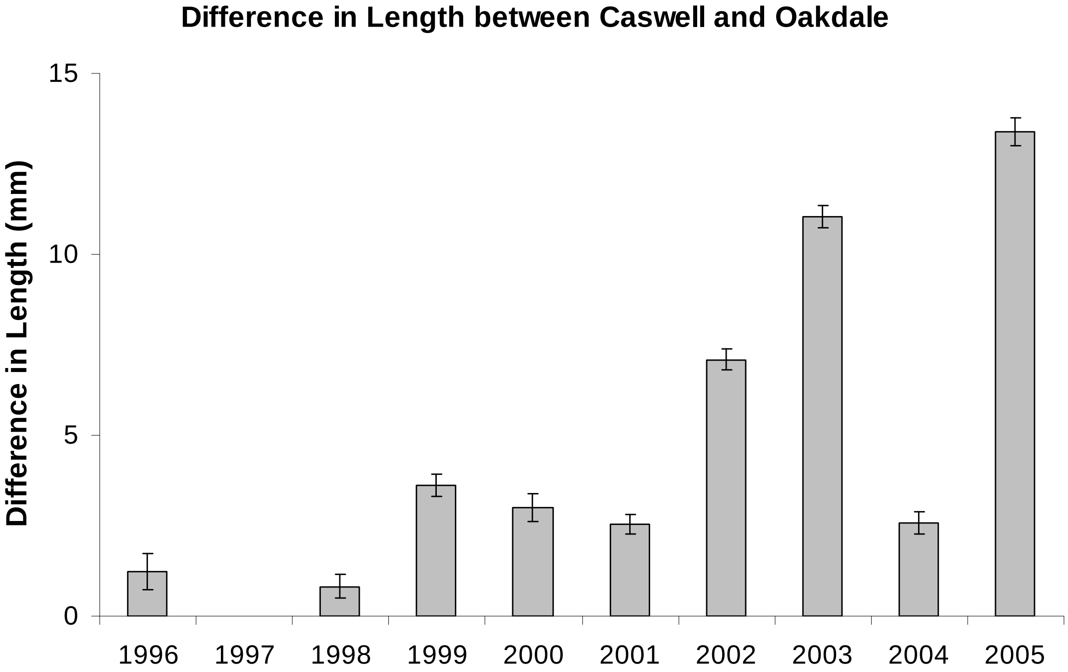


Figure 32. Differences in mean length of juvenile Chinook salmon sampled at Caswell compared to Oakdale (i.e., Caswell length minus Oakdale length) across Julian weeks 9 through 20 (Feb. 26 to May 20). Errors bars denote 95% confidence intervals.

Factors affecting body size

We found moderately strong associations between the relative length indices for each site (i.e., Table 20) and annual measures of flow and juvenile abundance. In these analyses, we first used means of environmental conditions over the period February 15 through April 1. We reasoned that conditions during this early could be critical to determining the early growth trajectories of juveniles. Moreover, to assess potential affects on growth, the length index for Oakdale was of primary interest. Several factors such as size-dependent mortality and juvenile rearing between sites could confound the interpretation of annual differences in length at Caswell. As measures of the potential affects of competition on growth, we used the sum of annual abundances of parr and smolts passing Oakdale, as well as the total passage at Oakdale (Table 12). In some respects, we would expect parr and smolt abundances to be a better measure because most fry had passed Oakdale before the period used to assess differences in annual lengths (February 26 – May 20).

Correlations between the Oakdale length index and mean conditions at Oakdale were 0.60 for flow, -0.33 for temperature, and 0.17 for turbidity (Table 16). Correlations for length versus the abundance indices were -0.37 for parr and smolts and -0.53 for total passage. Linear regressions of the Oakdale length index as a function of each predictor variable did not reveal any significant relationships. Example relationships are shown for flow (P = 0.08), temperature (P = 0.38), and parr and smolt abundance (P = 0.32) in Figure 33A-C. The strongest association was for flow (P = 0.08) followed by total passage (P = 0.14).

Table 21. Correlations between annual length indices and annual variables for passage conditions at Oakdale: mean flow at OBB (Feb. 15–April 1); mean temperature (Feb. 15–April 1); mean turbidity (Feb. 15–April 1); passage abundance of parr and smolt at Oakdale; and total juvenile passage at Oakdale.

	Oakdale Length Index	Caswell Length Index	Difference between sites
Flow	0.60	0.11	-0.63
Temperature	-0.33	0.01	0.48
Turbidity	0.17	0.19	0.11
Parr and Smolts	-0.37	-0.44	-0.13
Total Passage	-0.53	-0.65	-0.12

We also examined regressions using log-transformed values of each predictor to assess potential nonlinear relationships. A significant relationship was found between the Oakdale length index and log-transformed total passage (P = 0.02, R-square = 59%) (Figure 33D). The relationship implies a strong density-dependent affect on body size whereby juveniles experience higher growth rates (reduced competition) when abundances are low (Figure 33D). This relationship is largely driven by the data for 1996. In this year, lengths of parr and smolts were much higher than in subsequent years (Table 20; Figure 31), whereas total passage at Oakdale was particularly low (Table 10). For all other variable, using log-transformed values did not improve the regressions.

The relationship between temperature and length was surprising because it implied a negative effect of temperature on growth (Figure 33B), which is opposite to what we would expect for the range of temperatures experienced by early migrants. Mean temperatures at Oakdale (February 15 - April 1) were below average in 1996, 1998 and 1999, and well above average in 2004 and 2005 (Figure 34). This pattern bares little resemblance to the annual length index for Oakdale (Figure 31). Temperatures were lowest in 1999, for which body size was below average as well, but 1999 also had the highest total passage at Oakdale (Table 10).

We examined other periods over which to compute means for environmental conditions at Oakdale (e.g., across periods similar to that used for deriving the length index), however, these measures yielded similar results. In addition, correlations and regressions using the Caswell length index and environmental conditions did not reveal strong associations that differed from Oakdale analysis.

Finally, there was a moderate association between flow and the index of annual differences between Caswell and Oakdale lengths (Table 20; Figure 32). For example, the correlation between OBB flow and the length-difference index was -0.63 (Table 16). The linear regression for this relationship had a P-value of 0.06. As implied by this relationship, the years in which Caswell lengths were much greater than those at Oakdale were years with low flow (e.g., 2002, 2003, and 2005).

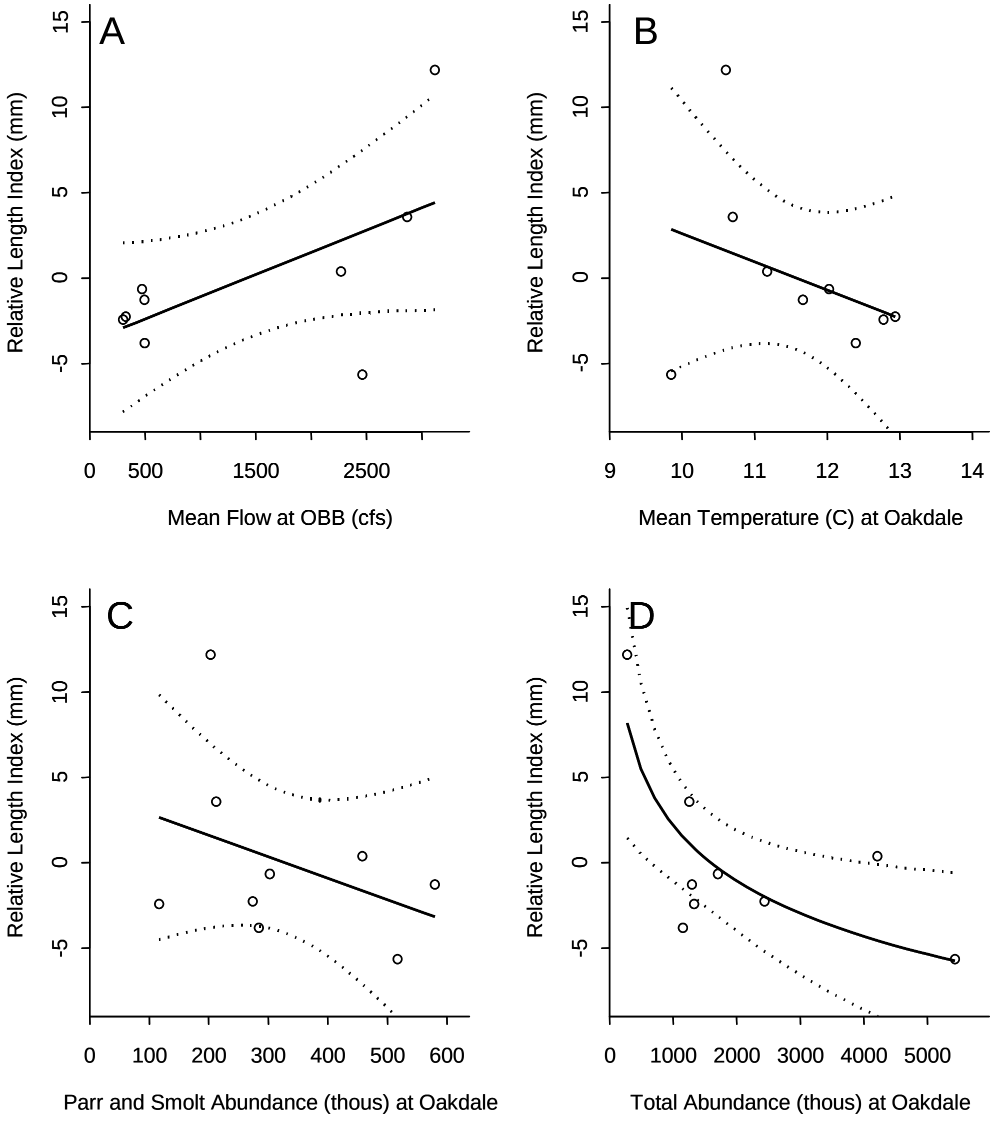


Figure 33. Linear regressions of the annual length index for Oakdale as a function of (A) **mean flow at OBB (Feb. 15–April 1),** (B) **mean temperature at Oakdale (Feb. 15–April 1),** (C) **passage abundance of parr and smolt at Oakdale, and** (D) **log-transformed total juvenile passage at Oakdale. Dashed lines indicate the 95% confidence interval for the regression line.**

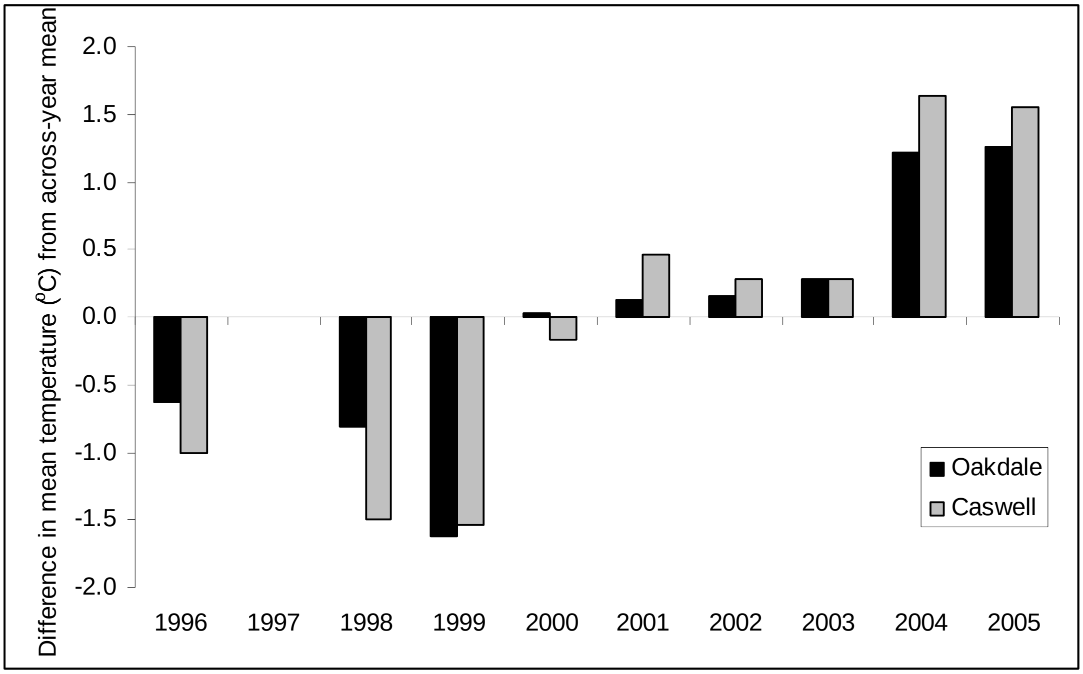


Figure 34. Difference in mean weekly temperature (˚C) from across-year mean from February 15-April 1.

Passage timing

We investigated the potential effects of changes in flow, turbidity, and precipitation on the migration behavior of the juvenile Chinook salmon by comparing these variables against daily passage estimates at the Oakdale and Caswell trap sites. It has been well established that variations in flow can influence the migration of juvenile Chinook salmon, in particular fry, in the Stanislaus River (e.g., Cramer and Demko 1993; Demko 2004). Thus, our primary purpose was to develop a series of exploratory plots so that the data could be readily compared across years 1996-2005, and to gather any new insight from recent years of data.

In the following sections, we provide brief summaries for each environmental variable and example plots for three years (1999, 2001, and 2005). A complete set of plots for each variable across all years with available data are provided in Appendix A. Also included in Appendix A are annual plots of daily passage estimates with superimposed values for daily mean length of juveniles. We also examined the potential effects of stream temperature, but temperatures did not appear to strongly influence passage timing of juveniles either within or between migration seasons. These plots are therefore not included in Appendix A, but are readily available.

Effects of flow

A consistent pattern in migrations of juvenile Chinook salmon observed in all years was an extensive downstream dispersal of newly emerged fry from late January through early March. Throughout this period, large pluses of fry were invariably associated with increases in flow of one form or another. In years with sustained high flows during fry migration (e.g., 1998 and 1999), fry movement passed Oakdale was more evenly distributed across weeks than in low flow years, and fry pulses appeared to occur for sustained periods after a somewhat delayed response to a steady, multi-day increase in flow (e.g., Figure 35). In contrast, in years with predominantly low flows during fry migration, it appeared that only small fluctuations in flow were necessary to initiate mass movements of fry passed Oakdale (e.g., Figure 36 and Figure 37). Note that in 2001, fry appeared to respond in mass numbers to rain-driven freshets that increased flows by less than 50 cfs at either the OBB or RIP gauges (Figure 36). Consequently, fry pulses in low flow years were typically much more sporadic and short in duration (e.g., 1-3 days) than in years with higher flows during fry migration.

Demko (2004) observed that while substantial passage of fry occurred during relatively small pulse flows (< 750 cfs) at Oakdale, these flows were not sufficient to sustain fry migration to the Caswell site (e.g., Figure 36). Our passage estimate corroborate yield similar findings. For example, the proportion of fish passing Caswell relative to Oakdale was approximately 81% and 46% during large increases in flow of approximately 4,100 cfs and 2,400 cfs in 1998 (Jan 28- Mar 5) and 1999 (Jan 18 – Feb 1) respectively. Conversely, the proportion of fry passing Caswell versus Oakdale during comparative small pulse flows of about 400 cfs and 70 cfs in 2000 (Jan 23 – 28) and 2001 (Feb 10 – 16) was only 12% and 0.1 % respectively.

In general, downstream migrations of parr and smolts were not as strongly influenced by variations in flow (e.g., Figure 36). As indicated in previous reports of juvenile Chinook migration in the Stanislaus River, the magnitude of flow may play a greater role in influencing smolt migration than variability in flow conditions (Demko et al. 2000).

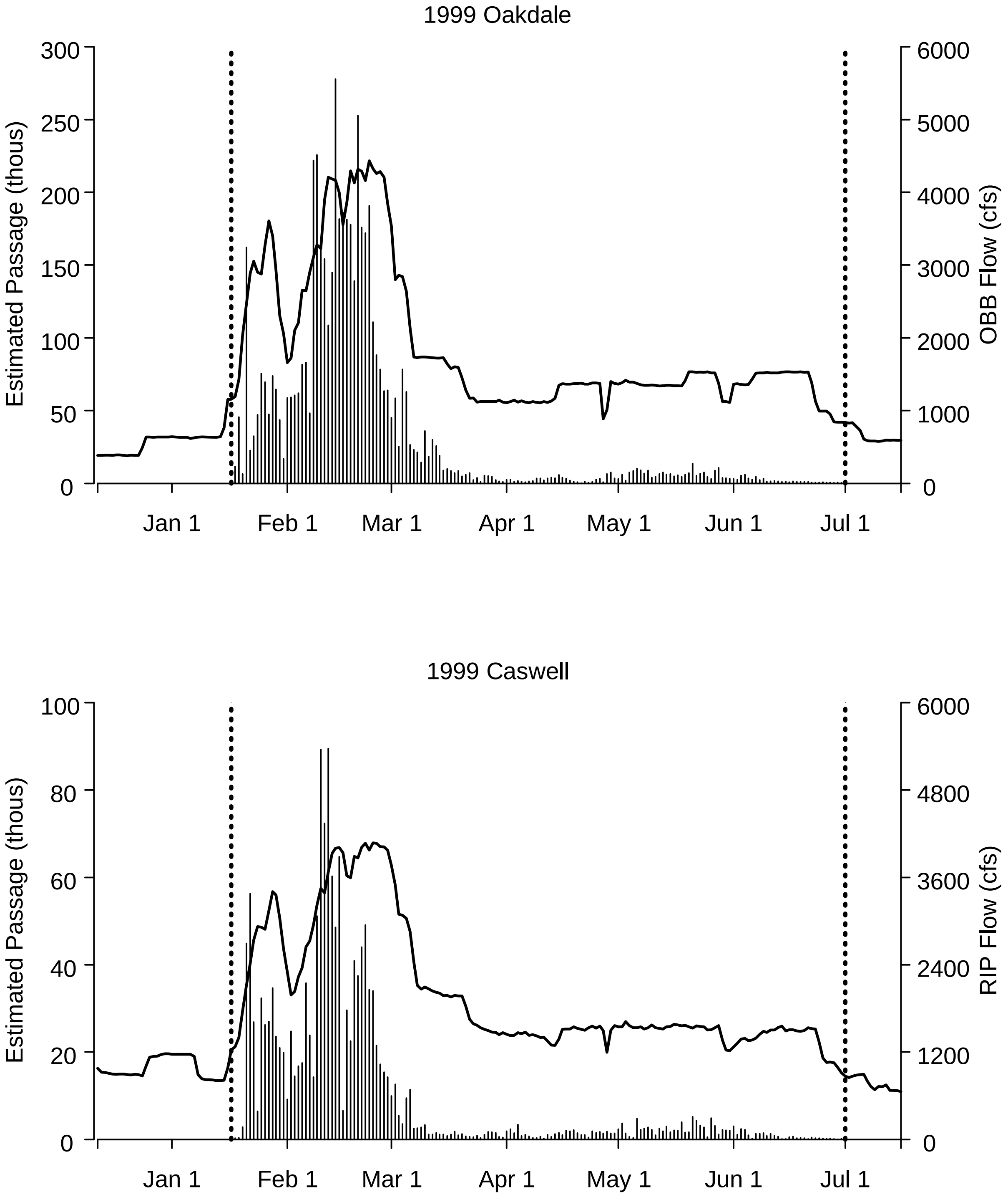


Figure 35. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 1999. Dotted lines indicate the start and end dates of trapping.

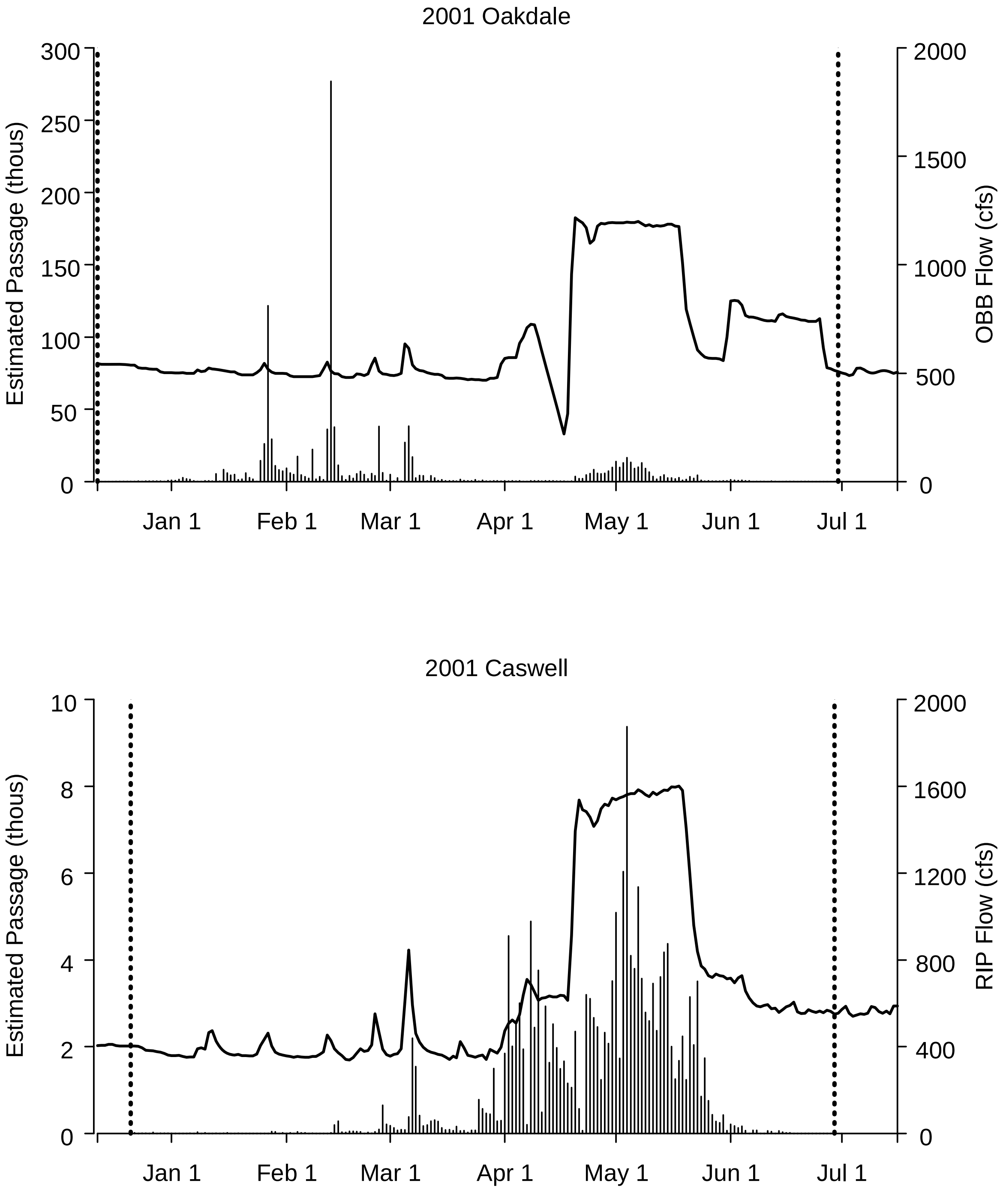


Figure 36. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 2001. Dotted lines indicate the start and end dates of trapping.

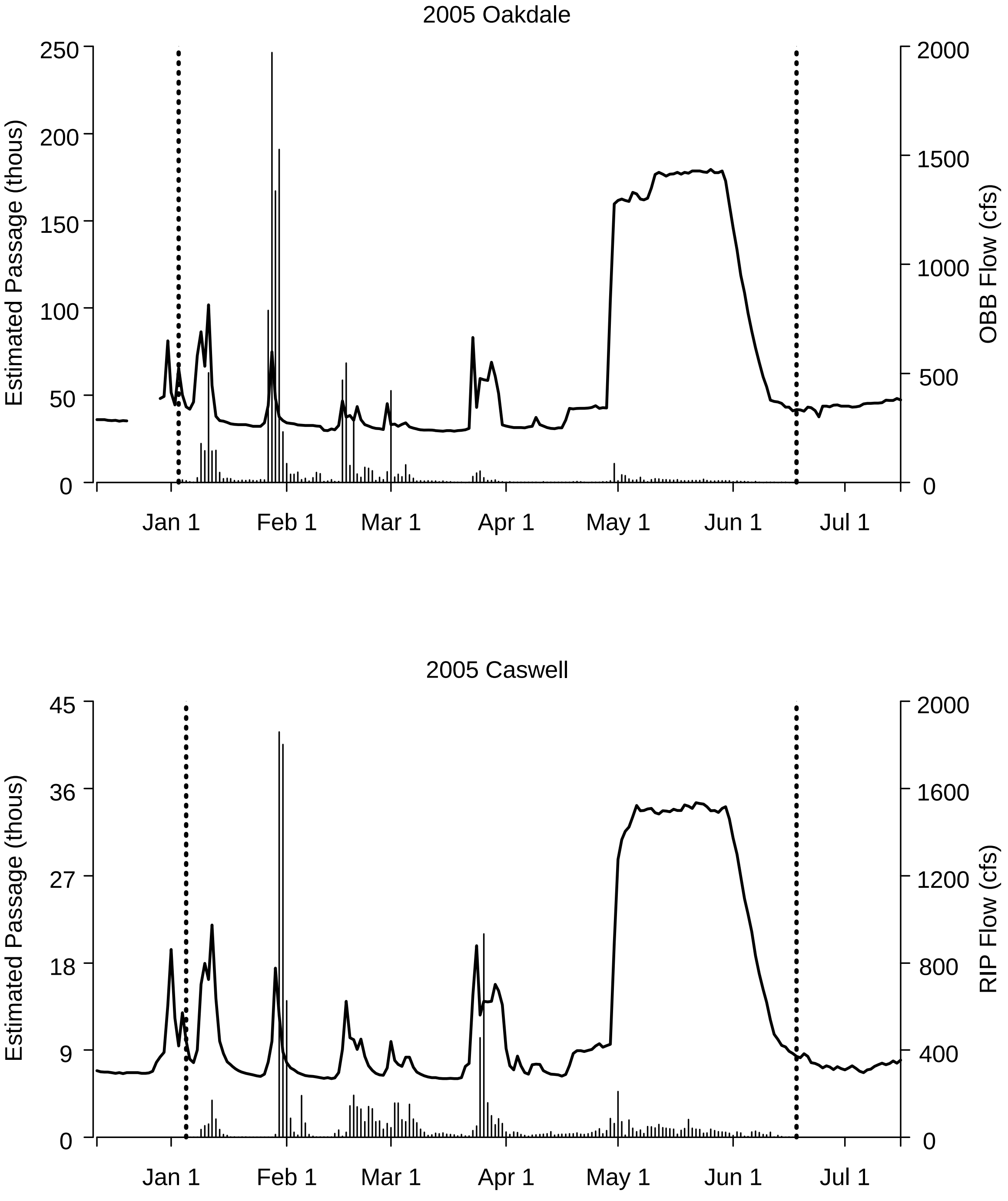
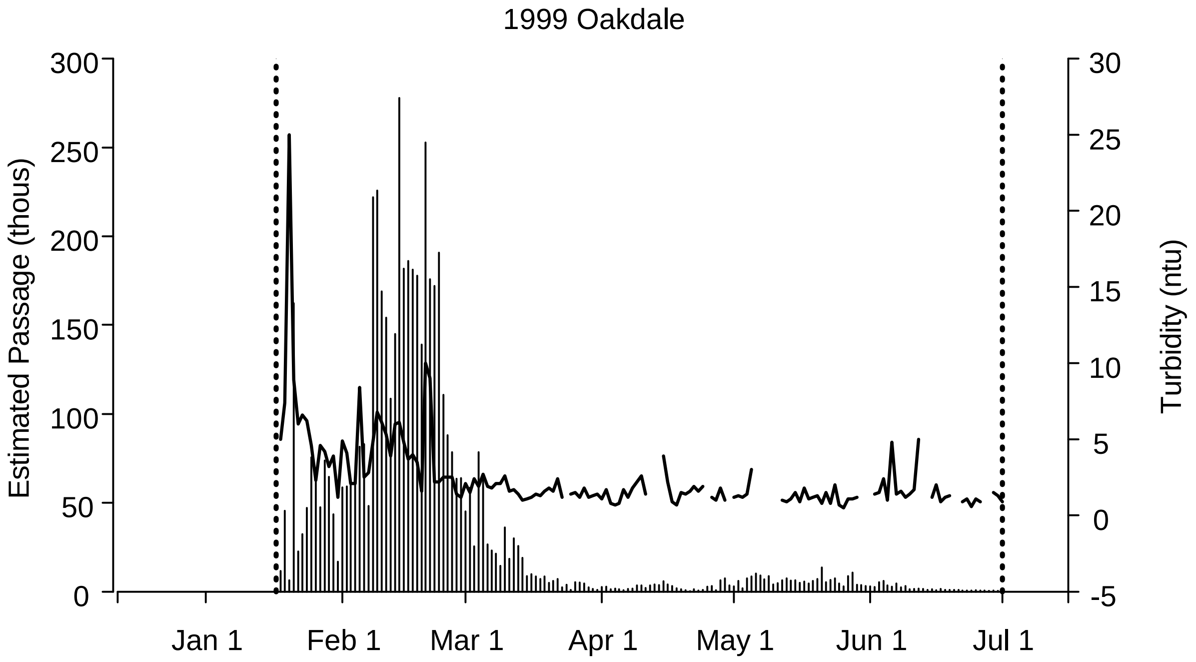


Figure 37. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 2005. Dotted lines indicate the start and end dates of trapping.

