Effects of the Ocean and River Environments on the Survival of Snake River Stream-Type Chinook Salmon

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EXECUTIVE SUMMARY

The U.S. National Marine Fisheries Service (NMFS) studied the success of transporting spring chinook salmon smolts during the years 1983-1990 (excluding 1988) from Lower Granite Dam (river mile107.5 of the Snake River) to below Bonneville Dam (river mile 146 of the Columbia River). During this eight-year period, approximately 350,000 smolts were coded-wire tagged, and subsequently recovered as adults in a fish trap at Lower Granite Dam. To estimate survival, we calculated the recovery fraction (number recovered/number tagged). Our analysis revealed that survival was related to smolt migration timing and that survival varied among years.

Of the juveniles marked, those migrating earlier in the season (16-22 April) had an average adult recovery of 1 per 870; later migrants (19 April-8 June) had an average adult recovery of 1 per 349, representing a 2.5-fold increase over the migration season. The greatest contrast was seen in 1990, when there was a 5-fold increase in recovery for later versus earlier migrants.

We performed a generalized linear model (GLM) analysis using 18 physical and biological variables to determine which were the best predictors of adult returns. The age of return over the study period was the best explanatory variable, showing the percentage of total returns was 9%, 58%, and 33% for the 3-,4-, and 5-year-olds, respectively. This reflects the effect of age of maturity on the numbers returning. Three to five-fold more fish mature to make their spawning run at age 4 and 5 than at age 3. Of the riverine and oceanographic variables considered, the spring transition explained the most year-to-year variations in survival. It was also clear that smolts migrating later in a given year generally yielded higher adult returns. This was not related to an increase in fish size or discharge with the advance of the season, but may be due, in part, to a greater mix of wild outmigrants (compared to hatchery outmigrants) later in the season. However, a separate analysis of hatchery and wild fish in 1990 suggests that both experienced better survival as the season progressed. Alternatively, the increased survival over the season may indicate that lower smolt densities later in the season, or improved estuary/nearshore oceanographic conditions, produced greater survivals.

Finally, we incorporated our findings in a model of the survival of transported fish for use in CRiSP and other life-cycle models.

ACKNOWLEDGMENTS

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Introduction

Recently researchers have turned to the problem of determining the influence environmental variables have had on the survival of salmonids in the nearshore ocean environment. Studies suggest that the most critical period for survival is the juvenile's early ocean life (Pearcy 1992). During the juvenile stage, salmon are more vulnerable to a wider range of predators because of smaller size and limited experience, and more vulnerable to slight fluctuations in food supply, which are driven by coastal upwelling. That early ocean residence is critical to survival is supported by the correlation of jack returns to older fish returns, suggesting that return percentages are set during the first year of life (Gunsolus 1978; Peterman 1982).

Although much emphasis in the literature has been placed on decadal variation in survival (Francis and Hare 1994), also important are data demonstrating significant interannual and in-season variability of survival. It is understanding these sources of variability that allows us to improve survival through the optimal hatchery release numbers and timing, transportation schedules, and harvest regulations.

Changes in nearshore ocean currents reflect in-season shifts in coastal conditions influencing salmon survival (Beamish 1995; Anderson 1997). Higher productivity occurs along the coast between the spring transition and fall transition dates. The spring transition, which is a switch from strong southerly winds to weak northerly winds, marks the change from lower to higher productivity, accompanied by a change in the Columbia River plume, the direction of coastal currents. After the spring transition, a coastal jet with currents greater that 15 km/d develops on the shelf off Oregon and Washington and a southward undercurrent in deeper waters over the shelf and slope (Pearcy 1992). This produces episodic upwelling of cold, nutrient rich water, which produces conditions favorable to salmon growth and survival. The processes associated with these transitions are described by Hickey (1979, 1989), Huyer et al. (1979), Huyer (1977, 1983), Strub et al. (1987) and Landry et al. (1989). Francis et al. (1989) hypothesized that the survival of juveniles is favorable if ocean entry occurs during this period of higher productivity.

An important problem in understanding how the nearshore ocean affects survival involves separating the mortality experienced in the river environment from that of the ocean and estuarine environments. Groups of fish tagged at a Columbia River dam and recovered as adults reflect the effects of both the river and ocean environments on survival. One way to separate the river mortality from the estuary/ocean mortality is to use tagged fish that are transported to below Bonneville Dam. Transported fish escape predators in the reservoirs such as the northern squawfish and seagulls, and they escape hazards encountered at the dams such as nitrogen supersaturation and turbines. The estuary/ocean effects on survival may therefore be better represented in the study of transported fish than in fish that migrate downriver unaided.

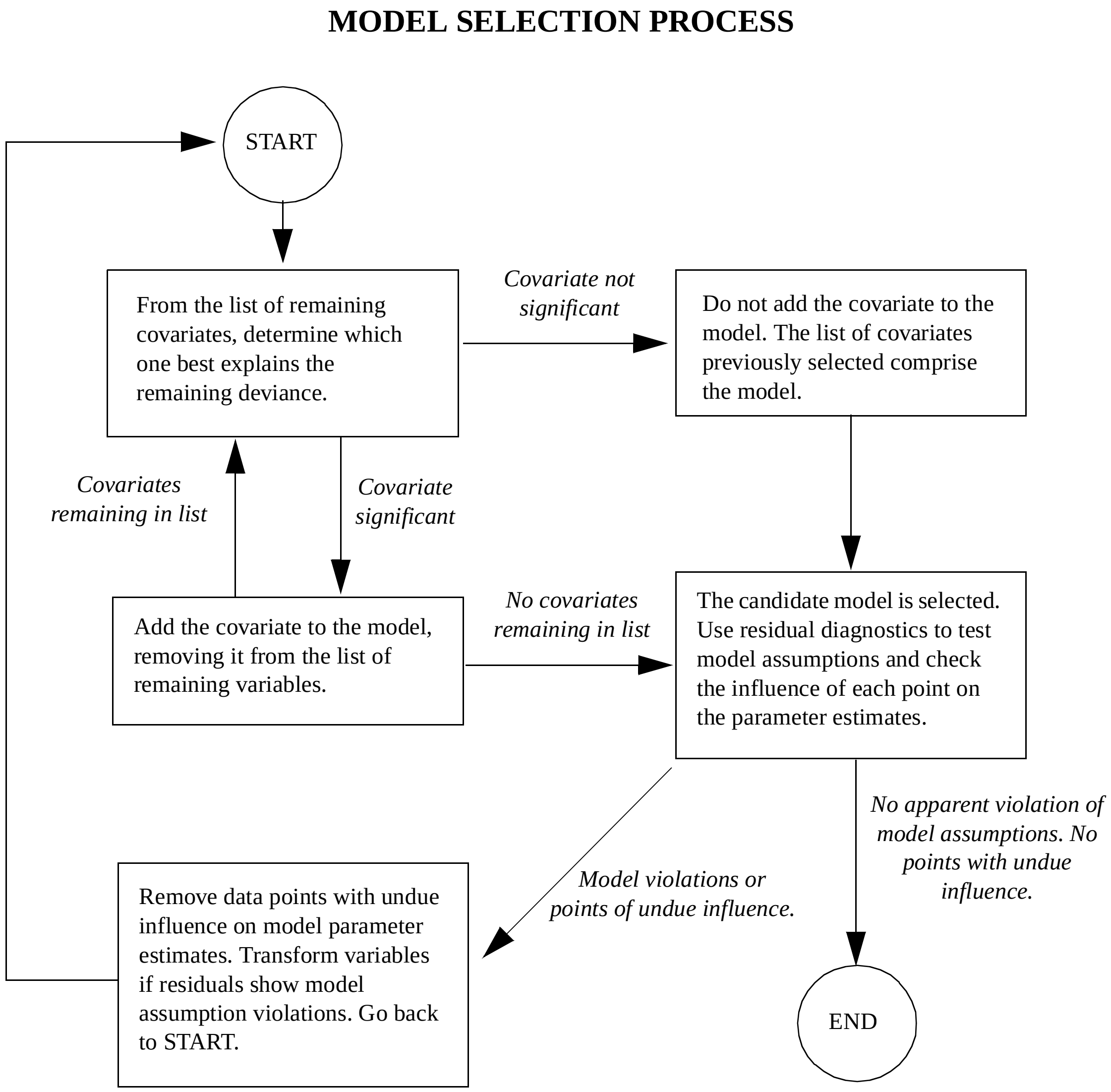

FIGURE 1 We selected covariates which had the best explanatory ability, discarding those with little.

The tagging program implemented by NMFS during the years 1983-1990 offered an excellent opportunity to study interannual variation in survival of transported fish which represented a mix of both hatchery and wild stocks. In this eight-year study, 350,000 smolts were tagged, and adults were subsequently recovered in the fisheries, at dams, and in hatcheries. We focussed on the returns at Lower Granite because recoveries at hatcheries and in fisheries were a very small percentage of the returns and their inclusion may have skewed the returns due to non-random sampling. For these fish, we calculated recovery percentages, defined as the percentages of tagged smolts that were recovered as adults. Since different tags were used among and within years, we were able to test for a relationships between recovery fractions and several biological and environmental variables. For example, we tested whether shorter adult lengths correlated with smaller return rates, to learn if poorer growth conditions contributed to higher mortality.

Previous studies have focussed on salinities (Blackbourn 1985), sea surface temperatures (Holtby and Scrivener 1989; Holtby et al. 1990), or coastal upwelling (Pearcy 1992) as predictors of salmon survival in the near-shore ocean. These predictors have been used with varying degrees of success. In our study, we tested the potential role of 18 variables; among these were annual spring and fall transition dates, wind velocity (which drives coastal upwelling), time of migration within a season, hatchery release numbers, and fish lengths (mm) at recovery.

Our goal was to select, from among this list of the biological and environmental variables, those that best explained the adult return rates of transported smolts. To select the most suitable variables, we used Generalized Linear Model (GLM) analysis (McCullagh and Nelder 1989). We used a step-wise regression analysis, using the deviance (analogous to variance) as a measure of the explanatory ability of various variables. At each step of the procedure, we selected the variable that best described the remaining deviance in the data. Having selected the best predictor in step k, we then proceeded to step $k + 1$, selecting the variable that best explained the remaining deviance. The procedure ended when all the remain covariates or their interactions were insignificant and the residual diagnostics revealed no violations of the underlying model assumptions (FIGURE 1).

The GLM analysis demonstrated the ability of migration timing in explaining within-year variation in survival, and the ability of spring transition date, length of summer, hatchery release number and flow in explaining between-year variation. The model selected, which may be incorporated into CRiSP, the Columbia River Salmon Passage Model (Anderson *et al.* 1996), can be used to reflect the influence of various management scenarios on post-mainstem survival and provide estimates of uncertainty. It also suggests what environmental variables should be further examined for their potential influence on salmon survival in other retrospective analyses such as Deriso *et al.* (1996) and Paulsen and Hinrichsen (1997).

Materials and Methods

Study Area

The study area encompassed the Snake River from Lower Granite Dam (river mile 107.5) to the lower Columbia River downstream of Bonneville Dam (river mile 146) (FIGURE 2). Fish were tagged and then barged to locations downstream of Bonneville.

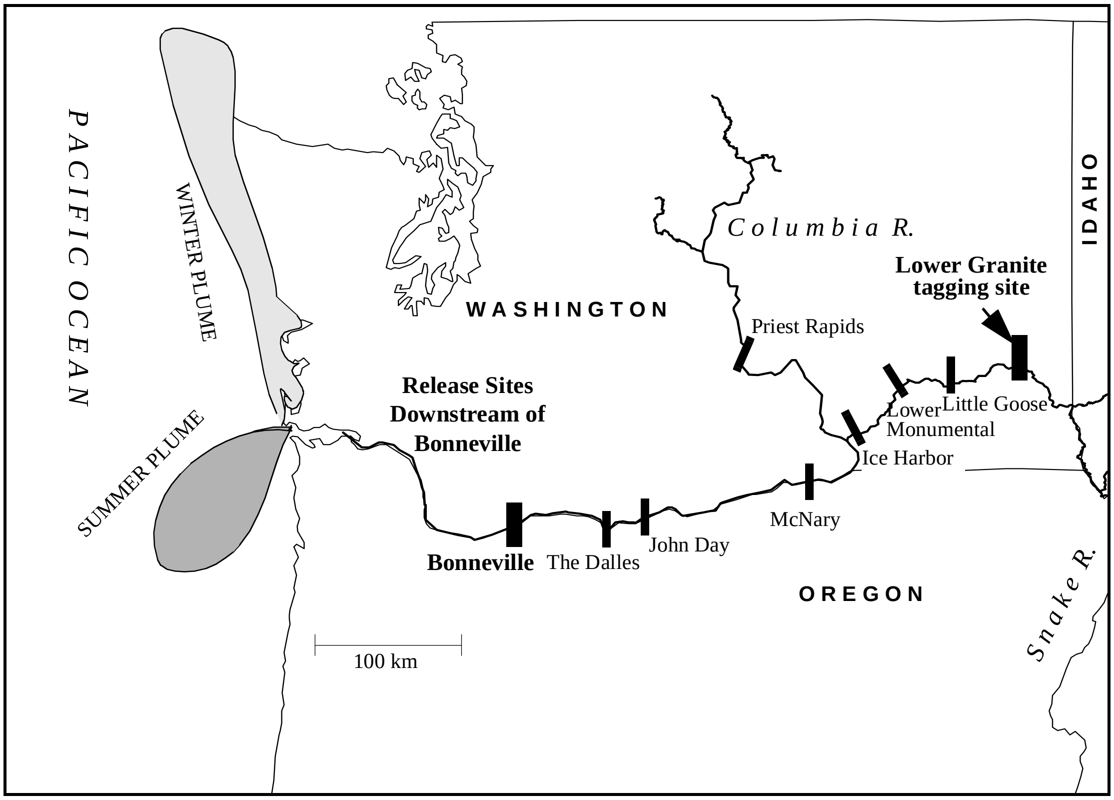

FIGURE 2 Tagging and release locations of spring chinook originating in the Snake River Basin. Fish were coded-wire tagged at Lower Granite Dam (river mile 107.5) on the Snake and transported below Bonneville Dam (river mile 146.1) on the Columbia River. They were recovered as adults in a Lower Granite fish trap. Fish migrating before the spring transition encounter the Columbia River plume in its winter configuration, after the; those migrating after the spring transition and prior to the fall transition encounter the plume in its summer configuration.

Data

Smolt tagging. Over the years 1983-1990 (excluding 1988), a total of 351,456 stream-type chinook smolts were marked at Lower Granite Dam with coded wire tags and freeze brands during the outmigration each year, and transported by barge for release below Bonneville Dam within 48 hours of tagging. There were 50 unique tag groups identified for the study. The period of tagging varied little from year to year, usually starting in early April and continuing into late May. However, in 1990 tagging continued into early June. Smolts were marked according to the procedures described by Matthews *et al.* (1987).

TABLE 1 Covariate list.

Variable	Definition
Hrelease	Total hatchery release in the Snake River Basin
LGRflow	Discharge (in KCFS) at Lower Granite Dam
PNI	Pacific Northwest Index
Age	The age effect represented as a factor variable with 3 levels: ages 3, 4, and 5
Year	The juvenile outmigration year effect represented as a factor variable with 7 levels
Period	The period effect represented as a factor variable with 3 levels: early, middle, and late migration
Slength	Length of summer as the number of days between the spring and fall transitions
Strans	The day of the year of the spring transition
Ftrans	The day of the year of the fall transition
LGRtemp	The temperature (°C) measured at Lower Granite Dam
BONtemp	The temperature (°C) measured at Bonneville Dam
Astoriaflow	Flow (KCFS) measured at Astoria
Firstday	For each tagged group, the first day of the year of tagging
Deltatrans	For each tagged group, the number of days between the median migration date and the spring transition
Lastday	For each tagged group, the last day of the year of tagging
Windvel	The mean N-S wind velocity (m/s) at the mouth of the Columbia
Length	Length of returning adults (mm)
Solar	The solar radiation ($\mathrm{kWh} \cdot \mathrm{m}^{-2} \cdot \mathrm{d}^{-1}$) measured at Astoria

All fish received an adipose fin clip, a freeze brand, and a coded wire tag. To provide estimates of the variance of survival *within* as well as among the study years, smolts were marked in replicated groups of approximately 5,000 fish. Each group received its own tag code.

Over the tagging study (1983-1990), delayed mortality due to handling and tagging was insignificant, varying annually between 0.3-1.3% (See Williams and Matthews [1995] for the 1986-1990 values). The exception was when personnel from another agency ran anesthetizer improperly in 1985. Delayed mortalities for fish tagged prior to 5 May averaged 1.9%; after 5 May they averaged 18.0%. Even so, the later fish had higher adult returns rates than earlier fish, and survival rates of late returning fish probably would have been even higher if marked smolts had not been suffocated in the preanesthetizer due to the use of a weaker anesthetic solution later in the tagging season.

The 18 covariates used in the model analysis are described below, and the variable names used to represent them are listed in TABLE 1.

First and last Day of tagging (Firstday and Lastday). The first and last day of tagging for each release group was recorded during the study. These data were obtained from the National Marine Fisheries Service annual reports on the evaluation of transportation (1983-1990) (e.g., Matthews et al. [1987]). These were used to estimate migration timing.

Adult recoveries. Adults were recovered 1-3 years after their year of smolt outmigration. Recovery sites included the ocean and river commercial fisheries, river sports fisheries, Indian ceremonial fisheries, survey streams, hatcheries, and river traps. A trap in a fish ladder at Lower Granite Dam was the primary recovery site and other sites had minimal recoveries. For example, of the spring chinook salmon tagged in 1984 at Lower Granite Dam, 73% of the recoveries were at the Lower Granite Dam trap, 15% at hatcheries, 6% at river sports fisheries, 2% at the Indian fishery, 2% at the commercial river fishery, 1% in streams surveyed, and 0% in the ocean fishery. The data used in this report contains the Lower Granite river trap data exclusively. It is the only recovery site where the percentage of migrants collected (known as the collection efficiency) is not thought to vary. The fish trap efficiency, f, is estimated at about 40% (i.e., $f = 0.40$) from a yearly aggregate determined over a couple of years. It is unknown by how much this expansion number varies over the migration season, but we need only assume that it does not vary systematically among tagged groups. Thus, to estimate actual survival (in percent), one must multiply the recovery percentage by $1/f$. The adult recovery data are summarized in TABLE 2. Notice that the best mean recovery percentage corresponded with outmigration year 1990 (0.367%), and the worst, outmigration year 1989 (0.061%)(FIGURE 3).

Adult length and age at maturity (Length and Age). Evaluation of smolt-to-adult survival was based upon the percentage of the tagged smolts that were recovered as adults in the Lower Granite fish trap. Upon recovery, each adult's freeze brand, age at maturity (in years), and length (mm) were recorded.

Flow and temperature at Lower Granite and Bonneville dams (LGRflow, LGRtemp, and BONtemp). We obtained daily flow (KCFS) and temperature (°C) at Lower Granite and Bonneville dams from the U. S. Army Corp of Engineers (ACOE). These data can be obtained from the Annual Fish Passage Reports for the years 1983-1990 or from the DART (Data Access in Real Time) World Wide Web database maintained at the University of Washington by the Columbia Basin Research Group[1].

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[1] See the Dart database World Wide Web pages at http://www.cqs.washington.edu/dart/dart.html.

TABLE 2 Summary of unexpanded spring chinook tagging and recovery at Lower Granite Dam.

			Adult Returns							
			Age 3		Age 4		Age 5		Total	
Outmigration Year	Period of Tagging	Smolts Tagged	Return	Percent Return	Return	Percent Return	Return	Percent Return	Return	Percent Return
1983	21 April - 25 May	44,648	10	.022	99	.222	15	.034	124	0.278
1984	16 April - 15 May	46,173	11	.024	40	.087	24	.052	75	0.162
1985	12 April - 22 May	45,420	11	.025	52	.114	38	.084	101	0.222[a]
1986	10 April - 3 June	45,005	7	.016	41	.091	26	.058	74	0.164
1987	10 April - 27 May	50,207	12	.024	66	.131	13	.026	91	0.181
1989	11 April - 30 May	75,295	3	.004	24	.032	19	.025	46	0.061
1990	13 April - 08 June	44,708	8	.018	71	.159	85	.190	164	0.367
Totals:		351,456	62	.018	393	.112	220	.063	675	0.192

[a] Returns were artificially lowered due to improper anesthesia techniques during handling and marking.

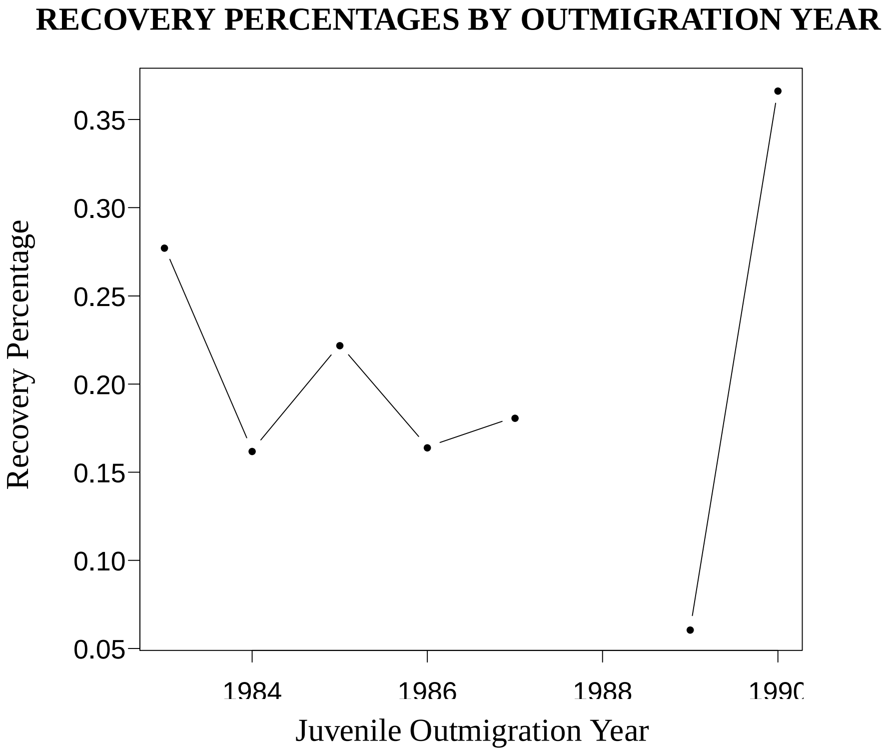
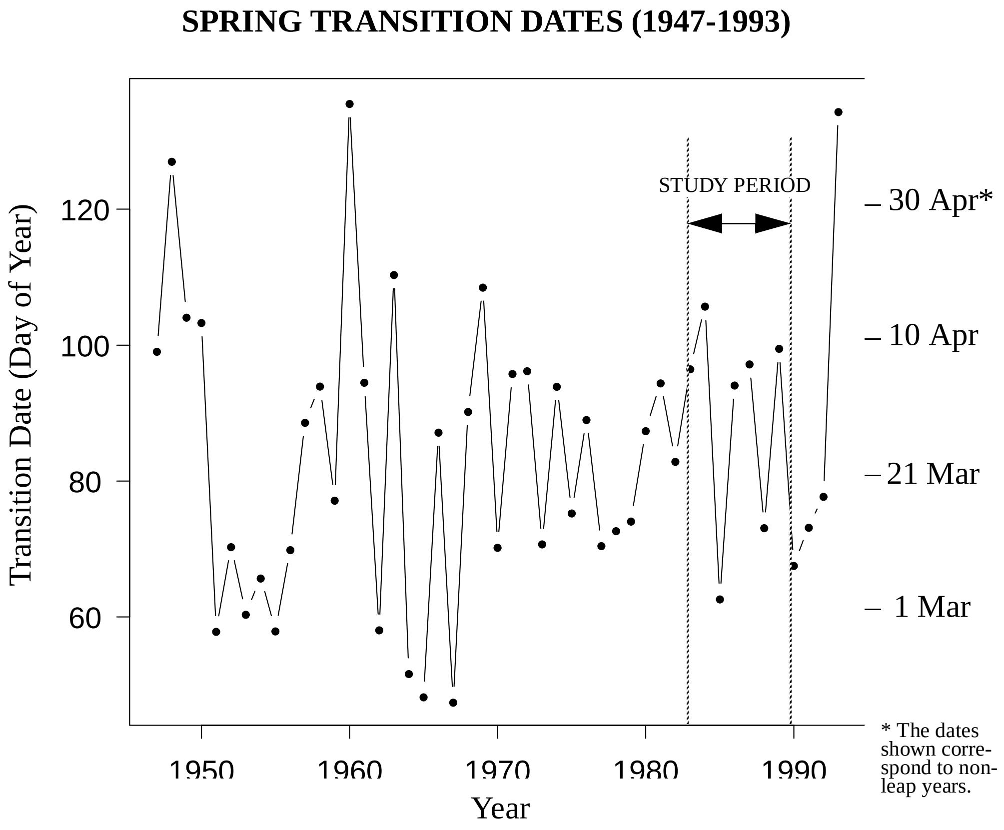


FIGURE 3 Average unexpanded recovery percentages by outmigration year. Observed adult return rates ranged from a low of 0.061% (1 in 1,639) in 1989 to 0.367% (1 in 272) in 1990. On average, approximately 2 fish were recaptured as adults for every 1,000 juveniles tagged and released. The trap efficiency was roughly estimated at 0.4, so the true average number of adults returning was about 5 per 1,000 juveniles.

*Flow at Astoria (Astoriaflow).*We reconstructed daily discharge (KCFS) at Astoria using eight long-term gages within the Columbia River Basin (Wendell Tangborn,personal communication, HYMET Company, 2366 Eastlake East, Seattle, Washington 98102). These flows represented the approximate freshwater input rates from the Columbia River Basin into the Pacific Ocean, and they affected the dimensions of the Columbia River plume at sea (Barnes et al. 1972, Fiedler and Laurs 1990). Previous studies showed that the surface water in the region covered by the Columbia River plume has higher rates of photosynthesis than ambient waters and contains more phytoplankton (Anderson 1964). Thus the dimensions of the plume, affected by the total Columbia discharge, influences the food supply available to juvenile salmon as they enter the near-shore ocean.

Wind-related covariates (Strans, Ftrans, Slength, Deltatrans, and Windvel). Each year, along the Pacific Coast of North American between San Francisco (38 °N Latitude) and the Queen Charlotte Islands (52 °N Latitude), the coastal winds switch from the southerly winds of winter to the northerly winds of summer producing a transition in wind called the *spring transition*. Conversely, the yearly switch back from the northerly winds of summer to the southerly winds of winter produce a *fall transition*. The summer winds, which occur after the spring transition and prior to the fall transition, are known to be favorable for upwelling—a process that transports the nutrients to the ocean surface, feeding the near-shore food chain. Estimates of the transition dates were derived from smoothed synthetic winds computed by the ocean surface currents model OSCURS (Ingraham and Miyihara 1988), which used daily sea level atmospheric pressure fields for years 1983 to 1990 as input (FIGURE 4). From the spring transition dates and the tagging periods described above, we computed *Deltatrans*, representing the difference (in days) between the mean date of transport and the spring transition date for each tagged group of juvenile chinook. The daily north-south component of the synthetic wind velocity (m/s), averaged over April-June, was also used as a predictor variable, *Windvel*. Wind velocity is a determinant of coastal upwelling. Higher velocity northwesterly winds induce stronger episodic upwelling of cold, nutrient-rich water off the shelf.



* The dates shown correspond to non-leap years.

FIGURE 4 Spring Transition dates (as day of the year) at the Columbia River's mouth estimated from the synthetic winds generated by OSCURS. During 1947-1993, the spring transition date varied from day 48 (17 Feb) to 136 (15 May). For this study, only the spring transition dates during 1983-1990 were used.

Solar radiation (Solar). Monthly solar radiation ($\mathrm{kWh} \cdot \mathrm{m}^{-2} \cdot \mathrm{d}^{-1}$) at Astoria was obtained from the Renewable Resource Data Center supported by the U.S. Department of Energy's National Renewable Energy Laboratory Resource Assessment Program[1] (NREL 1994). Data uncertainty, as reported by NREL, was approximately ±9 %. The monthly data were averaged over April-June to produce an annual value for 1983-1990.

Total hatchery release number (Hrelease). We obtained an estimate of the early hatchery output in the Snake River drainage over the years 1983-1990. We used the total number of hatchery spring and summer chinook released in the Snake River Basin (Fish Passage Center 1994).

Pacific Northwest Index (PNI). This index is constructed as the average of the standard normal deviates of three parameters (Ebbesmeyer et al. 1989; Ebbesmeyer and Strickland 1995): air temperature at Olga, Washington; precipitation at Cedar Lake in the Cascade foothills; and snow pack depth at the Paradise Ranger Station, Mount Rainier, WA. The index has been used to track decadal variations in the Pacific Northwest climate during the 1900s and has been found to co-vary with certain biological variables such as the Oyster Condition Index (Schoener and Tufts, 1987).

We defined the factor variables *Year*, *Period*, and *Age* to gauge the year-to-year variation in the data, the within-year variation (based on migration timing, and the variation between age-groups, respectively. The factor *Year* contains seven categories, one for each year of tagging. *Period* categorizes each tagged group as early, middle, or late, depending on their time of tagging (TABLE 3). It was impossible to define consistent time divisions for this factor variable since tags were changed at different times from year-to-year, but they were defined so that they occurred at approximately the same time each year. We use this factor variable only briefly show the significance of migration timing in a contigency table before showing its effect in a GLM analysis which uses the exact days of tagging. Finally, *Age* represents the age at recovery (3, 4, or 5 years). The returns by period and year are summarized in TABLE 4.

Data Analysis

We analyzed the recovery data using GLM techniques, which allow regression of count data against continuous and categorical predictors. The response in the GLM analysis is the recovery proportion, which is a survival index, defined as the number of tagged adult recoveries divided by the number of smolts tagged. The model selection procedure is a step-wise regression analysis (FIGURE 1). For selecting the optimal predictors, we examined the Akaike Information (*AIC*) p-values at each step of the regression (Akaike 1973). All possible models obtained by adding a single term to the

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[1] See the World Wide Web solar radiation database at http://rredc.nrel.gov/solar/.

current model were fit, and the *AIC* statistic computed. In most cases, the model selected at a given step was that having the smallest value for the *AIC* statistic.

The fundamental unit of recapture was a collection of fish trapped at Lower Granite Dam by age. Let n_{ik} represent the number of fish with tag code i, from an initial release of R_i that were observed in the inspected sample when release group i is in age group k ($k = 1$ for age 3 fish, $k = 2$ for age 4 fish, and $k = 3$ for age 5 fish). Let p_{ik} be the recovery proportion, namely, n_{ik}/R_i. This was our age-specific survival index which included the influence of age at maturity. In this study, there were 50 different tag codes and 3 different age groups, which gave rise to $N = 150$ observations of p_{ik}. To estimate the actual return rate of spring chinook to Lower Granite, we first estimated the fraction of fish that were sampled upon return, f, estimated at about 40% for the Lower Granite fish trap. We assume this value was constant over the years of study, which gives an estimated total return proportion of

$$y_{ik} = \left(\frac{1}{f}\right)\frac{n_{ik}}{R_i} = \frac{p_{ik}}{f} . \tag{1}$$

How do we interpret y_{ik} in terms of the salmon’s life history? Caution is needed. This return proportion contains information about the survival as well as maturation. For example, if all fish return at age 3, we do not know if this occurred because all fish matured at age 3, or fish destined for maturity at age 4 or age 5 simply died. Without making assumptions about the maturity schedule of salmon or their survival schedule, it is impossible to separate survival and maturity. Mathematically, we write

$$y_{i1} = S_{i0}\delta_{i1}M_{i1} , \tag{2}$$

$$y_{i2} = S_{i0}(1 - M_{i1})S_{i1}\delta_{i2}M_{i2} ,$$

$$y_{i3} = S_{i0}(1 - M_{i1})S_{i1}(1 - M_{i2})S_{i2}\delta_{i3}M_{i3} ,$$

where S_{i0} is the survival from transport to age 3, S_{i1} is the ocean survival from age 3 to age 4, and S_{i2} is the ocean survival from age 4 to age 5; δ_{ik} represents the age-specific survival rate for fish during their upstream spawning migration; M_{ik} is the fraction of fish maturing at age $k + 2$, $k = 1, 2, 3$. Notice that $M_{i1} + M_{i2} + M_{i3} = 1$.

If we prefer to write the survivals as functions of the return proportions, y_{ik}, the maturity fractions and the upstream migration survivals, we have

$$\begin{aligned} S_{i0} &= y_{i1}/\delta_{i1}M_{i1} \qquad (3) \\ S_{i1} &= \left(\frac{y_{i2}}{y_{i1}}\right)\left[\frac{\delta_{i1}M_{i1}}{(1-M_{i1})\delta_{i2}M_{i2}}\right] \\ S_{i2} &= \left(\frac{y_{i3}}{y_{i2}}\right)\left[\frac{\delta_{i1}M_{i2}}{(1-M_{i2})\delta_{i3}M_{i3}}\right] \quad . \end{aligned}$$

At marking it was unknown what proportion of fish in each release group had which particular maturity schedules and differential sampling of different stocks may have influenced the return rates. This emphasizes the importance of accounting for differences in returns based on differing age structure, which we discuss later in the paper.

We treat n_{ik} as the response variable, use the log link function, and assume an underlying scaled poisson distribution for these observations (Green and MacDonald 1987; Cormack and Skalski 1992). The mean of p_{ik} is θ_{ik}, In the scaled poisson distribution, the variances are proportional to the means, so that $var(p_{ik}) = \phi\theta_{ik}$. The general log-linear model used is of the form

$$\log(\theta_{i,k}) = \sum_{l} \beta_{k,l} x_{i,k,l} , \qquad (4)$$

where $\beta_{k,l}$ represents the various parameters to be estimated (sometimes age-specific, sometimes not), and $x_{i,k,l}$, the components of the l covariates used.

We have chosen the scaled poisson distribution because it is used successfully with data in which the “successes,” in this case the number of fish recovered at various ages, are rare. The scale factor is present because the variance in the data tends not be be simply equal to the mean as an unscaled poisson distribution would assume. Fortunately, as McCullagh and Nelder (1989) point out, the second-order properties of the parameter estimates are insensitive to the assumed distributional form: they depend mainly on the assumed variance-to-mean relationship and independence. We treat the age-specific observations as independent because of the large releases and small recoveries. In this case the observations are approximately independent. This occurs because, when the probability of recovery is low and the number of observations is large, a multinomial distribution (which models the dependence among age-specific observations) is approximately equal to a product of independent poisson distributions.

In fact, aggregating over the age-specific recoveries is not desirable for this data set. If we were to aggregate the data over age of return, we would loose important scientific information (i.e. changes in age distribution of fish over-time, whether by survival differences or age-at-maturity differences) and furthermore, it can mask the appearance of interactions and dramatically reduce the degrees of freedom in our case, we would loose 2/3 of the degrees of freedom. Therefore, we see little value in aggregating over age as a reviewer recommended.

