APPENDIX E.
COMPARISON OF SPAWNER-RECRUIT DATA WITH ESTIMATES OF EDT SPAWNER-RECRUIT PERFORMANCE

This chapter was drafted in 2004 and has not been revised for 2010.

APPENDIX E. COMPARISON OF SPAWNER-RECRUIT DATA WITH ESTIMATES OF EDT SPAWNER-RECRUIT PERFORMANCE

Tables

Figures

E.1. Introduction

In the Lower Columbia River tributaries, the Ecosystem Diagnosis and Treatment (EDT) model was used to develop salmon and steelhead population performance goals for the Washington Department of Fish and Wildlife (WDFW), develop the habitat strategy for the Lower Columbia River Fish Recovery Board (LCFRB), and to identify specific habitat restoration projects. The EDT model is habitat based and estimates the expected salmon and steelhead performance in the environment used by these anadromous fish (Lestelle et al. 1996). WDFW rated habitat for the EDT model in Grays River, Skamokawa Creek, Elochoman River, Mill Creek, Abernathy Creek, Germany Creek, Cowlitz River below the Barrier Dam, Toutle River, Coweeman River, Kalama River, North Fork Lewis River below Merwin Dam, East Fork Lewis River, Salmon Creek, Washougal River, Duncan Creek, Hamilton Creek, Hardy Creek, Wind River, and the White Salmon River. This includes thousands of miles of habitat and stream reaches.

Empirical information was not available for all 45 EDT environmental attributes for any reach. For most reaches there was no empirical information available. To estimate the values when no empirical information was available, derived information or expanded information from adjacent or similar reaches was used. Only a limited amount of expert opinion was used for rating current environmental habitats and this occurred for attributes, where there were no quantitative rules (i.e. riparian function and harassment) or for historical information. For a more detailed description of the rationale behind the expansion of empirical information, and the use of derived information and professional judgment see the documentation reports (i.e. Rawding, Glaser, VanderPloeg, and Pittman 2004) or the EDT Stream Reach Editor (SRE) where reach specific data quality and source information is kept. To be consistent between subbasins, the use of expanded and derived information and professional judgment was standardized and comparisons between reaches or subbasins can be made because the data is standardized. This is the underlying assumption behind the development and use of the LCRFB habitat strategy.

In addition to the habitat data, salmon and steelhead life history information is required for the EDT model. For most individual fall Chinook populations, there was information available on adult age structure, sex ratio, and fecundity. However for steelhead data was limited to the Wind, Kalama, and Toutle Rivers. For steelhead, the Kalama River dataset was used as a default when no other information was available because it is the most comprehensive. For chum salmon, less data was available and a common set was combined from many sources. Juvenile life history patterns and ocean survival were standardized from all races and the Columbia River capacity and survival estimates were derived from the Framework Process (Marcot et al. 2002).

The EDT model is a statistical model that explains the performance of salmon and steelhead based on the mechanisms of how salmon move through their environment (MBI 2002). To do this, EDT constructs a working hypothesis for a population within a subbasin based on the model and datasets used to populate the model. Mobrand Biometrics Inc (MBI) suggests three criteria for judging the usefulness of these type of models: 1) its predictions are consistent with observations, 2) it provides a clear and reasonable explanation for the observations, and 3) it provides useful guidance for management and enhancement.

Many models rely on data other than empirical data (ie Bayesian Belief Network). However, the use of non-empirical data has been a specific concern regarding the use of the EDT model in the context of salmon and steelhead recovery. WDFW welcomes the use of empirical information in the EDT model but this data was not always available when constructing the current database. Rather than waiting for more information WDFW has advocated using the “best available science” to move forward toward recovering salmon and steelhead populations that are listed under the Endangered Species Act (ESA). WDFW recommends funding surveys to collect key parameters that drive the model including habitat types, wood, percentage of fines in spawning gravel, bed scour, peak flow, low flow, maximum width, and minimum width.

E.2. Methods

The relationship between stock size and recruitment is a keystone in fishery science, because this function translates into the development of reference points used to set sustainable fisheries, and perform population viability analysis (Hilborn and Walters 1992, Chilcote 2000). However, these data sets are problematic due to environmental variation and observational errors (Hilborn and Walters 1992).

In basins with significant proportions of hatchery spawners, the estimates of spawners and recruits can be very uncertain. For fall Chinook salmon only a small percentage of all the hatchery fish are marked for identification with coded-wire-tags (CWT). To estimate the number of hatchery fall Chinook salmon present in a population, the adults recovered with CWT are expanded by the juvenile or adult tag rate. This expansion often indicates there were more hatchery fish present than total fish present. In addition, hatchery fish may have a different reproductive success in the stream and unless this is known and accounted for the estimate of recruits will be biased. Therefore, streams with significant hatchery populations were excluded from the analysis except for steelhead populations were the reproductive success was estimated (Chiclote at al 1986, Leider et al. 1990, and Hulett et al.1993). These criteria substantially reduced the number of streams to be considered for comparison with EDT.

Observational uncertainty includes measurement and sampling error when estimating the number of spawners and recruits (Francis and Shotton 1997). Spawning escapement estimation methods can be generally categorized as count, mark-recapture, redd counts, and peak count expansion. Counts are direct counts of fish trapped and passed over a weir or barrier. These counting facilities are rare and only a few populations are monitored with direct counts. Counts are assumed to have no sampling or measurement error, and represent the most accurate measure of escapement.

Mark-Recapture (M-R) is used by WDFW at partial barriers to estimate adult summer steelhead abundance using the pooled or stratified Petersen method (Seber 1982 and Arnason et al 1997). Adults are floy tagged and recaptured at upstream traps or “captured” through snorkeling, which is often called mark-resight (Rawding and Cochran 2001a). Juvenile estimates are made using the trap efficiency method (Rawding and Cochran 2001b). For M-R to be accurate the assumptions of the method must be met and WDFW conducts experiments to ensure these assumptions are not being substantially violated. The precision of the estimate is a function of the number of marks and recaptures. In general, WDFW’s goal for precision, is that the 95% confidence interval (CI) to be less than 25% but in many cases they are less than 10%. When the assumptions and precision goals are met, these estimates rank just below direct counts for use in spawner-recruit analysis.