Effects of turbidity

Turbidity was strongly associated with large pulses of migrating fry in some years, though this effect was not consistent across all years. In years with sustained high flows during fry migration (e.g., 1998 and 1999), mean turbidity levels were above average at both trap sites, but extreme turbidity events were relatively rare, especially for Oakdale. Under these conditions, fry migration was more evenly distributed across weeks, and fry pulses did not appear to be strongly associated with fluctuations in turbidity (e.g., Figure 38). However, a high turbidity event was recorded at Caswell in early February of 1999, and was associated with several days of high juvenile passage at Caswell (Figure 38).

More obvious associations between turbidity and fry passage were observed in years with moderate to low flow, such as 2001 (Figure 39) and 2005 (Figure 40). In low flow years, there appeared to be a greater tendency for extreme increases in turbidity and corresponding migrations of fry that coincided with natural freshets. In particular, several extreme turbidity events (> 20 or 30 NTU) occurred at both trap sites in 2005 and were associated with high passage rates at both sites. For example, in what appears to be rain-driven freshet, flows at OBB briefly rose from 274 cfs on January 26 to 599 cfs on January 28 (a modest 325 cfs increase), with turbidity at Oakdale peaking at 30 NTU (Figure 40). In the four days from January 27-30, an estimated 703 thousand fry passed the Oakdale trap. Flows at Ripon increased from 289 cfs on January 27 to 777 cfs on January 29 (a 488 cfs increase), with turbidity at Caswell peaking at 40 NTU. Passage at Caswell increased dramatically from January 30 to February 1, with an estimated passage of 96 thousand fry. Thus, an estimated 14% of fry passing Oakdale also passed Caswell. Given the relatively low increase in flow, it seems likely that the high turbidity levels were instrumental in encouraging fry to continue migrating and/or reducing their risk or predation during migration.



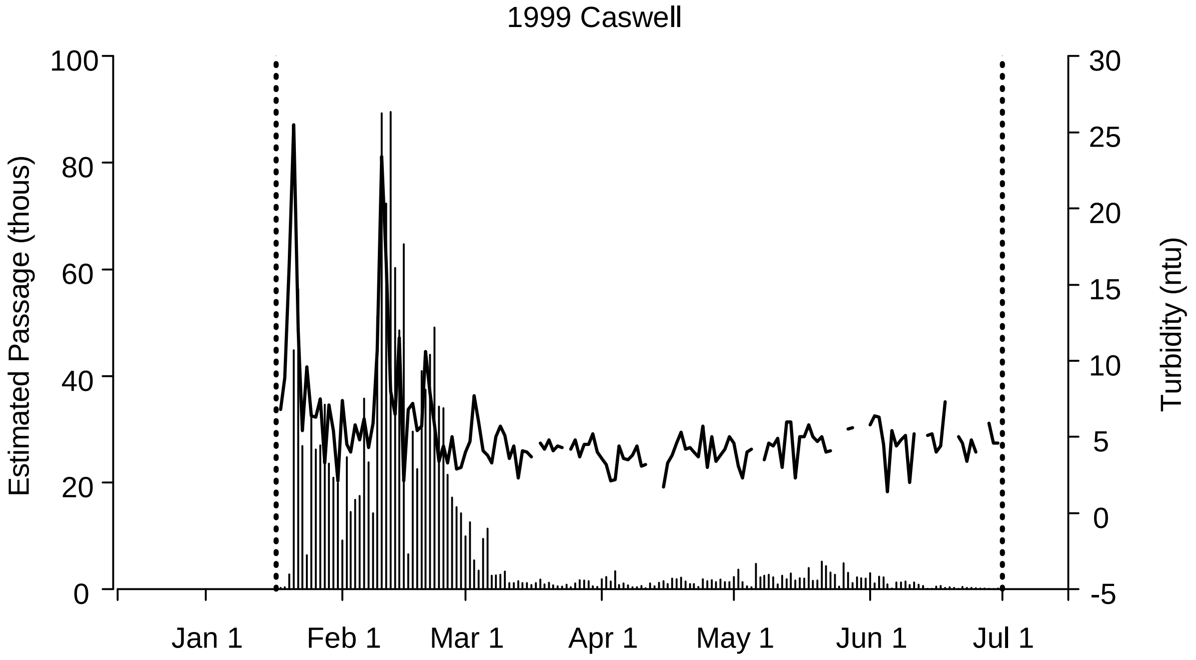
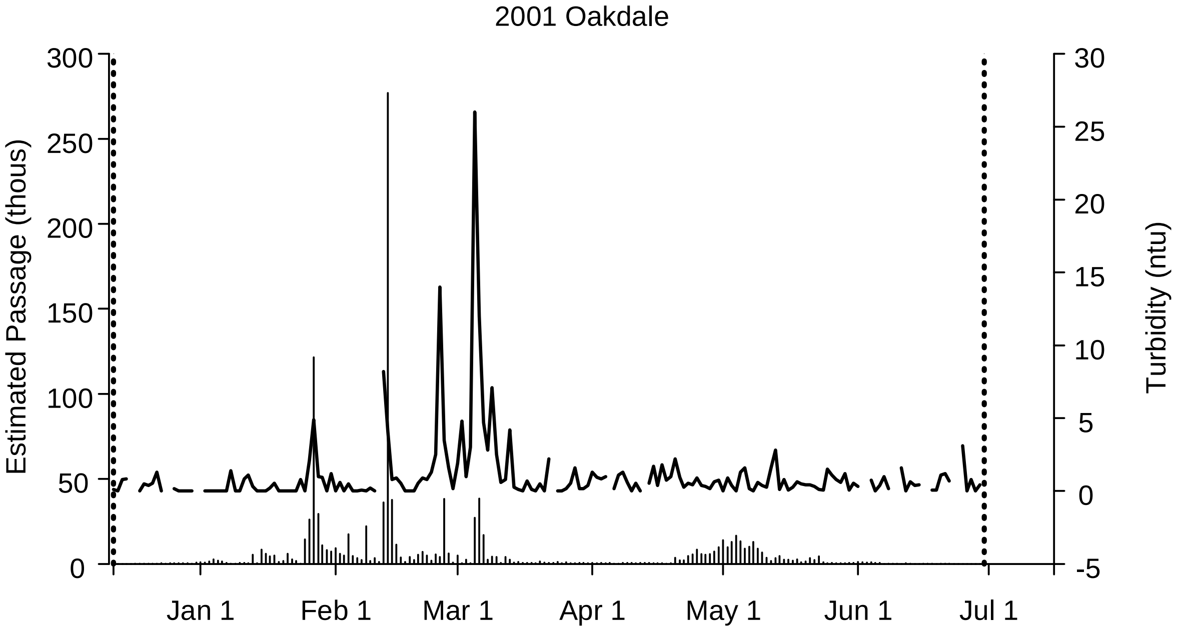


Figure 38. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 1999. Dotted lines indicate the start and end dates of trapping.



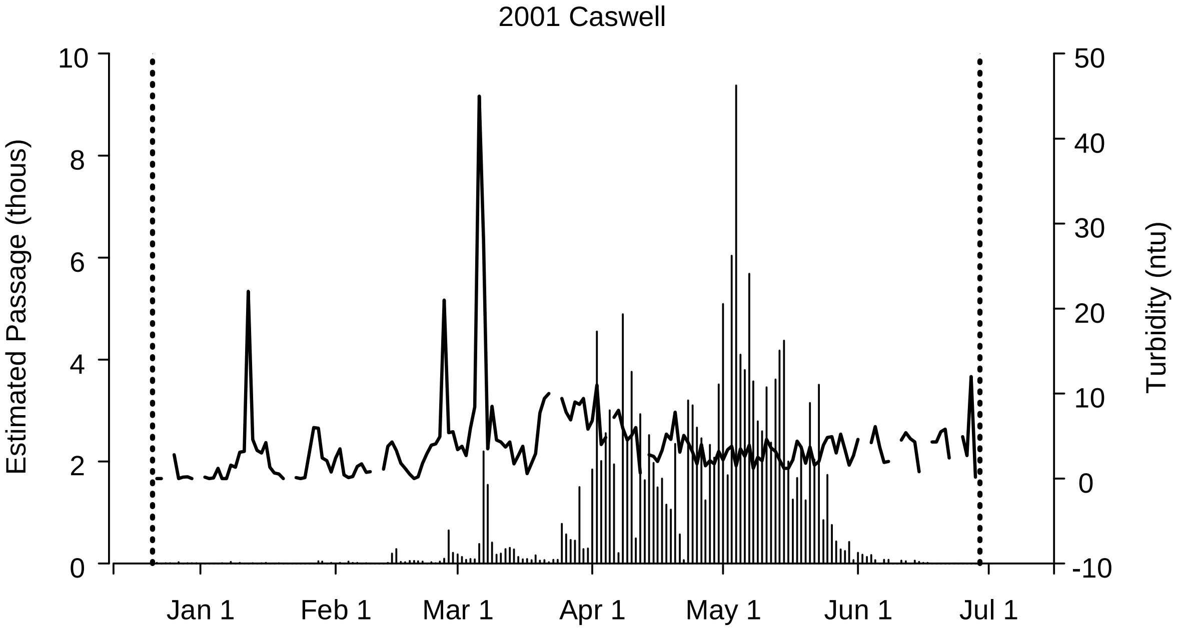


Figure 39. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 2001. Dotted lines indicate the start and end dates of trapping.

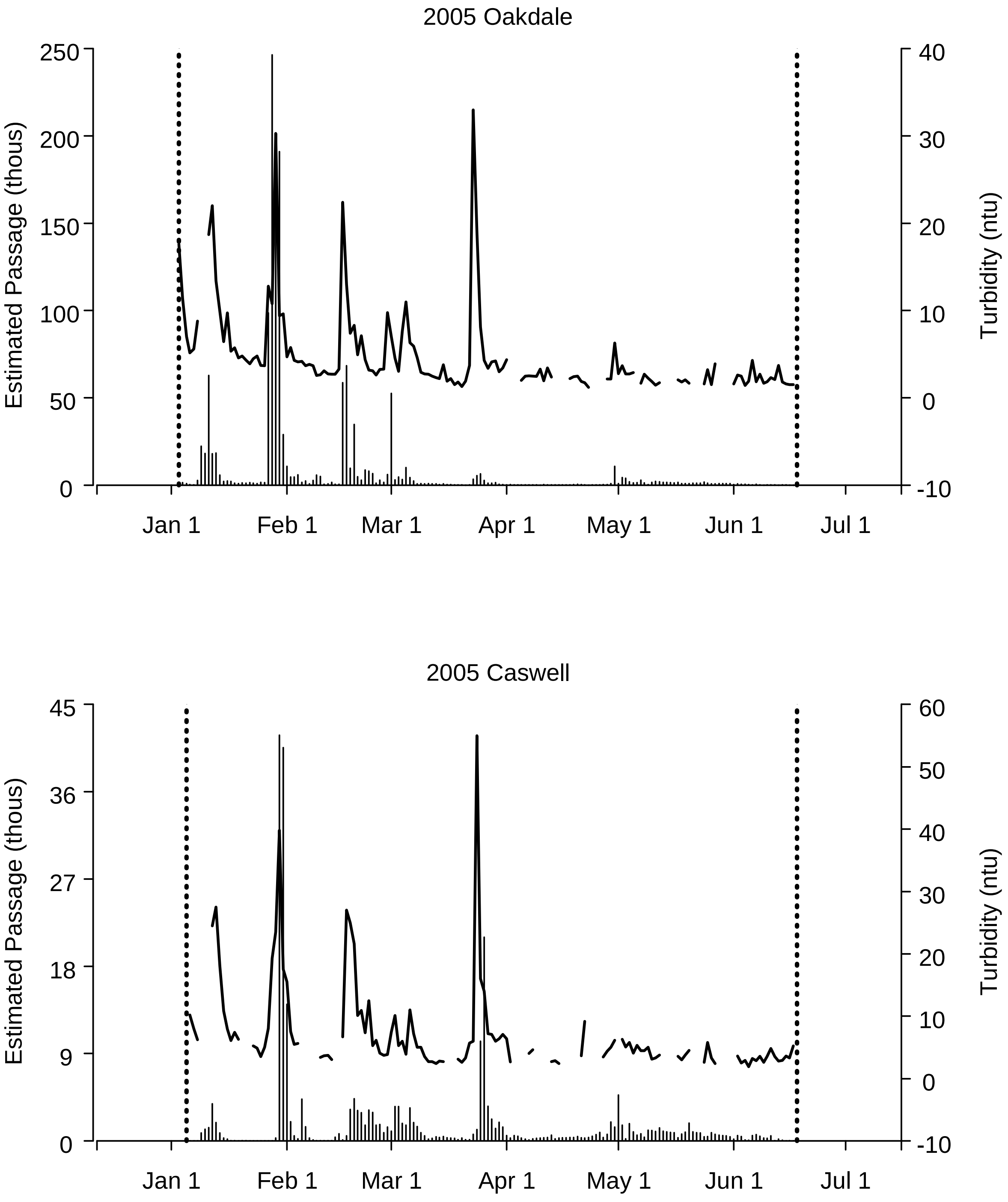
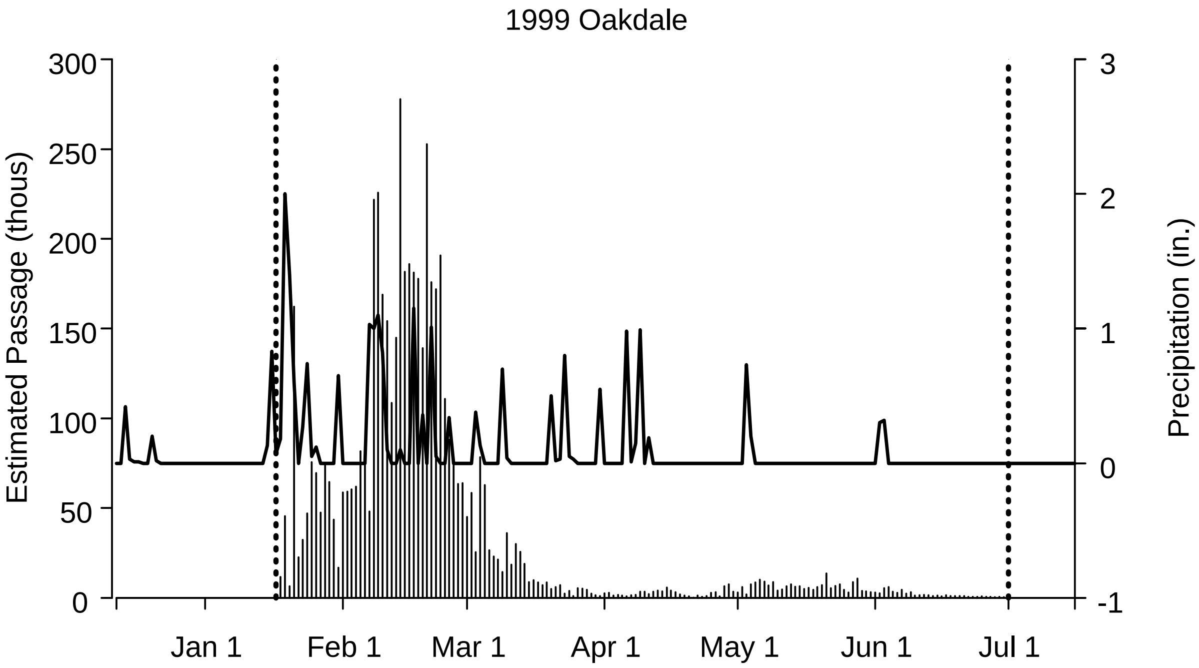


Figure 40. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 2005. Dotted lines indicate the start and end dates of trapping.

Effects of precipitation

Precipitation measured at New Melones ranged from about 0-3 inches per day between December 12 and July 16 across all years. In high flow years, rainfall had a relatively minor effect on the stream hydrograph compared with large flow releases from Goodwin Dam. There were instances, however, where rain events appeared to be associated with spikes in turbidity and increased passage at both sites (e.g., early February of 1999; Figure 41 and Figure 38). During lower flow years, mass movements of fry were often stimulated by rain-driven freshets (e.g., Figure 42 and Figure 43). As noted above, the freshets in 2001 resulted in flow increases of less than 50 cfs (Figure 36), yet several hundred thousands fry were estimated to have passed Oakdale (Figure 42). In years such as 2004 and 2005, sharp increases in precipitation were clearly associated with natural pulse flow events (freshets), substantial increases in turbidity, and a corresponding increase in passage of fry (e.g., Figure 40). Although the effects of precipitation, turbidity, and flow were highly correlated in most cases, fry passage in 2002 provided some evidence that rainfall alone can be an important factor in stimulating the downstream migration of fry (see Figures in Appendix A). Sharp, periodic increases in fry passage between mid January and mid March of 2002 occurred during relatively stable flow conditions with little variation in turbidity. These peaks in fry passage appeared to coincide closely with rainfall events, suggesting that under some circumstances, small rain events alone can be an important environmental cue stimulating downstream migration of fry.



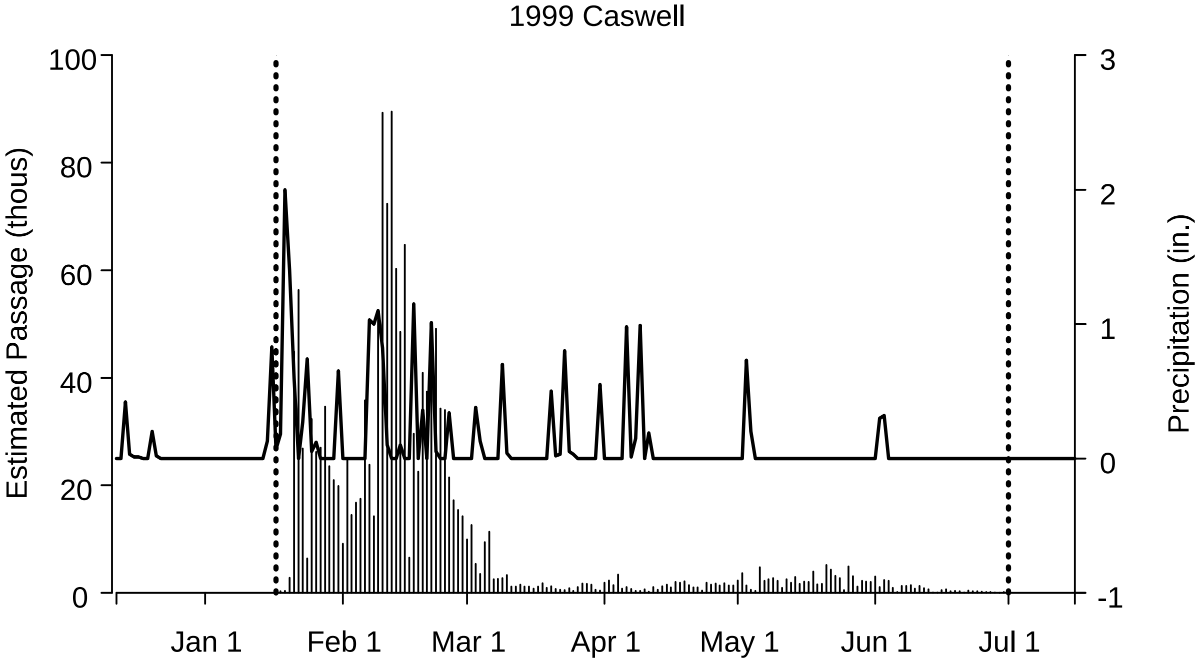


Figure 41. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones, 1999. Dotted lines indicate the start and end dates of trapping.

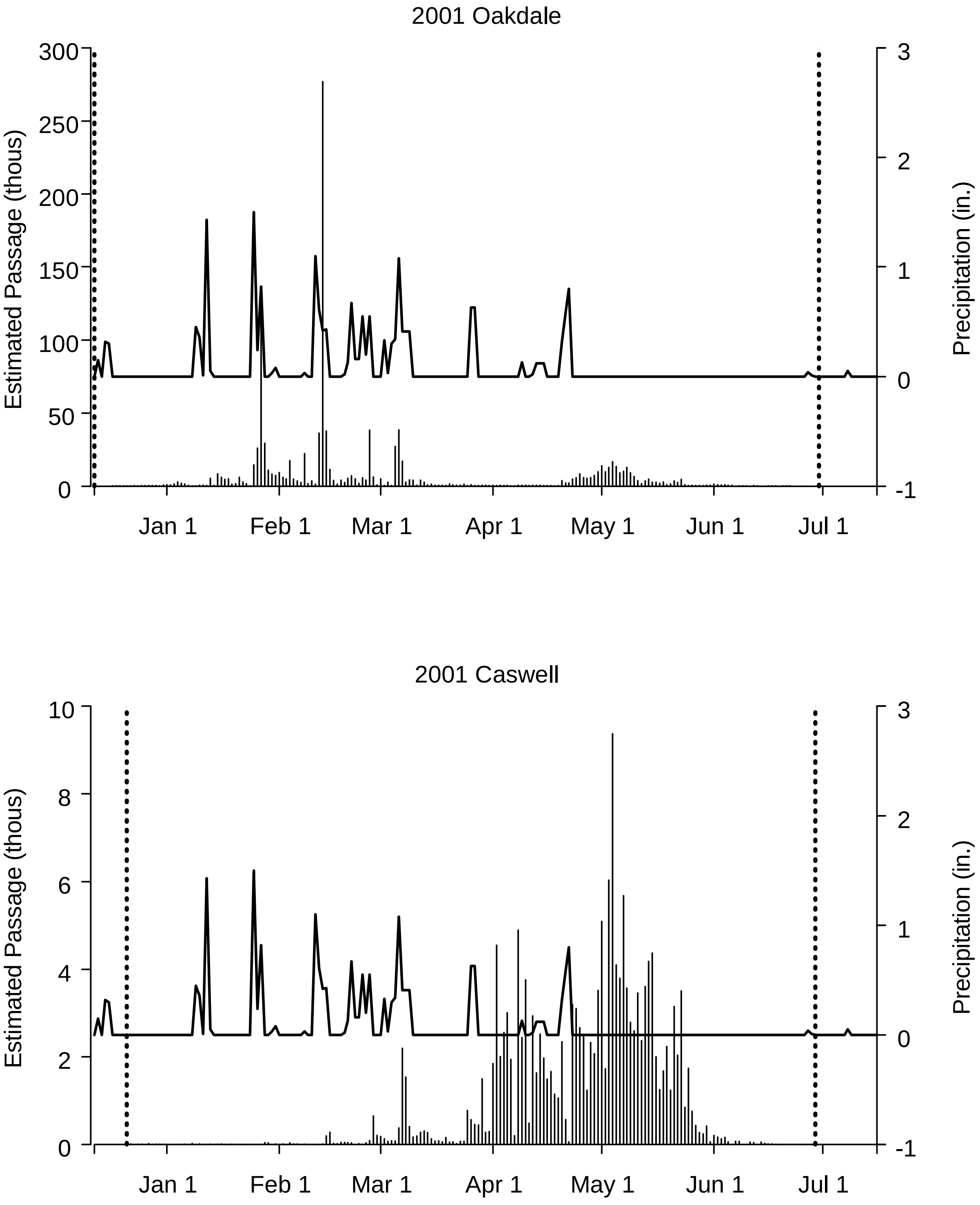
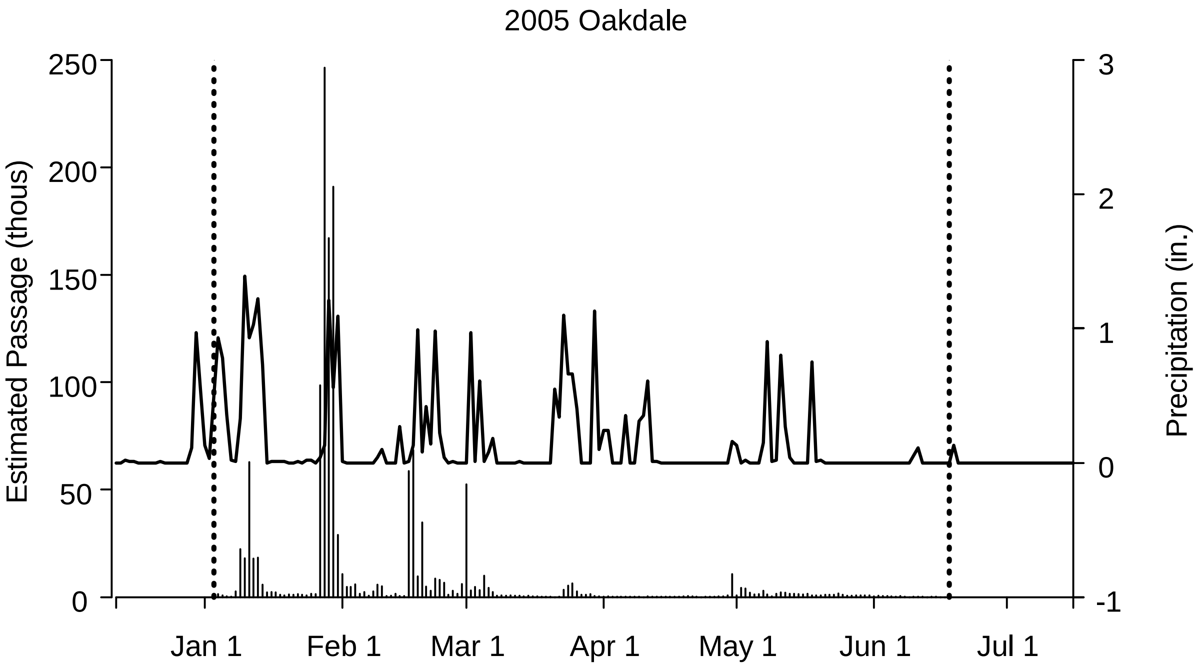


Figure 42. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones 2001. Dotted lines indicate the start and end dates of trapping.



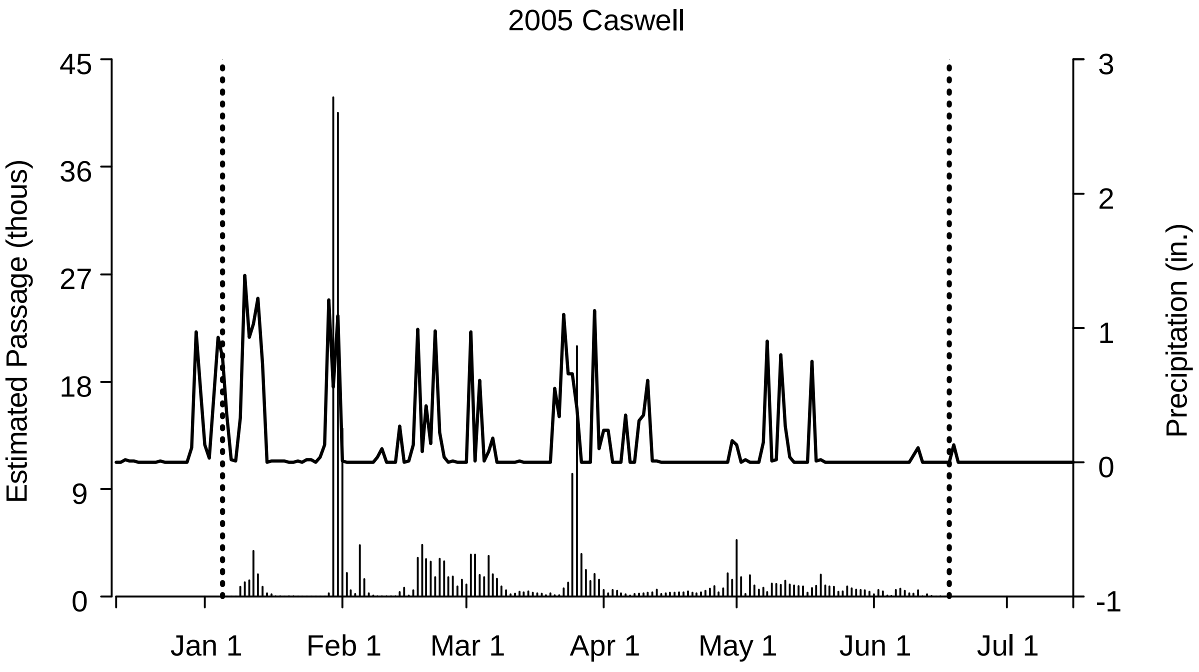


Figure 43. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones, 2005. Dotted lines indicate the start and end dates of trapping.