TABLE 3 Period definitions.

	Period		
Year	Early	Middle	Late
1983	**	21-27 Apr	29 Apr - 25 May
1984	16-21 Apr	22-28 Apr	29 Apr - 15 May
1985	12-18 Apr	19-26 Apr	29 Apr - 22 May
1986	10-20 Apr	20-28 Apr	28 Apr - 3 Jun
1987	10-20 Apr	20-28 Apr	30 Apr - 27 May
1989	11-22 Apr	22-27 Apr	1-30 May
1990	13-21 Apr	21 Apr - 2 May	2 May - 8 Jun

TABLE 4 Summary table for unexpanded returns of spring chinook salmon

	Period						Yearly Total	
	Early		Middle		Late			
Year	Returns	Percent Returns	Returns	Percent Returns	Returns	Percent Returns	Returns	Percent Returns
1983	NA	NA	62 (24,792)	.250	62 (19,856)	.312	124 (44,648)	.278
1984	1 (10,155)	.010	44 (27,713)	.159	30 (8,305)	.361	75 (46,173)	.162
1985	9 (9,893)	.091	34 (17,414)	.195	58 (18,113)	.320	101 (45420)	.222
1986	23 (20,002)	.115	27 (10,000)	.270	24 (15,003)	.160	74 (45,005)	.164
1987	31 (13,998)	.221	17 (14,218)	.120	43 (21,991)	.196	91 (50,207)	.181
1989	27 (28,582)	.094	15 (35,369)	.042	4 (11,344)	.035	46 (75,295)	.061
1990	20 (14,000)	.143	31 (14,000)	.221	113 (16,708)	.676	164 (44,708)	.367
Totals:	111 (96,630)	.115	230 (143506)	.160	334 (111,320)	.300	675 (351,456)	.192

Step-wise GLM analysis. We used a step-wise procedure to determine an optimal, parsimonious model. The many continuous and categorical variables described above were used as predictors, and were included or excluded in the final model according to their explanatory ability. In addition to the GLM analysis, contingency tables were derived to test the ability of *Age*, *Year*, and *Period* to predict the survival index.

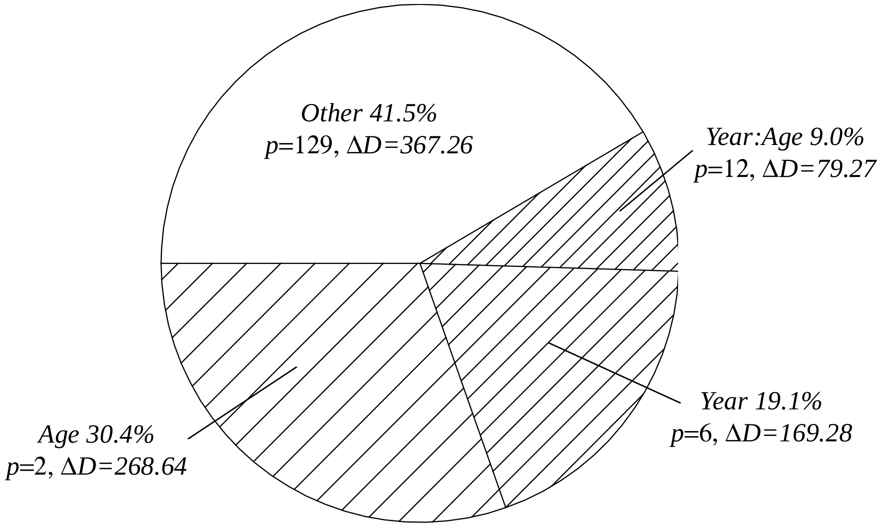
We performed model diagnostics including plots of Anscombe residuals and Cook's Distance (Anscombe 1953, Cook and Weisberg 1982, Chambers and Hastie 1992) to check for violations of model assumptions and for points of undue influence on the regression results. Since the Cook's Distance of the i th observation is proportional to the release size, R_i, it was necessary to divide it by R_i to obtain a useful measure of influence. This allowed us to judge whether points of high influence were due simply to relatively large release sizes.

We analyzed four models, each derived based on the inclusion or exclusion of certain influential data points. In *Model A*, we derived a model based on all the data, and it included all main effects and interactions found significant. In *Model B*, we omitted the highly influential observations #68 and #150. In *Model C*, we omitted #68, #150 and #147. Finally, in *Model D*, we used the all of the data, but only included main effects and two-way interactions that were significant in *Model C*. Its parameter estimates, however, were based on all the data, not a subset.

Results

Factor variables: *Age*, *Year*, and *Period*

The factors *Age*, *Year*, and *Period* were significant in the GLM analysis and in the contingency tables. In themselves, *Age* and *Year* and their interaction, represented by 20 parameters, explain 58.5% of the data's deviance (FIGURE 5). The remaining 41.5% of the total deviance was attributable to variables such as flow, temperature, or fish condition: those factors which vary within a year. The deviance associated with the random component of the model, the non-systematic component of the model, is also contained in the remaining 41.5% of the total deviance.



GLM APPORTIONMENT OF DEVIANCE TO *AGE*, *YEAR*, AND THEIR INTERACTION

FIGURE 5 The deviance pie chart for *Age* and *Year* and their interaction. Most of the deviance in the spring chinook returns is explained by the factors *Age* and *Year* along with their interaction term *Year:Age*. The deviance ascribed to the category "Other" contains the deviance attributable to within-year effects and to a random model component.

Age. Of the three factors considered, *Age* explained the most of deviance ($\Delta D = 268.64$, d.f. = 2), 30.4% of the total (TABLE 5). (Recall that *Age* represents the age composition of adult returns from a group tagged as juveniles during their outmigration year). Furthermore, a contingency table (TABLE 6) demonstrated significant between-year differences in the age distribution of returning fish. These differences were caused mainly by the age distributions observed in years 1983 and 1990; respectively, the years with the lowest and highest hatchery releases during the study. In 1983, there was a larger proportion of Age 4 fish in the returns than expected (based on the averages over all years) and a smaller number of Age 5 fish than expected (FIGURE 6). Thus the outmigrants of 1983 generally returned at a younger age than others.

In contrast, from the juveniles tagged in 1990, there was a larger number of Age 5 fish observed than expected based on the average over all years and fewer Age 4 fish, indicating a shift in distribution weighted toward older fish. Considering all years grouped together, 9.19% of the returning fish were Age 3, 58.2% were Age 4, and 32.6% were Age 5. During 1983, 79.0% were Age 4 and only 12.1% were Age 5. During 1990, 43.3% were Age 4 and 51.8% Age 5 (TABLE 6 and FIGURE 6).

TABLE 5 Analysis of deviance for the *Age* effect.

	Goodness-of-fit			Differences			
Model	Deviance χ^2	Pearson χ^2	d.f.	Deviance	Pearson	d.f.	p-value
1	884.450	1283.55	149	NA	NA	NA	NA
1 + Age	615.813	968.73	147	-268.64	-314.82	-2	1.406e-09

$\chi^2 = 268.64$, $\hat{\phi} = 6.59$, d.f. = 2, p-value = 1.406e-09

TABLE 6 *Age* and *Year* (year of outmigration) contingency table.

Year	Age 3		Age 4		Age 5		Totals
1983	10	*(11.39)	****99**	(72.20)	**15**	(40.41)	124
1984	11	(6.89)	40	(43.67)	24	(24.44)	75
1985	11	(9.28)	52	(58.80)	38	(32.92)	101
1986	7	(6.80)	41	(43.08)	26	(24.12)	74
1987	12	(8.36)	66	(52.98)	**13**	(29.66)	91
1989	3	(4.23)	24	(26.78)	19	(14.99)	46
1990	8	(15.06)	**71**	(95.48)	**85**	(53.45)	164
Totals	62		393		220		675

$\chi^2 = 75.087$ (Pearson chi-square with Yates continuity correction) d.f=12, p-value=3.538e-11

$G^2 = 79.274$ (chi-square statistic from likelihood ratio test)

* The expected cell counts are given in parentheses.

**The shaded cell counts are significantly different from their expected counts at the 0.05 level.

If hatchery releases were driving the interaction between outmigration year and age of recovered adults, then we would expect to see younger age-at-recovery corresponding to migration years of high hatchery releases, and older age-at-recovery, to migration years of low hatchery releases. (Assuming that larger hatchery releases result in greater proportions of hatchery fish among the tagged groups). This is because hatchery fish generally mature earlier than wild fish. However, just the opposite pattern was seen in the 1983-1990 data. The largest hatchery release coincided with 1990, when 11.7 million hatchery spring chinook were released into the Snake River, but the age-at-recoveries were *older*, not younger than average. The smallest hatchery release was 2.6 million in 1983, but the recovered adults from the 1983 outmigrants had a *younger* age distribution, not an older one. This may indicate that in years with high hatchery releases, hatchery fish make up a smaller portion of the returns. The returns from the outmigration of 1990 may have contained a greater portion of wild fish, in spite of the large number of hatchery fish released, because tagging occurred later in the season when wild fish made up a greater portion of the outmigration. Another factor which can affect the age-at-maturity of returning adults is the size of the hatchery smolts. Larger hatchery smolts tend to produce younger adult returns.

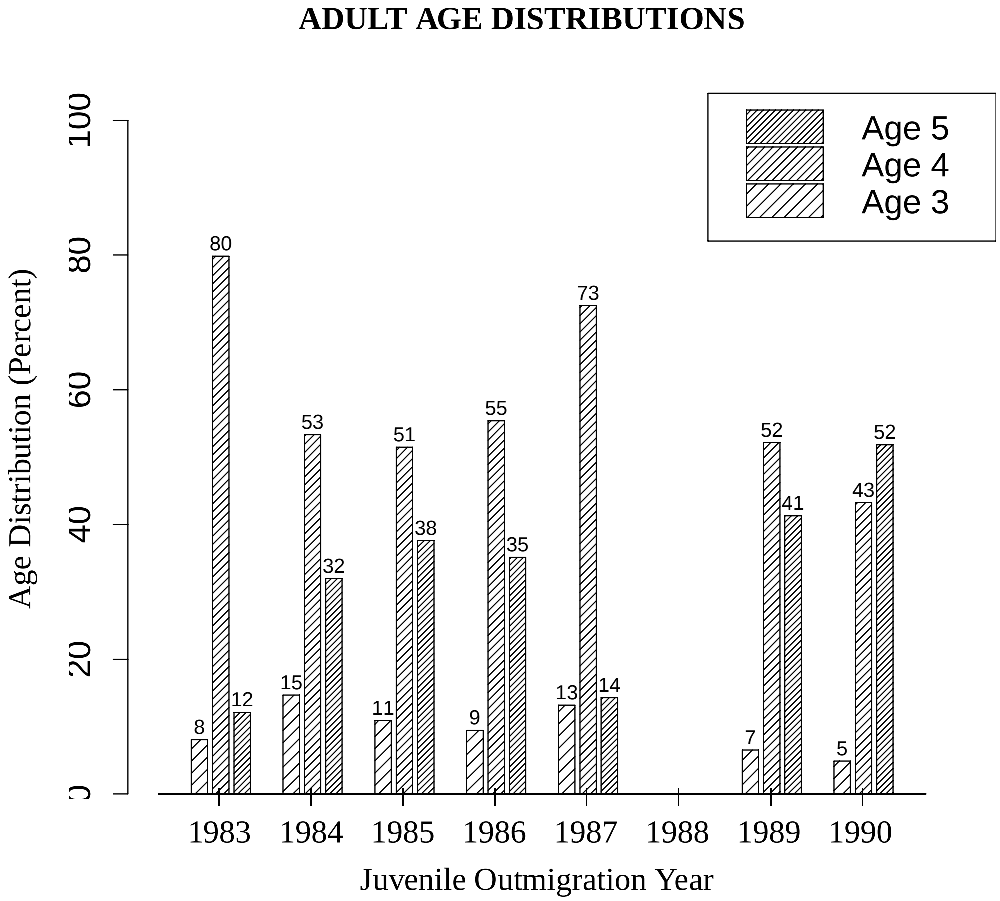


FIGURE 6 Age distribution of returning fish. Both varying age at maturity and age-specific ocean mortality can contribute to changes in age distribution.

Year. The factor *Year* is second to *Age* as an explanatory variable, explaining 19.14% of the total deviance, or 27.49% of the deviance left after extracting the *Age* effect ($\Delta D = 169.28$, d.f. = 6) (TABLE 7). The interaction between *Year* and *Age*, *Year:Age* explains just 8.96% of the total deviance, or 12.87% of the deviance after Age is extracted ($\Delta D = 79.27$, d.f. = 12). Although the deviance explained by this interaction is small, its chi-square value of $\Delta D / \hat{\phi} = 23.66$ is significant, with a p-value of 0.02256 when compared to a chi-square distribution with 12 degrees of freedom (TABLE 8). Thus a predictor variable that varies on an annual basis may interact with *Age* to produce a significant effect.

TABLE 7 Analysis of deviance for *Year* effect.

	Goodness-of-fit			Differences			
Model	Deviance χ^2	Pearson χ^2	d.f.	Deviance	Pearson	d.f.	p-value
1	884.45	1283.55	149	NA	NA	NA	NA
1 + Year	715.17	846.58	143	-169.28	-436.97	-6	7.260e-05

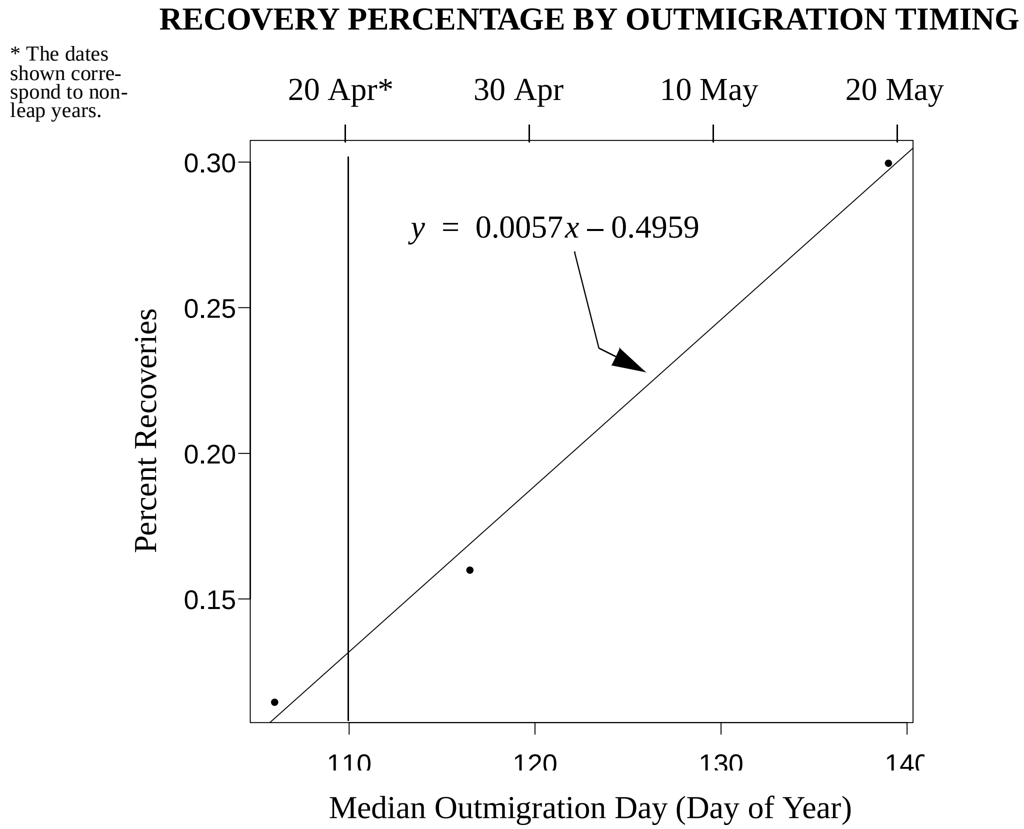
$\chi^2 = 169.28$, $\hat{\phi} = 5.92$, d.f. = 6, p-value = 7.260e-05

TABLE 8 Analysis of deviance for testing the *Age* and *Year* interaction.

	Goodness-of-fit			Differences			
Model	Deviance χ^2	Pearson χ^2	d.f.	Deviance	Pearson	d.f.	p-value
1	884.450	1283.55	149	NA	NA	NA	NA
1 + Age	615.813	968.73	147	-268.64	-314.82	-2	1.406e-09
$1 + Age + Year$	446.530	587.94	141	-169.28	-380.79	-6	3.477e-07
$1 + Age \times Year$	367.260	432.08	129	-79.27	155.86	-12	.02256

$\chi^2 = 79.27$, $\hat{\phi} = 3.35$, d.f. = 12, p-value =.02256

Period. The factor *Period* was included in the model to provide an assessment of how recoveries may be influenced by migration timing within a season. The maximum length of a period was one month, and the shortest, one week (TABLE 3). We were unable to select the period divisions that matched from year-to-year because tags were not changed on the same days from year-to-year. However, we later examine the within-year variation based on a finer time scale that does not rely on these rought divisions; instead we use the last day (*Lastday*) and first day of tagging (*Firstday*) for each tagged group, where certain tags were used for not more than a day. The *Period* variable explained 11.38% of the total deviance ($\Delta D = 79.27$, d.f. = 3), and was significant, with a p-value of 5.62e-04 (TABLE 9). More importantly, the period-based returns showed a tendency for fish tagged later in the season to survive better. This pattern is evident in the years 1983, 1984, 1985, and 1990 (four of the seven years) and, totaling over all years, the returns are 0.115%, 0.160%, and 0.300% for the early, middle, and late periods, respectively (TABLE 4 and FIGURE 7).


RECOVERY PERCENTAGE BY OUTMIGRATION TIMING

* The dates shown correspond to non-leap years.

FIGURE 7 On the whole, fish migrating later in the season showed better returns than those migrating earlier. The linear regression shown indicates that a 10 day delay in migration timing means an increase in recovery percentage of 0.06.

TABLE 9 Analysis of deviance for *Period* effect.

	Goodness-of-fit			Differences			
Model	Deviance χ^2	Pearson χ^2	d.f.	Deviance	Pearson	d.f.	p-value
1	884.45	1283.55	149	NA	NA	NA	NA
1 + Period	783.78	988.79	147	-100.67	-294.76	-2	5.626e-04

$\chi^2 = 100.67$, $\hat{\phi} = 6.73$, d.f. = 2, p-value =.5.626e-04

Correlation of covariates.

Some of the covariates were found to be highly correlated (TABLE 10). In multi-regression modeling it is best to avoid including correlated predictor variables in the final model. We do this by using representatives of the various groups of correlated predictors. Below we identify these various correlated groups.

Spring transition (Strans). The predictors *Deltatrans* ($r = 0.79$), *Slength* ($r = -0.89$) and the date of the *Strans* are correlated. *Deltatrans*, defined as the difference between the mean tagging day for a group and the date of the spring transition. Therefore, a later spring transition day results in a larger *Deltatrans*. The Length of summer is defined as the difference between the spring and fall transition dates in days. Since the fall transition date tends to be more stable than the spring transition date, the summer length tracks the spring transition date (e.g., an early spring transition generally means a longer summer).

Last Day Tagged (Lastday). The last day that a group was tagged (day of the year), water temperature at Bonneville Dam ($r = 0.76$), the first day of tagging ($r = 0.89$), and the period of tagging ($r = 0.85$), were correlated. The correlation was high among all of these variables because all increased from April to June. The high correlation between *Lastday* and *Firstday* shows that if *Lastday* is included in the model neither *Firstday*, or the median tagging day defined as (*Lastday* + *Firstday*)/2 should be excluded. (Note that the last and first day of tagging is not restricted to the period definitions in TABLE 3, but are the precise beginning and end days of tagging for each group of juveniles tagged with a unique code.)

Lower Granite Flow (LGRflow). Snake River flow at Lower Granite (*LGRflow*) was correlated with the flow estimated for Astoria (*Astoriaflow*) ($r = 0.81$) in the lower Columbia River.

Hatchery Release Numbers (Hrelease). Since the number of hatchery fish released in the Snake River Basin tended to increase over the years of study 1983-1990, the ordinal factor *Year* (outmigration year) and predictor *Hrelease* were correlated $(r = 0.84)$.

Adult Length (Length). Not surprisingly, the length of adult spring chinook returning to Lower Granite Dam was correlated with their age of return ($r = 0.98$). It was, in fact, the only covariate we considered, which was correlated with *Age* (considered

TABLE 10 Correlation of covariates.

	Year	Spring Transition	Fall Transition	Summer Length	Hatchery Release	L. Gran. Temp.	Bonneville Temp.	L. Gran Flow	Astoria Flow	First Day Tagged	Last Day Tagged	Delta Transition	Solar Radiation	Wind Velocity	Adult Length	Age	Period	P.N.I.
Year	1.00	-.17	.51	.38	**.84**	.20	.22	-.45	-.42	.01	-.02	-.12	-.26	-.03	-.06	0.00	-.11	-.53
Spring Transition	-.17	1.00	-.03	**-.89**	-.25	-.26	-.13	.28	.08	-.36	-.17	**.79**	.58	.06	-.05	0.00	-.09	-.52
Fall Transition	.51	-.03	1.00	.48	.26	.32	.26	-.51	-.71	.04	-.09	0.00	.53	-.62	-.07	0.00	-.04	.31
Summer Length	.38	**-.89**	.48	1.00	.33	.38	.23	-.47	-.39	.05	.11	-.69	-.27	-.33	.01	0.00	.06	-.32
Hatchery Release	**.84**	-.25	.26	.33	1.00	-.05	.02	-.09	-.06	-.01	-.02	-.17	-.41	-.14	-.03	0.00	-.13	-.66
L. Gran. Temp.	.20	-.26	.32	.38	-.05	1.00	.72	-.25	-.28	.65	.67	-.61	-.02	-.10	-.01	0.00	.58	-.04
Bonneville Temp.	.22	-.13	.26	.23	.02	.72	1.00	-.08	0.00	**.78**	**.76**	-.59	-.03	-.12	-.01	.01	**.85**	-.02
L. Gran Flow	-.45	.28	-.51	-.47	-.09	-.25	-.08	1.00	**.81**	.05	.07	.16	-.01	.06	.03	0.00	.14	.06
Astoria Flow	-.42	.08	-.71	-.39	-.06	-.28	0.00	**.81**	1.00	.12	.20	-.05	-.34	.20	.05	0.00	.23	-.22
First Day Tagged	.01	-.36	.04	.05	-.01	.65	**.78**	.05	.12	1.00	**.89**	-.62	.01	-.05	0.00	0.00	**.85**	.04
Last Day Tagged	-.02	-.17	-.09	.11	-.02	.67	**.76**	.07	.20	**.89**	1.00	-.72	-.19	.01	.01	0.00	**.84**	-.13
Delta Transition	-.12	**.79**	0.00	-.69	-.17	-.61	-.59	.16	-.05	-.62	-.72	1.00	.48	.05	-.04	0.00	-.61	.41
Solar Radiation	-.26	.58	.53	-.27	-.41	-.02	-.03	-.01	-.34	.01	-.19	.48	1.00	-.33	-.04	0.00	-.04	**.91**
Wind Velocity	-.03	.06	-.62	-.33	-.14	-.10	-.12	.06	.20	-.05	.01	.05	-.33	1.00	.04	0.00	-.02	-.31
Adult Length	-.06	-.05	-.07	.01	-.03	-.01	-.01	.03	.05	0.00	.01	-.04	-.04	.04	1.00	**.98**	.01	-.02
Age	0.00	0.00	0.00	0.00	0.00	0.00	.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**.98**	1.00	0.00	0.00
Period	-.11	-.09	-.04	.06	-.13	.58	**.85**	.14	.23	**.85**	**.84**	-.61	-.04	-.02	.01	0.00	1.00	.04
P.N.I.	-.53	.52	.31	-.32	-.66	-.04	-.02	.06	-.22	.04	-.13	.41	**.91**	-.31	-.02	0.00	.04	1.00

The shaded cells indicate that the correlation is greater than 0.75.

an ordinal factor). The average lengths of the fish returning were 490.56, 729.26, 876.76 mm for age 3,4, and 5 fish, respectively.

Pacific Northwest Index (PNI). The *PNI*, a measure of air temperature, precipitation, and snow pack, was correlated with solar radiation at Astoria (*Solar*) ($r = 0.90$). Further analysis revealed that its correlation with solar radiation was spurious; over a longer time period (1961-1990) correlation was poor ($r = 0.117$, $n = 30$).

GLM analysis overview

Age turned out to be the single most important covariate in the data. In model examined, it accounted for 30-40% of the total deviance (FIGURE 8). *Lastday,* a measure of outmigration timing, was the next most important covariate, explaining 15-18% of the data. Next, was the covariate *Strans*, the spring transition date, which explained between 3-5% of all the data's variation and a large portion of the yearly variation (16-26% of it). Much of the remaining yearly variation is explained by *Slength*, *Hrelease,* and *LGRflow* (36-42% of the total deviance explainable by yearly differences).

In our opinion, *Model C*, derived with the influential observations #68, #147, and #150 removed, was superior to the other three models. Although several interactions were significant when the highly influential observations are included in the analysis (*Model A*), all but one interaction disappears in their absence (*Model C*). This calls into question their inclusion in the final model. The only truly robust significant interaction is *Age:Hrelease*. It accounts for a full 70% of the deviation attributable to year-to-year differences in the *Age* of recoveries.

Model A

The GLM analysis singled out the age of return (*Age*), the last day of tagging (*Lastday*), and the spring transition date (*Strans*) as having the best relationship with return percentage. Together, these three covariates explained 60.3% of the total deviance, with $\Delta D = 467.12$, out of a total deviance of 884.46 (FIGURE 8). The final model selected was

$$1 + LGRflow + Age \times Hrelease + Lastday \times (Strans + Slength + Age)\ . \quad \textit{(Model A)}$$

By order of importance, the explanatory variables selected for the model were *Age*, *Lastday, Strans*, *Slength*, *LGRflow,* and *Hrelease* (TABLE 9). Some interactions among these covariates were also significant, the most important being *Age:Hrelease*. Together the interactions, with their six parameters, accounted for 11.3% of the total deviance. The analysis of deviance tables for each step of the model selection process are given in Appendix A.

Age. The factor *Age*, consisting of just two parameters, was found to explain a large amount of the deviance in the data. In all, it accounted for 30.4% of the total deviance ($\Delta D = 268.64$, d.f.=2), the largest amount of any single covariate used in the model, probably because fish tend to mature at ages 4 and 5, and much less often at age 3 (TABLE 6).

GLM APPORTIONMENT OF DEVIANCE

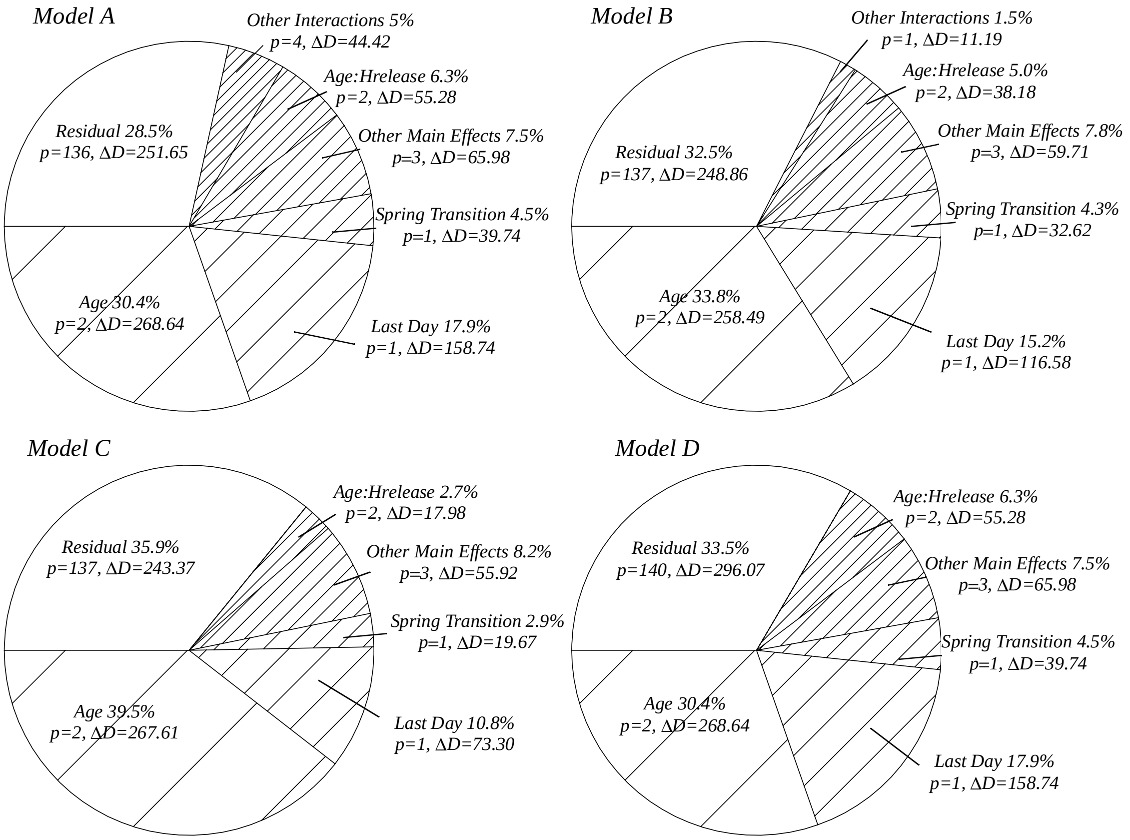


FIGURE 8 *Model A*, with 13 parameters explained 72% of the deviance; *Model B*, with 10 parameters, 68%; *Model C*, with 9 parameters, 64%; *Model D*, with 9 parameters, 67%. Generally, age (*Age*) accounted for 30-40% of the total deviance and *Lastday*, which represents migration timing, 10-20%. Although the spring transition date (*Strans*) explained only 3-5% of the total deviance, it described about 25-40% of the deviance attributable to the outmigration year effect alone.

TABLE 11 Step-wise regression results (*Model A*).

Model	D	d.f.	ϕ	ΔD	Δ d.f.	p-value
1	884.45	149	NA	NA	NA	NA
+ *Age*	615.81	147	6.5900	268.64	2	1.4062e-09
+ *Lastday*	457.07	146	3.4005	158.74	1	8.3479e-12
+ *Strans*	417.32	145	3.1841	39.74	1	4.1081e-04
+ *Slength*	400.01	144	3.2202	17.31	1	2.0419e-02
+ *LGRflow*	366.89	143	2.6691	33.22	1	4.2740e-04
+ *Hrelease*	351.42	142	2.6681	15.47	1	1.6027e-02
+ *Age:Hrelease*	296.14	140	2.2272	55.28	2	4.0792e-06
+ *Lastday:Strans*	274.03	139	2.0453	22.11	1	1.0096e-03
+ *Lastday:Slength*	263.90	138	2.0460	10.13	1	2.6045e-02
+ *Age:Lastday*	251.71	136	1.9730	12.18	2	4.5608e-02

Last day of tagging (Lastday). The covariate *Lastday* was significant because of the tendency (based on all years combined) for juveniles migrating later in the season (April-June) to show a higher adult return percentage. This pattern was evident in a plot of the residuals from the regression model $1 + Age \times Year$ against the last day tagged (FIGURE 9). Although, the residuals showed much variation not accounted for by this covariate, *Lastday* explained 16.7% of the deviance beyond that explained by *Age*, *Year*, and their interaction. In *Model A*, where the factor *Year* was not explicitly present, it explained 17.9% of the total deviance (FIGURE 8).

Spring transition (Strans). The spring transition date best accounted for the between-year variation in the data, explaining 23.5% of the deviance that was ascribed specifically to a *Year* effect. Its relationship with the return percentage was evident in its plot against the Anscombe residuals of the model $1 + Age \times Lastday$ (FIGURE 10). Once the effects of *Age*, *Lastday*, and their interaction were removed, we saw that a later spring transition date generally brought greater survival. In the years where the spring transition was in early March, the annual mean residuals were positive (0.3-0.4). In the years where it occurred relatively late (early to mid April), the annual mean residuals were zero or less (-0.8-0).

Other covariates. Although there were other significant effects present in the model beyond *Age*, *Lastday*, and *Strans*, they varied from year to year as did the spring transition date, and together they explained only 7.5% of the total deviance (FIGURE 8). These covariates were, in order of importance: *Slength*, *LGRflow*, and *Hrelease*.

Interactions. The most important interaction was *Age:Hrelease*. It explained all of 70% of the deviation attributable to year-to-year differences in *Age* composition of the adult recoveries. Other interactions were also significant, but their significance was largely dependent on the inclusion of three highly influential observations. These suspect interactions were *Lastday:Strans*, *Lastday:Slength*, and *Lastday:Age (*TABLE 9*)*.

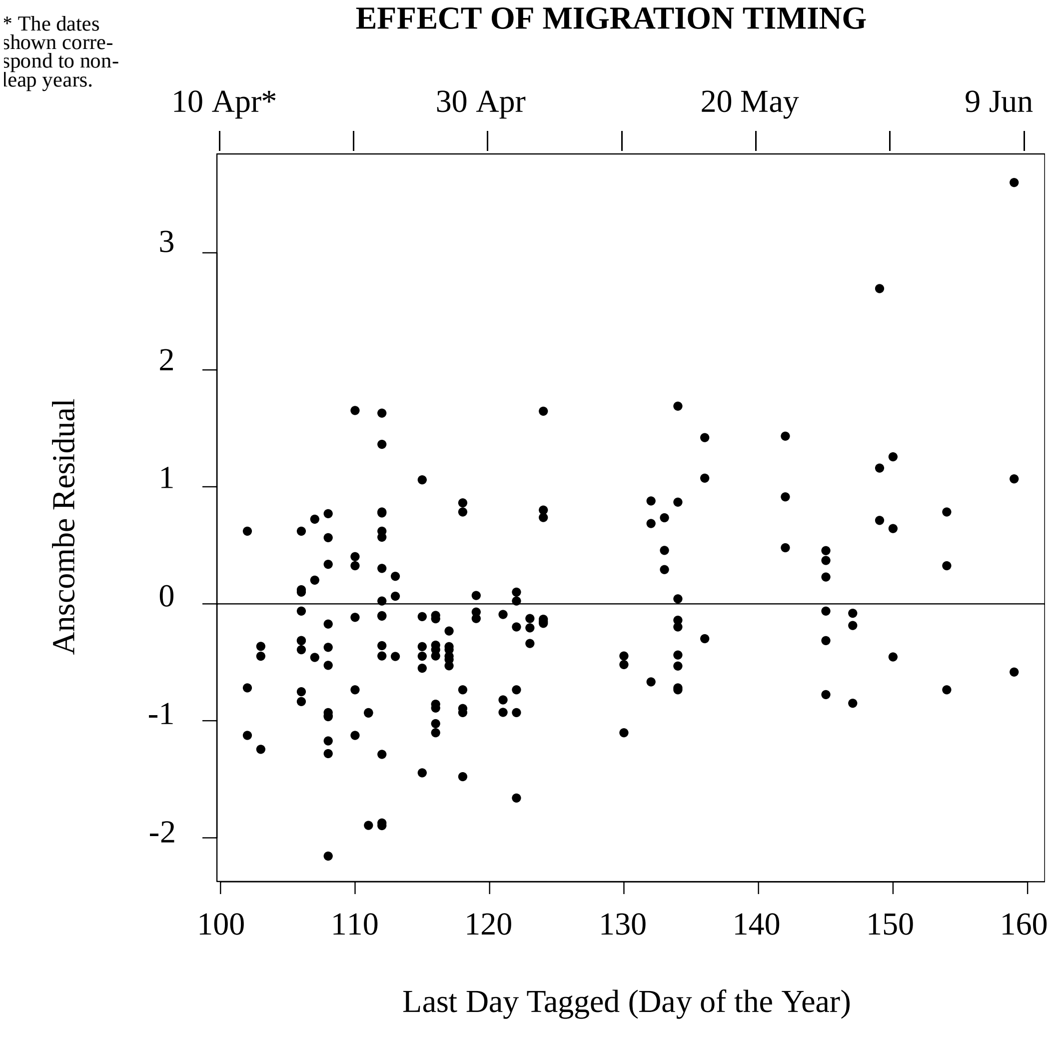


FIGURE 9 The plot of the Anscombe residuals of the model 1 + *Age*×*Year* against the last day of tagging for each release group demonstrated that once the effects of *Year, Age*, and their interaction was removed, that there was a strong relationship between the return percentage and the last tagging day (*Lastday*). All else being equal, there was a tendency for later migrants to have greater return percentages than earlier migrants. All 150 observations were included in the analysis.