Redd surveys are used for winter steelhead since other methods are not available (Freymond and Foley 1986). Redd counts are a combination of a cumulative count of redds in some tributary reaches, an expansion of supplemental redd surveys, an expansion of average redd density to unsurveyed tributaries, and an Area-Under-the-Curve (AUC) estimate for the mainstem. Only redd survey data from the SF Toutle River is used in this analysis because the valley is open to get accurate AUC counts from a helicopter and tributaries are surveyed frequently enough that population estimates are expanded for only a few reaches.

Peak Count Expansion (PCE) is used for fall Chinook salmon estimates. In these basins, a population estimate was made by tagging Chinook carcasses using the Jolly-Seber (JS) model (Seber 1982). As with the Petersen method, the JS estimate is only valid if the assumptions are met and care is taken to ensure the assumptions were not violated. The PCE factor is developed by comparing the peak count of lives and deads to the total population estimate from carcass tagging. This one time PSE is used to expand previous and future peak counts into a population estimate.

Chum salmon abundance is often estimated using AUC (Ames 1984). Surveyors count the number of live chum salmon spawning and are asked to estimate their "observer efficiency" or the percent of the population they see based on water conditions. The periodic counts are plotted over the course of the season and the number of fish days is estimated by the AUC. The AUC is divided by the average residence time to develop the estimate. Redd counts, PCE, and AUC methodologies are potentially the least precise of the estimates because annual variance estimates are unknown, observation efficiency is varies between surveyors, true observer efficiency estimate is unknown, annual residence time is variable, and the standard residence time from other studies may be slightly different than the actual residence time.

The original EDT model and subsequent datasets focused on ESA listed species, which included chum salmon, Chinook salmon, and steelhead. Coho salmon modeling was not fully funded in the subbasin planning effort due to lack of resources. To fully cover coho salmon, additional reaches need to be added since this species has a preference for small creeks not used by other species. Coho salmon were only fully included in the Elochoman River, and Skamokawa, Mill, Abernathy, Germany, and Salmon Creeks.

For Columbia River tributaries spawner-smolt data is a measure of tributary production and the smolt estimate is the number of smolts leaving the tributary. Recent studies have indicated ten fold changes in ocean variability as measured by smolt to adult survival (NRC 1996 , Rawding 2001, and ODFW unpublished). Spawner-smolt data are less variable than spawner-adult data because spawner-adult data also include assumptions from the Framework about survival conditions in the mainstem and estuary from limited studies (Marcot et al. 2002). For Chinook salmon assumptions about ocean harvest rates are also included. Since there are less assumptions spawner-smolt data is a better measure for ensuring consistency with EDT than spawner-adult data.

One output of the EDT model is a Beverton-Holt (BH) spawner-recruit curve for adults or smolts (Beverton and Holt 1957, Mousalli and Hilborn 1987, and Lestelle et al 1996). To determine if EDT outputs are consistent with observations, EDT spawner-recruit curves will be compared to actual spawner-recruit data. In Table E9-1 and Table E9-2 are the populations with spawner-recruit data used for comparison with the EDT model. These datasets represent the most accurate information available for comparison with EDT model.

Table E9-1 Populations used in comparing the predicted EDT Beverton-Holt Curve with actual spawner and smolt data.

Stock	Escapement	Recruits	Age	Comments
Trout Cr	Weir Count	M-R at trap	scales	Some years adjustment when trap not operational and hatchery fish present
Wind R.	M-R at trap	M-R at trap	scales	One year juvenile scale data missing and adjustment for hatchery reproductive success to smolt stage
Cedar	M-R at trap	M-R at trap	All age 2	adjustment for hatchery reproductive success to smolt stage

Table E9-2. Populations used in comparing the predicted EDT Beverton-Holt Curve with actual spawner and adult recruit data.

Stock	Escapement	Recruits	Age	Comments
Washougal Summer steelhead	Mark-Resight snorkel survey	Same as escapement plus CRC & C&R estimate.	Use Kalama Scales	Used current estimates of snorkel efficiency from M-R estimates to adjust historical counts
Kalama Steelhead – summer & winter populations combined	Mark-Resight snorkel survey for summers and weir count for winters	Same as escapement plus CRC & C&R estimate.	Scales	Used estimates of successful jumpers and snorkel efficiency from M-R estimates to adjust historical counts
Wind River Summer Steelhead	Mark-Resight snorkel survey	Same as escapement plus CRC & C&R estimate.	Scales used avg for some years	Used current estimates of snorkel efficiency from M-R estimates to adjust historical counts
SF Toutle Winter Steelhead	Redd survey	Same as escapement plus CRC & C&R estimate.	Use Kalama Scales	
NF Toutle Winter Steelhead	Weir Count	Same as escapement but no fishery	Scales	
Coweeman Fall Chinook	Carcass Tagging Expansion	Same as escapement but Cowlitz CWT used to estimate fishery	Scales	
EF Lewis Fall Chinook	Carcass Tagging Expansion	Same as escapement but Cowlitz CWT used to estimate fishery	Scales	
NF Lewis Fall Chinook	Carcass Tagging Expansion	Same as escapement but Lewis wild CWT used to estimate fishery	Scales	
Grays River Chum Salmon	Carcass Tagging Expansion and AUC	Assume no fishery	Scales	

The EDT datasets were populated by WDFW and run on the MBI website (http://www.mobrand.com/edt). Results from the website were provided in "Report 1" , which provided an estimate of productivity and capacity for the BH spawner curves for adults and juveniles. The EDT model is deterministic and provides no estimates of uncertainty. The observed spawner-recruit data was fit to the same BH model used by EDT using maximum likelihood estimation (MLE) and assuming lognormal error Hilborn and Waters 1992).

$$R = (\alpha S / (1+ \alpha S/\beta)) * e^{\varepsilon t} \qquad (1)$$

Where:

R = the number of recruits measured as adults or smolts
S = the number of spawners
α = the intrinsic productivity of the stock, and
β = the freshwater carrying capacity of the stock
$^{\varepsilon t}$ = a normal distributed random variable ($N(0,\sigma)$)

A non-linear search over α, β, and σ was used to minimize the negative log-likelihood and estimate the parameters. A two-dimensional confidence interval on α and β was estimated using a likelihood profile by search over all values that provided a likelihood within a specified range of the negative log-likelihood (Hudson 1971, Hilborn and Mangel 1997). To estimate a 95% confidence region, a chi-squared distribution with two degrees of freedom was used to contour all negative likelihood values three greater than minimum value. The 95% confidence contour created an ellipse with a negative correlation between α and β. If the EDT point estimate of α, β was within the 95% confidence region from the spawner-recruit data, there was no significant difference between the two model estimates.

