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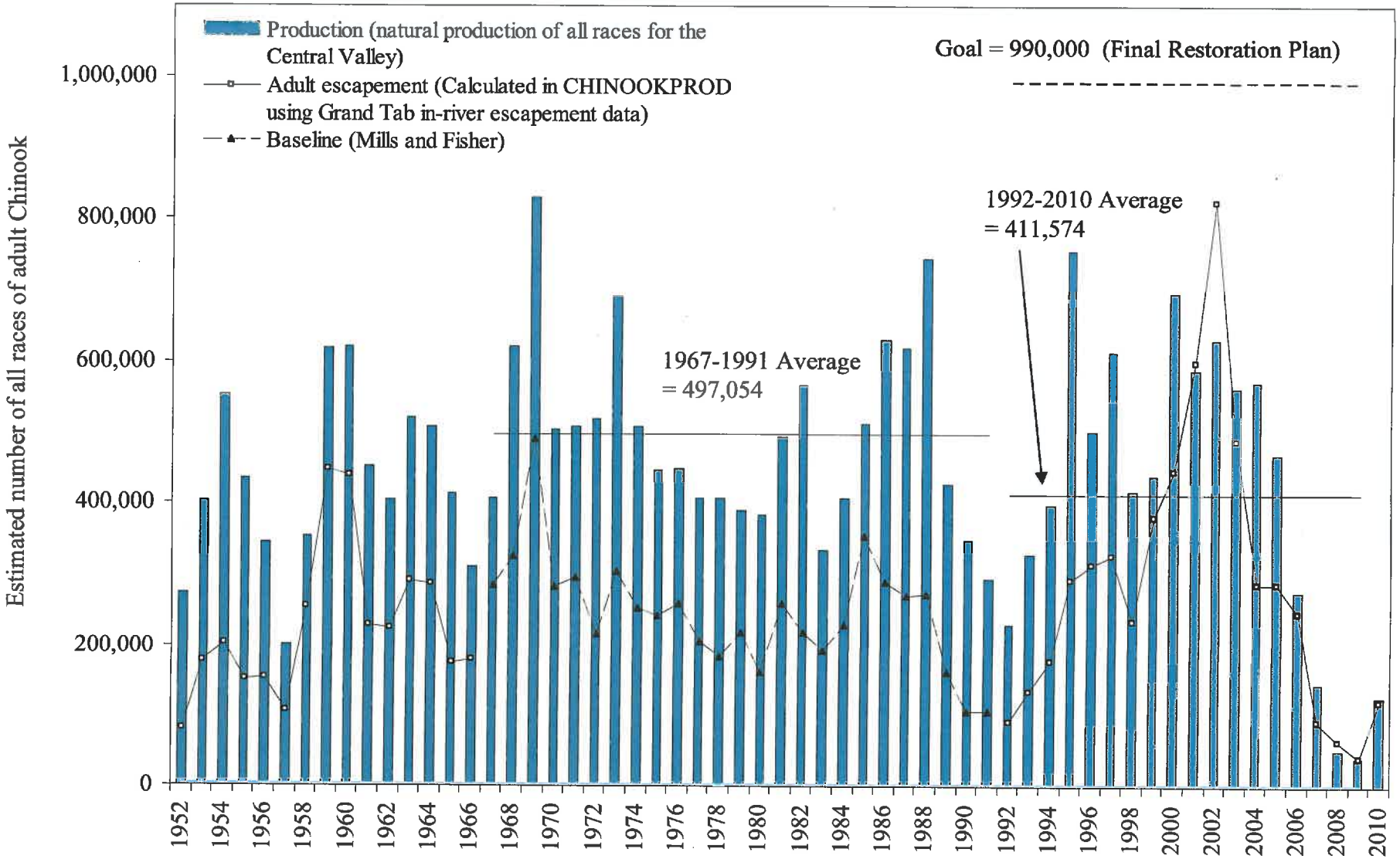


Figure 1. Estimated yearly natural production and in-river escapement of all races of adult Chinook Salmon in the Central Valley rivers and streams. 1952 - 1966 and 1992 - 2010 numbers are calculated in CHINOOKPROD using CDFG Grand Tab in-river escapement data (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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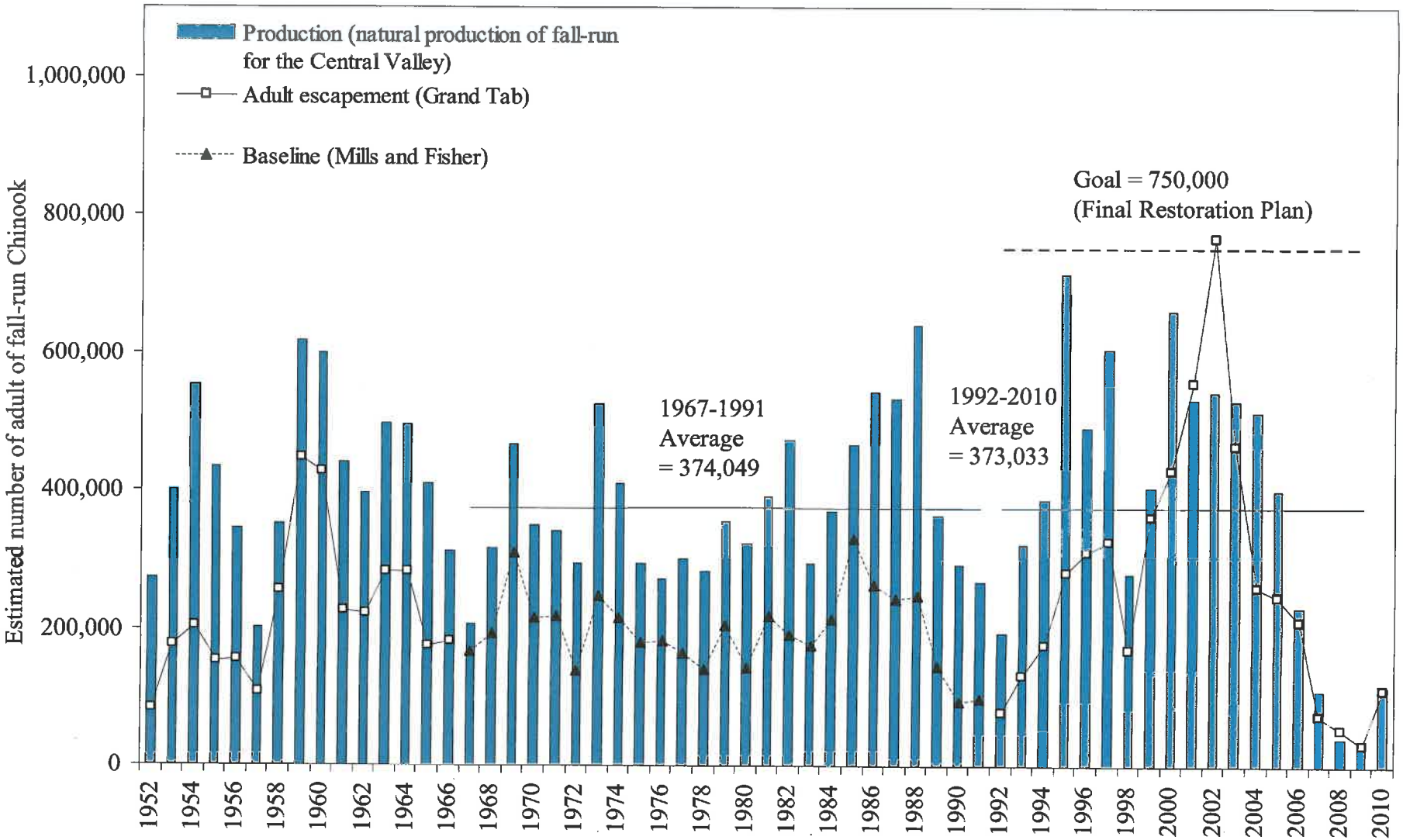


Figure 2. Estimated yearly natural production and in-river escapement of adult fall-run Chinook salmon in the Central Valley rivers and streams. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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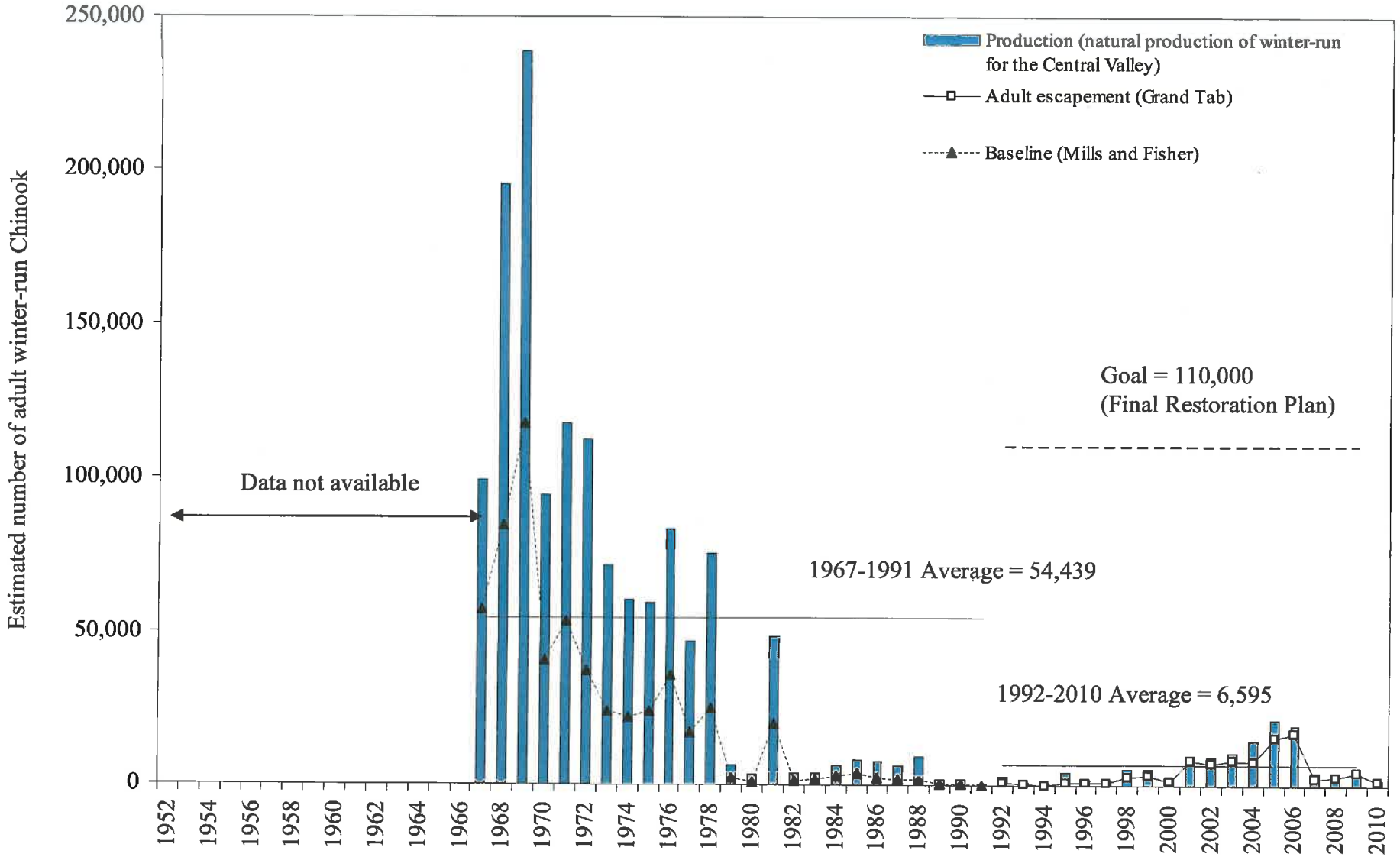


Figure 3. Estimated yearly natural production and in river escapement of adult winter-run Chinook salmon in the Central Valley rivers and streams. 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967-1991) are from Mills and Fisher (CDFG, 1994).

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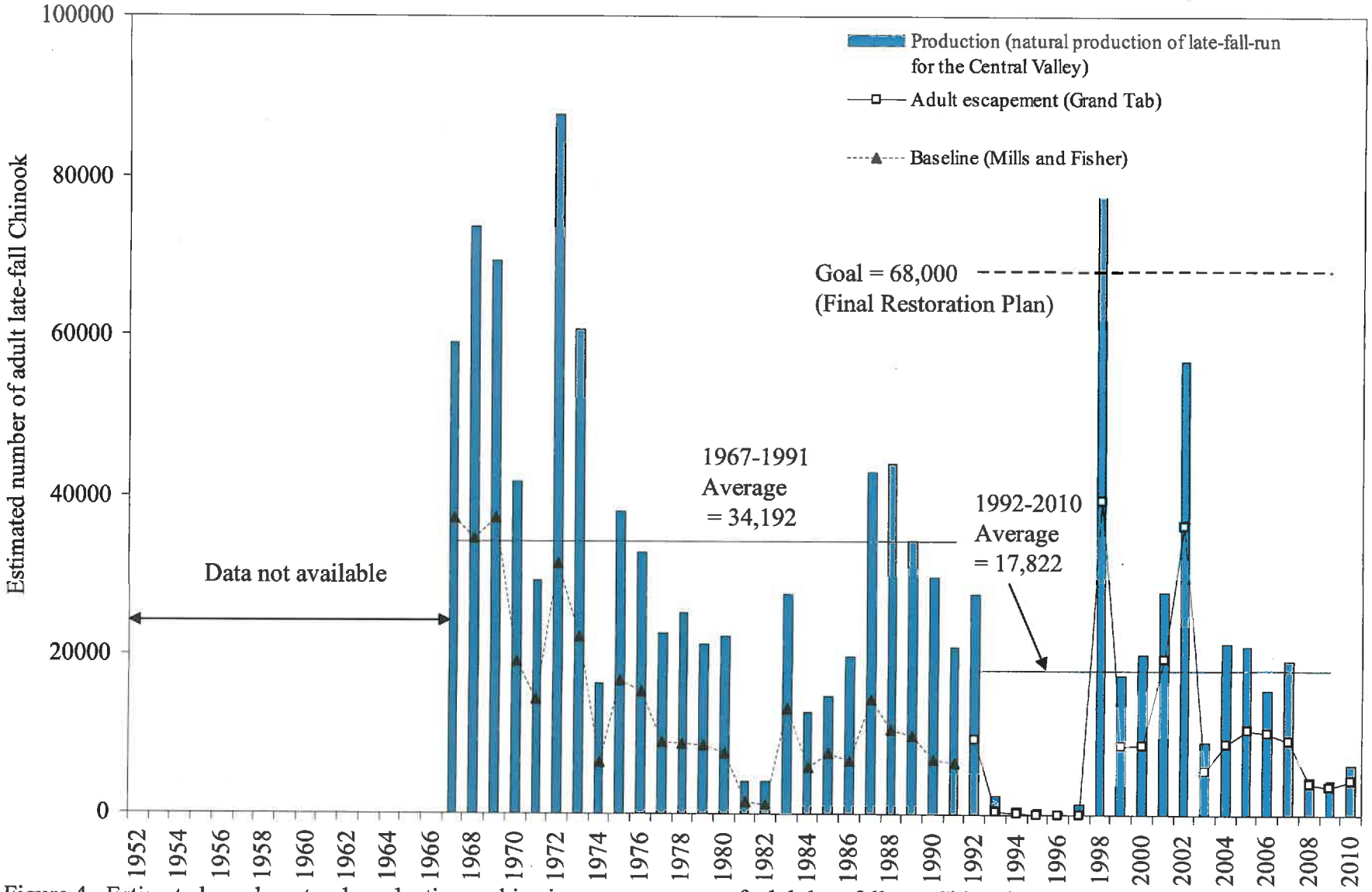


Figure 4. Estimated yearly natural production and in-river escapements of adult late-fall-run Chinook salmon in the Central Valley rivers and streams. 1992 – 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991)are from Mills and Fisher (CDFG, 1994).

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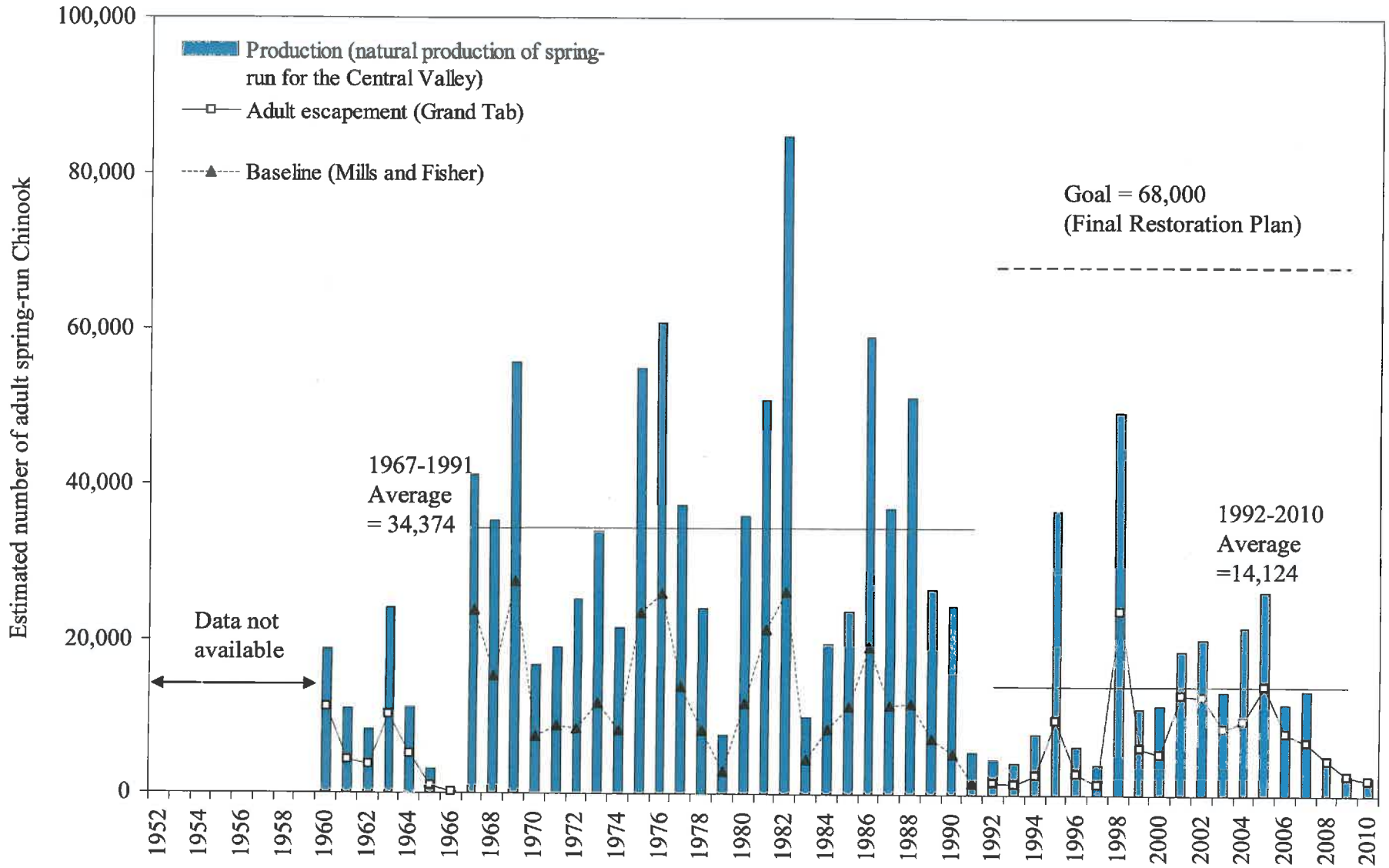


Figure 5. Estimated yearly natural production and in-river escapement of adult spring-run Chinook salmon in the Central Valley rivers and streams. 1960 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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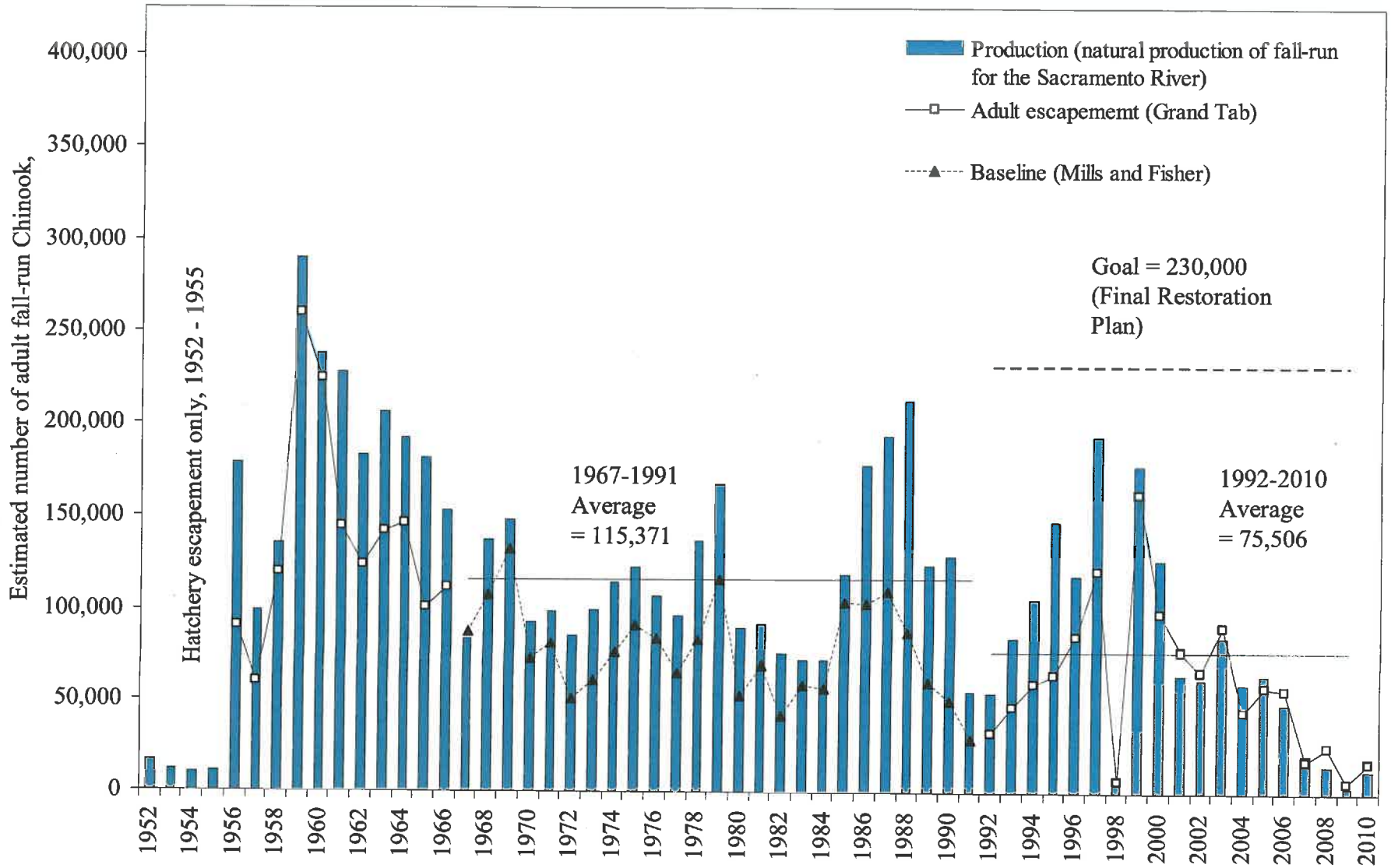


Figure 6. Estimated yearly natural production and in-river escapement for the entire mainstem Sacramento River adult fall-run Chinook salmon. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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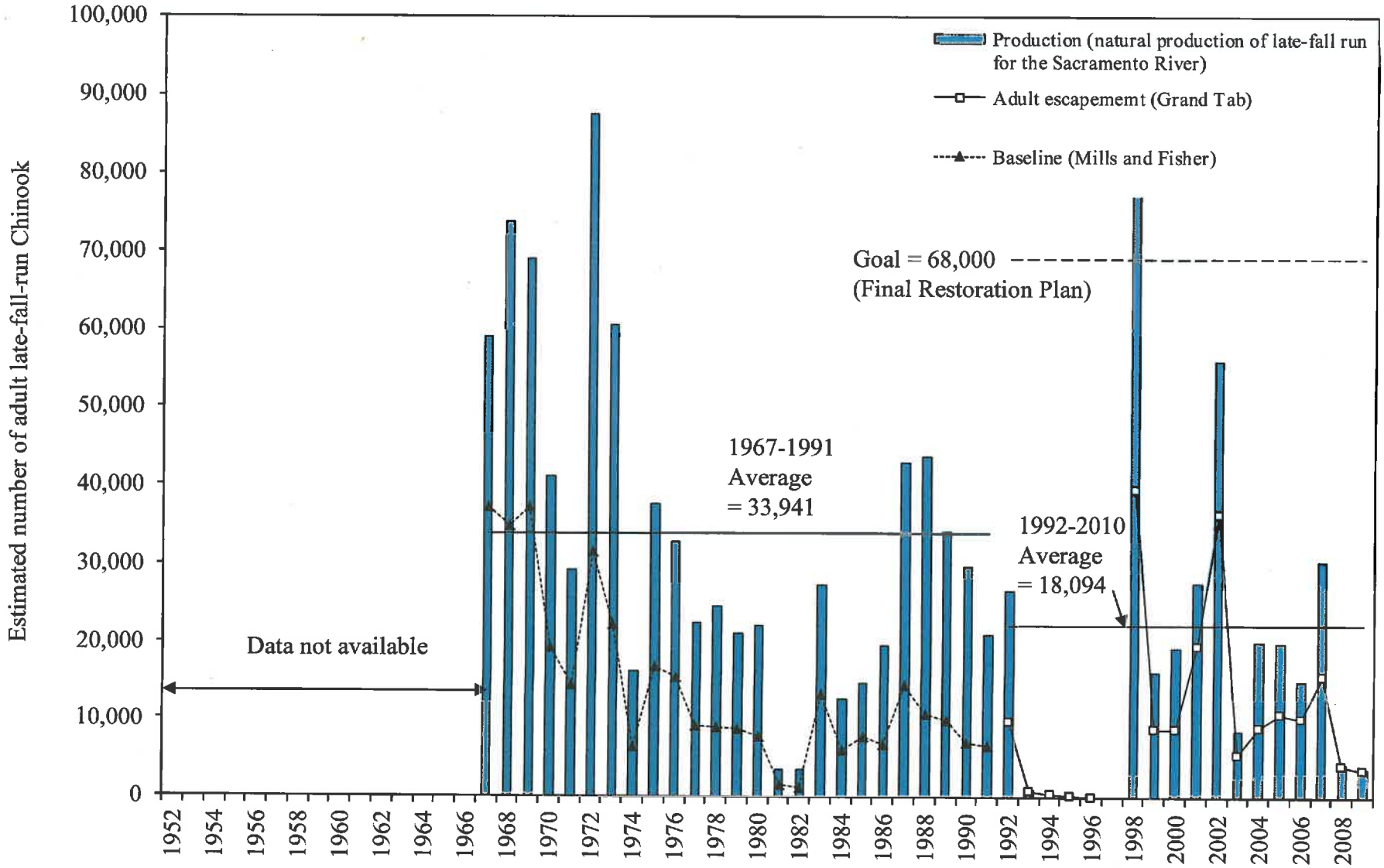


Figure 7. Estimated yearly natural production and in-river adult escapement for above RBDD mainstem Sacramento River late-fall-run Chinook salmon. 1992 -2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 – 1991) are from Mills and Fisher (CDFG, 1994).

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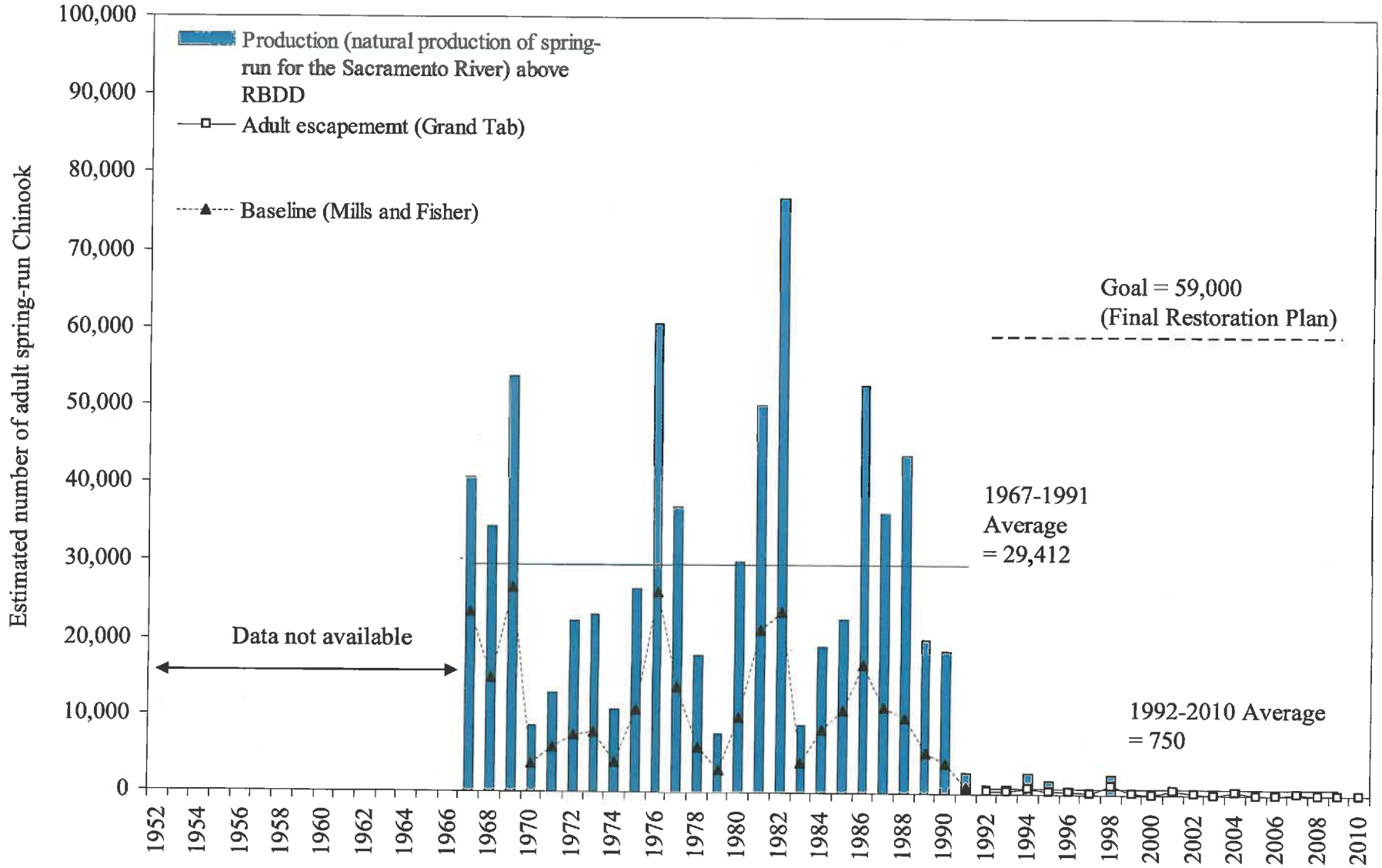


Figure 8. Estimated yearly natural production and in river adult escapement for above RBDD mainstem Sacramento River spring-run Chinook salmon. 1992-2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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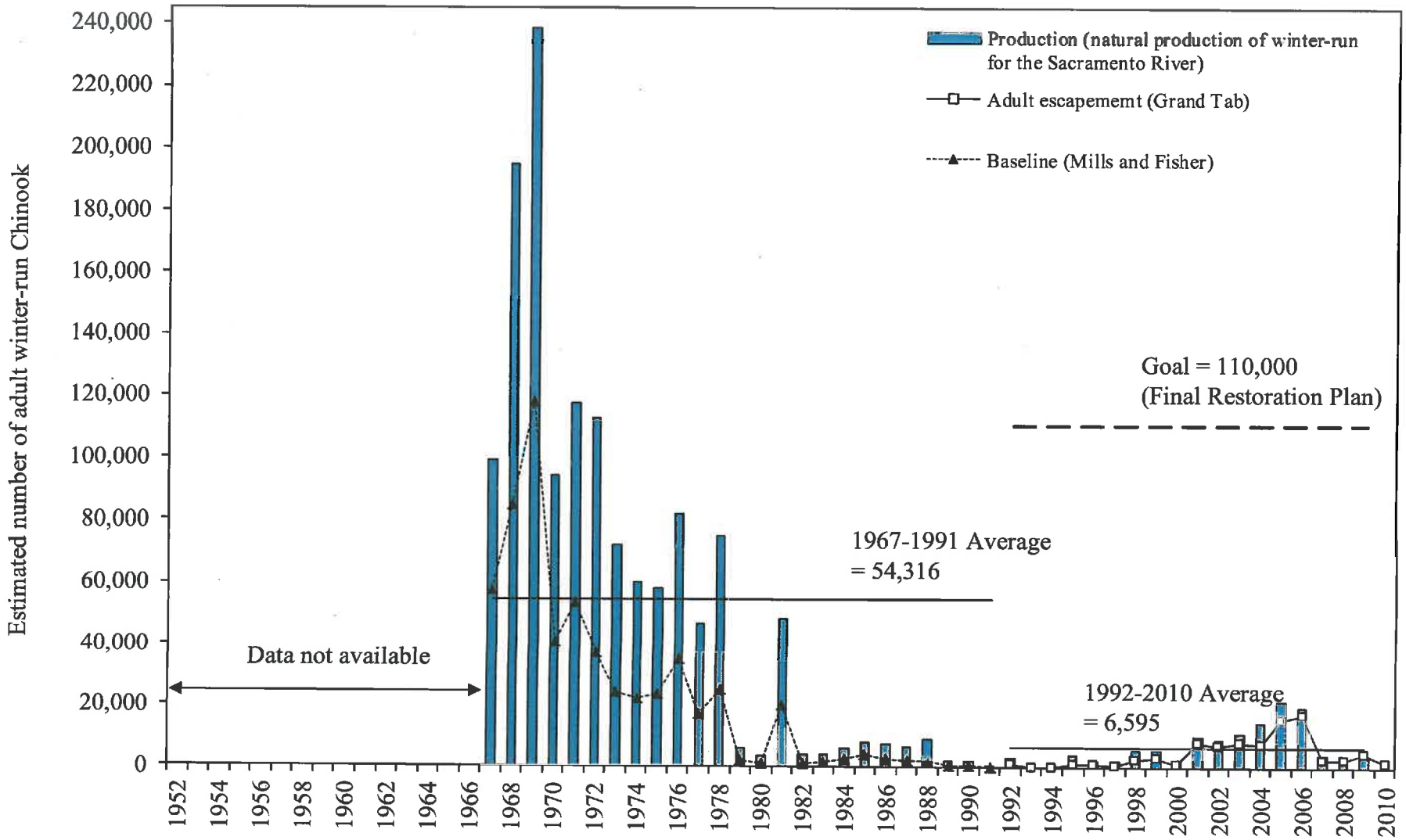