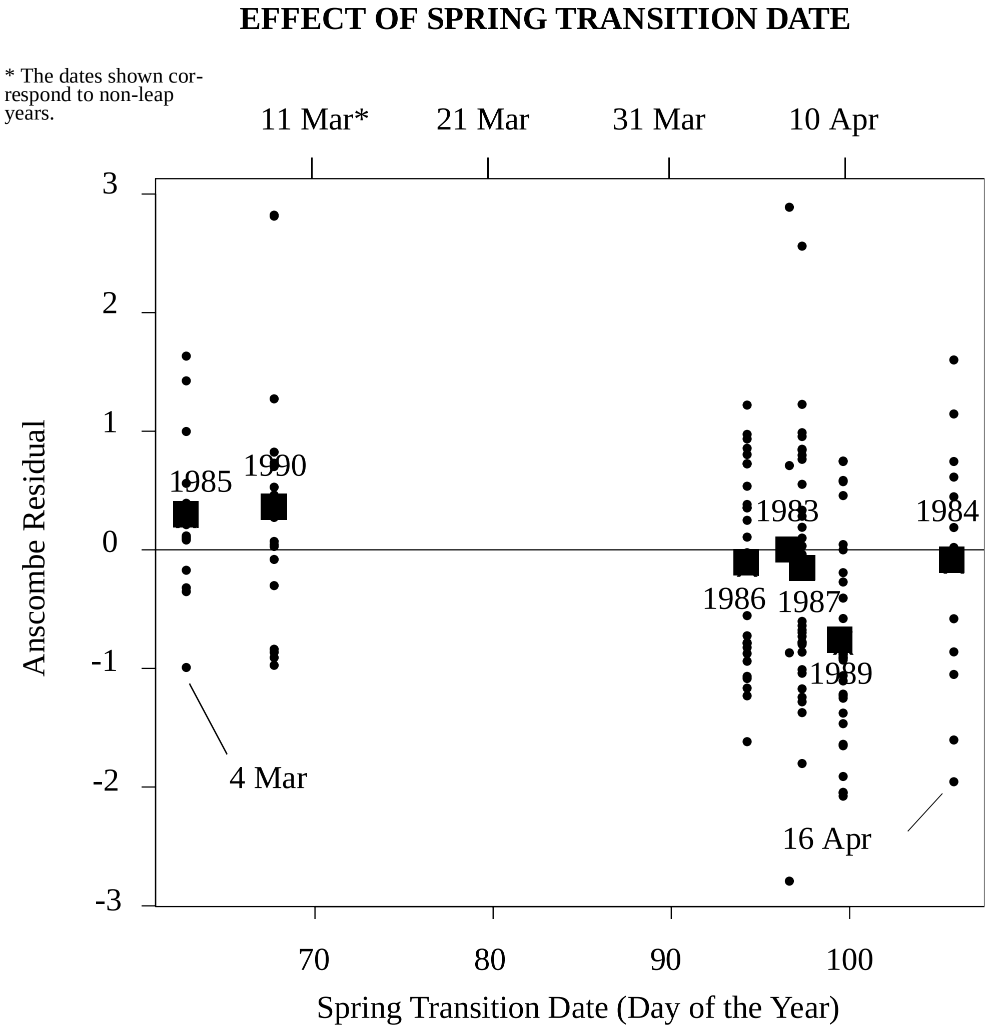


FIGURE 10 The plot of the Anscombe residuals of the model 1 + *Age* × *Lastday* against the spring transition date (*Strans*) for each release group demonstrated that once the effects of *Age*, *Lastday,* and their interaction were removed, there was a decreasing relationship between the return percentage and the spring transition date. The blackened boxes represent the annual mean of the residuals. All else being equal, there was a tendency for juveniles to show a better return percentage in years when the spring transition arrived earlier. Among the study years, the spring transition date varied from 4 March to 16 April. All 150 observations were included in the data set.

Model parameters (Model A). The parameter estimates verify that all of the main effects and interactions of the model are significant (TABLE 12). It is difficult to draw conclusions about the sign of the influence of the various covariates on the recovery percentage. For example, we know that an early spring transition date resulted in better recovery percentage. However, the coefficient of *Strans* was positive, suggesting just the opposite. This is because the spring transitions negative effect was not contained in the coefficient of its main effect, but in the coefficient of its interaction with *Lastday.* The solution was to look at the fitted surfaces; they showed clearly the relationships between the covariates and recovery percentages.

TABLE 12 Parameter estimates[a] (*Model A*).

Parameter	Value	Std.Error	t value
(Intercept)[b]	-7.033314e+01	2.798558e+01	-2.513191712*
Age4	1.387145e+00	1.697945e+00	0.816955388
Age5	-2.875757e+00	1.760645e+00	-1.633354342
Lastday	6.033967e-01	2.283650e-01	2.642247021*
Strans	2.717936e-01	1.051465e-01	2.584904561*
Slength	1.866762e-01	9.384319e-02	1.989234975*
LGRflow	-9.490755e-03	3.376792e-03	-2.810583344*
Hrelease	-1.378150e-07	5.793141e-08	-2.378933852*
AgeTwoHrelease	-4.078866e-10	6.050855e-08	-0.006740975
AgeThreeHrelease	1.821905e-07	6.451879e-08	2.823835509*
Lastday:Strans	-2.608987e-03	8.606416e-04	-3.031443672*
Lastday:Slength	-1.773722e-03	7.681138e-04	-2.309192014*
Age4Lastday	3.692181e-03	1.296584e-02	0.284762202
Age5Lastday	2.122867e-02	1.341705e-02	1.582215419

[a] We use the *treatment* form of coding for the factor *Age* (Chambers and Hastie 1992).

[b] The intercept represents the level for age 3 fish.

Note: * denotes significance at the $\alpha = 0.05$ level. We compare the t-value with a standard normal distribution.

Fitted surface (Model A). The fitted surface, represented by contour plots over the interior of the data, illustrated the relationship between each covariate and the return percentage (Appendix B). The nine plots represented a 6-dimensional surface, where the response variable was taken as the linear predictor, $logit(p)$. The fitted surfaces revealed quickly the relationship between the response variable and its covariates, and also showed distinctive patterns of interaction among the covariates. When no interaction was present among the covariates depicted, the contour lines were parallel. Although these predicted surfaces show a high degree of interaction, we discovered that all, except the interaction between *Age* and *Hrelease,* were due to just three observations, and therefore must be viewed skeptically.

Of all interactions explored, the interaction between the hatchery release numbers, *Hrelease*, and the factor *Age* had the most explanatory power. (In fact, as discussed later, all other interactions previously discussed will become insignificant with the removal of a few observations.) This interaction was evident in the plot of the predicted surface (FIGURE B.10-FIGURE B.12). The plot shows that, in general, larger hatchery releases mean lower return percentages. However, the effect of the hatchery release was tempered by age. In the five-year-olds, the hatchery release size made little difference. This is evident in the loss of density of contour lines along a vertical line drawn through age 5. If no interaction were present, then the density of the contour lines would not change with *Age*.

Cook's distance (Model A). Observations #150 and #68 had the greatest influence as measured by their Cook's distance, having values of 1.94e-05 and 1.05e-05, respectively. These values represent the change in parameter estimates when the regression is performed in the observation's absence (FIGURE 11). Observation #150 is the fraction of fish returning as five-year-olds that migrated late in the season (29 May - 09 June). The return of this group was high: 0.960% compared with an average of 0.063% for all 5-year-olds during the study. A group of returning 4-year-olds, represented by observation #68, was also large, 0.324% compared with an average of 0.112% for all 4-year-olds.

Anscombe residuals (Model A). The Anscombe residuals for *Model A* were approximately normally distributed, suggesting that the scaled poisson distribution is a good model for fitting the data (FIGURE 12). The six largest Anscombe residuals were #8, #96, #86, #104, #68, and #15. There were no apparent outliers among the 150 residuals: each was within 2.33 standard deviations of zero. However, since observation #68 has a large Anscombe residual *and* a high Cook's distance, it is suspect, and therefore regressions were run in its absence (See models *B* and *C*).

COOK'S DISTANCE

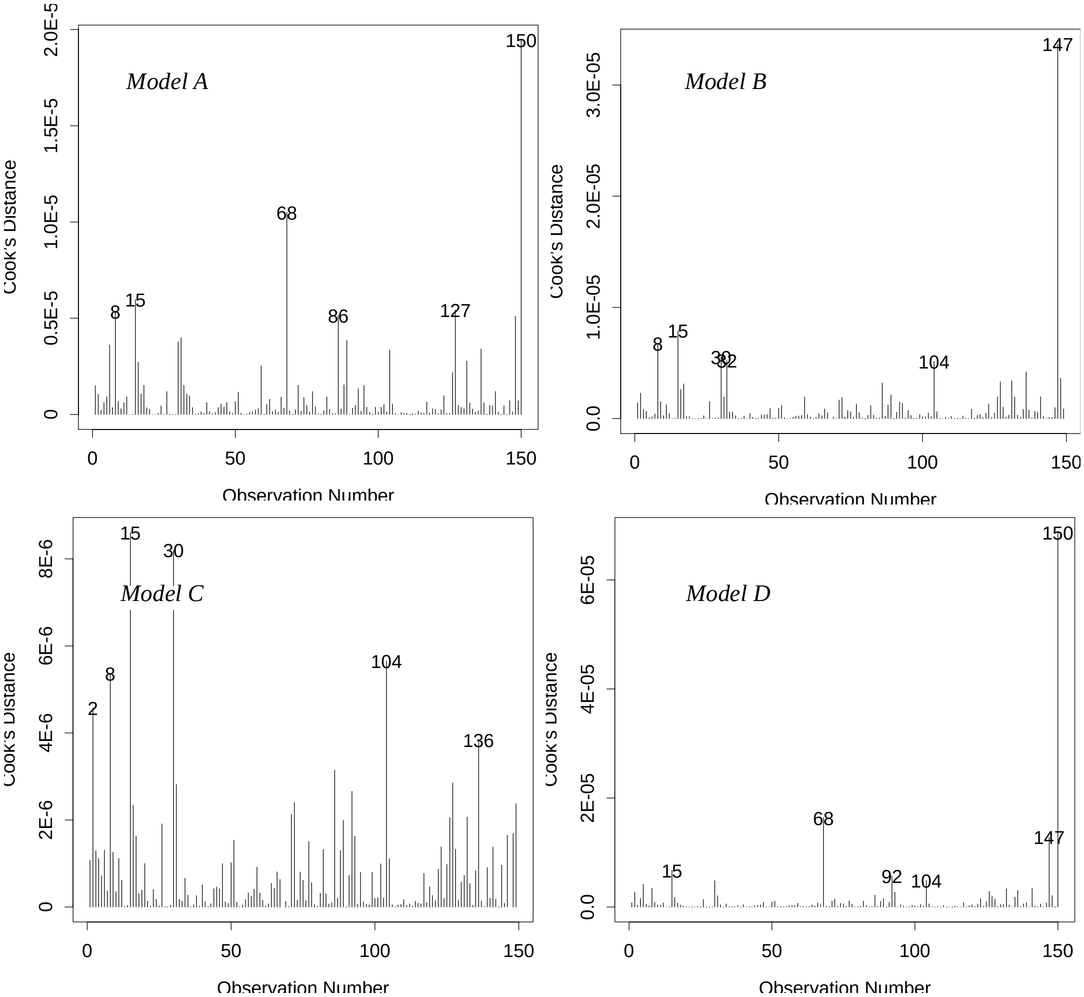


FIGURE 11 Cook's distance measured for each observation: *Model A*, where all 150 observations were present; *Model B,* where observations #68 and #150 were omitted; *Model C*; where observations #68, #147, and #150 were omitted; and *Model D,* where all 150 observations are included but, of the interactions, only *Hrelease:Age* was included. Of these four plots, *Model C* had the best characteristics; no one point dominated the regression to the degree seen in the other plots.

PROBABILITY PLOTS OF ANSCOMBE RESIDUALS

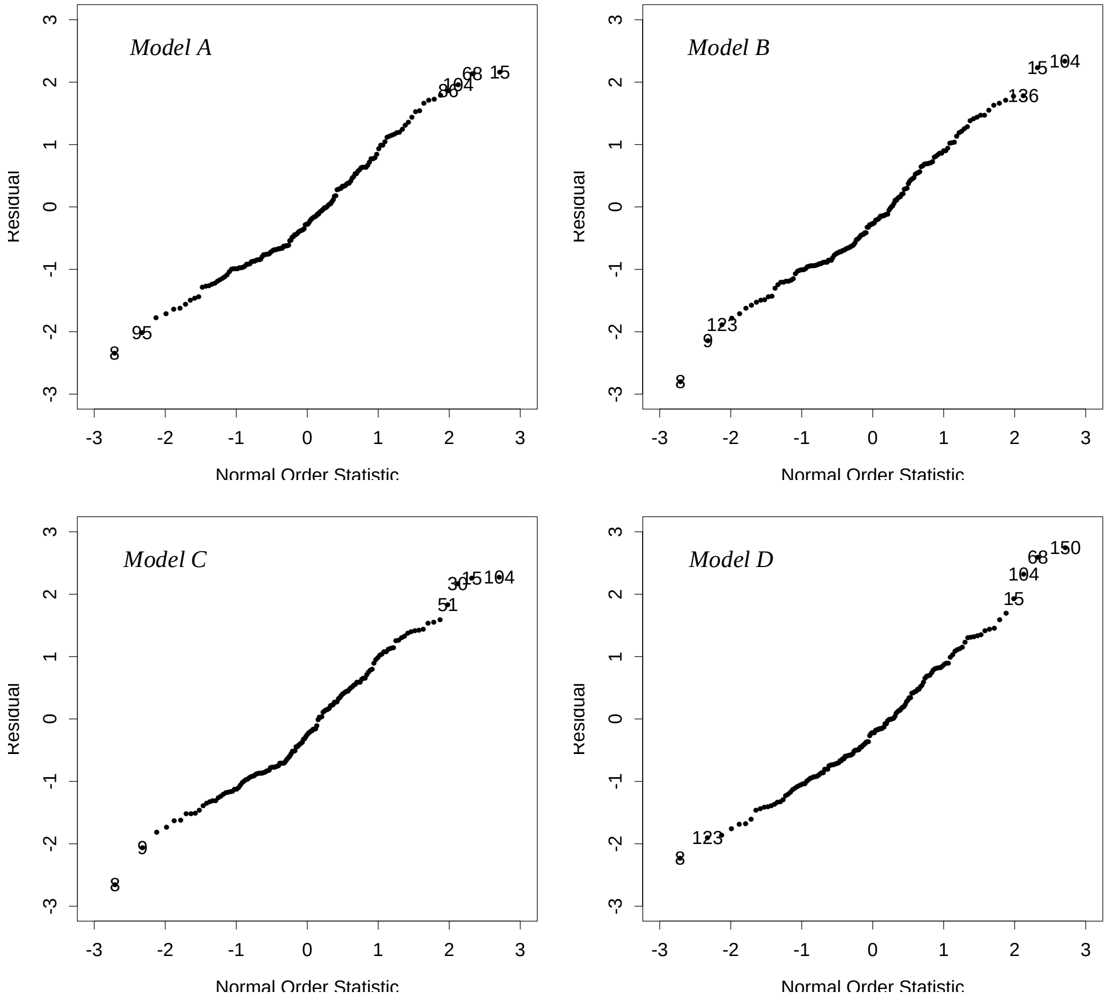


FIGURE 12 Probability plot of the Anscombe residuals for the four different models explored: *Model A*, where all 150 observations were present; *Model B*, where observations #68 and #150 were omitted; *Model C*, where observations #68, #147, and #150 were omitted; and *Model D*, where all 150 observations were included but, of the interactions, only *Hrelease:Age* were included. The residuals lie approximately in a straight line, and were therefore approximately normally distributed.

Model B

Because observations #68 and #150 had such large influence on the model choice, we determined how the model selection changed in their absence. When these observations were removed, the significance of the main effects remained, but two of the interaction terms, *Lastday:Slength* and *Age:Lastday*, lost their explanatory power (TABLE 13). Thus the significance of these two interaction terms hinges on the inclusion of observations #150 and #68 — just two observations out of 150. This argues for removing these interactions from the final model. The total deviance in the data changed from 884.45 to 765.63. The model selected was

$$1 + Slength + LGRflow + Age \times Hrelease + Lastday \times Strans \qquad \text{(Model B)}$$

TABLE 13 Step-wise regression results (*Model B*).

Model	D	d.f.	ϕ	ΔD	Δ d.f.	p-value
1	765.63	147	NA	NA	NA	NA
+ *Age*	507.14	145	4.4416	258.49	2	2.2037e-13
+ *Lastday*	390.56	144	2.7438	116.58	1	7.1093e-11
+ *Strans*	357.94	143	2.5795	32.62	1	3.7662e-04
+ *Slength*	336.50	142	2.5104	21.44	1	3.4758e-03
+ *LGRflow*	317.05	141	2.2348	19.45	1	3.1751e-03
+ *Hrelease*	298.23	140	2.1958	18.82	1	3.4179e-03
+ *Age:Hrelease*	260.06	138	1.9277	38.18	2	5.0036e-05
+ *Lastday:Strans*	248.87	137	1.8517	11.19	1	1.3960e-02
+ Lastday:Slength	**242.67**	**136**	**1.8740**	**6.20**	**1**	**6.8932e-02**
+ Age:Lastday	**237.67**	**134**	**1.8690**	**4.99**	**2**	**2.6293e-01**

Note: The shaded rows are those associated with insignificant interactions. In *Model A*, these interactions were all significant. When observations #68 and #150 were excluded, their explanatory ability was lost.

Model parameters (Model B). A table of the model parameter estimates and their p-values demonstrated that the spring transition date, *Strans*, was not significant as a main effect (TABLE 14). Its explanatory power was contained in the interaction term *Lastday:Strans*. When this interaction term was removed, spring transition becomes significant with a t-value of -5.21. All other main effects were significant at the 0.05 level in the presence of interactions terms.

Predicted surface (Model B). The predicted surface changed markedly when the interactions *Lastday:Slength* and *Age:Lastday* were removed.(Appendix C). In fact, at all points on the fitted surface, the relationship between migration timing, represented by *Lastday*, and return percentage was positive.

The interaction between *Age* and *Hrelease* was still evident in the alternative predicted surface. The surface showed that the hatchery release numbers affected the return percentage of age 3 and 4 fish, but had little effect on age 5 fish (FIGURE C.10-FIGURE C.12). It was also evident that larger hatchery releases were associated with a poorer return percentages. This is troubling since there were currently 8-10 hatchery smolts for every wild one during the outmigration.

In terms of the main effects included in the alternative model, the covariates the *Lastday* had a positive effect on return percentage, while the other continuous predictor variables, *Strans*, *Slength*, *LGRflow*, and *Hrelease*, all had a negative effect. The factor *Age* was more complex, showing the best returns among the age 4 fish, with the poorest returns among the age 5 fish. This pattern was also clear in the raw data, with age 3, 4, and 5 contributing to 8.6%, 54.2%, and 37.2% of the returns, respectively (TABLE 6).

Cook's distance. (Model B). The Cook's distance for *Model B* showed that observation #147 was extremely influential in the absence of observations #68 and #150 (FIGURE 11). Its influence of 3.4e-05 was 30 times as large as the average Cook's distance. This argued for conducting a GLM analysis which excluded observation #147 in addition to #68 and #150 (See *Model C*).

Anscombe Residuals (Model B). The Anscombe residuals showed no unusual deviation from normality (FIGURE 12). The largest residuals were from observations #8 and #104. Observation #8 was overestimated by the regression and #104 was underestimated. In all models, these observations yielded large residuals (FIGURE 12). All the residuals were within 3 standard deviations of zero, meaning that none were obvious outliers.

TABLE 14 Parameter estimates[a] (*Model B*).

	Value	Std. Error	t value
(Intercept)[b]	-6.143536e+00	4.528341e+00	-1.356685797
Age4	1.816591e+00	4.453547e-01	4.078975288*
Age5	-1.766676e-01	5.056966e-01	-0.349354904
Lastday	8.032438e-02	2.236855e-02	3.590952060*
Strans[c]	3.057133e-02	3.629654e-02	0.842265775
Slength	-3.101568e-02	9.452830e-03	-3.281100182*
LGRflow	-9.574186e-03	3.320826e-03	-2.883073460*
Hrelease	-1.334856e-07	5.591597e-08	-2.387254006*
Age4Hrelease	4.144096e-10	5.843541e-08	0.007091754
Age5Hrelease	1.759856e-07	6.316073e-08	2.786313328*
Lastday:Strans	-6.448110e-04	2.640887e-04	-2.441645790*

[a] We use the *treatment* form of coding for the factor *Age* (Chambers and Hastie, 1992).

[b] The intercept represents the level for age 3 fish.

[c] The spring transition date, *Strans*, is not significant as a main effect. Its explanatory power is contained in the interaction term *Lastday:Strans*. When this interaction term is removed, spring transition becomes significant with a t-value of -5.21.

Note: * denotes significance at the $\alpha = 0.05$ level. We compare the t-value with a standard normal distribution.

Model C

Model C was our preferred model. It contained only one interaction term, *Age:Hrelease*, and the GLM analysis confirmed that other interactions (significant in models A and B) depended upon three highly influential points. When observations #68, #147, and #150 were omitted from the analysis, the main effects from *Model A* remained significant, but several of the interactions did not (TABLE 15). Only one of the four originally significant interactions, *Age:Hrelease*, remained significant. The other interactions were therefore excluded from the final model:

$$1 + Strans + Slength + LGRflow + Age \times Hrelease . \qquad \text{(Model C)}$$

Model parameters (Model C). The t-values of the parameter estimates confirmed that each of the covariates selected in the regression process retained their significance in the presence of all other selected covariates (TABLE 16). They also confirmed the strong explanatory ability of *Age*, *Strans*, and *Slength*. The parameterized model is

$$\log(p_k) = \mu + \alpha_k + \beta_1 Lastday + \beta_2 Strans + \beta_3 Slength + \qquad (5)$$

$$\beta_4 LGRflow + \beta_5 Hrelease + \gamma_i Hrelease,$$

where μ is the intercept, α_k represents the main effect for age k, $(\alpha_1 = 0)$; β_j, $j = 1, 2, 3, 4, 5$ are the coefficients of *Lastday, Strans, Slength, LGRflow,* and *Hrelease*, respectively; and γ_k represent the slopes associated with hatchery release for age k $(\gamma_1 = 0)$. This model could be coded into CRiSP (see TABLE 16 for parameter estimates).

Predicted surface (Model C). The predicted surface shows the absence of interactions except for *Age:Hrelease (*Appendix D*)*. Notice that, except for the plots in which *Age* is an axis variable, the contour lines are evenly spaced. This makes the curves simpler to analyze, and the influence of the covariates more clear. The effect of increased *Lastday* (later migration) is positive. The effects of increased hatchery release (*Hrelease*), spring transition date (*Strans*), summer length (*Slength*), and Lower Granite flow (*LGRflow*) are all negative.

Cook's distance (Model C). Of the four models explored, the Cook's distance plot of Model C was the most favorable. Its distances were more evenly distributed than other models' (FIGURE 11).

Anscombe residuals (Model C). The Anscombe residuals for Model C lie approximately on a straight line on the normal probability plot. The residuals showed no great departure from normality and none were outliers.

TABLE 15 Step-wise regression analysis (*Model C*).

Model	D	d.f.	ϕ	ΔD	Δ d.f.	p-value
1	677.85	149	NA	NA	NA	NA
+ *Age*	410.24	144	2.8617	267.61	2	0.0
+ *Lastday*	336.94	143	2.2131	73.30	1	8.6499e-09
+ *Strans*	317.27	142	2.1827	19.67	1	2.6798e-03
+ *Slength*	299.31	141	2.1359	17.96	1	3.7350e-03
+ *Hrelease*[a]	274.46	140	1.9837	24.85	1	4.0163e-04
+ *LGRflow*	261.36	139	1.8855	13.11	1	8.3779e-03
+ *Age:Hrelease*	243.37	137	1.8006	17.98	2	6.7804e-03
+ Lastday:Strans	**237.96**	**136**	**1.7711**	**5.41**	**1**	**8.0425e-02**
+ Lastday:Slength	**233.15**	**135**	**1.7934**	**4.81**	**1**	**1.0149e-01**
+ Age:Lastday	**232.63**	**133**	**1.8216**	**0.52**	**2**	**8.6662e-01**

a Hrelease enters the model before LGRflow in *Model C*. In *Models A* and *B*, it entered the model after *LGRflow.*

Note: The shaded rows are those associated with insignificant interactions. In *Model A*, these interactions were all significant. When observations #68,#147, and #150 were excluded, their explanatory ability was lost.

TABLE 16 Parameter estimates[a] (*Model C*).

	Parameter	Value	Std.Error	t value
(Intercept)[b]	μ	5.259555e-01	2.952027e+00	0.178167575
Age4	α_2	1.815835e+00	4.414806e-01	4.113056698*
Age5	α_3	8.031983e-02	5.035075e-01	0.159520638
Lastday	β_1	2.221172e-02	3.948313e-03	5.625623313*
Strans	β_2	-4.710386e-02	1.041271e-02	-4.523688016*
Slength	β_3	-3.005124e-02	9.293900e-03	-3.233436479*
LGRflow	β_4	-9.168515e-03	3.254275e-03	-2.817375615*
Hrelease	β_5	-1.144056e-07	5.497523e-08	-2.081038213*
Age4Hrelease	γ_2	4.479957e-10	5.799609e-08	0.007724584
Age5Hrelease	γ_3	1.282011e-07	6.424384e-08	1.995539161*

[a] We use the *treatment* form of coding for the factor *Age* (Chambers and Hastie, 1992).

[b] The intercept represents the level for age 3 fish.

Note: * denotes significance at the 0.05 level.

Model D

Model D is simply *Model C*, but its parameters, unlike our Model C analysis, were estimated with the highly influential data points, #68, #149, and #150 included. Since all the data were included, the step-wise GLM table matched that of *Model A*, except *Age:Hrelease* was the only interaction allowed in the model.

$$1 + Strans + Slength + LGRflow + Age \times Hrelease \qquad \textit{(Model D)}$$

Model parameters (Model D). How did the model parameters change when all observations are left in the model but *Model C* is selected, which omits all interactions but *Age:Hrelease*? First of all, many of the covariates had a greater influence on return percentage, as demonstrated by their larger t-values (TABLE 17). When observations #48, #147, and #150 were omitted, the coefficients of *Lastday*, *LGRflow*, and *Age2:Hrelease* had t-values of 5.6, -2.8, and 2.8, respectively. When the observations were put back into the model, the t-values of the coefficients increased in magnitude to 7.6, -4.1, and 4.2, respectively. It is, therefore, easy to understand why the data points had a large influence.

The sign of the significant parameters remained the same when the three influential observations were included in the analysis. This means that, except for *Hrelease* which has an interaction, there was no change in the *sign* of the relationship between the covariates and return percentage. *Lastday* had a positive influence, and *Strans*, *Slength*, *LGRflow* had a negative influence. The exception to this was the effect of *Hrelease*. At ages 3 and 4, larger hatchery releases gave poorer returns; but at age 5, they gave greater returns.

TABLE 17 Parameter estimates[a] (*Model D*).

	Value	Std. Error	t- value
(Intercept)b	2.347178e+00	3.155136e+00	0.74392298
Age4	1.853132e+00	4.812352e-01	3.85078180*
Age5	-2.602469e-01	5.465300e-01	-0.47618046
Lastday	2.890710e-02	3.808462e-03	7.59023042*
Strans	-5.427043e-02	1.090741e-02	-4.97555516*
Slength	-3.800109e-02	9.877478e-03	-3.84724607*
LGRflow	-1.377577e-02	3.388840e-03	-4.06504097*
Hrelease	-1.179153e-07	5.994490e-08	-1.96706158*
Age4Hrelease	-9.404548e-10	6.300037e-08	-0.01492777
Age5Hrelease	1.931193e-07	6.750036e-08	2.86101092*

[a] We use the treatment form of coding for the factor *Age* (Chambers and Hastie, 1992).

[b] The intercept represents the level for age 3 fish.

Note: * denotes significance at the 0.05 level.

Cook's distance (Model D). Of all the models considered, this one had the most disturbing Cook's distance plot (FIGURE 11). Observation #150 had tremendous influence on the parameters of the model; with a Cook's distance of 6.9e-05, it is 53 times larger than the average over all observations, 1.3e-06. This argues for using *Model C*, which excludes the three points of highest influence.

Anscombe residuals (Model D). The residuals appeared to be approximately normal based on a probability plot (FIGURE 12). As in all models considered, observation #8, located 2.22 standard deviations from the mean, had the largest negative residual, and corresponded to an unusually low return (1 fish returned, a four-year-old, out of 10,155 tagged). The largest positive residual, which was observation #150, located 2.75 standard deviations from the mean, corresponded to an unusually large return for a tagged group (out of 2,708 fish tagged, 1 out of every 100 fish tagged was recovered as a five-year-old).

Discussion

Although it is perhaps the least important variable from a management point of view, of the variables considered, *Age* was the most important in explaining the deviance in the data. It explained between 30-40% of the total deviance. This is due to the dominance of age 4 and 5 recoveries compared to smaller Age 3 recoveries. It was therefore important to eliminate the *Age* effect from the data set so that we could see the influence of variables such as migration timing and spring and fall transitions more clearly. Once this was done, the variable *Lastday*, which is a measure of outmigration timing, and *Strans*, the spring transition date, were identified as important explanatory variables.

The interaction between *Age* and *Year* represented the year-to-year differences observed in the age distribution of the recoveries. There are two good reasons to believe that this effect was due to changes in age-at-maturity and not ocean mortality. (1) Ocean mortality is usually set during the first year in the ocean and should affect ages 3, 4, and 5 fish equally, producing no shift in the age structure of returning adults. (2) If later ocean mortality was driving the differences in age distribution, we would expect the small return of Age 5 fish from the fish tagged in 1983 (15 compared to an expected number of 40.4) to be accompanied by a small number of Age 4 fish returning from the fish tagged in 1984. This was not observed. Similarly, the small return of Age 4 adults from the group tagged in 1990 (71 compared to an expected number of 95.5) should have been accompanied by a small return of Age 5 adults from the group tagged in 1989. This, also, was not observed. These observations suggest that the shifts in age distribution were due more to differing age-at-maturity, caused perhaps by changing differences in the relative mix of hatchery and wild fish, rather than ocean mortality.

Survival was generally improved for later migrants, increasing on average by a factor of 3 for fish arriving 45 days later at Lower Granite Dam (see *Model C* fitted curves). This survival increase was not due to greater fish size. Plots of fish length against the recovery dates of spring chinook at Lower Granite dam during 1989, 1993, 1994, and 1995 showed no increase in size over the tagging period (FIGURE 13). The increase was more likely due to better fish condition or better estuary or ocean conditions. It may also have been due to a higher proportion of wild fish tagged later in the season. Wild fish are known to survive better than hatchery fish. However increasing survival over the season appears to apply to both hatchery and wild fish as demonstrated in the PIT-tag data of 1990, where adult recoveries were separated into hatchery and wild fish using scale analysis (TABLE 18).

TABLE 18 Adult returns to Lower Granite Dam of spring/summer chinook salmon smolts marked and transported from the dam in 1990.

Dates marked	Number of smolts marked[a]		Observed adult returns[b]		Total adult return estimates[c]	
	Number	Type	Number	Percent	Number	Percent
13-18 Apr	**5,938**	**hatchery**	**9**	**0.15**	**23**	**0.40**
	1,062	wild	2	0.19	5	0.50
18-21 Apr	**6,218**	**hatchery**	**7**	**0.11**	**18**	**0.30**
	782	wild	2	0.26	5	0.60
21-25 Apr	**6,256**	**hatchery**	**10**	**0.16**	**25**	**0.40**
	744	wild	7	0.94	18	2.40
25 Apr-2 May	**6,039**	**hatchery**	**12**	**0.20**	**30**	**0.50**
	961	wild	2	0.21	5	0.50
2-14 May	**6,203**	**hatchery**	**12**	**0.19**	**30**	**0.50**
	797	wild	9	1.10	23	2.90
14-29 May	**4,857**	**hatchery**	**34**	**0.70**	**85**	**1.80**
	2,143	wild	23	1.10	58	2.70
29 May-8 Jun	**1,177**	**hatchery**	**10**	**0.85**	**25**	**2.10**
	1,531	wild	25	1.63	63	4.10
Totals	**36,688**	**hatchery**	**94**	**0.26**	**235**	**0.60**
	8,020	wild	70	0.87	175	2.20
Grant Total	44,708	combined	164	0.37	410	0.90

[a] Numbers of hatchery and wild smolts based upon outmigration timing data from PIT-tagged smolts detected at Lower Granite Dam, and presumes 15% of the overall smolt outmigration were wild fish.

[b] Hatchery and wild adult returns based upon scale analysis.

[c] Estimated adult returns are observed adult returns adjusted (by a factor of 2.5) for trapping efficiency at Lower Granite Dam.

Higher survival later in the season, we emphasize, was not attributable to increased flow during the outmigration, because flow showed no increasing or decreasing trends over the outmigration seasons. The correlation between *LGRflow* and *Lastday* is only 0.07 for the seven years we analyzed (TABLE 10). In fact, survival was negatively related to flow in all models considered (once the effects of the other model covariates are factored out).