CONCLUSIONS

We found a significant ($P < 0.05$) relationship between flows at OBB and the annual survival-rate estimates, whereby higher flow was associated with higher survival. However, this relationship was highly dependent on the fry component of the migration. A high fraction (28% to 81%) of the fry passing Oakdale were also estimated to have passed Caswell in years with moderate flows during fry migration (1998-2000), but only 1% to 13% of migrating fry were estimated to have passed Caswell in years with lower flows (2001-2005). In contrast to fry, abundance ratios for parr and smolts more consistent across years, and were only weakly correlated with flows. This suggests that variations in flow or other conditions experienced by these life stages are less critical to parr and smolt survival than for fry. However, we did not explicitly test such hypotheses because abundance ratios for parr and smolts are potentially confounded as measures of survival rate if juveniles rear extensively between the trap sites.

We also found a significant, positive relationship between turbidity and overall survival rates. Mean turbidity levels were correlated with mean flows across years, so it is difficult to determine the relative importance of these variables from a statistical perspective. Nevertheless, the observed variations in annual flows undoubtedly have stronger effects on passage conditions and overall survival rates than the observed ranges in mean turbidity. Rather, it appears that turbidity can greatly enhance fry migration success to Caswell during periodic freshets when turbidity levels spike (e.g., > 20 NTU). Such conditions were more likely to occur during the fry migration period under sustained low flows (e.g., 2004 and 2005). Survival rates did not appear to be strongly related to variations in temperature across years.

Body size

We found moderately strong associations between mean lengths at Oakdale and annual measures of flow and juvenile abundance. The only significant relationship, however, was between mean length and log-transformed values of total passage at Oakdale. This relationship implied a strong density-dependent effect on body size, suggesting that juveniles experienced higher growth rates (reduced competition) when abundances were low. The relationship was largely driven by the data for 1996, for which juveniles were especially large and total passage at

Oakdale was the lowest on record. Variations in juvenile length did not appear to be strongly related to either temperature or turbidity conditions.

There were also obvious differences in mean lengths between the Oakdale and Caswell sites. Juveniles migrating past Caswell (February 26 – May 20) were found to significantly larger than those at Oakdale in all years. Differences ranged from just 0.8 mm in 1998 to 13.4 mm in 2005. These differences between Caswell and Oakdale lengths were most prominent in years with low flow, such as during March and April of 2002, and throughout most of the parr and smolt migration in 2003 and 2005. These results suggests that juveniles may rear extensively between the trap sites, especially in low flow years. Alternatively, such patterns could also arise if predation of juveniles is strongly size dependent, such that smaller individuals suffer much higher mortality rates.

Juvenile Rearing

We found additional evidence that juveniles rear extensively between the trap sites. We examined ratios of Caswell versus Oakdale passage abundance computed across weekly intervals and across discrete length groups (5 mm intervals). A high abundance ratio implies a large number of fish at Caswell relative to Oakdale. In many years, the weekly abundance ratios were quite low during fry migration (January - February), but then increased rapidly and often peaked above one during parr migration (March - April) before declining again during late parr and smolt migration (May). These patterns strongly suggest that juveniles rearing between the trap sites provided additional contributions to the passage at Caswell, often for numerous weeks during parr migration, for example. Similarly, there were several years for which the length-based abundance ratios were very high (e.g., > 1) across several length groups (predominantly within the parr size class). Clear examples of this evidence of juvenile rearing were found for years with moderate to high flows (e.g., 1998 and 2000) as well as low flows (e.g., 2004 and 2005).

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APPENDIX A

Juvenile Chinook salmon passage versus Flow

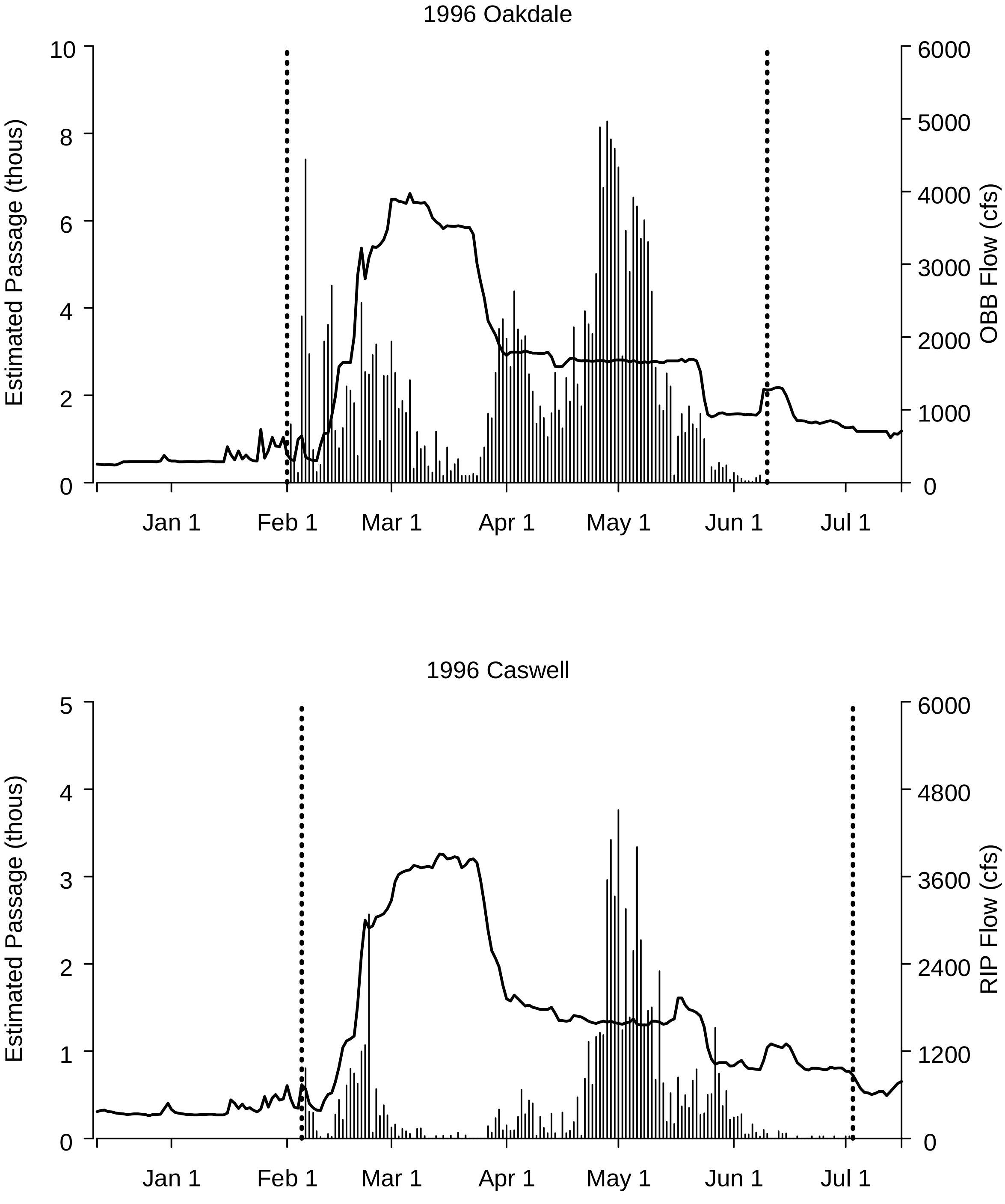
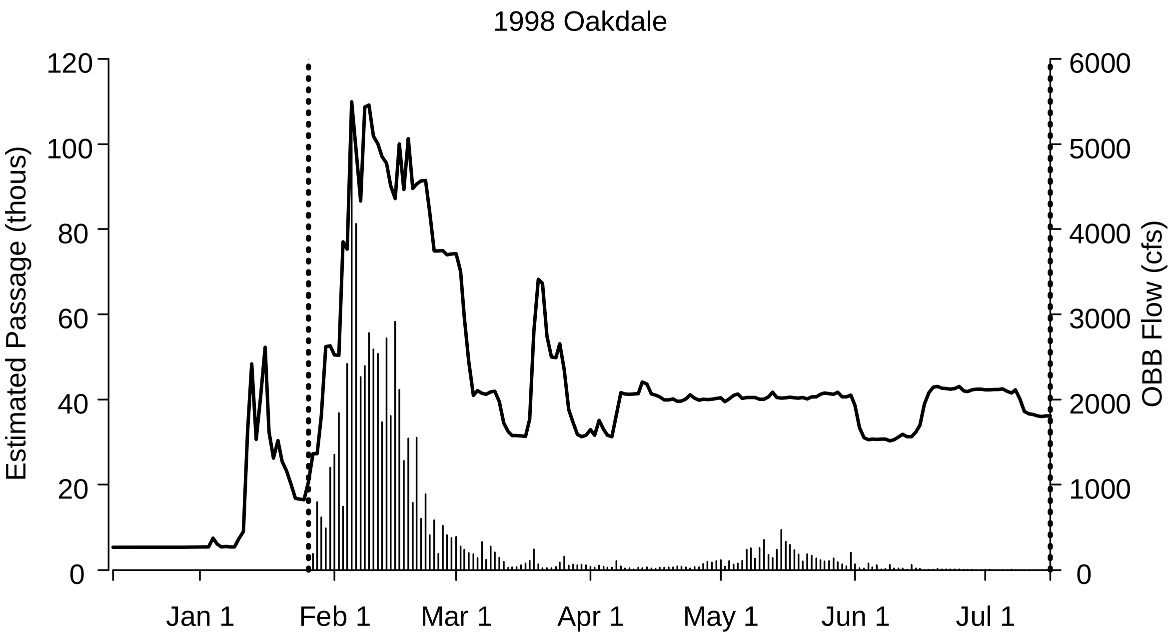


Figure A-1. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 1996. Dotted lines indicate the start and end dates of trapping.



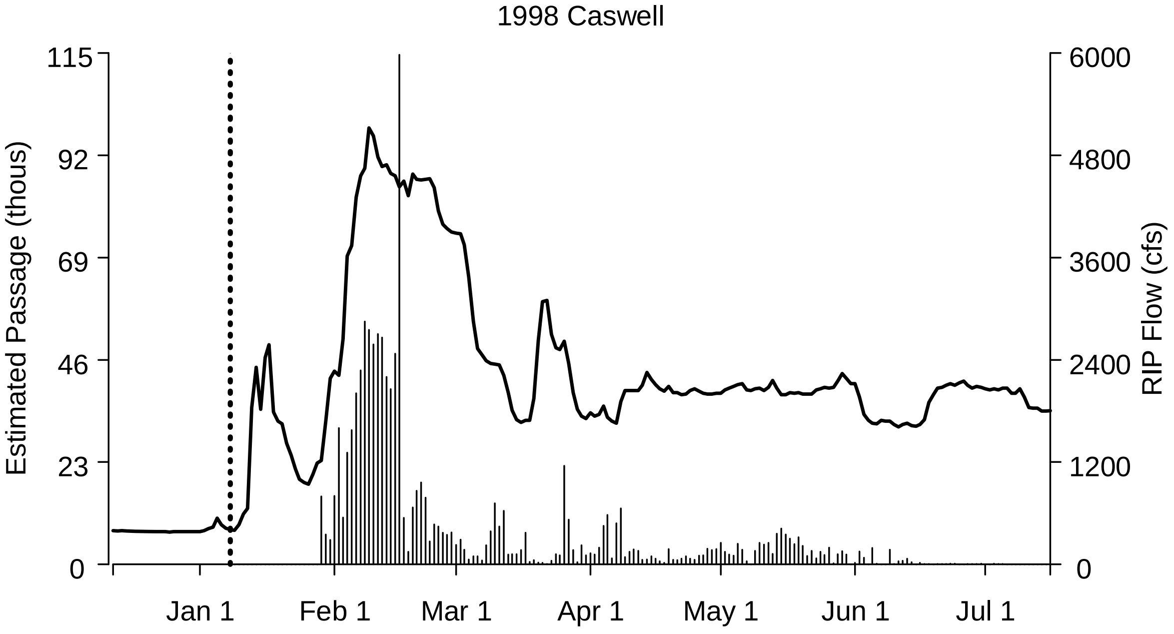
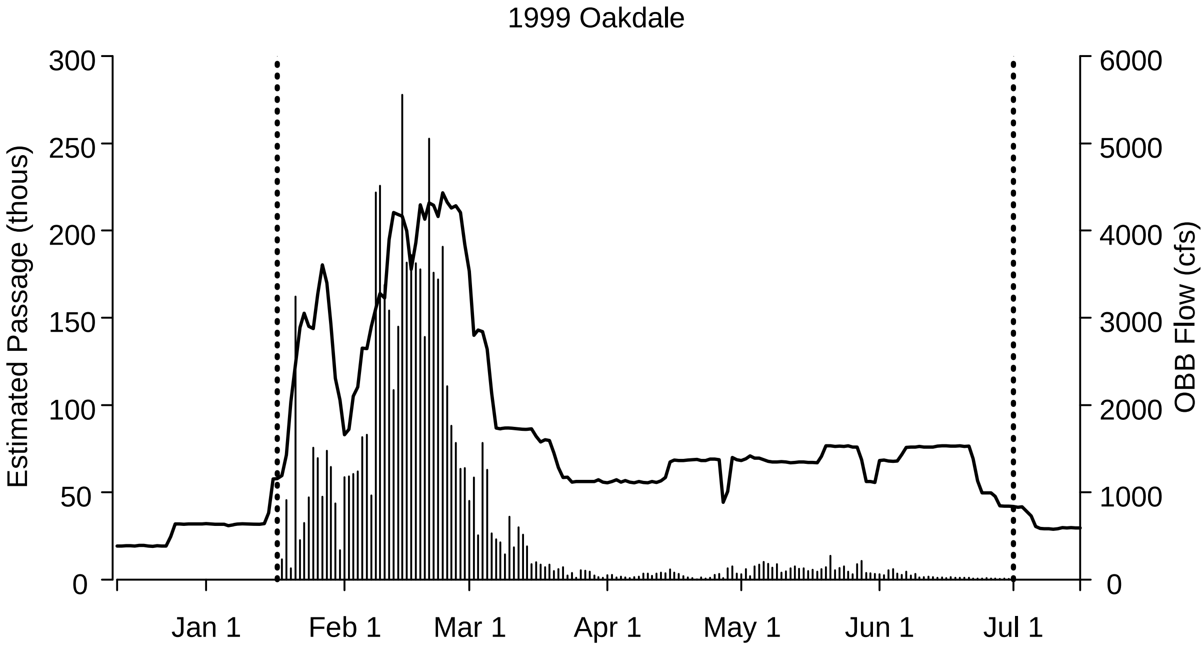


Figure A-2. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 1998. Dotted lines indicate the start and end dates of trapping.



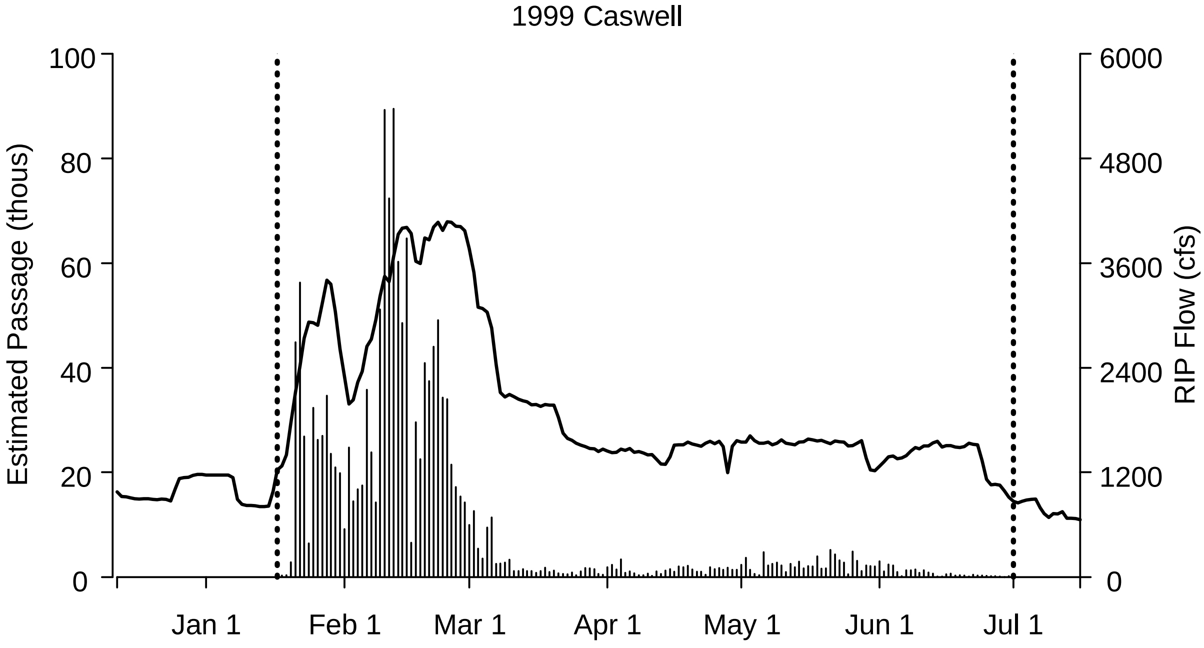
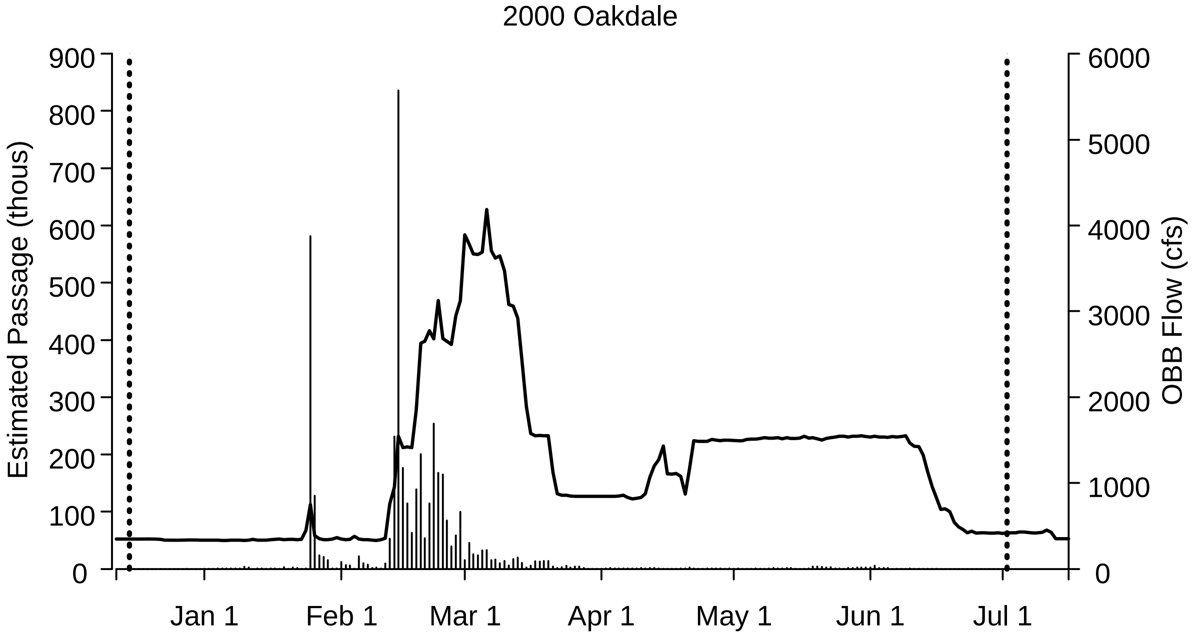


Figure A-3. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 1999. Dotted lines indicate the start and end dates of trapping.



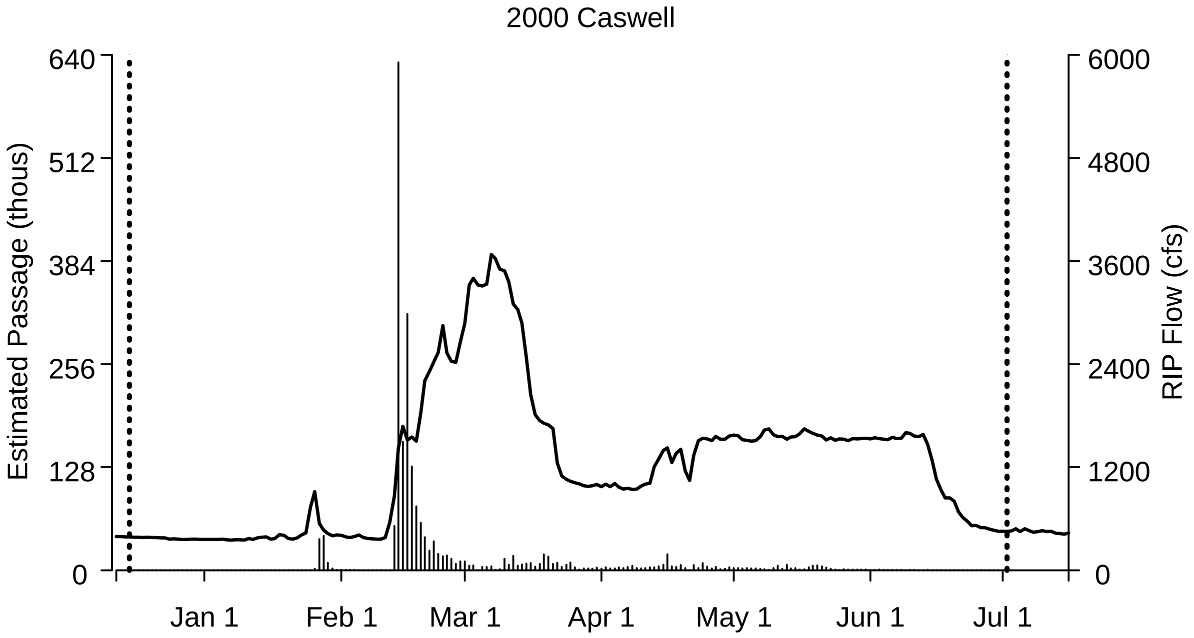
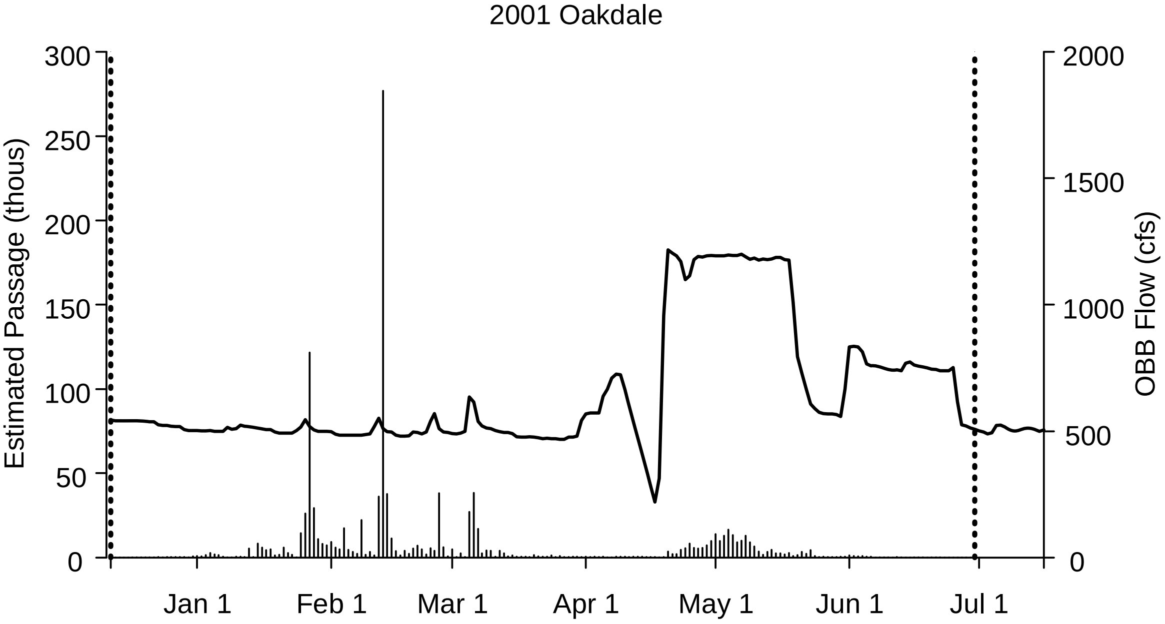


Figure A-4. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 2000. Dotted lines indicate the start and end dates of trapping.



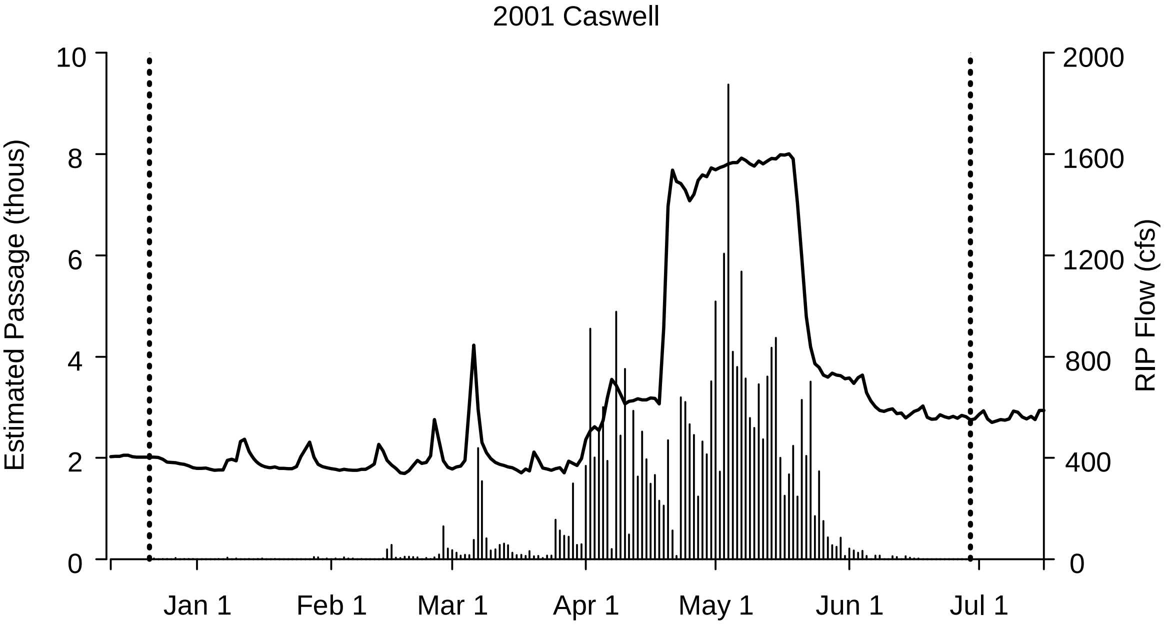
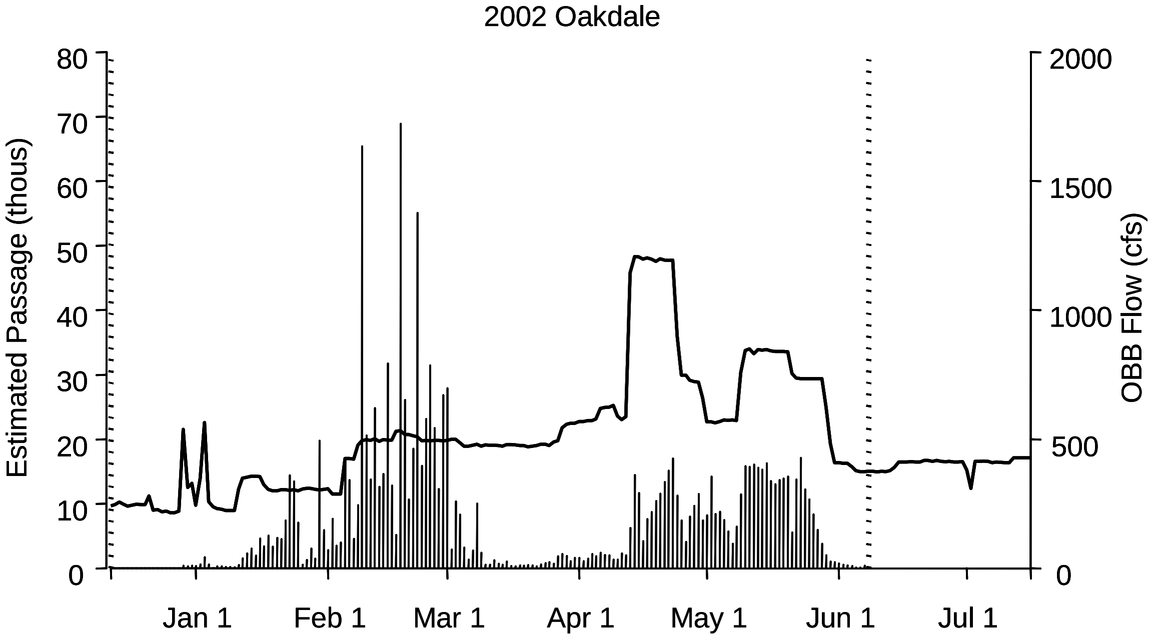


Figure A-5. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 2001. Dotted lines indicate the start and end dates of trapping.