E.3. Results and Discussion

A comparison of EDT generated spawner-recruit curves with the spawner-recruit curves generated from the data was considered. To estimate a spawner recruit relationship from the data Hilborn and Walters (1992) recommend that: 1) data used in spawner-recruit analysis have low measurement error due to the destructive relationship of measurement error on these curves (Ludwig and Walters 1981), 2) the relation be examined for time series bias especially due to auto-correlated environmental events (Hilborn and Starr 1984), 3) the data be non-stationary due to variability in ocean regimes (Hare and Francis 1994) with productive periods (pre-1977 and post 1999) and an unproductive period in between, and 4) the data have sufficient contrast to determine the relationship. If data meet the recommendations and a spawner-recruit curve was generated than a comparison could be developed comparing the fit the EDT and data derived curves. Most of the data sets are too sparse or provide insufficient contrast for direct comparisons. Therefore, the EDT model was said to have a good fit if the predicted BH curve ran through the observed data and if the point estimates (α, β) from the EDT model fell within the 95% confidence region from MLE of these same parameters from the observed data.

EDT model was designed to predict average performance, as measured by smolt and adult productivity, capacity, and abundance, of the modeled population over specified environmental conditions. Spawner-smolt estimates are more likely to reflect average environmental conditions due to less environmental variation in freshwater (Cramer 2000). A comparison of EDT spawner-smolt curves to the three steelhead spawner-smolt datasets is found in Figure E9-1 and Figure E9-2. The EDT curves passes through the individual data points reasonably well for all data sets. The point estimate (α, β), depicted by a white sun in the graphs, from the EDT analysis is within the 95% contour from the spawner-recruit data. Based on population monitoring protocols, these datasets are the best datasets to compare to the EDT model.

The adult steelhead comparisons are found in Figure E9-2 (Figure E9-3, and Figure E9-4). While the Wind River smolt dataset compared favorably with the EDT output, the adult dataset does not (Figure E9-2). This is due to the relatively recent adult dataset, that was collected primarily during an unproductive ocean regime during the late 1980's and 1990's. Recent returns, which are not included in the dataset because the full brood year has not returned, indicate the new spawner recruit data will fall at or above the EDT line.

Figure E9-3 contains the winter steelhead populations within the Toutle subbasin. The EDT performance estimate for the North Fork Toutle River above the Sediment Retention Structure (SRS) is outside the 95% confidence interval. The EDT analysis indicated that all steelhead production occurs in the tributaries and production from the mainstem Toutle River above the SRS is not possible due to sediment still working its way downstream after the eruption of Mt. St. Helens. The EDT model indicates that steelhead are very sensitive to sediment concentrations near the levels modeled in the Toutle subbasin. A slight change in the mainstem rating would increase steelhead capacity and the mainstem and the EDT point estimate would fall within the 95% contour.

The SF Toutle River had less sediment and recovered more rapidly after the eruption of Mt. St. Helens than the NF Toutle River. This dataset begins in the mid-1980's and has continued to the present. It exhibits a high level of variation due to favorable ocean conditions in the mid-1980s and unfavorable conditions through the rest of the period. The EDT estimate falls within the center of the 95% confidence region (Figure E9-3).