Figure 9. Estimated yearly natural production and in river adult escapement for above RBDD mainstem Sacramento River winter-run Chinook salmon. 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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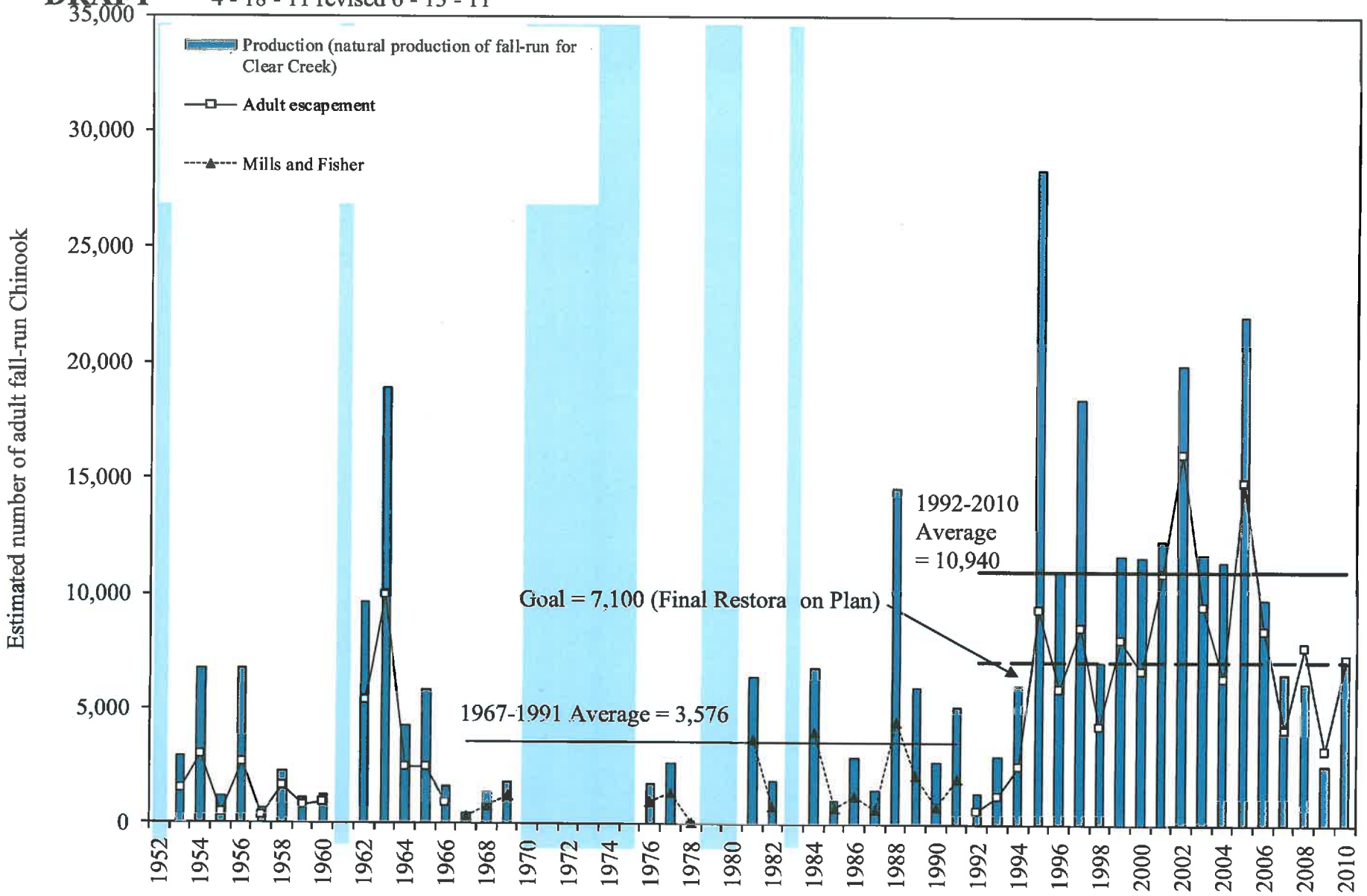


Figure 10. Estimated yearly natural production and in river adult escapement of Clear Creek fall-run Chinook salmon. = data was not available for 1952, 1961, 1970-1975, 1979, 1980, 1983. 1953 – 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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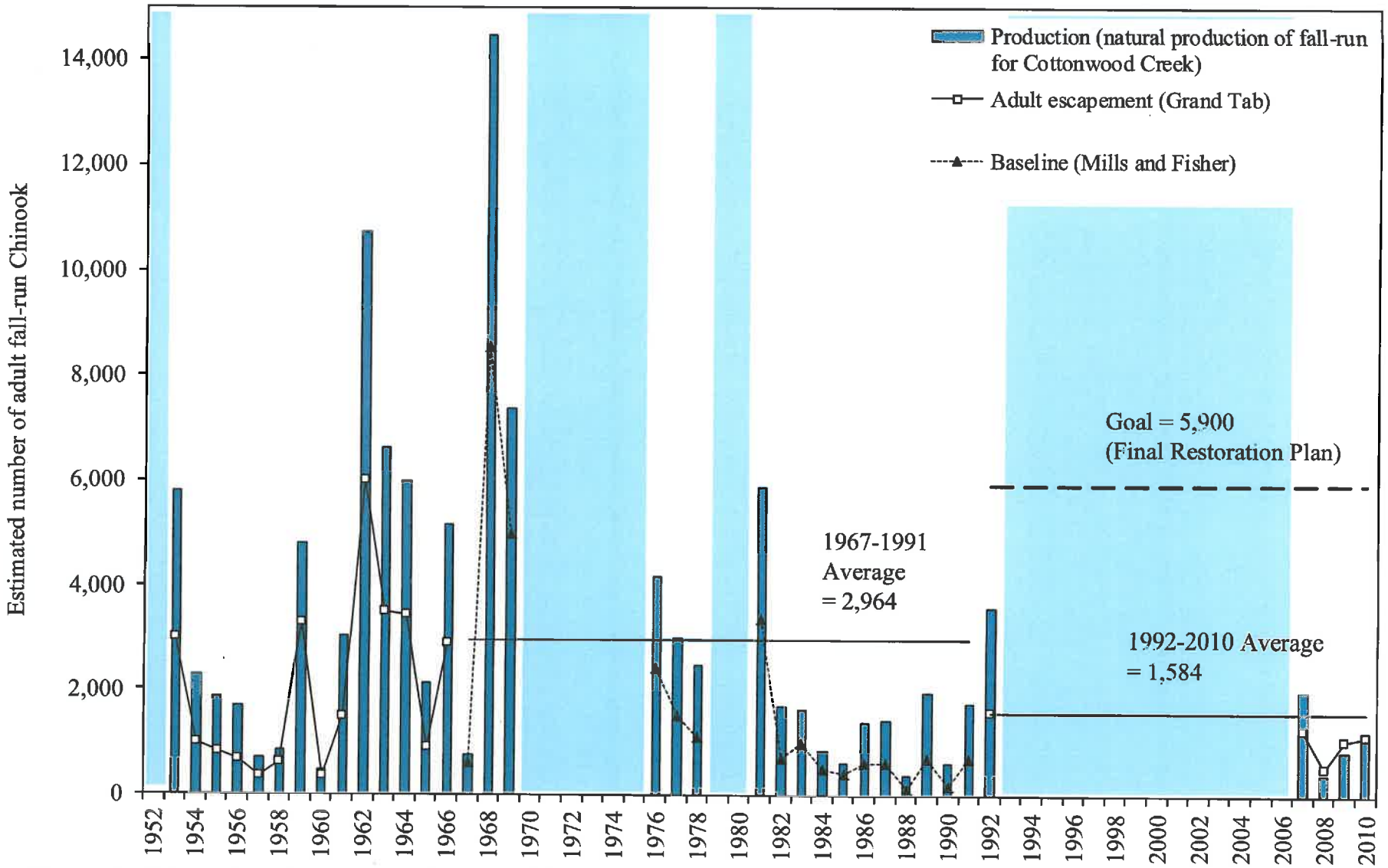


Figure 11. Estimated yearly natural production and in river adult escapement of Cottonwood Creek fall-run Chinook salmon. = data was not available for 1952, 1970 - 1975, 1979 - 1980 and 1993 - 2005. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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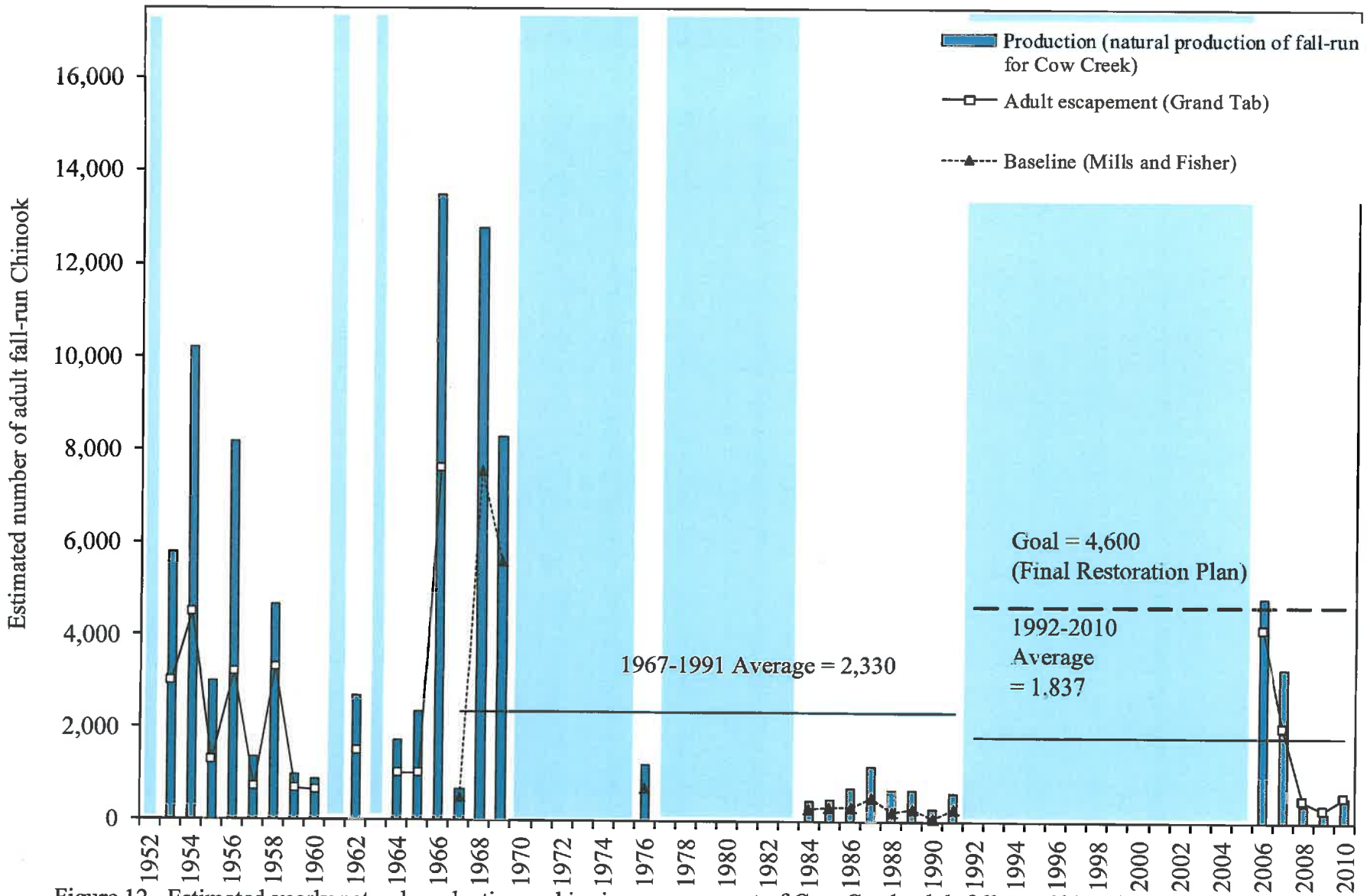


Figure 12. Estimated yearly natural production and in river escapement of Cow Creek adult fall-run Chinook salmon. = data was not available for 1952, 1961, 1963, 1970 - 1975, 1977 - 1983, and 1992 - 2005. 1952 – 1966 and 1992-2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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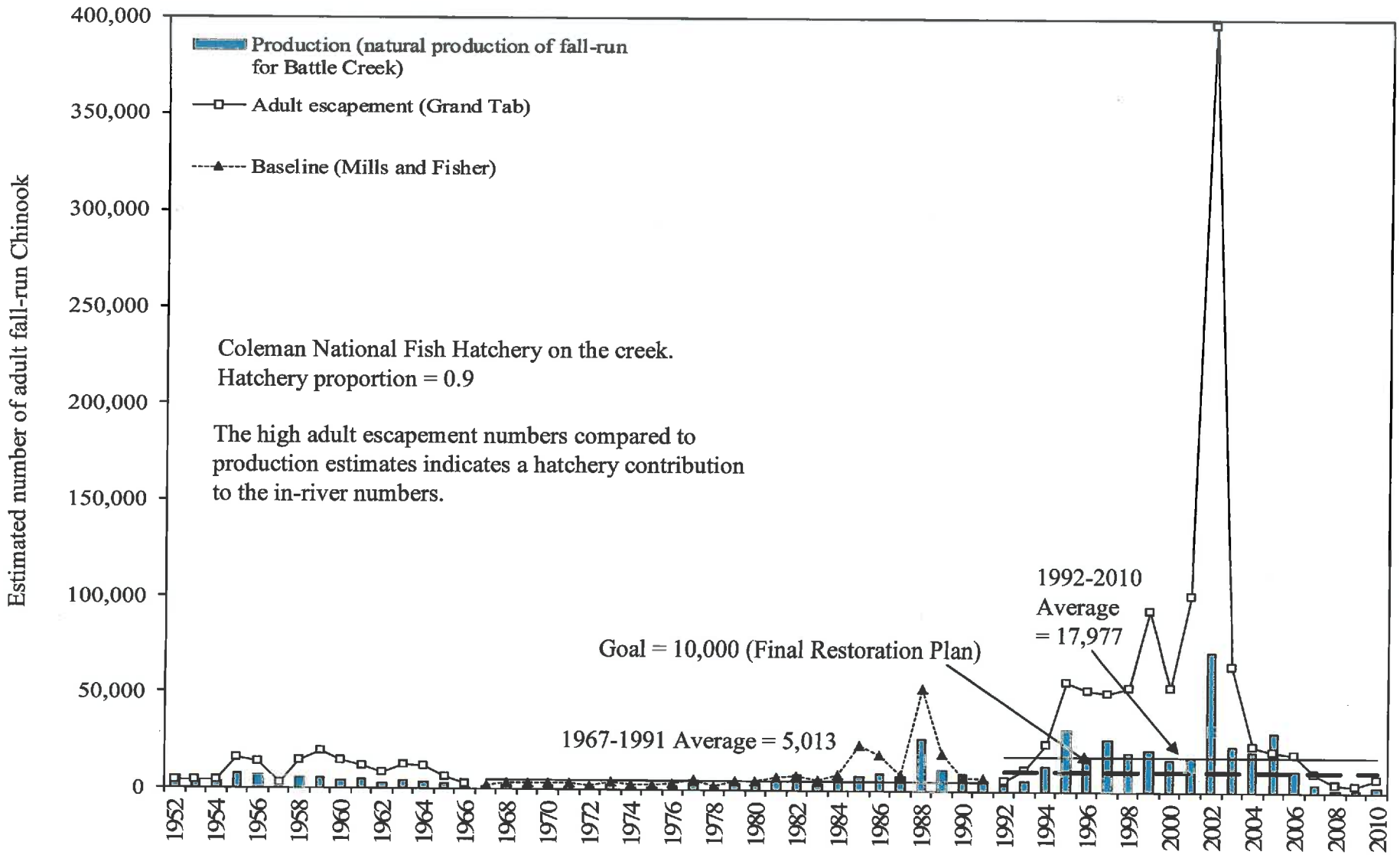


Figure 13. Estimated yearly natural production and in river escapement of Battle Creek adult fall-run Chinook salmon. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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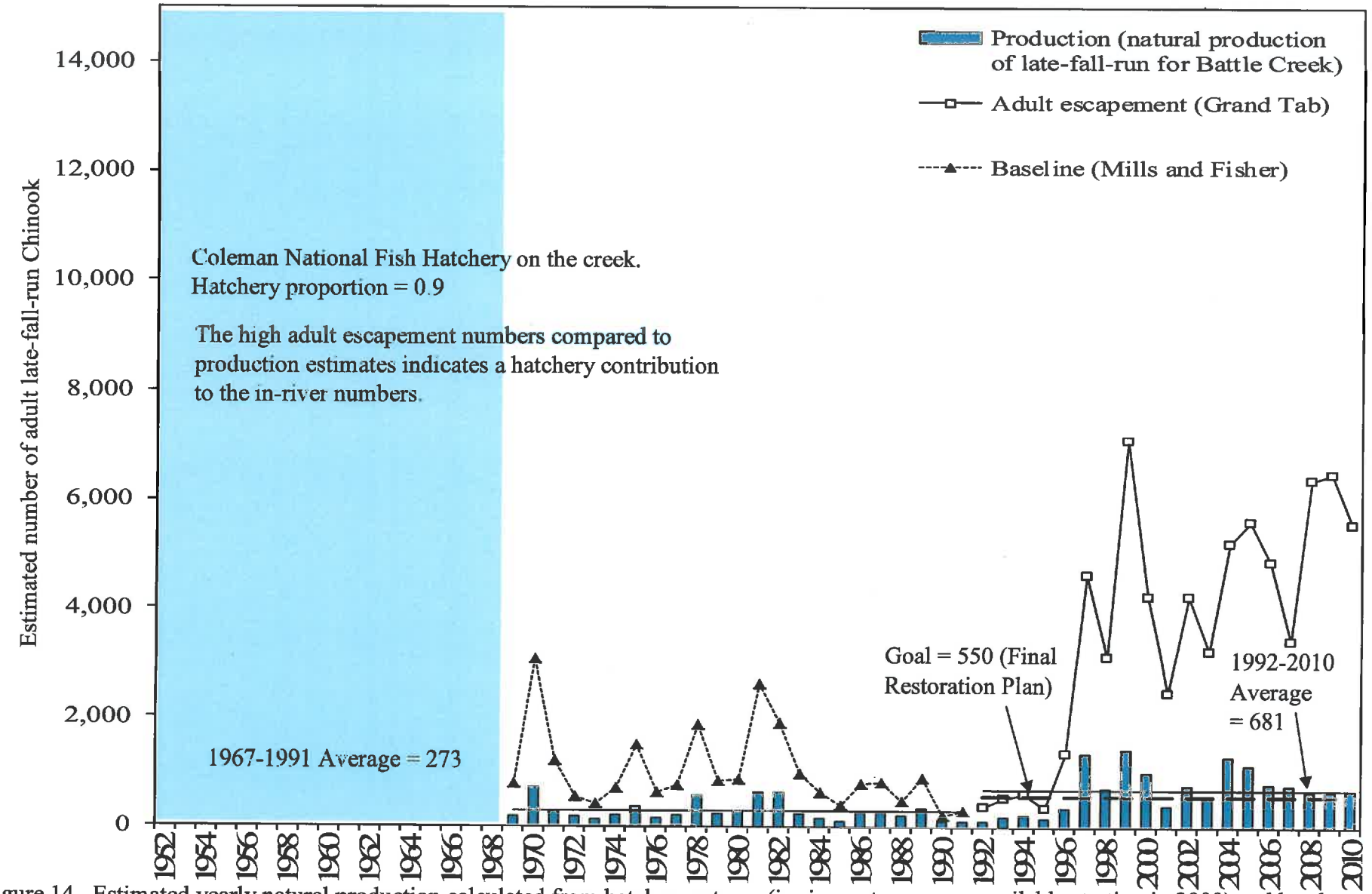


Figure 14. Estimated yearly natural production calculated from hatchery returns (in river returns were available starting in 2000) and hatchery returns of Battle Creek adult late-fall-run Chinook salmon. 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). = data was not available for 1952-1968. Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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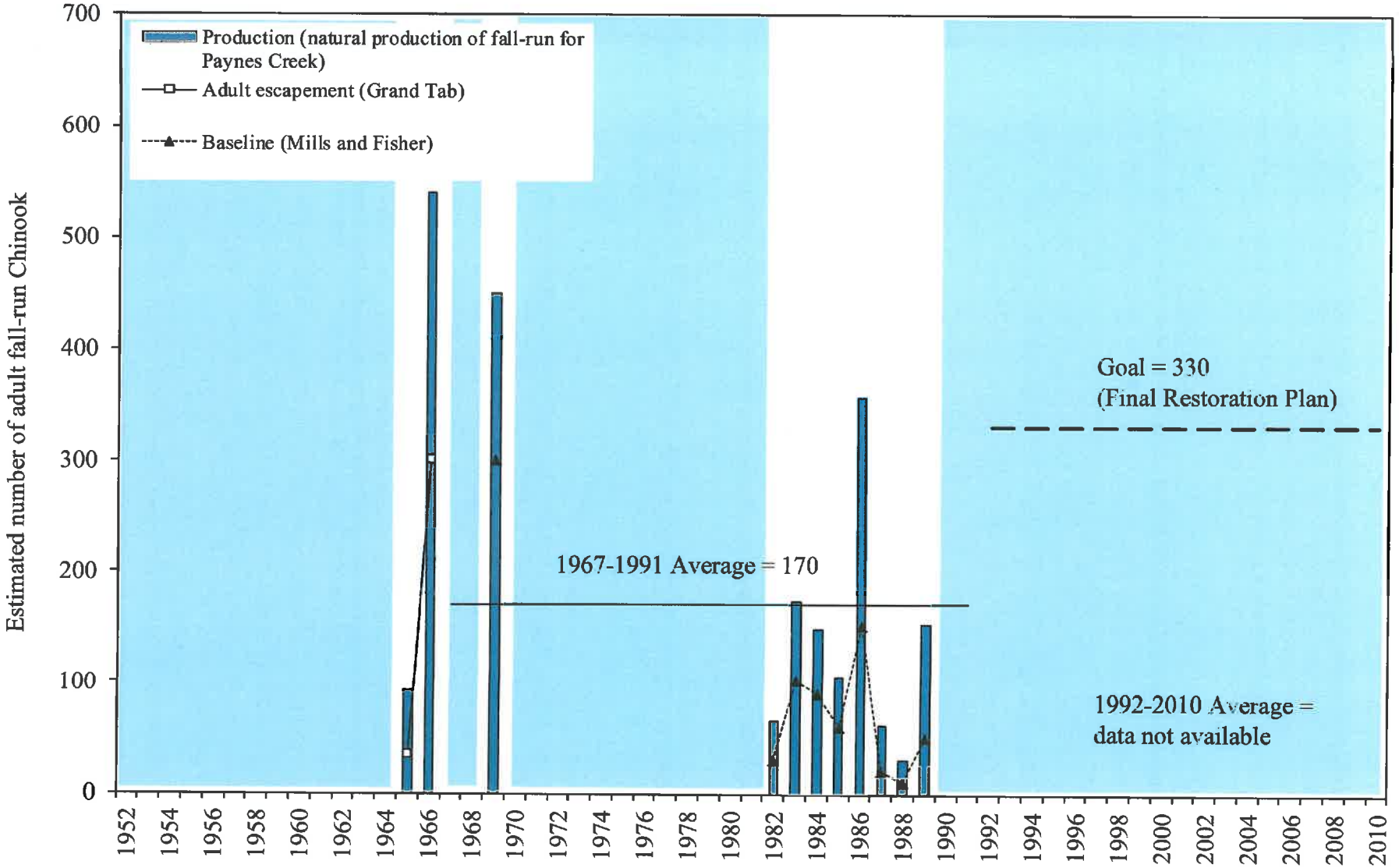


Figure 15. Estimated yearly natural production and in river escapement of Paynes Creek adult fall-run Chinook salmon. = data was not available for 1952 - 1964, 1967 - 1968, 1970 - 1981, and 1990 - 2010 1965-1966 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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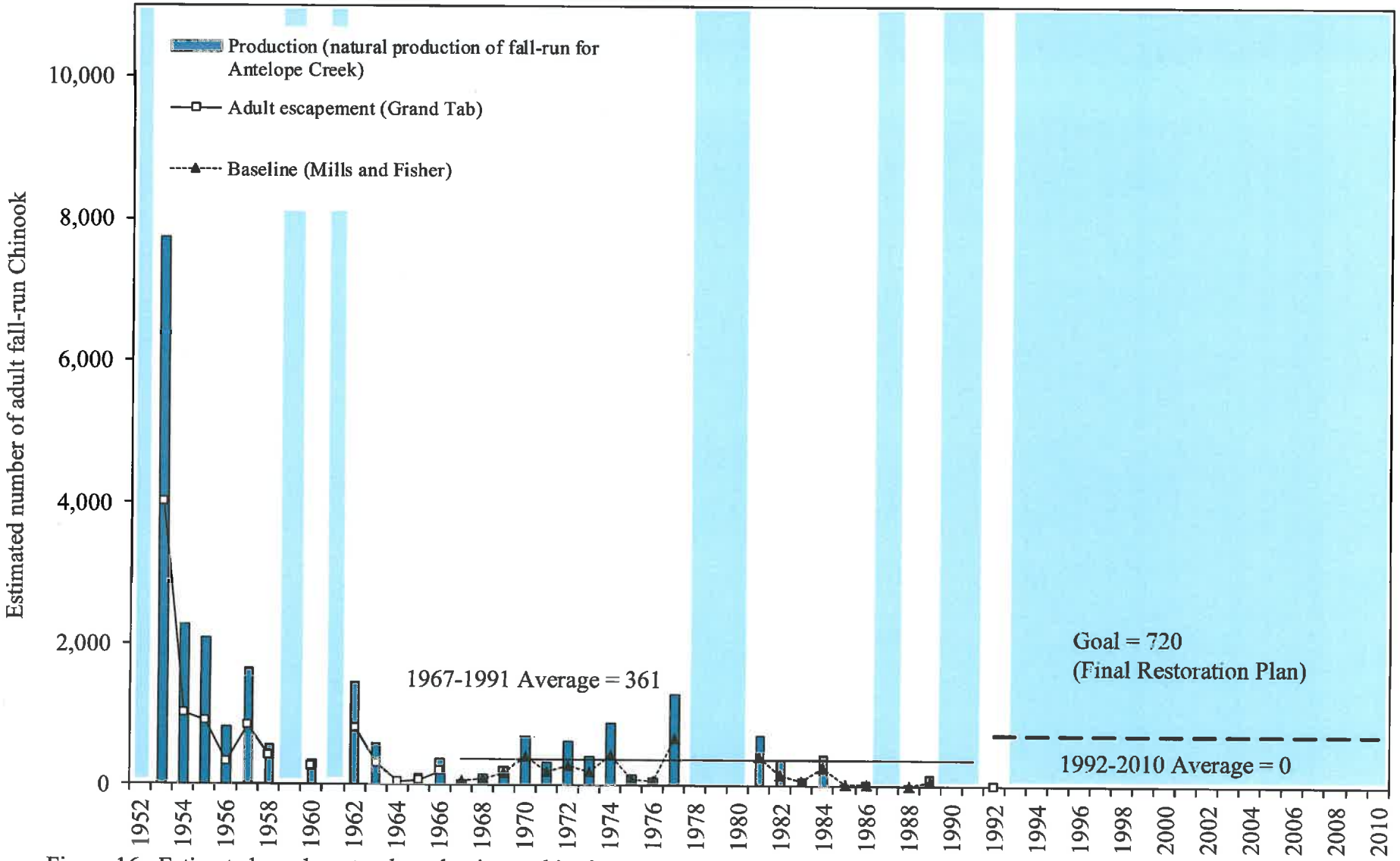


Figure 16. Estimated yearly natural production and in river escapement of Antelope Creek adult fall-run Chinook salmon. ▭ = data was not available for 1952, 1959, 1961, 1978 - 1980, 1987, 1990, 1991, and 1993 – 2010. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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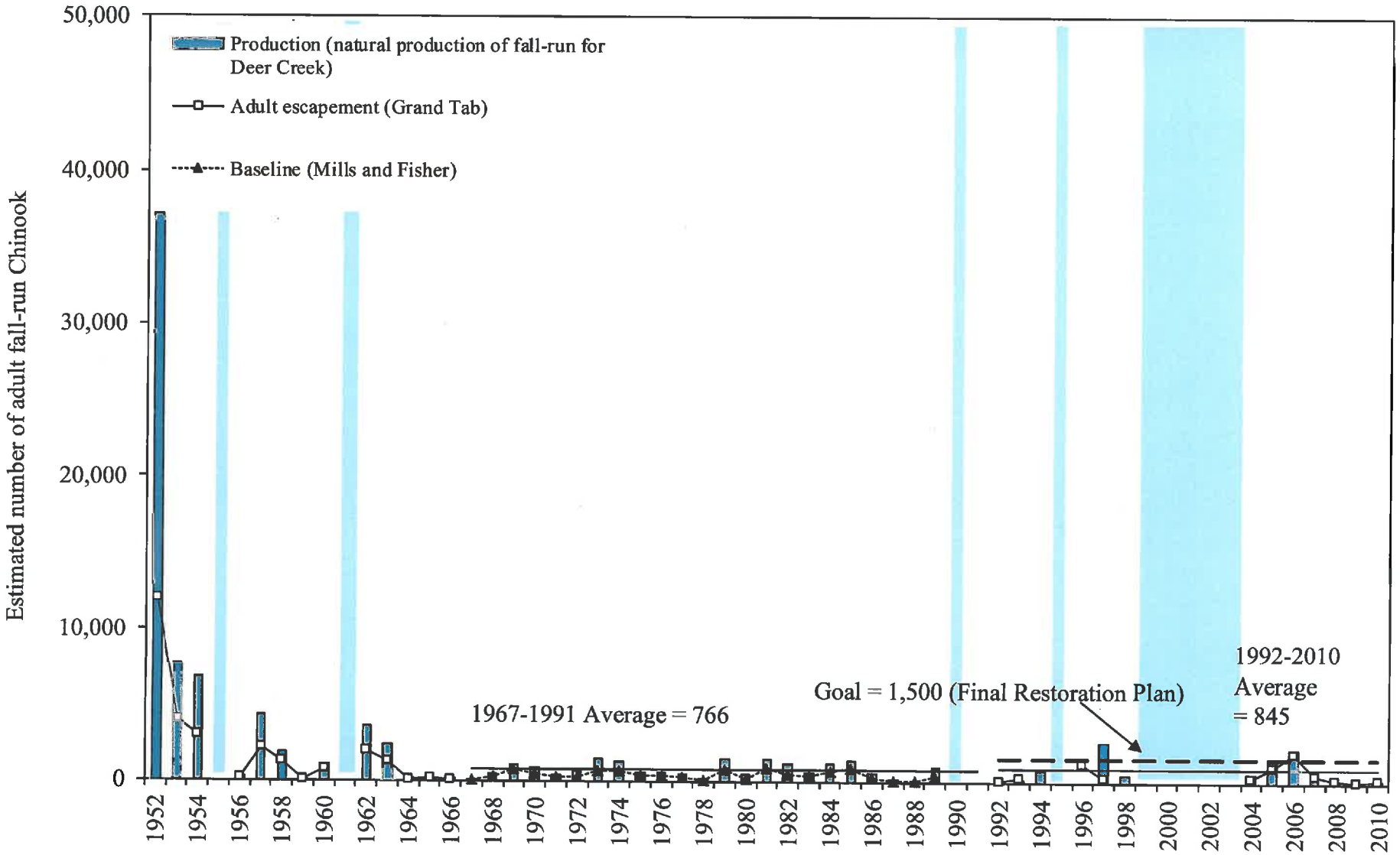


Figure 17. Estimated yearly natural production and in river escapement of Deer Creek adult fall-run Chinook salmon. = data was not available for 1955, 1961, 1990 - 1992, 1995, 1996, and 1999 - 2003. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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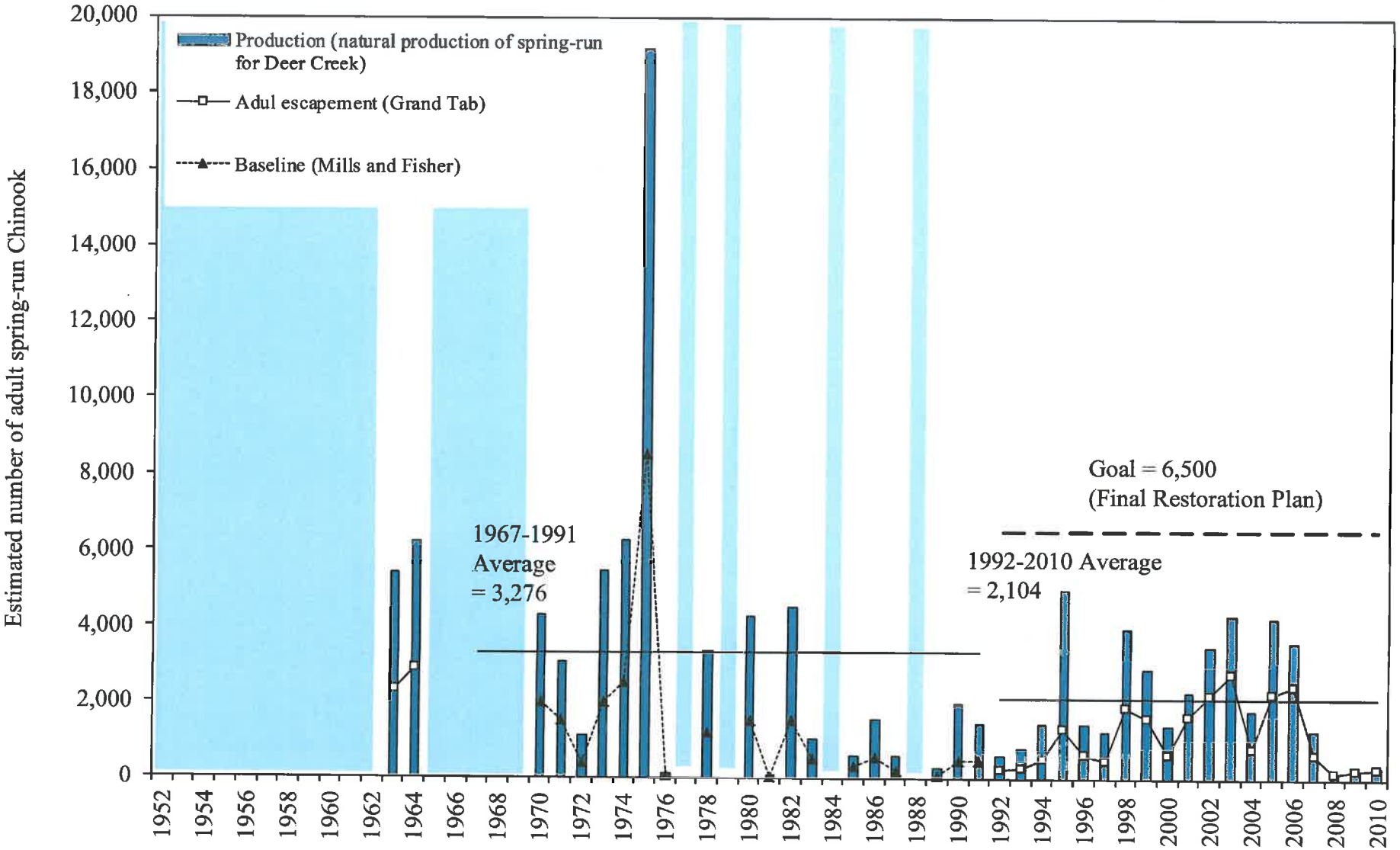


Figure 18. Estimated yearly natural production and in river escapement of Deer Creek adult spring-run Chinook salmon. = data was not available for 1952 - 1962, 1965 - 1969, 1977, 1979, 1984, and 1988. 1952 - 1966, and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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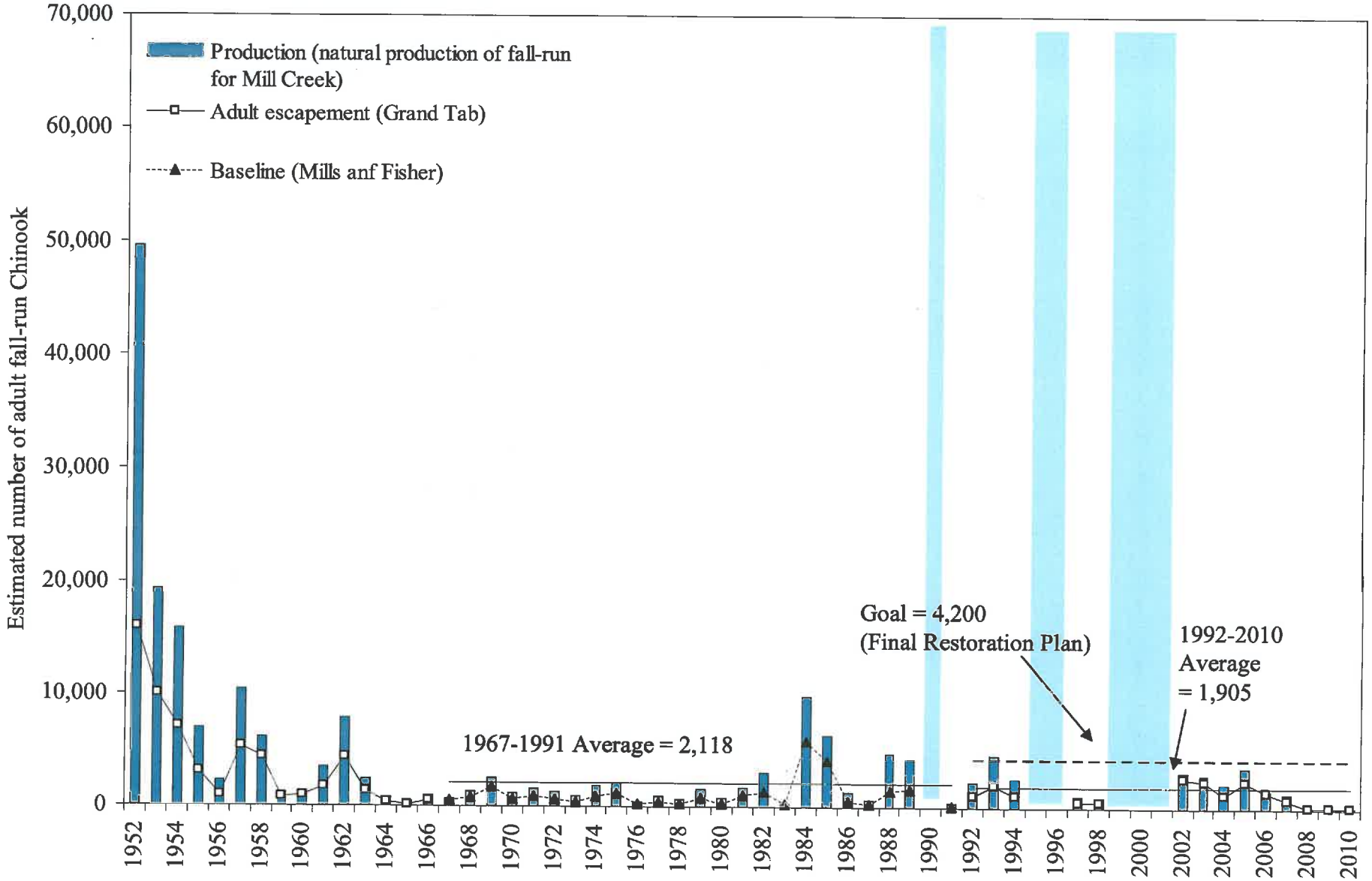


Figure 19. Estimated yearly natural production and in river escapement of Mill Creek adult fall-run Chinook salmon. ▭ = data was not available for 1990, 1995 - 1996, and 1999 - 2001. 1952 -1966 and 1992 – 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 – 1991) are from Mills and Fisher (CDFG, 1994).