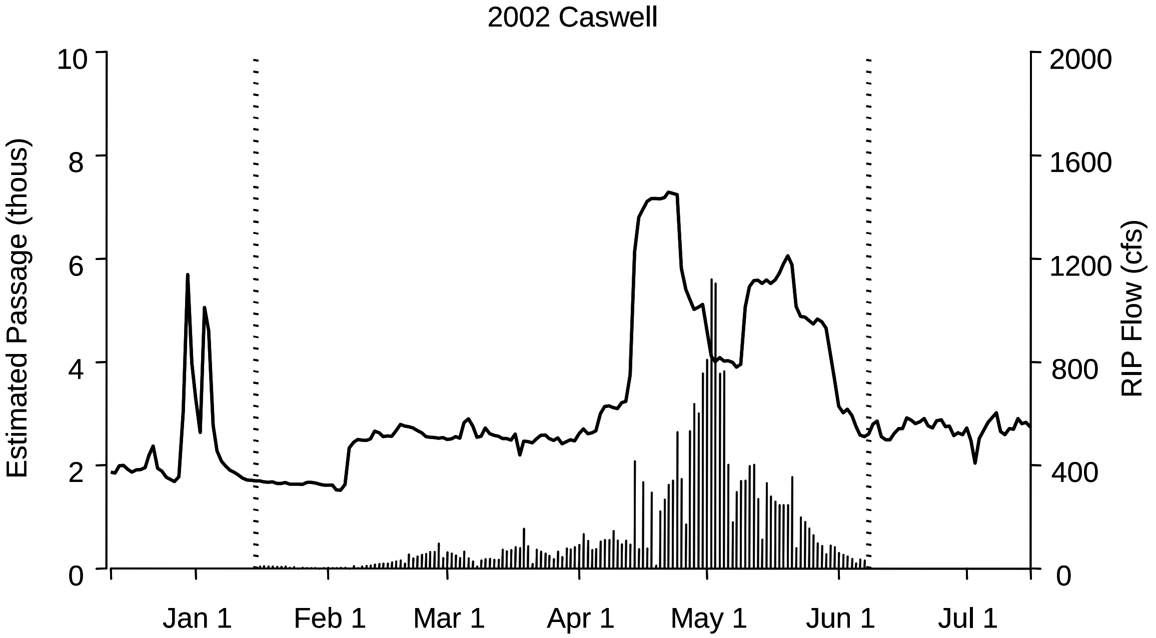
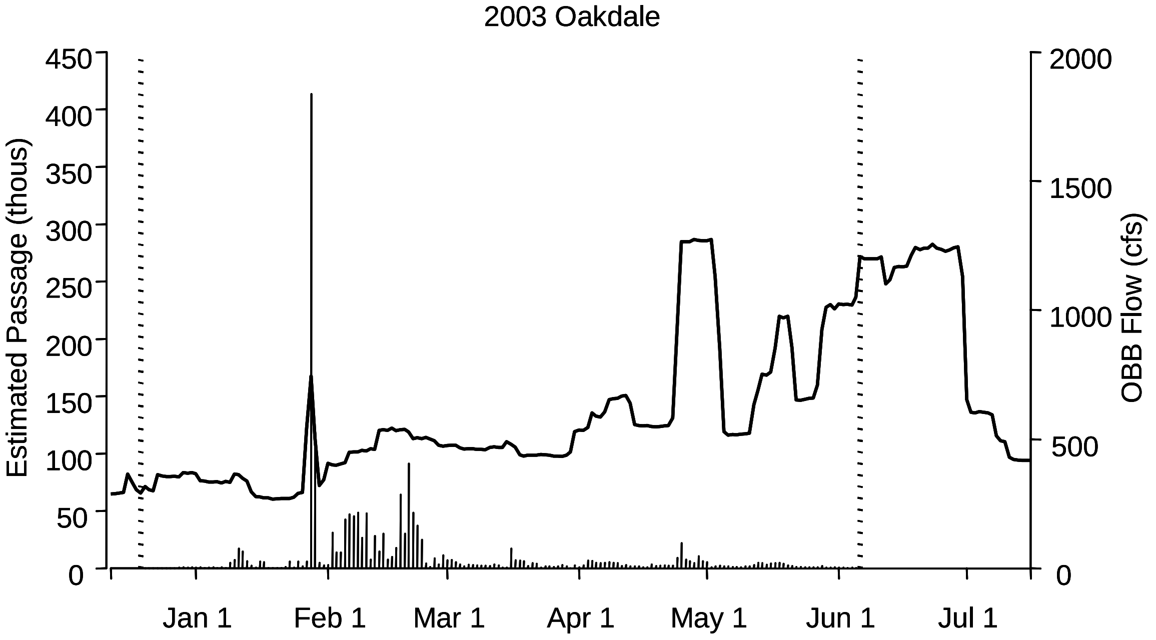


Figure A-6. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 2002. Dotted lines indicate the start and end dates of trapping.



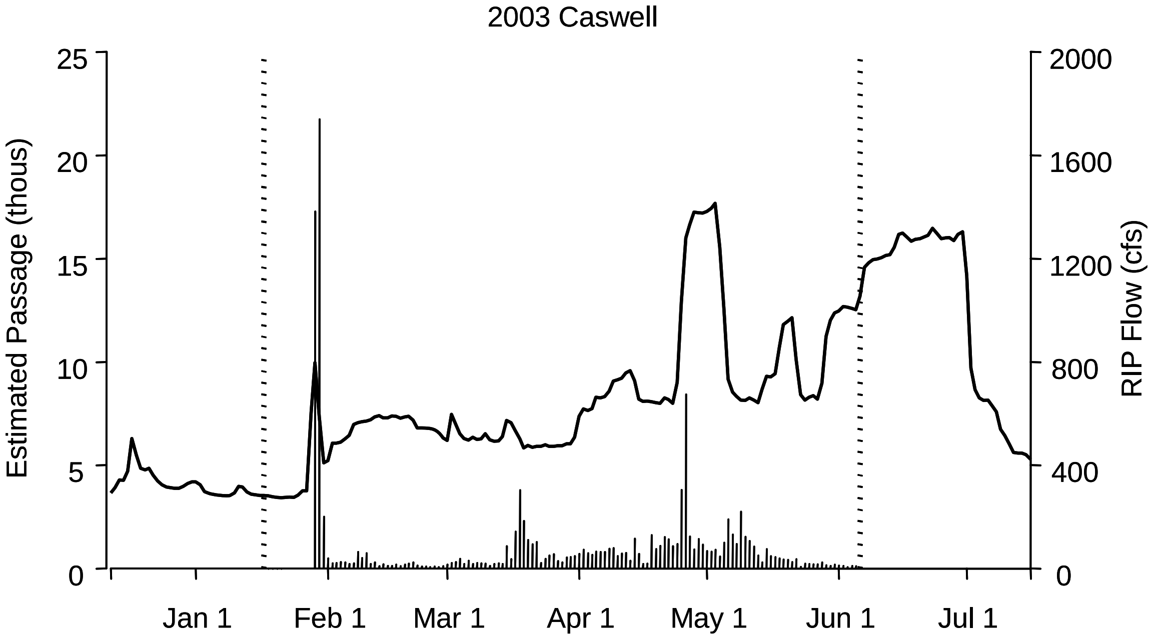


Figure A-7. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 2003. Dotted lines indicate the start and end dates of trapping.

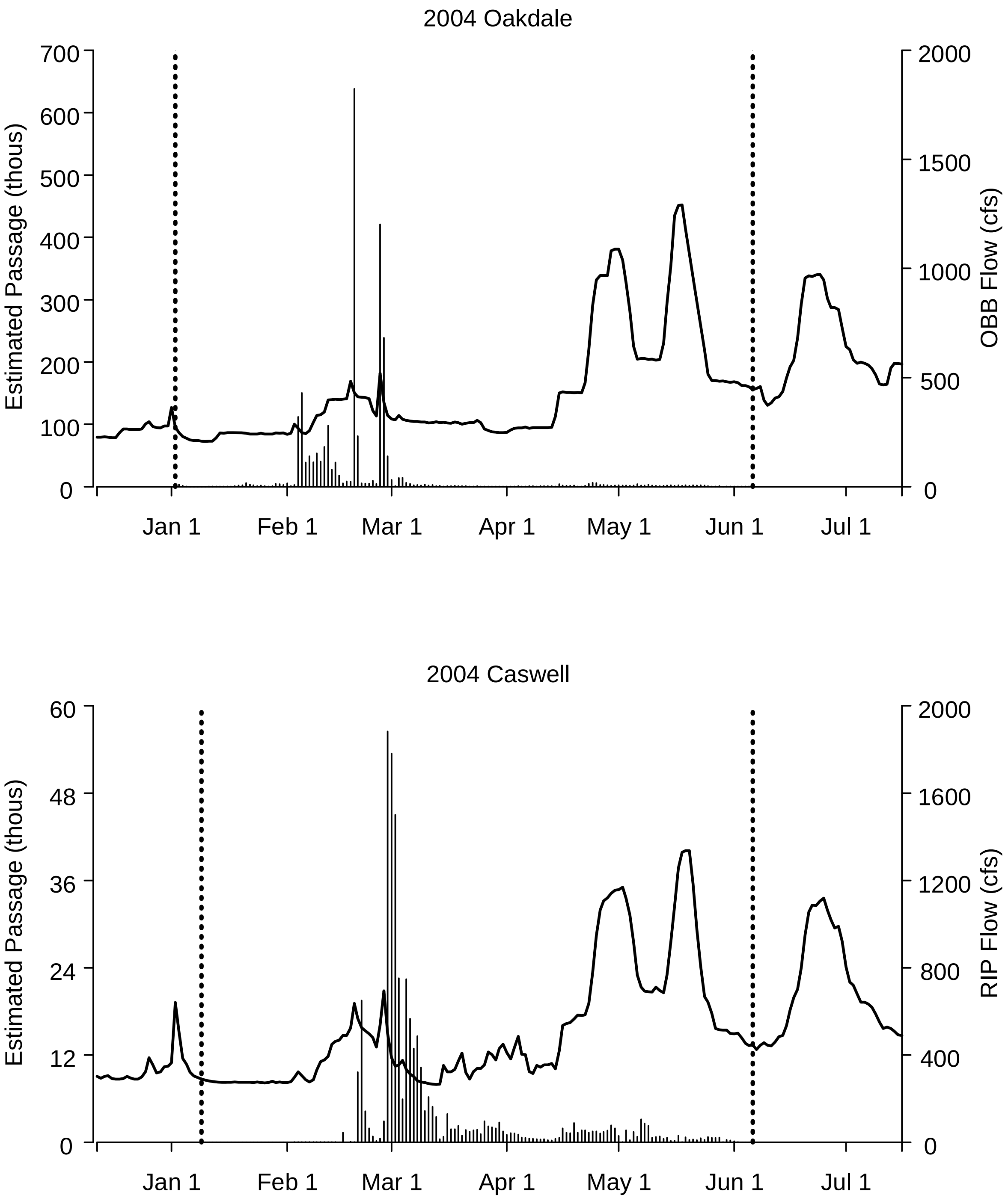


Figure A-8. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 2004. Dotted lines indicate the start and end dates of trapping.

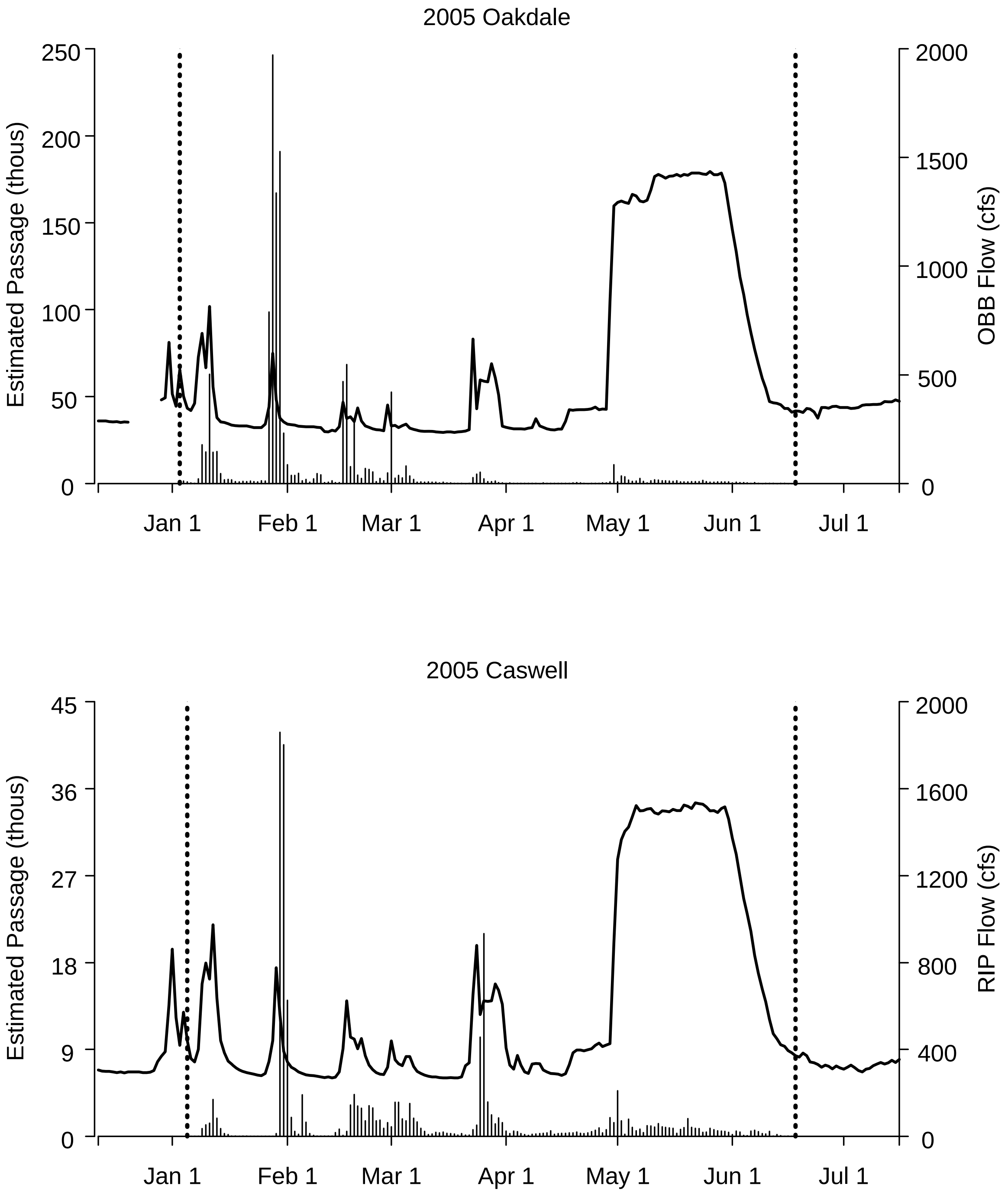


Figure A-9. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean daily discharge (cfs) in the Stanislaus River at Orange Blossom Bridge (OBB) and Ripon (RIP), 2005. Dotted lines indicate the start and end dates of trapping.

Juvenile Chinook salmon passage versus Turbidity

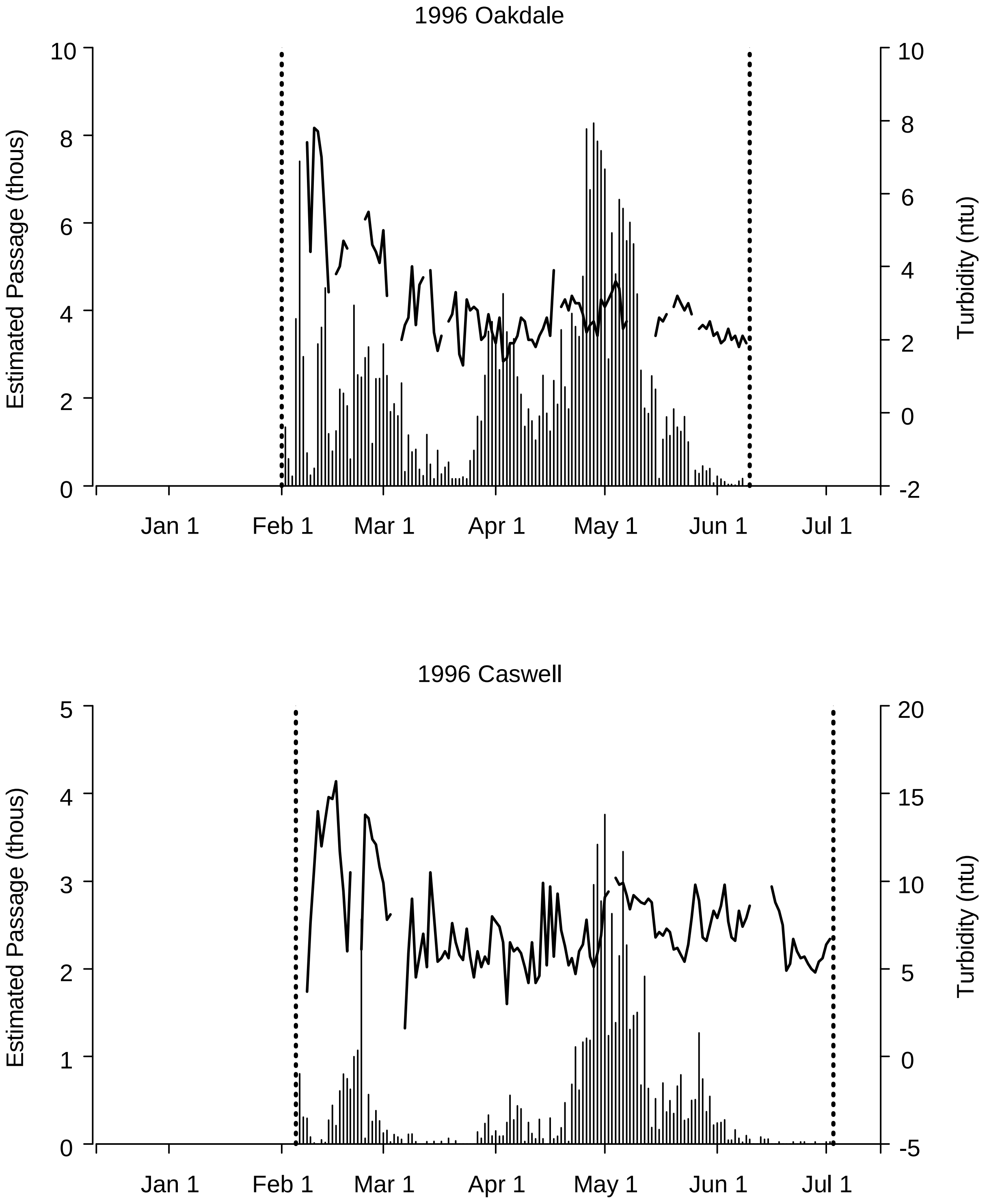
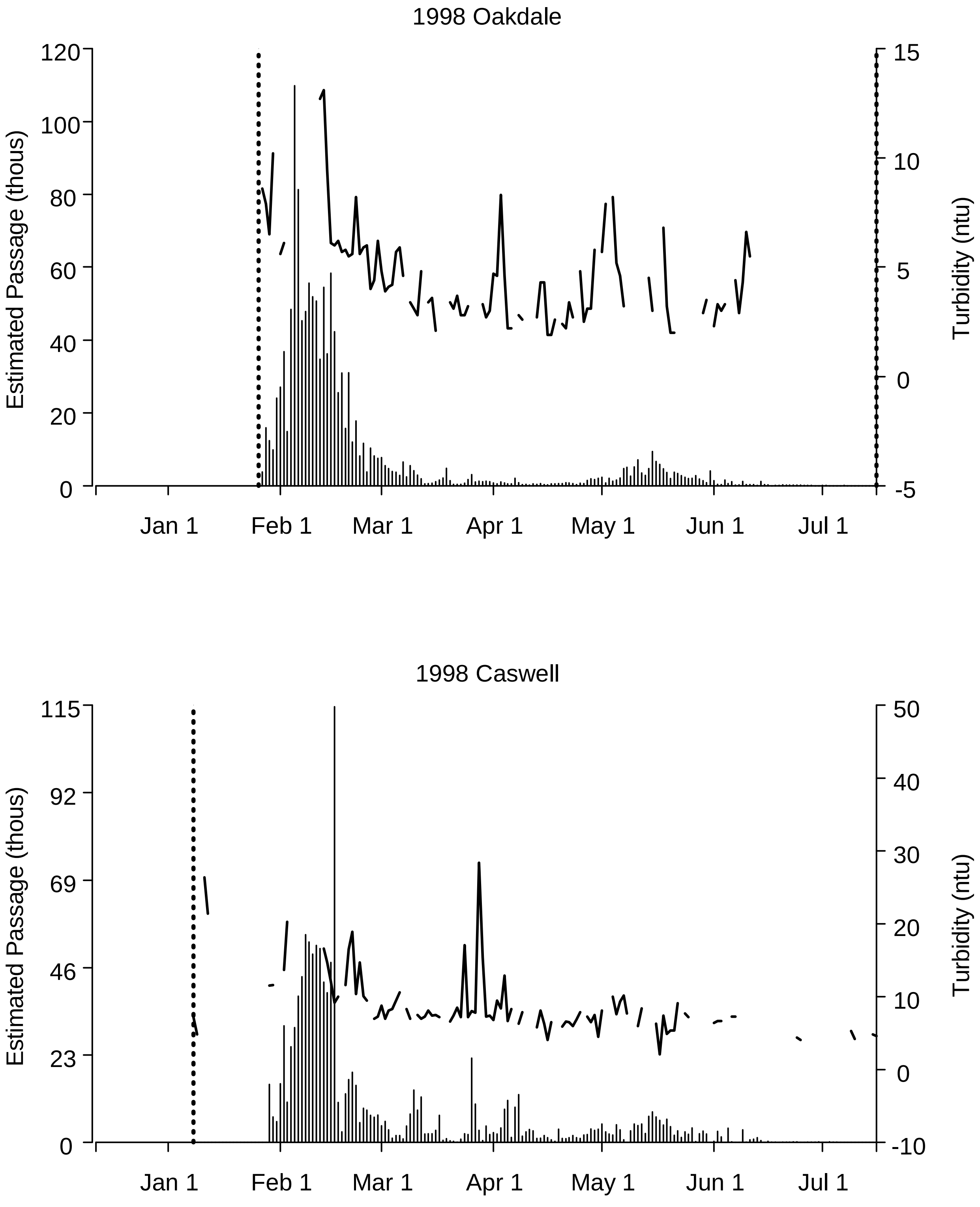
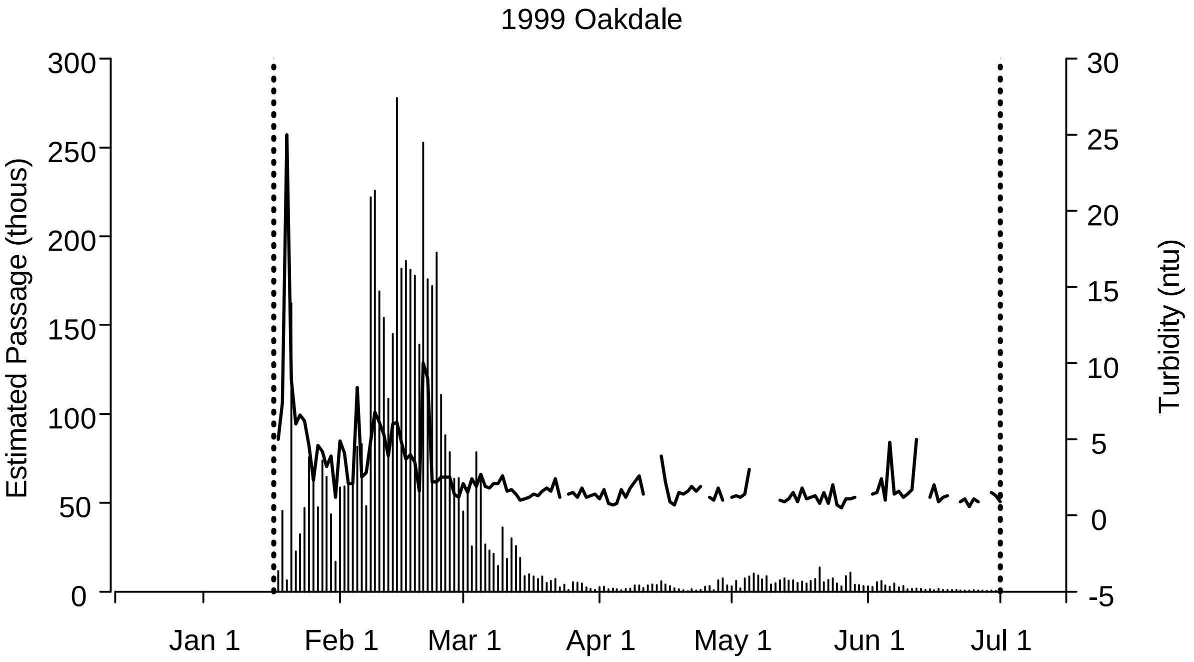


Figure A-1. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 1996. Dotted lines indicate the start and end dates of trapping.


1998 Oakdale

1998 Caswell

Figure A-2. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 1998. Dotted lines indicate the start and end dates of trapping.