LENGTHS OF CHINOOK SMOLTS AT LOWER GRANITE DAM

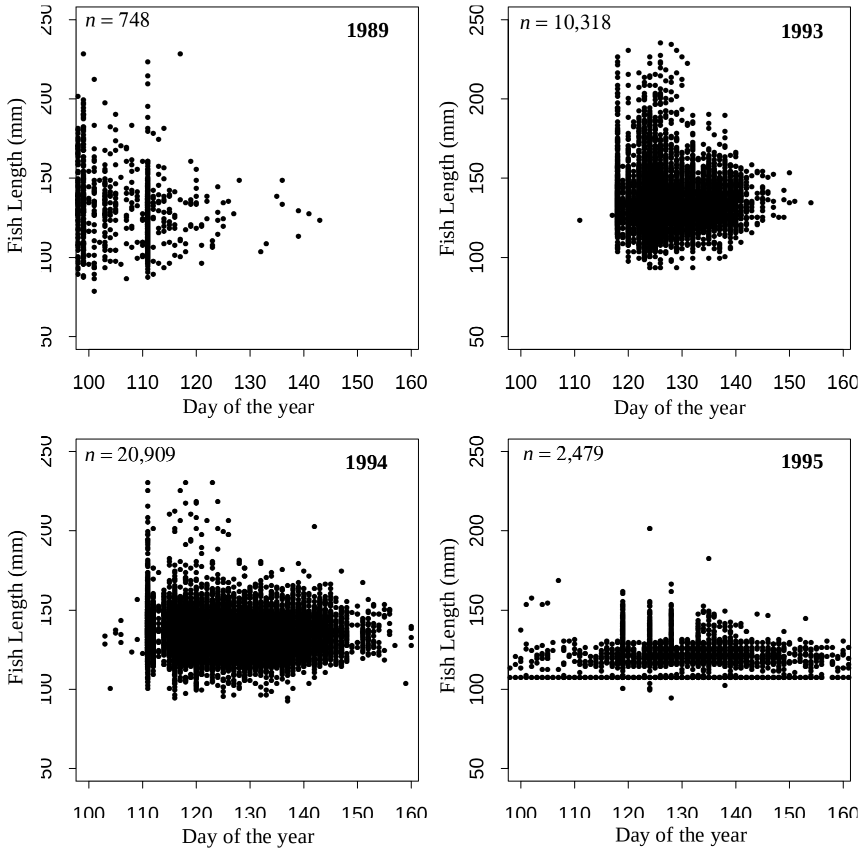


FIGURE 13 Lengths of juvenile spring chinook captured at Lower Granite Dam during the migration seasons of 1989, 1993, 1994, and 1995. These fish were pit-tagged and recovered at Lower Granite Dam. There was no clear trend for increasing fish size during days 100-160 (10 Apr - 9 Jun).

The spring transition date was the best covariate for describing year-to-year variation in the data. Adult return rates were higher when the spring transition date occurred earlier in the year. The spring transition is the abrupt switch from the southerly winds of winter to the northerly winds of summer, signaling the start of coastal upwelling. This upwelling brings nutrients to the ocean surface, resulting in a plankton bloom. Interestingly, the spring transition usually occurred before tagging began, so that the onset of upwelling, creating a productive coastal zone, had started prior to outmigrant tagging. Tagging did not begin until 10-21 April of each year, but the spring transition occurred from 4 March-16 April. This, along with the observation that returns were better when the transition was earlier, suggests that there is a lag before the productive zone provides its optimal benefit to salmon. It appears that the earlier the productive zone is set-up, the greater its benefit.

Over the last century, the spring transition timing has changed greatly from year-to-year, but generally occurs earlier than it did at the turn of the century, and fall transition, generally later, making summer approximately a month longer than it once was (Ebbesmeyer et al. 1996). It is unknown what effect this trend in the transitions has had on salmon production over the last century, but our results suggest the effect may have been significant.

Managers responsible for planning the release timing of hatchery smolts should begin to consider spring transition timing; if it occurs later in the year than normal, it may be beneficial to delay releases. In any case, as standard practice, it may be better to delay and spread out the releases over time to better match the outmigration characteristics of wild fish.

A monitoring program to synchronize the release of hatchery fish with near-shore productivity is possible with existing technology. In-situ instruments, known as profiling pump-and-probe flourometers, which were developed at Brookhaven National Lab in New York, can be used to continuously measure chlorophyll and primary production (Kolber and Falkowski 1993). These could be placed off the continental shelf, one at every degree of latitude, to measure primary production in the Columbia River plume.

The length of summer (as measured by the time between the spring and fall transitions) was also significant once the effect of the spring transition was removed. In general, this meant that later fall transition resulted in poorer survival. This suggests that a later fall transition provided no benefit to spring chinook salmon. This may occur because the productivity of the coast diminishes greatly well before the fall transition. This may also occur because the juvenile spring chinook salmon leave the transitional domain, which extends northward to about 52°N, before the fall transition occurs. Indeed, spring chinook salmon are known to migrate out of the near-shore area rapidly compared to fall chinook salmon and other species.

Greater flow during the outmigration season did not appear to produce greater returns. This contradicts the idea that higher flow provides a benefit to transported fish by increasing fish health. Our analysis suggests that other variables, such as oceanographic conditions or developmental variables, are more important in determining return percentages.

Larger hatchery releases were associated with poorer returns, suggesting a density-dependent survival. Smith et al. (1985) found that the density of stocked fish negatively influenced the success of outplant programs. The negative correlation between hatchery release numbers and adult return rates suggests competition among chinook for food.

Another possibility is that wild fish naturally show greater return rates. When more hatchery fish are released, more are tagged, and the overall return percentage diminishes. In terms of biomass, this effect may be even greater because hatchery fish are generally 2-10 times larger than wild fish, particularly when steelhead are also considered. Ecologically, larger releases of hatchery steelhead may be even more detrimental to wild chinook salmon survival than large releases of hatchery chinook salmon.

To summarize the effects of hatchery fish, Marnel (1986) showed that interactions between hatchery and wild fish can: (1) transmit disease, (2) cause hybridization, (3) lead to predation on wild fish by hatchery fish, (4) cause competition, (5) alter growth and survival of wild fish, and (6) displace wild fish. These negative interactions argue for a greater scrutiny of hatchery programs, and a need to produce a smaller number of smolts, focussing on quality instead of quantity.

The Pacific Northwest Index, although proven useful for tracking decadal variation in climate and certain biological variables such as the Oyster Condition Index (Schoener and Tufts, 1987) and the total salmon production in the Columbia Basin (unpublished data), it was not influential at the interannual time scale. Considering the time scales at which the important environmental variables act is essential. Since 1977, the Northwest has been in a predominantly warm/dry regime which is tracked well by the PNI. The NMFS transportation studies (1983-1990) considered in this paper were conducted entirely within this regime, thought to be unfavorable to salmon production. Within this short span of 8 years, one is able to examine only inter- and intra-annual variation, not decadal variation. Inter-annual variation was best explained by the spring transition date, and intra-annual variation, by migration timing.

Conclusions

Below are several conclusions we reached on the study of stream-type chinook tagged as juveniles during (1983-1990).

1. Adults returned predominantly at age 4. Of the returns during the study period, 9% were age 3; 58%, age 4; and 33%, age 5. Of the covariates considered, age was most significant and explained the most variation in return percentage.
2. Within a migration season, later migrants showed greater return percentages than earlier migrants. This was not due to an increase in size, but perhaps to increased experience, or a more favorable estuary/ocean environment due to fewer predators or greater growth potential. It was not due to increasing flow over the migration season—the correlation between flow and migration date was weak (less than 0.1)
3. Spring transition date during the year of juvenile outmigration was the best predictor among those explaining year-to-year variation (as opposed to within-year variation). All else being equal, an earlier spring transition was associated with greater survival.
4. A longer summer (defined as the time between spring and fall transitions) in the year of juvenile outmigration appeared less favorable to returns than a shorter summer.
5. Higher flow at Lower Granite Dam did not produce higher return percentages. In fact, higher flow was negatively correlated with adult return rates. Flow at Astoria, a positive correlate of Lower Granite Flow, was also negatively related to adult return rates.
6. Larger hatchery releases in the Snake River may result in smaller return percentages. Large steelhead releases accompanied the larger releases of chinook salmon hatchery fish.
7. The Pacific Northwest Index (PNI), solar radiation, age-specific length of returning fish, and wind velocity (which drives coastal upwelling) were not significantly related to adult return rates. Some of these variables, such as the PNI, may be important only over longer time scales.

Recommendations

1. Incorporate our final selected statistical model in CRiSP and other life-cycle models to account for variability in survival related to the near-shore ocean environment. The optimal model, based on its simplicity and its ability to explain the data, is given in equation (4), and the parameter estimates are given in TABLE 16.
2. More transportation studies are needed. The GLM analysis should be extended throughout the river basin to explore the influence of near-shore ocean conditions. Analysis of data collected throughout the Columbia Basin and over a longer time span should be carried out.
3. Hatcheries should consider shifting their focus from releasing larger numbers of smolts in the Columbia River system to releasing smaller number of smolts, concentrating on quality instead of quantity.
4. Hatchery managers should consider timing their releases to correspond to more favorable nearshore ocean conditions as measured by the timing of the spring transition, or direct measurements of plankton abundance in the Columbia River plume. We could deploy profiling pump-and-probe flourometers to measure chlorophyll and primary production continuously in the Columbia River plume. These could be placed at 1 degree Latitude intervals along the continental shelf so that hatchery releases may be timed with favorable near-shore conditions. At any rate, releases should be adjusted to mimic the very protracted outmigration of wild smolts that NMFS has reported, in essence reducing intra-specific competition and increasing the probability that a good portion of the outmigrants will experience favorable nearshore ocean conditions.

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GLOSSARY

General

CRiSP. Columbia River Salmon Passage model developed at the University of Washington.

NMFS. The National Marine Fisheries Service.

Climate, Oceanography, and Biology

Age at maturity. The age of a salmon at the time of its maturity. Salmon captured during their spawning run in the Columbia River are considered mature. Age is measured from the time the salmon is a fertilized egg, which is the time that its parents spawned, usually in the fall.

Fall transition. The switch from the predominantly northerly winds of summer to the southerly winds of winter off the Pacific coast of North America in an area varying from approximately San Francisco, California to northern Vancouver Island, Canada. In this report, the fall transition date is reported as the day that the fall transition occurs at the mouth of the Columbia River (46 °N. latitude).

Flow. Discharge in KCFS, 1000s of cubic feet per second.

OSCURS. The Ocean Surface Current Simulation model developed by James Ingraham of NOAA. The model uses daily sea level atmospheric pressure fields as input.

Pacific Northwest Index or **PNI**. An index constructed as the average of the standard normal deviates of three parameters: air temperature at Olga, Washington; precipitation at Cedar Lake in the Cascade foothills; and snow pack depth at the Paradise Ranger Station, Mount Rainier, Washington.

Solar radiation. Radiation from the sun measured in kilowatt hours per square meter per day at the earth’s surface ($kWh \cdot m^{-2} \cdot d^{-1}$).

Spring transition. The switch from the predominantly southerly winds of winter to the northerly winds of summer off the pacific coast of North America in an area ranging from approximately San Francisco, California to northern Vancouver Island, Canada. In this report, the spring transition date is reported as the day that the spring transition occurs at the mouth of the Columbia River (46 °N. latitude).

Stream-type chinook salmon. A chinook salmon which spends a year or more in freshwater before migrating to the ocean. On the Columbia River Basin, these salmon are also called “yearlings.”

Statistics.

AIC. The Akaiki selection criterion. It is defined as

$$AIC = D + 2p\hat{\phi},$$

where D is the deviance, p is the number of parameters estimated, and $\hat{\phi}$ is the estimated dispersion parameter.

Anscombe residual. A transformation of the response and predicted values that makes their difference approximately normal. The transformation is performed by a function $A(\cdot)$ defined

$$A(\cdot) = \int \frac{d\mu}{V^{1/3}(\mu)} ,$$

where μ is the mean of the response variable and V is the mean of the response variable. For the scaled poisson distribution, we use the transformation

$$A(y) = \frac{3}{2} y^{2/3} .$$

The Anscombe residuals,

$$\frac{\frac{3}{2}(y^{2/3} - \mu^{2/3})}{\left(\mu \cdot \sqrt{\frac{\phi}{R}}\right)^{1/6}} ,$$

where R is the release size and ϕ is the scale parameter, have an approximate standard normal distribution.

Deviance. D. The discrepancy in a model fit which is proportional to twice the difference between the maximum log likelihood achievable and that achieved by the model under investigation. The smaller the deviance, the better the model fit. It is analogous to the variance in the normal-theory linear models.

Dispersion parameter. ϕ. Also called the *scale parameter.* When one divides the deviance by the dispersion parameter, one obtains the scaled deviance, which is distributed approximately as a chi-square random variable.

Factor. A covariate used in a regression analysis which is categorical (*i.e.*, it does not vary continuously). In this paper age at maturity, which is identified by year, is considered a factor variable.

GLM. A generalized linear model. This class of GLMs includes as special cases: linear regression and analysis-of-variance models, logit and probit models, and log-linear models. These share properties that lead to a common method for computing parameter estimates.

Link function. In a GLM, a function that transforms the response variable in a way that makes its mean a linear function of the covariates. Throughout this paper, the link function is $\log(\cdot)$.

Parameter. An intercept or coefficient in the GLM model which needs to be estimated.

Release. A group of fish with a unique tag identification which is released into the river or barged below Bonneville Dam. The recovery rates of the releases are used to estimate survival.

Scaled deviance. D^*. The deviance divided by the dispersion parameter. It is twice the difference between the maximum log likelihood achievable and that achieved by the model under investigation. Like the variance in Normal-theory models it follows, approximately, a chi-square distribution.

APPENDIX A: STEPWISE GLM ANALYSIS (*MODEL A*)

TABLE A.1 Analysis of deviance for first step (Main Effects). Compared to the model containing only a grand mean: *Response* = 1.

Model	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
1 + *Years*	715.17	143	5.9201	169.28	786.21	6	7.2604e-05
1 + *Periods*	783.79	147	6.7265	100.67	810.69	2	5.6265e-04
1 + *Age*	**615.81**	**147**	**6.5900**	**268.64**	**642.17**	**2**	**1.4062e-09**
1 + *Strans*	825.82	148	7.4240	58.63	840.67	1	4.9492e-03
1 + *Ftrans*	875.49	148	8.5955	8.96	892.68	1	3.0713e-01
1 + *Slength*	859.42	148	7.9831	25.03	875.39	1	7.6614e-02
1 + *Hrelease*	875.86	148	9.1133	8.59	894.08	1	3.3148e-01
1 + *LGRtemp*	791.47	148	6.6052	92.98	804.68	1	1.7548e-04
1 + *BONtemp*	823.14	148	7.0053	61.31	837.16	1	3.0932e-03
1 + *LGRflow*	863.86	148	7.9857	20.59	879.83	1	1.0382e-01
1 + *Astoriaflow*	883.95	148	8.6133	0.50	901.18	1	8.0991e-01
1 + *Firstday*	798.95	148	7.1518	85.50	813.25	1	5.4488e-04
1 + *Lastday*	725.71	148	5.4184	158.74	736.54	1	6.2076e-08
1 + *Deltatrans*	714.94	148	5.7106	169.51	726.36	1	5.0848e-08
1 + *Solar*	813.93	148	6.8822	70.52	827.69	1	1.3689e-03
1 + *Windvel*	882.57	148	8.5686	1.89	899.70	1	6.3902e-01
1 + *Pni*	848.41	148	7.3417	36.04	863.10	1	2.6722e-02
1 + *Length* + *Age:Length*[a]	584.17	146	6.1248	300.28	620.92	3	1.2870e-10

[a] Although 1 + *Length* + *Age:Length* explains the greatest amount of the deviance and has the smallest AIC, its significance, as we shall see, is mostly a consequence of the *Age* factor.

TABLE A.2 Analysis of deviance for second step (Main Effects). Compared to the model containing only a grand mean and *Age*: *Response* = 1 + *Age*.

Added Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+*Years*[a]	446.53	141	4.1698	169.28	496.57	6	3.4768e-07
+ *Periods*	515.15	145	4.6444	100.67	533.72	2	1.9649e-05
+ *Strans*	557.18	146	5.2556	58.63	567.69	1	8.3733e-04
+ *Ftrans*	606.85	146	6.5725	8.96	619.99	1	2.4285e-01
+ *Slength*	590.78	146	5.8640	25.03	602.51	1	3.8829e-02
+ *Hrelease*	607.22	146	7.2114	8.59	621.64	1	2.7496e-01
+ *LGRtemp*	522.83	146	4.6593	92.99	532.14	1	7.9180e-06
+ *BONtemp*	557.49	146	5.0496	58.32	567.58	1	6.7507e-04
+ *LGRflow*	595.22	146	5.9761	20.59	607.17	1	6.3412e-02
+ *Astoriaflow*	615.32	146	6.5764	0.50	628.47	1	7.8319e-01
+ *Firstday*	530.31	146	5.0362	85.50	540.38	1	3.7824e-05
+ *Lastday*	**457.07**	**146**	**3.4005**	**158.74**	**463.87**	**1**	**8.3479e-12**
+ *Deltatrans*[b]	446.30	146	3.4788	169.51	453.26	1	2.9398e-12
+ *Solar*	545.29	146	4.7763	70.52	554.84	1	1.2175e-04
+ *Windvel*	613.93	146	6.4855	1.89	626.90	1	5.8978e-01
+ *Pni*	579.77	146	5.1733	36.04	590.12	1	8.3060e-03
+ *Length* + *Age:Length*[c]	561.90	144	5.6742	53.91	595.94	3	2.3314e-02

[a] Although *Years* explains the greatest amount of deviance, its AIC is larger than that of *Lastday*. Furthermore, we are interested in physical parameters that can help explain the year-to-year variation which the importance of the *Years* variable makes evident. Therefore we choose *Lastday* as our next most important covariate.

[b] Although, as a predictor, *Deltratrans* is slightly superior to *Lastday*, the two are highly correlated, and are not both needed in the model. We use *Lastday* as the covariate of choice so that we may understand the separate role played by the spring transition date.

[c] Notice that the model 1 + *Length* + *Age:Length* looses its explanatory power when *Age* is extracted from the model (compare with the previous table).

TABLE A.3 Analysis of deviance for third step (Main Effects). Compared to the model *Response* = 1 + *Age* + *Lastday.*

Added Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Years*[a]	360.16	140	2.8670	96.91	394.56	6	7.3457e-06
+ *Periods*[b]	454.44	144	3.3903	2.62	468.01	2	6.7910e-01
+ *Strans*	**417.32**	**145**	**3.1841**	**39.74**	**423.69**	**1**	**4.1081e-04**
+ *Ftrans*	452.12	145	3.4456	4.94	459.02	1	2.3099e-01
+ *Slength*	438.79	145	3.2756	18.28	445.34	1	1.8162e-02
+ *Hrelease*	456.02	145	3.4660	1.04	462.96	1	5.8299e-01
+ *LGRtemp*	456.89	145	3.4222	0.17	463.74	1	8.2180e-01
+ *BONtemp*	449.65	145	3.3522	7.42	456.35	1	1.3686e-01
+ *LGRflow*	428.29	145	2.9692	28.78	434.23	1	1.8494e-03
+ *Astoriaflow*	450.18	145	3.2458	6.89	456.67	1	1.4510e-01
+ *Firstday*	451.28	145	3.3513	5.79	457.98	1	1.8875e-01
+ *Deltatrans*[c]	416.53	145	3.1360	40.54	422.80	1	3.2400e-04
+ *Solar*[d]	421.35	145	3.1937	35.72	427.74	1	8.2493e-04
+ *Windvel*	452.45	145	3.3465	4.62	459.14	1	2.4007e-01
+ *Pni*	438.51	145	3.2264	18.56	444.96	1	1.6472e-02
+ *Length* + *Age:Length*	421.72	143	3.2574	35.35	441.27	3	1.2559e-02

[a] Although *Years* explains the greatest amount of deviance, it contains 6 d.f. Because we are interested in physical parameters that can help explain the year-to-year variation, we choose *Strans* as our next most important covariate.

[b] The factor *Periods* loses its explanatory power once *Lastday* is included in the model.

[c] *Deltratrans* explains only slightly more deviation than the spring transition date. It is highly correlated with *Strans*, and therefore we loose nothing by selecting *Strans* as the “best” covariate.

[d] Solar radiation explains almost as much of the deviance as *Strans*.

TABLE A.4 Analysis of deviance for second step (Main Effects). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans*.

Added Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Years*[a]	360.16	140	2.8670	57.16	388.83	6	1.2831e-03
+ *Periods*	413.72	143	3.2011	3.61	426.52	2	5.6942e-01
+ *Ftrans*[b]	400.01	144	3.2202	17.31	406.45	1	2.0417e-02
+ *Slength*	**400.01**	**144**	**3.2202**	**17.31**	**406.45**	**1**	**2.0419e-02**
+ *Hrelease*	402.82	144	3.2013	14.50	409.22	1	3.3330e-02
+ *LGRtemp*	416.82	144	3.2066	0.50	423.23	1	6.9203e-01
+ *BONtemp*	407.15	144	3.1175	10.18	413.38	1	7.0810e-02
+ *LGRflow*	408.98	144	2.9907	8.35	414.96	1	9.4797e-02
+ *Astoriaflow*	417.01	144	3.1742	0.31	423.36	1	7.5273e-01
+ *Firstday*	412.53	144	3.1510	4.79	418.83	1	2.1749e-01
+ *Deltatrans*	416.53	144	3.1598	0.79	422.85	1	6.1603e-01
+ *Solar*	406.58	144	3.1345	10.75	412.84	1	6.4066e-02
+ *Windvel*	411.17	144	3.1345	6.15	417.44	1	1.6116e-01
+ *Pni*	415.48	144	3.1761	1.85	421.83	1	4.4593e-01
+ *Length* + *Age:Length*	399.88	142	3.1830	17.45	418.97	3	1.3975e-01

[a] Although *Years* explains the greatest amount of deviance, it contains 6 d.f. Because we are interested in physical parameters that explain the year-to-year variation, we choose *Slength* as our next most important covariate.

[b] Notice that *Ftrans* and *Slength* explain the same amount of deviance. This is because *Slength* is the difference between *Ftrans* and *Strans*, and the deviance explained by *Strans* has been extracted in the model fit. A similar argument explains why *Deltatrans* and *Firstday* explain the same amount of remaining deviance.

TABLE A.5 Analysis of deviance for second step (Main Effects). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans* + *Slength*.

Added Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Years*	360.16	140	2.8670	39.85	383.09	6	7.6176e-03
+ *Periods*	399.01	142	3.2508	1.00	412.02	2	8.5763e-01
+ *Ftrans*	399.99	143	3.2411	0.02	406.49	1	9.3797e-01
+ *Hrelease*	391.85	143	3.2214	8.16	398.29	1	1.1140e-01
+ *LGRtemp*	397.14	143	3.2271	2.87	403.60	1	3.4559e-01
+ *BONtemp*	398.68	143	3.1967	1.33	405.08	1	5.1907e-01
+ *LGRflow*	**366.89**	**143**	**2.6691**	**33.22**	**372.23**	**1**	**4.2740e-04**
+ *Astoriaflow*	374.09	143	2.7975	25.93	379.68	1	2.3321e-03
+ *Firstday*	398.61	143	3.2033	1.40	405.02	1	5.0808e-01
+ *Deltatrans*	396.31	143	3.1488	3.71	402.60	1	2.7799e-01
+ *Solar*	399.46	143	3.2229	3.71	405.90	1	6.7767e-01
+ *Windvel*	399.80	143	3.2229	0.56	405.90	1	6.7767e-01
+ *Pni*	400.01	143	3.2427	0.00	406.50	1	9.9628e-01
+ *Length* + *Age:Length*	393.28	141	3.2225	6.73	412.62	3	5.5434e-01

TABLE A.6 Analysis of deviance for second step (Main Effects). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans* + *Slength* + *LGRflow.*

Added Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Years*	346.11	139	2.6875	20.78	367.61	6	1.0192e-01
+ *Periods*	365.93	141	2.7285	0.97	376.84	2	8.3754e-01
+ *Ftrans*	365.56	142	2.6738	1.34	370.90	1	4.7942e-01
+ *Hrelease*	**351.42**	**142**	**2.6681**	**15.47**	**356.75**	**1**	**1.6027e-02**
+ *LGRtemp*	366.89	142	2.6888	0.00	372.27	1	9.7592e-01
+ *BONtemp*	360.98	142	2.6289	5.91	366.24	1	1.3379e-01
+ *Astoriaflow*	365.07	142	2.6739	1.82	370.42	1	4.0954e-01
+ *Firstday*	364.82	142	2.6519	2.07	370.12	1	3.7644e-01
+ *Deltatrans*	365.41	142	2.6369	1.48	370.68	1	4.5315e-01
+ *Solar*	359.69	142	2.6602	7.20	365.02	1	9.9991e-02
+ *Windvel*	364.50	142	2.7101	2.39	369.92	1	3.4720e-01
+ *Pni*	358.60	142	2.6730	8.29	363.95	1	7.8249e-02
+ *Length* + *Age:Length*	354.11	140	2.6367	12.79	369.93	3	1.8315e-01

TABLE A.7 Analysis of deviance for second step (Main Effects). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans* + *Slength* + *LGRflow* + *Hrelease.*

Added Term(s)[a]	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Years*	346.11	139	2.6875	5.30	362.24	6	5.7791e-01
+ *Periods*	350.95	140	2.7037	0.46	361.77	2	9.1771e-01
+ *Ftrans*	350.25	141	2.6533	1.16	355.56	1	5.0780e-01
+ *LGRtemp*	350.62	141	2.6726	0.80	355.96	1	5.8375e-01
+ *BONtemp*	346.38	141	2.6094	5.04	351.60	1	1.6459e-01
+ *Astoriaflow*	348.75	141	2.6623	2.67	354.08	1	3.1688e-01
+ *Firstday*	350.97	141	2.6626	0.45	356.30	1	6.8244e-01
+ *Deltatrans*	341.70	141	2.5362	9.72	346.77	1	5.0274e-02
+ *Solar*	351.32	141	2.6853	0.10	356.69	1	8.4569e-01
+ *Windvel*	348.85	141	2.6604	2.56	354.17	1	3.2625e-01
+ *Pni*	351.06	141	2.6858	0.35	356.44	1	7.1682e-01
+ *Length* + *Age:Length*	345.28	139	2.6687	6.14	361.29	3	5.1273e-01

[a] None of the terms are significant.

TABLE A.8 Analysis of deviance for (Interactions). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans* + *Slength* + *LGRflow* + *Hrelease.*

Added Interaction Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Age:Lastday*	332.32	140	2.4314	19.10	342.05	2	1.9696e-02
+ *Age:Strans*	321.54	140	2.4372	29.88	331.29	2	2.1761e-03
+ *Age:Slength*	331.89	140	2.5422	19.53	342.06	2	2.1484e-02
+ *Age:LGRflow*	347.48	140	2.6788	3.94	358.19	2	4.7941e-01
+ *Age:Hrelease*	**296.14**	**140**	**2.2272**	**55.28**	**305.05**	**2**	**4.0792e-06**
+ *Lastday:Strans*	330.43	141	2.3837	20.99	335.20	1	3.0041e-03
+ *Lastday:Slength*	341.05	141	2.5067	10.36	346.07	1	4.2017e-02
+ *Lastday:LGRflow*	351.40	141	2.6848	0.01	356.77	1	9.4132e-01
+ *Lastday:Hrelease*	341.98	141	2.5300	9.43	347.04	1	5.3480e-02
+ *Strans:Slength*	350.25	141	2.6810	1.16	355.61	1	5.0980e-01
+ *Strans:LGRflow*	351.15	141	2.6769	0.26	356.51	1	7.5340e-01
+ *Strans:Hrelease*	350.74	141	2.6812	0.68	356.10	1	6.1485e-01
+ *LGRflow:Slength*	349.17	141	2.6575	2.24	354.49	1	3.5812e-01
+ *LGRflow:Hrelease*	342.82	141	2.5790	8.60	347.98	1	6.7872e-02
+ *Slength:Hrelease*	351.40	141	2.6868	0.01	356.78	1	9.4082e-01

TABLE A.9 Analysis of deviance for (Interactions). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans* + *Slength* + *LGRflow* + *Hrelease* + *Age*:*Hrelease.*

Added Interaction Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Age*:*Lastday*	279.26	138	2.0837	16.88	287.60	2	1.7423e-02
+ *Age*:*Strans*	292.73	138	2.2072	3.40	301.56	2	4.6245e-01
+ *Age*:*Slength*	295.68	138	2.2507	0.46	304.69	2	9.0343e-01
+ *Age*:*LGRflow*	291.71	138	2.2441	4.43	300.69	2	3.7299e-02
+ *Lastday*:*Strans*	**274.03**	**139**	**2.0453**	**22.11**	**278.12**	**1**	**1.0096e-03**
+ *Lastday*:*Slength*	284.44	139	2.1191	11.70	288.68	1	1.8787e-02
+ *Lastday*:*LGRflow*	296.08	139	2.2415	0.06	300.57	1	8.7376e-01
+ *Lastday*:*Hrelease*	285.26	139	2.1461	10.88	289.55	1	2.4364e-02
+ *Strans*:*Slength*	295.83	139	2.2460	0.31	300.32	1	7.0996e-01
+ *Strans*:*LGRflow*	295.72	139	2.2338	0.42	300.19	1	6.6405e-01
+ *Strans*:*Hrelease*	295.99	139	2.2449	0.14	300.48	1	7.9948e-01
+ *LGRflow*:*Slength*	294.82	139	2.2318	1.32	299.29	1	4.4250e-01
+ *LGRflow*:*Hrelease*	284.94	139	2.1286	11.20	289.20	1	2.1817e-02
+ *Slength*:*Hrelease*	295.45	139	2.2287	0.69	299.90	1	5.7716e-01

TABLE A.10 Analysis of deviance for (Interactions). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans* + *Slength* + *LGRflow* + *Hrelease* + *Age*:*Hrelease* + *Lastday*:*Strans.*

Added Interaction Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Age*:*Lastday*[a]	262.71	137	1.9658	11.32	270.57	2	5.6168e-02
+ *Age*:*Strans*	270.56	137	2.0307	3.47	278.69	2	4.2596e-01
+ *Age*:*Slength*	273.59	137	2.0629	0.44	281.84	2	8.9812e-01
+ *Age*:*LGRflow*	270.35	137	2.0593	3.68	278.59	2	4.0939e-01
+ *Lastday*:*Slength*	**263.90**	**138**	**2.0460**	**10.13**	**267.99**	**1**	**2.6045e-02**
+ *Lastday*:*LGRflow*	270.72	138	2.0427	3.31	274.81	1	2.0317e-01
+ *Lastday*:*Hrelease*	273.64	138	2.0553	0.39	277.75	1	6.6154e-01
+ *Strans*:*Slength*	272.06	138	2.0713	1.97	276.21	1	3.2990e-01
+ *Strans*:*LGRflow*	273.61	138	2.0508	0.42	277.71	1	6.4905e-01
+ *Strans*:*Hrelease*	271.88	138	2.0688	2.15	276.02	1	3.0803e-01
+ *LGRflow*:*Slength*	271.90	138	2.0425	2.13	275.99	1	3.0727e-01
+ *LGRflow*:*Hrelease*	271.30	138	2.0280	2.73	275.36	1	2.4609e-01
+ *Slength*:*Hrelease*	274.02	138	2.0620	0.01	278.14	1	9.3419e-01

[a] The interaction term *Age*:*Lastday* explains slightly more of the deviance than *Lastday*:*Slength*, but takes up one more degree of freedom. This is reflected in the AIC, which argues for including *Lastday*:*Slength* in the model. The p-value argues for selecting the latter as the best interaction term.

TABLE A.11 Analysis of deviance for (Interactions). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans* + *Slength* + *LGRflow* + *Hrelease* + *Age*:*Hrelease* + *Lastday*:*Strans* + *Lastday*:*Slength.*

Added Interaction Term(s)	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Age*:*Lastday*	**251.71**	**136**	**1.9730**	**12.18**	**259.60**	**2**	**4.5608e-02**
+ *Age*:*Strans*	260.15	136	2.0276	3.75	268.26	2	3.9692e-01
+ *Age*:*Slength*	263.39	136	2.0648	0.51	271.65	2	8.8381e-01
+ *Age*:*LGRflow*	260.36	136	2.0610	3.54	268.60	2	4.2416e-01
+ *Lastday*:*LGRflow*	263.77	137	2.0597	0.13	267.89	1	8.0451e-01
+ *Lastday*:*Hrelease*	261.38	137	2.0354	2.52	265.45	1	2.6600e-01
+ *Strans*:*Slength*	263.10	137	2.0646	0.80	267.23	1	5.3362e-01
+ *Strans*:*LGRflow*	263.88	137	2.0595	0.01	268.00	1	9.3913e-01
+ *Strans*:*Hrelease*	262.55	137	2.0629	1.34	266.68	1	4.2004e-01
+ *LGRflow*:*Slength*	263.27	137	2.0501	0.62	267.37	1	5.8190e-01
+ *LGRflow*:*Hrelease*	259.32	137	2.0471	4.57	263.42	1	1.3500e-01
+ *Slength*:*Hrelease*	263.68	137	2.0554	0.21	267.79	1	7.4820e-01

TABLE A.12 Analysis of deviance for (Interactions). Compared to the model *Response* = 1 + *Age* + *Lastday* + *Strans* + *Slength* + *LGRflow* + *Hrelease* + *Age*:*Hrelease* + *Lastday*:*Strans* + *Lastday*:*Slength* + *Age*:*Lastday.*

Added Interaction Term(s)[a]	D	d.f.	ϕ	ΔD	AIC	Δ d.f.	p-value
+ *Age*:*Strans*	250.80	134	1.9837	0.91	258.73	2	7.9451e-01
+ *Age*:*Slength*	251.47	134	1.9912	0.24	259.44	2	9.4149e-01
+ *Age*:*LGRflow*	247.98	134	1.9883	3.73	255.94	2	3.9155e-01
+ *Lastday*:*LGRflow*	251.50	135	1.9880	0.22	255.47	1	7.4204e-01
+ *Lastday*:*Hrelease*	250.87	135	1.9721	0.84	254.82	1	5.1420e-01
+ *Strans*:*Slength*	250.87	135	1.9976	0.85	254.86	1	5.1531e-01
+ *Strans*:*LGRflow*	251.68	135	1.9907	0.03	255.66	1	9.0364e-01
+ *Strans*:*Hrelease*	250.40	135	2.0003	1.32	254.40	1	4.1744e-01
+ *LGRflow*:*Slength*	251.26	135	1.9782	0.45	255.22	1	6.3231e-01
+ *LGRflow*:*Hrelease*	248.29	135	1.9765	3.42	252.25	1	1.8842e-01
+ *Slength*:*Hrelease*	251.59	135	1.9809	0.12	255.55	1	8.0633e-01

[a] None of the remaining interaction terms are significant.

APPENDIX B: FITTED CURVES FOR *MODEL A*

The following figures demonstrate the effects of the covariates of *Model B* and their interactions. In *Model A*, no observations were omitted from the data set. The fitted curves are on the scale of the linear predictor, $\log(p)$.