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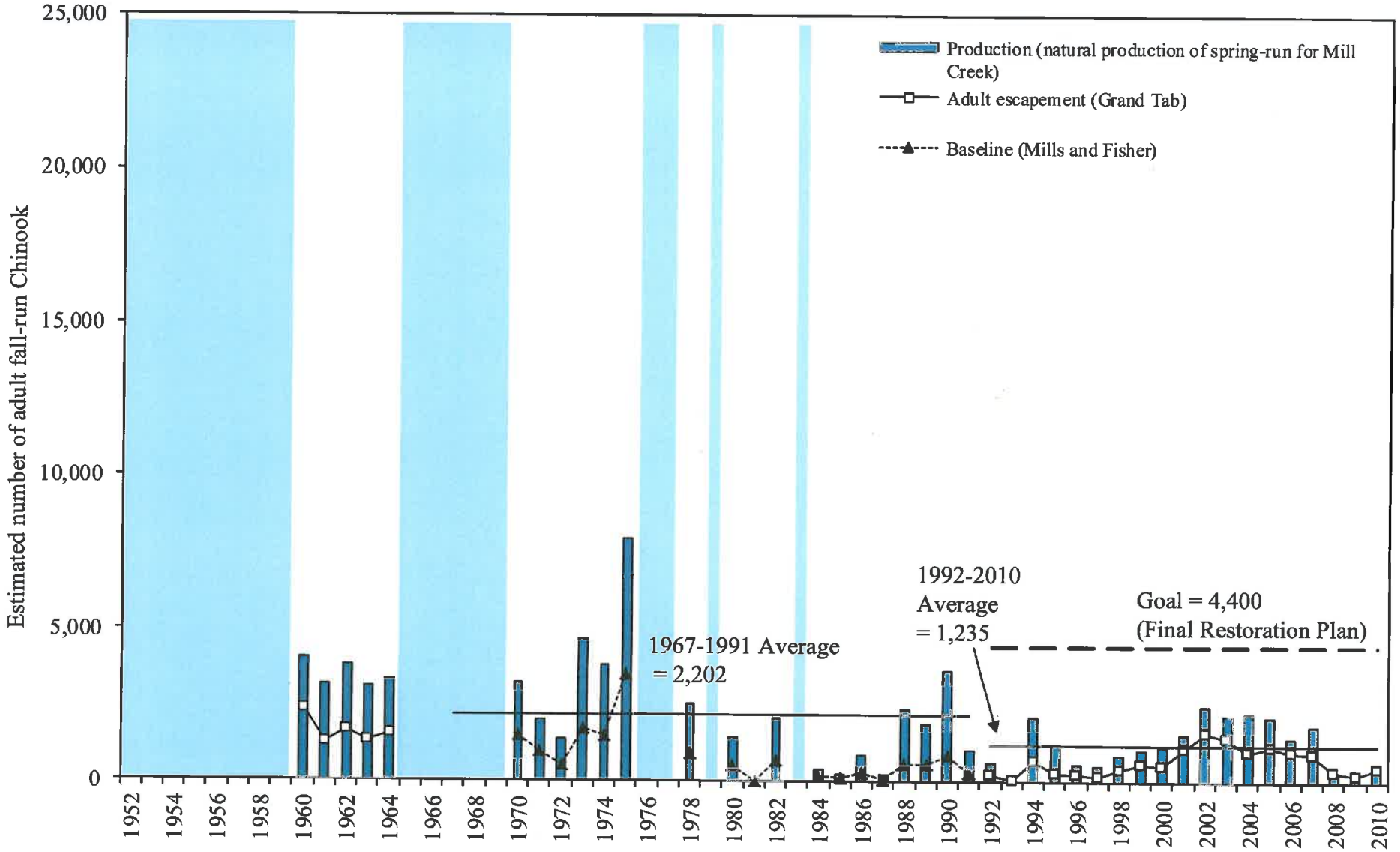


Figure 20. Estimated yearly natural production and in river escapement of Mill Creek adult spring-run Chinook salmon. = data was not available for 1952 - 1959, 1965 - 1969, 1976, 1977, 1979, and 1983. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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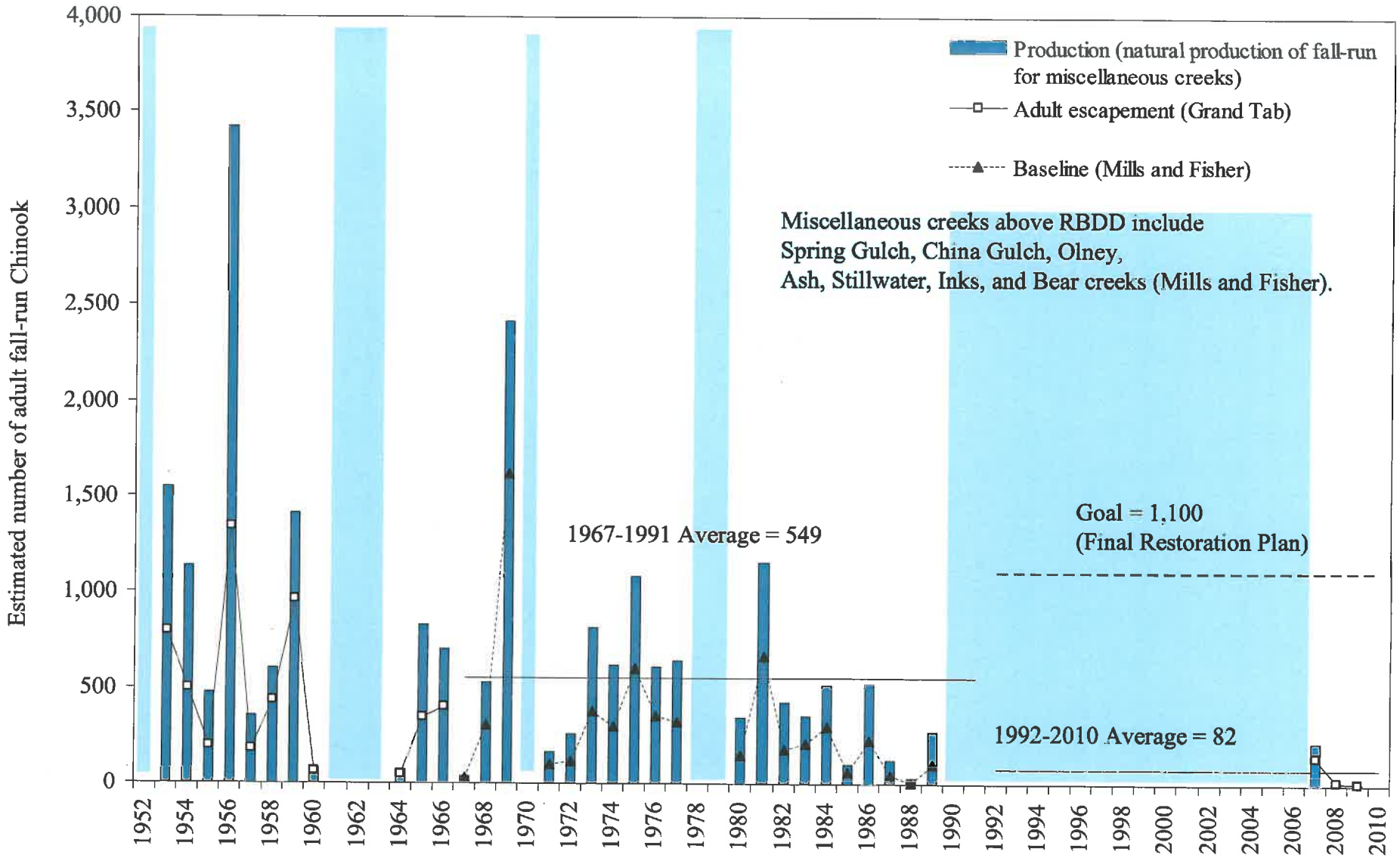


Figure 21. Estimated yearly natural production of miscellaneous creeks adult fall-run Chinook salmon above RBDD. ▭ = data was not available for 1952 -1955, 1963 – 1968 and 1970 – 2006. 1952 – 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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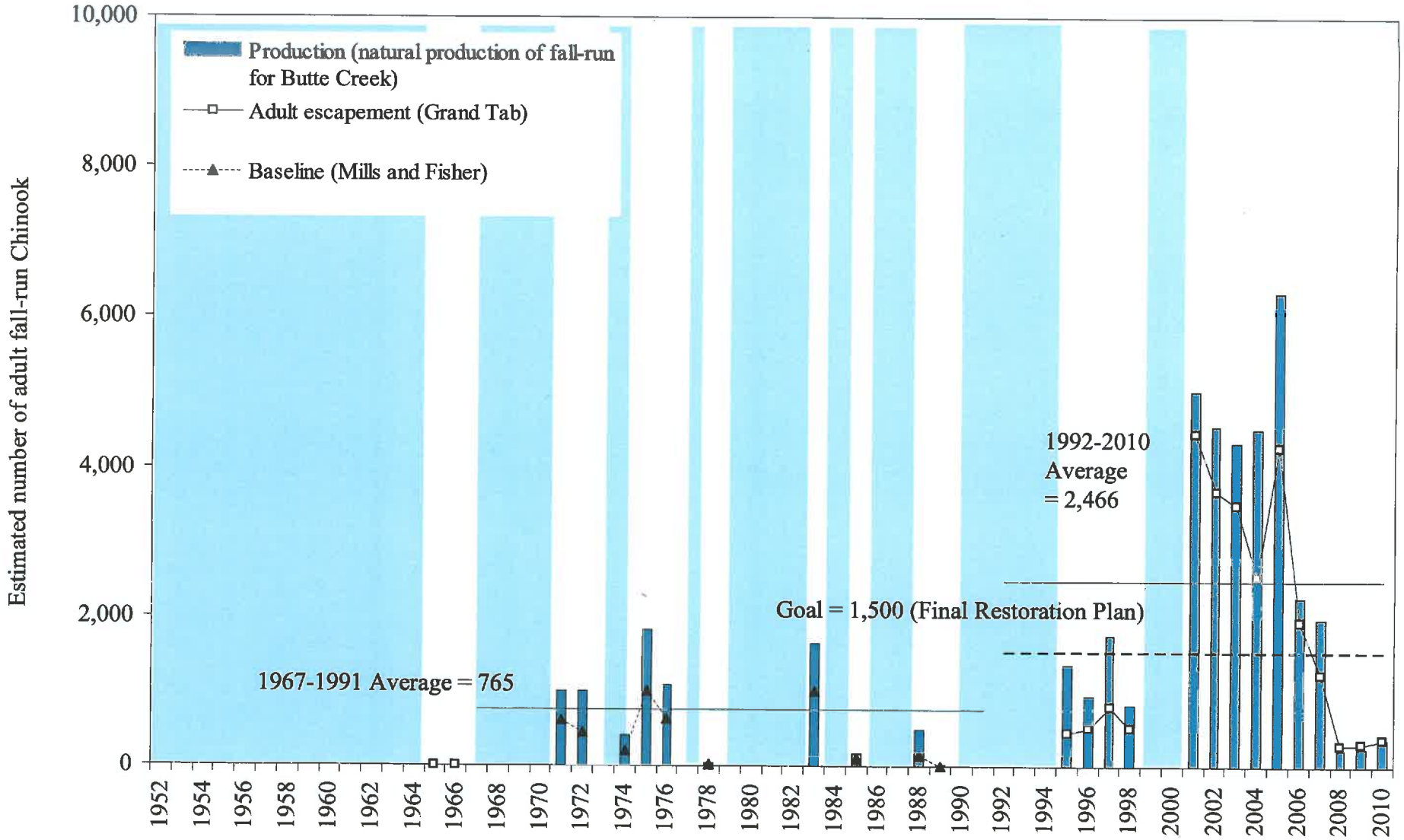


Figure 22. Estimated yearly natural production and in river escapement of Butte Creek adult fall-run Chinook salmon. = data was not available for 1952 - 1964, 1967 - 1970, 1973, 1977, 1979 - 1982, 1984, 1986,1987, 1990 -1994, and 1999 - 2001. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 – 1991) are from Mills and Fisher (CDFG, 1994).

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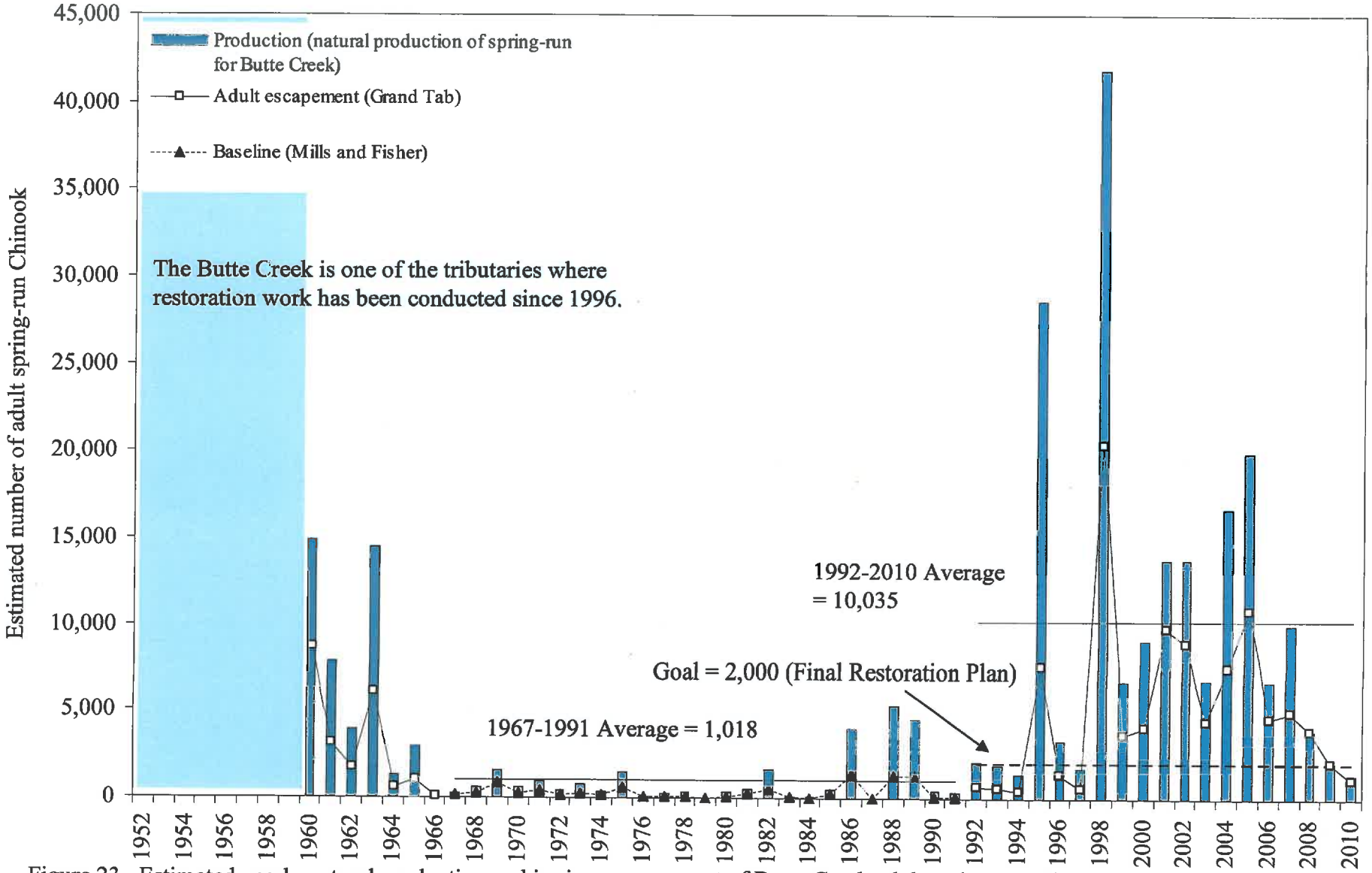


Figure 23. Estimated yearly natural production and in river escapement of Butte Creek adult spring-run Chinook salmon. 1952- 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). ▭ = data was not available for 1952 - 1959. Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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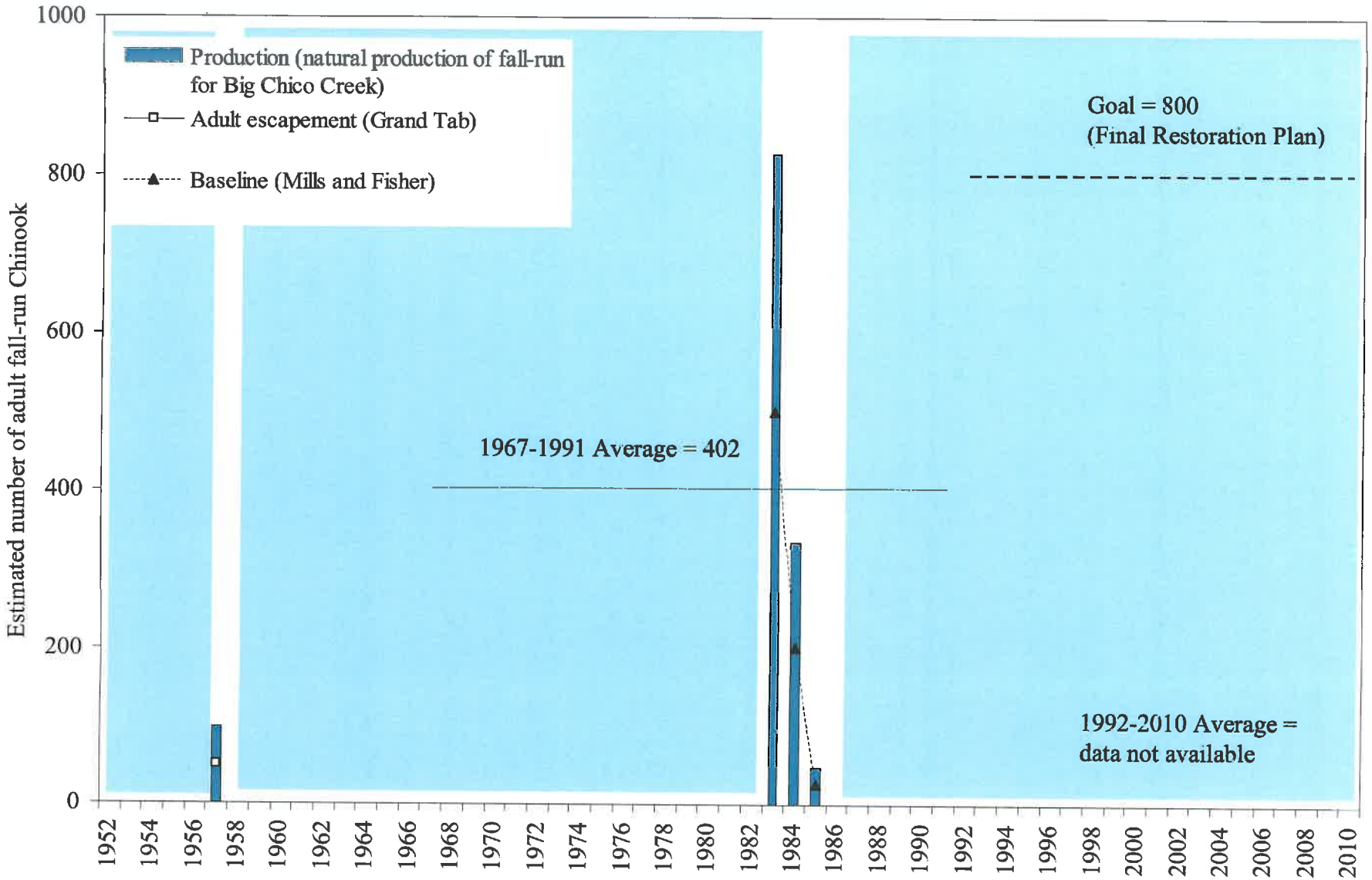


Figure 24. Estimated yearly natural production, and in river escapements of Big Chico Creek adult fall-run Chinook salmon. ▭ = data was not available for 1952 - 1956, 1958 - 1982, and 1986 - 2009. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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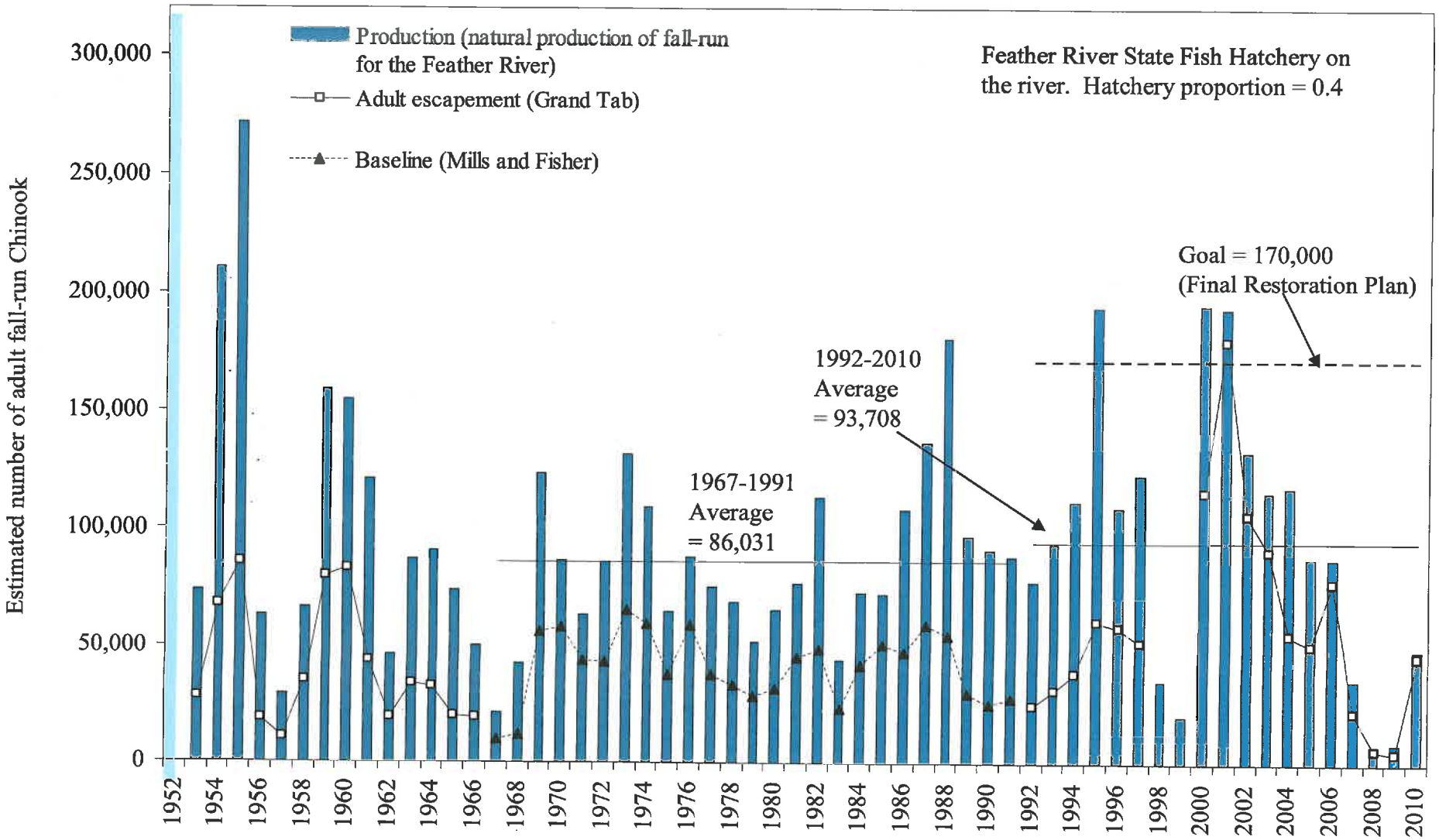


Figure 25. Estimated yearly natural production, and in river escapements of Feather River adult fall-run Chinook salmon. In-river escapements were not available for 1998 and 1999. 1952 - 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994). 1998 and 1999 are hatchery escapement only. Starting in 2005 only fall-run returns are used for hatchery escapement.

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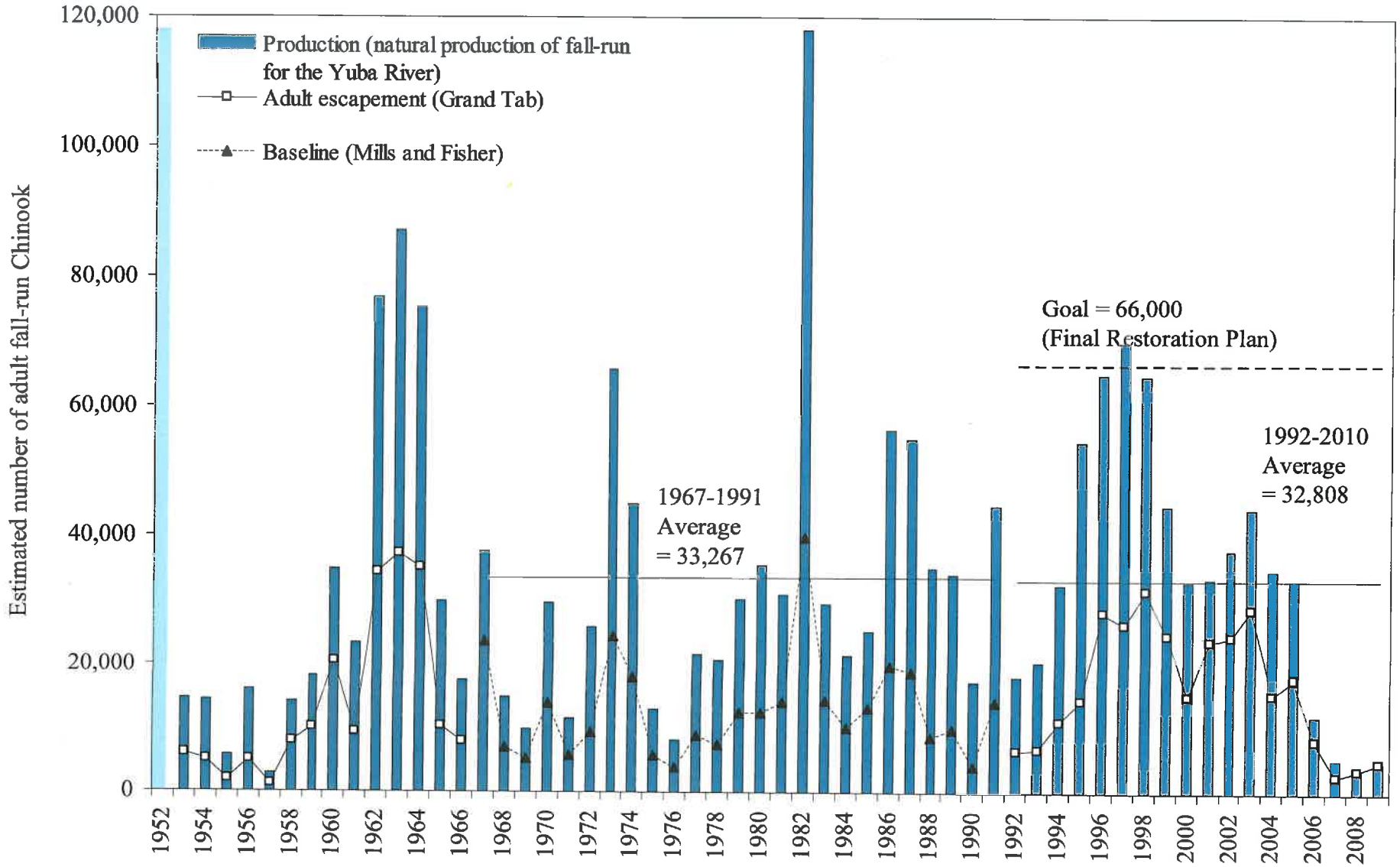


Figure 26. Estimated yearly natural production and in river escapement of Yuba River adult fall-run Chinook salmon. 1967-1991 baseline numbers are from Mills and Fisher (CDFG, 1994). 1952 - 1966 and 1992-2010 numbers are from CDFG Grand Tab (February 2, 2011). ▭ = data was not available for 1952.

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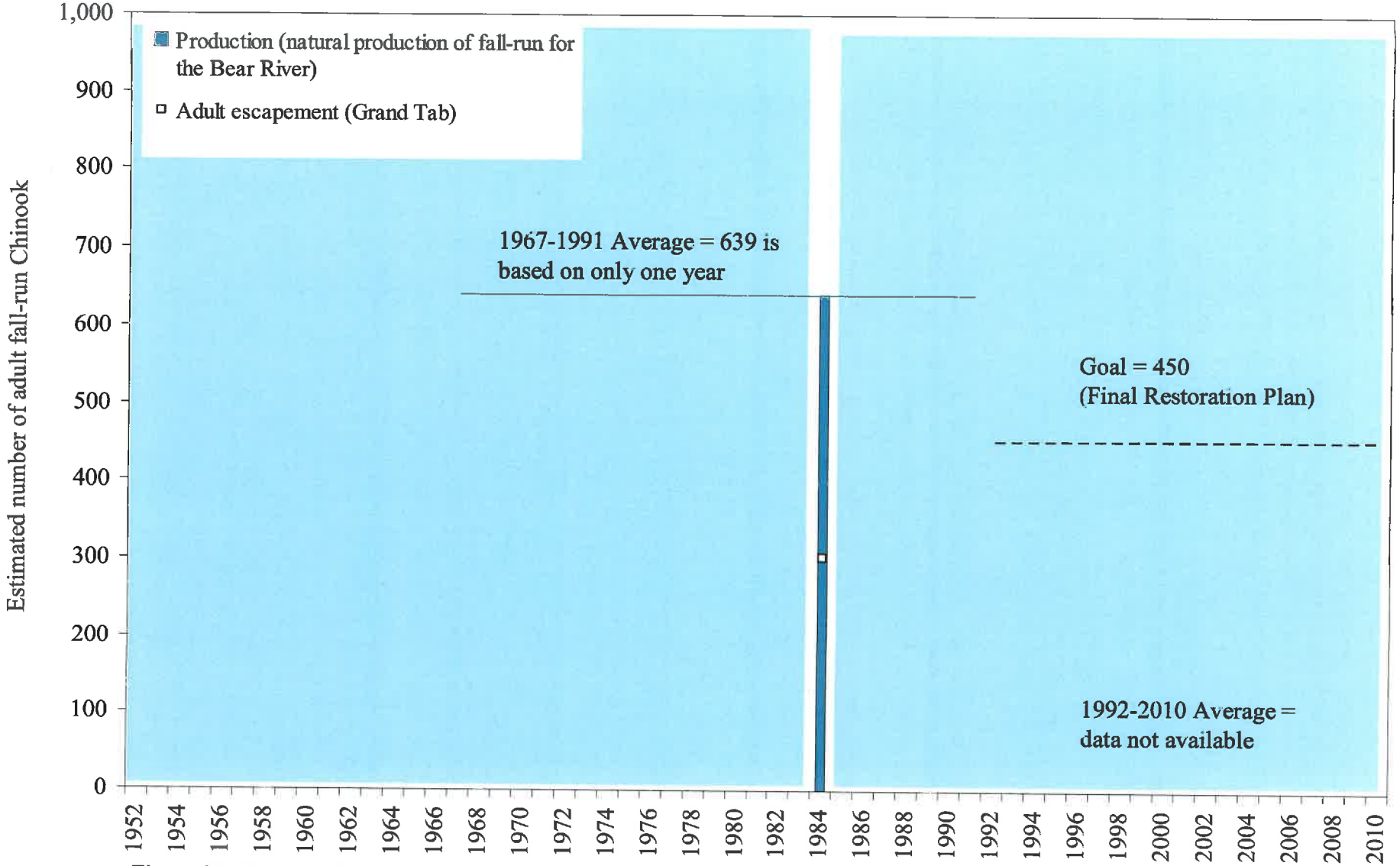


Figure 27. Estimated yearly natural production and in river escapement of Bear River adult fall-run Chinook salmon. = data was not available for 1952 - 1983, and 1985 – 2010. Numbers are from CDFG Grand Tab (February 2, 2011).