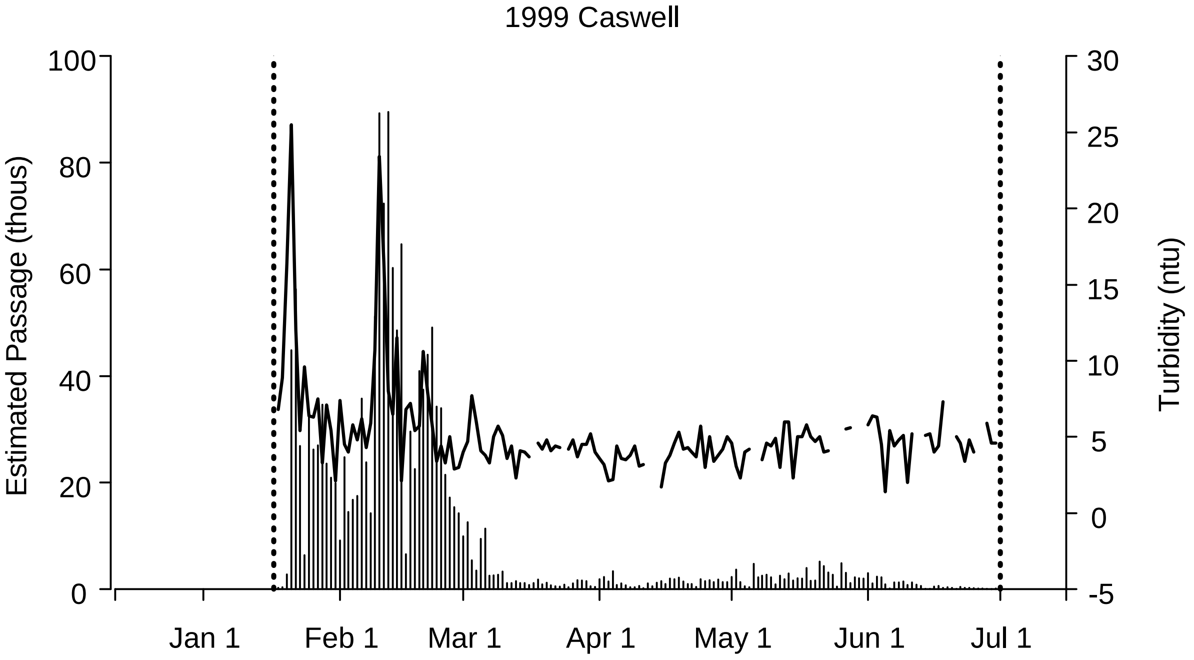
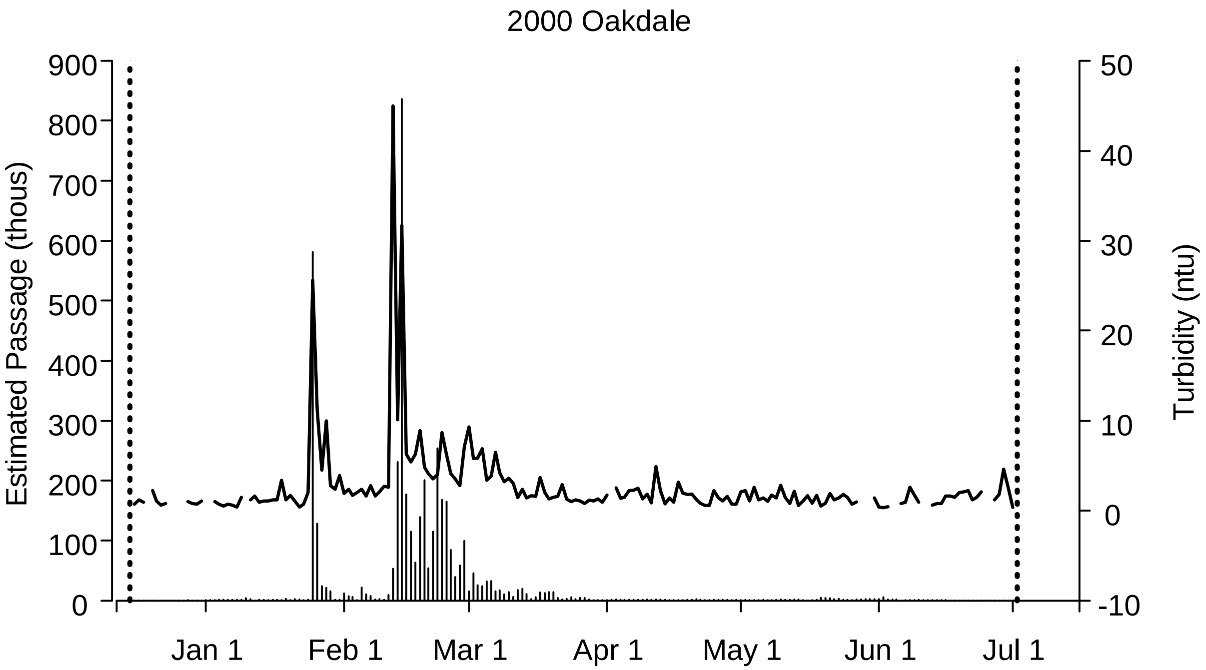


Figure A-3. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 1999. Dotted lines indicate the start and end dates of trapping.



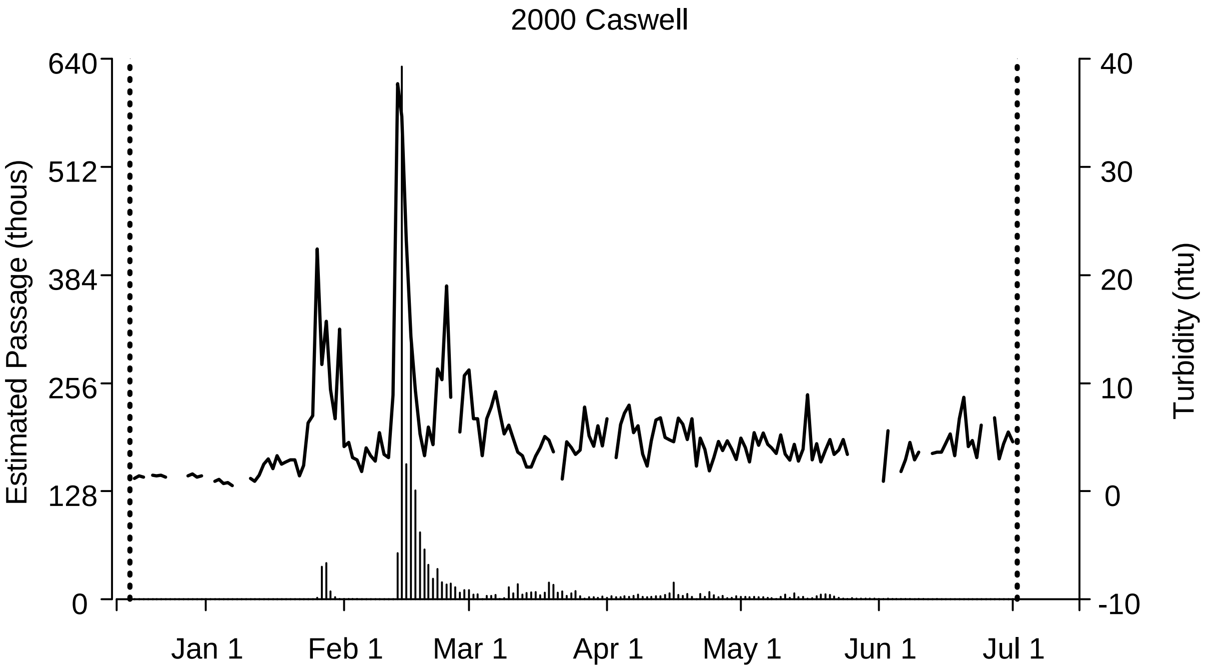
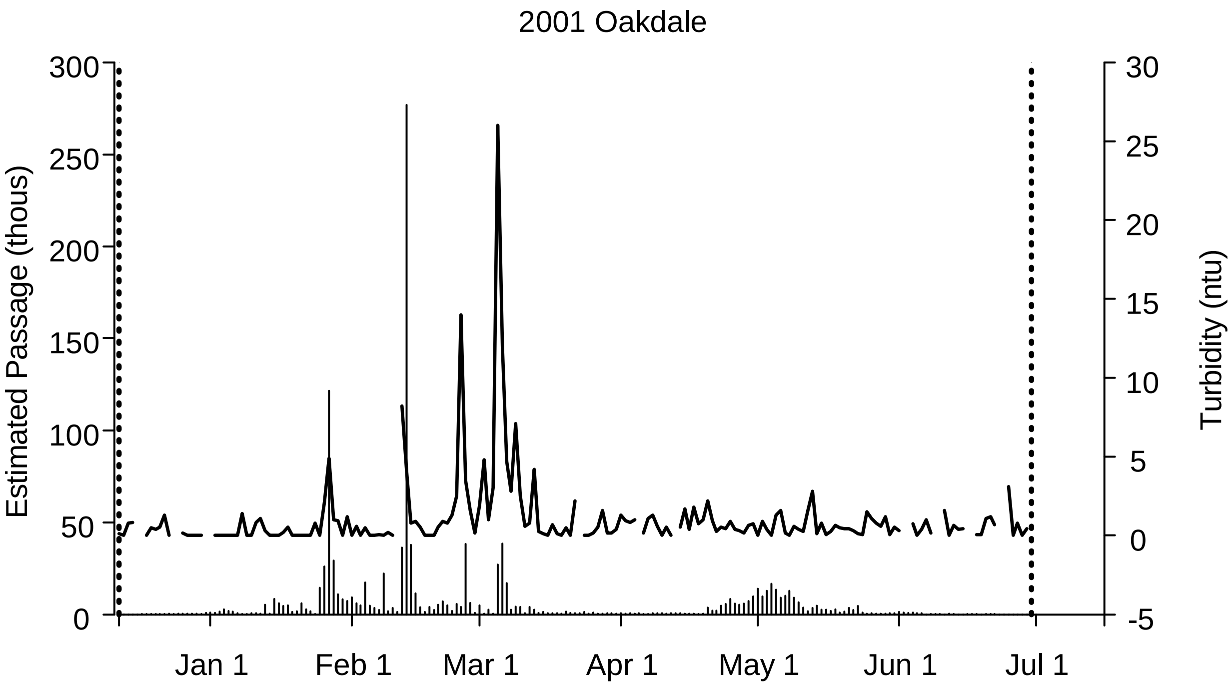


Figure A-4. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 2000. Dotted lines indicate the start and end dates of trapping.



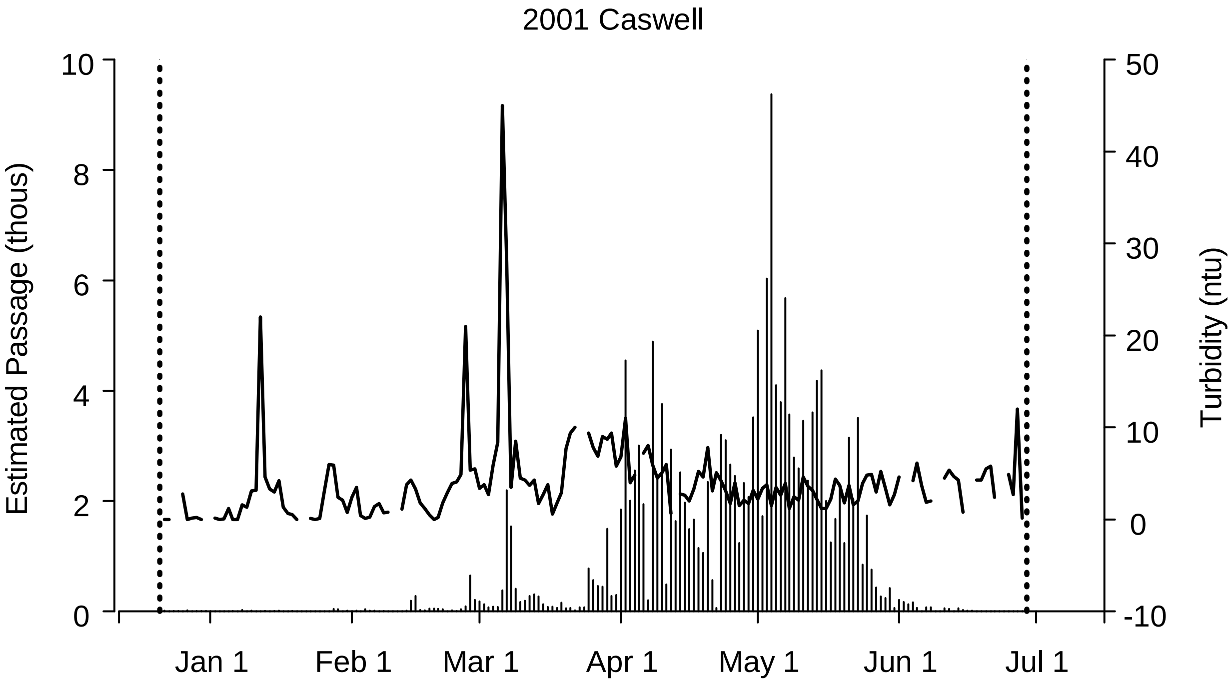
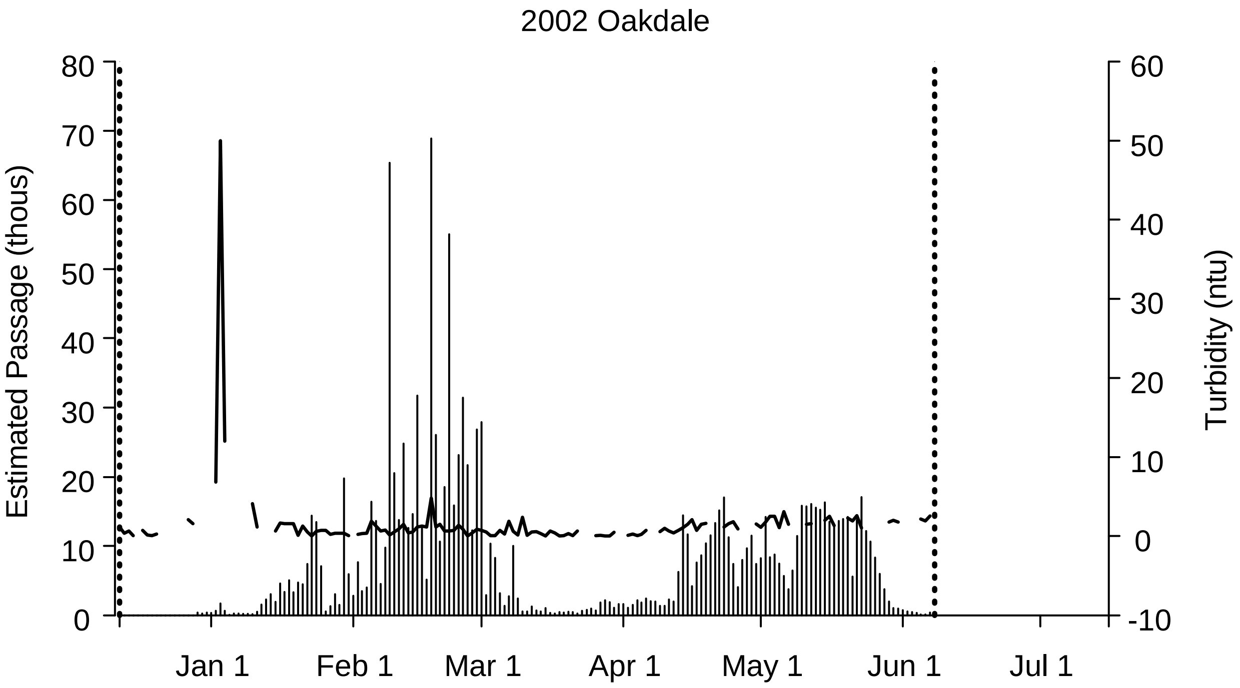


Figure A-5. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 2001. Dotted lines indicate the start and end dates of trapping.


2002 Oakdale

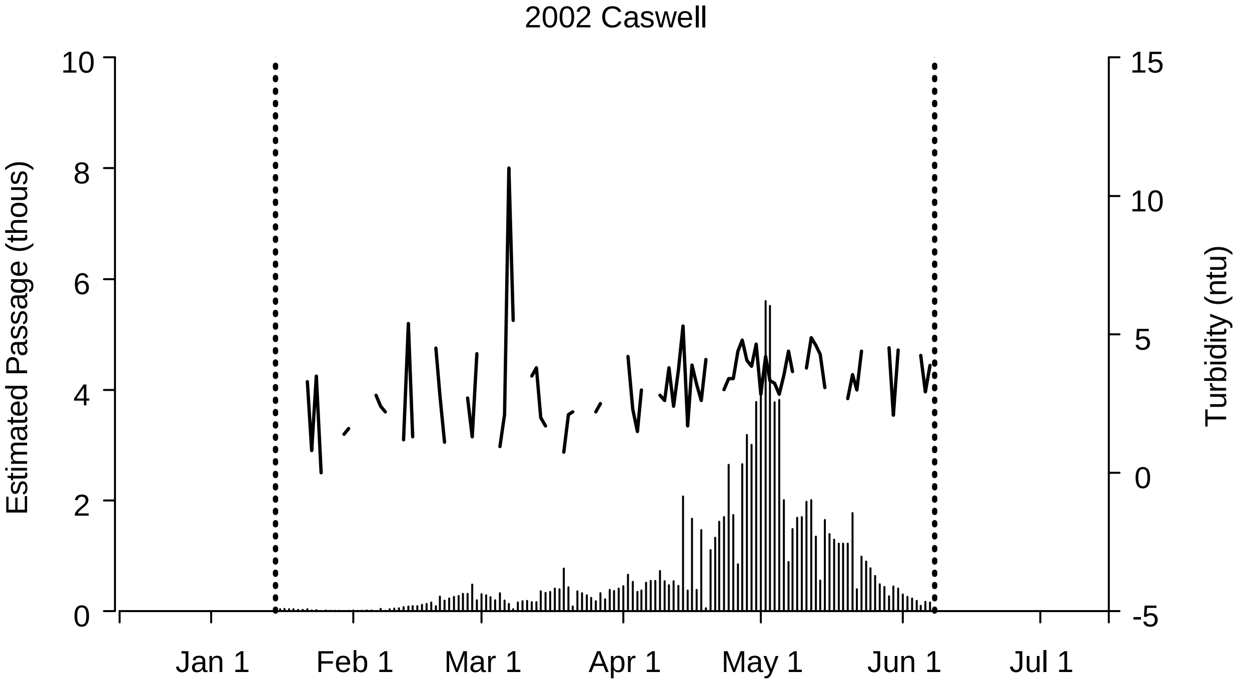
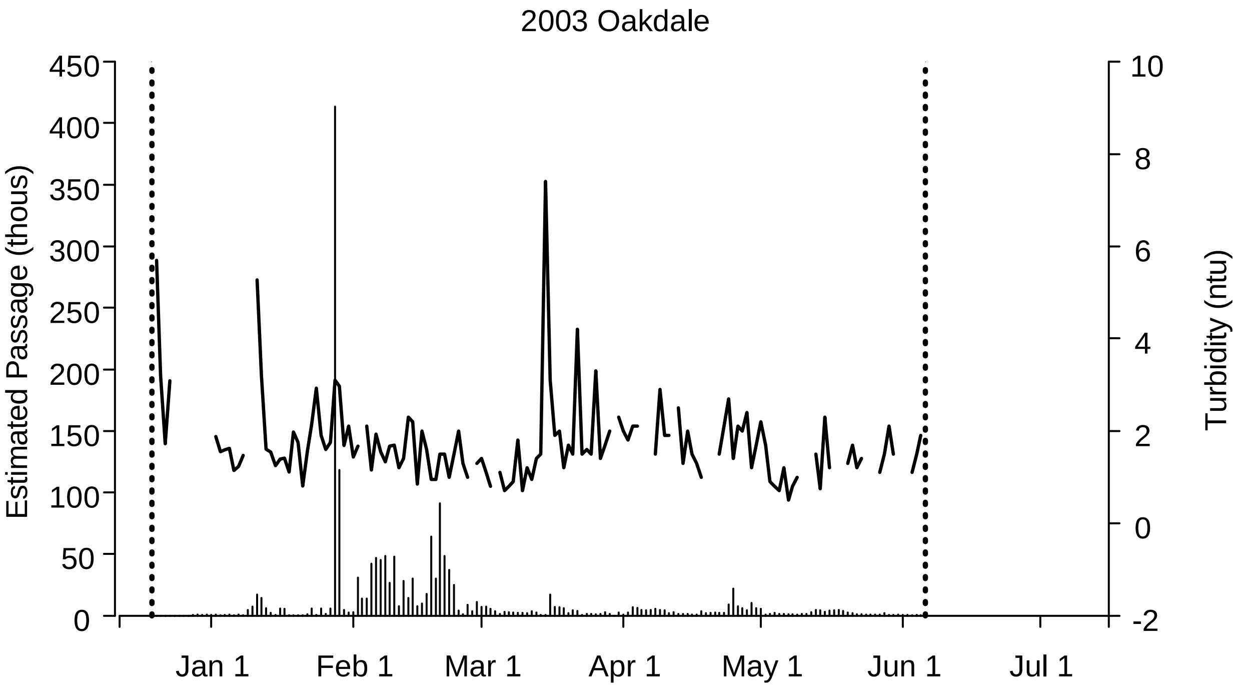

2002 Caswell

Figure A-6. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 2002. Dotted lines indicate the start and end dates of trapping.



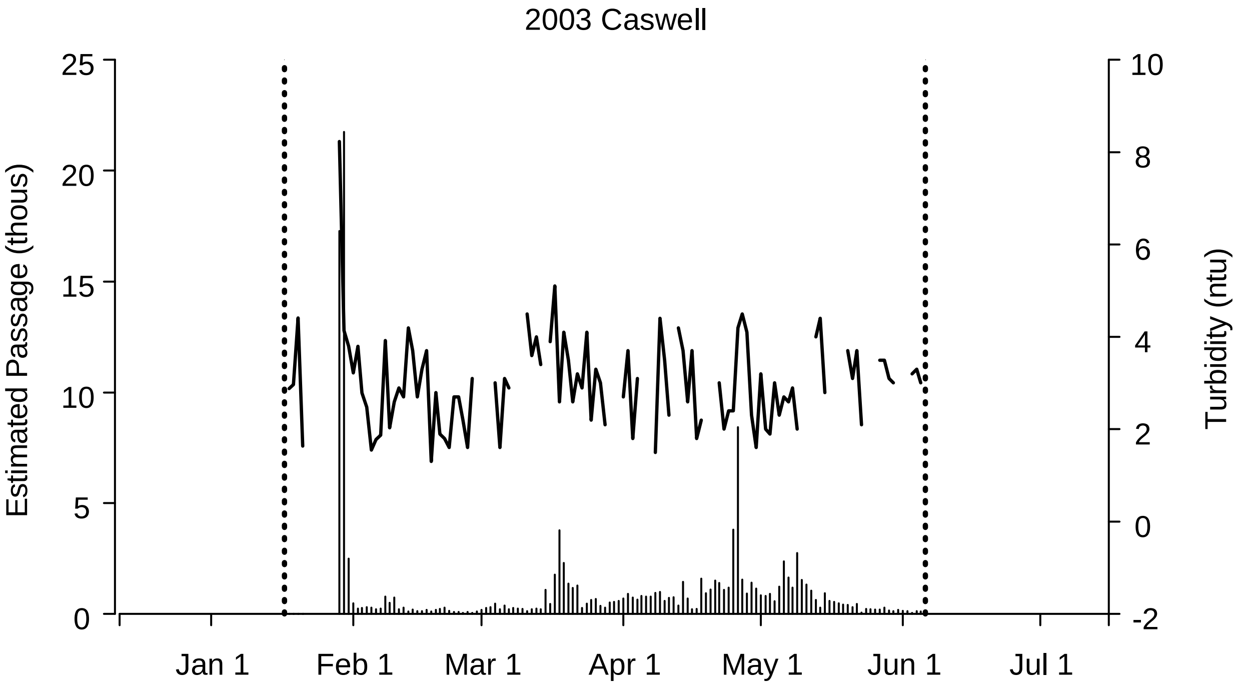
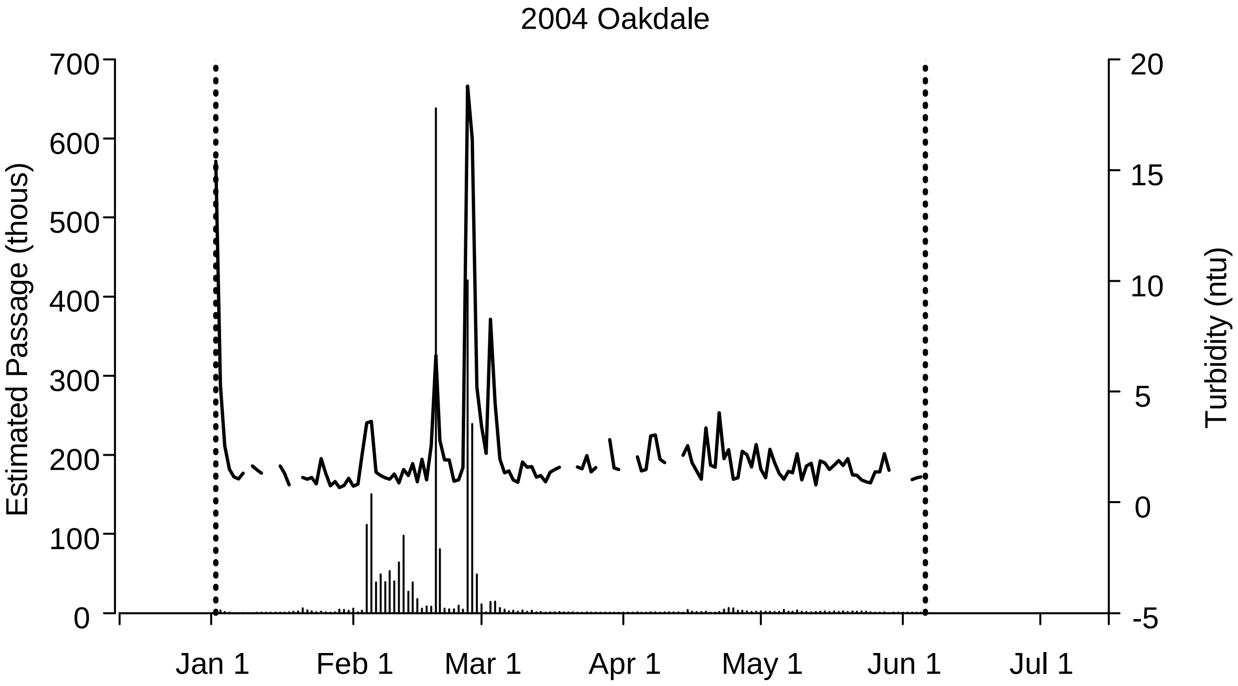


Figure A-7. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 2003. Dotted lines indicate the start and end dates of trapping.



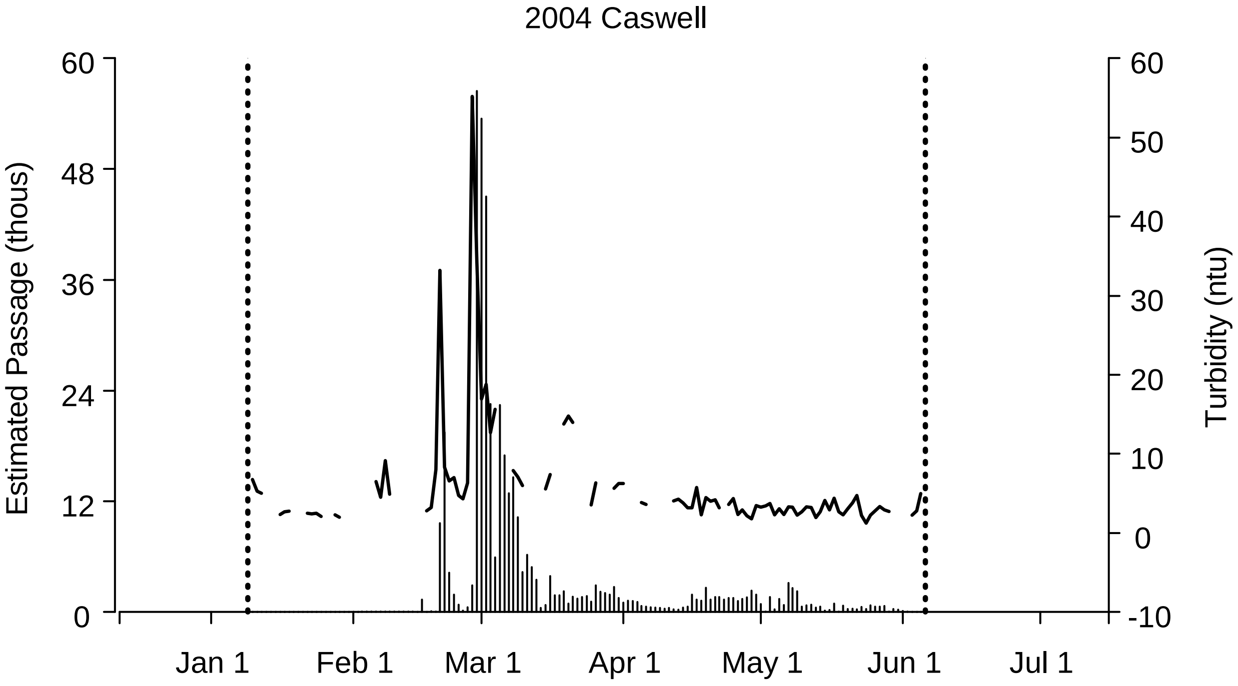
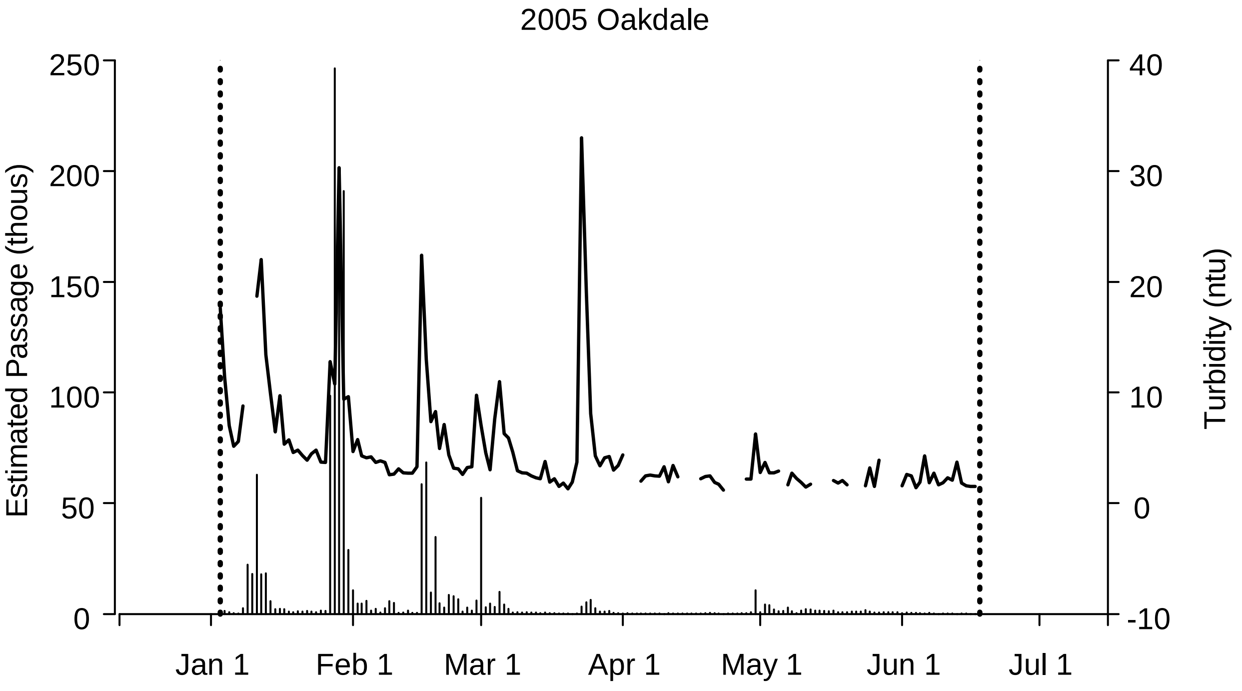


Figure A-8. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 2004. Dotted lines indicate the start and end dates of trapping.