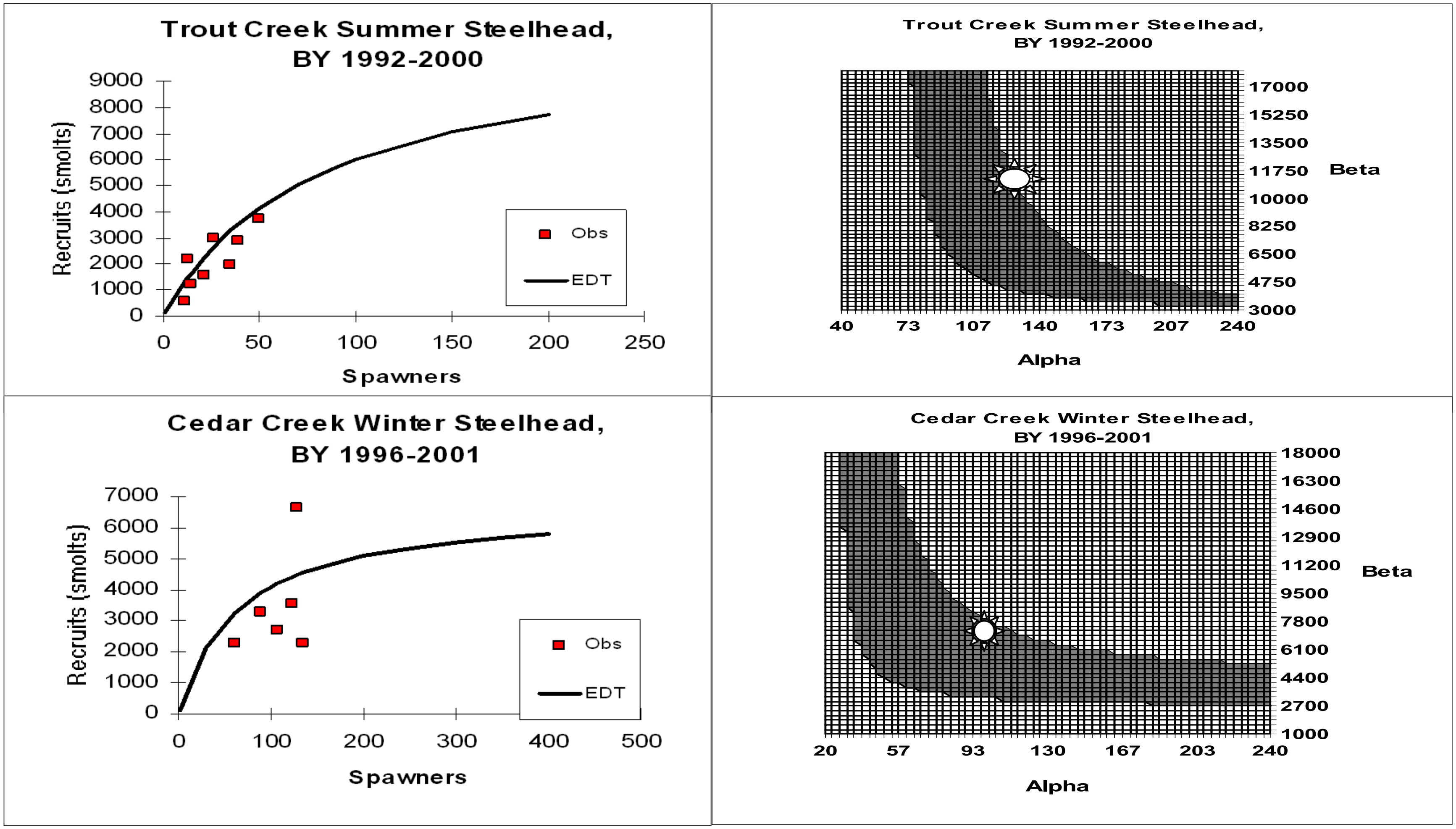

Figure E9-1. Comparison of EDT estimates of the Beverton-Holt spawner curve (solid line) with observed data (red squares) and the 95% confidence region determined by maximum likelihood analysis (dark grey pattern) compared to the EDT (α, β) point estimate (white sun).

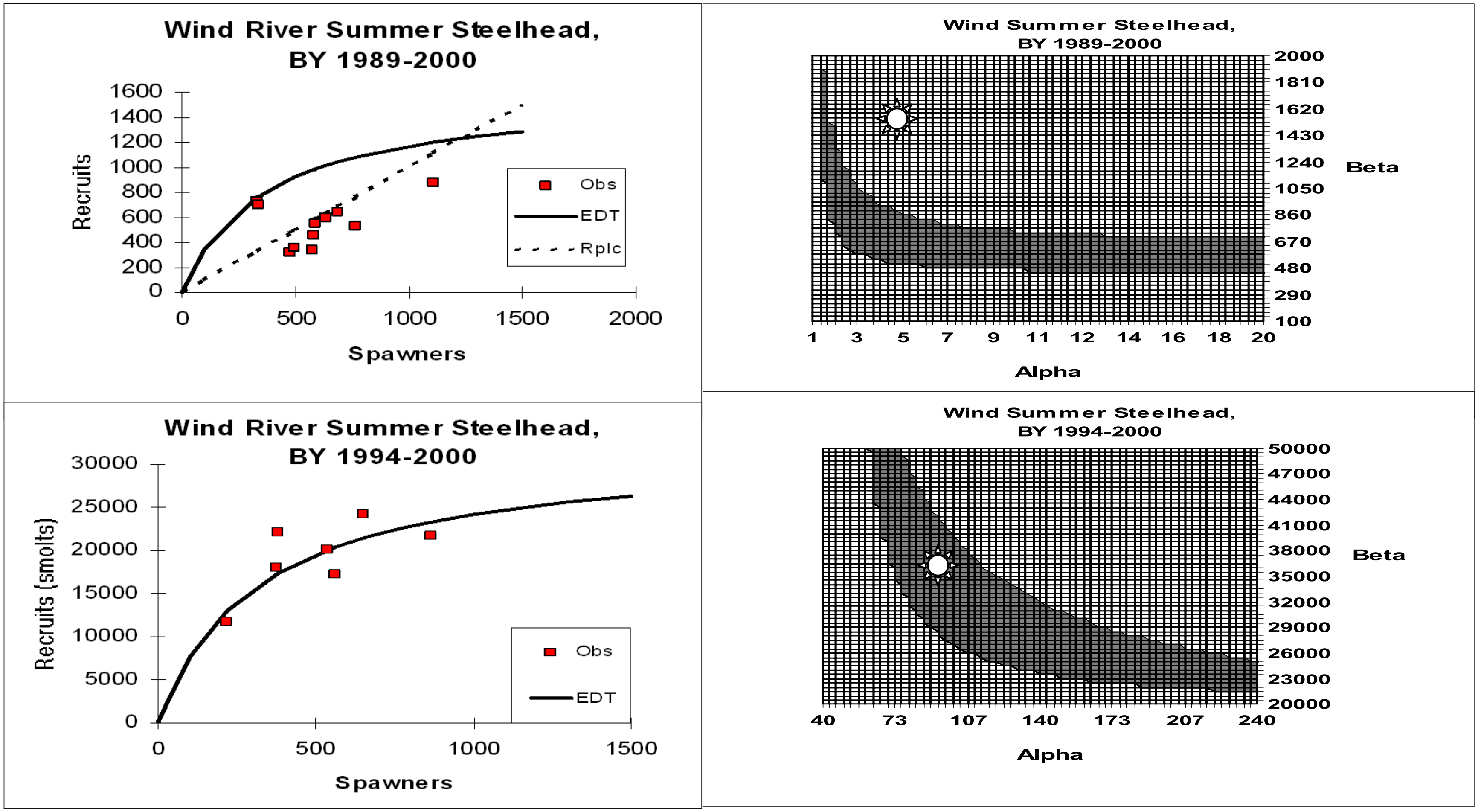

Figure E9-2. Comparison of EDT estimates of the Beverton-Holt spawner curve (solid line) with observed data (red squares) and the 95% confidence region determined by maximum likelihood analysis (dark grey pattern) compared to the EDT (α, β) point estimate (white sun).

Figure E9-4 contains the two longest steelhead datasets from the Washougal and Kalama Rivers. Both summer and winter steelhead are passed above Kalama Falls Hatchery (KFH). Since the exact spawning and rearing distribution of both races is unknown, a generic EDT steelhead population was modeled. Both wild and hatchery steelhead have been passed above KFH. The relative fitness of hatchery steelhead in the Kalama River is less than wild steelhead (Leider et al. 1990 and Hulett et al. 1996). Specific brood year data was used to reduce the effectiveness of hatchery spawners when available, otherwise the average reproductive success was used. The eruption of Mt. St. Helens resulted in high stray rates into the Kalama River; therefore the returns influenced by this event were not used in this analysis (Leider 1989). Due to the hatchery program, escapements of hatchery and wild steelhead approached equilibrium levels and the spawner-recruit data are not very informative about the productivity of the stock. The EDT estimate of performance is slightly outside this 95% confidence region. In reviewing the EDT outputs, the survival of juvenile steelhead overwintering in the mainstem was reduced due to estimates of bed scour in these canyon reaches. This pattern was observed in other basins with larger canyons and a monitoring program for bed scour using TFW protocols should be established to address this uncertainty (WFPB 1997).