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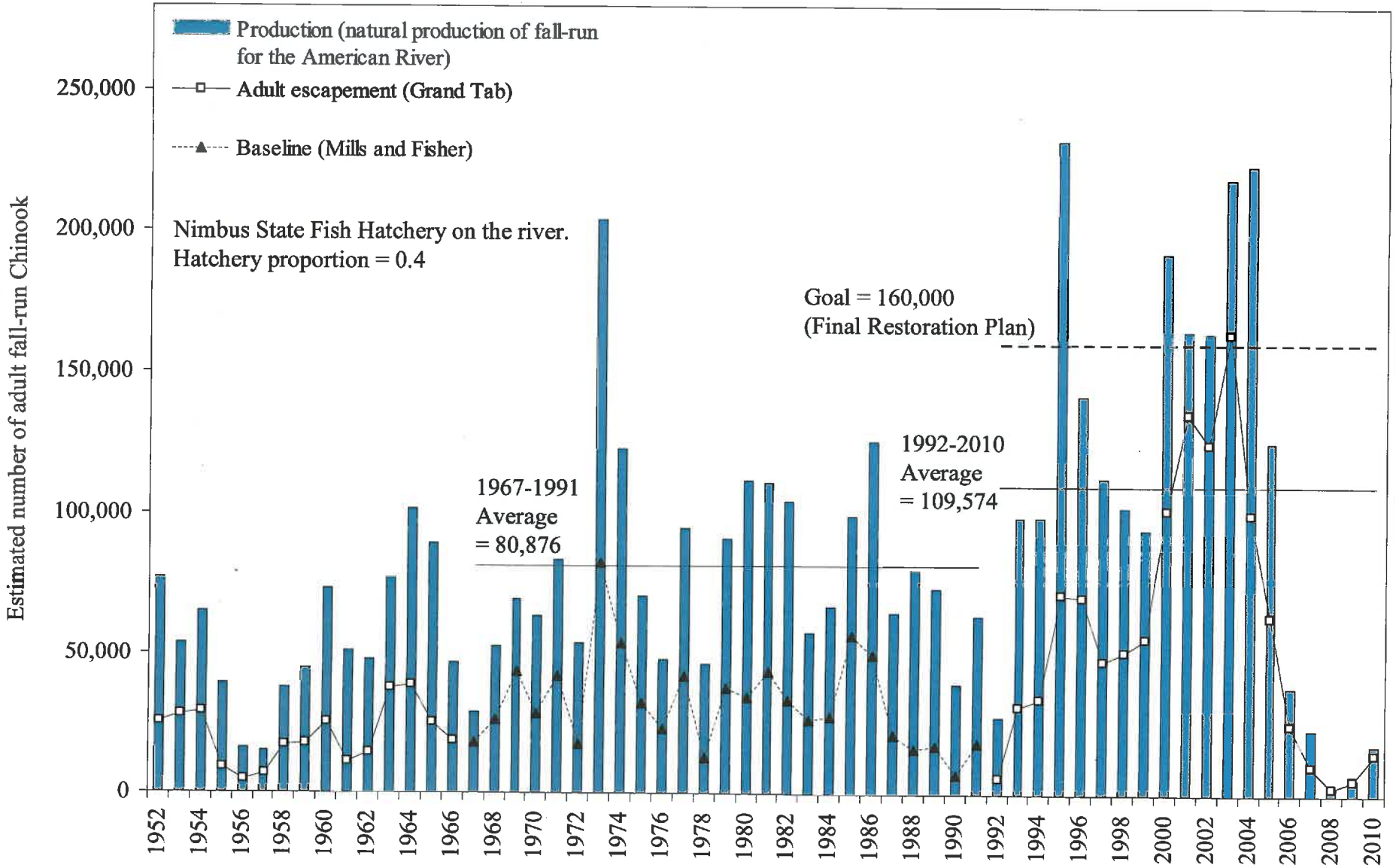


Figure 28. Estimated yearly natural production and in river escapement of American River adult fall-run Chinook salmon. 1952 - 1966, and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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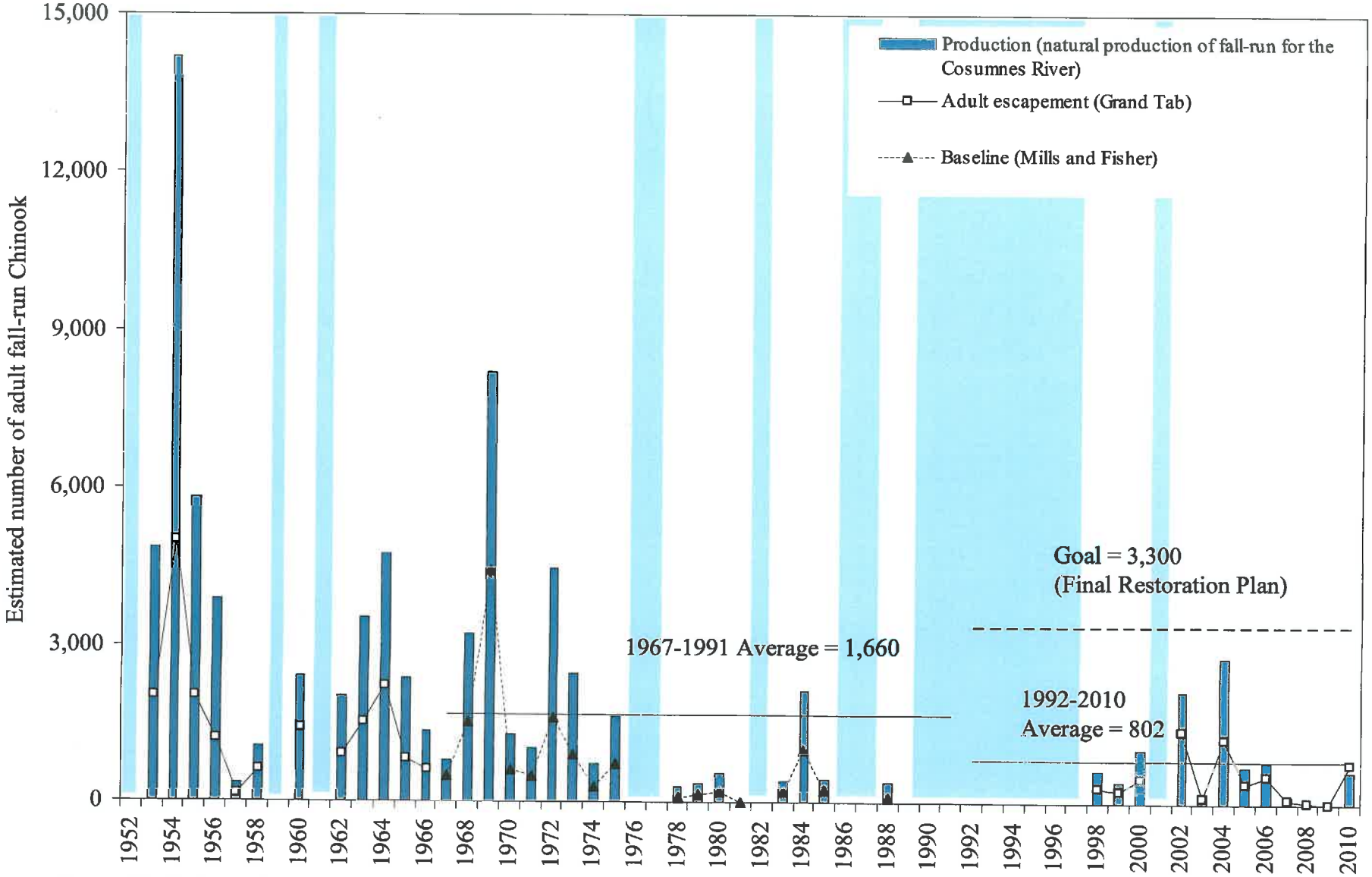


Figure 29. Estimated yearly natural production and in river escapement of Cosumnes River adult fall-run Chinook salmon. = data was not available for 1952, 1959, 1961, 1976-1977, 1982, 1986, 1987, 1989 - 1997, and 2001. 1952-1966 and 1992-2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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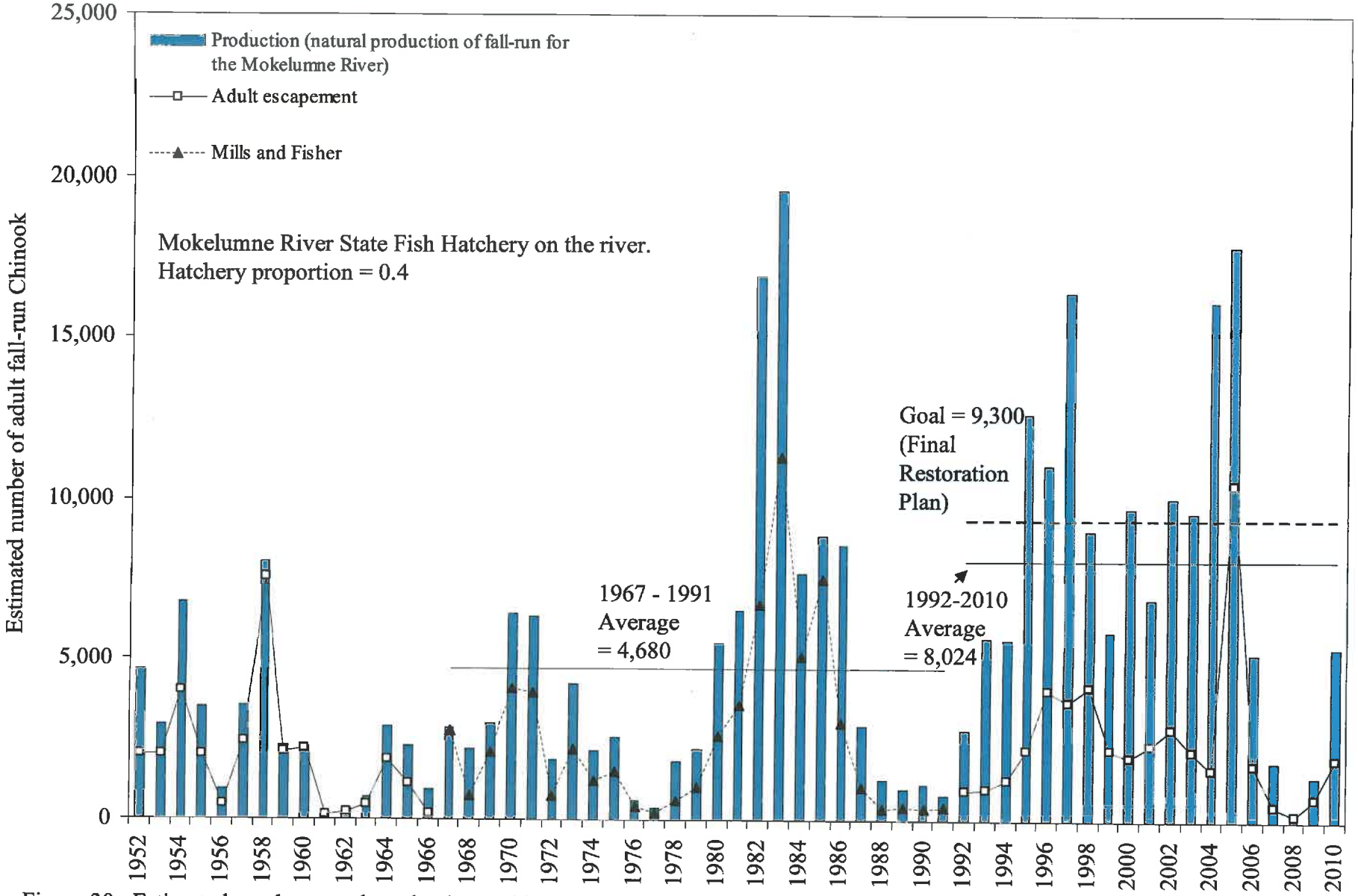


Figure 30. Estimated yearly natural production and in river escapement of Mokelumne River adult fall-run Chinook salmon. In river escapement numbers were not available for 2001. 1952 – 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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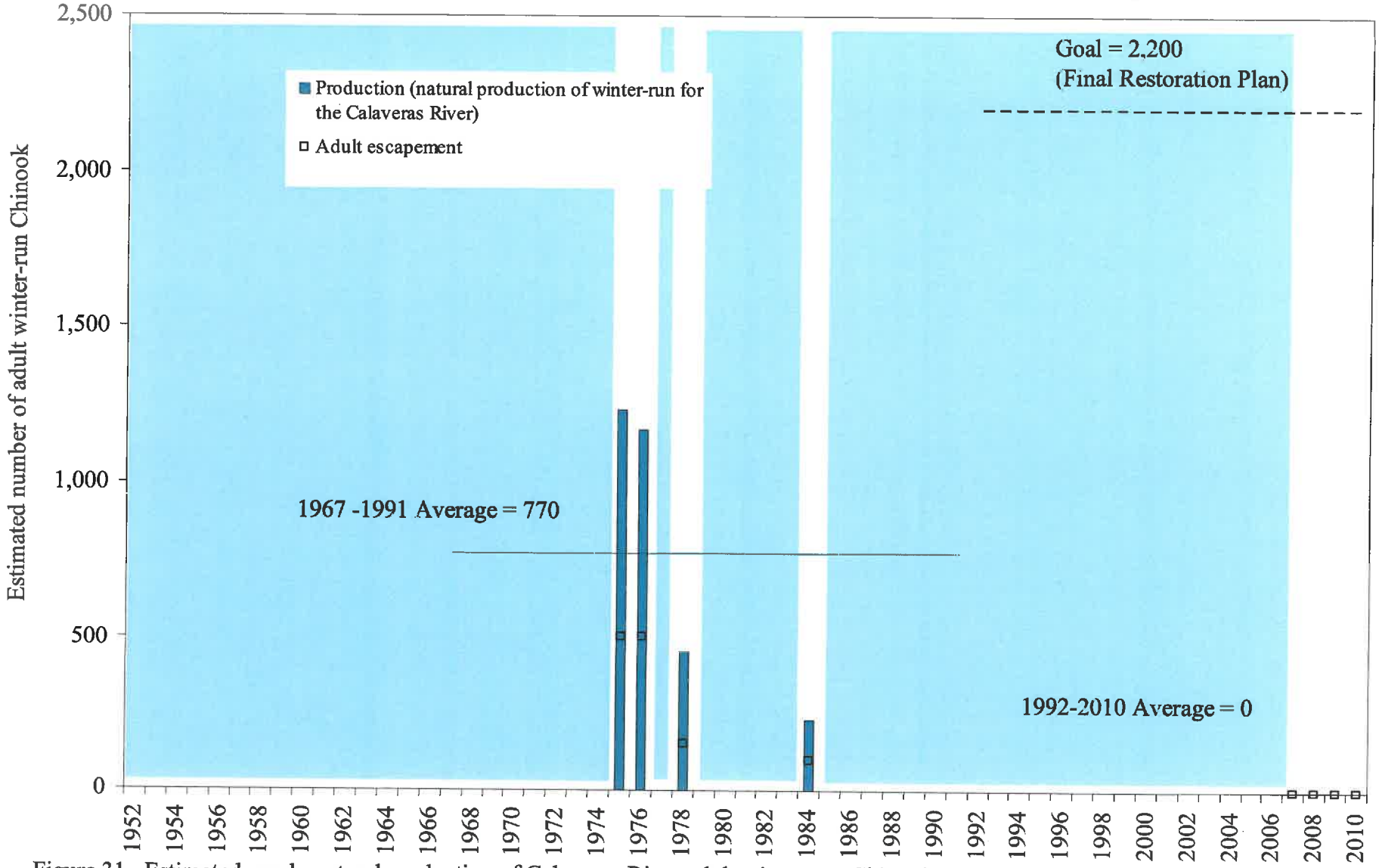


Figure 31. Estimated yearly natural production of Calaveras River adult winter-run Chinook salmon. ▭ = data was not available for 1952 - 1974, 1977, 1979 – 1983, and 1985 - 2006. 1952 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers from Mills and Fisher (CDFG, 1994) were not available.

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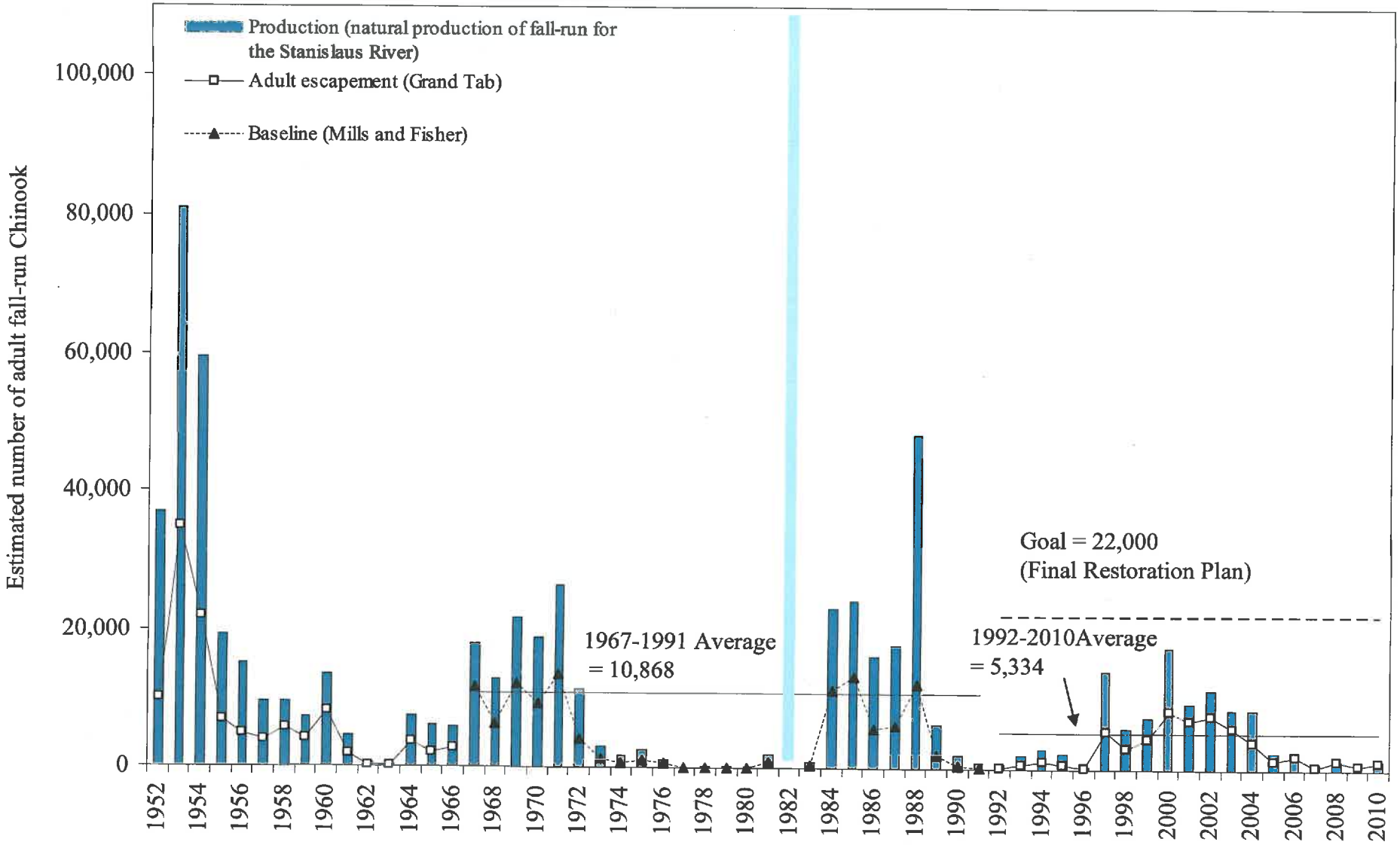


Figure 32. Estimated yearly natural production and in river escapement of Stanislaus River adult fall-run Chinook salmon. 1952 – 1966 and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994). = data was not available for 1982.

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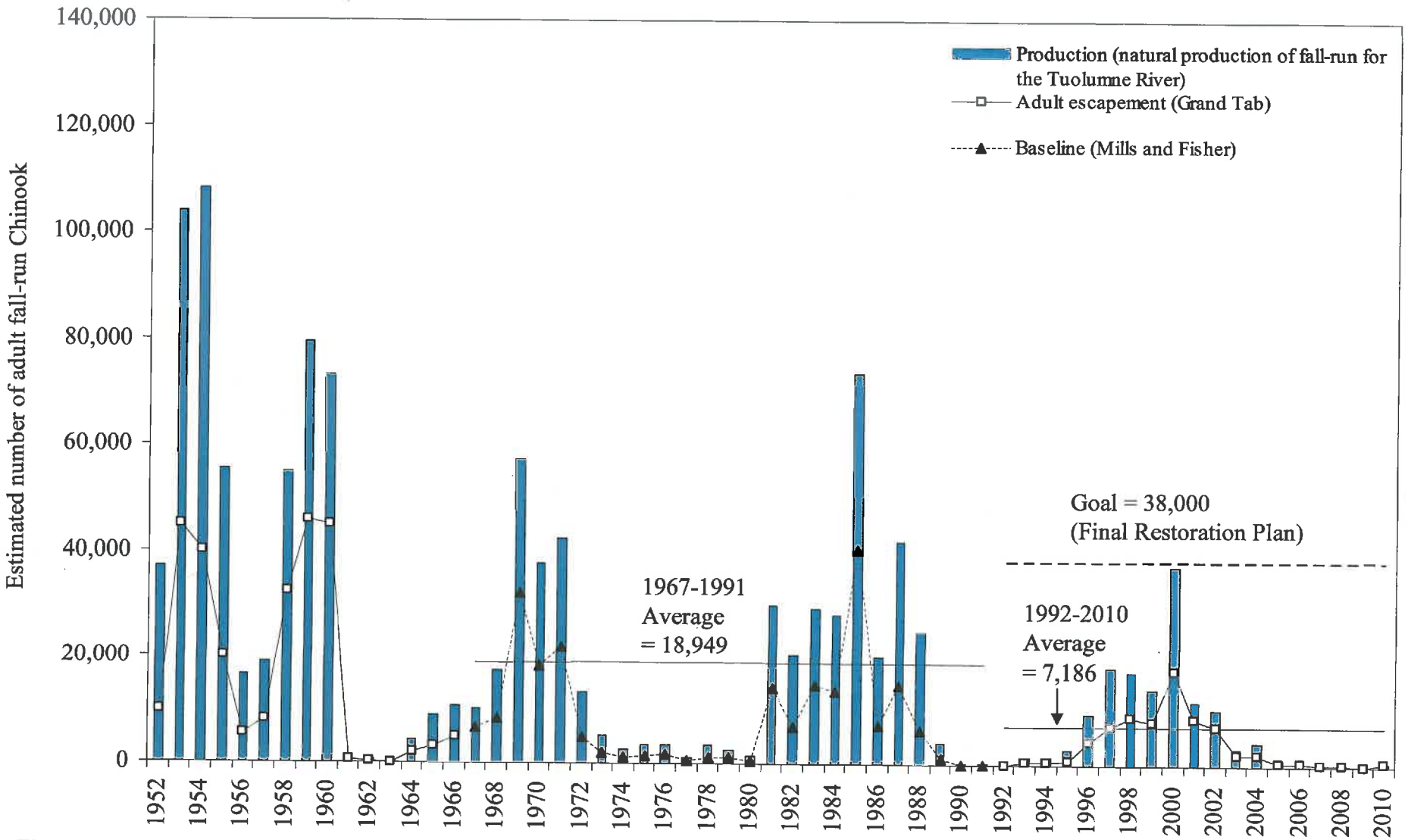


Figure 33. Estimated yearly natural production and in river escapement of Tuolumne River adult fall-run Chinook salmon. 1952 - 1966, and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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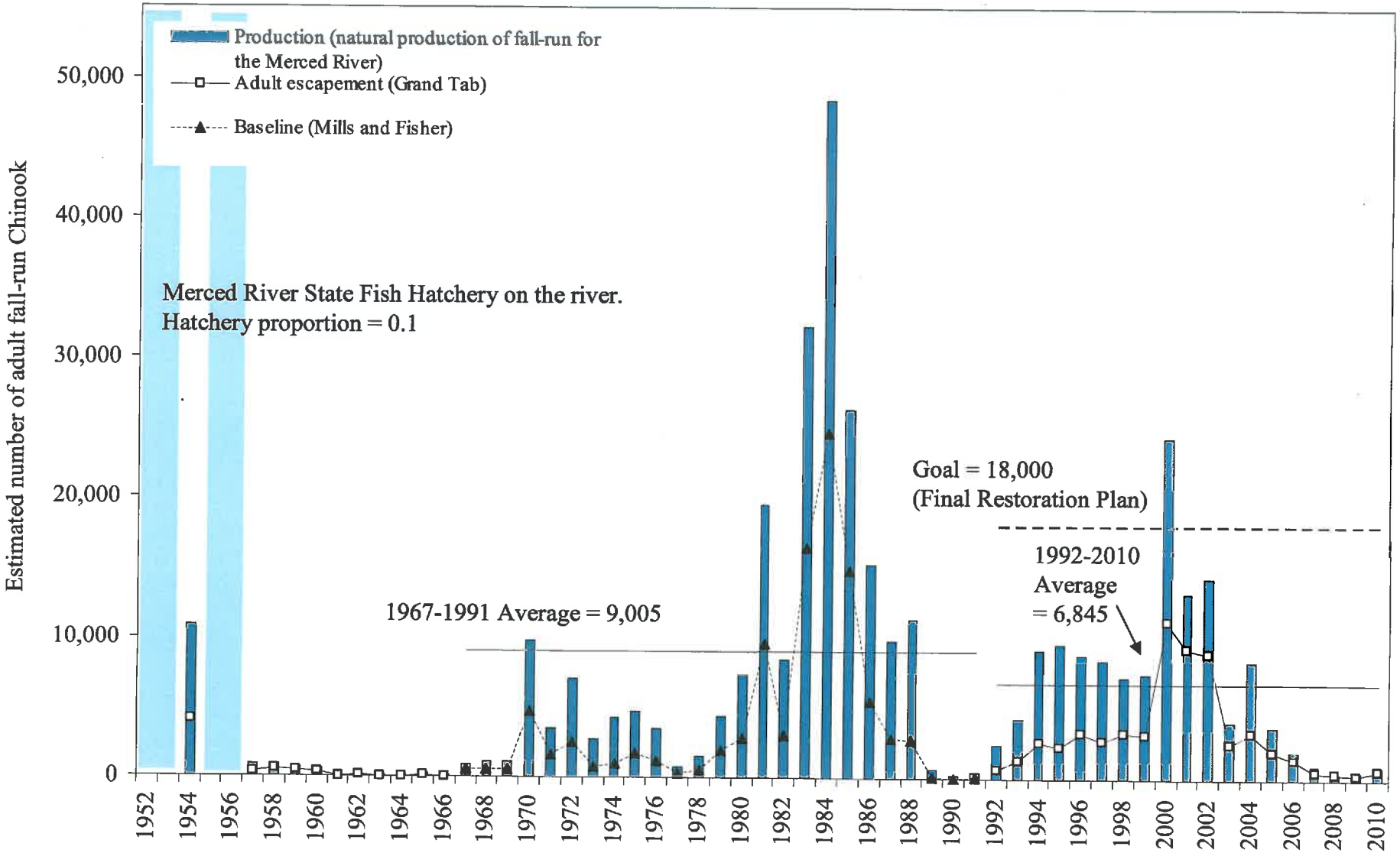


Figure 34. Estimated yearly natural production and in river escapement of Merced River adult fall-run Chinook salmon. 1952 - 1966, and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). ▭ = data was not available for 1952 - 1953, and 1955 - 1956. Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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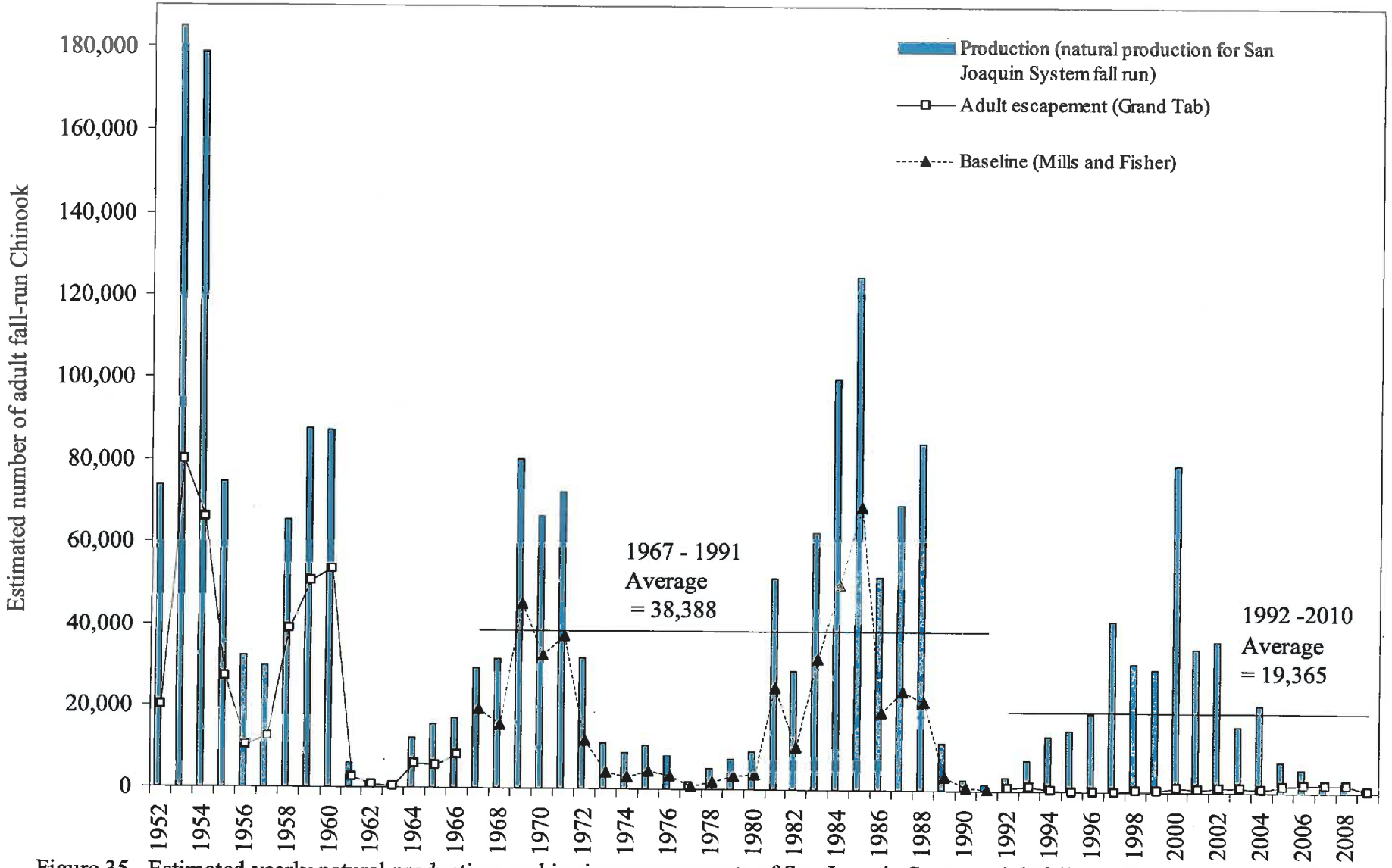


Figure 35. Estimated yearly natural production, and in river escapements of San Joaquin System adult fall-run Chinook salmon. The San Joaquin System is the sum of the Stanislaus, Tuolumne, and Merced Rivers. 1952 - 1966, and 1992 - 2010 numbers are from CDFG Grand Tab (February 2, 2011). Baseline numbers (1967 - 1991) are from Mills and Fisher (CDFG, 1994).