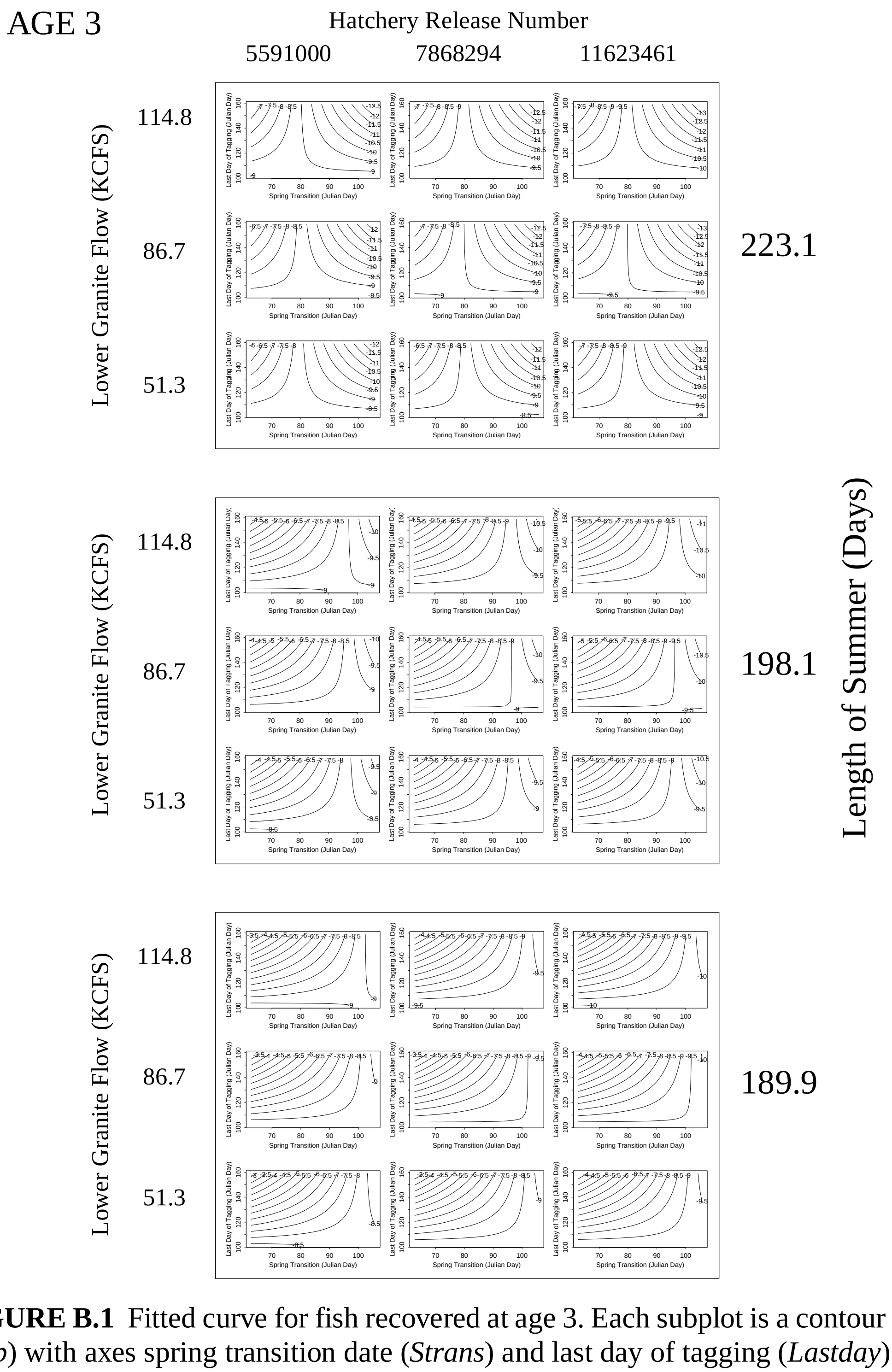

FIGURE B.1 Fitted curve for fish recovered at age 3. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

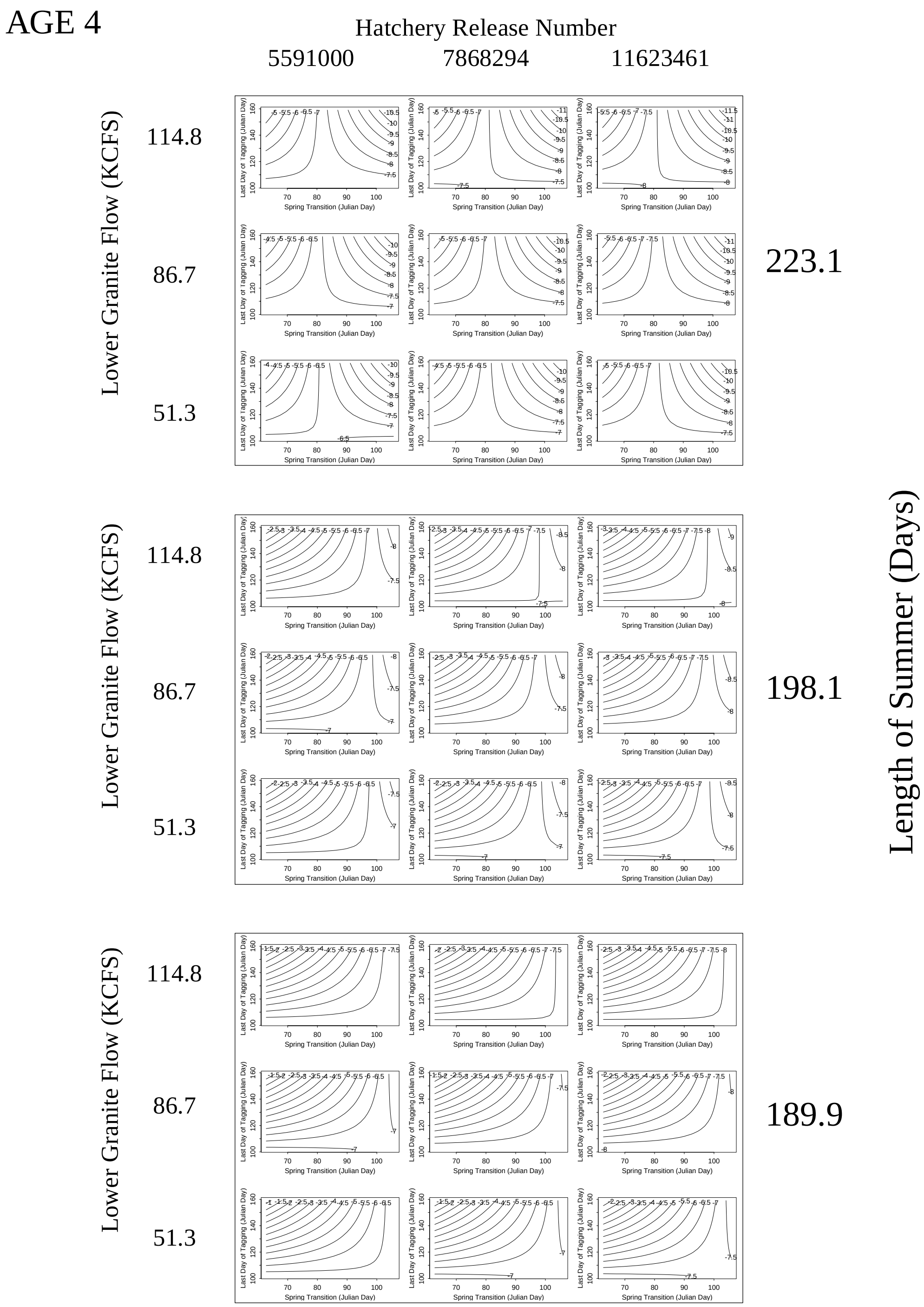

FIGURE B.2 Fitted curve for fish recovered at age 4. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

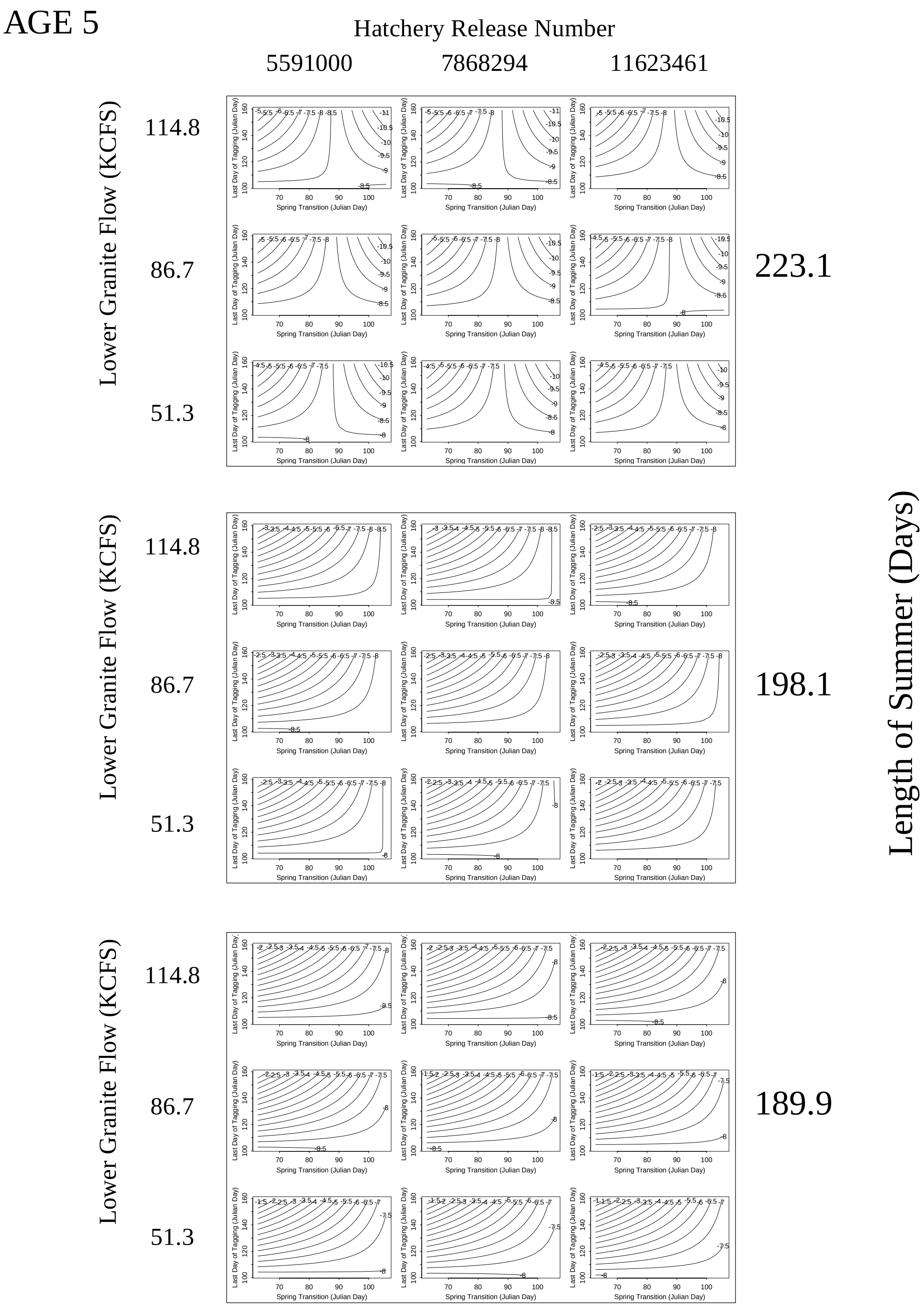

FIGURE B.3 Fitted curve for fish recovered at age 5. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

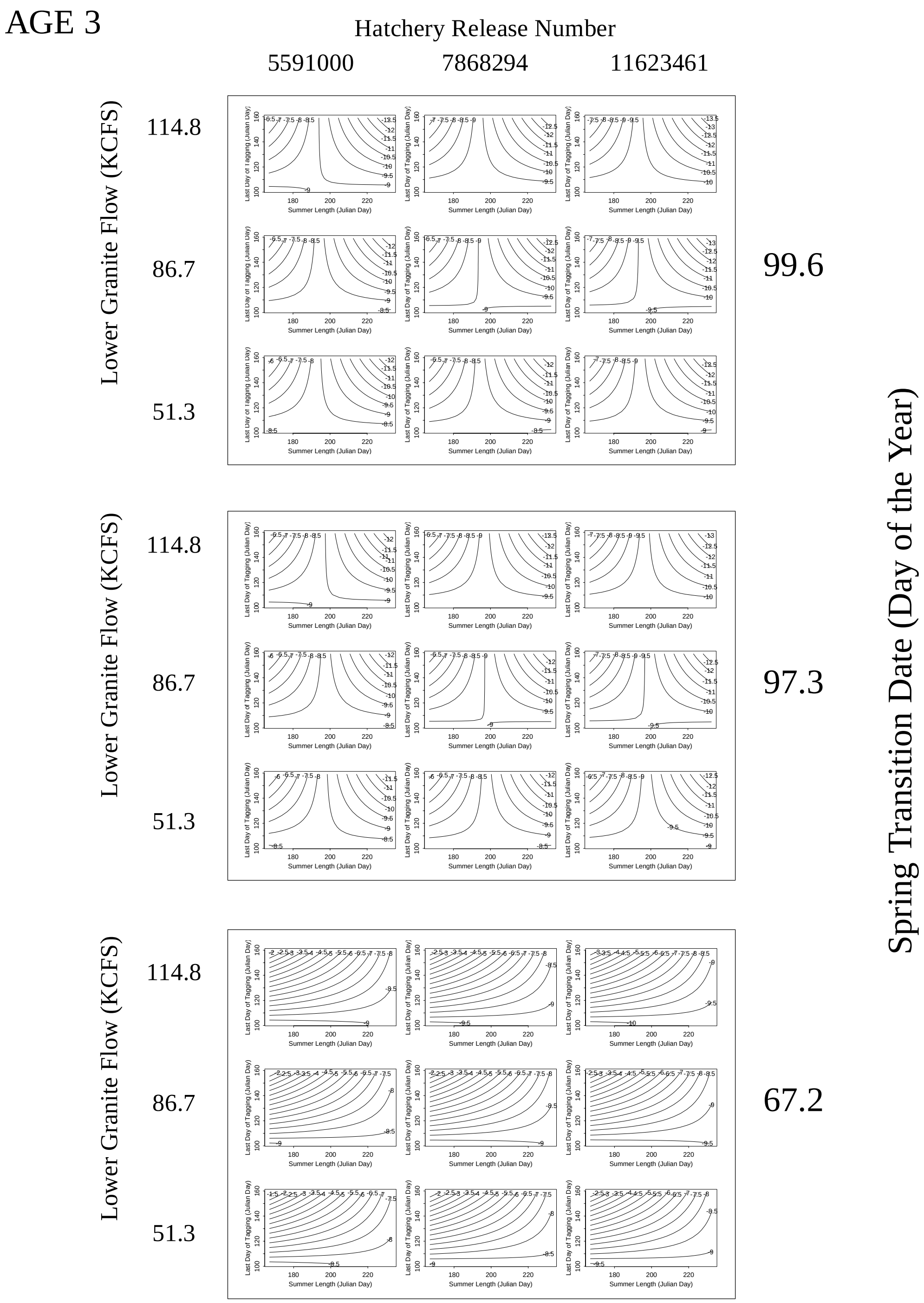

FIGURE B.4 Fitted curve for fish recovered at age 3. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

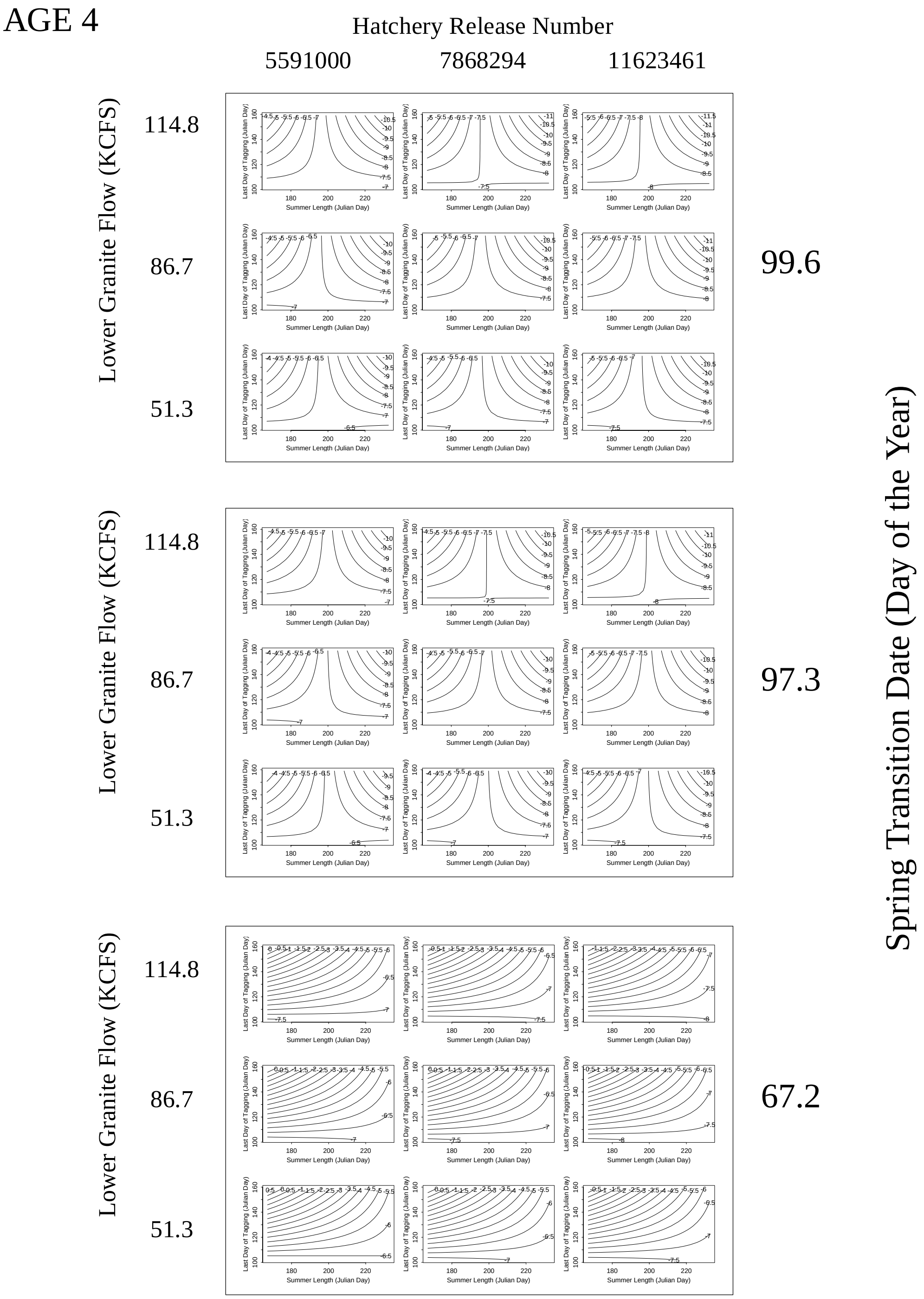

FIGURE B.5 Fitted curve for fish recovered at age 4. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

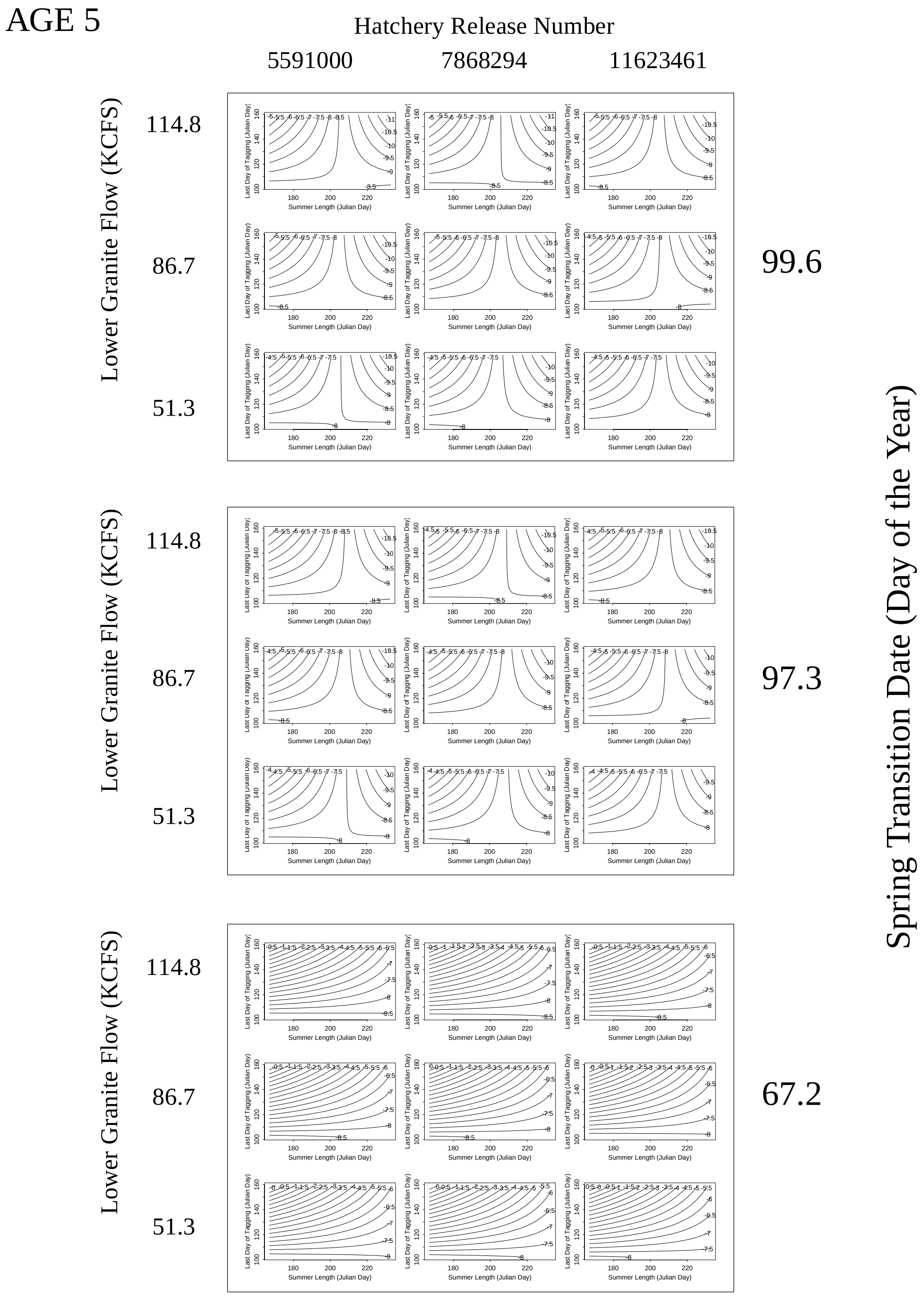

FIGURE B.6 Fitted curve for fish recovered at age 5. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

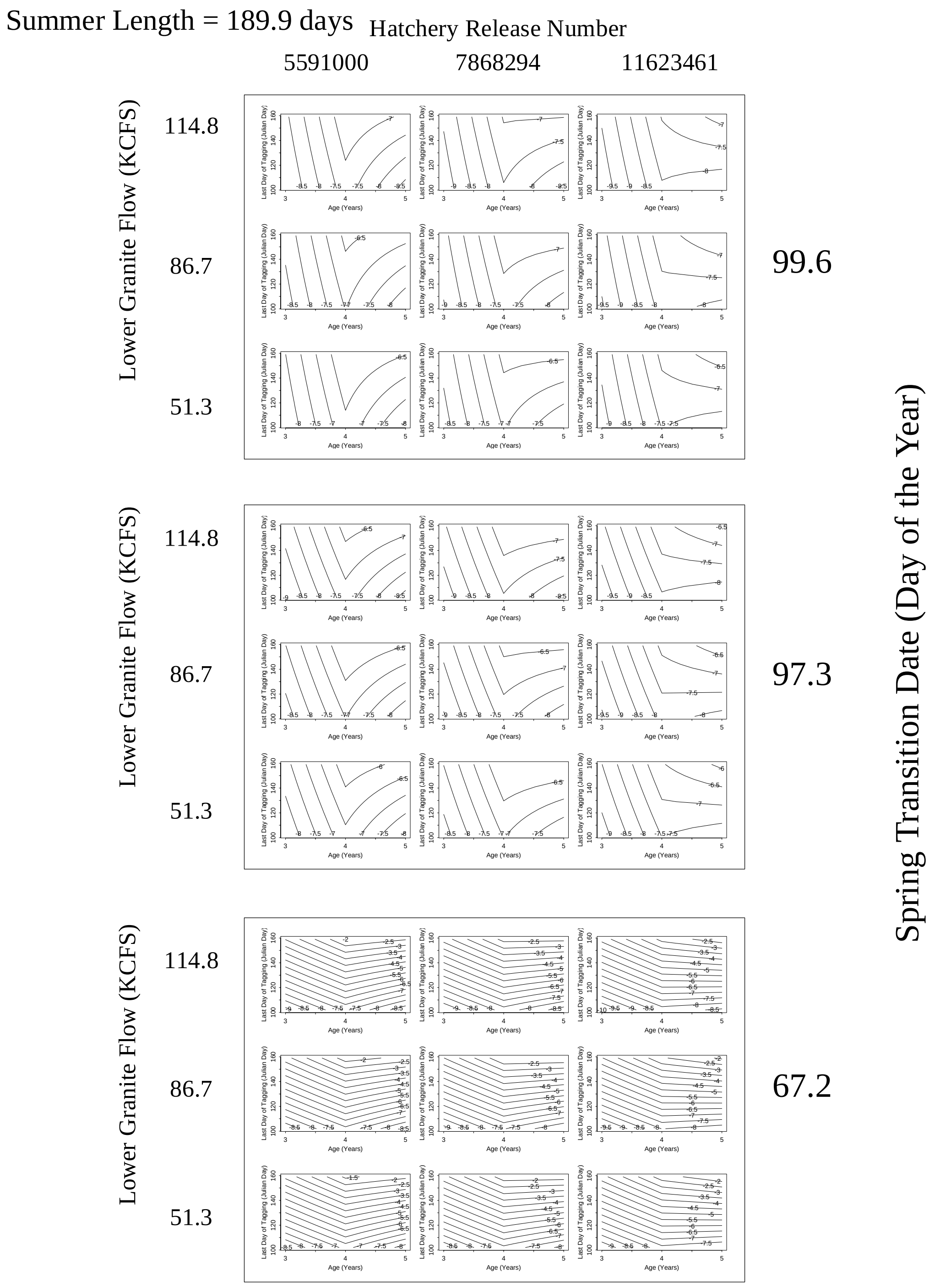

FIGURE B.7 Fitted curve for fish migrating during a summer lasting 189.9 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday*).

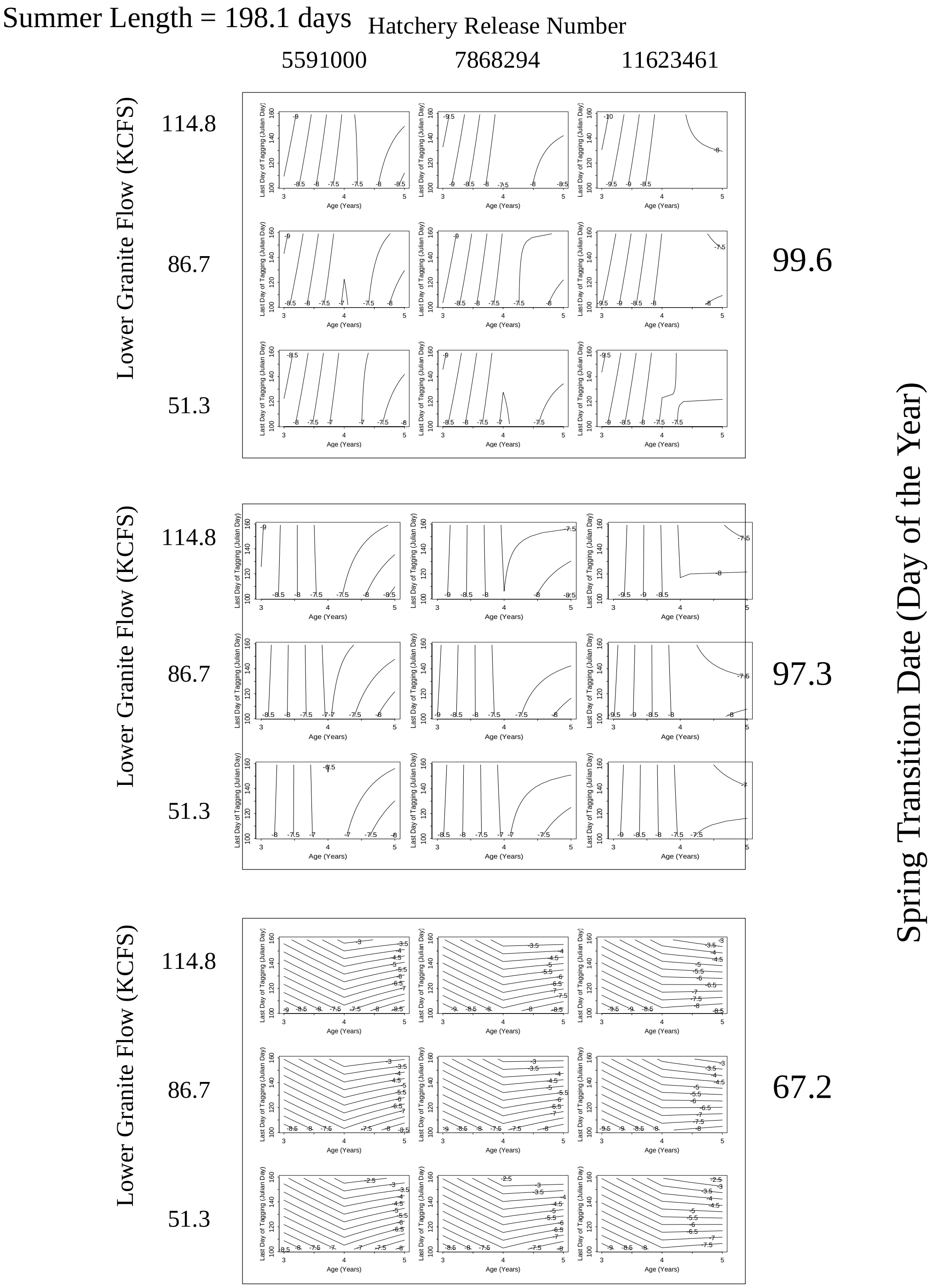

FIGURE B.8 Fitted curve for fish migrating during a summer lasting 198.1 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday*).

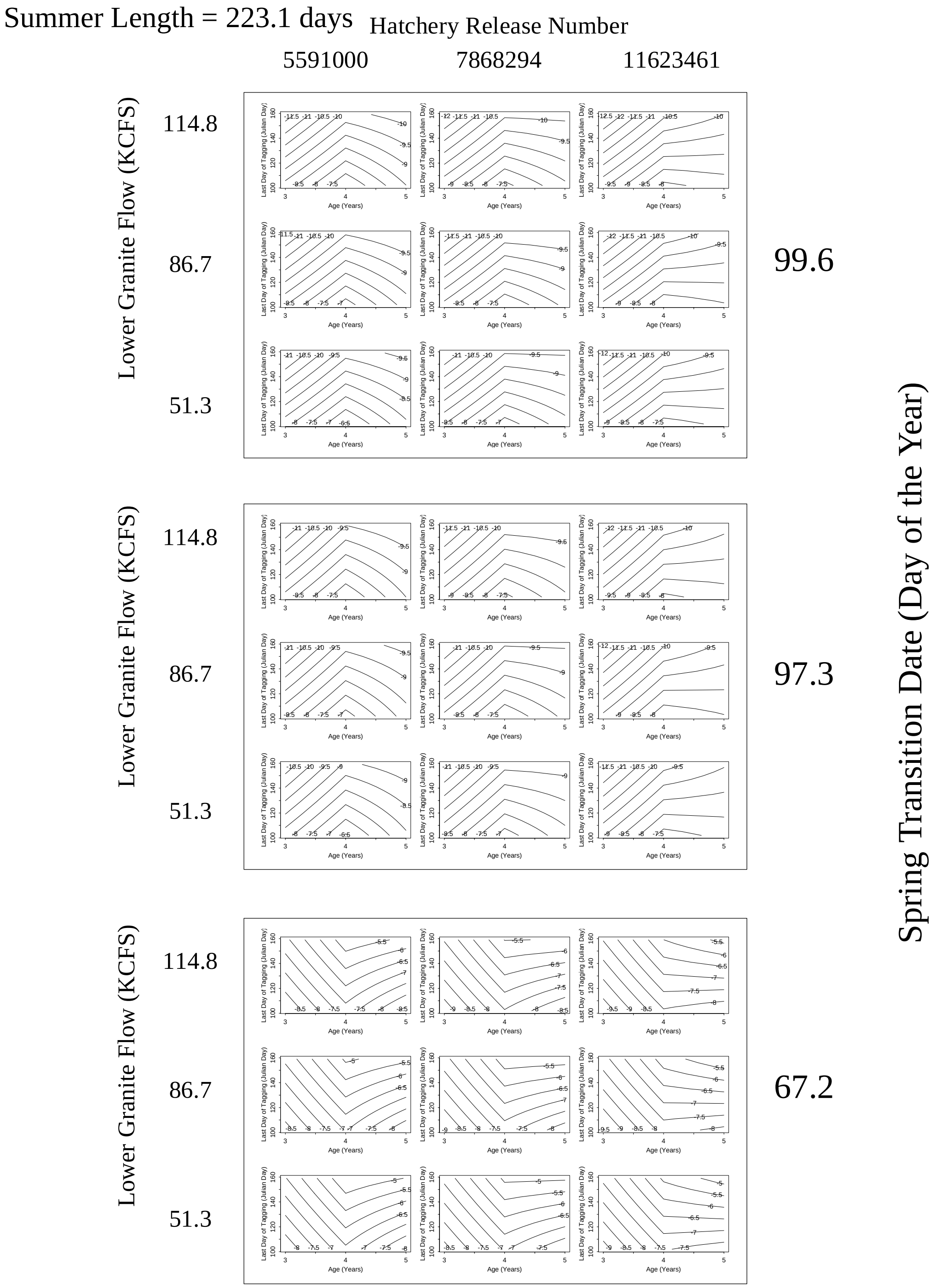

FIGURE B.9 Fitted curve for fish migrating during a summer lasting 223.1 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday)*.