The Washougal River summer steelhead population has been monitored by snorkeling from the 1950's to the early 1970's and monitoring was re-initiated in 1985. Recently, these snorkel counts were standardized and population estimates were made using PCE from snorkeling. During the course of the data collection, the ocean regime has cycled through productive and unproductive periods (Hare and Francis 1994) and the data is highly variable. The EDT point estimate falls within the 95% contour (Figure E9-4).

Most fall Chinook populations are associated with a hatchery program. Due to the potential uncertainties and lack of specific data, only three fall Chinook populations were identified for comparison with the EDT model. Tule populations on the Coweeman and EF Lewis are shown in Figure E9-5. As mentioned above these populations are monitored using a PCE of live and dead counts and index reaches are expanded to estimate the entire population. To estimate ocean harvest, these stocks were assumed to have interception and maturity rates similar to the Cowlitz Hatchery CWT groups. Given these assumptions, there is an unknown amount of measurement error in the spawner-recruit data. When the EDT fit is plotted against both populations the fit is reasonable. The point estimate for the Coweeman population is within the 95% confidence region, while the EF Lewis estimate is not (Figure E9-5). The MLE of capacity in the EF Lewis River was over 100,000 adults which not feasible for this small basin.

Lewis River fall Chinook are classified as a bright population. This population has a different life history pattern than the typical tule population. The Lewis River bright stock was modeled with extended freshwater rearing and higher smolt to adult survival due to their larger outmigration size. As with other populations, the spawner-recruit data is highly variable and the BH model had a poor fit to the data. The EDT fit to the data was through the middle of the scatter plot and point estimate is within the 95% confidence region (Figure E9-6).

The Grays River chum salmon dataset was the only one available for this species for a comparison with the EDT model because other datasets are too recent or other counts represent an unknown and potentially varying portion of the escapement. Similar to the tule spawner-recruit dataset, this dataset has an unknown amount of measurement error. There were no stock specific estimates of harvest and the recruits in this dataset are post harvest recruits. The original MLE were unrealistic and two data points with the lowest escapement were eliminated from the dataset to obtain a realistic convergence. The BH curve from EDT provides a reasonable estimate of chum performance and the point estimate falls within the 95% confidence region (Figure E9-6).

E.4. Summary

Overall, the EDT model passed the criteria that salmon performance is consistent with observed data. Estimates of spawner-recruit performance as measured by the BH model were similar between the MLE fit to observed data and the EDT estimate based on the quantity and quality of available habitat when recruits were measured as smolts. All three point estimates from the EDT model were within the 95% confidence region from the observed data. When recruits were measured as adults the MLE of the BH parameters were some times realistic and sometimes unrealistic due to high variability in datasets and the lack of data at low spawning densities. For the remaining nine adult datasets, five EDT point estimates were within the 95% confidence region, two under estimated performance, one over estimated performance, and the EF Lewis was off due to lack of a realistic MLE of the BH parameters from the observed data. Population monitoring should be expanded to add additional stocks to assess risk and check the reasonableness of the EDT model. Some current spawning ground survey programs should be improved to increase the accuracy and precision of the population estimates.

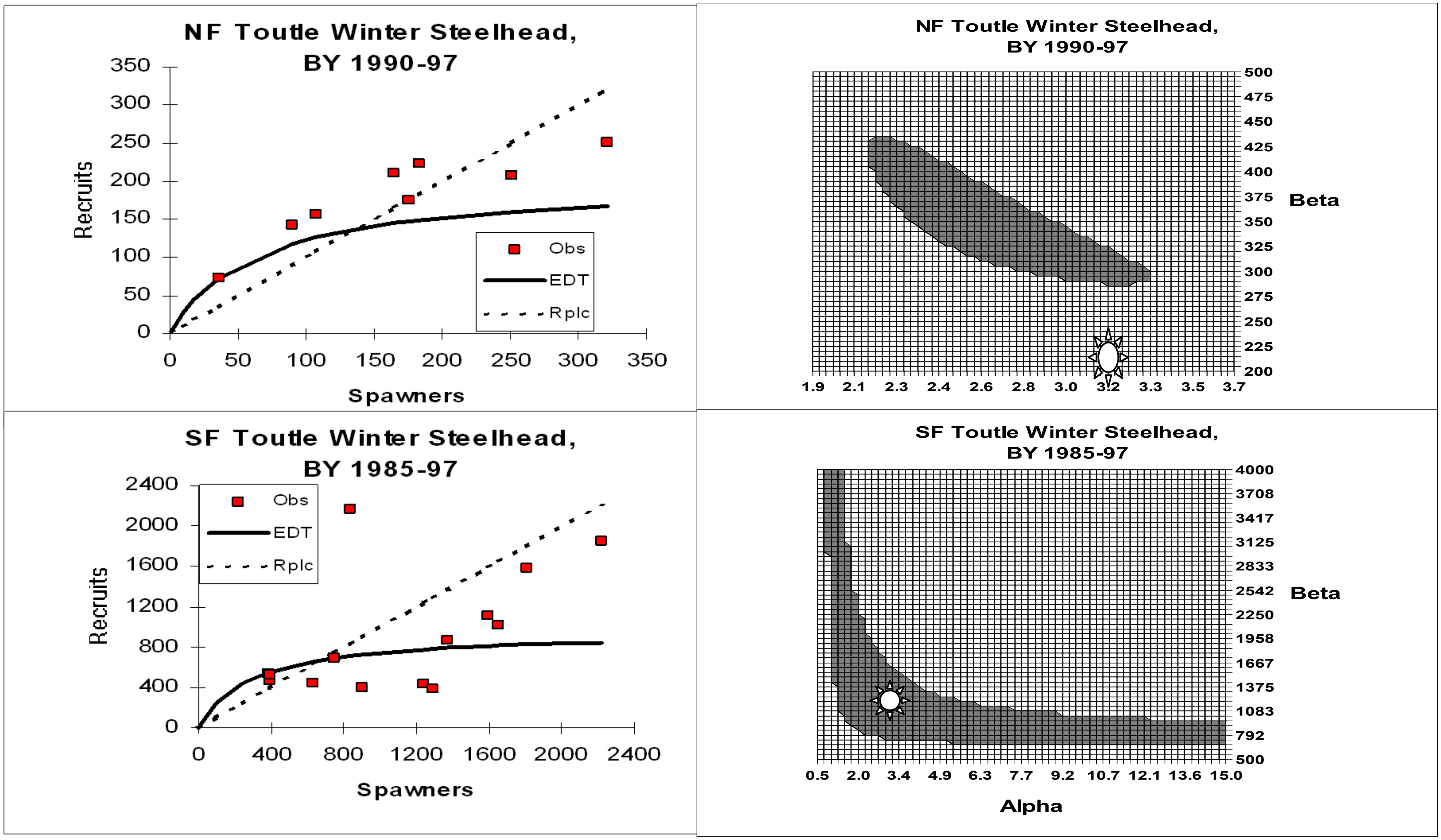

Figure E9-3. **Comparison of EDT estimates of the Beverton-Holt spawner curve (solid line) with observed data (red squares) and the 95% confidence region determined by maximum likelihood analysis (dark grey pattern) compared to the EDT (α, β) point estimate (white sun).**