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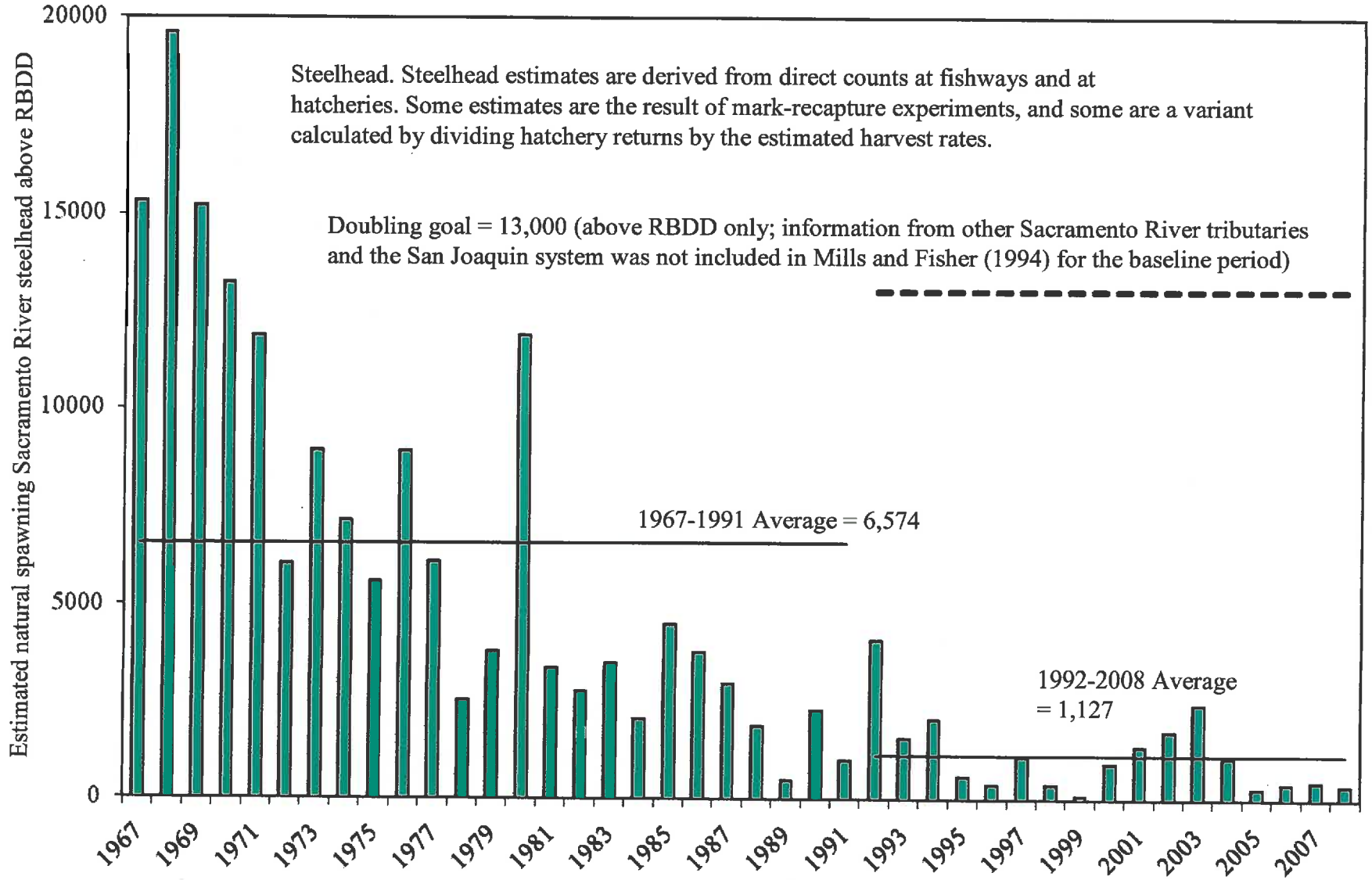


Figure 36. Estimated yearly number of natural spawning of steelhead on the Sacramento River, upstream of the RBDD (Mills and Fisher, 1994). Data for 1992-2008 is from CDFG, Red Bluff. 2008 sampling was curtailed in June due to high water temperatures.

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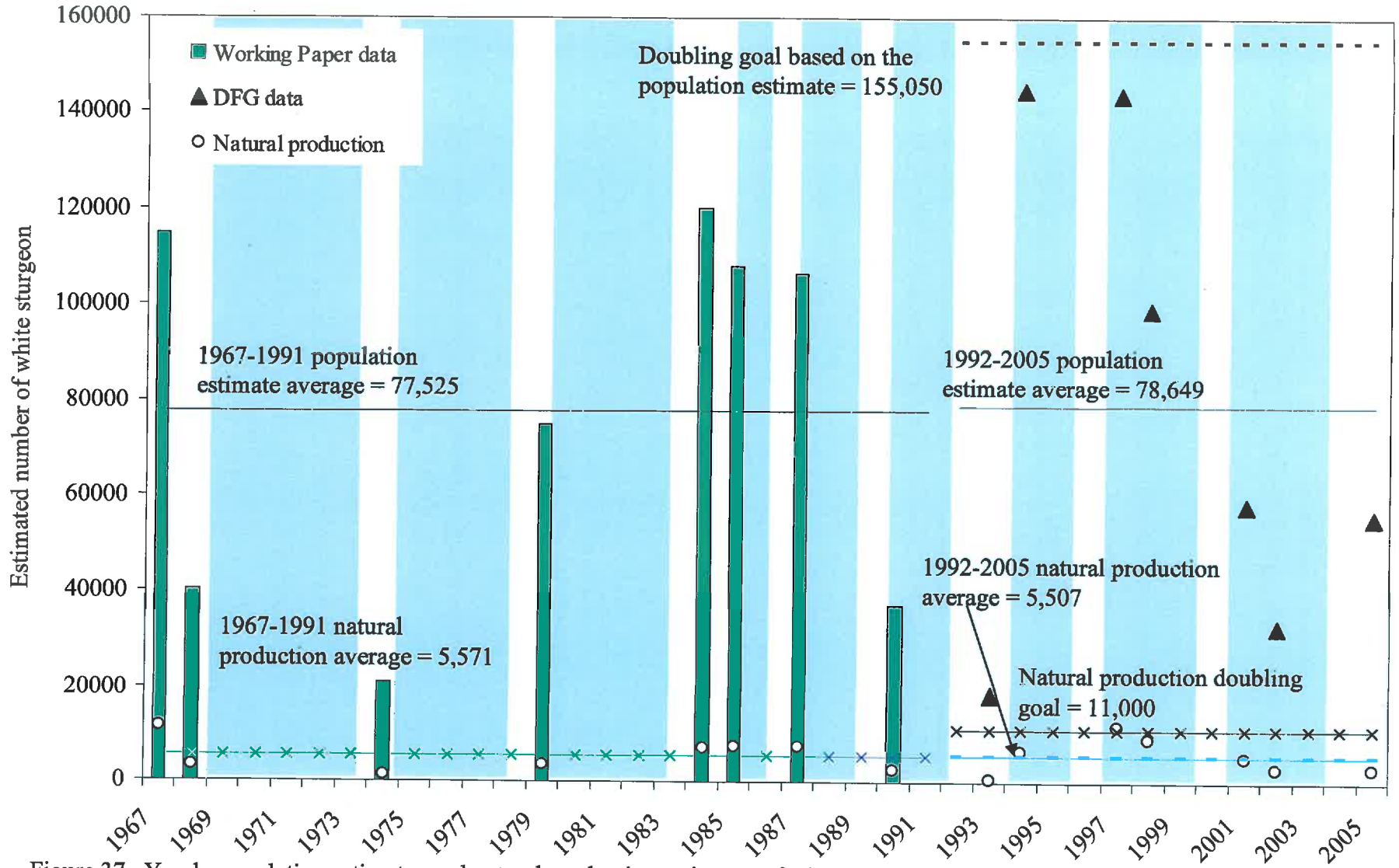


Figure 37. Yearly population estimates and natural production estimates of white sturgeon in the Central Valley. Population estimates are for >= 40 inch fish, while natural production estimates are based on age 15 fish. 1967-1991 baseline numbers are from the Working Papers on Restoration Needs, Vol. 3 (1995), and 1992-2001 numbers are from CDFG, Bay Delta. ▭ = data was not available for 1991-1992, 1995-1996, 1999-2000, and 2003-2004.

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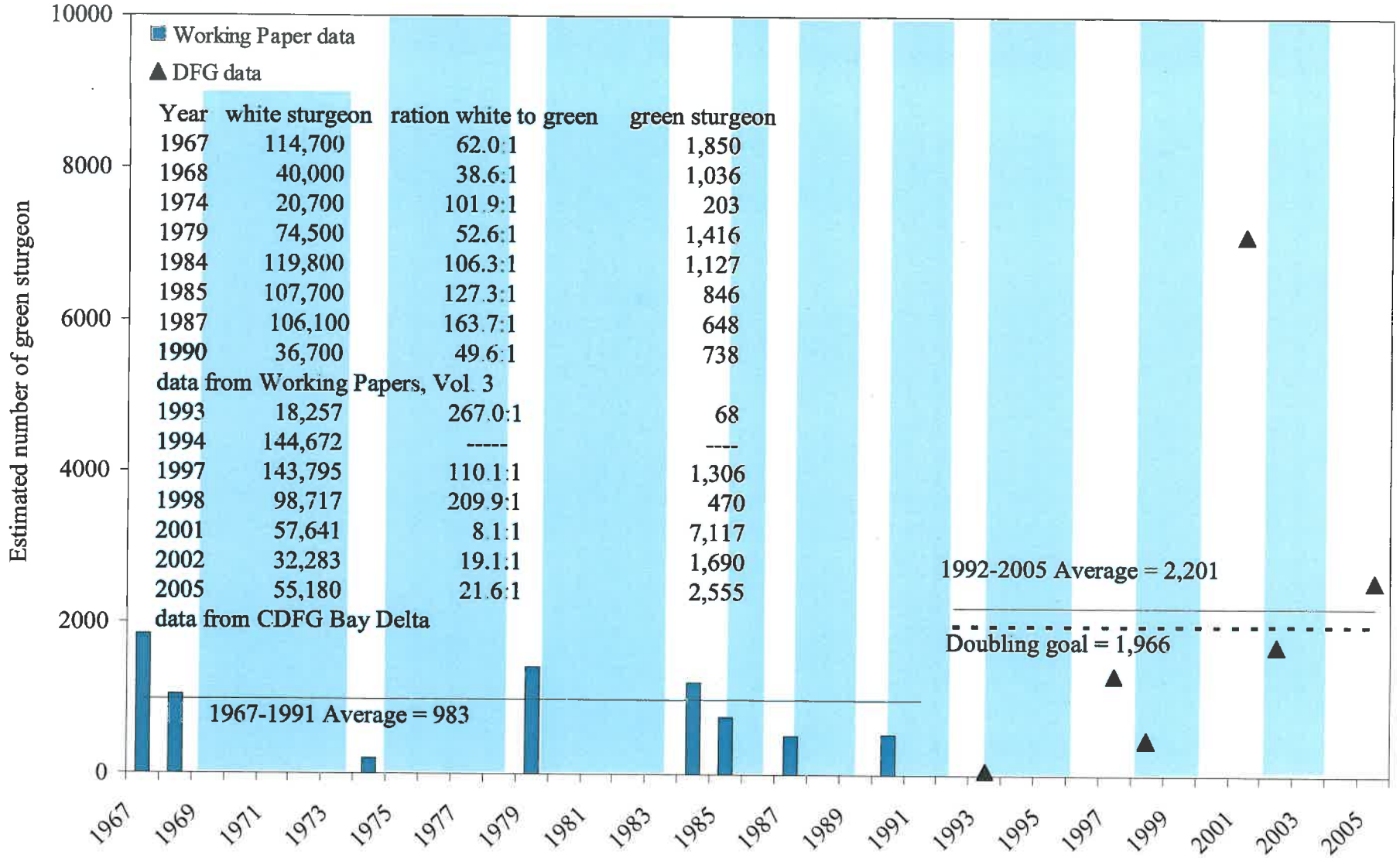


| Year | white sturgeon | ration white to green | green sturgeon |
|---|---|---|---|
| 1967 | 114,700 | 62.0:1 | 1,850 |
| 1968 | 40,000 | 38.6:1 | 1,036 |
| 1974 | 20,700 | 101.9:1 | 203 |
| 1979 | 74,500 | 52.6:1 | 1,416 |
| 1984 | 119,800 | 106.3:1 | 1,127 |
| 1985 | 107,700 | 127.3:1 | 846 |
| 1987 | 106,100 | 163.7:1 | 648 |
| 1990 | 36,700 | 49.6:1 | 738 |
| data from Working Papers, Vol. 3 | | | |
| 1993 | 18,257 | 267.0:1 | 68 |
| 1994 | 144,672 | ----- | ---- |
| 1997 | 143,795 | 110.1:1 | 1,306 |
| 1998 | 98,717 | 209.9:1 | 470 |
| 2001 | 57,641 | 8.1:1 | 7,117 |
| 2002 | 32,283 | 19.1:1 | 1,690 |
| 2005 | 55,180 | 21.6:1 | 2,555 |
| data from CDFG Bay Delta | | | |

Figure 38. Yearly estimated abundance of green sturgeon in the Central Valley. 1967-1991 baseline numbers are from the Working Paper on Restoration Needs, Vol. 3 (1995), and 1992-2005 numbers are from CDFG, Bay Delta. ▭ = data was not available for 1969-1973, 1975-1978, 1980-1983, 1986, 1988-1989, 1991-1992, 1994-1996, 1999-2000, and 2004-2005. Green sturgeon estimates were based on a ratio of white to green sturgeon captured during those years when DFG was sampling for these fish.

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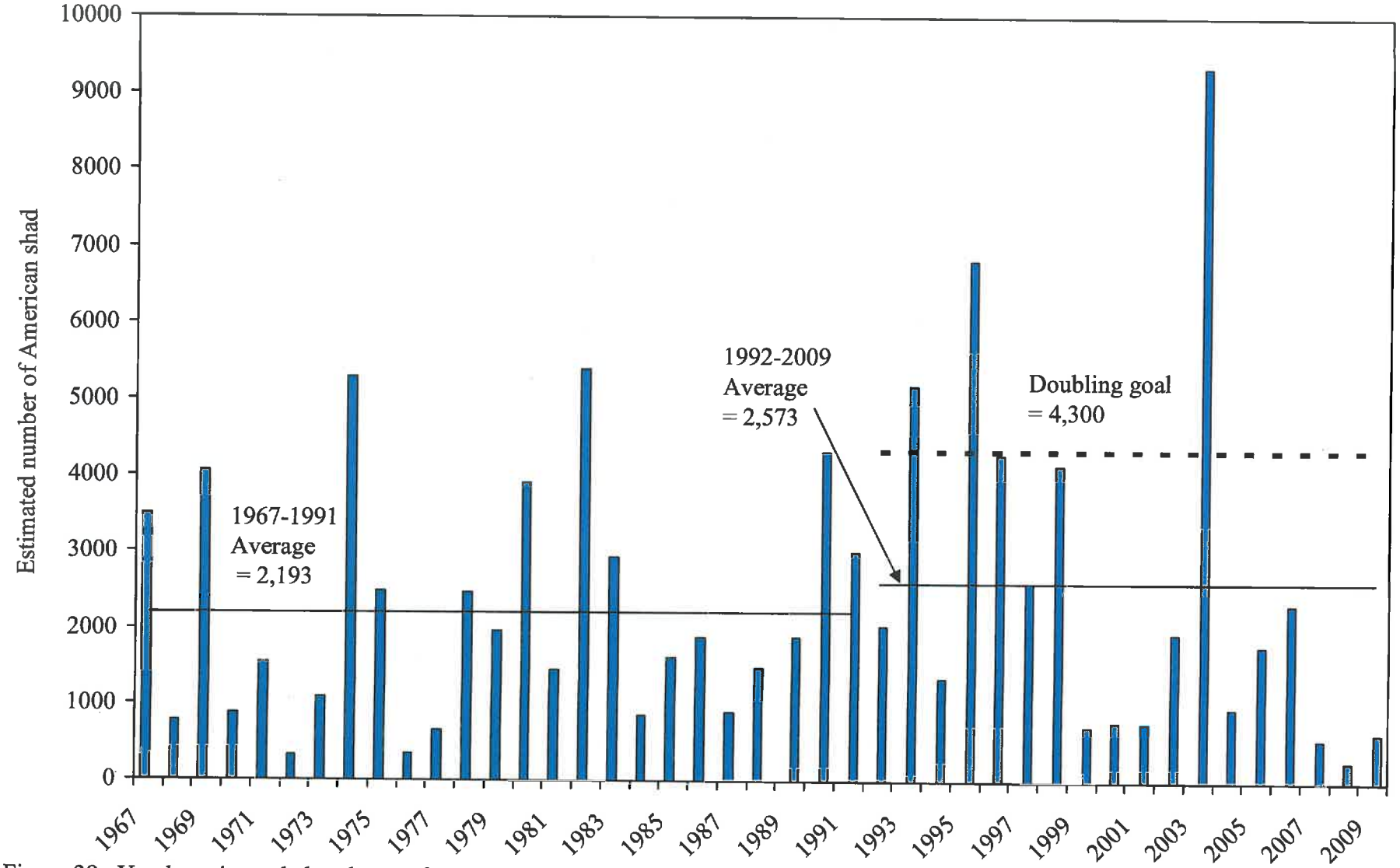


Figure 39. Yearly estimated abundance of American shad in the Central Valley, 1967 through 2005. Data, based on juvenile abundance from CDFG, Central Valley Bay Delta Branch (CVBDB) fall midwater trawl, was used as an index of production. 1967 – 1988 data is from the Working Papers, Vol.3, and 1989 – 2009 data is the from CDFG, CVBDB midwater trawl website. The Working Papers and CVBDB site a young-of year index .

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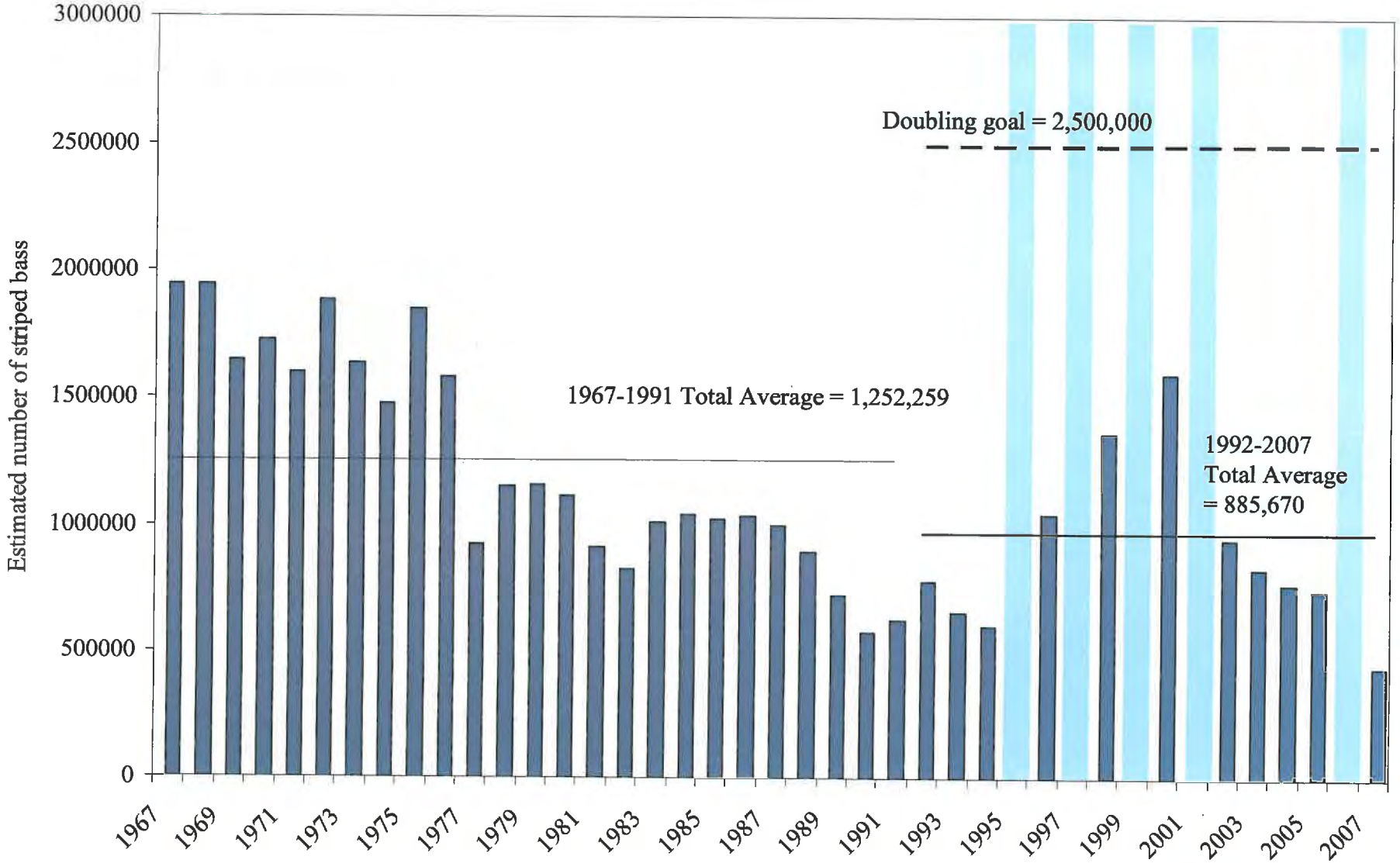


Figure 40. Yearly estimated abundance of adult sized (> 15 inches before 1982, and > 16.5 inches thereafter) striped bass in the Central Valley. Data is from the Mills and Fisher (1967-1991), and CDFG, Bay Delta (1992-2007). ▭ = data was not available for 1995, 1997, 1999, 2001, and 2006.

# Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival

**T.R. Sommer, M.L. Nobriga, W.C. Harrell, W. Batham, and W.J. Kimmerer**

**Abstract**: In this study, we provide evidence that the Yolo Bypass, the primary floodplain of the lower Sacramento River (California, U.S.A.), provides better rearing and migration habitat for juvenile chinook salmon (*Oncorhynchus tshawytscha*) than adjacent river channels. During 1998 and 1999, salmon increased in size substantially faster in the seasonally inundated agricultural floodplain than in the river, suggesting better growth rates. Similarly, coded-wire-tagged juveniles released in the floodplain were significantly larger at recapture and had higher apparent growth rates than those concurrently released in the river. Improved growth rates in the floodplain were in part a result of significantly higher prey consumption, reflecting greater availability of drift invertebrates. Bioenergetic modeling suggested that feeding success was greater in the floodplain than in the river, despite increased metabolic costs of rearing in the significantly warmer floodplain. Survival indices for coded-wire-tagged groups were somewhat higher for those released in the floodplain than for those released in the river, but the differences were not statistically significant. Growth, survival, feeding success, and prey availability were higher in 1998 than in 1999, a year in which flow was more moderate, indicating that hydrology affects the quality of floodplain rearing habitat. These findings support the predictions of the flood pulse concept and provide new insight into the importance of the floodplain for salmon.

**Résumé** : Notre étude démontre que le canal de dérivation Yolo, la principale plaine d'inondation de la région aval de la rivière Sacramento (Californie, É.-U.), offre de meilleurs habitats pour l'alevinage et la migration des jeunes Saumons Quinnat (*Onchorhynchus tshawytscha*) que les bras adjacents de la rivière. En 1998 et 1999, la taille des saumons a augmenté plus rapidement dans la plaine d'inondation agricole, sujette aux débordements saisonniers de crue, que dans la rivière, ce qui laisse croire à de meilleurs taux de croissance. De plus, des jeunes saumons marqués à l'aide de fils de métal codés et relâchés dans la plaine d'inondation étaient plus gros au moment de leur recapture et avaient des taux de croissance apparente plus élevés que des poissons relâchés dans la rivière en même temps. L'amélioration des taux de croissance dans la plaine de débordement résultait en partie d'une consommation significativement plus importante de proies, le reflet d'une plus grande disponibilité des invertébrés de la dérive. Un modèle bioénergétique laisse croire que le succès de l'alimentation a été meilleur dans la plaine d'inondation que dans la rivière, en dépit du coût métabolique d'alevinage significativement plus grand dans les eaux plus chaudes de la plaine d'inondation. Les indices de survie des poissons marqués et relâchés dans la plaine d'inondation étaient quelque peu plus élevés que ceux des poissons de la rivière, mais les différences n'étaient pas statistiquement significatives. La croissance, la survie, le succès de l'alimentation et la disponibilité des proies étaient tous supérieurs en 1998 par comparaison avec 1999, une année à débit plus modéré, ce qui indique que l'hydrologie affecte la qualité des habitats d'alevinage dans la plaine d'inondation. Nos résultats appuient les prédictions du concept de pulsion de crue (flood pulse concept) et mettent en lumière l'importance de la plaine d'inondation pour le saumon.

[Traduit par la Rédaction]

## Introduction

Although the trophic structure of large rivers is frequently dominated by upstream processes (Vannote et al. 1980), there is increasing recognition that floodplains plays a major role in the productivity and diversity of riverine communities (Bayley 1995). Based largely on observations from relatively undisturbed river–floodplain systems, Junk et al. (1989) proposed the flood pulse concept, which predicts that annual inundation is the principal force determining productivity and biotic interactions in river–floodplain systems. Floodplains can provide higher biotic diversity (Junk et al. 1989) and increased production of fish (Bayley 1991; Halyk and Balon 1983) and invertebrates (Gladden and Smock 1990). Potential mechanisms for floodplain effects include increased habitat diversity and area (Junk et al. 1989), large inputs of

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terrestrial material into the aquatic food web (Winemiller and Jepsen 1998), and decreased predation or competition due to intermediate levels of disturbance (Corti et al. 1997). Nonetheless, the degree to which floodplains support riverine ecosystems remains poorly understood, particularly in regulated and temperate rivers. Uncertainties about river–floodplain relationships are due, in large part, to the difficulty in separating the relative contribution of floodplain versus channel processes and sampling problems in seasonal habitats, which are frequently subject to extreme environmental variation.

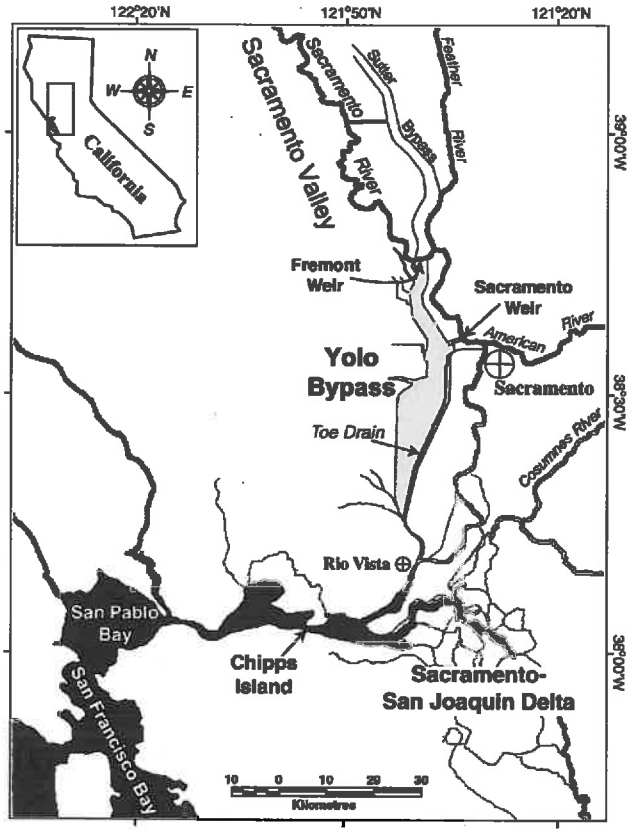
In the this study, we examined the relative importance of floodplain and riverine habitat to juvenile chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River (California, U.S.A.), a large regulated river (Fig. 1). The system is particularly well suited to a comparative study, because young salmon migrating down the lower Sacramento River to the San Francisco Estuary in wet years have two alternative paths: they may continue down the heavily channelized main river or they may pass through the Yolo Bypass, an agricultural floodplain bordered by levees. We had two reasons to believe that the floodplain might be important habitat for young salmon. First, years of high flow are known to enhance populations of a variety of species in the San Francisco Estuary (Jassby et al. 1995) and the survival of chinook salmon (Kjelson et al. 1982). However, the specific mechanisms for these benefits have not been established. Possible reasons for the positive effects of flow on fish include increased habitat availability, migration cues, food supply, larval transport, and reduced predation rates (Bennett and Moyle 1996). Floodplain inundation is one of the unique characteristics of wet years, during which the Yolo Bypass is likely to be a significant migration corridor for young chinook salmon in the Sacramento Valley. During high-flow events, the Yolo Bypass can convey >75% of the total flow from the Sacramento River basin, the major producer of salmon among tributaries of the San Francisco Estuary. Second, floodplains are known to be among the most important fish-rearing areas in a variety of river systems, yet in developed regions, the availability of this habitat has been greatly reduced by channelization and levee and dam construction (Rasmussen 1996). A high degree of habitat loss may greatly enhance the biological significance of remnant floodplains in heavily modified systems, such as the San Francisco Estuary and its tributaries.

This study tests the hypothesis that the agricultural floodplain provides better habitat quality than the adjacent river channel. For the purpose of this analysis, we focus on salmon growth, feeding success, and survival as indicators of habitat quality. Obviously, there are many other possible measures of habitat quality, such as reproductive output of adults or physiological indicators. However, we believe that the chosen suite of parameters is reasonably representative of habitat quality. For example, Gutreuter et al. (2000) successfully used growth as a factor to test the hypothesis that floodplain inundation had a major effect on fish production.

The San Francisco Estuary is one of the largest estuaries on the Pacific Coast (Fig. 1). The system includes downstream bays (San Pablo and San Francisco) and a delta, a broad network of tidally influenced channels that receive inflow from the Sacramento and San Joaquin rivers. The estuary and its tributaries have been heavily altered by levees, dams, land reclamation activities, and water diversions. The primary floodplain of the Sacramento River portion of the delta is the Yolo Bypass, a 24 000-ha leveed basin that conveys excess flow from the Sacramento Valley, including the Sacramento River, Feather River, American River, Sutter Bypass, and westside streams. The 61 km long floodplain floods seasonally in winter and spring in about 60% of years, and is designed to convey up to 14 000 $m^3 \cdot s^{-1}$. During a typical flooding event, water spills into the Yolo Bypass via the Fremont Weir when Sacramento Basin flows surpass approximately 2000 $m^3 \cdot s^{-1}$. Except during extremely high flow events, the mean depth of the floodplain is generally less than 2 m, creating broad shoal areas. During dry seasons, the Toe Drain channel, a permanent riparian corridor, remains inundated as a result of tidal action. At higher levels of Sacramento Basin flow (e.g., >5000 $m^3 \cdot s^{-1}$), the Sacramento Weir is also frequently operated. Agricultural fields are the dominant habitat type in Yolo Bypass, but approximately one-third of the floodplain area is natural vegetation, including riparian habitat, upland habitat, emergent marsh, and permanent ponds.

There are four races of chinook salmon in the Sacramento Valley: winter, spring, late fall, and fall run (Yoshiyama et al. 2000). Historical data indicate that all races have de-

**Fig. 1.** The location of Yolo Bypass in relation to the San Francisco Estuary and its tributaries. The San Francisco Estuary encompasses the region from San Francisco Bay upstream to Sacramento. Feather River Fish Hatchery is located on the Feather River approximately 112 km upstream of Yolo Bypass.

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creased in abundance since the 1950s, but the spring, winter, and late-fall runs have shown the most pronounced declines. There are multiple causes for these long-term reductions, including habitat loss, habitat degradation, water diversions, and oceanic conditions. In the present study, we focused on the fall run, the numerically dominant race in the Sacramento Valley. The typical life-history pattern for these salmon is for young to migrate from the tributaries to the bay–delta area at the "fry" stage (Brandes and McLain 2001), when most individuals are approximately 35- to 70-mm fork length (FL). In low flow years, there may be substantial upstream rearing in the Sacramento River. Peak juvenile emigration from the tributaries occurs during winter and spring (Kjelson et al. 1982).

## Materials and methods

### Physical conditions

During 1998–1999, flow measurements in Yolo Bypass and the adjacent stretch of the Sacramento River were obtained from gauges operated by the U.S. Geological Survey (USGS). Daily water temperatures for each site were calculated as the mean of maximum and minimum daily measurements for single stations in the Sacramento River (USGS) and a temperature recorder (Onset Corp.) installed in the Yolo Bypass Toe Drain channel (Fig. 1). However, from 1 February to 26 March 1998, these data were not available for Yolo Bypass. During this period, before the recorder was installed, discrete measurements were taken at the same location, typically during mid or late morning.

### Fish sampling

Salmon FL (mm) was measured during January–April in 1998 and 1999 on samples collected with 15-m beach seines (4.75-mm mesh). Samples were collected weekly at five core locations located around the perimeter of the Yolo Bypass, during periods when the basin was flooded. After the bypass drained, additional samples were collected at random locations around the perimeter of ponds near the core locations. Comparative data on salmon size in the adjacent reach of the Sacramento River were collected by the U.S. Fish and Wildlife Service (USFWS) at five beach-seine sites, using techniques similar to those used when the the bypass was flooded.

FLs of salmon obtained from beach-seine sampling were compared to determine whether there was evidence of major differences in salmon size between the Yolo Bypass and the Sacramento River. However, these data were not considered unambiguous evidence of growth differences, because the two systems were open to immigration and emigration during much of the study, and migrating salmon include multiple races of salmon that cannot be readily separated. We addressed this issue by using paired releases of coded-wire-tagged (CWT) juvenile salmon in Yolo Bypass and the Sacramento River. This approach allowed comparisons of growth among fish of similar origin and provided a relative estimate of migration time and survival. The salmon were produced and tagged at the Feather River Fish Hatchery and released on 2 March 1998 and 11 February 1999. The release sites were in Yolo Bypass below Fremont Weir (52 000 in 1998; 105 000 in 1999) and in the adjacent reach of the Sacramento River (53 000 in 1998; 105 000 in 1999). The fish had a mean FL of 57.5 ± 0.5 mm (SE) in 1998 and of 56.8 ± 0.4 mm (SE) in 1999. A small portion of each group was subsequently collected by trawling at the seaward margin of the delta at Chipps Island, which is located downstream of the confluence of the Yolo Bypass and the Sacramento River (Fig. 1). The USFWS Chipps Island survey samples a single channel location with a midwater trawl towed at the surface (Baker et al. 1995; Brandes and McLain 2001). Ten 20-min tows were made each day, except during March in 1998 and 1999, when sampling was conducted every other day. Data on migration time (days) and FL (mm) were recorded for fish recaptured from each release group. Apparent growth rate was also calculated for each fish, as: (FL of individual at Chipps Island – mean FL of CWT release group) × (migration time)$^{-1}$. Survival indices of the paired CWT releases were calculated by USFWS by dividing the number of fish recovered for each release group at Chipps Island by the number released, corrected for the fraction of time and channel width sampled (Brandes and McLain 2001).

### Diet

We performed diet comparisons on fall-run juvenile salmon (33–81 mm) collected in beach-seine samples during February–March of 1998 and 1999 from the Yolo Bypass (103 individuals) and the Sacramento River (109 individuals). Fish samples were tagged and stored individually in a deep freeze. After thawing, stomachs were removed from the fish and the contents were identified (using a dissecting microscope) to order (insects and arachnids), genus (crustaceans), or phylum (rarely eaten taxa such as oligochaetes). To develop average invertebrate length estimates, up to 10 individuals of each prey type encountered were measured. Prey dry weight estimates were calculated from average lengths, using regression equations for delta crustaceans obtained from J. Orsi (California Department of Fish and Game, Stockton, CA 95205, unpublished data) and from literature sources. Diet results were compared as an index of relative importance (IRI) (Shreffler et al. 1992) for each month. The index was calculated as: IRI = (% numeric composition + % weight composition) × % frequency of occurrence.