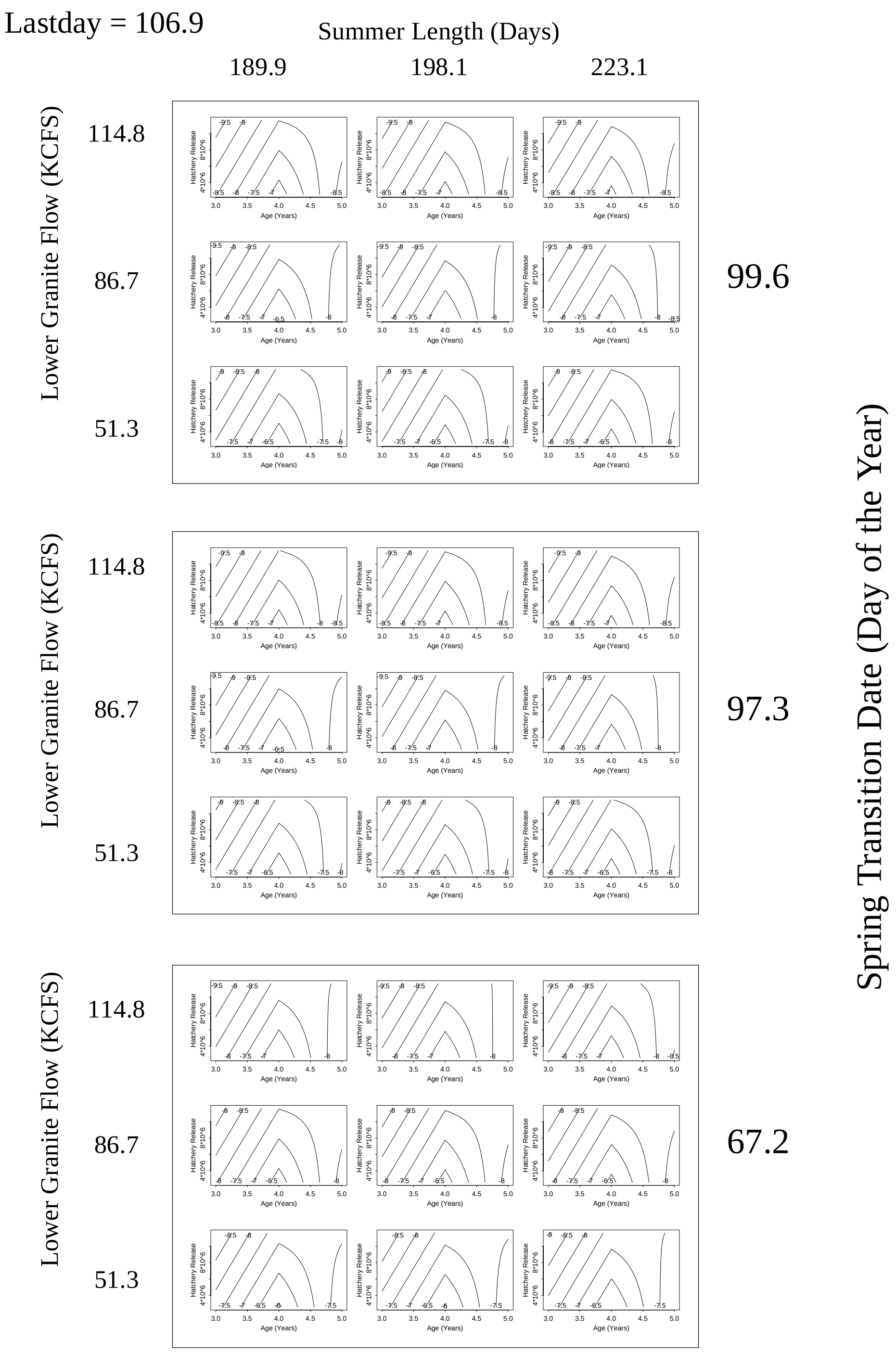

FIGURE B.10 Fitted curve for fish migrating before day of the year 106.9. Each subplot is a contour plot of log(*p*) with axes age (3, 4, or 5 years) and hatchery release (*Hrelease*).

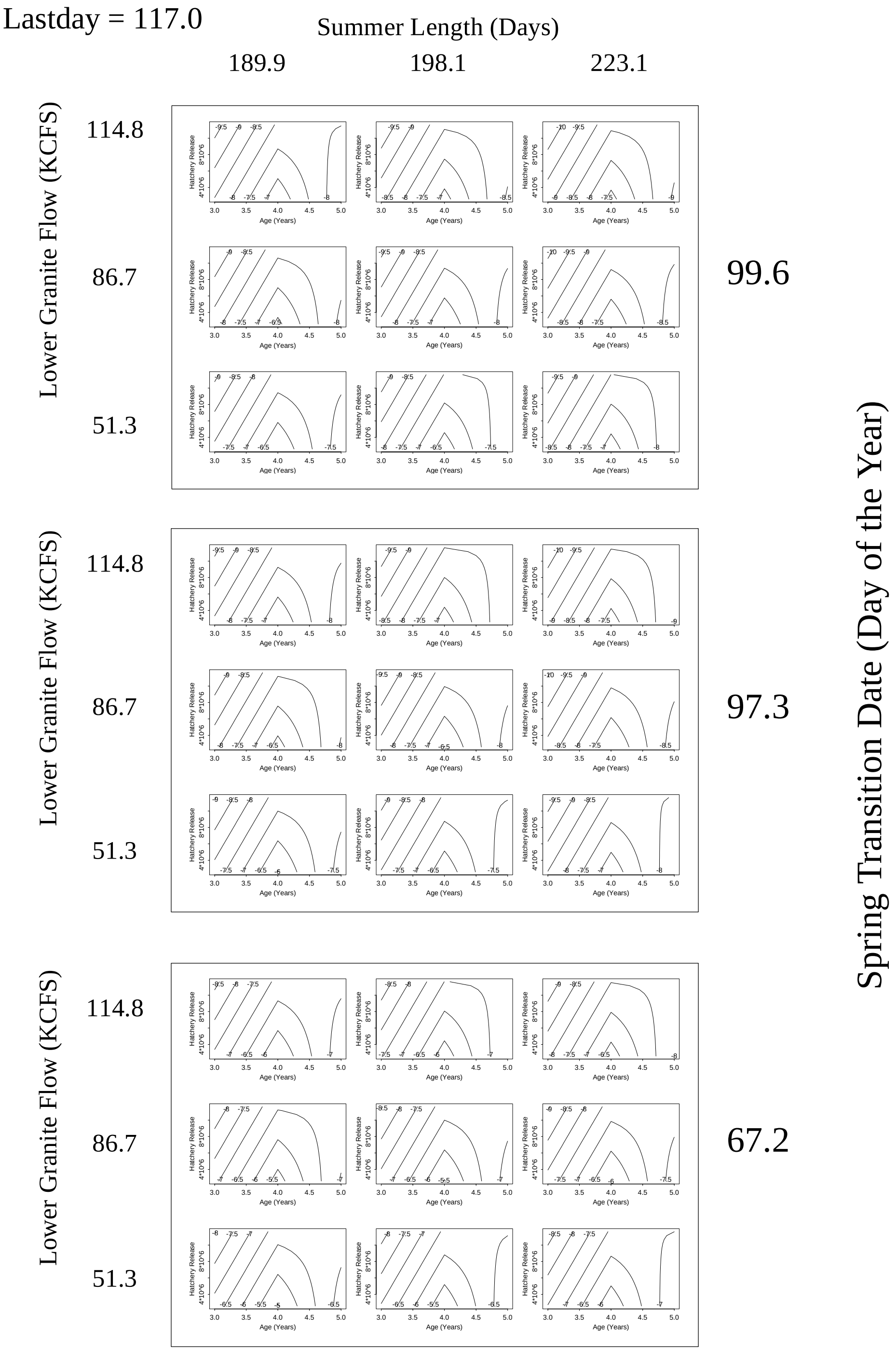

FIGURE B.11 Fitted curve for fish migrating before day of the year 117.0. Each subplot is a contour plot of log(*p*) with axes age (3, 4, or 5 years) and hatchery release (*Hrelease*).

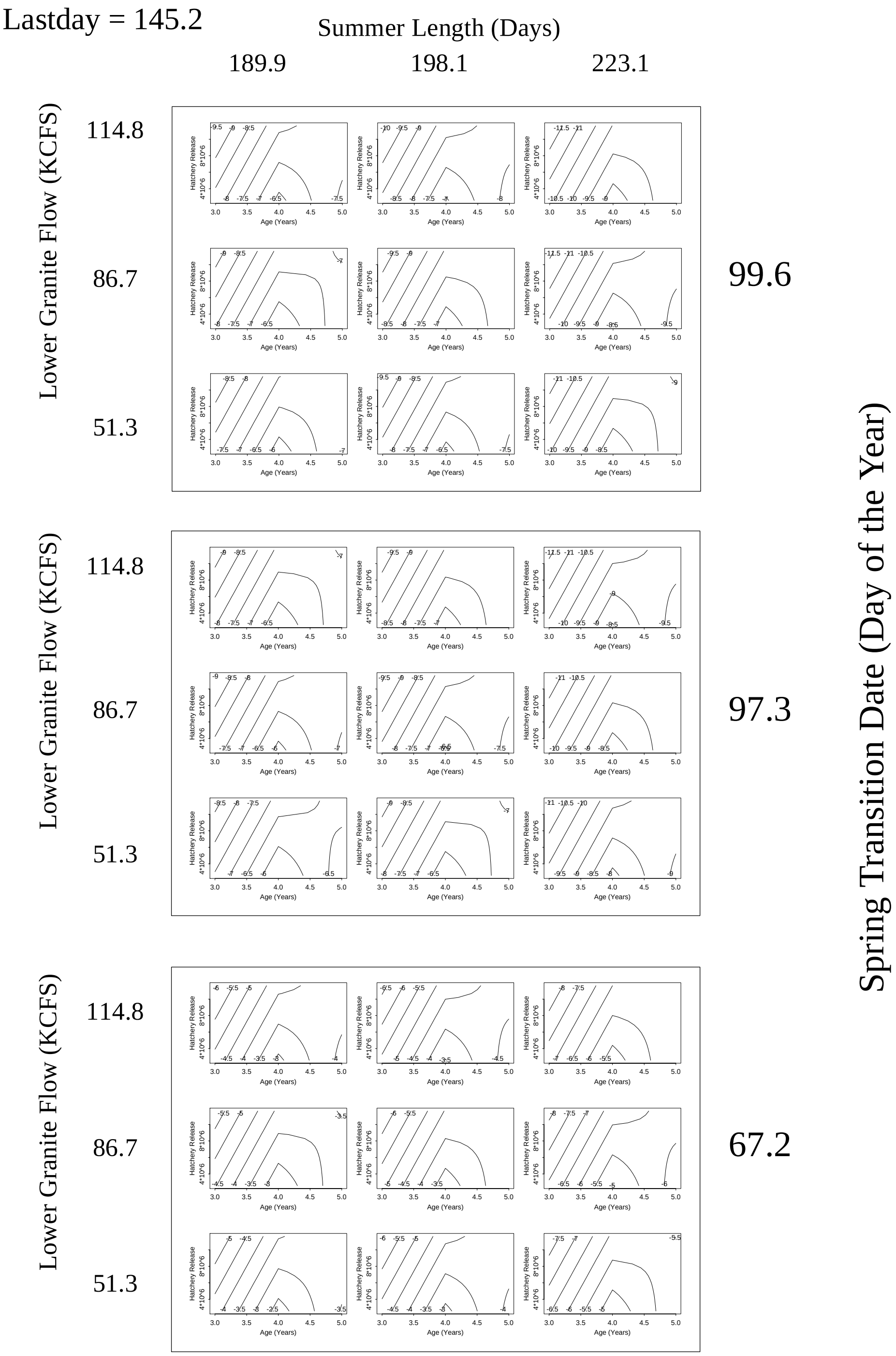

FIGURE B.12 Fitted curve for fish migrating before day of the year 145.2. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and hatchery release (*Hrelease*).

APPENDIX C: FITTED CURVES FOR *MODEL B*

The following figures demonstrate the effects of the covariates of *Model B* and their interactions. In *Model B*, observations #68 and #150 are omitted from the data set. The fitted curves are on the scale of the linear predictor, $\log(p)$.

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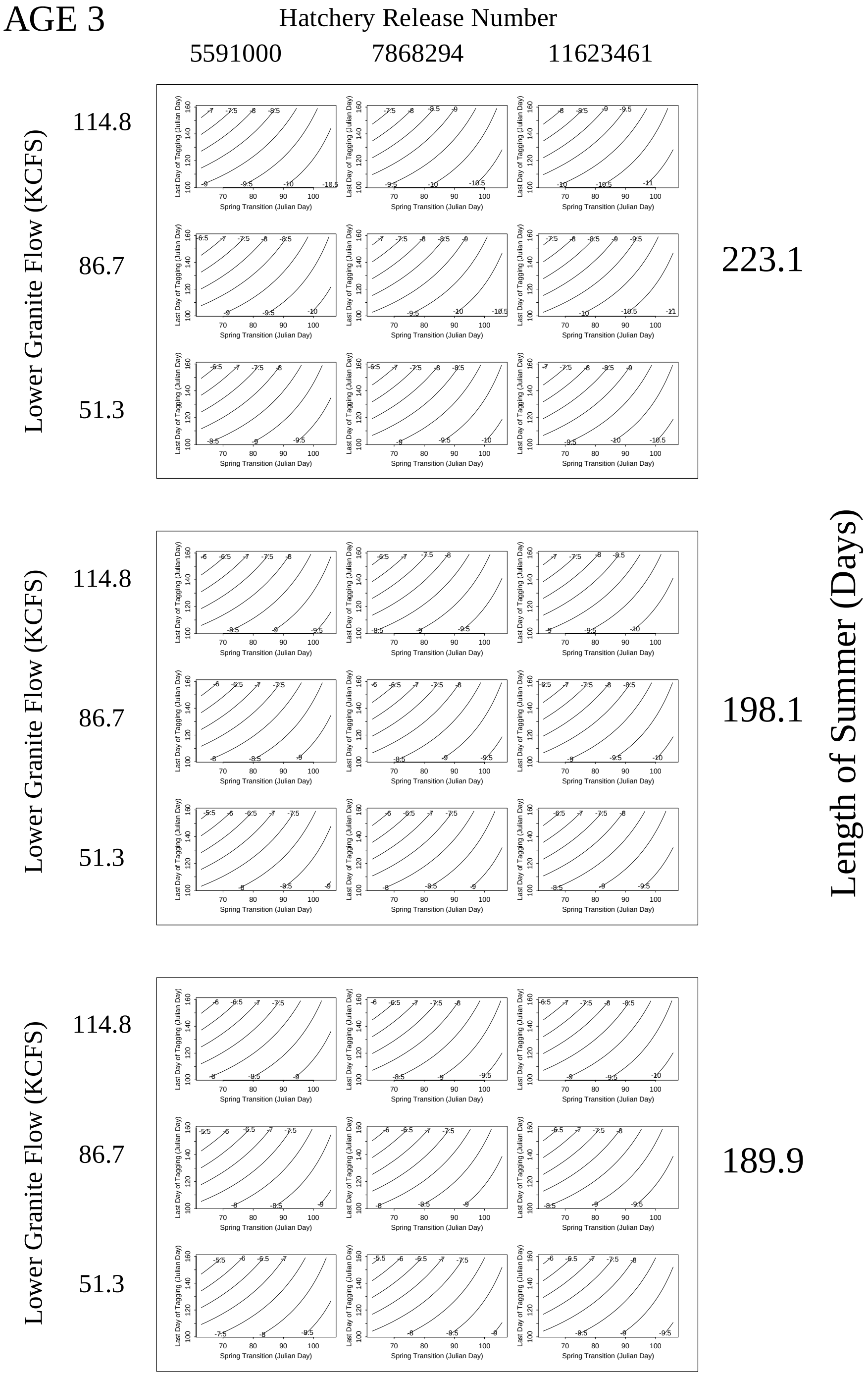

FIGURE C.1 Fitted curve for fish recovered at age 3. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

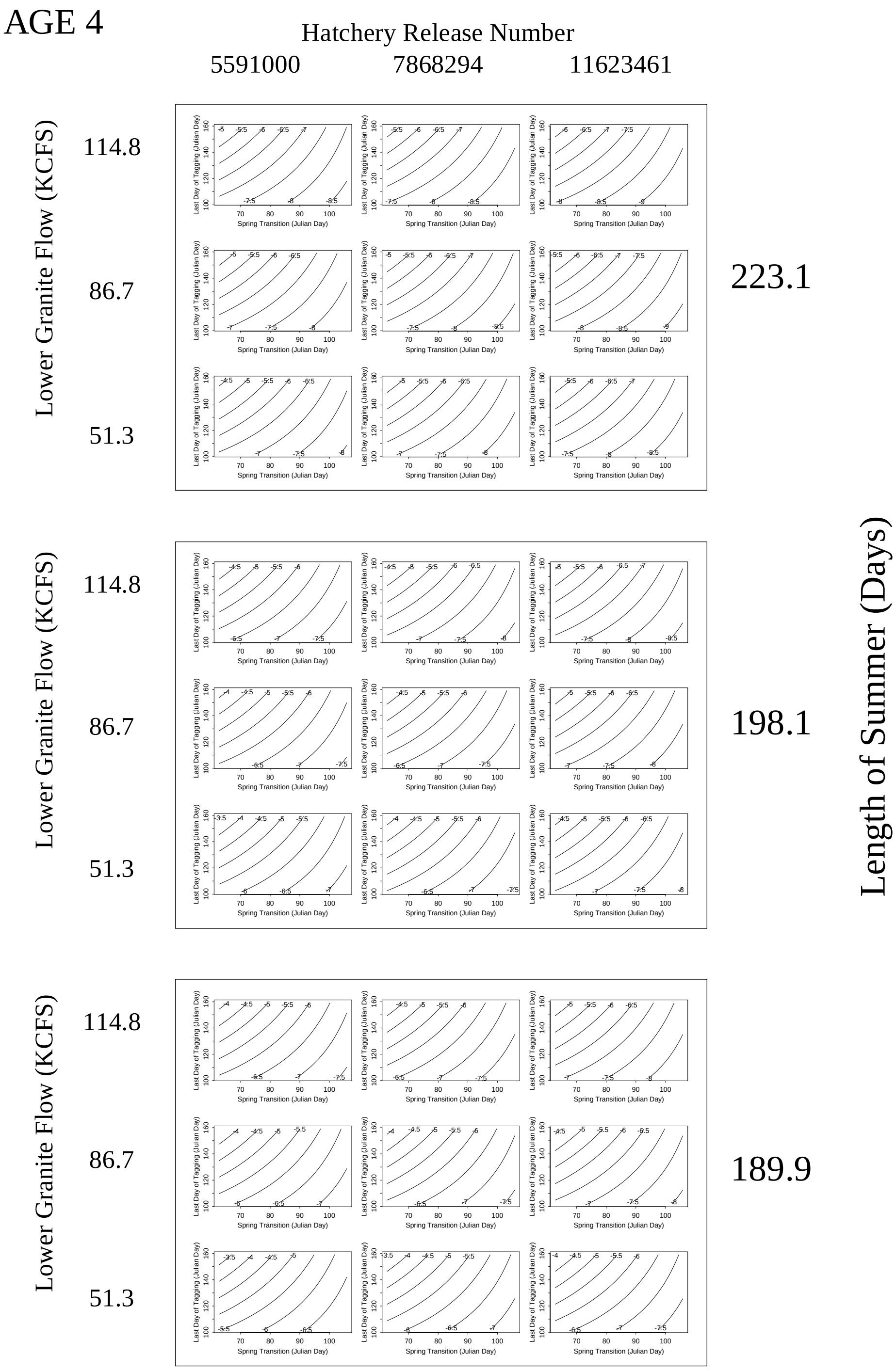

FIGURE C.2 Fitted curve for fish recovered at age 4. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

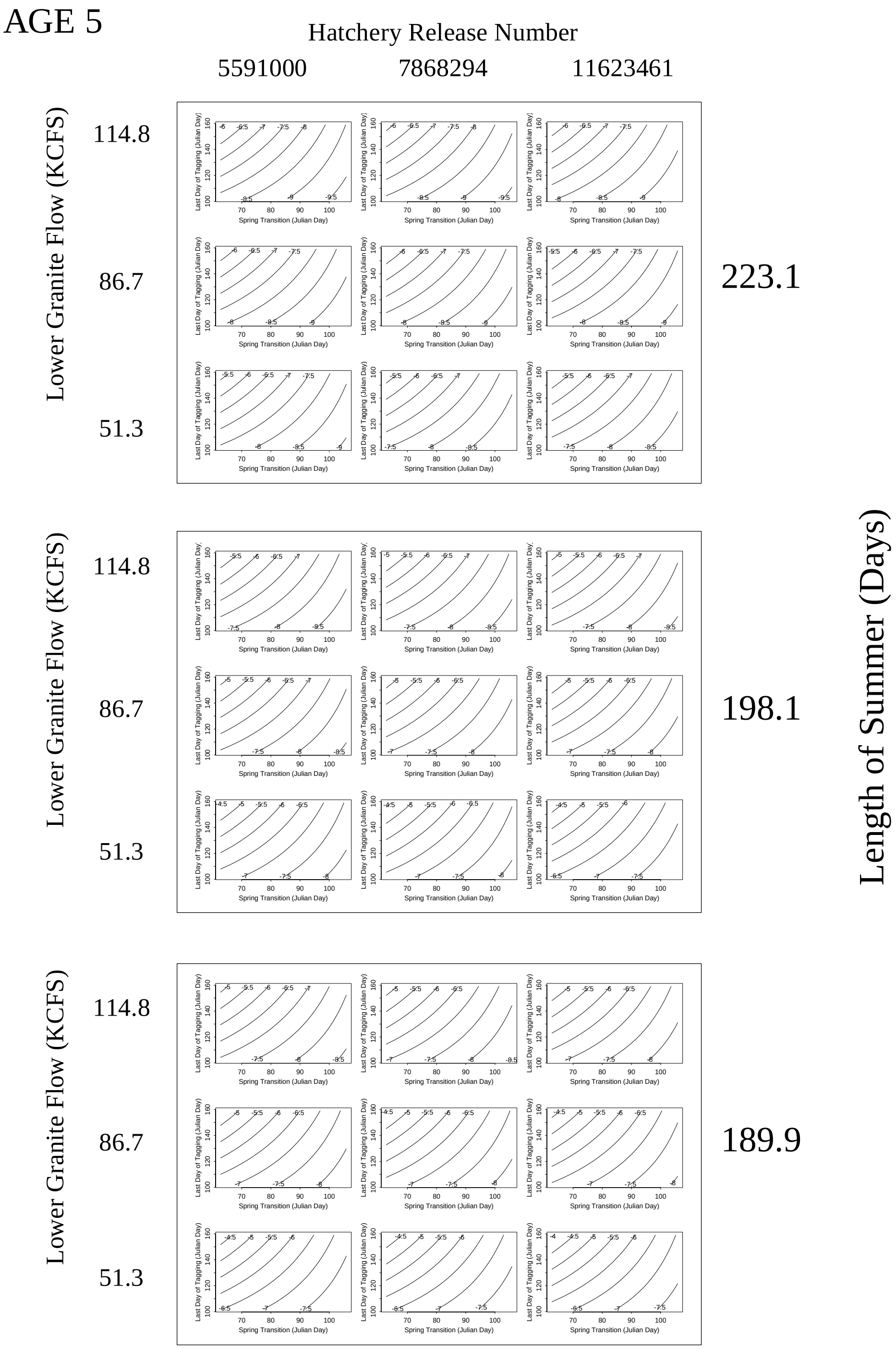

FIGURE C.3 Fitted curve for fish recovered at age 5. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

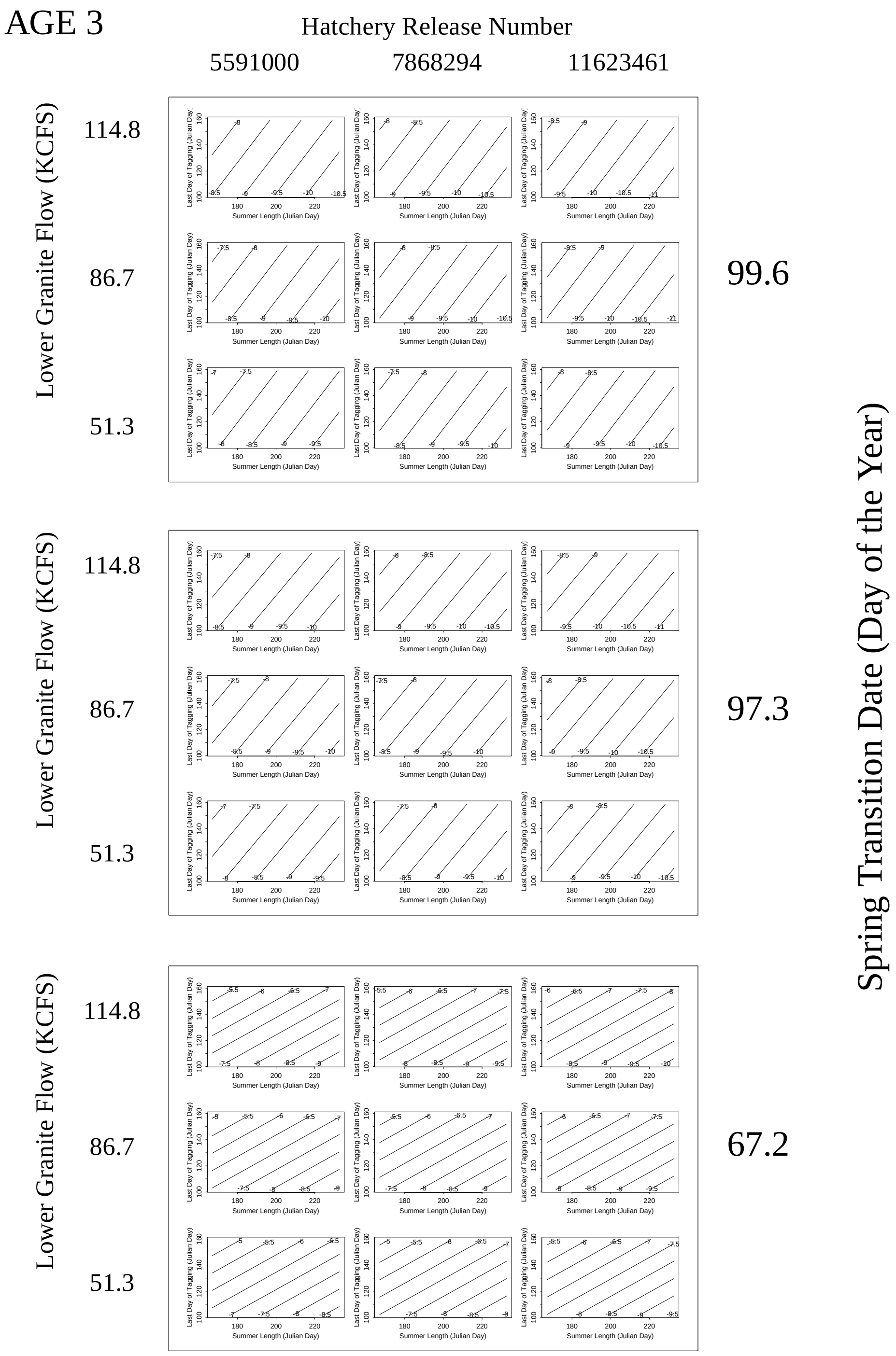

FIGURE C.4 Fitted curve for fish recovered at age 3. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

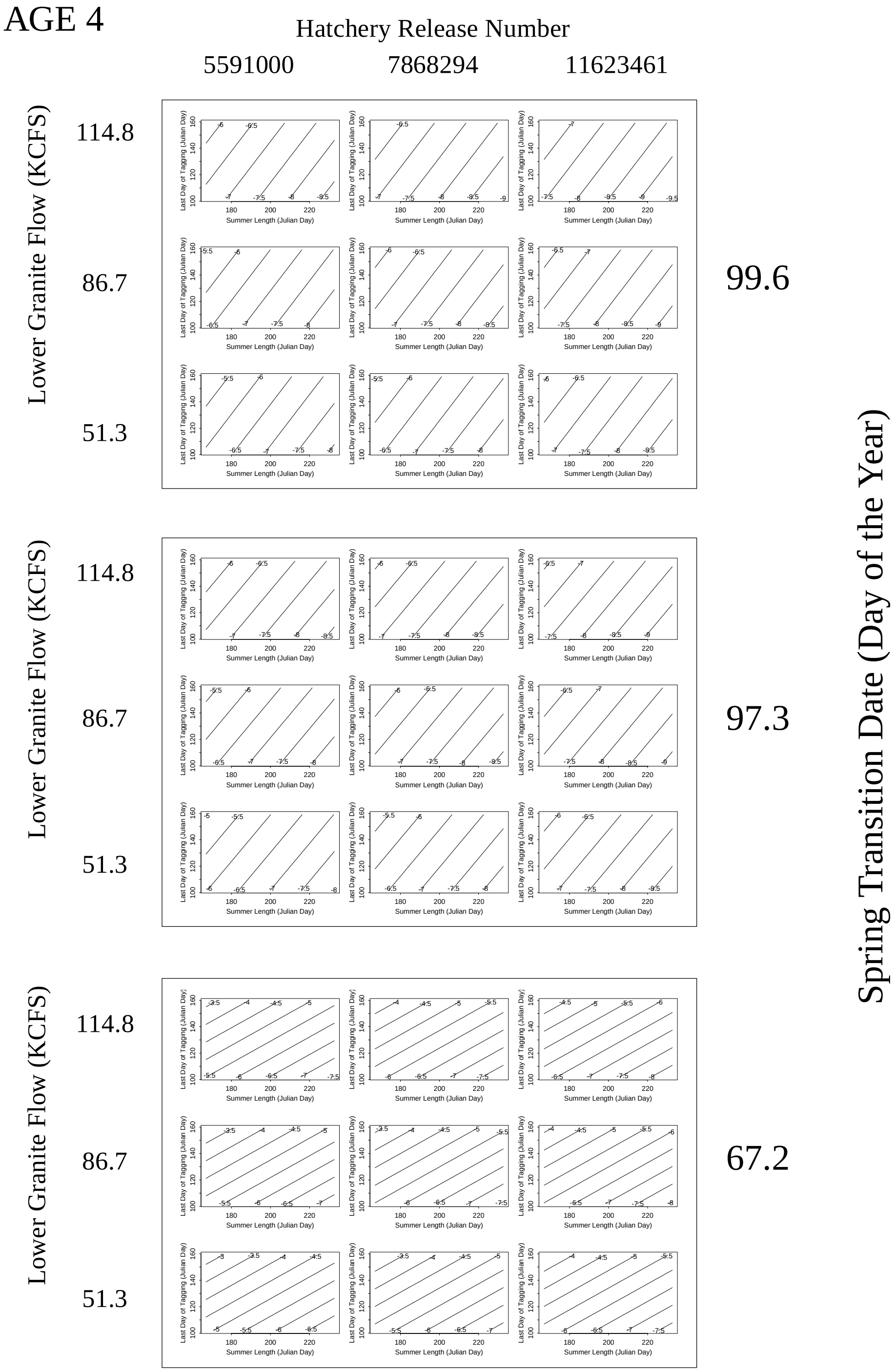

FIGURE C.5 Fitted curve for fish recovered at age 4. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

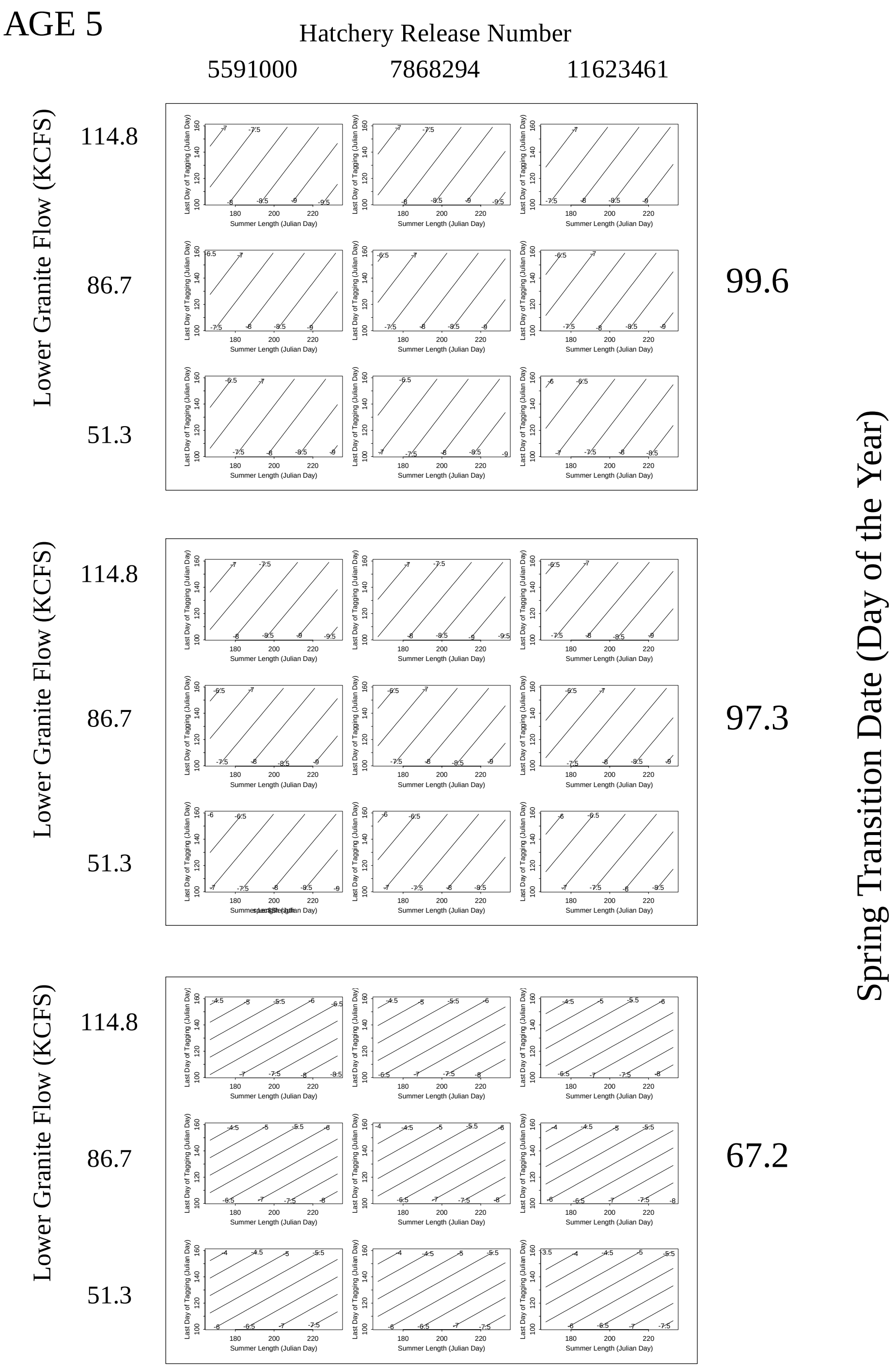

FIGURE C.6 Fitted curve for fish recovered at age 5. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

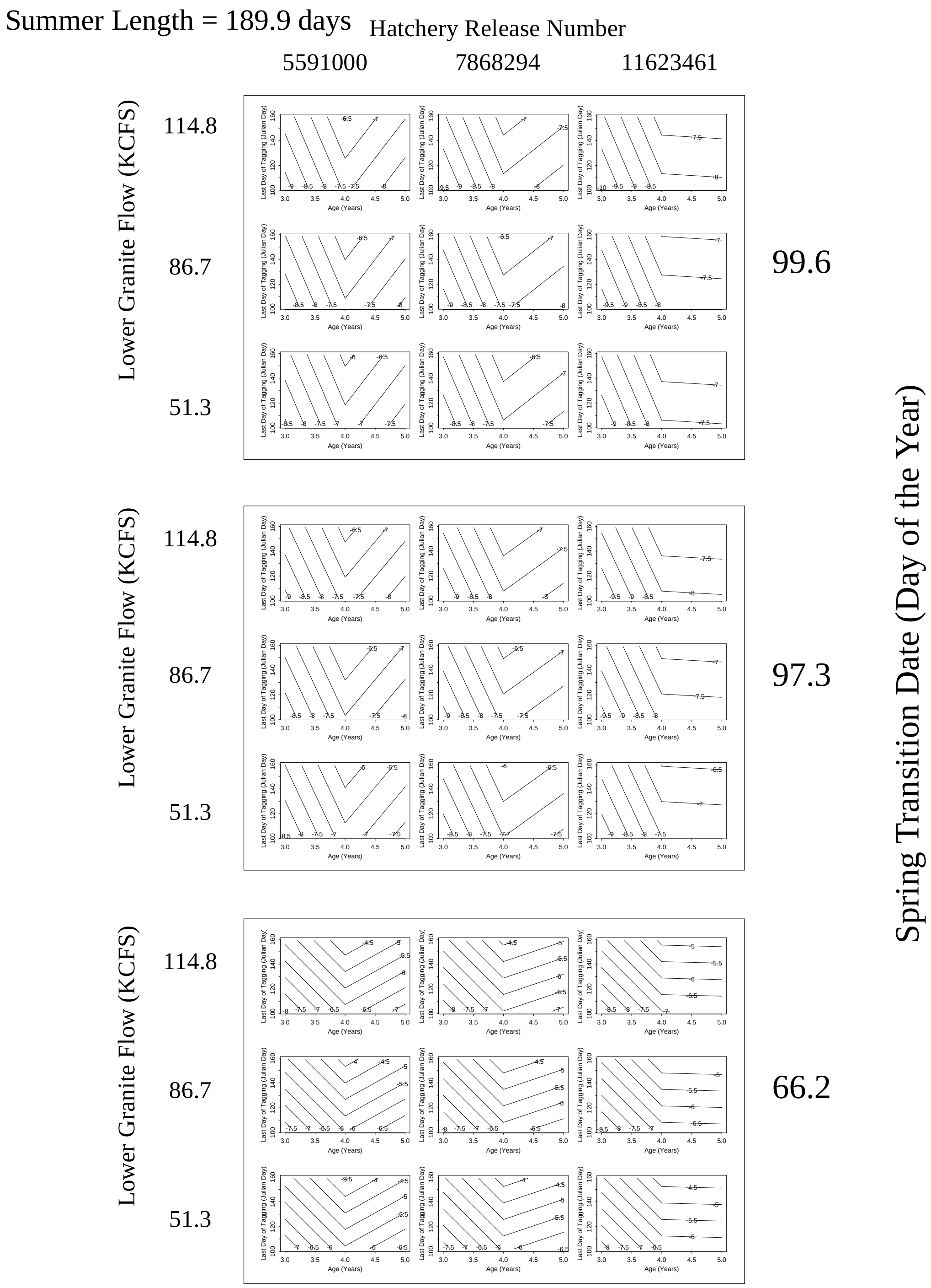

FIGURE C.7 Fitted curve for fish migrating during a summer lasting 189.9 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday*).