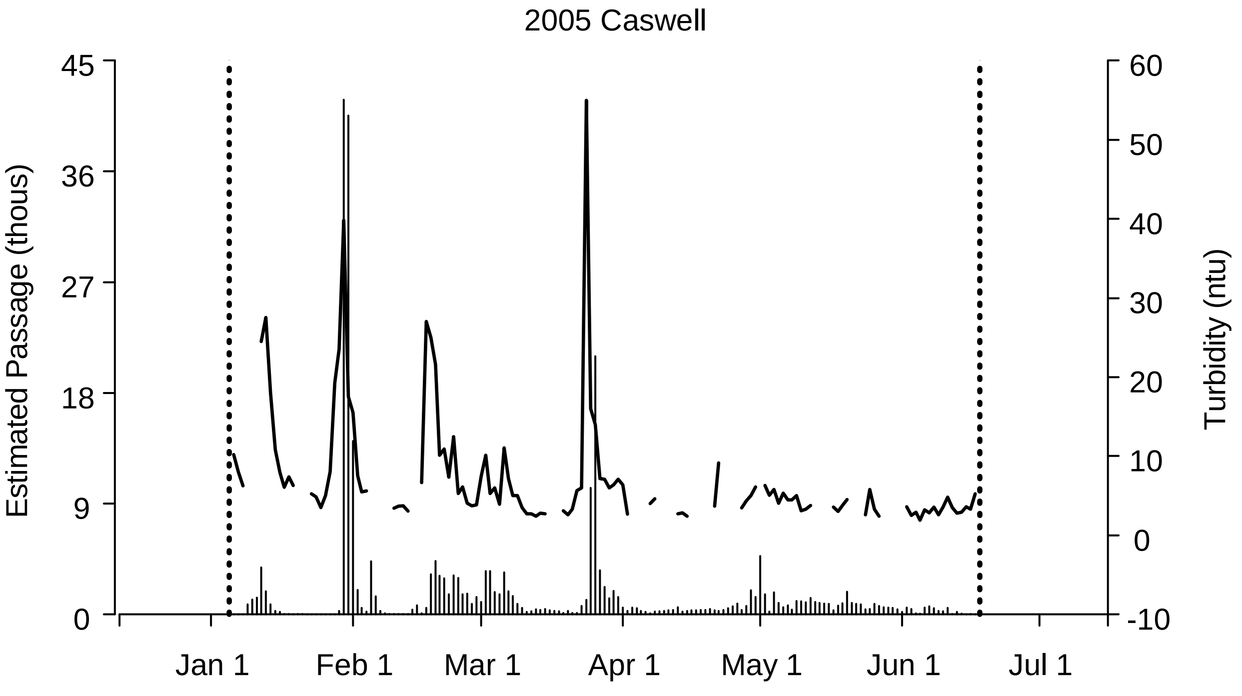
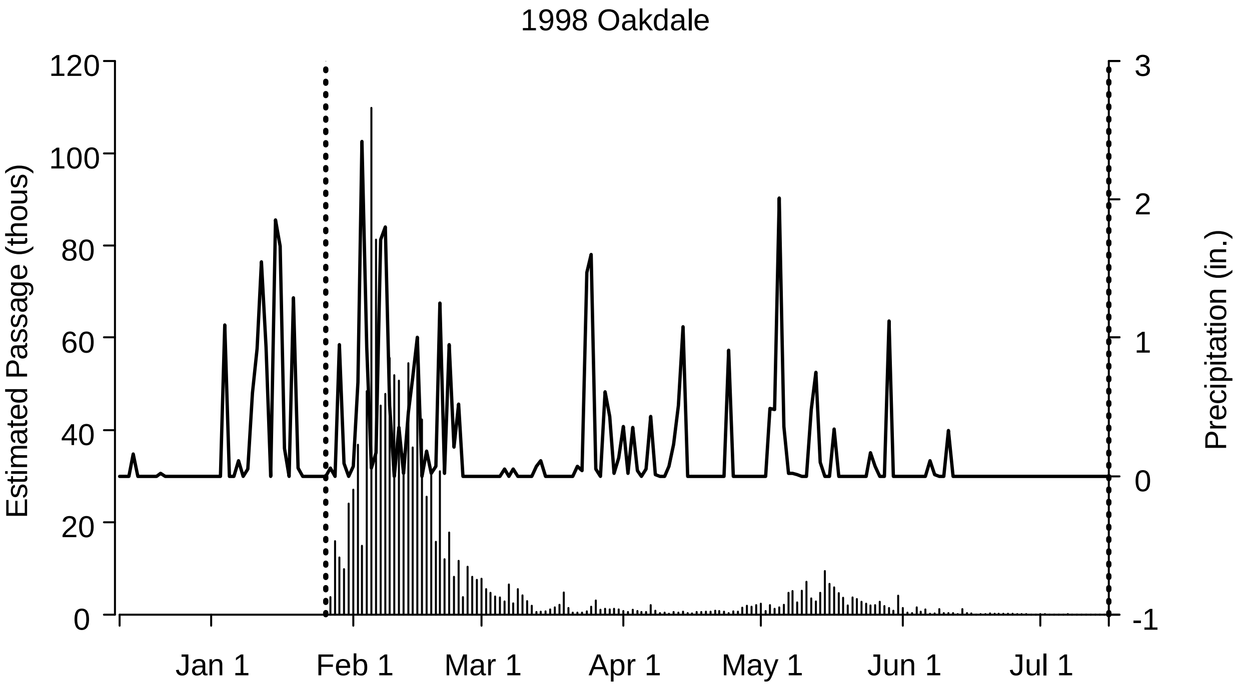


Figure A-9. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and stream turbidity (ntu) recorded at each trap site, 2005. Dotted lines indicate the start and end dates of trapping.

Juvenile Chinook salmon passage versus Precipitation



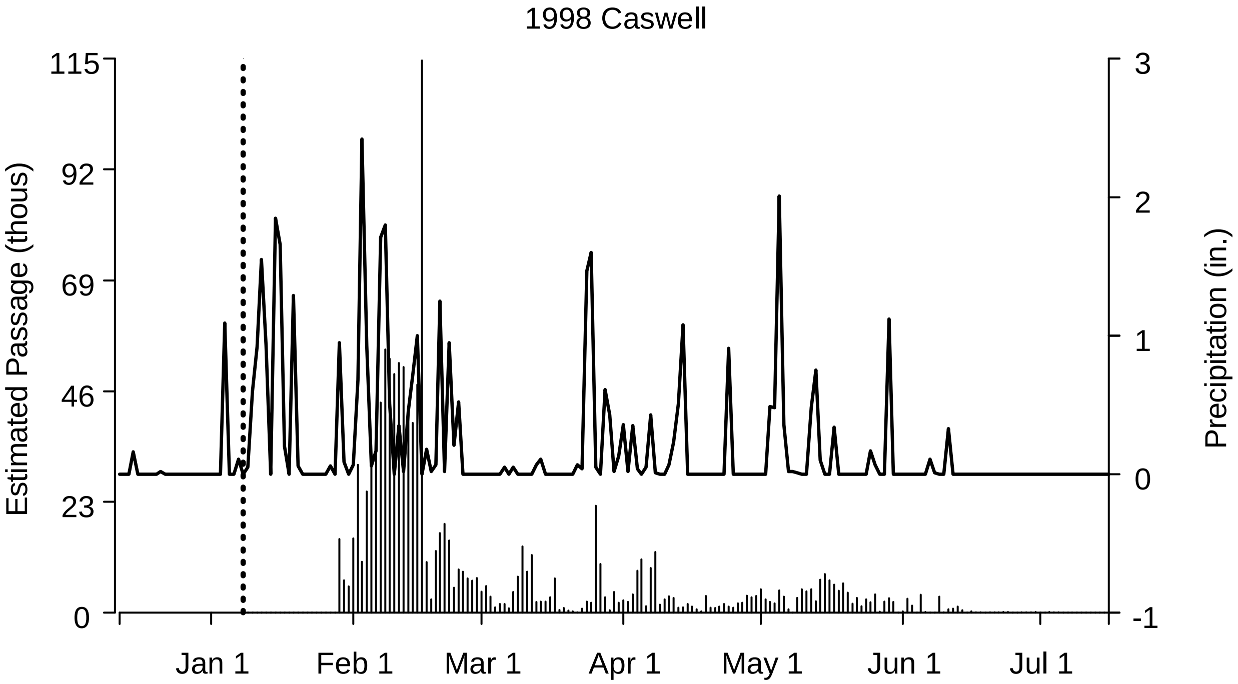
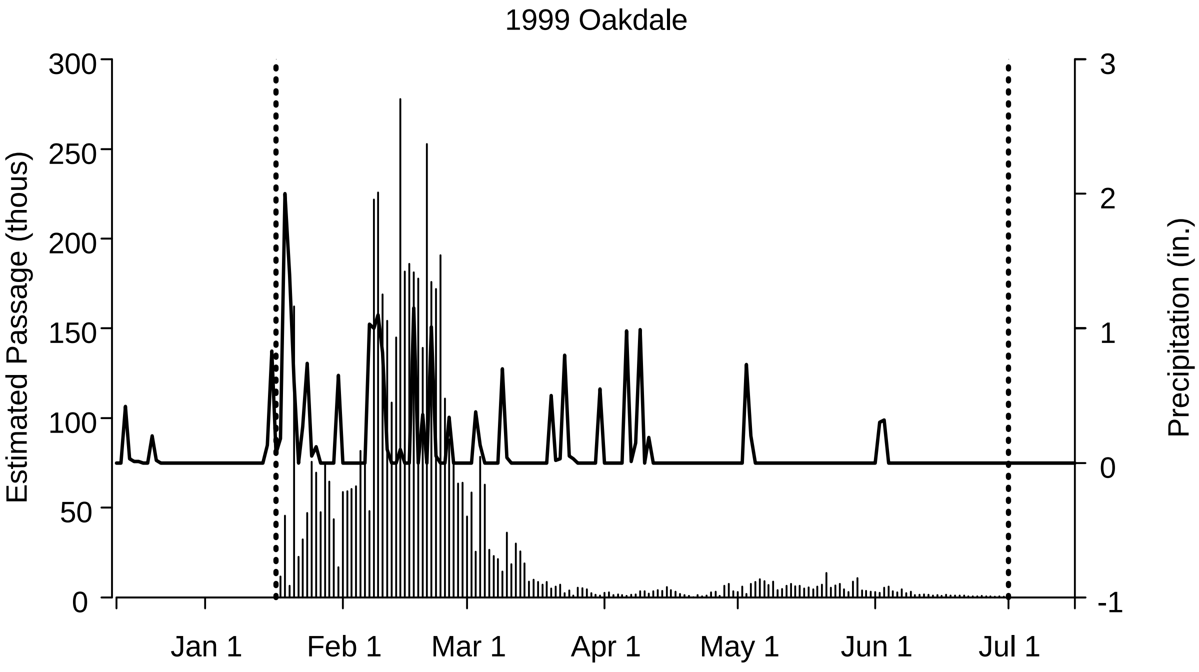


Figure A-10. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at New Melones, 1998. Dotted lines indicate the start and end dates of trapping.



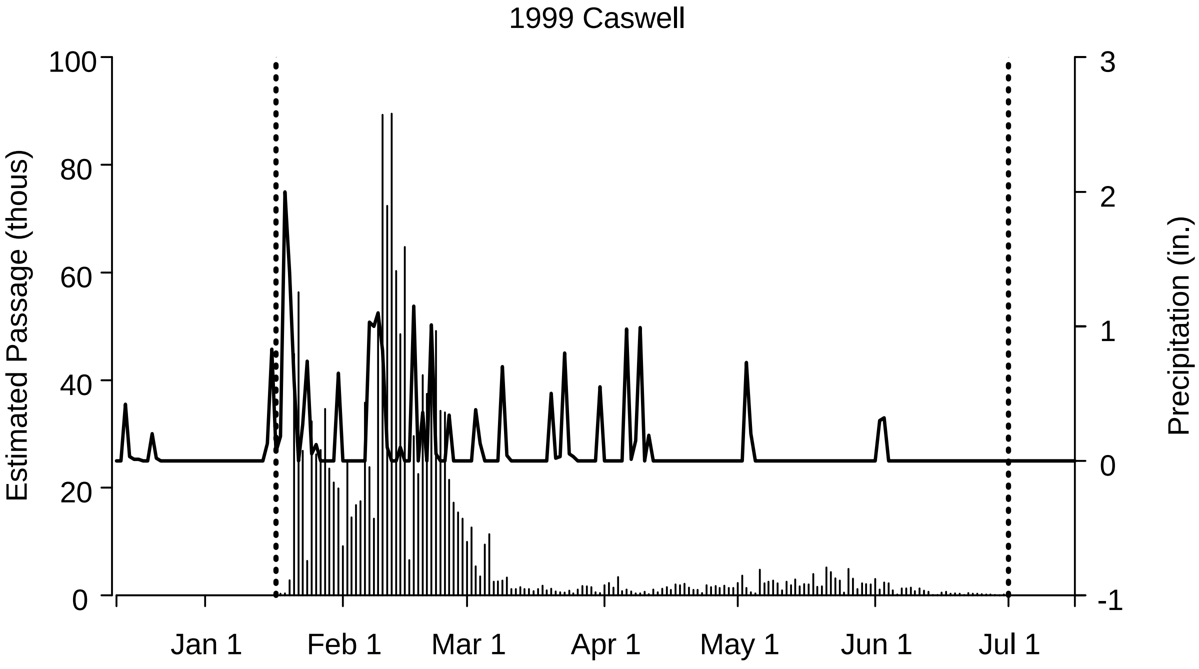


Figure A-11. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones, 1999. Dotted lines indicate the start and end dates of trapping.

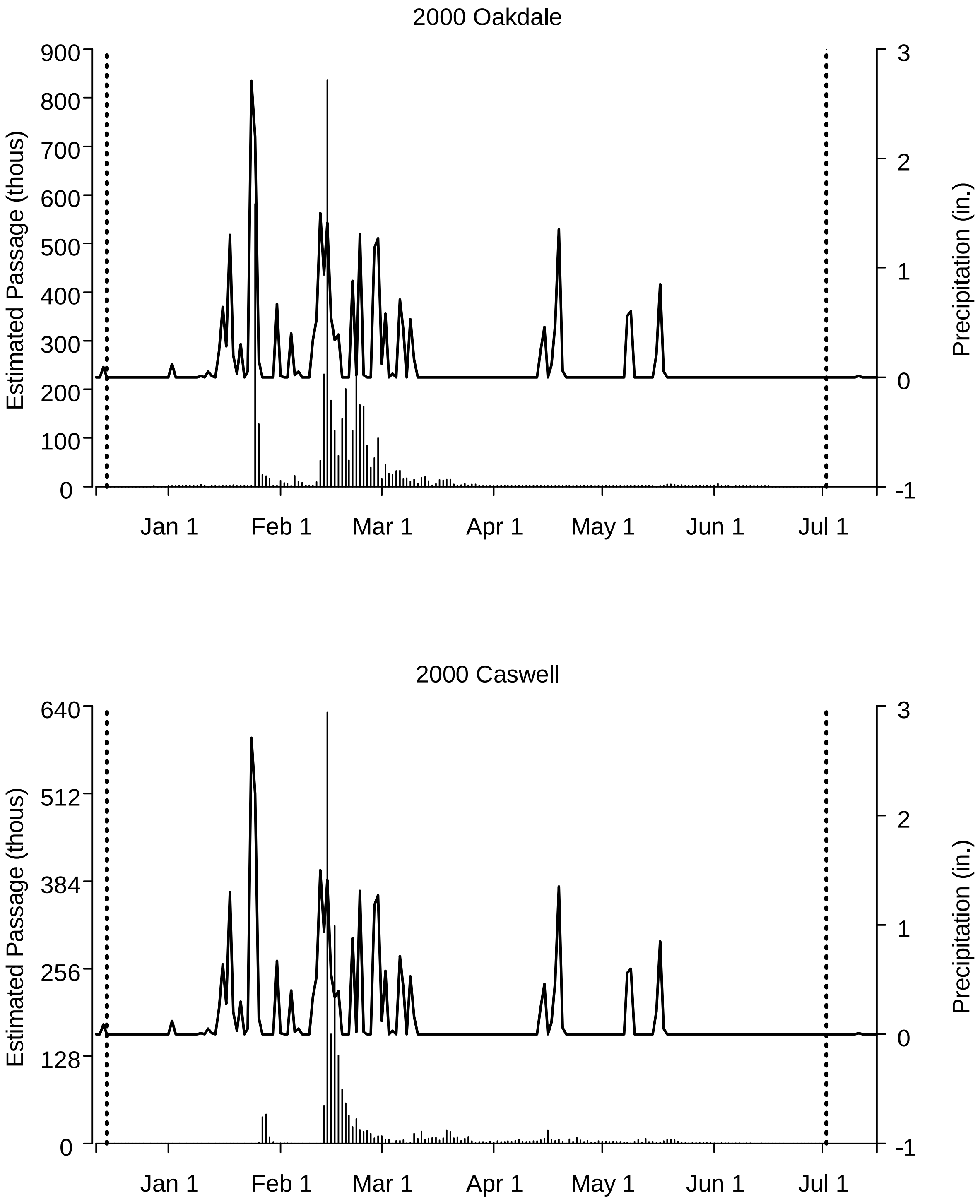
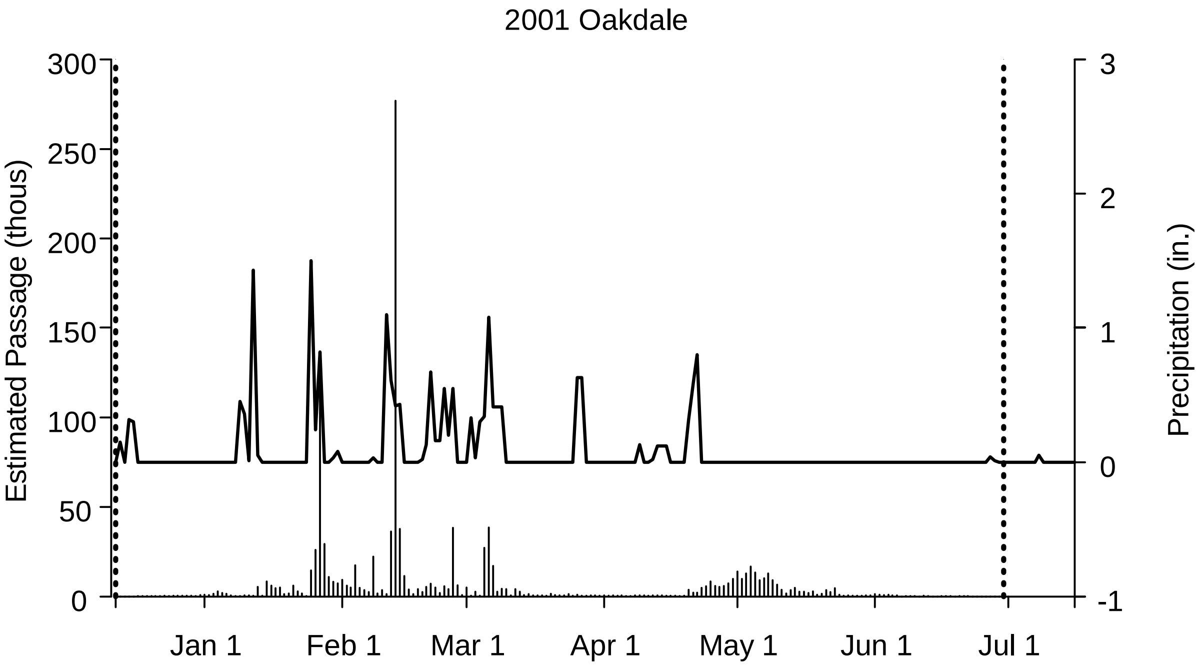


Figure A-12. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at each trap site, 2000. Dotted lines indicate the start and end dates of trapping.



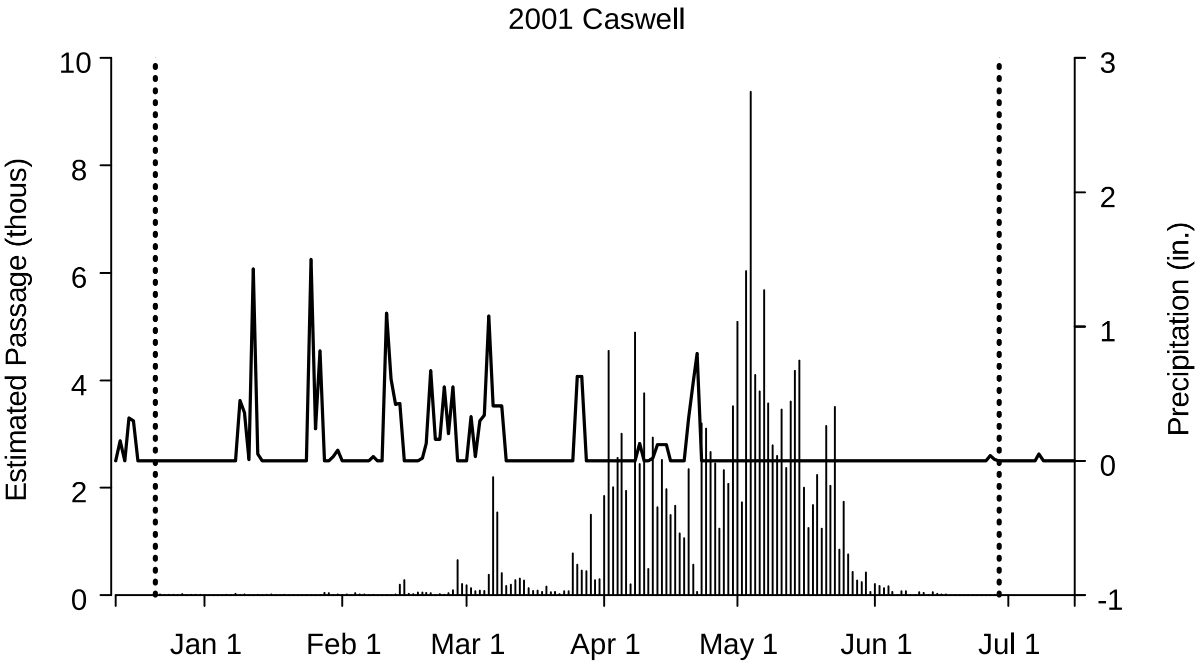


Figure A-13. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones 2001. Dotted lines indicate the start and end dates of trapping.

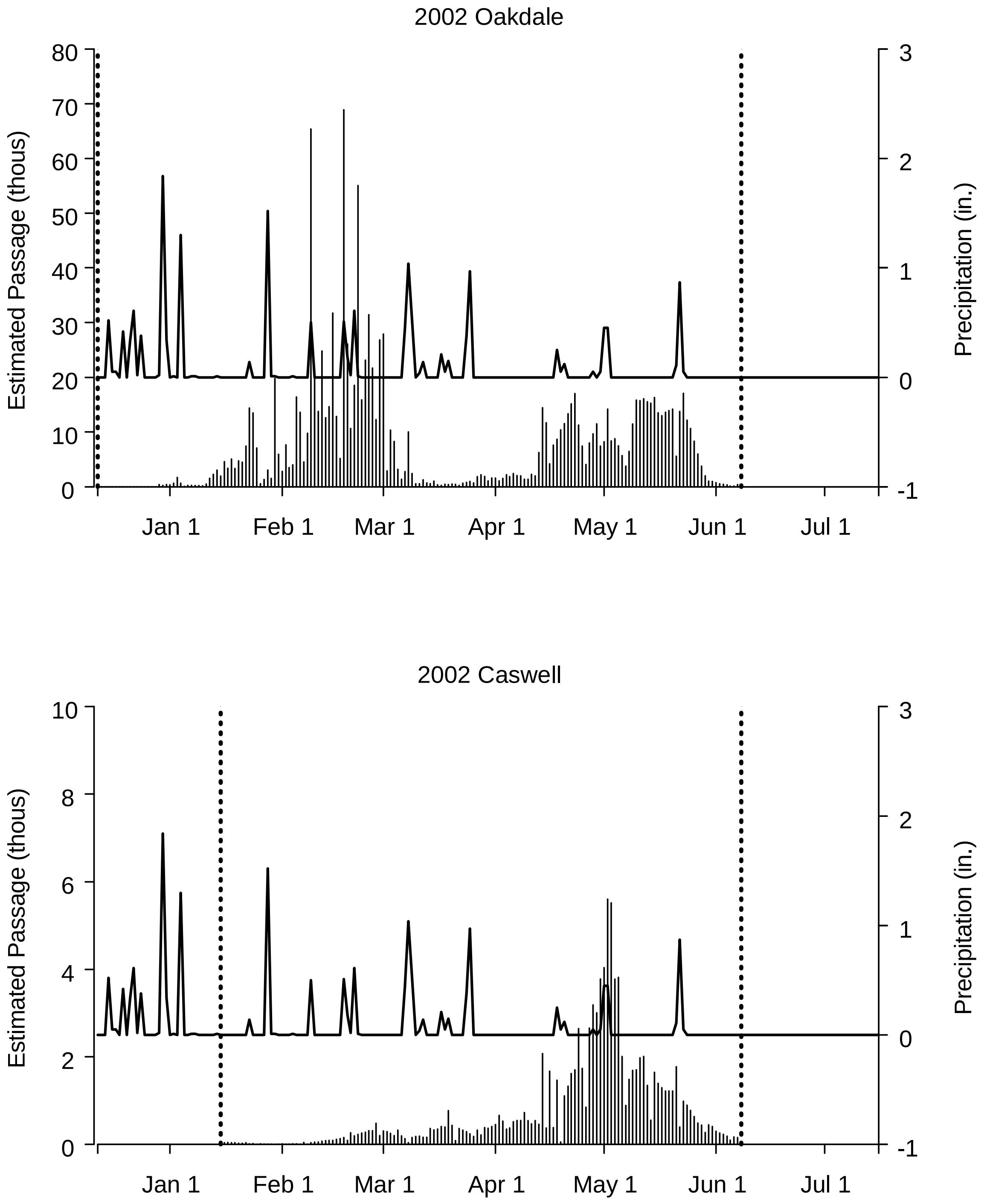
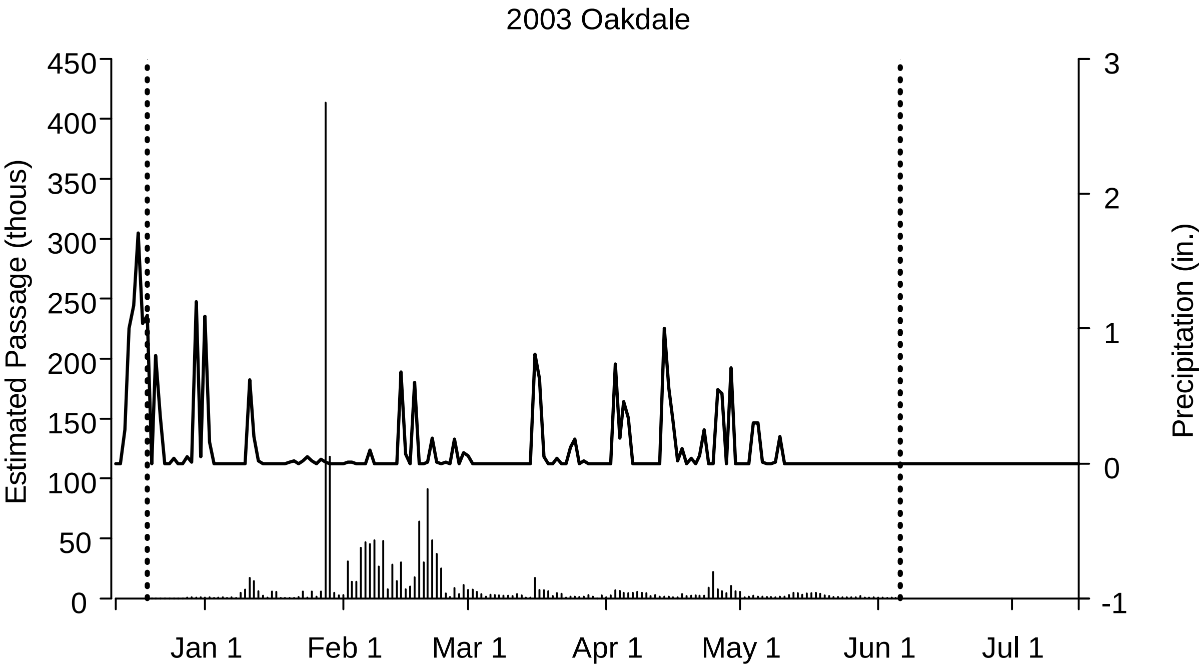


Figure A-14. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones, 2002. Dotted lines indicate the start and end dates of trapping.