### Prey availability

Invertebrates were sampled in February–March of 1998 and 1999, to examine prey availability in the Yolo Bypass and the Sacramento River. Sampling was not designed as a comprehensive evaluation of spatial and temporal variation of prey. Rather, it was intended to provide information on whether variation in salmon diets between the two locations was consistent with gross differences in prey type or relative abundance. We focused on Diptera (adults, pupae, and larvae) and crustacean zooplankton, which comprised over 90% of the diets of Yolo Bypass and Sacramento River juvenile salmon. Weekly drift samples were collected at fixed stations on the Yolo Bypass and the Sacramento River during periods when the floodplain was inundated. The sampling points were located away from overhanging vegetation and bank eddies, in water velocities of approximately 15–60 cm·s$^{-1}$, depending on flow. Net (500-μm mesh) dimensions were 0.46 × 0.3 m mouth and 0.91 m length. The nets were fished for approximately 30 min during midmorning, to coincide with the time period when most fish-stomach samples were taken. Sample volume was calculated using a flowmeter (General Oceanics Model 2030R) and net dimensions. Drift samples were stored in ethanol or formaldehyde, then identified to family or order using a dissecting microscope. In 1998, zooplankton were collected in the Yolo Bypass at two fixed stations with battery-operated rotary-vane pumps with a mean flow rate of 17 L·min$^{-1}$. Samples were taken via pipes with outlets at multiple locations beneath the water surface. Discharge was directed into a 150 μm mesh net held in a basin on the bank. Flow rate was recorded at the beginning and end of the sample period, which varied from 1 to 6 h. No samples were taken in the Sacramento River during a comparable period in 1998. In 1999, zooplankton samples were taken with a Clarke–Bumpus net (160-μm mesh, diameter 0.13 m, length 0.76 m) placed in surface flow in the Yolo Bypass and Sacramento River. Sample volume was recorded as for the drift net. Zooplankton samples were concentrated and stored in 5%

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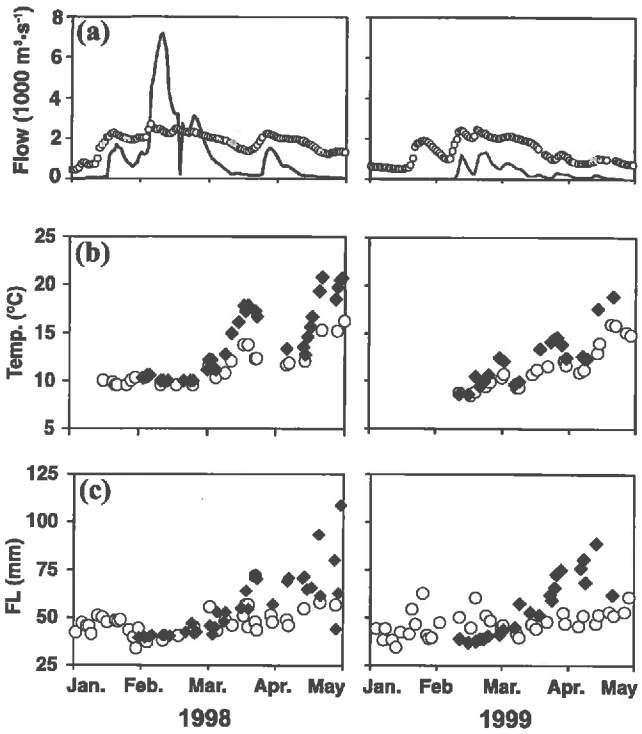
**Fig. 2.** Chinook salmon size versus physical conditions in Yolo Bypass and the Sacramento River during winter and spring in 1998 and 1999. (*a*) Mean daily flow ($m^3 \cdot s^{-1}$) in Yolo Bypass (solid line) and the Sacramento River (circles). (*b*) Mean water temperature (°C) in Yolo Bypass (solid symbols) and the Sacramento River (open symbols). (*c*) Mean daily chinook salmon FL for Yolo Bypass (solid symbols) and Sacramento River (open symbols) beach-seine stations. For presentation purposes, only the daily mean FLs are shown; however, individual observations for February–March were used for statistical analyses.




formaldehyde, for later identification to genus using a dissecting microscope.

### Bioenergetics

Feeding success was examined in two ways: (1) prey biomass estimated from stomach contents and (2) prey biomass estimated as a function of maximum theoretical consumption. For the first measure, we used the previously described stomach-content data to calculate total-prey biomass for individual fish.

A limitation of using prey biomass as a measure of feeding success between locations is that thermal history affects how consumption alters growth rate (Hewett and Kraft 1993). As will be discussed in further detail, water temperatures were significantly higher in the Yolo Bypass floodplain than in the Sacramento River. To correct for this problem, our second approach used bioenergetic modeling to incorporate the metabolic effects of water temperature. We used methods similar to those of Rand and Stewart (1998) to calculate a wet weight ration index, which uses prey biomass for each sampled individual as a proportion of the theoretical maximum daily consumption. The stomach-content data were used as our estimate of prey biomass for individual fish. The theoretical maximum daily consumption rate ($C_{max}$) was modeled using Fish Bioenergetics 3.0 (Hanson et al. 1997), using observed body size and water temperature at the time each beach-seine sample was collected. The model input also required fish mass, which we estimated from FL data, using length–weight relationships from Sacramento River juvenile salmon (Petrusso 1998). The caloric value of the prey was taken from weight conversion factors provided by Hanson et al. (1997). Model parameters were derived from those of Stewart and Ibarra (1991) for chinook salmon. The model was run for individual fish collected at each sampling location in 1998 and 1999.

**Table 1.** Robust regression statistics for Yolo Bypass and Sacramento River salmon FLs for 1998 and 1999.

| | 1998 | | 1999 | |
|---|---|---|---|---|
| | Parameter ± SEM | *t* | Parameter ± SEM | *t* |
| Intercept | 29.4±0.6 | 46.8 | 23.5±0.5 | 43.7 |
| Location | 6.4±0.6 | 10.2 | 11.1±0.5 | 20.6 |
| Day | 0.3±0.01 | 34.5 | 0.3±0.01 | 48.5 |
| Location:day | −0.14±0.01 | −18.4 | −0.21±0.01 | −33.6 |

**Note:** The *t* values are all highly significant ($p < 0.0001$).

We emphasize that the second approach provides an *index*, rather than an *absolute* measure of feeding success. The wet weight ration index is conceptually analogous to "*P*" in Hanson et al. (1997), a model parameter that indicates what fraction of $C_{max}$ is obtained over the course of the day. The major difference is that *P* is based on prey consumption over a 24-hour period, whereas our wet weight ration index is based on instantaneous measurements of stomach contents, which may not represent mean trends over the entire day. An additional limitation is that the Stewart and Ibarra (1991) model parameters were developed for adult salmon and we applied the model to juveniles. We did not have sufficient field or laboratory data to develop bioenergetic-model parameters specific to the earliest life stages. Nonetheless, other studies (Rand and Stewart 1998) have demonstrated that similar wet weight ration indices can provide an effective technique for comparing relative salmonid feeding success between seasons and years.

### Statistical analysis

Overlapping temperature measurements from continuous recorders and the discrete measurements during 26 March – May 1998 were analyzed with Wilcoxon's matched-pairs test, to determine whether the two methods yielded different results. Mean water temperature for Yolo Bypass and the Sacramento River during the primary period of floodplain inundation (February–March) was analyzed with a generalized linear model with a variance function that increased with the mean squared, since variances were not homogeneous (Venables and Ripley 1997). Salmon FL measurements for Yolo Bypass and the Sacramento River during February–March of 1998 and 1999 were compared with a robust iteratively reweighted least squares regression procedure ("rlm"; Venables and Ripley 1997), because we detected substantial numbers of outliers in preliminary graphical evaluations of the data. Initial analyses revealed a substantial difference in the effects of location between years, so years were analyzed separately. Results from the CWT and bioenergetic studies were analyzed using a factorial-design analysis of variance, to evaluate the effects of location (Yolo Bypass, Sacramento River) and year (1998, 1999). Residuals from each model were examined graphically, to confirm that they met the assumption of normality and homogeneity of variance. Cochran and Levene's tests were also used, to test the assumption of homogeneity of variance. Logarithmic transformation was performed where necessary.

## Results

### Physical conditions

Yolo Bypass was inundated in 1998 and 1999 but the hydrology was substantially different in the two years (Fig. 2).

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**Table 2.** Results of salmon collections at Chipps Island for 1998 and 1999 coded-wire-tagged groups released concurrently in Yolo Bypass and the Sacramento River.

| | 1998 | | 1999 | |
|---|---|---|---|---|
| | Yolo Bypass | Sacramento River | Yolo Bypass | Sacramento River |
| Fork length (mm) | 93.7±2.0 | 85.7±1.4 | 89.0±2.6 | 82.1±1.7 |
| Migration time (days) | 46.2±2.3 | 55.4±3.5 | 58.2±2.8 | 58.6±4.1 |
| Apparent growth rate (mm·day$^{-1}$) | 0.80±0.06 | 0.52±0.02 | 0.55±0.06 | 0.43±0.03 |
| Survival index | 0.16 | 0.09 | 0.09 | 0.07 |
| Sample size | 9 | 10 | 9 | 8 |

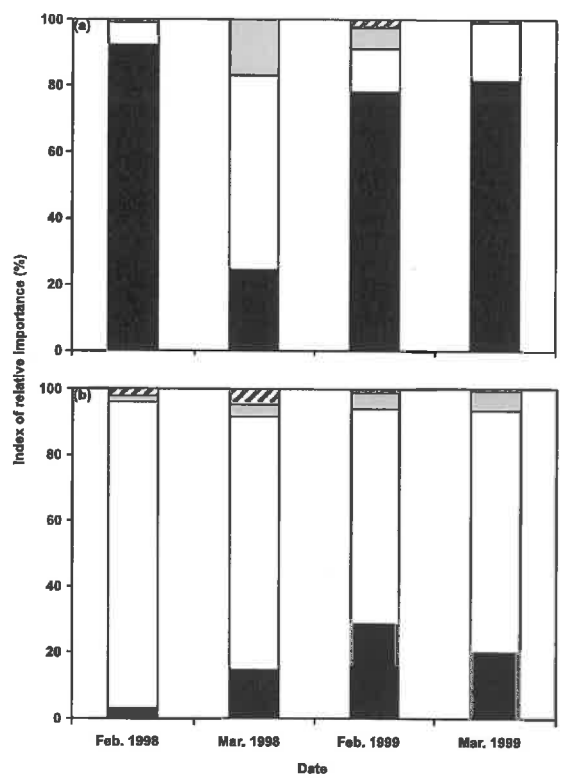
**Note:** Values for FL, migration time, and apparent growth rate are mean ± standard error (SEM).

The first year was extremely wet, with multiple flow pulses and a peak flow of 7200 m$^3$·s$^{-1}$. In 1999, floodplain hydrology was more moderate, with a peak of 1300 m$^3$·s$^{-1}$. Flows in the Sacramento River were much less variable than in the floodplain and generally remained at or below 2000 m$^3$·s$^{-1}$, a level within the design capacity (3100 m$^3$·s$^{-1}$) of the channel. Overlapping sampling between the continuous-temperature recorders and the discrete measurements during March–May 1998 showed a mean difference of 0.9°C between the two approaches, but this disparity was not statistically significant (Wilcoxon's matched-pairs test, $p > 0.25$). In 1998 and 1999, temperatures increased fairly steadily throughout the study period; however, in both years, temperature levels in Yolo Bypass were up to 5°C higher than those in the adjacent Sacramento River during the primary period of inundation, February–March. Temperature in the Yolo Bypass was described in 1998 by $T_y = -7.7 \pm 2.1 + (1.9 \pm 0.2)T_s$ and in 1999 by $T_y = -3.5 \pm 1.2 + (1.5 \pm 0.1)T_s$, where $T_y$ is the temperature of the Yolo Bypass, $T_s$ is the temperature of the Sacramento River, and the range for each value is the 95% confidence limit.

### Fish growth, migration time, apparent growth rate. and survival

Salmon increased in size substantially faster in the Yolo Bypass than in the Sacramento River during each of the study years (Fig. 2). Robust regression results showed that the effect of location was highly significant ($p < 0.00001$) in each year (Table 1). This result is consistent with the CWT data (Table 2), which showed that the 1998 and 1999 Yolo Bypass CWT release groups had significantly larger mean length ($F = 14.34$, $p = 0.0006$) and higher apparent growth rates ($F = 20.67$, $p = 0.0007$) than the Sacramento River release groups. There was also a statistically significant effect of year: both release groups had larger mean sizes ($F = 4.42$, $p = 0.04$) and higher apparent growth rates ($F = 16.47$, $p = 0.0002$) in 1998 than in 1999. The 1998 Yolo Bypass CWT group showed the fastest migration time, arriving an average of at least 9 days ahead of any other release group. However, there was no statistically significant ($F = 2.22$, $p = 0.15$) effect of release location on migration time in the analysis of variance (ANOVA). As for fish size and apparent growth rate, mean migration time was slower in 1999 than in 1998 ($F = 5.60$, $p = 0.02$). There was no statistically significant interaction between location and year for salmon size ($F = 0.07$, $p = 0.78$), apparent growth rate ($F = 1.62$, $p = 0.21$), or migration time ($F = 1.8$, $p = 0.18$). The survival indices were somewhat higher for CWT groups released in the Yolo Bypass than for those released in the Sacramento River for both 1998 and 1999. However, the lowest coefficient of variation based on a Poisson distribution of the CWT recaptures is 32%, and the actual (unknown) distribution of counts is likely to have higher variance than a Poisson distribution. Clearly the confidence limits of the paired survival indices would overlap, so the differences are not statistically significant.

**Fig. 3.** Chinook salmon diet during February and March of 1998 and 1999 in Yolo Bypass (*a*) and the Sacramento River (*b*). The index of relative importance (*y*-axis) is defined in the text. Diptera (solid bars), zooplankton (open bars), other aquatic prey (shaded bars), and other terrestrial prey (striped bars) are shown for each month.




### Diet

The diet of young salmon in the Yolo Bypass was dominated by dipterans, principally chironomid pupae and adults (Fig. 3). The second most common prey item was zooplank-

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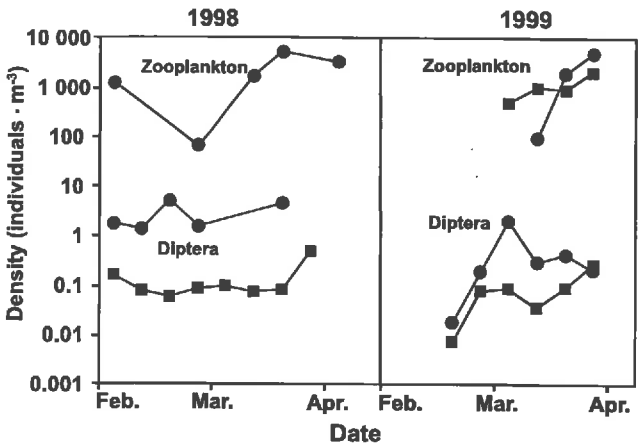
**Fig. 4.** $Log_{10}$-scaled weekly abundance (individuals·$m^{-3}$) of zooplankton and Diptera in Yolo Bypass (circles) and the Sacramento River (squares) during 1998 and 1999. Note that 1998 zooplankton data were not available for the Sacramento River.




ton, mostly cladocerans and copepods. Except for March 1998, zooplankton comprised less than 15% of the Yolo Bypass diets. Other aquatic (mainly amphipods and collembola) and terrestrial (mainly ants and arachnids) prey were relatively minor diet items. As for the floodplain samples, dipterans and zooplankton comprised over 90% of the diets of Sacramento River salmon; however, zooplankton were the dominant prey item in all months. Other aquatic (mostly amphipods, oligochaetes, and collembola) and terrestrial (mostly ants and other terrestrial insects) prey were consumed infrequently.

### Prey availability

The drift samples contained many of the same taxa observed in the salmon diets, with Diptera (principally chironomids) as the major type at both sampling locations. However, the density of Diptera was much higher in the Yolo Bypass than in the Sacramento River (Fig. 4), particularly in 1998, when densities were consistently an order of magnitude higher. In general, dipteran drift densities were higher at each location in 1998 than in 1999. There was little difference in zooplankton density in the Yolo Bypass between 1998 and 1999 or between Yolo Bypass and the Sacramento River in 1999.

### Bioenergetics

Young salmon from the Yolo Bypass had higher total-prey weights ($F = 39.2$, df = 1, $p < 0.0001$) than those from the Sacramento River (Fig. 5). The bioenergetic-modeling results showed that Yolo Bypass salmon also had higher wet weight ration indices than those from the Sacramento River ($F = 19.3$, df = 1, $p < 0.0001$). The interaction between location and year was significant for both the wet weight ration indices ($F = 10.0$, df = 1, $p = 0.02$) and the prey weights ($F = 4.7$, df = 1, $p = 0.03$).

## Discussion

Chinook salmon that rear in the Yolo Bypass floodplain have higher apparent growth rates than those that remain in the adjacent Sacramento River channels. Mean length increased faster in the Yolo Bypass during each study year, and CWT fish released in the Yolo Bypass were larger and had higher apparent growth rates than those released in the Sacramento River. It is possible that these observations are due to higher mortality rates of smaller individuals in the Yolo Bypass or of larger individuals in the Sacramento River; however we have no data or reasonable mechanism to support this argument.

Apparent growth differences between the two areas are consistent with water temperature and stomach-content results. We found that the Yolo Bypass floodplain had significantly higher water temperatures and that young salmon from the floodplain ate significantly more prey than those from the Sacramento River. The wet weight ration indices calculated from bioenergetic modeling suggest that the increased prey availability in Yolo Bypass was sufficient to offset increased metabolic requirements from higher water temperatures. Higher water temperatures in the Yolo Bypass are expected as a result of the shallow depths on the broad floodplain. Increased feeding success in the Yolo Bypass is consistent with trends in prey availability. While Yolo Bypass and the Sacramento River had similar levels of zooplankton, Yolo Bypass had more dipteran prey in the drift, particularly in 1998. Studies of juvenile chinook salmon diets by Rondorf et al. (1990) showed that zooplankton were the least-favored prey items. Therefore, the dominance of zooplankton in the diets of Sacramento River salmon probably reflects a relatively low availability of other more energetically valuable prey items.

Recoveries of paired releases were too few to determine whether the higher survival indices for the Yolo Bypass release groups represent actual survival differences or random variation. Additional validation is needed from new release studies and from CWT recoveries in the adult ocean fishery and escapement. Nonetheless, the hypothesis that floodplain rearing could improve survival is substantiated by the growth data and bioenergetic modeling. Faster growth rates reflect improved habitat conditions, which would be expected to lead to improved survival, both during migration and later in the ocean. Elevated Yolo Bypass survival rates are also consistent with significantly faster migration rates in 1998, the likely result of which would be reduced exposure time to mortality risks in the delta, including predation and water diversions.

Improved survival is consistent with other habitat differences between the Yolo Bypass floodplain and the Sacramento River channel. We estimate that complete inundation of the Yolo Bypass creates a wetted area approximately 10 times larger than the reach of the Sacramento River we studied. This level of inundation is equivalent to a doubling of the wetted area of the entire delta portion of the San Francisco Estuary. Much of the floodplain habitat consists of broad shoals composed of soil and vegetation that are typical of the low-velocity conditions selected by young salmon (Everest and Chapman 1972). An increase in rearing area should reduce competition for food and space and perhaps reduce the probability of encountering a predator. In contrast, the Sacramento River channel is relatively narrow, with steep rock-reinforced banks and little shallow habitat. Migration through the Yolo Bypass corridor would also prevent

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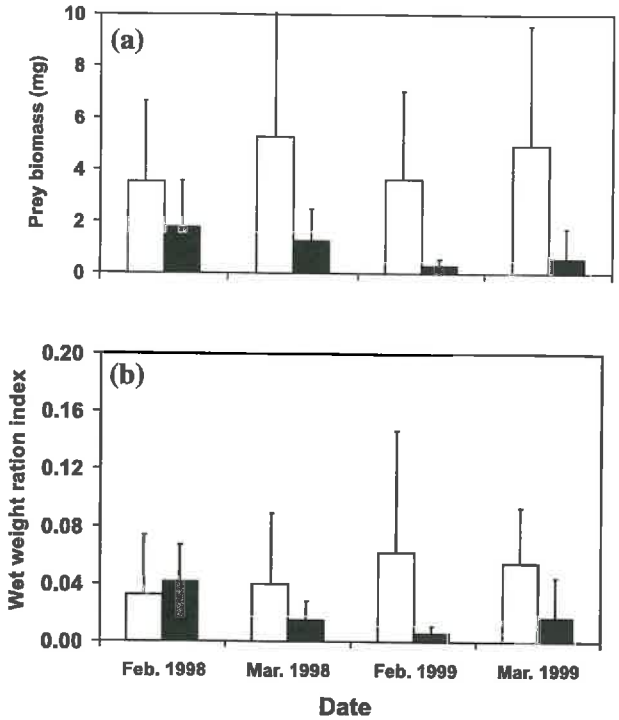
fish from entering the channels of the central delta, in which there are various risks, including major water diversions (Brandes and McLain 2001). However, the Yolo Bypass is a less-stable environment, with stranding risks when flood waters recede. The relatively well-drained topography of the Yolo Bypass floodplain may help to reduce the magnitude of this problem. This is not to say, however, that access to floodplain rearing habitat represents the only mechanism to account for possible improvements in juvenile salmon survival in wetter years. Other covariates, such as reduced water temperature (Baker et al. 1995), reduced predation losses from higher turbidity (Gregory and Levings 1998), and reduced water diversion effects (Kjelson et al. 1982), also contribute to improved wet-year survival of salmon that migrate through the San Francisco Estuary.

The results from this study suggest that hydrology may affect salmon feeding success, migration, and survival in both floodplain and river habitat. The CWT results indicate that salmon grew faster, migrated faster, and may have had better survival rates in 1998 than in 1999. One clear difference between the years is that the flow pulses were higher and of longer duration in 1998 than in 1999. Higher flow could directly increase migration rates through higher water velocities and have multiple indirect effects on growth through factors such as food supply or water temperature. The abundance of Diptera in drift samples was substantially higher in 1998 than in 1999 in both locations. The significant interaction between location and year for both prey weights and the wet weight ration index indicates that the combined effects of diet and water temperature under 1998 hydrology should have resulted in higher growth rates. Higher growth rates and faster migration times in 1998 may, in turn, have improved survival by reducing predation risk. Higher-flow conditions in 1998 increased the quantity and duration of floodplain rearing area, perhaps reducing resource competition and predator encounter rates. Increased flow duration and magnitude in 1998 could also have improved survival on the floodplain by reducing stranding risks.

These results provide new insight into the significance of seasonal floodplain habitat for salmon rearing, which has been studied primarily in perennial waterways such as estuaries and rivers (Healey 1991; Kjelson et al. 1982). Indeed, this is the first study we are aware of demonstrating that off-channel floodplain provides major habitat for chinook salmon. We do not believe that the benefits of the floodplain to chinook salmon are unique to Yolo Bypass. Initial results from the Cosumnes River, an undammed watershed in the delta, show similar growth enhancements for juvenile chinook salmon that rear on the floodplain rather than in adjacent river channels (Peter Moyle, University of California, Davis, CA 95616, personal communication). Moreover, the benefits of the floodplain to salmon are consistent with findings for other fish species. Sommer et al. (1997) found that the Yolo Bypass provides major spawning, rearing, and foraging habitat for the native cyprinid Sacramento splittail (*Pogonichthys macrolepidotus*). The spawning and rearing of fish on floodplains has been reported in diverse locations that range from small streams (Halyk and Balon 1983; Ross and Baker 1983) to large rivers (Copp and Penaz 1988) in both temperate (Gehrke 1992; Turner et al. 1994) and tropical (Winemiller and Jepsen 1998) locations. The growth effects of floodplain habitat have been described for several tropical locations (Welcomme 1979); however, the present study and the results of Gutreuter et al. (2000) represent the only examples from temperate rivers of which we are aware.

**Fig. 5.** Feeding success results for Yolo Bypass (open bars) and Sacramento River (solid bars) juvenile salmon during 1998 and 1999. (*a*) Estimated prey weights in stomach contents. (*b*) Wet weight ration indices. Means and standard errors are shown.




Differences between the invertebrate communities in floodplains versus river channels have been reported by Castella et al. (1991). The exceptional production of drift invertebrates on the Yolo Bypass floodplain is consistent with the results of Gladden and Smock (1990), who found that invertebrate production was one to two orders of magnitude greater on the floodplain than in adjacent streams. Although we did not monitor benthic invertebrates, results from other studies of large rivers indicate that benthic biomass may be up to an order of magnitude higher in the floodplain (Junk et al. 1989). The Yolo Bypass drift invertebrate results contrast with the results for zooplankton, which were not particularly abundant on the floodplain. This finding is comparable with that of Welcomme (1979), who reported that densities of zooplankton in natural floodplains are frequently low, except for low-water periods and localized concentrations near habitat interfaces such as shorelines.

The mechanism for greater abundance of drift invertebrates in the Yolo Bypass remains unclear, but is unlikely to be an artifact of land use on the floodplain. Possible explanations for increased drift abundance include increased food supply (e.g., primary production or detritus), more habitat, and longer hydraulic residence times. For each of these mechanisms, Yolo Bypass probably provides functions similar to more "natural" floodplains. Improved food supply is supported by the work of Jassby and Cloern (2000), whose

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modeling studies suggest that the Yolo Bypass should have enhanced phytoplankton production as a result of its large surface area and shallow depth. Inputs of fertilizers from agriculture in the Yolo Bypass would not be important contributing factors, as nitrogen and phosphorous are rarely limiting to phytoplankton production in the delta (Ball and Arthur 1979). Like less-disturbed floodplains in other regions (Junk et al. 1989), invertebrate production in the Yolo Bypass may be stimulated by an increased availability of detritus in the food web. Alternatively, the trends in invertebrate abundance we observed may be a consequence of physical differences between floodplain and channel habitat. Inundation of the floodplain may increase the amount of habitat for benthic invertebrates, a major source of drift biomass. Given the larger surface area and lower velocities in Yolo Bypass, the floodplain probably has a much longer hydraulic residence time than the Sacramento River, reducing the rate at which drift invertebrates would be flushed out of the system. Increased habitat area and hydraulic residence time would also have been functional characteristics of the historical floodplain.

In the broader context, the results for salmon and drift invertebrates are consistent with the flood pulse concept, which predicts that floodplains should yield greater fish and invertebrate production than channel habitat (Junk et al. 1989). This finding is significant in that the flood pulse concept was developed primarily on the basis of relatively undisturbed rivers, whereas our study was conducted in a regulated river with a floodplain dominated by agricultural uses. Gutreuter et al. (2000) showed similar enhancements in fish growth from floodplain inundation in the Upper Mississippi River, another large regulated river. These studies suggest that floodplains can maintain important functional characteristics even in heavily modified rivers. In the case of the San Francisco Estuary and its tributaries, we do not claim that floodplain inundation is the primary factor regulating the productivity of the system. The Yolo Bypass floodplain may be seasonally more productive than the Sacramento River for some fish and invertebrates, but we have no data regarding its contribution during dry months or years. Nonetheless, the results of the present study and of Sommer et al. (1997) are sufficient to demonstrate that the floodplain represents one of the most biologically important habitat types in the region. We believe that proposed large-scale restoration activities in the San Francisco Estuary and its tributaries (Yoshiyama et al. 2000) that would increase the area and connectivity of the floodplain offer particular promise for native fish populations such as chinook salmon and Sacramento splittail.

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[Article]

# Habitat Use and Stranding Risk of Juvenile Chinook Salmon on a Seasonal Floodplain

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*Abstract.*—Although juvenile Chinook salmon *Oncorhynchus tshawytscha* are known to use a variety of habitats, their use of seasonal floodplains, a highly variable and potentially risky habitat, has not been studied extensively. Particularly unclear is whether a seasonal floodplain is a net "source" or a net "sink" for salmonid production. To help address this issue, we studied salmon habitat use in the Yolo Bypass, a 24,000-ha floodplain of the Sacramento River, California. Juvenile salmon were present in the Yolo Bypass during winter–spring; fish were collected in all regions and substrates of the floodplain in diverse habitats. Experimental releases of tagged hatchery salmon suggest that the fish reared on the floodplain for extended periods (mean = 33 d in 1998, 56 d in 1999, and 30 d in 2000). Floodplain rearing and associated growth are also supported by the significantly larger size of wild salmon at the floodplain outlet than at the inlet during each of the study years. Several lines of evidence suggest that although the majority of young salmon successfully emigrated from the floodplain, areas with engineered water control structures had comparatively high rates of stranding. Adult ocean recoveries of tagged hatchery fish indicate that seasonal floodplains support survival at least comparable with that of adjacent perennial river channels. These results indicate that floodplains appear to be a viable rearing habitat for Chinook salmon, making floodplain restoration an important tool for enhancing salmon production.

A large downstream movement of fry to provide dispersal to rearing areas is typical of ocean-type Chinook salmon *Oncorhynchus tschawytcha* (Healey 1991). Rearing areas include channel and off-channel habitat in natal and nonnatal streams and their estuaries (Bjornn 1971; Kjelsen et al. 1982; Levy and Northcote 1982; Swales et al. 1986; Swales and Levings 1989; Healey 1991; Shreffler et al. 1992). Recently, Sommer et al. (2001b) observed that juvenile Chinook salmon also live on seasonal floodplains. Large rivers and streams typically have dynamic floodplains varying in size from several to thousands of hectares, unless their channels are heavily confined by topography (e.g., streams at high elevation or confined by canyons or levees). Floodplains are known to be of major importance to aquatic ecosystems in most regions; large rivers typically favor the development of a fauna adapted to colonize this habitat (Welcomme 1979; Junk et al. 1989; Sparks 1995). As a result, it is reasonable to expect dispersing salmonid fry show some ability to use seasonal habitat. In support of this hypothesis, Sommer et al. (2001b) reported that food resources and water temperatures on the seasonal floodplain of a large river were superior to those in an adjacent perennial channel, resulting in enhanced growth rates of young salmon. Despite some evidence that enhanced growth on the floodplain improved fry–smolt survival in the estuary, Sommer et al. (2001b) did not address any effects on adult production.

Intuitively, rearing in seasonal floodplains or intermittent streams seems risky because these habitats are among the most dynamic on earth (Power et al. 1995). It is still unknown whether seasonally dewatered habitats are a net "source" or a "sink" for salmonid production relative to production in permanent stream channels (Brown 2002). In particular, the high degree of seasonal flow fluctuation characteristic of floodplain habitat could cause major stranding events and increase mortality rates of young salmon (Bradford 1997; Brown 2002). For resident taxa in intermittent streams, the benefits of very large flow fluctuations appear to outweigh costs associated with a variable environment (Spranza and Stanley 2000). This issue continues to be a key concern for regulatory agencies that evaluate off-channel restoration projects or proposed flow fluctuations for possible effects on fishes (Brown 2002; Bruce Oppenheim, NOAA Fisheries, personal communication).

Here, we describe spatial and temporal trends in juvenile Chinook salmon habitat use and stranding in a large California river floodplain. Our study was conducted in the Yolo Bypass, the primary floodplain of the Sacramento River, the major pro-

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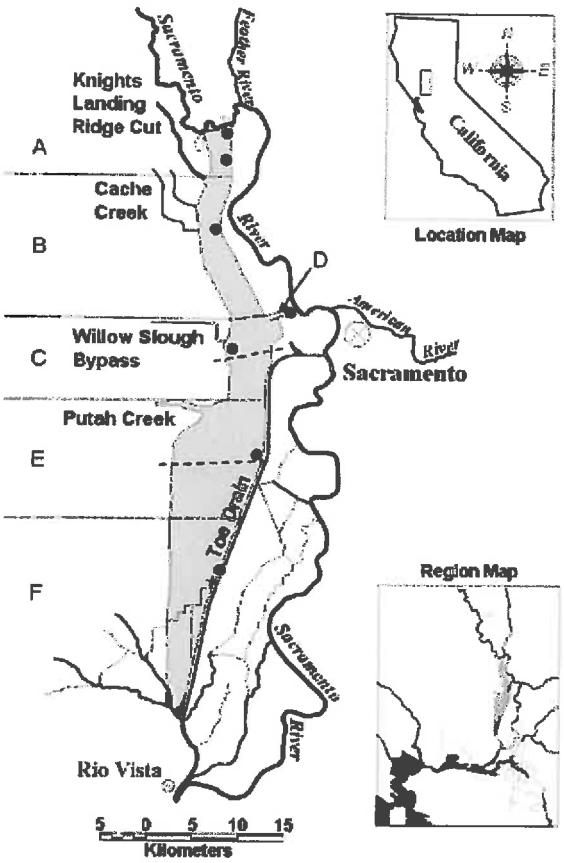


FIGURE 1.—Location of Yolo Bypass in relation to the San Francisco Bay–Delta and its tributaries. Fremont Weir is the upper (northern) edge of the Yolo Bypass. The major regions of the floodplain are delineated from north to south and correspond to the following codes: (A) Fremont Weir; (B) Cache Creek sinks; (C) Yolo Bypass Wildlife Area; (D) Sacramento Bypass; (E) Putah Creek Sinks; and (F) Liberty Island. The sampling locations are identified as follows: beach seine sites (solid circles); screw trap (star); and purse seine transects (dotted lines).

ducer of salmon in the San Francisco estuary (Figure 1). Because the Yolo Bypass can convey 75% or more of the total flow from the Sacramento River basin (Sommer et al. 2001a), this floodplain can be expected to be a migratory pathway for a substantial number of juvenile Chinook salmon. A major objective of our study was to collect basic information about the timing, duration, and habitat use of salmon on floodplains. We hoped that these data would provide insight into whether a floodplain is a net source (i.e., with rearing benefits) or a net sink (i.e., with high mortality because of stranding or predation) for salmon populations. The major hypotheses evaluated were as follows: (1) salmon occur in all major habitat types and geographic regions; (2) floodplains provide rearing habitat for salmon and are not simply a migration corridor; and (3) stranding of juvenile salmon does not have a major population-level effect on survival of the fish that use floodplain habitat. We addressed these hypotheses by sampling wild fish throughout the floodplain, experimentally releasing tagged fish, and using hydrologic modeling and measurements of physical conditions to describe how habitat varied over the study period.

## Study Area

The San Francisco Estuary and its two component regions, Sacramento–San Joaquin Delta and downstream bays (Figure 1), make up one of the largest estuaries on the Pacific coast of North America. Major changes to the system have included diking and isolation of about 95% of the wetlands, introduction of exotic species, channelization, sediment inputs from hydraulic mining, and discharge of agricultural and urban chemicals (Nichols et al. 1986; Kimmerer 2002). The Estuary receives most freshwater via the Delta, which drains approximately 100,000 km$^2$. Most precipitation occurs upstream of the Delta during winter and spring, resulting in a greater than 10-fold seasonal range of daily freshwater flow into the estuary. However, the hydrograph is substantially altered by dams on each of the major rivers. Peak flow pulses typically occur during winter, but dam operations can reduce the magnitude of the pulses, particularly in dry years, when much of the inflow is captured behind reservoirs (Mount 1995; Kimmerer 2002). The historically prominent spring flow pulse from snowmelt is at present muted except during heavy, late-season storms. For the past several decades, much of the spring snowmelt has been stored in reservoirs and released during summer and autumn, periods of historically lower flow. As much as 65% of the net Delta flow during summer and autumn is diverted from the channels by two large water diversions (the State Water Project and the Central Valley Project); additional water is diverted by 2,200 pumps and siphons for irrigation (Kimmerer 2002).