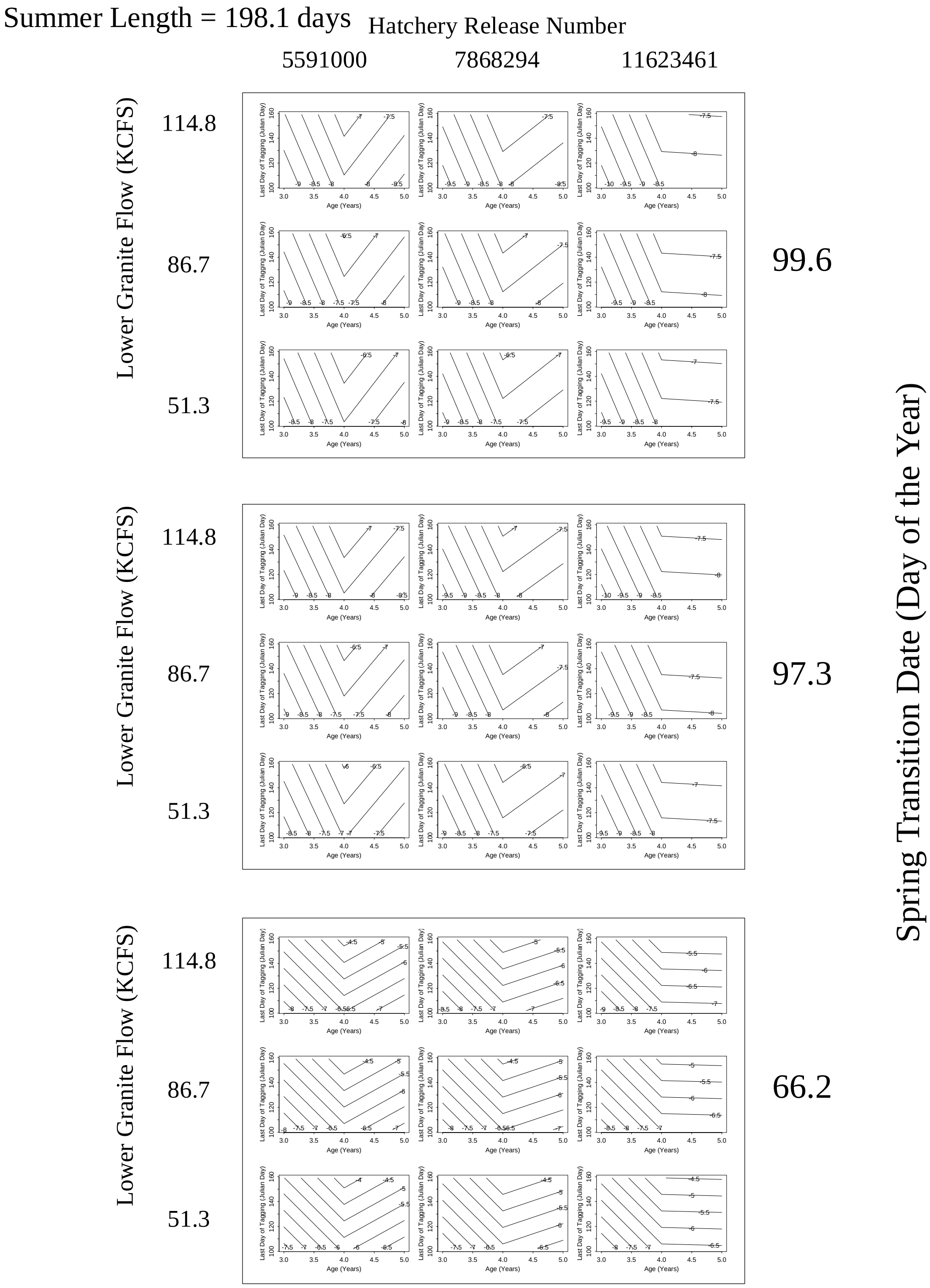

FIGURE C.8 Fitted curve for fish migrating during a summer lasting 198.1 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday*).

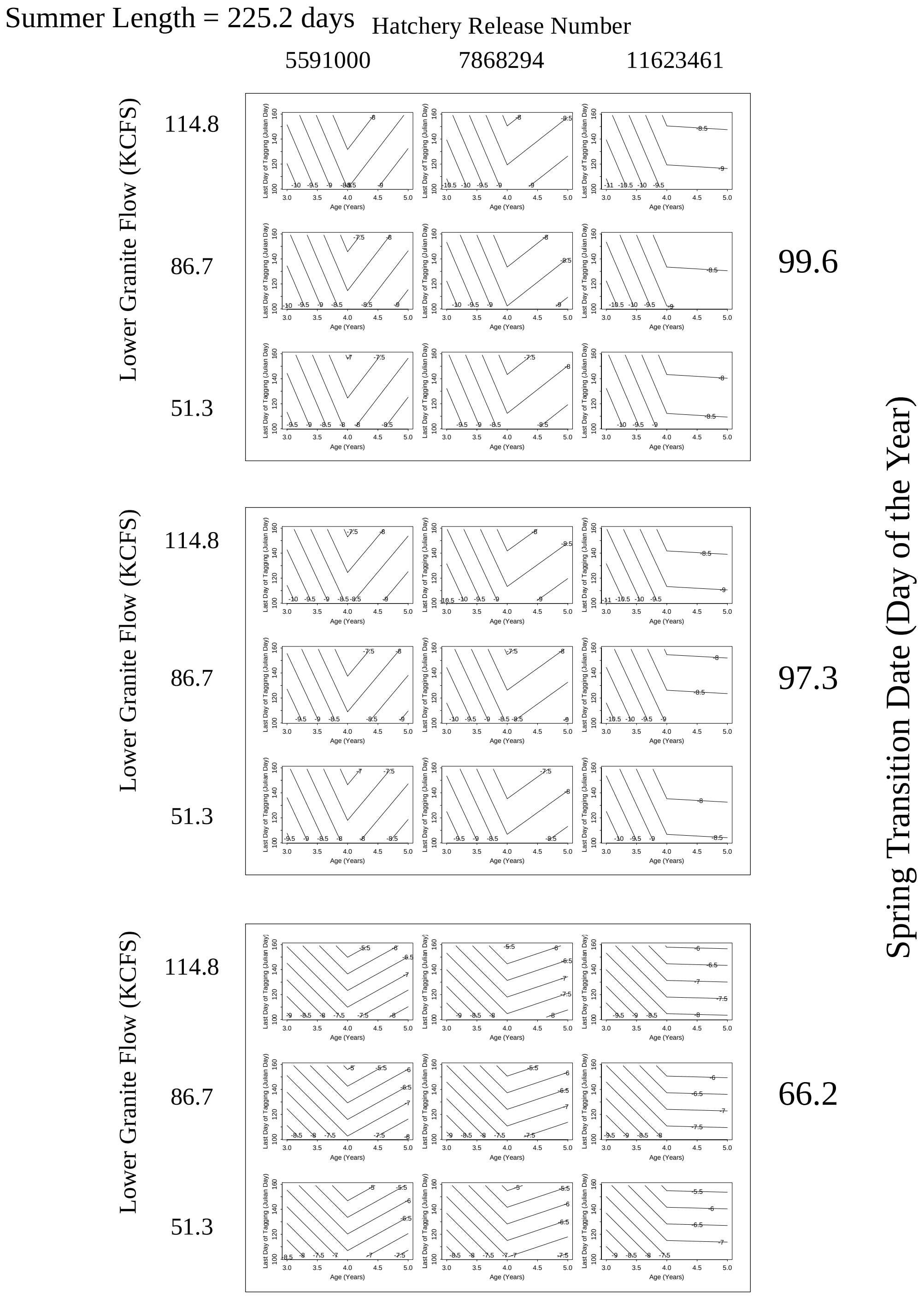

FIGURE C.9 Fitted curve for fish migrating during a summer lasting 225.2 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday*).

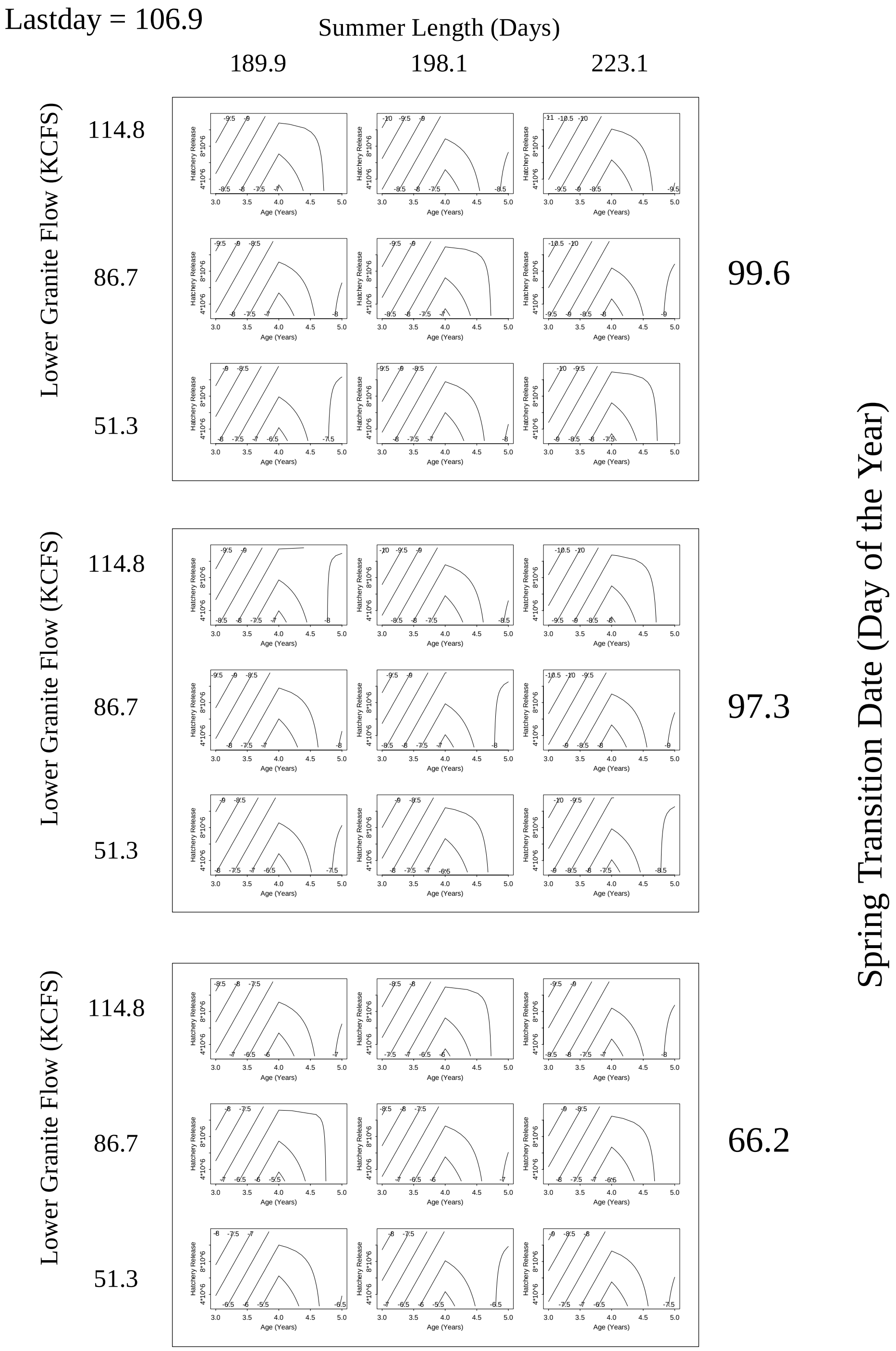

FIGURE C.10 Fitted curve for fish migrating before day of the year 106.9. Each subplot is a contour plot of log(*p*) with axes age (2, 4, or 5 years) and hatchery release number (*Hrelease*).

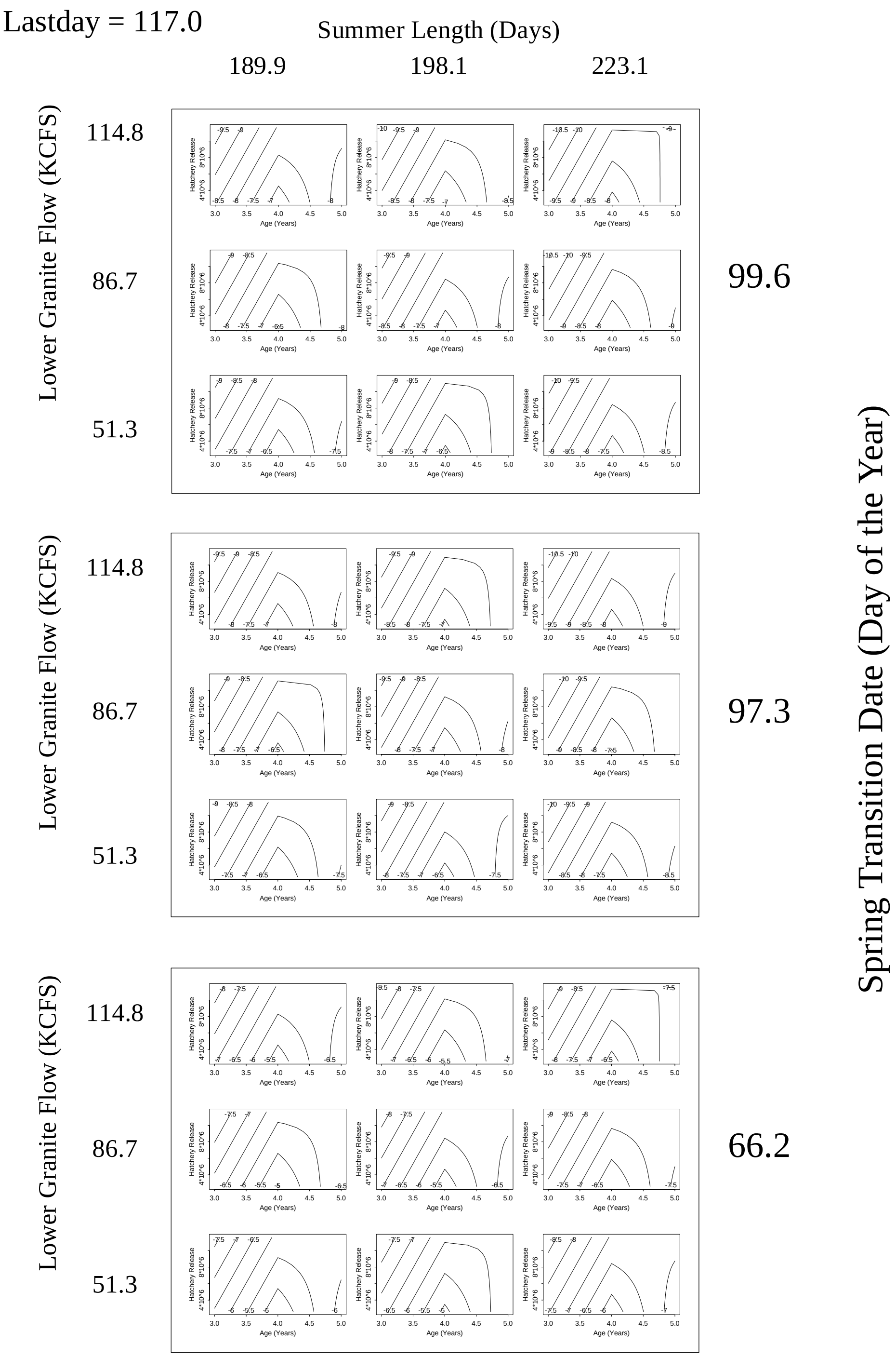

FIGURE C.11 Fitted curve for fish migrating before day of the year 117.0. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and hatchery release number (*Hrelease*).

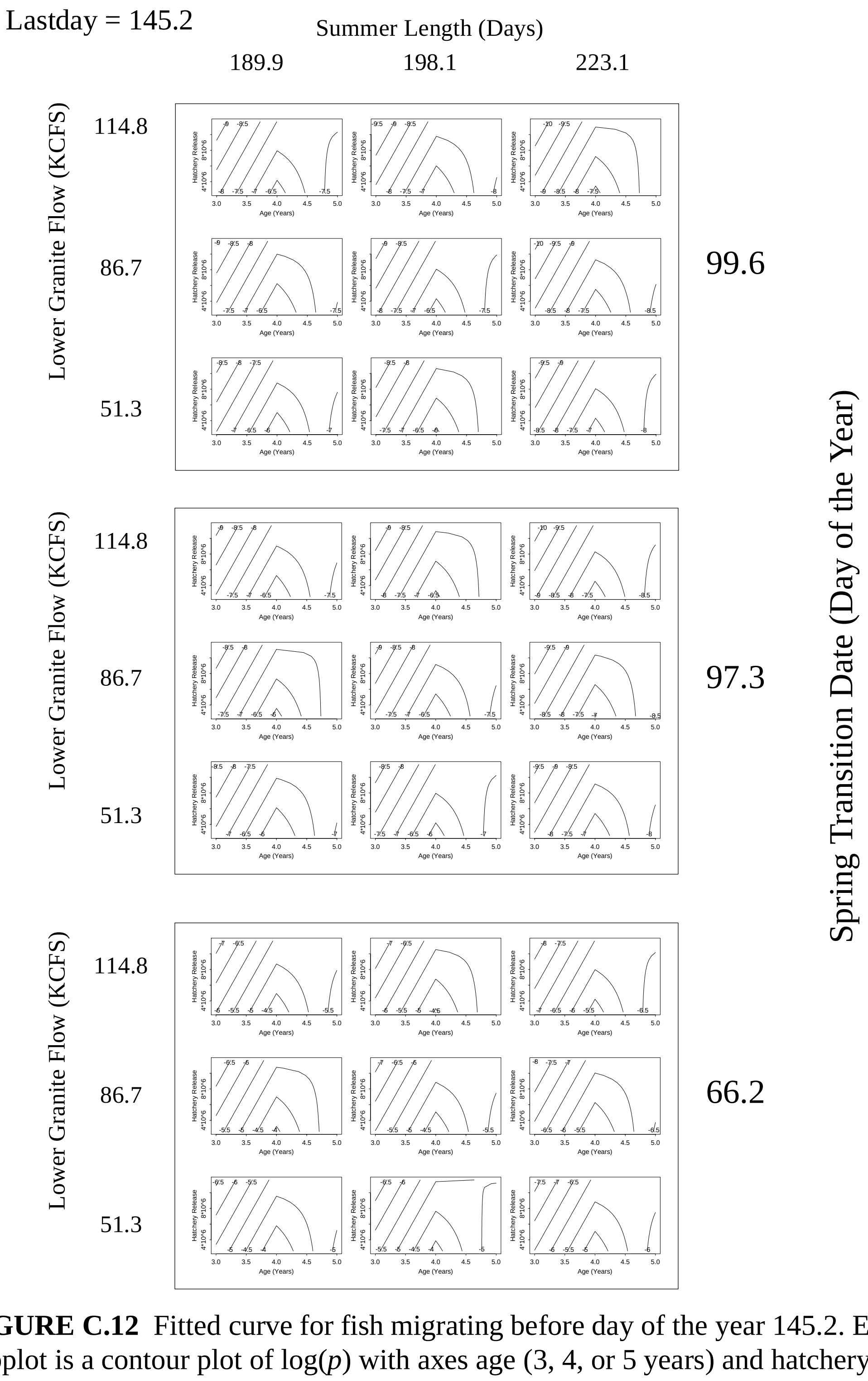

FIGURE C.12 Fitted curve for fish migrating before day of the year 145.2. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and hatchery release number (*Hrelease*).

APPENDIX D: FITTED CURVES FOR *MODEL C*

The following figures demonstrate the effects of the covariates of *Model B* and their interactions. In *Model C*, observations #68, #147, and #150 are omitted from the data set. The fitted curves are on the scale of the linear predictor, $\log(p)$.

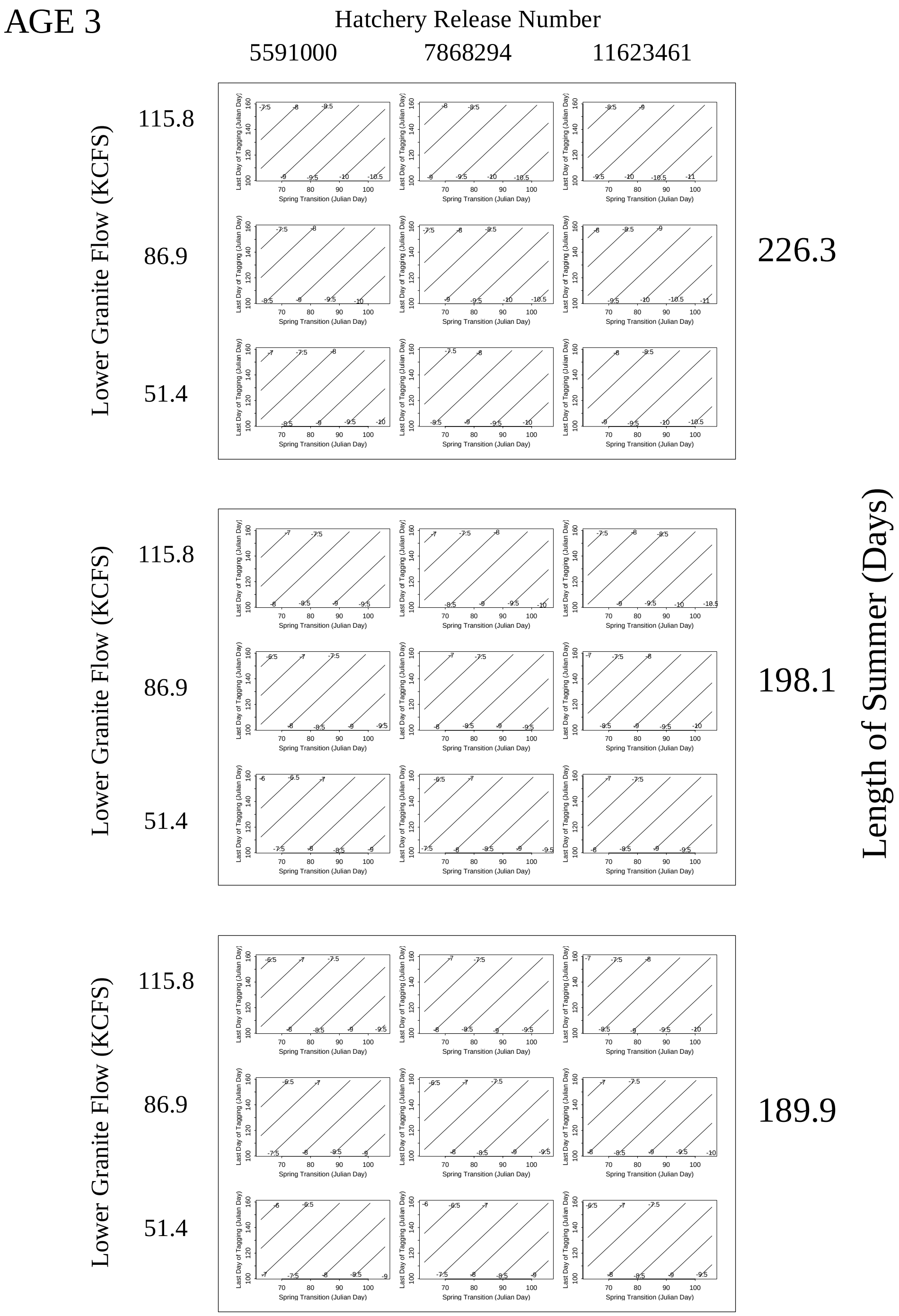

FIGURE D.1 Fitted curve for fish recovered at age 3. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

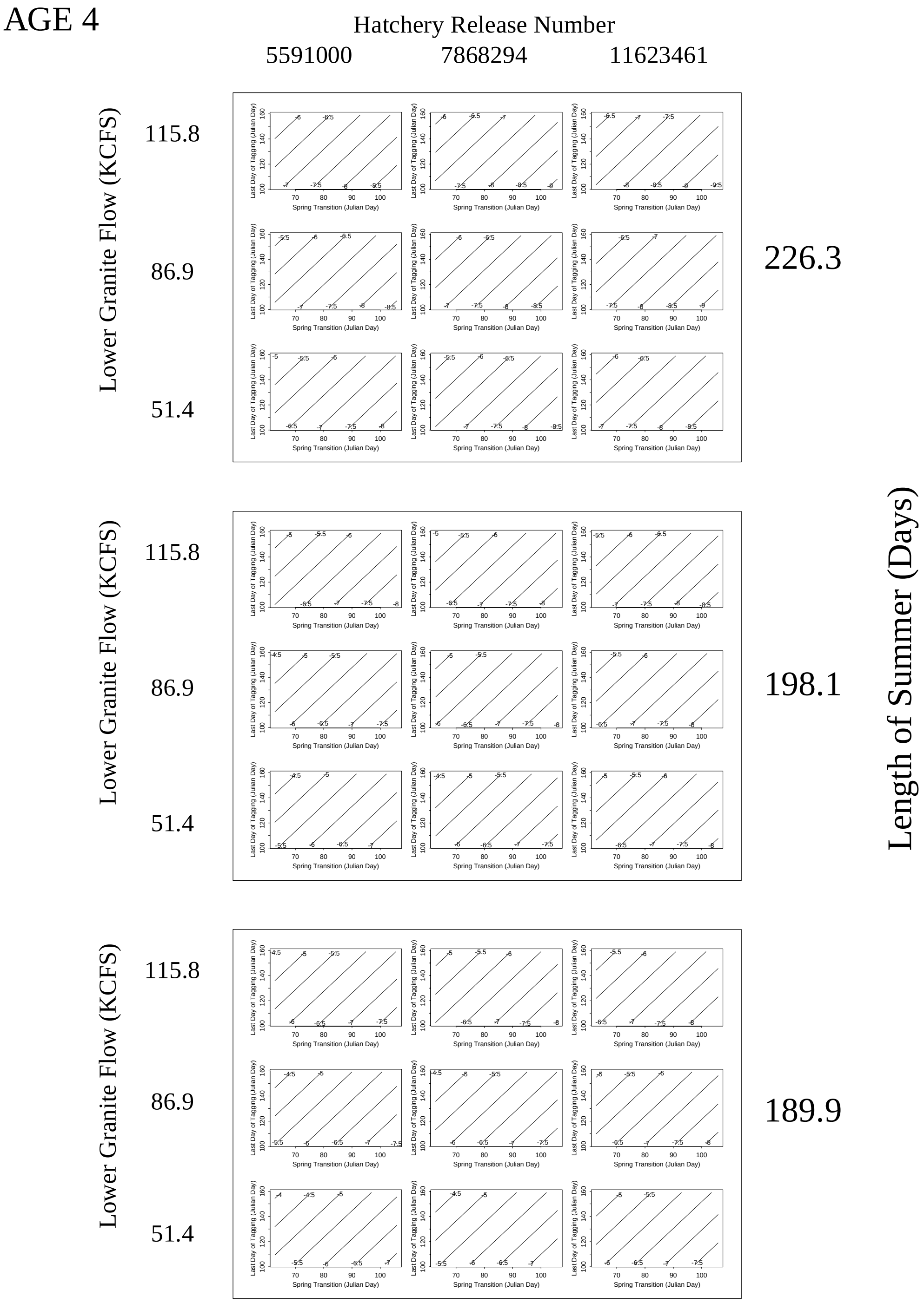

FIGURE D.2 Fitted curve for fish recovered at age 4. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

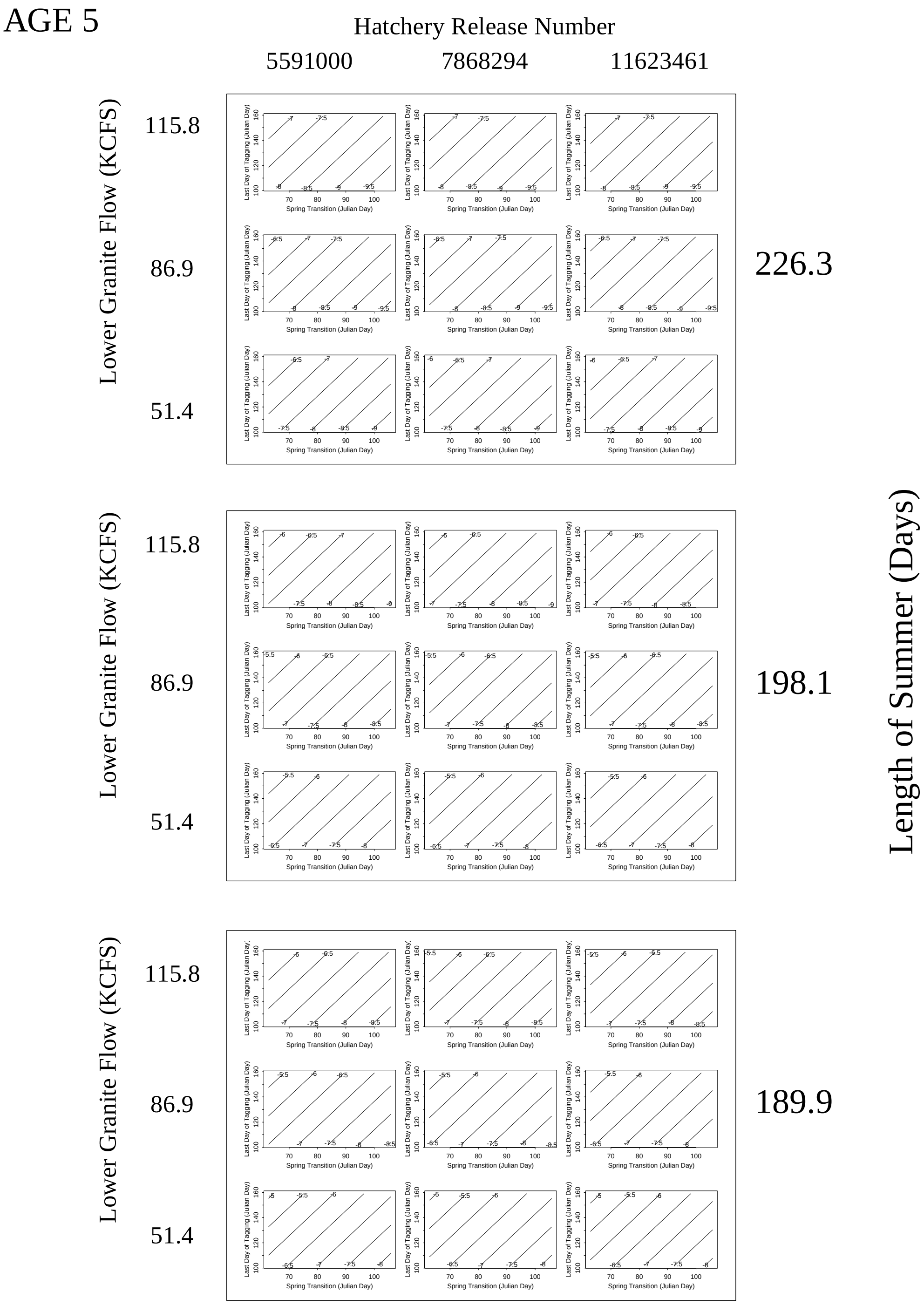

FIGURE D.3 Fitted curve for fish recovered at age 5. Each subplot is a contour plot of log(p) with axes spring transition date (*Strans*) and last day of tagging (*Lastday*).