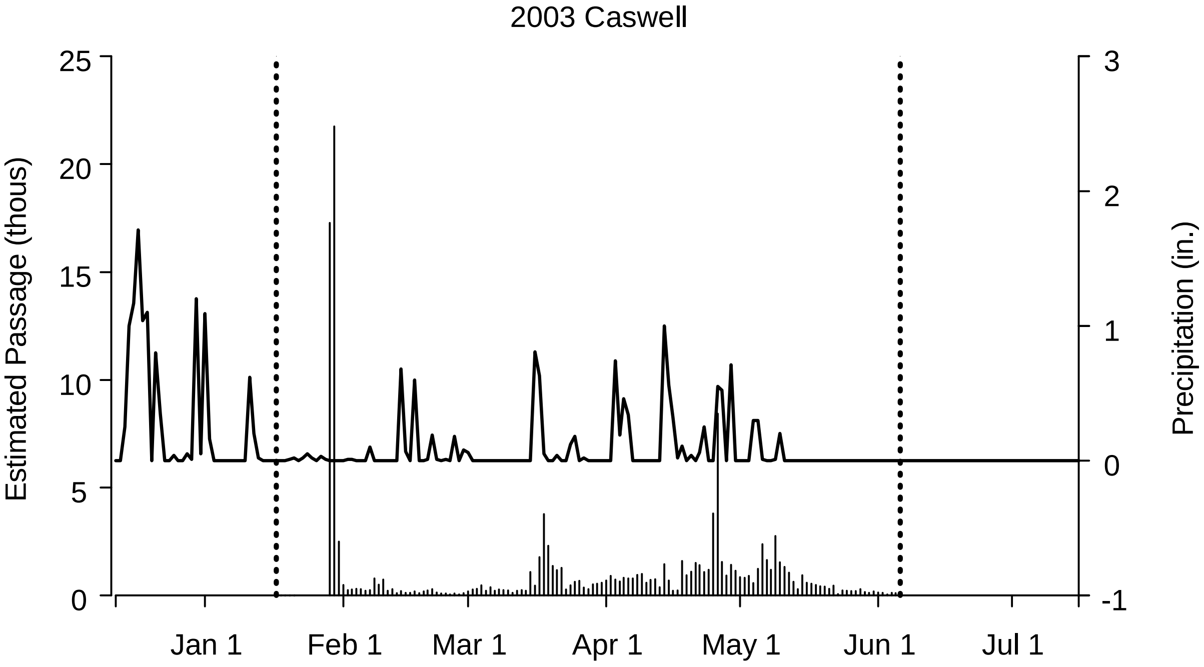
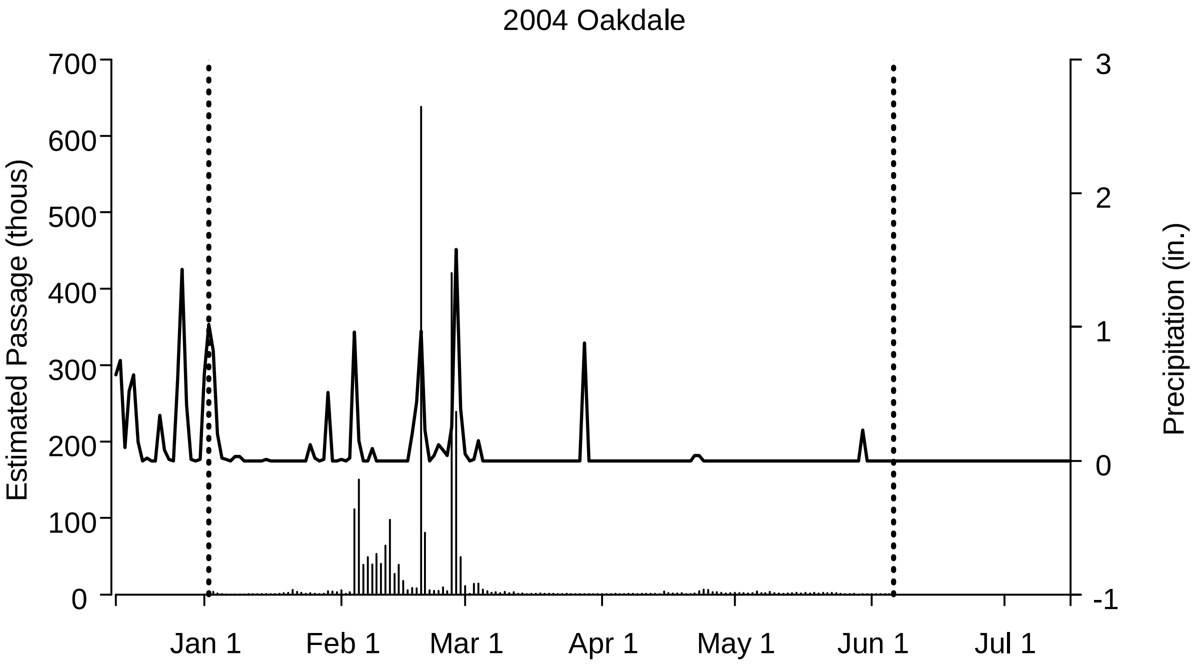


Figure A-15. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones, 2003. Dotted lines indicate the start and end dates of trapping.



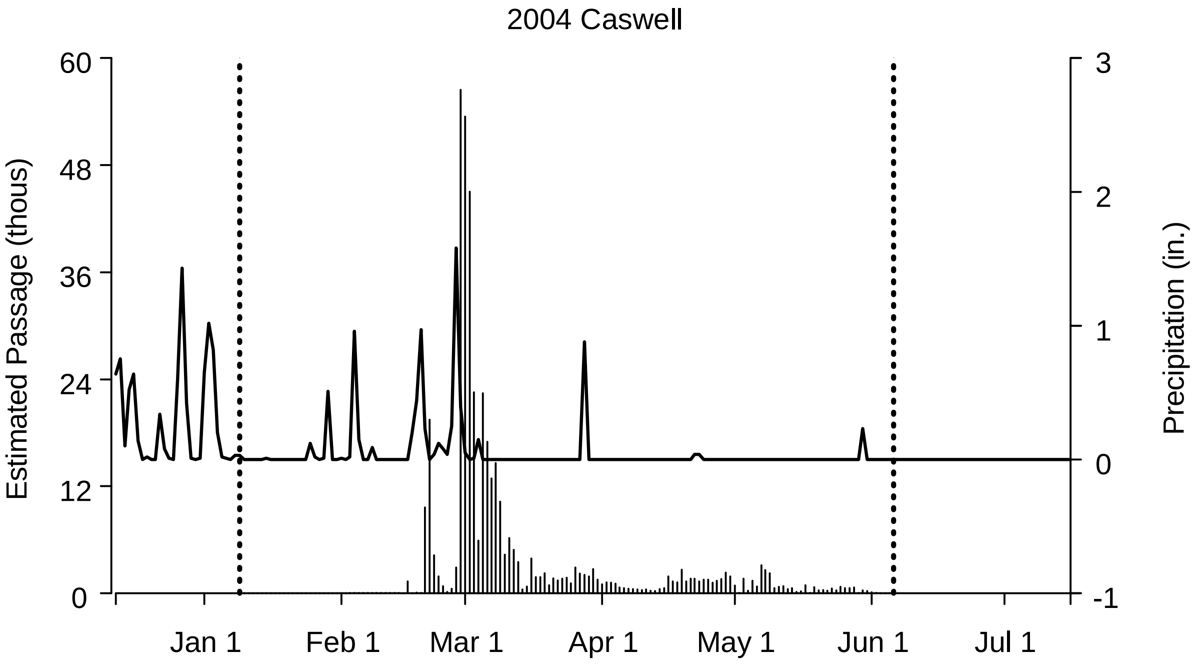
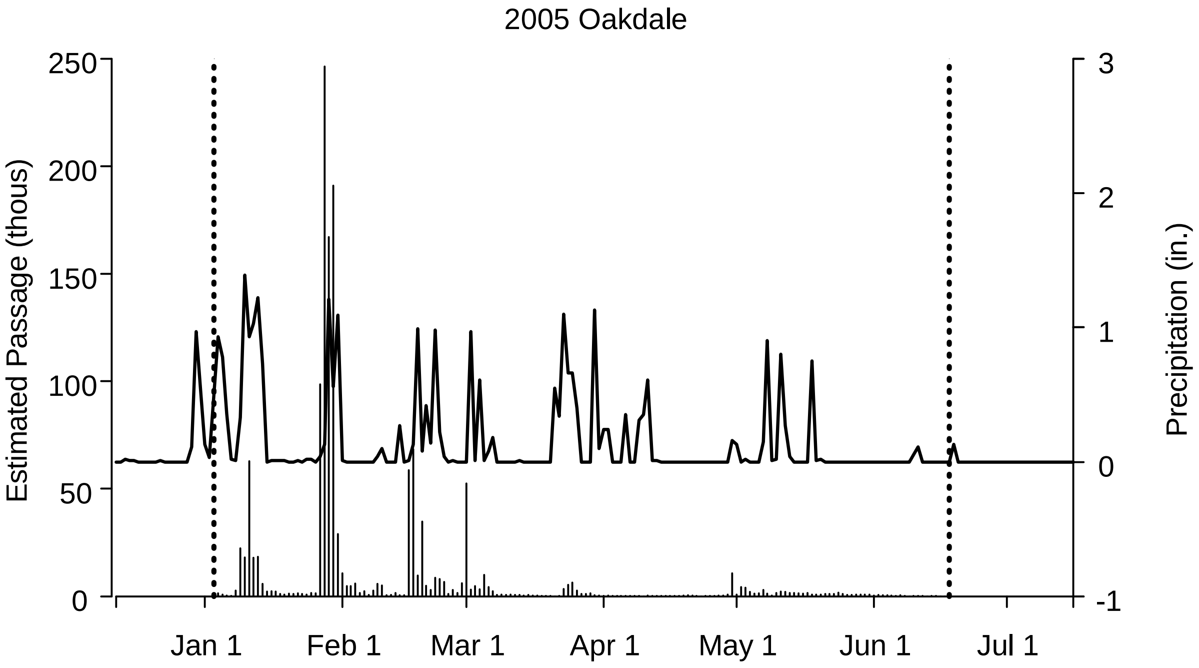


Figure A-16. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones, 2004. Dotted lines indicate the start and end dates of trapping.



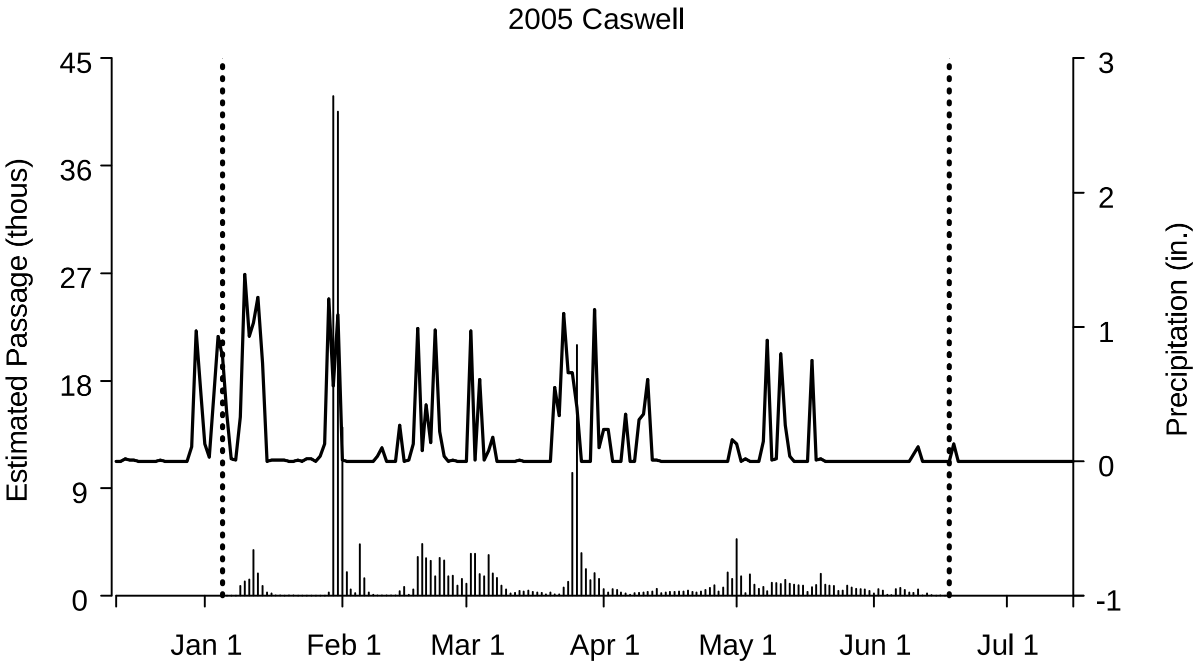
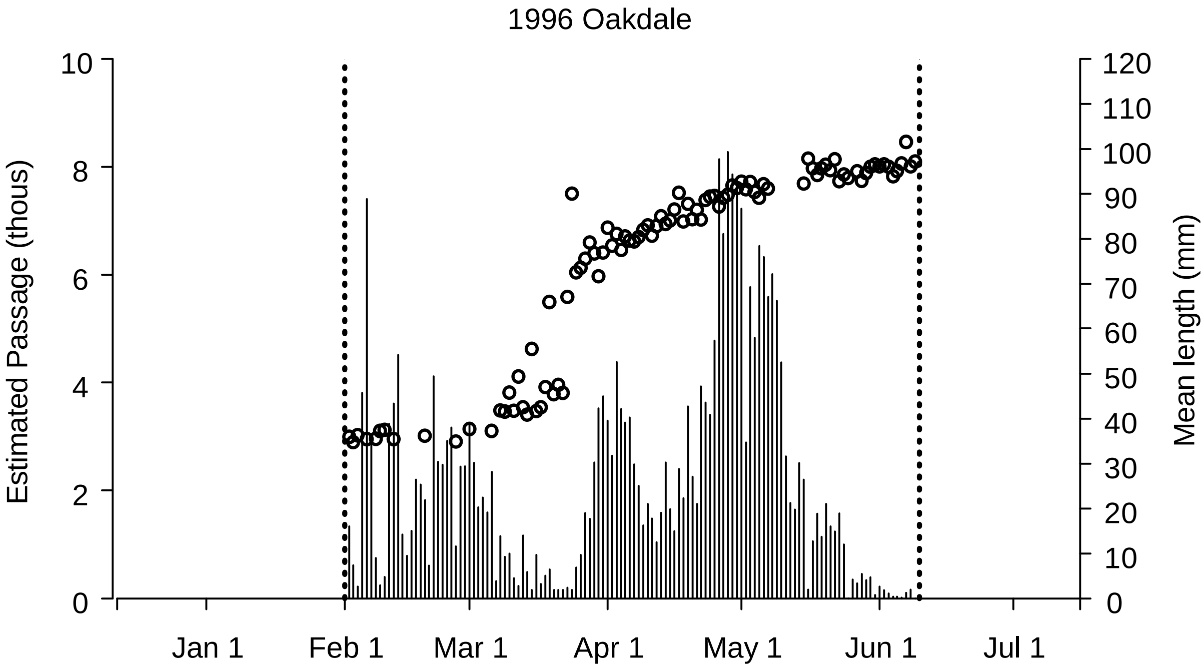


Figure A-17. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and precipitation (in.) recorded at at New Melones, 2005. Dotted lines indicate the start and end dates of trapping.

Juvenile Chinook salmon passage versus Mean length



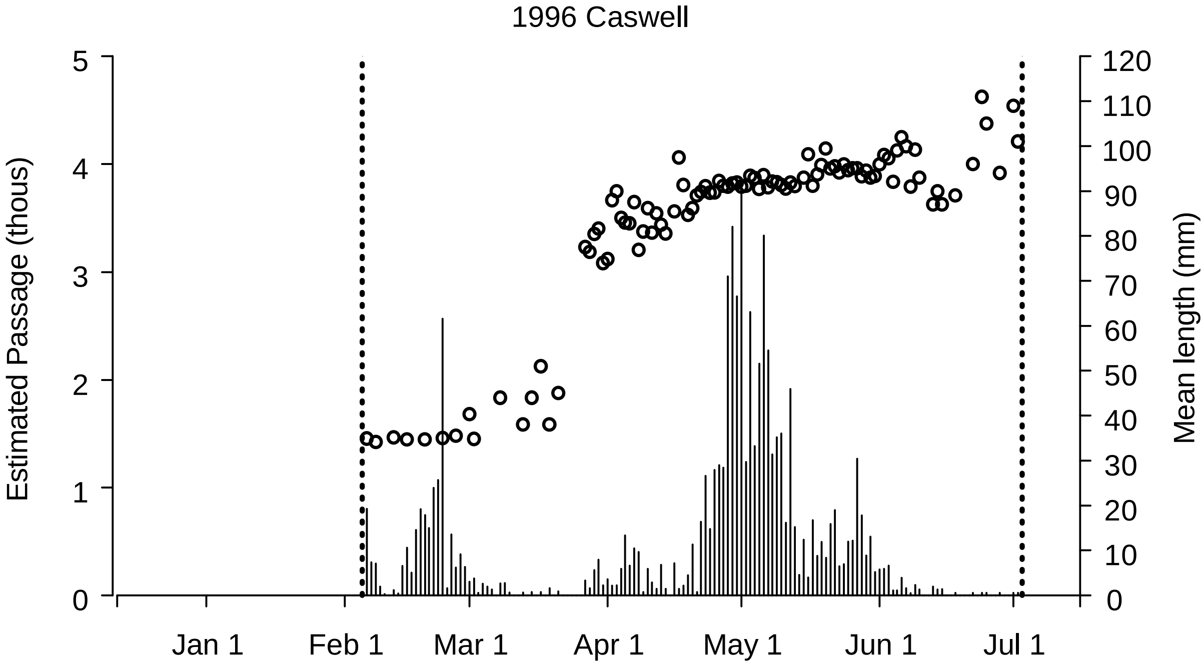


Figure A-18. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 1996. Dotted lines indicate the start and end dates of trapping.

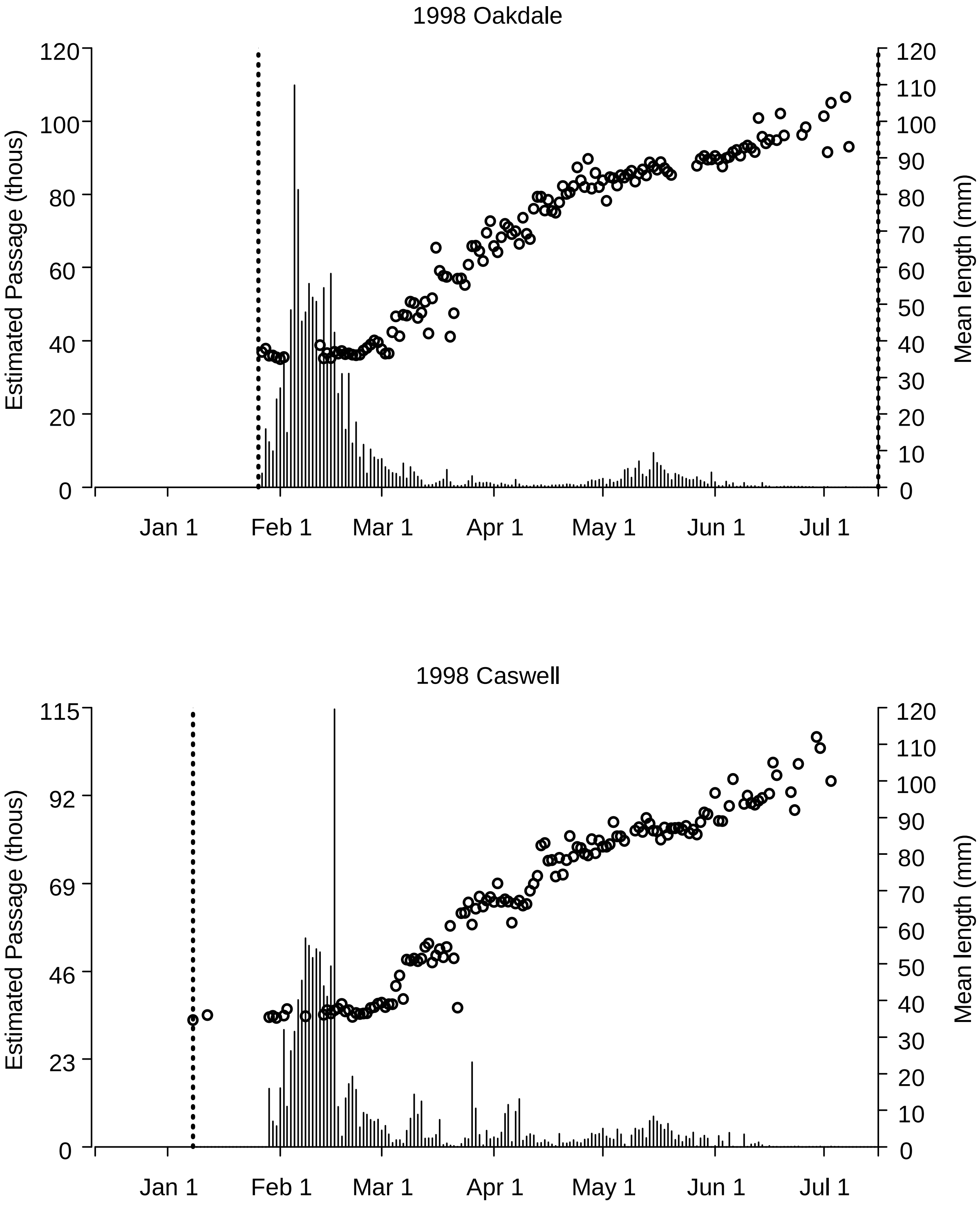
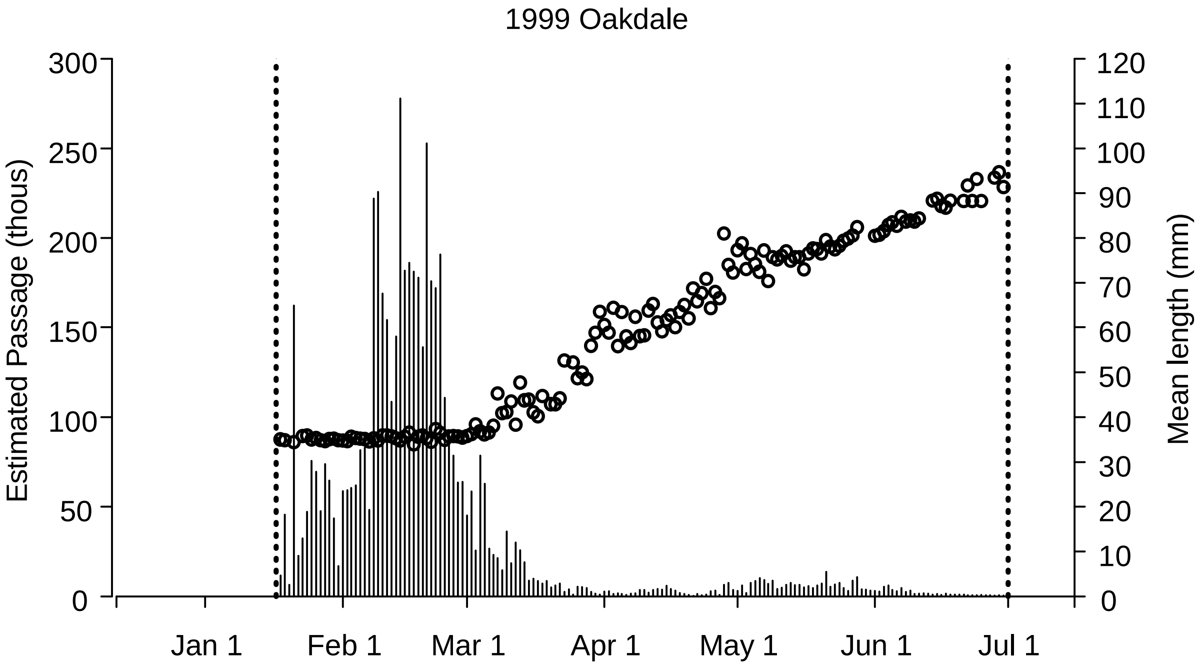


Figure A-19. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 1998. Dotted lines indicate the start and end dates of trapping.