The 24,000-ha Yolo Bypass is the primary floodplain of the Delta (Sommer et al. 2001a). The majority of the floodplain is leveed to protect surrounding cities from floodwaters, but levees confine flow through the bypass only under very high flow events. The Yolo Bypass currently floods an average of every other year, typically under high-flow periods in winter and spring. The Yolo Bypass has a complex hydrology, with inundation possible

from several different sources. The floodplain typically has a peak inundation period during January–March but can flood as early as October and as late as June. The primary input to the Yolo Bypass is through Fremont Weir in the north, which conveys floodwaters from the Sacramento and Feather rivers. During major storm events (e.g., >5,000 $m^3/s$), additional water enters from the east via the Sacramento Weir, adding flow from the American and Sacramento rivers. Flow also enters the Yolo Bypass from several small streams on its western margin, including Knights Landing Ridge Cut, Cache Creek, and Putah Creek. During much of the winter, water-suspended sediment levels in the Yolo Bypass and Sacramento River are high, generally resulting in secchi depths of less than 0.25 m. However, hydraulic residence times are typically longer in the Yolo Bypass than in the Sacramento River (Sommer et al. 2004). Floodwaters recede from the northern and western portions of the bypass along relatively even elevation gradients of 0.09% west–east and 0.01% north–south into a perennial channel on the eastern edge of the Bypass; they then rejoin the Sacramento River near Rio Vista. The majority of the Yolo Bypass is at present managed for wildlife in a mosaic that includes riparian, wetland, upland, and perennial pond habitats; however, a dominant land use during the past two decades, agriculture has decreased in recent years because of habitat restoration activities.

Our data collection focused on the fall-run juvenile Chinook salmon, currently the numerically dominant race in the Sacramento Valley (Yoshiyama et al. 2000). There are four races of Chinook salmon in the Sacramento Valley: winter, spring, late-fall, and fall-run. Like many other native fish, Chinook salmon in the San Francisco estuary and its tributaries have been adversely affected by such factors as habitat loss, water diversions, and species introductions (Bennett and Moyle 1996); as a result, the Sacramento River winter and spring run Chinook salmon are protected under the Federal Endangered Species Act. The typical life history pattern is for young fall-run salmon fry (approximately 35–70 mm fork length) to migrate from the tributaries during winter and spring to the estuary (Brandes and McLain 2001).

## Methods

*Physical habitat.*—Because seasonal hydrologic variability is a key characteristic of floodplain habitat, we reasoned that detailed data on changes in physical habitat would be necessary to evaluate the responses of young salmon. Daily flow data were obtained from gauging stations in the floodplain, and temperature data were collected using continuous temperature recorders (Sommer et al. 2001b). However, the vast area of Yolo Bypass made it impractical to directly measure other parameters, such as depth and surface area. As an alternative, we used a hydrologic model to estimate these parameters (Sommer et al. 2004). To summarize, the model treated Yolo Bypass as a "reservoir" described by (1) basin geometry and (2) flow and stage time series. The Yolo Bypass floodplain geometry was developed from 200 cross-sections with data collected at 300-m intervals by standard rod and level survey techniques. Mean daily stage and flow data were obtained from five gauging stations in the Yolo Bypass. For each date in the time series, we used linear interpolation between the gauging stations to estimate the stage at each cross-section. The estimated stage value was then used to calculate conveyance characteristics of each cross-section: area, width, and wetted perimeter. The daily results for each cross-section were used to estimate total surface area and mean depth. The large scale of the study reach did not allow validation of the depth estimates. As a partial validation of the model, Sommer et al. (2004) estimated total inundated area for the Yolo Bypass by using aerial photographs on days when the floodplain was inundated (February 8 and March 2, 1998) and when the floodplain was draining (April 28, 1998). To provide additional information about areas where fish stranding and consequent losses could occur, we estimated the portion of the area that was isolated ponds versus inundated area that was actively draining to the Delta (i.e., perennial channels and adjacent inundated area) on April 28, 1998.

*Fish habitat use.*—We used beach seine sampling to examine which regions and substrates of the floodplain were used by young salmon (hypothesis 1). During January through April of each year, a 15-m seine (3.2-mm mesh) was used to sample six regions of the Yolo Bypass (Figure 1). Fixed stations were used in each region during flooded periods. After floodplain drainage, samples were collected randomly within each region. For all periods, the primary substrate type of the habitat (sand, mud, gravel, pavement, or vegetation), fish species and size, and an estimate of the surface area swept by the seine were recorded. Habitat use during flood events was summarized in terms of the percentage of samples that contained salmon for each region and substrate type.

To provide additional information about habitat use, we conducted purse seine sampling along two transects (Figure 1). This sampling, performed in 1998 when the Yolo Bypass flow was relatively high (>850 $m^3/s$), used purse seines (30.5 m × 4.6 m, 4.75-mm mesh) set from a jet boat. Purse seining was conducted at 1–2 transects up to five times weekly, depending on hydrology. Hauls were made at random points in each of three habitat types (riparian, agricultural fields, and wetlands), the boundaries of which were established from aerial photographs taken before the Bypass was inundated. In the case of riparian habitat, hauls were made in clearings adjacent to trees to avoid snagging. We also recorded transect side (east or west half) for each haul because the western side of the Yolo Bypass was shallower and flow was dominated by inputs from westside streams rather than from Fremont or Sacramento weirs (Sommer et al. 2004). Most of these hauls were performed in areas exposed to at least a modest current. Additional limited paired sampling was conducted to examine possible differences between areas with and without velocity refuges. Low-velocity habitats sampled included downstream edges of levees, islands, and clusters of trees. Water velocities in randomly selected areas were approximately 0–0.05 m/s compared with greater than 0.33 m/s in adjacent exposed areas. Water depths were similar for each sampling pair. Differences in salmon densities for each habitat type were examined by using a Kruskal–Wallace test. A randomization *t*-test with 1,000 iterations (Haddon 2001) was used to compare salmon density on the east and west sides of the floodplain.

*Migration trends.*—To examine temporal trends in salmon migration through the floodplain (hypotheses 2 and 3), we operated a rotary screw trap (EG Solutions, Corvallis, Oregon) near the base of the Yolo Bypass during each study year. This technique was intended to provide an indication of the timing and duration of migration, rather than an absolute measure of the number of salmon emigrating the floodplain. During much of the sampling period the inundated width of the floodplain was 1–5 km, an area we considered too large for the traditional mark–recapture evaluations required to measure trap efficiency and total emigration (Roper and Scarnecchia 1996). A 1.5-m-diameter trap was used for the first 3 weeks of sampling in February 1998, after which a 2.4-m trap was used for all other sampling. We operated traps as often as 7 days each week, the daily effort varying from 1 to 24 h, depending on debris load and safety considerations. Fish number and size were recorded in all years. In 1998, young salmon were classified as fry (prominent parr marks) or transitional fish/smolts (faded parr marks, silver appearance).

*Floodplain residence time and growth.*—We used experimental releases of salmon with coded wire tags (CWTs) as our primary method to evaluate fish residence time on the floodplain (hypothesis 2). Fry (mean size = 57 mm fork length) from the Feather River Fish Hatchery (Figure 1) were tagged by using coded-wire half tags (Northwest Marine Technologies) and released in the Yolo Bypass below the Fremont Weir on March 2, 1998 (53,000 fry); February 11, 1999 (105,000 fry); and February 22, 2000 (55,000 fry). We assessed residence time in the Yolo Bypass from recoveries of tagged fish in the screw trap at the base of the floodplain.

We also examined, using the previously described beach seine data, whether there was evidence of long-term rearing of wild salmon in the floodplain. We compared the slopes of weekly fork length measurements for the two northern beach seine regions ("North") to the southernmost region ("South"), using a generalized linear model (GLM) with a Poisson distribution and log link variance function. We reasoned that major significant differences between the sizes of fish in the two areas provided evidence of extended rearing and growth of fish in the floodplain.

*Salmon survival and stranding.*—We used several independent data sources to examine whether salmon successfully emigrated from the floodplain (hypothesis 3). First, we compared survival of each of the Yolo Bypass CWT hatchery-reared salmon release groups with the survival of parallel CWT groups containing the same number of fish released into the Sacramento River (Sommer et al. 2001b). Recapture rates at the smolt stage of the 1998 and 1999 release groups had previously been analyzed by Sommer et al. (2001b); in the present study, we evaluated adult recoveries in the commercial and recreational ocean fisheries through 2003. Second, we examined stranding by using beach seine data (described previously) collected within a few weeks after the Sacramento River stopped flowing into the Yolo Bypass. Densities of salmon were compared with a randomization *t*-test (Haddon 2001) for (1) isolated earthen ponds (2) perennial channels, and any sites immediately adjacent to these water sources. The results for all years were pooled because of relatively low sample sizes for individual years. Data for each year

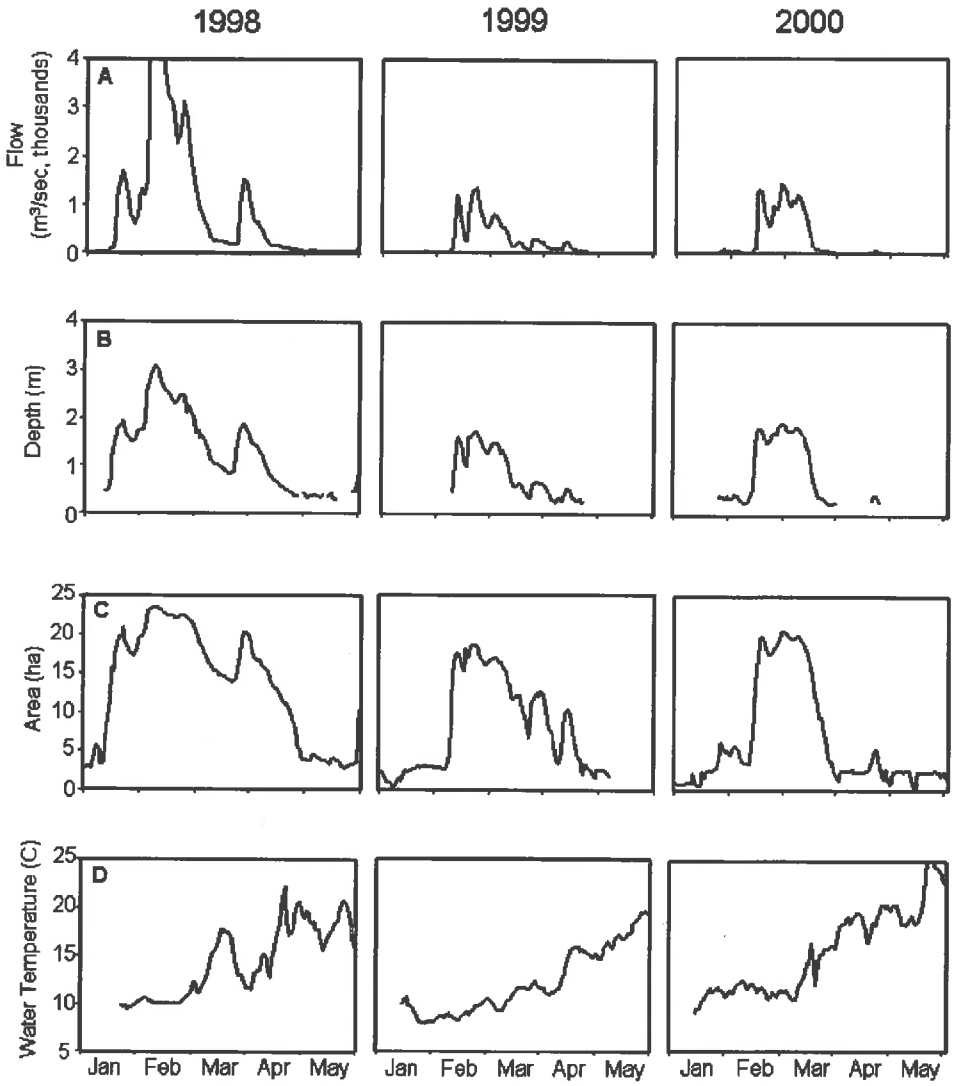


FIGURE 2.—Trends in physical variables for January–June 1998–2000: (A) mean daily flow in the Yolo Bypass; (B) simulated mean daily depth; (C) surface area; and (D) daily mean water temperature. The surface area data for 1998 and 2000 are from Sommer et al. (2004).

were first standardized for possible annual differences in abundance by conversion to $z$-scores; we then ran the randomization analysis using 1,000 iterations. We hypothesized that abundance of salmon would be equal in isolated ponds and contiguous water sources; that is, they would show no distinct "preferences." Our reasoning was that similar abundance levels would indicate successful emigration, because most of the water drains from the floodplain. To further understand factors that could affect stranding, we also used a randomization $t$-test to compare densities of fish in two types of isolated ponds: isolated earthen ponds and concrete weir scour ponds at Fremont and Sacramento weirs (Figure 1). Sampling effort was much greater in the isolated earthen ponds, so the randomization $t$-test was performed after randomly subsampling the earthen pond data from throughout the floodplain to provide equal sample sizes. We predicted that flood control structures would cause higher stranding than "natural" ponds. In addition, we examined trends in the catch of salmon in the screw trap data. We predicted that salmon catch would increase substantially during drainage because fish successfully emigrated the floodplain.

## Results

### *Physical Habitat*

The hydrographs varied substantially during the years of study (Figure 2A). In 1998 the hydrology

was wet (4.4-year recurrence flood event) and the Yolo Bypass was inundated during mid-January through mid-April and again in early June. The flow was lower in the other 2 years, when inundation occurred between mid-February and mid-March, peak flood events being at the 1.7-year recurrence interval in 1999 and at the 2.4-year recurrence interval in 2000. Surface area in the Yolo Bypass closely followed the flow peaks, the amounts of inundated area being successively smaller in each of the study years (Figure 2C). For the April 28, 1998, photographs, the total surface area of 5,050 ha was slightly lower than the model estimate of 6,700 ha. Based on the aerial photographs, we estimated that only 600 ha of the 5,050 ha comprised isolated ponds, the remainder being water that drained to the Delta. For all but peak flood events, mean water depth remained less than 1 m (Figure 2B). During peak flood events, mean depths did not exceed 2 m except in February 1998. Water temperature showed gradual increases throughout each study year (Figure 2D).

### *Fish Habitat Use*

We captured salmon in all regions of the floodplain and on all substrate types. During 1998–2000 flood events, salmon were captured in a high percentage of samples in each region (Figure 1) of the floodplain: (1) Fremont Weir (100%, $n$ = 13 samples); (2) Cache Creek Sinks (50%, $n$ = 16 samples); (3) Yolo Bypass Wildlife Area (77%, $n$ = 22 samples); (4) Sacramento Bypass (100%, $n$ = 7 samples); (5) Putah Creek Sinks (94%, $n$ = 11 samples); and (6) Liberty Island (100%, $n$ = 7 samples). Similarly, during 1998–2000 flood events we collected salmon on a high percentage of substrate types: (1) mud (70%, $n$ = 47 samples); (2) sand (100%, $n$ = 3 samples); (3) pavement (100%, $n$ = 8 samples); (4) vegetation (97%, $n$ = 32 samples); and 5) gravel (89%, $n$ = 9 samples).

Salmon densities as estimated by purse seine sampling were not significantly different between riparian (mean abundance = 46.9/ha, SE = 10.4, $n$ = 23), agricultural (mean abundance = 20.9/ha, SE = 6.1, $n$ = 35), or natural vegetated habitat types (mean abundance = 27.5/ha, SE = 5.6, $n$ = 31) based on a Kruskal–Wallis test ($H$ = 4.38, df = 2, $P$ = 0.112). There was also no statistically significant difference between the east (mean abundance = 29.5/ha, SE = 6.0, $n$ = 53) and west (mean abundance = 29.9/ha, SE = 6.7, $n$ = 36) sides of the Bypass as shown by a randomization $t$-test ($P$ = 0.95). Salmon were collected in six hauls in low-velocity habitat (mean abundance = 189/ha, SE = 24/ha), but none were collected in adjacent areas exposed to a current.

### *Floodplain Migration Trends*

Salmon migration as indicated by trends in screw trap catch was highly variable over the course of the study, but there were prominent peaks in Chinook salmon catch coincident with floodplain drainage during late March–April (Figure 3B). Additional smaller peaks in salmon catch also paralleled flow, mostly during February and March. The life history stage of salmon during 1998 was exclusively parr through the end of March, after which the majority showed signs of smoltification.

### *Floodplain Residence Time*

Based on recoveries of tagged fish in the screw trap, the mean residence time of CWT salmon was 33 d (range, 16–46 d; $n$ = 10) in 1998, 56 d (range, 4–76 d; $n$ = 49) in 1999, and 30 d (range, 28–37 d; $n$ = 25) in 2000. The size of fish was significantly larger ($P$<0.001; GLM) at the outlet of the floodplain than at the top (Figure 3C) during each of the study years.

### *Salmon Survival and Stranding*

The numbers of CWT fish recovered for the Yolo Bypass were higher than in the Sacramento River in 1998, similar in 1999, and lower in 2000 (Table 1). Densities of wild Chinook salmon were highly variable during floodplain drainage events, with no statistically significant difference between densities in isolated earthen ponds and contiguous water sources (Table 2). However, densities of salmon were significantly higher ($P$ < 0.0001; randomization $t$-test) in concrete weir scour ponds than in isolated earthen ponds (Table 3).

## Discussion

Research on migratory fishes reveals that these species frequently have alternative life histories that may be influenced by habitat use at early life stages (Clark 1968; Secor 1999). Under Clark's (1968) "contingent hypothesis," migratory taxa have divergent migration pathways that could help the species deal with environmental variability and heterogeneity. This theory is consistent with our understanding of Chinook salmon, which are adapted to the extreme hydrologic variability in western North America and show a range of life histories (Healey 1991; Bottom et al. 2005). In this context, the use of multiple habitats—including natal and nonnatal streams (Bjornn 1971; Scriv-

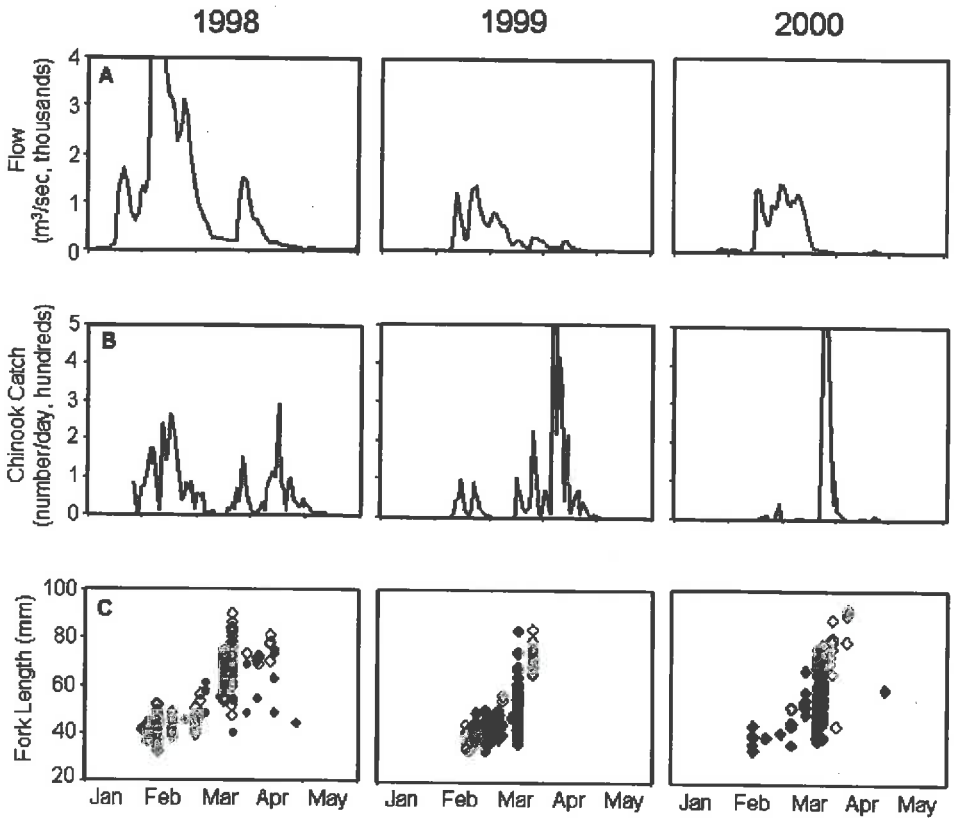


FIGURE 3.—Chinook salmon results during winter and spring 1998–2000: (A) mean daily flow; (B) salmon catch rates in screw trap sampling; and (C) salmon size for beach seine samples near the Yolo Bypass intake (solid symbols) and outlet (clear symbols).

ener et al. 1994), side channels and off-channel ponds (Swales et al. 1986; Swales and Levings 1989), low-elevation rivers (Kjelsen et al. 1982; Brown 2002), and estuaries (Healey 1991; Shreffler et al. 1992)—can be considered as part of an overall "bet-hedging" strategy that spreads risk across a variable environment. Despite the fact that seasonal floodplain represents perhaps the single most variable habitat available to salmon, our study suggests that floodplains are a viable rearing location for young fish.

TABLE 1.—Number of coded wire tags recovered in the ocean and commercial fisheries for Chinook salmon released in the Yolo Bypass and Sacramento River. The total number of tagged fish released in each location for each year is shown in parentheses. The survival ratio is calculated as the number of Yolo Bypass recoveries divided by the number of Sacramento River recoveries.

| Release group | 1998 (53,000) | 1999 (105,000) | 2000 (55,000) |
|---|---|---|---|
| Yolo Bypass | 75 | 136 | 27 |
| Sacramento River | 35 | 138 | 47 |
| Survival ratio | 2.14 | 0.99 | 0.57 |

At the beginning of our study, our conceptual model for floodplain habitat use was that young salmon move into the floodplain during high-flow events and spread throughout the broad expanse of seasonally inundated habitat. Among the wide variety of suitable substrates and habitat types for rearing, young salmon appear to seek out low-velocity areas. Moreover, floodplain habitat apparently is not simply a migration corridor; many young salmon actively rear on the highly productive floodplain habitat for extended periods of time, resulting in high growth rates. Our findings suggest that salmon emigrate from the seasonally inundated habitat both during flood events and during drainage. Juvenile Chinook salmon do not appear to be especially prone to stranding mortality; indeed, survival may actually be enhanced by floodplain rearing in some years. Our conceptual model was supported by our results and has a variety of management implications.

Salmon were present in a broad range of habitat and substrate types and were collected in all regions and sides of the Yolo Bypass floodplain. The

TABLE 2.—Densities of Chinook salmon (number/ha ± SE, with sample size in parentheses) collected in beach seine sampling during drainage events in 1998–2000. The sample locations are divided into isolated earthen ponds and contiguous water sources. Density differences were not statistically significant between the two pond types based on a randomization *t*-test of the pooled data for all years ($P = 0.79$; $n = 43$ for isolated ponds; $n = 59$ for contiguous water sources).

| Location type | 1998 | 1999 | 2000 |
|---|---|---|---|
| Isolated ponds | 206 ± 112 (30) | 890 ± 491 (8) | 126 ± 65 (5) |
| Contiguous water sources | 167 ± 79 (33) | 310 ± 104 (13) | 463 ± 123 (13) |

fact that they were present on the western half of the Bypass, where flows are dominated by Knights Landing Ridge Cut and Cache and Putah creeks, suggests that salmon spread throughout the floodplain after entering the basin by way of Fremont and Sacramento weirs. A few of these fish may have originated from a modest spawning population in Putah Creek (Marchetti and Moyle 2001). The fact that salmon were present in a wide range of habitat and substrate types and in different regions of the Yolo Bypass indicates that many areas of habitat were suitable, although this does not mean that there were no habitat preferences. Like many young fishes, much of the distribution of juvenile Chinook salmon can be explained by their association with shallow depths and low velocities (Everest and Chapman 1972; Roper et al. 1994; Bradford and Higgins 2001). The physical modeling indicated that mean depths were generally 1 m or less during all but peak flood periods, so much of the thousands of hectares of inundated habitat was probably within the shallow range typically preferred by young Chinook salmon (Everest and Chapman 1972). Our limited purse seine sampling suggested that young salmon were most abundant in low-velocity areas, which is consistent with previous studies in river and stream habitat (Everest and Chapman 1972; Roper et al. 1994; Bradford and Higgins 2001). We did not directly simulate water velocity in the present study; however, the relatively shallow water depth during flood events reflects the broad area of low-velocity rearing habitat created during flood events. We expect that this increase in rearing habitat in the Yolo Bypass provides foraging opportunities (Sommer et al. 2001b), reduced energy expenditure, and perhaps reduced probability of encounter with a predator (Ward and Stanford 1995).

Our results also suggest that fish rear in the system for extended periods rather than simply using it as a migration corridor. The mean residence time of 30–56 d for the 44-km reach between the floodplain release location and the screw trap is substantially longer than one would expect, given that (1) fingerlings are capable of migrating at rates of at least 6–24 km/d in low-elevation reaches of other large rivers (Healey 1991) and (2) one of our 1999 CWT fish was recovered just 4 days after being released, having traveled an estimated rate of 11 km/d. The fish were significantly larger at the base of the Yolo Bypass, suggesting that their period of residence in the floodplain was long enough to support substantial growth. Similarly, Sommer et al. (2001b) found that salmon showed higher growth rates in the Yolo Bypass than in the adjacent Sacramento River, primarily because of higher levels of invertebrate prey in the floodplain. A long period of rearing is also supported by the screw trap data, which showed that the densities of salmon were greatest during drainage of the floodplain. We believe that these peaks are a result of rearing salmon being forced off of the floodplain by receding flows. Temperature and salmon life history stage do not provide good alternative explanations for the emigration trends. In 1998, for example, water temperatures were relatively high by late March and salmon began smoltification shortly thereafter; yet the screw trap data indicate

TABLE 3.—Densities of Chinook salmon (number/ha ± SE, with sample size in parentheses) collected in beach seine sampling for earthen ponds and adjacent concrete weir ponds. Density differences were statistically significant between the two pond types based on a randomization *t*-test of the pooled data for all years ($P < 0.0001$; $n = 26$ for each pond type). Note that we used a randomly sampled subset of the earthen pond data to provide equal sample sizes for the comparison.

| Location type | 1998 | 1999 | 2000 |
|---|---|---|---|
| Earthen ponds | 186 ± 67 (63) | 531 ± 200 (21) | 369 ± 97 (18) |
| Concrete weir ponds | 2,717 ± 1,115 (14) | 14,208 ± 3,898 (12) | 4,181 ± 1,275 (3) |

that emigration did not peak until the end of April, when the floodplain drained. Perhaps the emigration trends are partially confounded by seasonal variation in salmon abundance. In the absence of trap efficiency data, we cannot estimate the proportion of the population that emigrated in winter versus spring events.

Several lines of evidence suggest that the majority of fish successfully emigrated from the floodplain. One important observation was that the area of isolated ponds was small relative to the overall area of the floodplain during both peak flood and drainage periods. As an example, in 1998, the wettest year we studied, the peak area of inundation was 24,000 ha, but the total inundated area dropped to 5,000 ha by late April. Of the 5,000 ha remaining at this point, our estimates from aerial photographs showed that isolated ponds took up only 600 ha. Put another way, isolated ponds represented just 12% of the wetted area in April and only 2.5% of the peak inundated area in winter. The same trend is evident in the area simulations for 1999 and 2000, when the peak area was 20,000 ha, but dropped to about 2,000 ha within a month. These results demonstrate that the Yolo Bypass drains fairly efficiently, leaving little isolated area where stranding can occur. This finding was somewhat unexpected, because many parts of the Yolo Bypass have natural topographic features or agricultural levees that could potentially impede drainage and fish emigration. Even if the area of isolated ponds is low, stranding could still be a substantial source of mortality if densities of fish in the remaining ponds were very high. However, we found no evidence that densities of fish stranded in isolated ponds were significantly higher than those in contiguous water sources that were draining to the Delta. The key point here is that most of the water drains from the floodplain and apparently the majority of the fish are leaving with the receding floodwaters. To help illustrate this issue, if we assume that mean densities of fish observed in Table 2 were representative of the entire wetted area of floodplain in April 1998, then the total number of fish in the 600 ha of isolated ponds would have been 123,600 salmon, lower than an estimate of 835,000 fish in the 5,000 ha of contiguous water sources. This conservative estimate also does not include the large numbers of fish that emigrated from the floodplain before April.

In addition to the beach seine and surface area data, we believe that trends in screw trap data support the hypothesis that stranding is not consistently a major problem on the floodplain. The screw trap data are somewhat ambiguous, because the large area of the floodplain makes it unreasonable to measure the efficiency of the trap. Therefore, we cannot accurately estimate the absolute number of salmon emigrating from the floodplain. However, we can at least examine the patterns of trap catch to evaluate likely mechanisms. Some of the possible patterns that we would expect to see for different factors are summarized in Figure 4. First, under the "trap efficiency" model, we would have expected dual peaks in the earliest and latest portions of flood events, when the screw trap would be sampling the highest portion of total flow (Figure 4A). If young salmon follow the "go with the flow" model, catch and flow peaks should be well-correlated (Figure 4B). Alternatively, if floodplains represent an important rearing habitat, we would expect catch trends to follow the "loitering" model, in which catch does not increase until drainage, when fish are forced from their rearing habitat by receding floodwaters (Figure 4C). Finally, if stranding were a major factor controlling catch trends, we would expect an early increase in catch as fish moved through the floodplain during inundation, but then catch should drop earlier than flow as young salmon became isolated from draining floodwaters (Figure 4D; "bathtub" model). Of these patterns, our data for the Yolo Bypass provide the strongest support for both the "go with the flow" and "loitering" models. In each year we saw obvious screw trap catch peaks associated with flow events, and additional prominent peaks associated with drainage. To summarize, apparently some of the fish move

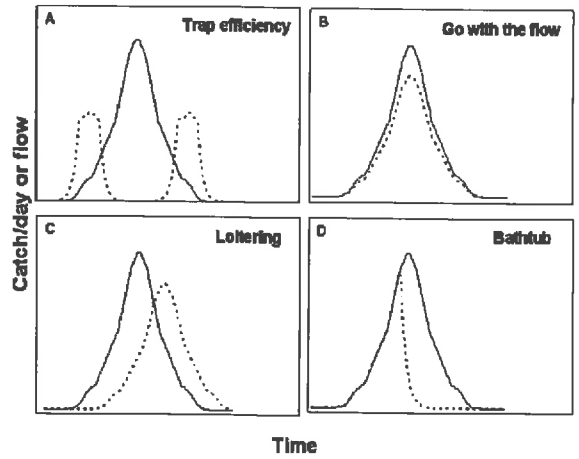


FIGURE 4.—Four conceptual models of expected screw trap catch (dotted line) relative to flow (solid line). See the Discussion for further details about each model.

through the floodplain in direct association with flow, whereas others remain as long as possible to rear on the floodplain. The screw trap trends show no evidence that stranding had a major influence on patterns of emigration.

Relatively low stranding rates on the Yolo Bypass floodplain are supported by observations from other seasonal floodplain habitat in the San Francisco estuary (Peter Moyle, University of California–Davis, personal communication) and other studies. Higgins and Bradford (1996) and Bradford (1997) report that juvenile salmonids are relatively mobile and that most avoid being stranded during moderate rates of stage change. Higgins and Bradford (1996) state that maximum recommended stage reduction levels for gravel bars of regulated rivers are typically 2.5–5 cm/h, much more than the 1 cm/h or less rates of change in mean water depth we observed during drainage in the present study. In his review of the ecology of fishes in floodplain rivers, Welcomme (1979) noted that the majority of fish emigrate from floodplain habitat during drainage.

Even if stranding is not a major source of mortality, this does not necessarily mean that floodplains are not sinks for salmon production. Of the possible sources of mortality, birds and piscivorous fishes may have benefited from stranded salmon (Brown 2002). As noted by Sommer et al. (2001a), major avian predation is unlikely because densities of wading birds are low relative to the thousands of hectares of rearing habitat available during flood events. We did not measure densities of fish predators, but believe that the creation of large areas of rearing habitat should create more refuges for young fish and decrease the probability of encounter with a predator.

Ultimately, it is survival data that allow us to differentiate source from sink habitat. The size and complexity of the San Francisco estuary made it very difficult to directly measure survival rates with statistical rigor (Newman and Rice 2002); however, our CWT release studies at least provide an indication of whether survival rates in the Yolo Bypass were substantially different from those in the Sacramento River, the adjacent migration corridor. The limited results suggest that fry–adult survival rates were at least comparable in the Yolo Bypass and the Sacramento River. Moreover, the 1998 results suggest that in some years, survival may actually be substantially higher for salmon that migrate through the floodplain. Although none of these CWT releases were replicated, the fact that Sommer et al. (2001b) reported similar results for fry-to-smolt survival for the same releases in 1998 and 1999 increases our confidence that the survival data are not spurious.

Our data indicate that floodplains are a viable rearing habitat for juvenile Chinook salmon. Hence, the most important management implication of our study is that seasonal habitat should be considered as part of restoration plans for this species. Despite frequent concerns that off-channel habitat could increase stranding mortality (Brown 2002; Bruce Oppenheim, NOAA Fisheries, personal communication), our results for a hydrologically variable seasonal floodplain suggest that one should be able to design restoration projects that do not create a population sink because of excessive mortality. This is not to say, however, that stranding mortality is never an issue on floodplain habitat. For example, in the Yolo Bypass we saw significantly higher stranding rates in the concrete weir scour ponds of Fremont and Sacramento weirs than in earthen ponds. This finding suggests that artificial water control structures can create unusual hydraulics that promote stranding. However, the total area of these concrete weir ponds was only 3 ha, much smaller than our estimate of 600 ha for total isolated pond area for April 1998 and insignificant compared with the peak inundated area of 24,000 ha area. Fixing the poor hydraulics at these water-control structures may, nonetheless, be an attractive option, particularly if the cost of the solution is relatively low or if it helps to address other fisheries issues such as adult fish passage. In the Yolo Bypass, the concrete weirs not only create stranding problems for juveniles but also frequently block upstream passage of adult salmon, sturgeon, and steelhead trout (Sommer et al. 2001a), thus creating an incentive to resolve both issues simultaneously.

Finally, we wish to acknowledge that even natural floodplain or well-designed restored floodplain habitat could at least occasionally be a population sink because of stranding or predation losses. Our study was conducted over 3 years for a single, large floodplain; we cannot rule out the possibility that floodplains may not have net benefits in other years or locations. As an example, fish densities in the Yolo Bypass were relatively low compared with those reported in some other studies (Levy and Northcote 1982; Swales et al. 1986; Swales and Levings 1989); perhaps young salmon behavior could be different at higher densities. However, the potential for such losses can still be consistent with effective management of salmon populations. Diverse life history strategies

provide bet-hedging for salmon populations in the highly variable environment of coastal tributaries (Secor 1999; Bottom et al. 2005). We therefore expect that young salmon will not thrive in all habitats in every year. In the case of highly variable seasonal environments such as floodplains, stranding losses might cause excessive mortality in some years, but the risks may be offset by increased rearing habitat and food resources in other years (Sommer et al. 2001b; Brown 2002).

## Acknowledgments

This study would not have been successful without the contributions of staff from the Interagency Ecological Program, which includes the California Department of Water Resources, California Department of Fish and Game, and U.S. Fish and Wildlife Service. The field assistance of W. Batham, R. Kurth, C. Messer, K. Malchow, F. Feyrer, and L. Grimaldo is gratefully acknowledged. This manuscript was substantially improved by the comments of P. Moyle, B. Herbold, F. Feyrer, T.G. Brown, and two anonymous reviewers. Funding was provided by the Interagency Ecological Program and CALFED.