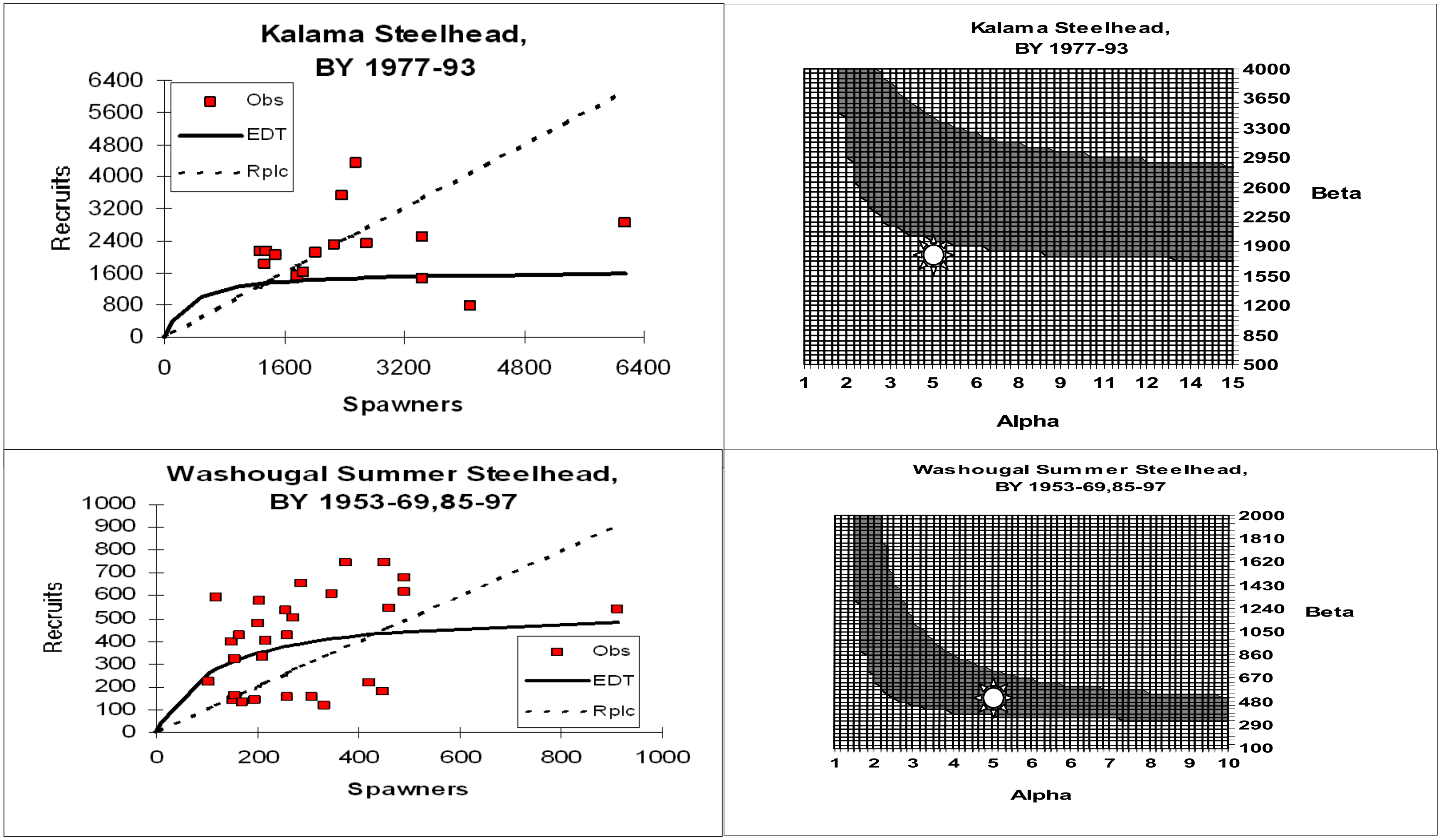

Figure E9-4. **Comparison of EDT estimates of the Beverton-Holt spawner curve (solid line) with observed data (red squares) and the 95% confidence region determined by maximum likelihood analysis (dark grey pattern) compared to the EDT (α, β) point estimate (white sun).**