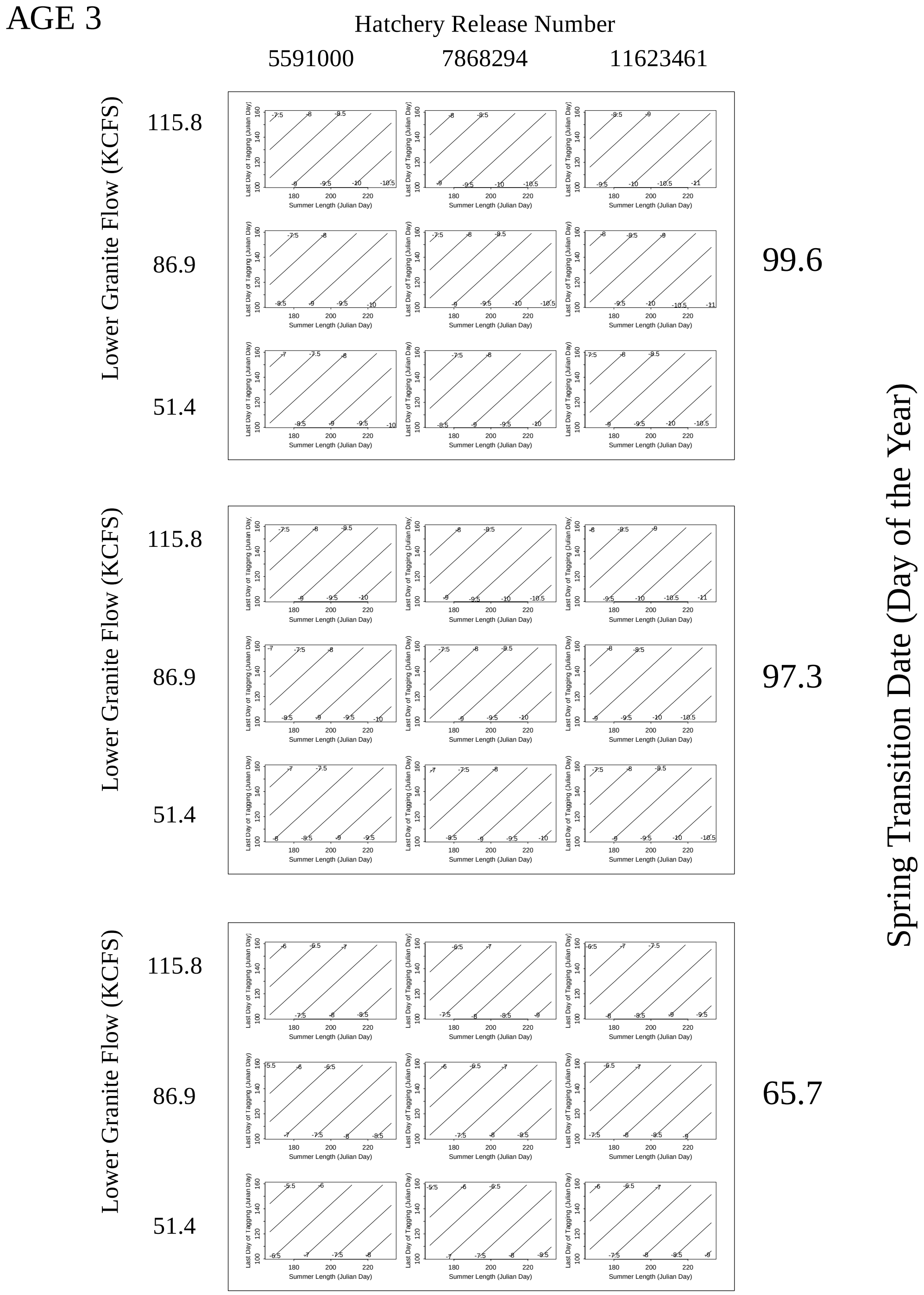

FIGURE D.4 Fitted curve for fish recovered at age 3. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

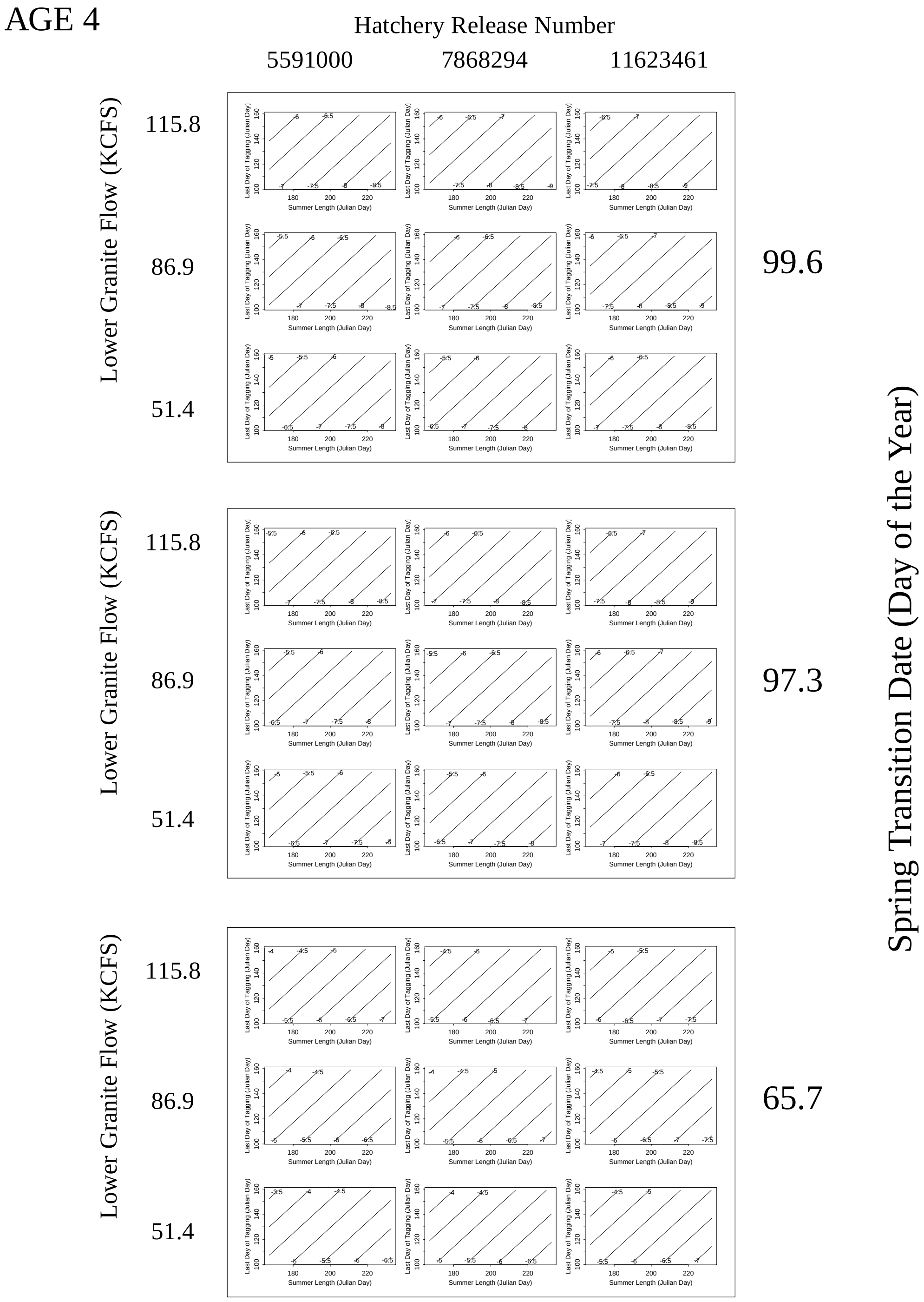

FIGURE D.5 Fitted curve for fish recovered at age 4. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

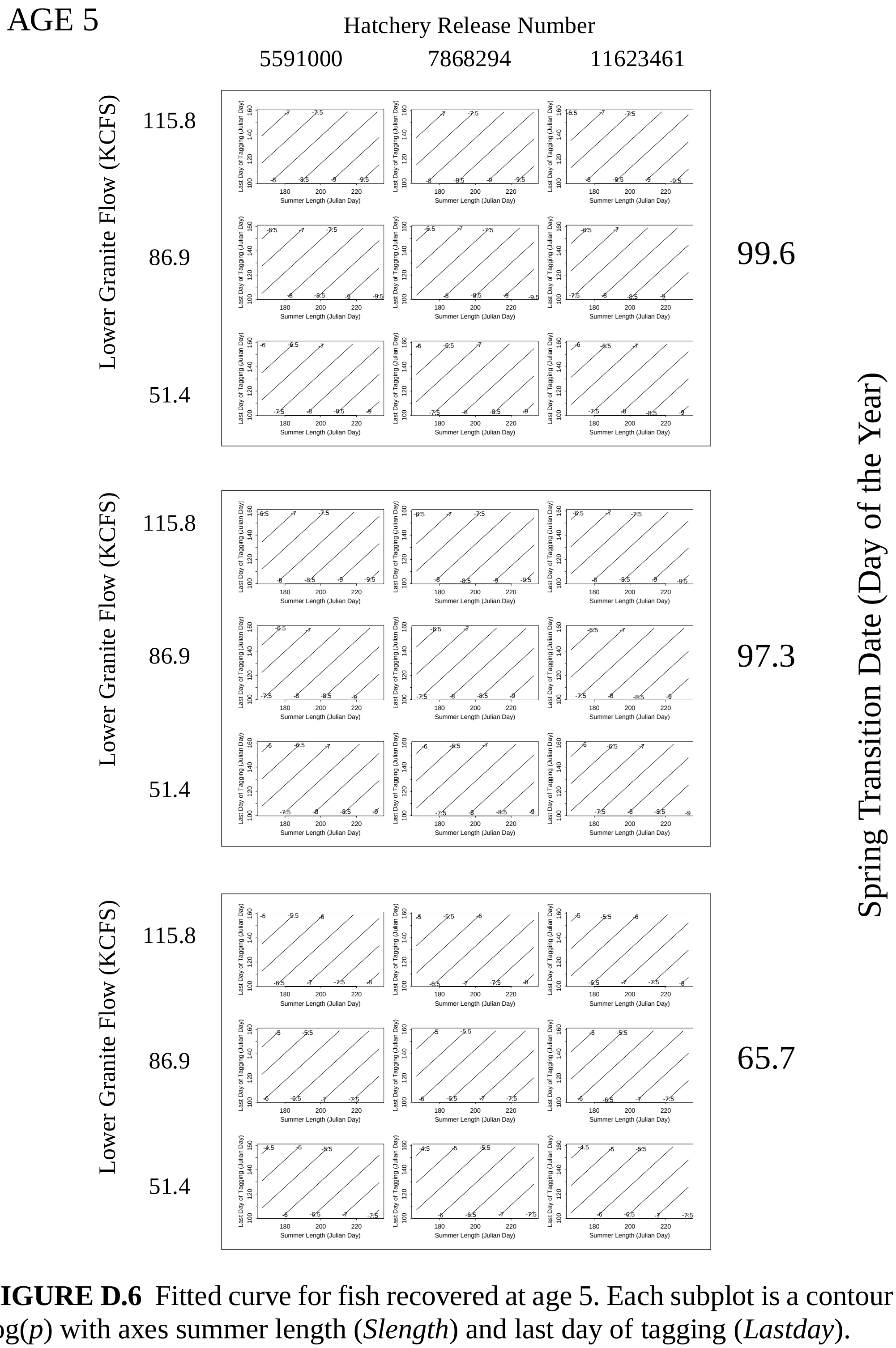

FIGURE D.6 Fitted curve for fish recovered at age 5. Each subplot is a contour plot of log(p) with axes summer length (*Slength*) and last day of tagging (*Lastday*).

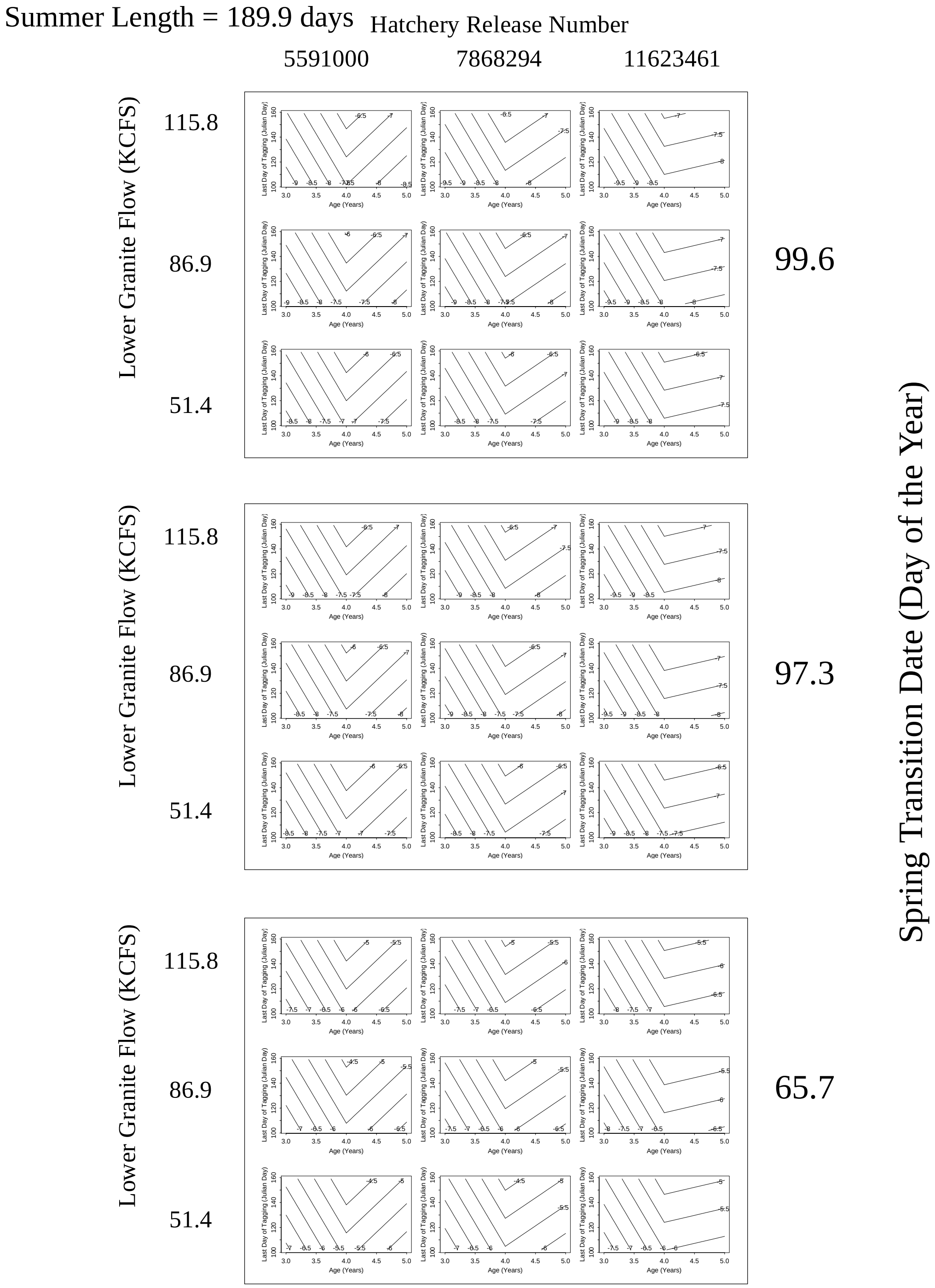

FIGURE D.7 Fitted curve for fish migrating during a summer lasting 189.9 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday*).

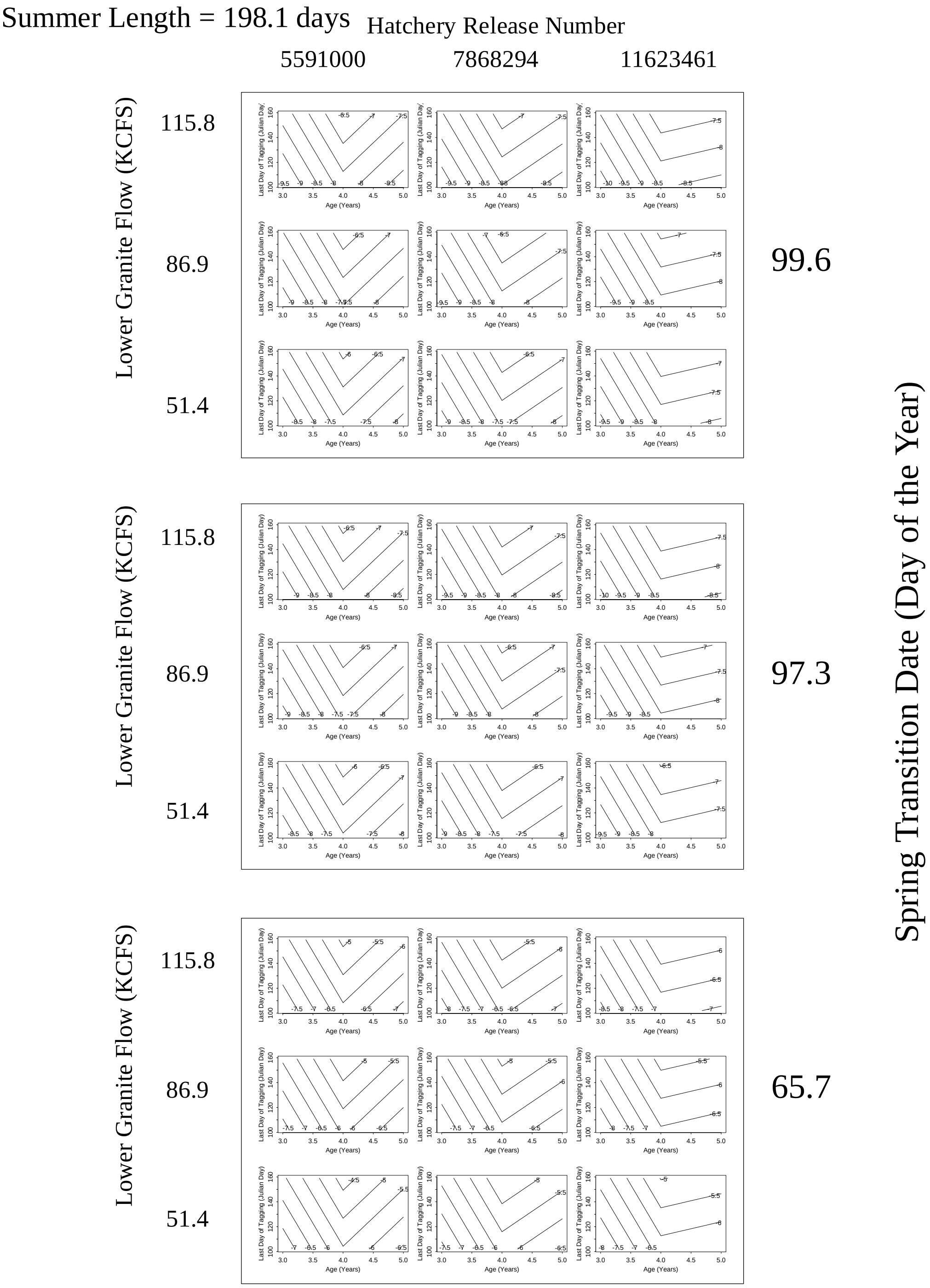

FIGURE D.8 Fitted curve for fish migrating during a summer lasting 198.1 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday*).

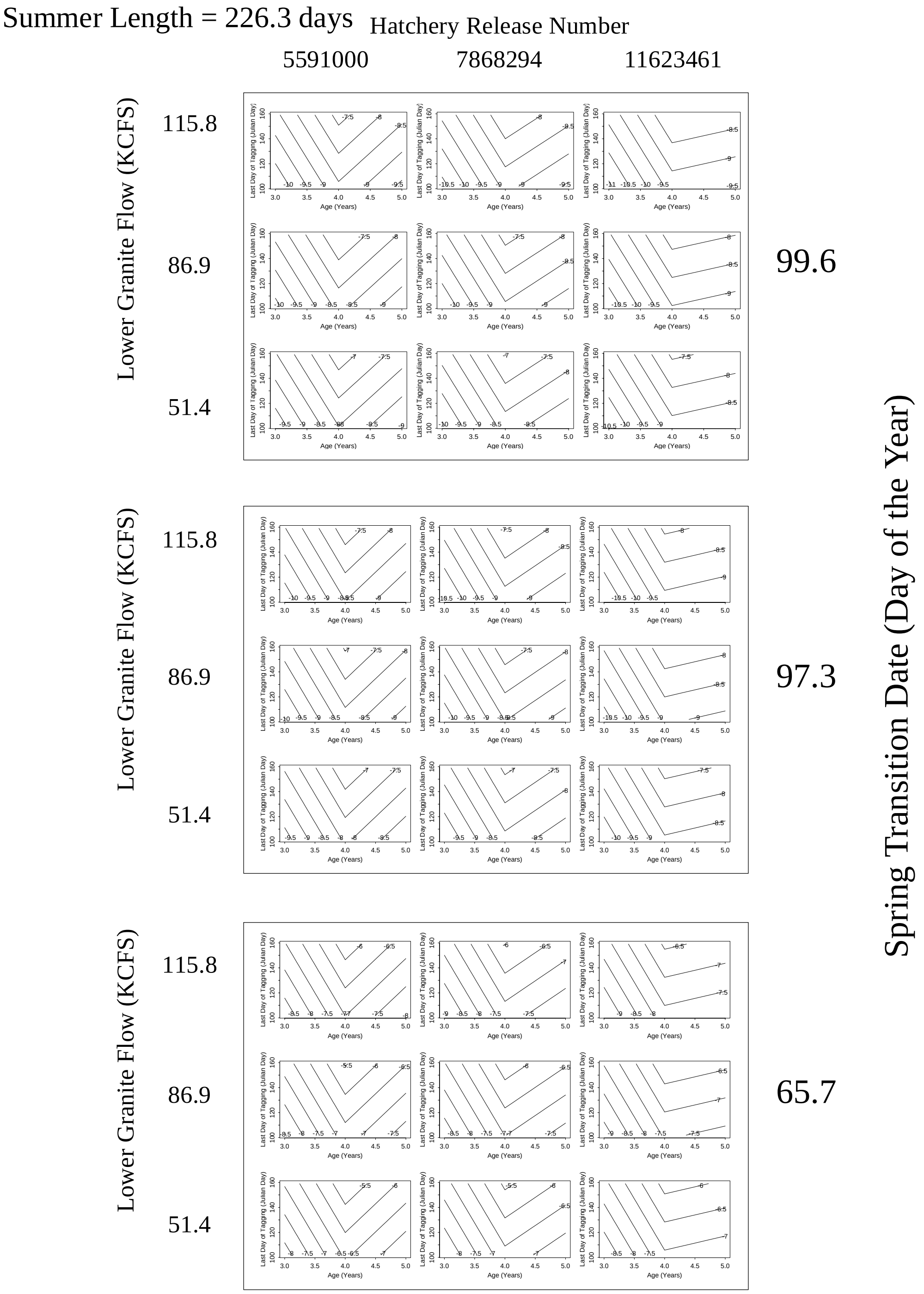

FIGURE D.9 Fitted curve for fish migrating during a summer lasting 226.3 days. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and last day of tagging (*Lastday*).

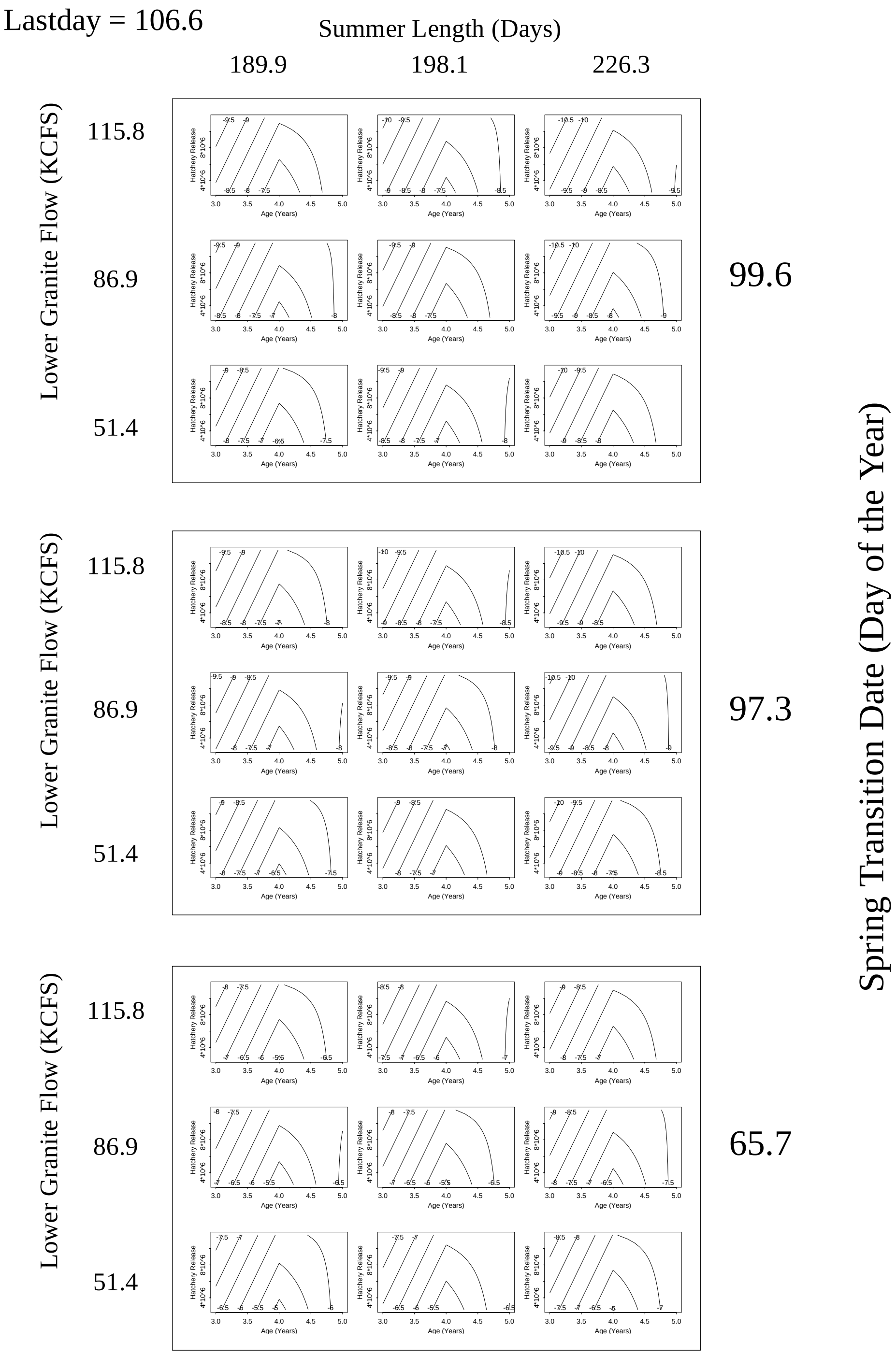

FIGURE D.10 Fitted curve for fish migrating before day of the year 106.6. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and hatchery release number (*Hrelease*).

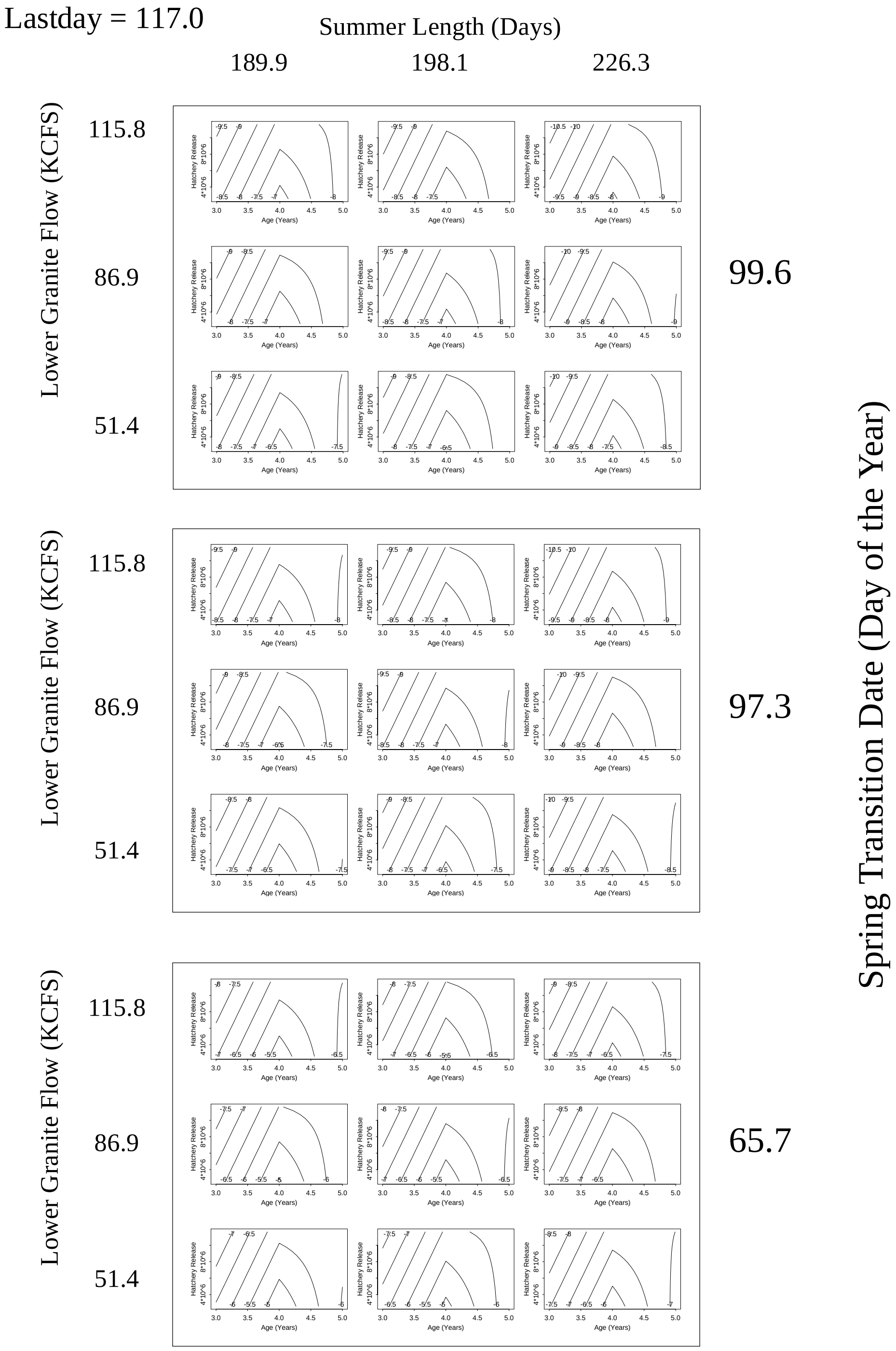

FIGURE D.11 Fitted curve for fish migrating before day of the year 117.0. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and hatchery release number (*Hrelease*).

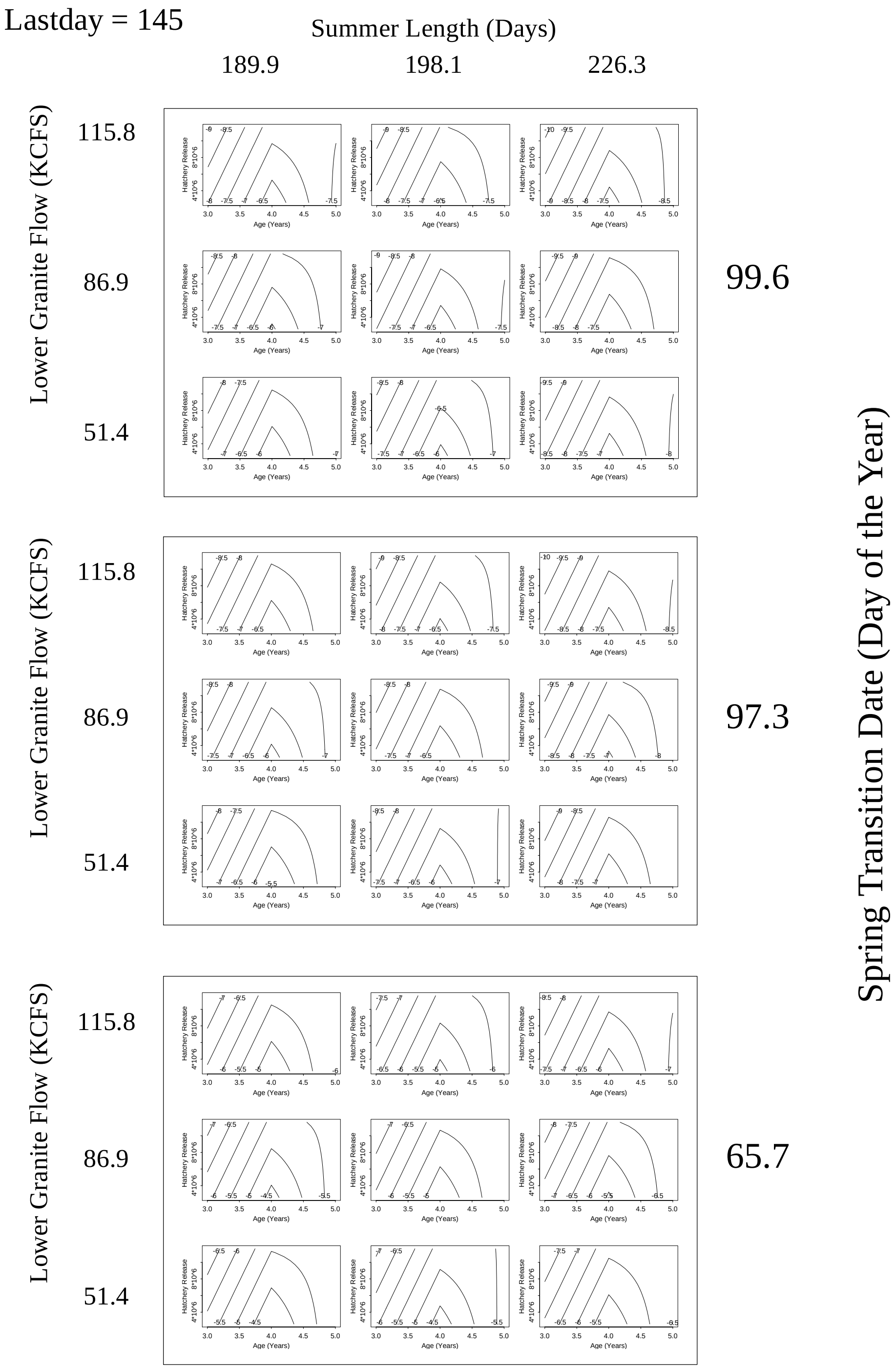

FIGURE D.12 Fitted curve for fish migrating before day of the year 145. Each subplot is a contour plot of log(p) with axes age (3, 4, or 5 years) and hatchery release number (*Hrelease*).