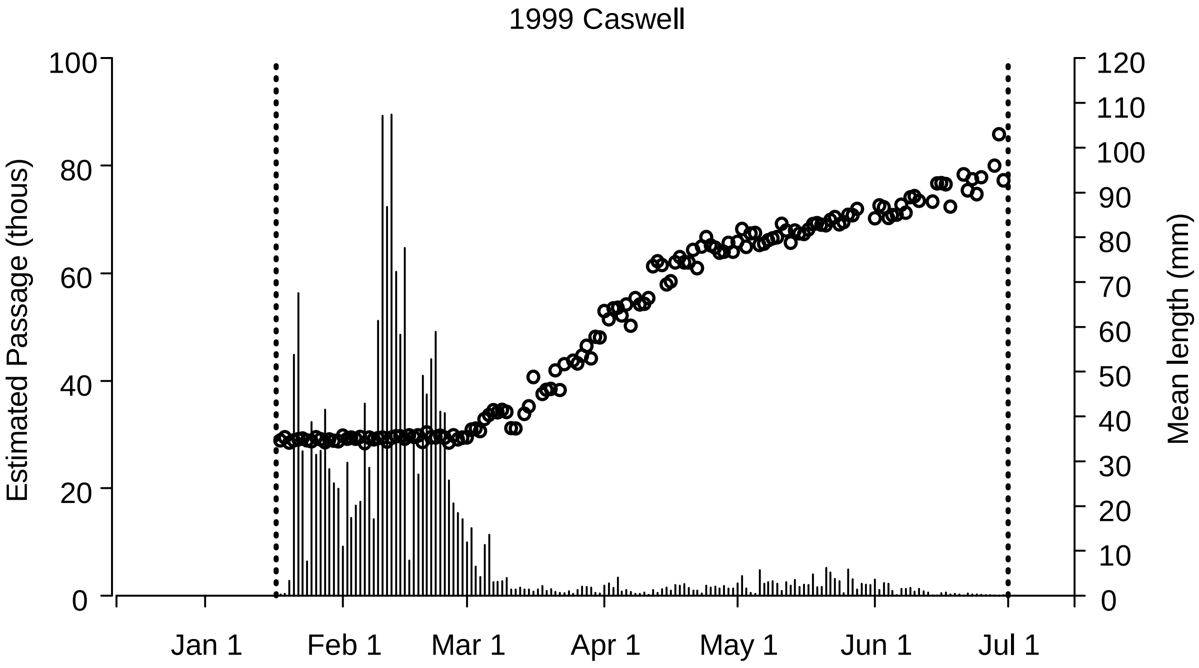
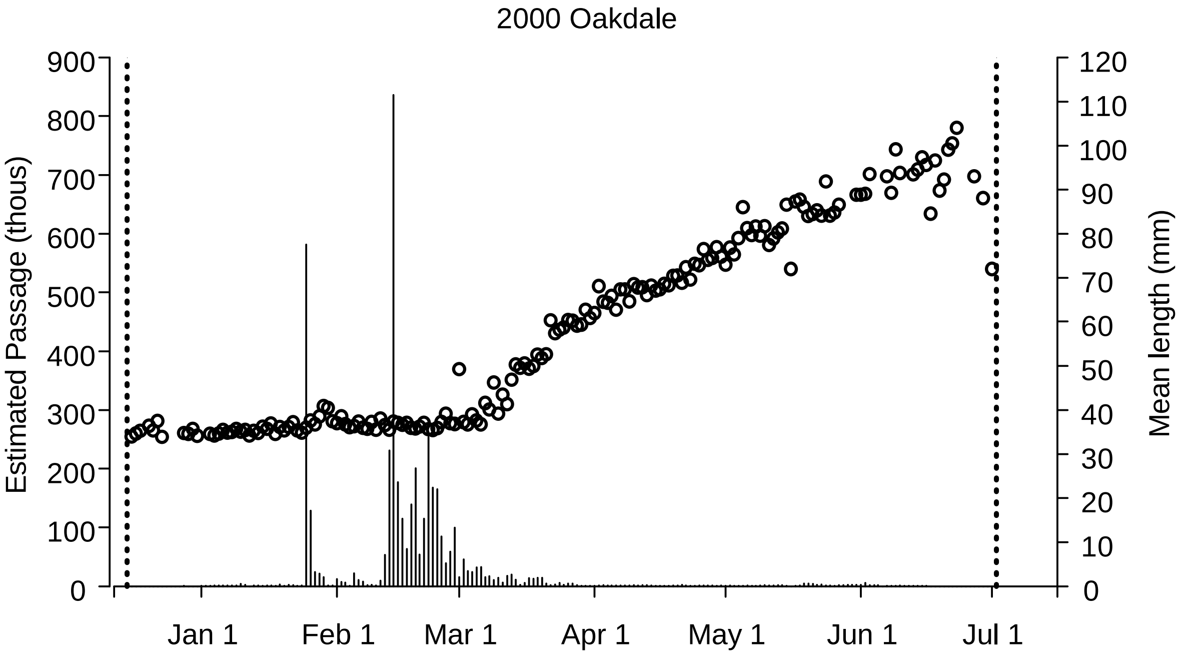


Figure A-20. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 1999. Dotted lines indicate the start and end dates of trapping.



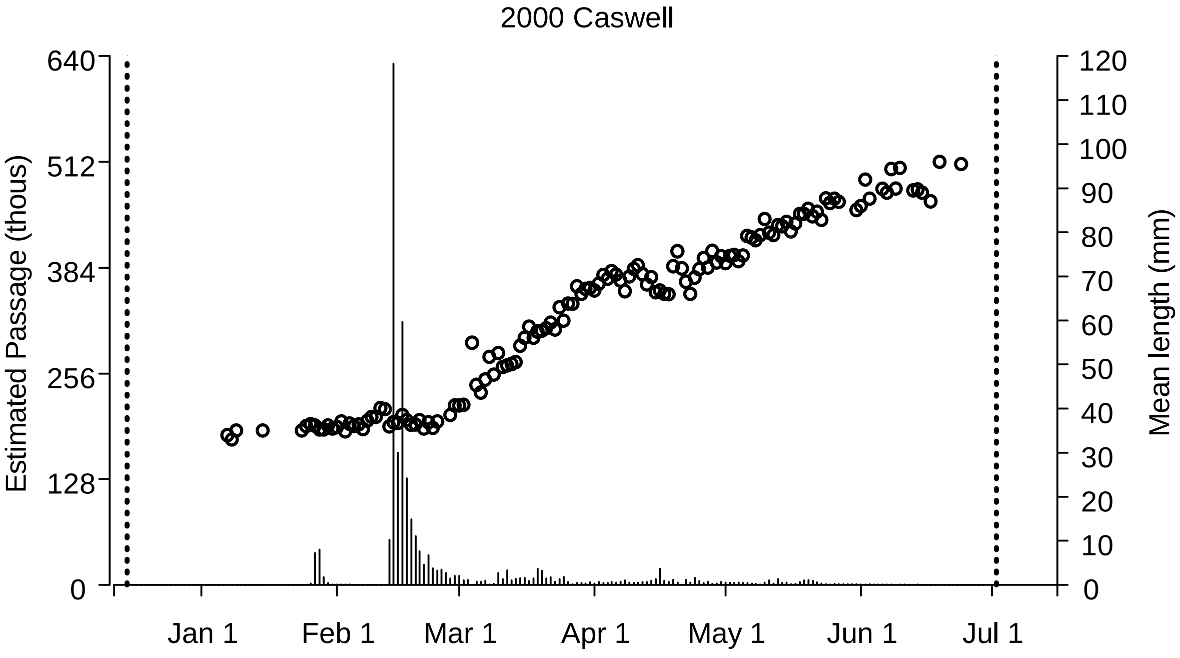
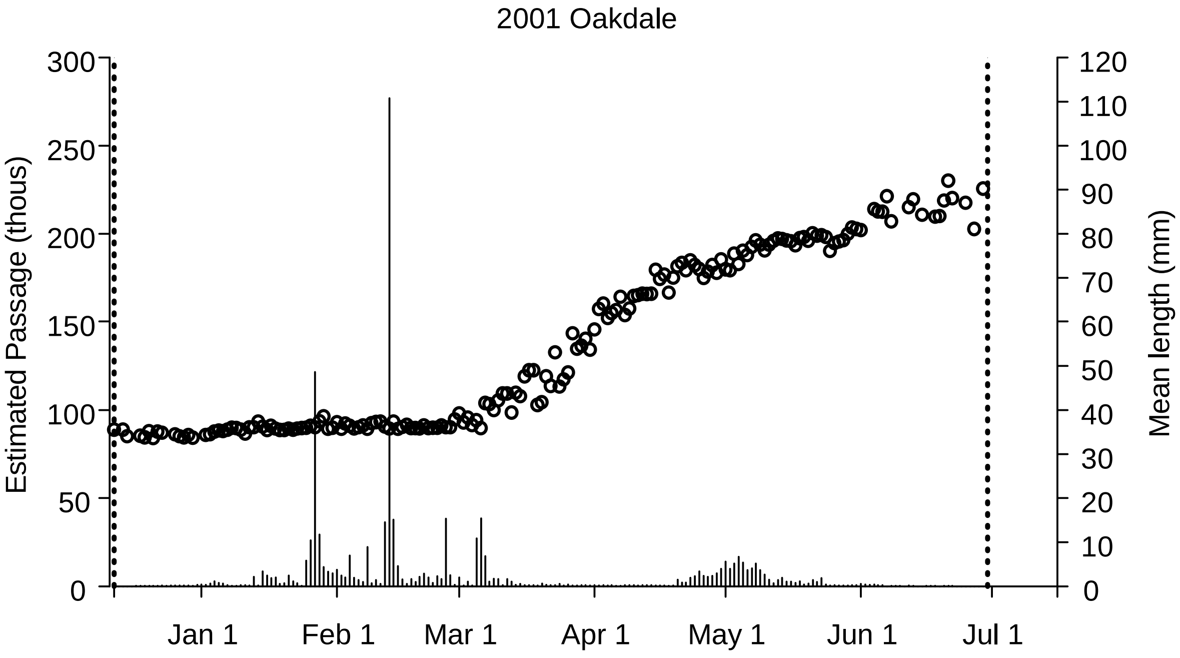


Figure A-21. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 2000. Dotted lines indicate the start and end dates of trapping.



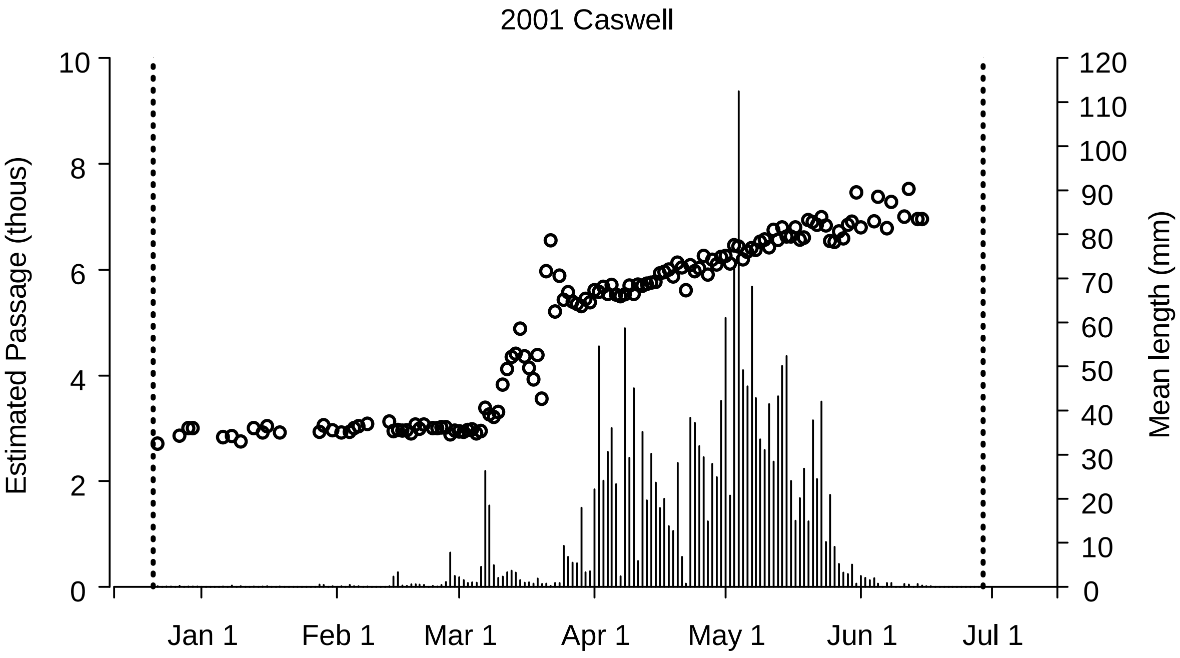
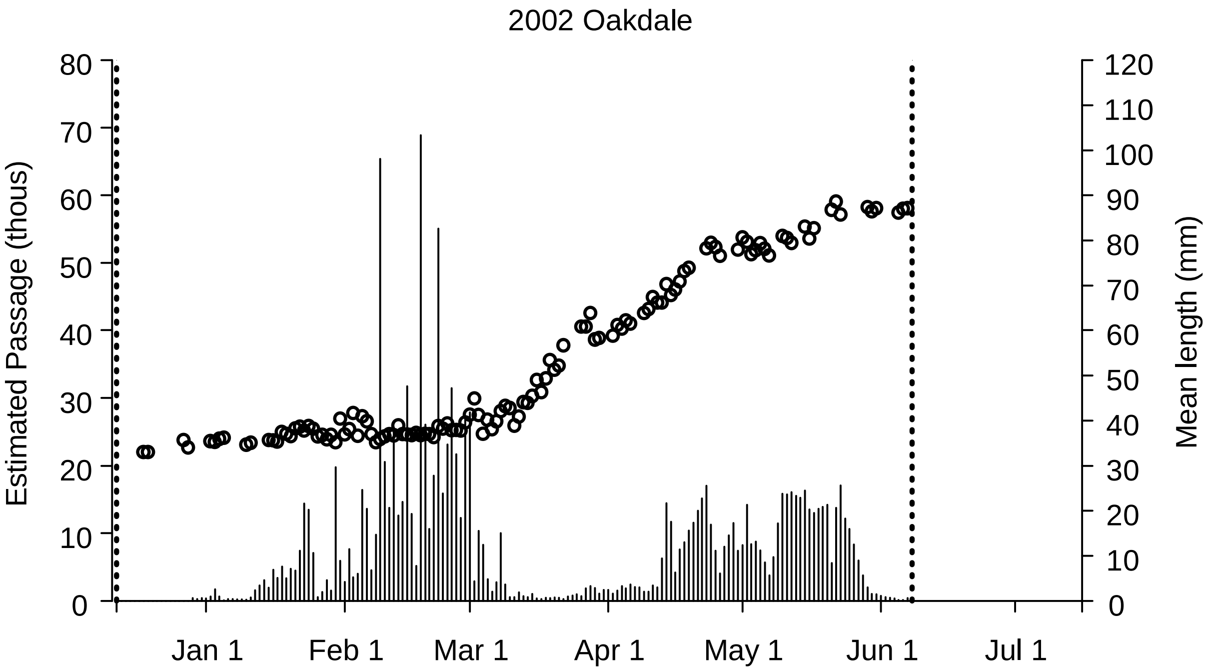


Figure A-22. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 2001. Dotted lines indicate the start and end dates of trapping.



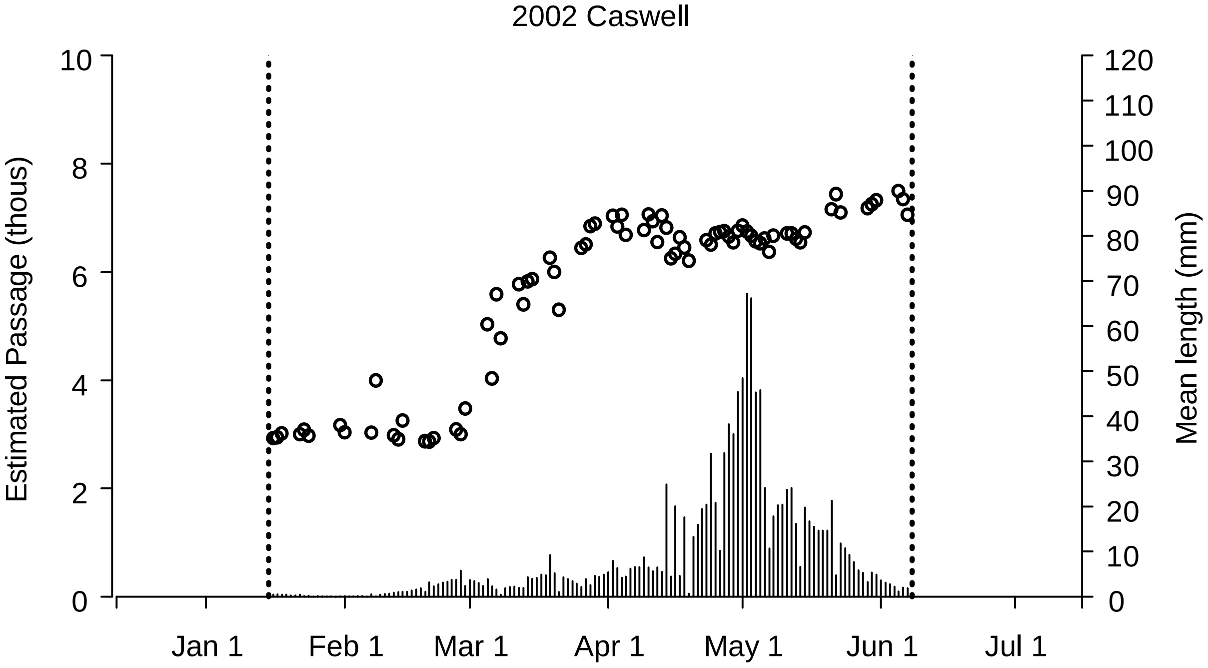


Figure A-23. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 2002. Dotted lines indicate the start and end dates of trapping.

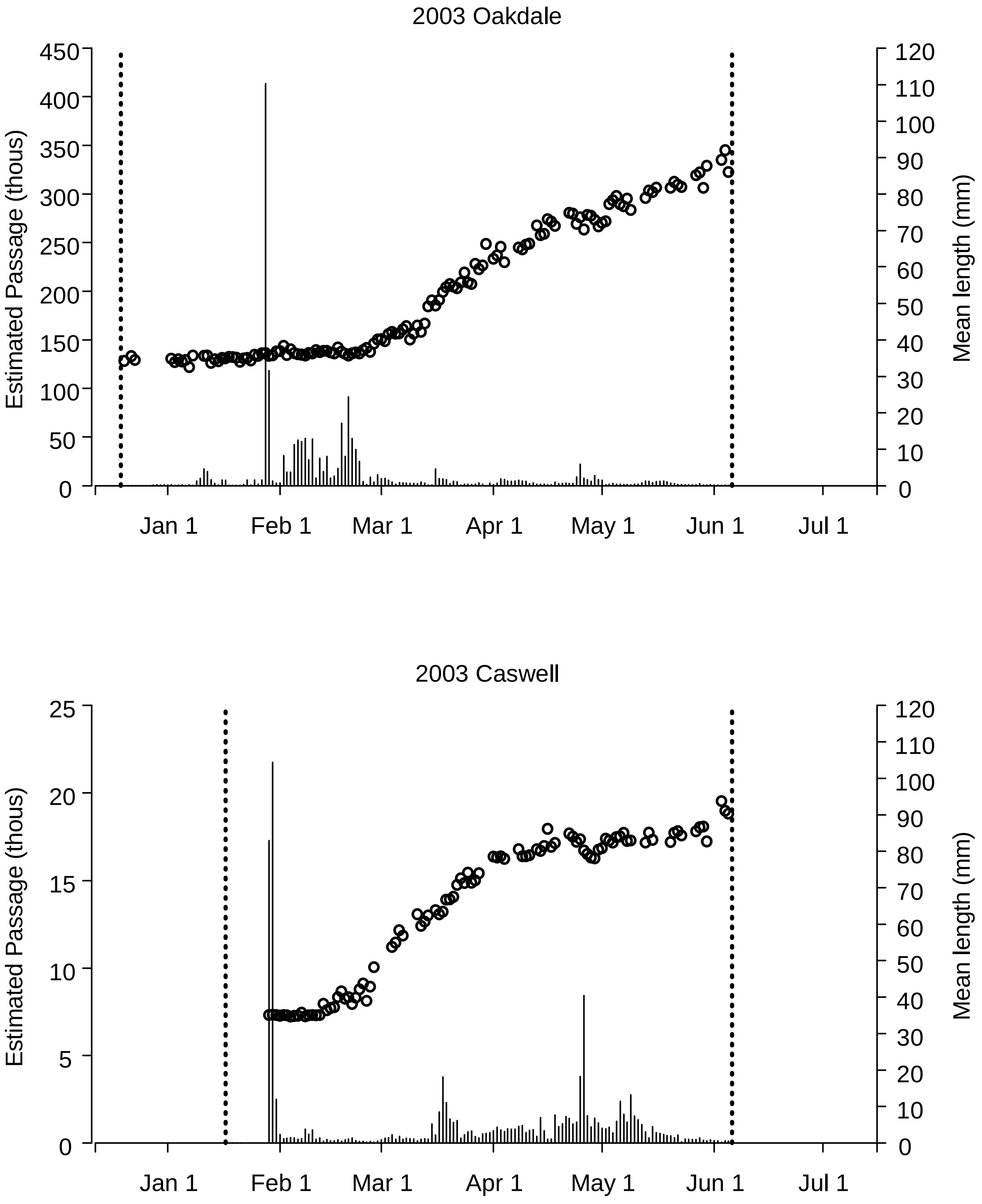
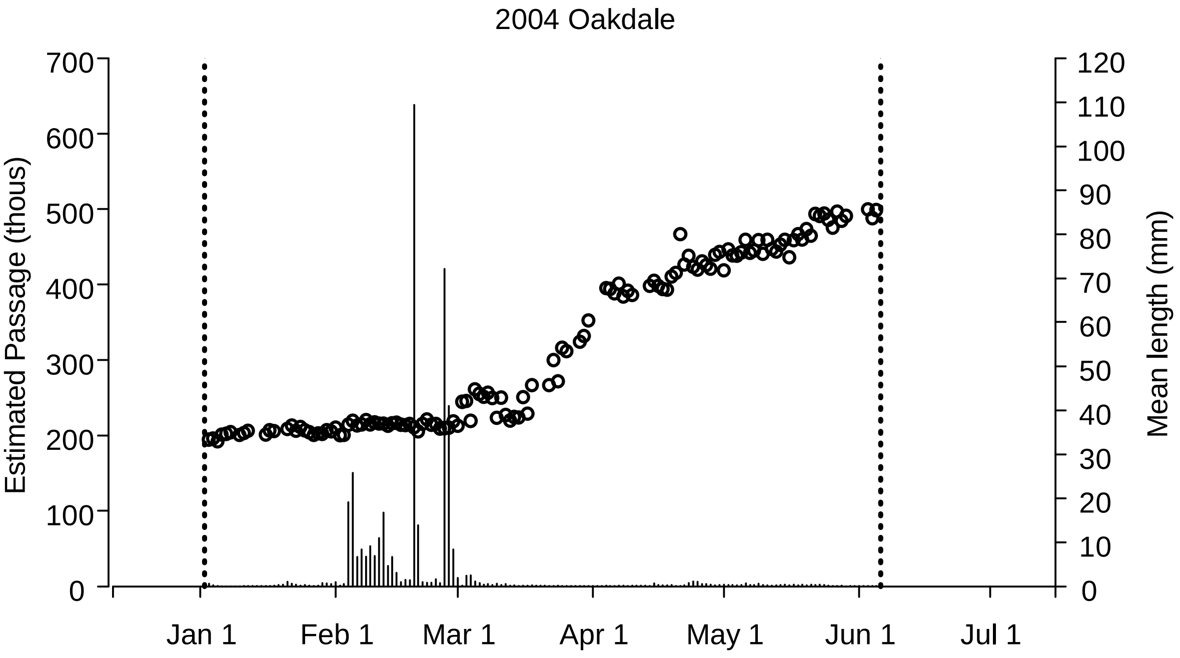


Figure A-24. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 2003. Dotted lines indicate the start and end dates of trapping.



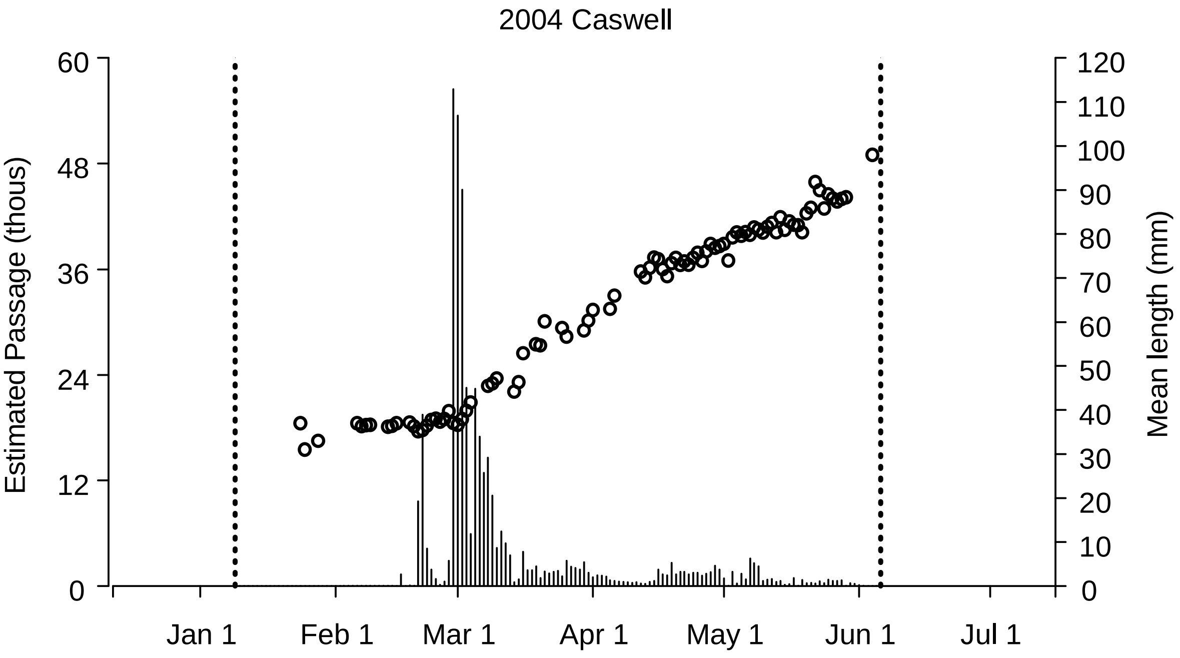


Figure A-25. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 2004. Dotted lines indicate the start and end dates of trapping.

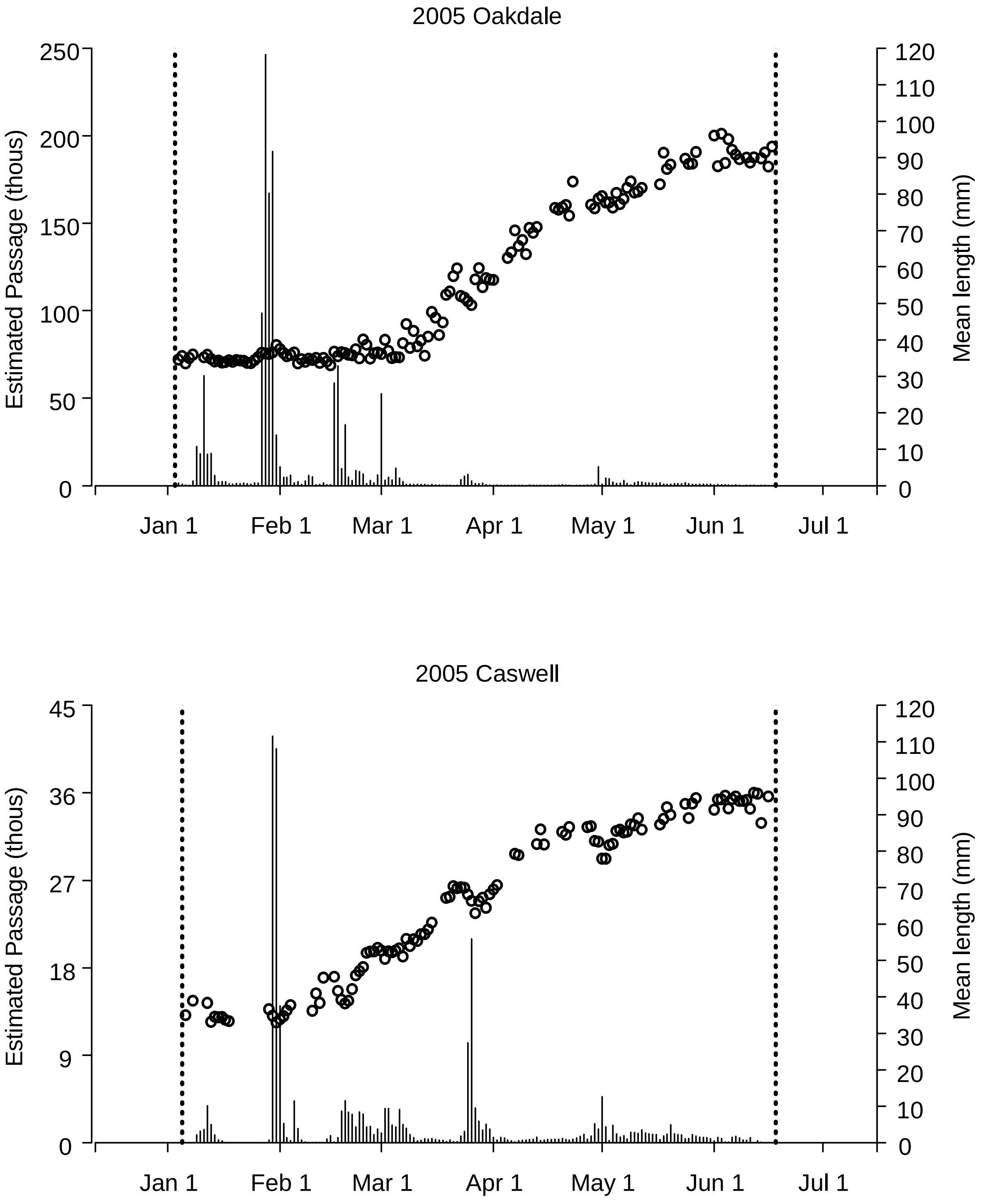


Figure A-26. Estimated total number of juvenile Chinook salmon passing the Oakdale and Caswell trap sites and mean length (mm) recorded at each trap site, 2005. Dotted lines indicate the start and end dates of trapping.