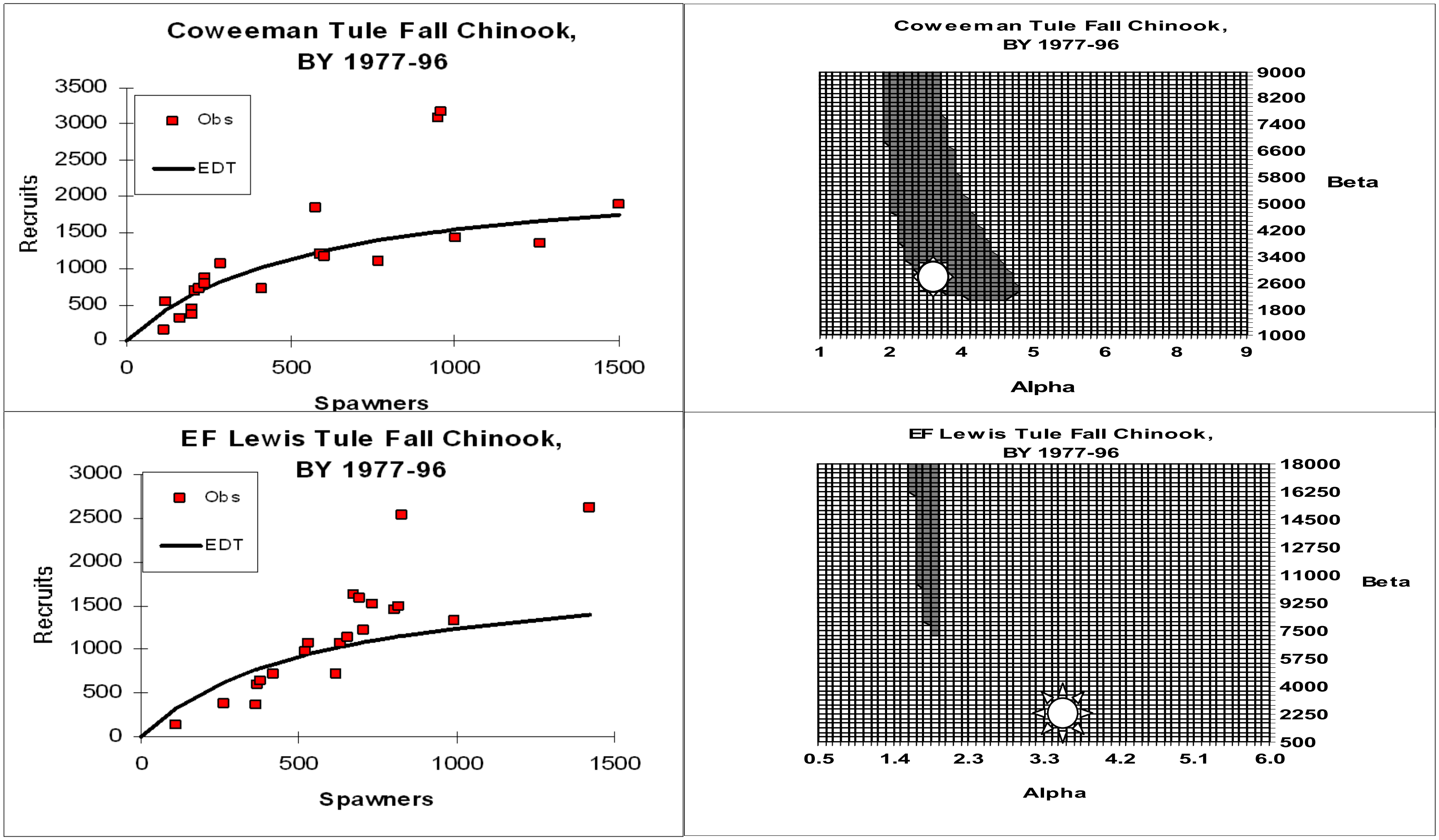

Figure E9-5. Comparison of EDT estimates of the Beverton-Holt spawner curve (solid line) with observed data (red squares) and the 95% confidence region determined by maximum likelihood analysis (dark grey pattern) compared to the EDT (α, β) point estimate (white sun).

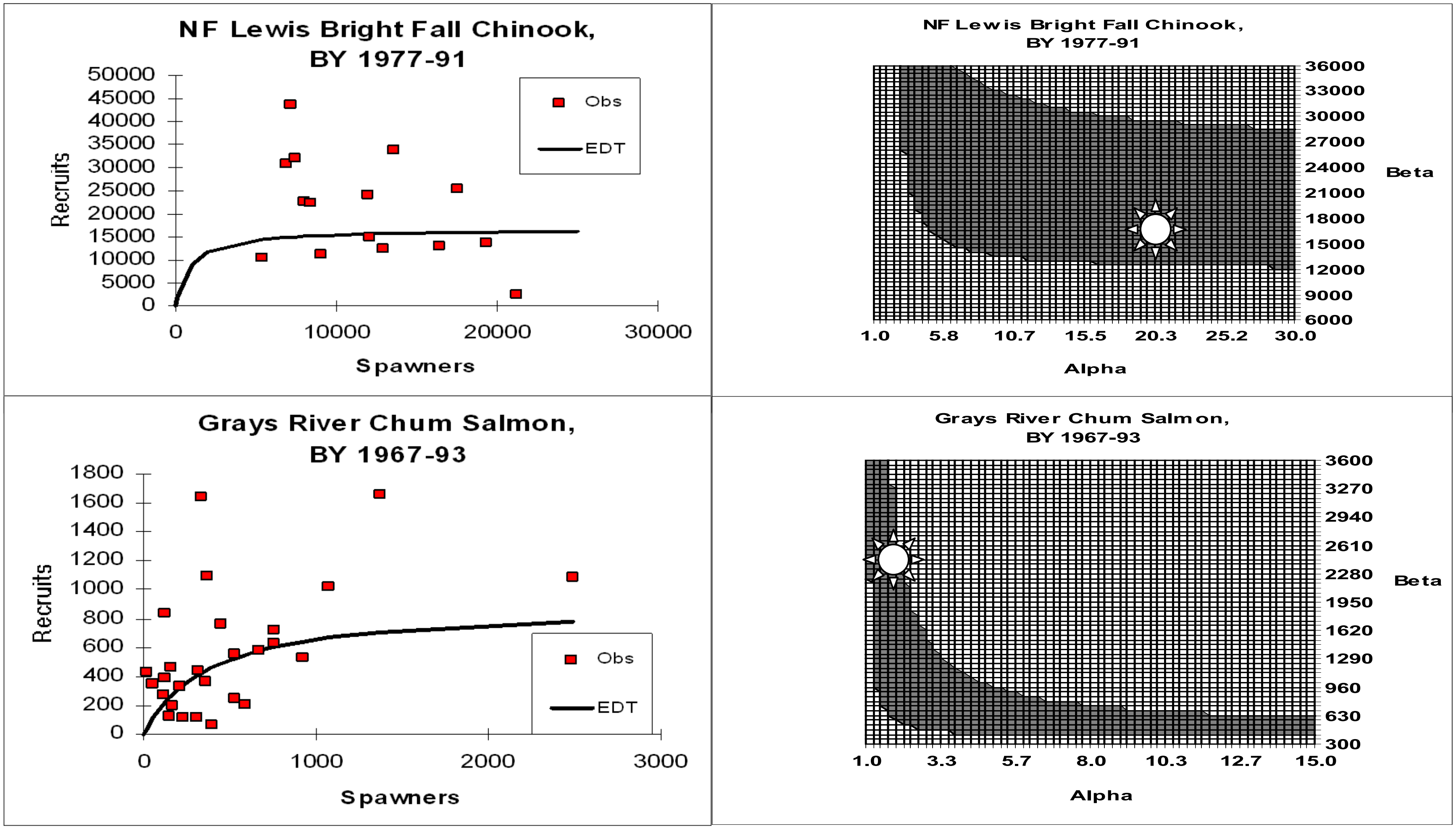

Figure E9-6. **Comparison of EDT estimates of the Beverton-Holt spawner curve (solid line) with observed data (red squares) and the 95% confidence region determined by maximum likelihood analysis (dark grey pattern) compared to the EDT (α, β) point estimate (white sun).**

E.5. References

Ames, J. 1984. Puget Sound chum salmon escapement estimates using spawner curve methodology. In Proceedings of the workshop on stream indexing for salmon escapement estimation. Edited by P.E.K. Symons and M. Waldichuk. Can. Tech. Rep. Fish. Aquat. Sci. No. 1326 pp 133-148.