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# Insights into the Problems, Progress, and Potential Solutions for Sacramento River Basin Native Anadromous Fish Restoration

Spring-Run Chinook Salmon in Mill Creek, California (Photo by Dave Vogel)

**April 2011**

**Prepared for:**

**Northern California Water Association**
**and**
**Sacramento Valley Water Users**

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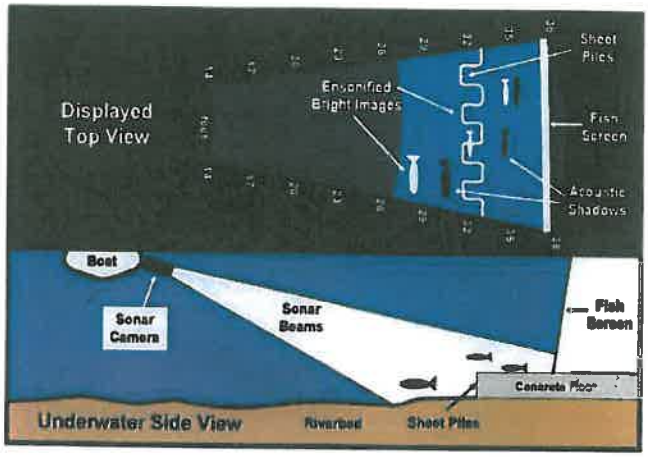



Figure 60. Schematics of DIDSON™ imaging at the base of a flat-plate fish screen. Bottom diagram shows orientation of sonar beams from the acoustic camera off the side of a boat and submerged objects at the fish screens. Top diagram shows the resultant corresponding sonar imaging of objects ensonified with acoustic shadows from the objects. (from Vogel 2008b)

From 1996 through 2010, Natural Resource Scientists, Inc. conducted 22 separate research projects on juvenile salmon (including four studies of predatory fish) in the Delta using acoustic or radio telemetry as a means to gain an improved understanding of fish movements and mortality (Vogel 2010a). The reason juvenile salmon telemetry studies were initiated in the Delta was to acquire detailed data on fish behavior, fish route selection through complex channels, and estimate fish survival in discrete reaches. Past efforts using traditional coded-wire tagging could not answer those critically important questions. Research findings from the telemetry investigations indicate that smolt survival assumptions and models must incorporate these new conclusions to avoid misinterpretation of data and improve quantitative estimates of fish survival and movements (Vogel 2010a).

The first successful use of telemetry on juvenile salmon in the Central Valley was conducted by Natural Resource Scientists, Inc. on behalf of EBMUD in 1996 and 1997. At that time, the specific behavior of juvenile salmon in the Delta was largely unknown. The initial studies quickly determined that the fish did not move as a school, but instead, dispersed, exhibiting a wide range in migratory behaviors in the complex Delta environment. Salmon moved many miles back and forth each day with the ebb and flood tides and the side channels (where flow was minimal) were largely unused. Site-specific hydrodynamic conditions present at flow splits when the fish arrived had a major affect in initial route selection. Importantly, some of the salmon were believed to have been preyed upon based on very unusual behavior patterns (Vogel 2010a).

Subsequent, additional juvenile salmon telemetry studies were conducted by Natural Resource Scientists Inc. on behalf of the USFWS and CALFED in the north Delta (Vogel 2001, Vogel 2004). Triangulating radio-tagged fish locations in real time (Figure 61) clearly demonstrated

how juvenile salmon move long distances with the tides and were advected into regions with very large tidal prisms, such as upstream into Cache Slough and into the flooded Prospect and Liberty Islands (Figure 62). During the studies, it was determined that some radio-tagged salmon were eaten by predatory fish in northern Cache Slough, near the levee breaches into flooded islands (discussed below). Also, monitoring telemetered fish revealed that higher predation occurred in Georgiana Slough as compared to the lower Sacramento River (Figure 63). As discussed previously, past coded-wire tagging studies found that salmon released into northern Georgiana Slough were found to have a higher mortality rate than fish released downstream of the slough in the Sacramento River (Brandes and McLain 2001).

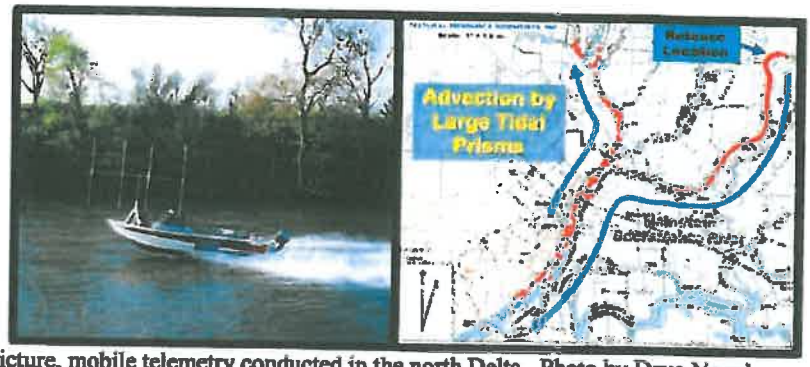



Figure 61. Left picture, mobile telemetry conducted in the north Delta. Photo by Dave Vogel.
Figure 62. Right picture, telemetered locations of approximately 100 radio-tagged salmon smolts released in the lower Sacramento River near Ryde (data from Vogel 2001 and Vogel 2004).

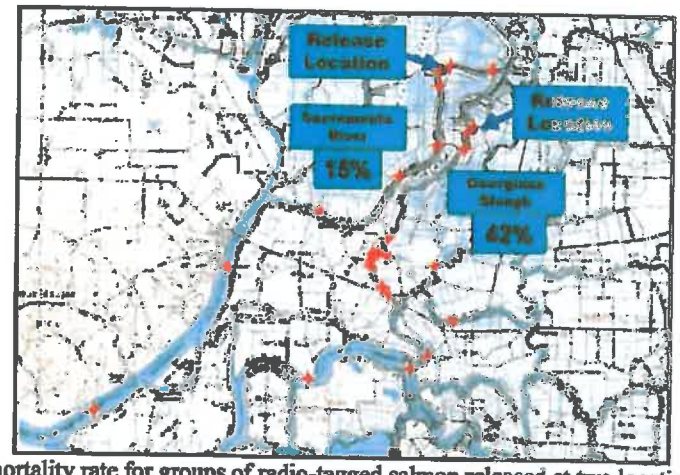
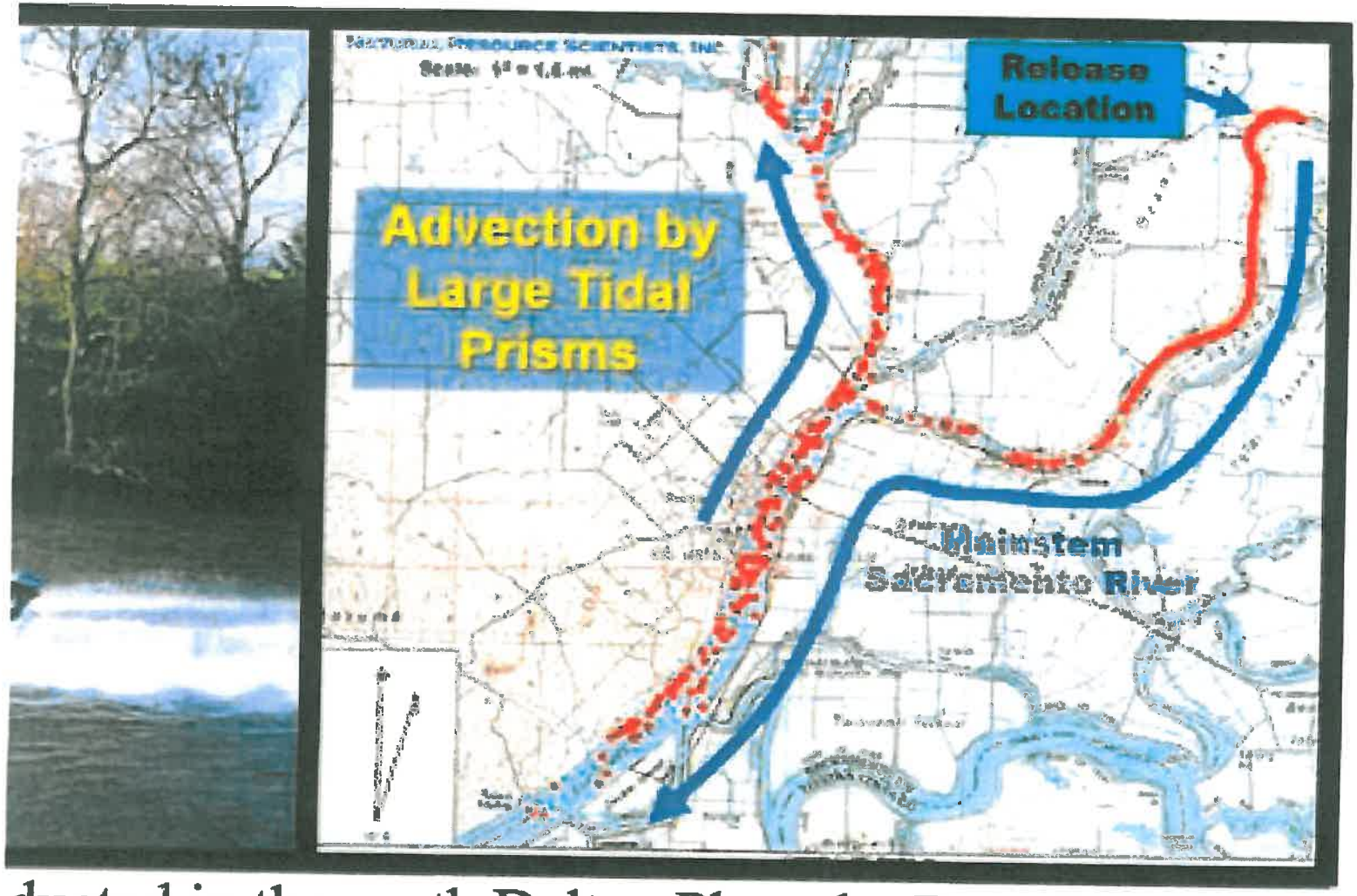



Figure 63. Estimated mortality rate for groups of radio-tagged salmon released at two locations in the north Delta and locations where radio-tagged salmon smolts were detected to have been preyed upon (Vogel 2001, Vogel 2004).

More recently, a 2007 study conducted by releasing acoustic-tagged juvenile salmon in the San Joaquin River found 116 motionless juvenile salmon transmitters in the lower San Joaquin River near the Stockton Waste Water Treatment Plant and a nearby bridge (Figure 64) (Vogel 2007b). This was an all-time record for the largest number of dead radio- or acoustic-telemetered juvenile




ducted in the north Delta. Photo by Dave Vogel.

ıs of approximately 100 radio-tagged salmon smolts released in the

vegetation at some sites in the Delta and water clarity. Increased water clarity for sight predators such as black bass and striped bass would presumably favor predatory fish over prey (*e.g.*, juvenile salmon). Fewer native fish species are found in *Egeria* stands compared to introduced fish species (Grimaldo and Hymanson 1999). Additionally, it has been hypothesized that high densities of *Egeria* in portions of the Delta may restrict juvenile salmon access to preferred habitats, forcing salmon to inhabit deep water or channel areas where predation risks may be higher (Grimaldo *et al.* 2000).

During recent years, there has been an emphasis to reclaim or create shallow, tidal wetlands to assist in re-recreating the form and function of ecosystem processes in the Delta with the intent of benefitting native fish species (Simenstad *et al.* 1999). Among a variety of measures to create such wetlands, Delta island levees either have been breached purposefully or have remained unrepaired so the islands became flooded. A recent example is the flooding of Prospect Island which was implemented under the auspices of creating shallow water habitat to benefit native fish species such as anadromous fish (Christophel *et al.* 1999). Initial fish sampling of the habitat created in Prospect Island suggested the expected benefits may not have been realized due to an apparent dominance of non-native fish (Christophel *et al.* 1999). Importantly, a marked reduction of sediment load to the Delta in the past century (Shvidchenko *et al.* 2004) has implications in the long-term viability of natural conversion of deep water habitats on flooded Delta islands into shallow, tidal wetlands. The very low rates of sediment accretion on flooded Delta islands indicate it would take many years to convert the present-day habitats to intertidal elevations which has potentially serious implications for fish restoration (Nobriga and Chotkowski (2000) due to likely favorable conditions for non-salmonid fish species that can prey on juvenile salmon. Studies of the shallow water habitats at flooded Delta islands showed that striped bass and largemouth bass represented 88 percent of the individuals among 20 fish species sampled (Nobriga *et al.* 2003).

There have likely been significant adverse, unintended consequences of breaching levees in the Delta. There is a high probability that site-specific conditions at the breaches have resulted in hazards for juvenile anadromous fish through the creation of favorable predator habitats. The breaches have changed the tidal prisms in the Delta and can change the degree in which juvenile fish are advected back and forth with the tides (Figure 61; previously discussed). Additionally, many of the breaches were narrow which have created deep scour holes favoring predatory fish. Sport anglers are often seen fishing at these sites during flood or ebb tides. Breaching the levees at Liberty Island is an example (Figure 72 and 73). Recent acoustic-tagging of striped bass in this vicinity confirmed a high presence of striped bass (Figure 74, D. Vogel, unpub. data).

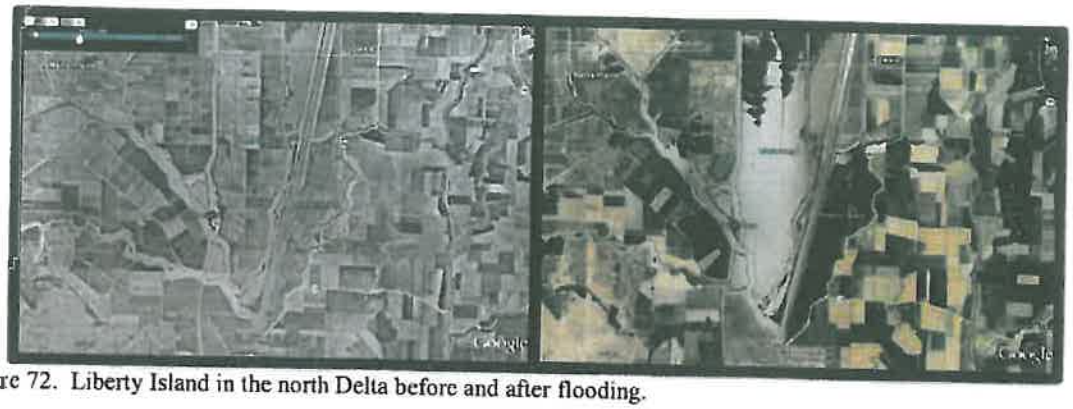


Figure 72. Liberty Island in the north Delta before and after flooding.

Figure 73. Liberty Island in the north Delta before and after flooding showing locations of narrow breaches in the levee.

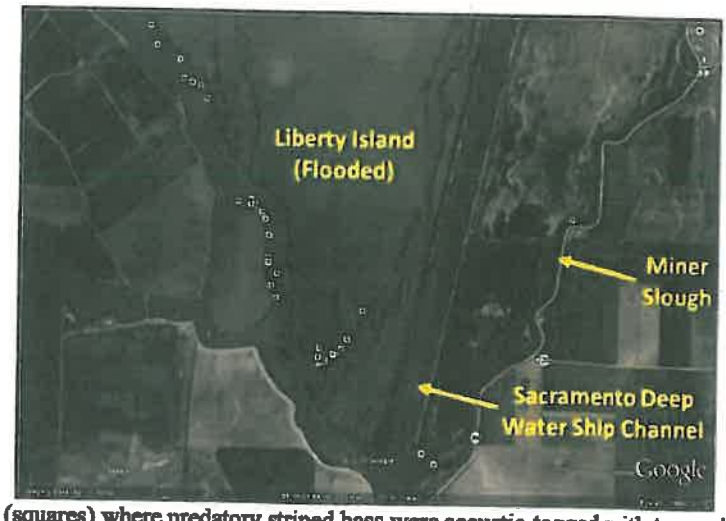



Figure 74. Locations (squares) where predatory striped bass were acoustic-tagged with transmitters during the winter of 2008 – 2009 in the north Delta near Liberty Island (D. Vogel, unpublished data).

**Jeff Opperman**
**Final Report for Fellowship R/SF-4**

My CALFED fellowship (R/SF-4) had three primary research areas: (1) how native fish use California floodplains; (2) developing a method to identify and quantify a particular type of floodplain in the Sacramento Valley; and (3) a white paper for CALFED that reviews, summarizes, and synthesizes research on floodplains generally, and Central Valley floodplains specifically.

***1. Native fish and floodplains.***

For this research I collaborated with Carson Jeffres, a graduate student at UC Davis (this research was his Master's thesis). We compared the growth rates of juvenile Chinook salmon between various floodplain and riverine habitats. This study built on previous work; (1) in the Yolo Bypass that found that juvenile Chinook grew faster in the flooded Bypass than in the nearby Sacramento River and; (2) in the Cosumnes Preserve which showed that native, wild juvenile Chinook salmon appeared to use the Cosumnes floodplain for rearing when it was inundated.

Juvenile salmon were obtained from a hatchery on the Mokelumne River and placed in enclosures within the Cosumnes River and floodplain (ten fish per enclosure). For two flood seasons (2004 and 2005), six enclosures were placed in each of three different habitat types in the floodplain and two locations in the river (30 enclosures total). Floodplain habitats included an ephemeral pond, flooded terrestrial herbaceous vegetation, and a pond that was permanent during the first year of the study and ephemeral during the second. The river locations were the river channel above the floodplain and the river channel below the floodplain.

The fish were measured at one week intervals, although measurement frequency declined during large flood events that made access difficult. In 2004 fish were measured three times over 4.5 weeks and in 2005 they were measured four times over 8 weeks. After the final measurement the fish were sacrificed and a sub-set were saved for a gut-content analysis.

In general, fish had faster growth rates in floodplain habitats than in the river. During periods of low, clear water, fish growth rates in the river site above the floodplain were comparable to those in the floodplain. However, during higher flows, with more turbid water, growth in the river above the floodplain was significantly lower than on the floodplain. Fish in the river below the floodplain, which was representative of intertidal delta habitat, were consistently low.

The main channel of the Cosumnes River, like those of many Central Valley rivers, is incised and lacks complexity. There are few side channels, backwaters, or accessible floodplain habitats (other than the Cosumnes Preserve). Thus, juvenile fish will tend to be displaced downstream during high flow events. In the Cosumnes, juvenile fish will be flushed downstream to either the intertidal delta or the floodplain. Among these two

habitats, the floodplain appears to provide significantly better habitat for rearing (Figure 1).

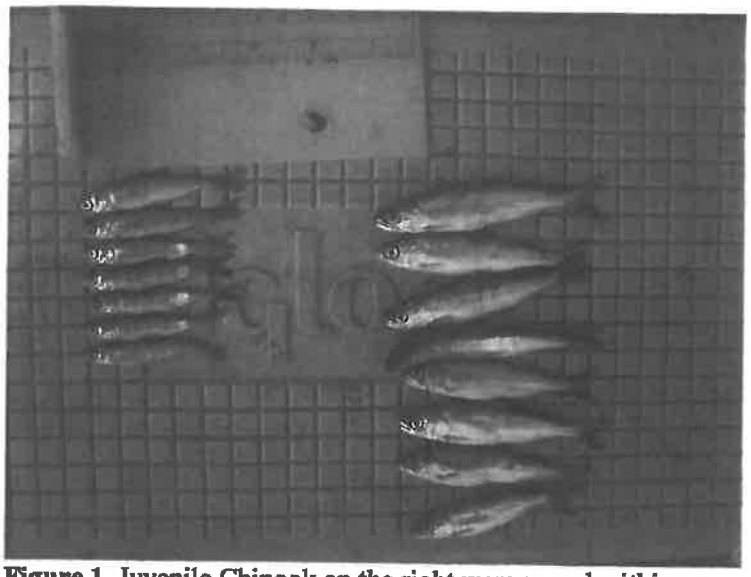


**Figure 1.** Juvenile Chinook on the right were reared within an enclosure within the Cosumnes River floodplain while those on the left were reared within an enclosure in the river below the floodplain (intertidal Delta habitat).

This study confirms that juvenile Chinook benefit from access to floodplain habitats. While river habitats comparable to those above the floodplain can support similar growth rates as the floodplain, this habitat is more variable. During high flows the river offers poor habitat and fish living in this type of habitat will tend to be displaced downstream. The floodplain can provide optimal growing conditions during such floods and likely offers superior habitat conditions to the downstream Delta.

The risk of fish stranding on the floodplain merits further research. However, initial research on the Cosumnes suggests that native fish tend to respond to cues that facilitate emigration from the floodplain during draining and that primarily non-native fish become stranded. This work further supports the concept that floodplain restoration can be an important strategy for restoring Central Valley salmon populations.

This research is summarized in:

Jeffres, C., J. Opperman, and P. B. Moyle. *Submitted.* Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. Submitted to Environmental Biology of Fishes.

This work has also been presented at the following conferences:

1. Floodplain Management Association 2005
2. Society for Ecological Restoration 2005
3. Riverine Hydroecology (Stirling, Scotland) 2006

***2. Identifying and mapping the floodplain inundated by the Floodplain Activation Flood.***

Working in collaboration with Phil Williams and Associates (PWA), we worked to define, identify, and quantify a particular type of floodplain: that which is inundated by a Floodplain Activation Flood (FAF). The FAF is a relatively frequent, long duration, spring-time flood that has particular value for native fish and food web productivity (see text on floodplain conceptual model below for further description of a Floodplain Activation Flood).

The FAF was defined as follows:

1. occurs in two out of three years (67% exceedance probability)
2. duration of at least one week
3. occurs between March 15 and May 15.

These criteria were applied to a series of paired gauges along the Sacramento River and within the Yolo Bypass. This process derived a flood stage elevation that corresponded to the FAF criteria. This flood stage was then used to develop a water surface that was applied to topography for the Sacramento River and surrounding floodplain (from US Army Corps of Engineers' Sacramento-San Joaquin Comprehensive Study), estimating the area of floodplain inundated during the FAF.

We found that there is very little floodplain area inundated by the FAF in the current Sacramento Valley. Nearly all floodplain that corresponds to the FAF is found within the Yolo Bypass.

This work is further described in:

Philip Williams & Associates, L., and J. J. Opperman. 2006. The frequently activated floodplain: quantifying a remnant landcape in the Sacramento Valley, San Francisco, CA.

Williams, P., J. Opperman, E. Andrews, S. Bozkurt, and P. Moyle. Quantifying activated floodplain on a lowland regulated river. *In preparation for* San Francisco Estuary and Watershed Science.

***3. The Central Valley Floodplain White Paper***

I am continuing to work on the floodplain white paper along with my co-author, Peter Moyle. A central part of the white paper is a conceptual model for Central Valley floodplains, briefly described below.

This work has been presented at the following conferences:

1. Floodplain Management Association, 2005
2. American Geophysical Union and the North American Benthological Society, 2005
3. Society for Ecological Restoration, 2005

4. State of the Estuary Conference, 2005
5. CALFED Science Conference, 2006
6. Riverine Hydroecology (Stirling, Scotland), 2006
7. State of Washington, the Ecological Value of High Flows, 2006

Brief overview of conceptual model:

Floodplains support high levels of biodiversity and are among the most productive ecosystems in the world. They provide a range of ecosystem services to human society, including storage and conveyance of flood flows, groundwater recharge, open space, recreational opportunities, and habitat for a diversity of species, many of them of economic importance. Among the world's ecosystem types, Costanza et al. (1997) ranked floodplains second only to estuaries in terms of the ecosystem services provided to society. In the Central Valley, the most important ecosystem services provided by floodplains include reduction of flood risk and habitat for numerous species, including commercially and recreationally valuable species (e.g., chinook salmon and waterfowl) and for endangered species. Recent research has demonstrated that floodplains provide necessary spawning habitat for the Sacramento splittail, an endemic minnow (Sommer et al. 1997) and that juvenile chinook salmon grow faster on floodplains than in main-stem river channels (Sommer et al. 2001b) (Figure 1). Productivity from floodplains can be exported to the Sacramento-San Joaquin Delta, where food limitation is likely one of the factors contributing to the decline of fish species (Jassby and Cloern 2000, Schemel et al. 2004). Further, in places such as the Yolo Bypass, ecologically valuable floodplains can be compatible with productive agriculture (Sommer et al. 2001a).

Recognizing these valuable services, state and federal agencies have expressed policy goals to restore floodplains in the Central Valley (CALFED Bay-Delta Program 2000). Further, flood management projects in the Central Valley now generally include a floodplain restoration component. To guide these restoration efforts, we convened a floodplain working group, composed of floodplain experts drawn from academia, agencies, NGOs, and the private sector, to define ecologically functional floodplains. This group described three primary components of ecologically functional floodplains:

- ***Connectivity*** between river and floodplain.
- ***Hydrological variability***
- ***Sufficient geographic scale*** for associated ecological benefits to be meaningful on a system- or population-scale.

We developed a conceptual model of floodplain processes based on the scientific literature, our collective experiences studying floodplains, and guidance from the floodplain working group (Figure 2). This conceptual model illustrates the linkages between physical and biological processes in floodplains and can be used to inform floodplain restoration projects.

***Organization of the conceptual model.***
A diverse range of flows influence floodplain geomorphic and ecological processes, ranging from flows below bankfull to large, rare, and highly erosive floods. Numerous aspects of these flows have geomorphic and ecological significance, including magnitude, frequency, duration, rates of change, and seasonality, as well as antecedent conditions on the floodplain. To simplify, our conceptual model focuses on three types of 'representative floods,' characterized by their frequency and magnitude, which are found in the blue boxes in the Hydrology portion of the model. These floods perform geomorphic work, described in the brown-outline boxes in the Geomorphology portion of the model. Hydrologic and geomorphic processes create the conditions for Ecosystem Responses and Processes to occur (green-outlined boxes). The Ecosystem Responses and Processes produce Ecological Benefits, the magnitudes of which are influenced by the geographic scale of floodplain. Two representative floods, the Floodplain Activation Flood and the Floodplain Reorganization Flood are illustrated in Figures 2 and 3 and described below.

**Two representative floods**
***Floodplain Activation Flood.*** The floodplain activation flood (FAF) is a small-magnitude flood that occurs relatively frequently (e.g., almost every year) (Figure 3). The FAF can be further defined in terms of seasonality and duration—for example a flood that lasts at least one week and occurs in the Spring. The following article by Betty Andrews defines a FAF in terms of frequency, season, and duration and then describes a process to map the floodplain that corresponds to the FAF in the Sacramento Valley. A long duration flood produces characteristic ecological benefits such as habitat for native fish spawning and rearing (Figure 1) and food web productivity. The duration of the flood is important as these processes cannot occur during a short event. The seasonality of the flood also influences which ecological processes occur (see the temporal scale bar (Winter  Late spring) in one of the ecological process boxes). The importance of duration and seasonality for a FAF is indicated by the question mark adjacent to the flood occurring in late January on the hydrograph in Figure 2 (a short, winter-time flood). Because floodplains can remain inundated for a period of time after the loss of direct connection with river flows, a series of short connections can also function as a floodplain activation flood.
***Floodplain Reorganization Flood.*** The floodplain reorganization flood is a greater magnitude flood that occurs less frequently (Figure 3). This higher energy flood produces geomorphic work including extensive erosion and deposition on the floodplain which creates heterogeneous floodplain topography. In turn, these dynamic events and heterogeneous topography create a diverse ecosystem with vegetation patches of varying age, species composition and structure, and floodplain water bodies of varying successional stage and connectivity to the river. The ecosystem processes that occur during a Floodplain Activation Flood take place within the mosaic of habitat features created during Floodplain Reorganization Floods.

**Conclusions**
The model illustrates the importance of hydrological variability for an ecologically functional floodplain. For example, a floodplain that rarely is inundated by a Floodplain

Activation Flood will not produce the ecological benefits of food web productivity or spawning and rearing habitat for native fish. A floodplain that is not subject to Floodplain Reorganization Floods will not maintain the mosaic of habitats (e.g., vegetation and water bodies of varying successional stages) that help support floodplain biodiversity. Therefore, floodplain restoration projects should not only focus on reintroducing connectivity between rivers and floodplains. Floodplain managers should also ask the following questions about this connectivity: how often, for how long, in what season, and of what magnitude? The answers to these questions will strongly influence the range of ecological benefits that the restored floodplain can provide.


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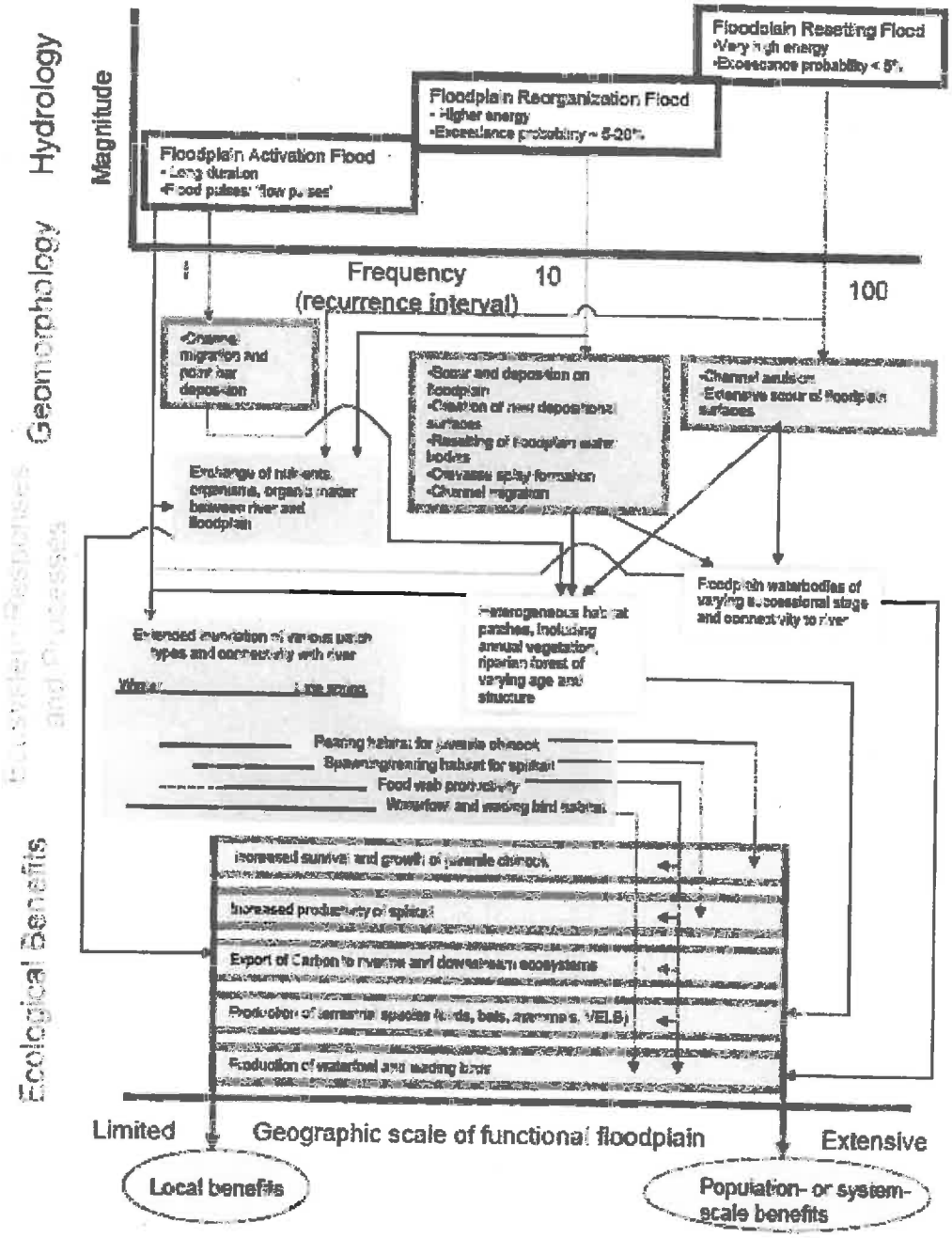
**Figure 2.** Floodplain Conceptual Model



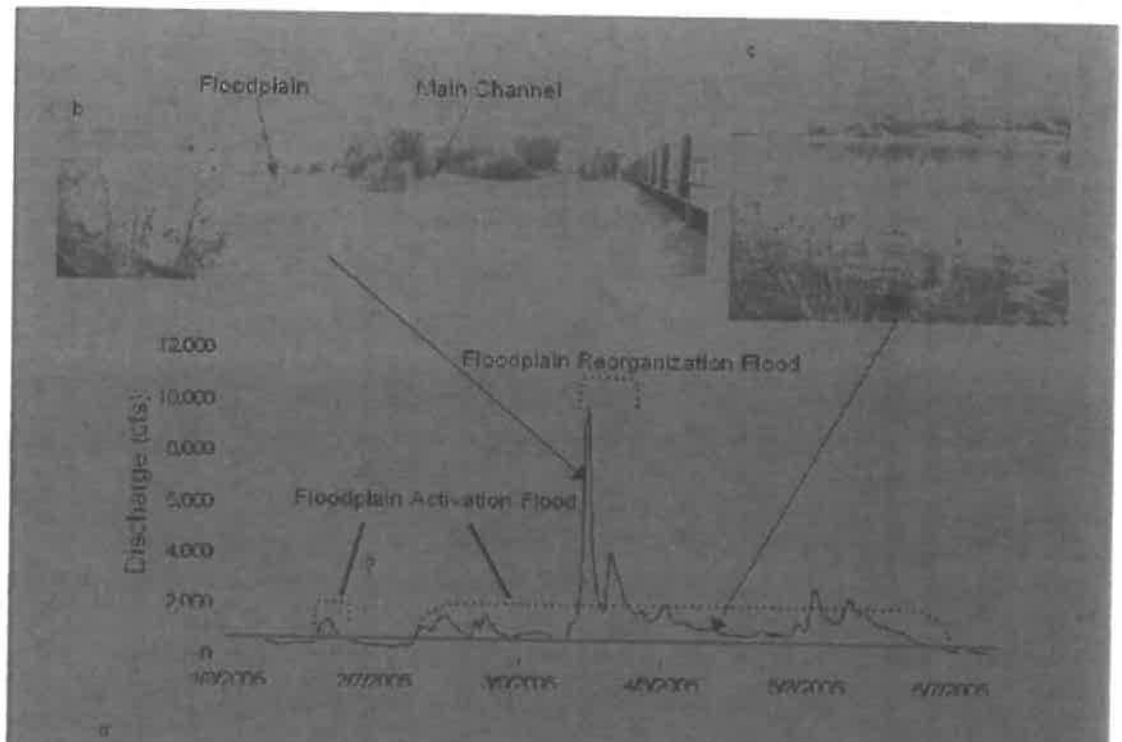



**Figure 3.** (a) Hydrograph from the Cosumnes River winter and spring 2005. The red line indicates the approximate discharge at which the river and floodplain are connected. The importance of duration and seasonality for a floodplain activation flood (FAF) is indicated by the question mark adjacent to the flood occurring in late January (i.e., this short, winter-time flood may not provide the ecological benefits associated with a FAF). (b) A floodplain reorganization flood on the Cosumnes River floodplain, March 23, 2005; (c) A floodplain activation flood on the Cosumnes River floodplain, April 2005. Note the development of algal mats in the water and on the vegetation.