Arnason, A.N., C.W. Kirby, C.J. .Schwarz, and J.R. Irvine. 1996. Computer analysis of marking data from stratified populations for estimation of salmon escapements and the size of other populations. Can. Tech. Rep. Fish. Aquat. Sci. No. 2106.

Beverton, R.J.H. and J.S. Holt. 1957. On the dynamics of exploited fish populations. Fisheries Investment Series 2, Vol. 19 U.K. Ministry of Agriculture and Fisheries, London.

Chilcote, M.W., S.A. Leider, and J.J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. Trans. Am. Fish. Soc. 115:726-735.

Chilcote, M. W. 2000. Conservation assessment of steelhead populations in Oregon. Oregon Department of Fish and Wildlife, Portland, Oregon. Unpublished.

Cramer,S.P. 2000. The effective of environmentally driven recruitment variation on sustainable yield for salmon populations. Pages 485-504. In E.E. Knudsen et al. (Eds) Sustainable Fisheries Management: Pacific Salmon. Lewis. Boca Raton.

Francis, R.I.C.C, and R. Shotton. 1997. "Risk" in fisheries management: a review. Can. J. Fish. Aquat. Sci. 54, 1699-1715.

Freymond, W. and S. Foley. 1986. Wild Steelhead: spawning escapements for Boldt Case Area Rivers. Fisheries Management Division. Washington Department of Game. Report No. 86-12. Olympia, WA.

Hare,S.R., and R.C. Francis. 1994. Climate change and salmon production in northeast Pacific Ocean, p. 357-372. In R.J. Beamsish (ed.) Climate Change and Northern Fish Populations. Can. Spec. Pub. Fish. Aquat. Sci. 121.

Hilborn,R. and P.J. Starr. 1984. Making stock-recruitment work. In P.E.K. Symons and M. Waldichuk (Eds.) Proceedings of the Workshop on Stream Indexing for Salmon Escapement Estimation. Can. Tech. Rep. on Fish. and Aquat. Sci. No. 1326, pp 227-244.

Hilborn,R. and C.J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty. Chapman and Hall. New York.

Hilborn,R. and M. Mangel. 1997. The Ecological Detective: Confronting models with data. Princeton: Princeton University Press.

Hudson, D.J. 1971. Interval estimation from the likelihood function. Proc. Roy. Stst. Soc. 33:256-262.

Hulett, P.L., C.W. Wagemann, and S.A. Leider. 1996. Studies of hatchery and wild steelhead in the lower Columbia region. Progress report for fiscal year 1995, report no. RAD 96-01.

Ledier, S,A. 1989. Increased straying by adult steelhead trout. *Salmon gairdneri*. Following the 1980 eruption of Mt. St. Helens. Environmental Biology of Fishes 24:219-229.

Leider, S.A., P.L. Hulett, J.J. Loch, and M.W. Chilcote. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. Aquaculture 88:239-252.

Lestelle, L.C., L.E. Mobrand, J.A. Lichatowich, and T.S. Vogel. 1996. Applied ecosystem analysis--a primer, EDT: the ecosystem diagnosis and treatment method. Project No. 9404600. Prepared for: Bonneville Power Administration, Portland, Oregon.

Ludwig, D. and C.J. Walters. 1981. Measurement error and uncertainty in parameter estimates for stock and recruitment. . Can. Journ. Fish. Aquat. Sci. 38:711-720.

Marcot, B. G., W.E. McConnaha, P.H. Whitney, T.A. O'Niel, P.J. Paquet, L.E. Mobrand, G.R. Blair, L.C. Lestelle, K.M. Malone, K.I. Jenkins. 2002. A multi-species framework approach to the Columbia River Basin. Northwest Power Planning Council. Portland,OR

Mobrand Biometrics Inc. 2002. Subbasin planning with EDT: A Primer. Mobrand Biometrics Inc. http://www.edthome.org/sbp/SBPandEDT.pdf

Moussalli, E., and R. Hilborn. 1986. Optimal stock size and harvest rate in multistage life history models. Can. Journ. Fish. Aquat. Sci. 43:135-141.

NRC 1996. Upstream: salmon and society in the Pacific Northwest. Report of the Committee on Protection and Management of Pacific Northwest Anadromous Salmonids. Natural Resource Council, National Academy Press, Washington D.C.

Rawding D. 2001. Stock-recruitment of wild winter and summer steelhead in the Kalama River, Washington. Wash. Depart. of Fish and Wild. Vancouver, WA. Unpublished draft.

Rawding, D. and P.C. Cochran. 2001. Wind River steelhead smolt and parr production monitoring during the 1999 spring outmigration. Wind River watershed project 1999 annual report. BPA. Contract No. 98A109728. Washington Department of Fish and Wildlife. Vancouver, WA.

Rawding, D and P.C. Cochran. 2001. Adult steelhead monitoring in the Wind River 1999-2001. Wind River watershed project 1999 annual report. BPA. Contract No. 98A109728. Washington Department of Fish and Wildlife. Vancouver, WA.

Rawding, D., B. Glaser, S. VanderPloeg, and N. Pittman. 2004. Documentation used in the Ecosystem Diagnosis and Treatment Model (EDT) for the Wind River Subbasin. Washington Department of Fish and Wildlife. Vancouver, WA.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. Second addition. Charles Griffin and Sons, Ltd. London.

Washington Forest Practice Board (WFPB). 1997. Standard methodology for conducting watershed analysis, version 4.0. Washington Forest Practices Board. Olympia, WA.