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NPAFC DOCUMENT NUMBER

NPAFC

Doc. No. 94

Rev. No. ______

Variation in marine growth rates of British Columbia pink and sockeye salmon stocks

by

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submitted to the

NORTH PACIFIC ANADROMOUS FISH COMMISSION

by

CANADA

October 1994

This paper may be cited in the following manner:
Welch, D.W. *Variation in marine growth rates of British Columbia pink and sockeye salmon stocks.* (NPAFC Doc. 94) 30 p. Dept. of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, B.C. Canada. V9R 5K6

ABSTRACT

Scale collections for three stocks of sockeye salmon (*Oncorhynchus nerka*) and two stocks of pink salmon (*O. gorbuscha*) from British Columbia were used to examine the changes occurring in freshwater and marine growth rates of salmon since the 1950s. Substantial between-stock differences in patterns of marine growth over time were evident, even for stocks whose natal rivers were nearby. In stocks with multiple ages at return, different age groups generally showed similar patterns of variation over time when specific ocean ages were considered. However, there is some evidence that the patterns are most consistent when considered as "offshore" (open ocean, pelagic), and "coastal" life history periods. Marine growth rates for ages when sockeye are far from the coast showed variation in scale growth rates, but no long-term trend. In contrast, marine growth during either or both the first and last years in the ocean (when sockeye pass through the coastal zone) often showed evidence of a trend towards decreasing marine growth rates with time. Similar patterns are evident for the more limited pink salmon time series, except here the pattern is reversed: marine growth during the coastal phase of the first year shows little or no trend. This suggests that the numbers of pink salmon smolts in coastal waters may be insufficient to affect their food supply at this time. Further work is needed to relate the annual changes in marine growth rates to the terminal size of salmon at return to coastal waters, and to establishing the oceanographic factors that lead to large changes in growth rates between years and life history periods.

INTRODUCTION

At the 1993 Annual Meeting of the North Pacific Anadromous Fish Commission the parties agreed that NPAFC and the North Pacific Marine Science Organization (PICES) should jointly examine the critical issue of the impact of change in the productivity of the North Pacific Ocean on Pacific salmon. Because salmon spend several years at sea before returning to spawn, the life history periods when the ocean environment has its major effects on salmon production are unclear. To provide finer scale data for studying this issue, I initiated a program to measure marine growth rates of salmon using existing scale collections for a number of Canadian salmon stocks. I report here on preliminary findings for three British Columbia sockeye salmon stocks, (Early Stuart, Skeena, and Nass), plus two pink salmon stocks (Fraser and Skeena rivers).

MATERIALS AND METHODS

The Department of Fisheries and Oceans (DFO) and the Pacific Salmon Commission (PSC) maintain extensive archival collections of salmon scales collected from major test fisheries conducted within the province of British Columbia. For initial analysis, I focussed on sockeye salmon collected from three of the largest sockeye populations in the province. The Fraser River is located in southern British Columbia, and contains many distinct sockeye salmon spawning populations. In order to select a homogeneous sample, the Early Stuart stock was chosen for analysis. This stock is unique in migrating very early in the summer, prior to other stocks of Fraser sockeye returning in significant numbers (Woodey 1987). As a result, variations in marine growth rates caused by measuring a scale sample composed of a mixture of stocks should be minimized. Whenever possible scale samples were selected for measurement from a window of ±3 days from the peak date of test fishery catches of Early Stuart sockeye in each year. Peak dates were determined with the help of PSC staff.

Run timing characteristics for individual sockeye stocks returning to either the Skeena and Nass river systems in Northern British Columbia are less clear. A gillnet test fishery situated near the mouth of each river is operated by DFO. Both river systems are major sockeye producers situated at the heads of fiords separated by about 100 km. The Nass River test fishery in particular is situated near the head of an extensive fiord system, making it less likely that Skeena River sockeye will contribute to the Nass test fishery. Conversely, the Skeena test fishery is situated to the south of the Nass, so the bulk of the fish returning to the Nass probably do not pass through the area where the Skeena test fishery operates.

The run timing characteristics of individual stocks within these systems are not well known. In order to reduce potential heterogeneity caused by stock compositions varying over the years, scale samples from each test fishery were selected from a time window of ±5 days of the average date of peak return to each test fishery. No Nass River test fishery scale samples were found in the archives for the 1967 sample year.

Early Stuart sockeye scales were measured for the period 1951-93 (43 yrs). Skeena and Nass River sockeye scale series mere measured for the 37 yr period 1957-93, and the 39 yr period 1955-93, respectively. A sample of 100 scales were digitized per year for age 4_2 Early Stuart sockeye, except for a few years where lesser numbers of scales were available. Analysis of these data indicated that the benefit from digitizing 100 scales was marginal, and target sample sizes for Nass and Skeena sockeye salmon were reduced to 80 scales per age group and year. In most cases these sample sizes were achieved, but sample sizes on the Nass and Skeena dropped to only a few scales in some years for less common age groups. These reduced sample sizes are reflected in the width of the ±2 SE bands around the means shown on individual fisheries. Only limited numbers of age 5_2 sockeye scales were available for the Early Stuart sockeye, reflecting the rarity of this life history pattern among upper Fraser sockeye stocks.

Scale measurements were made using a BioSonics Optical Pattern Recognition (OPR) video digitizing system. Scales were magnified using a microscope with attached video camera at 8X, and the signal sent to a Sony Trinitron 52 cm (25") large screen television monitor with built-in RGB jacks.

The normal setup of the OPR system sends the video output to a 35 cm (14") computer monitor. This monitor is capable of displaying the entire image of a pink salmon scale at sufficient magnification to resolve fine detail on the scale surface. However, it is not possible to display the entire surface of a sockeye scale on this monitor while maintaining sufficient magnification to allow good discrimination of scale features. The combined use of low power magnification on the microscope along with the large screen television monitor allows the entire sockeye scale to be displayed at one time while simultaneously providing detailed resolution of the circuli. This enabled the scale readers to make all scale measurements described below at once, without the need to change viewing magnifications.

Each scale was measured from the focus to the end of the freshwater and marine growth zones. Growth was measured on a 20□ventral angle to a line drawn perpendicular to the orientation of the circuli near the scale focus. This perpendicular line forms approximately the longest axis of the scale. The edge of the freshwater annulus was taken as the outer edge of a series of finely spaced and frequently broken-up circuli, and did not include "plus growth", freshwater growth that occurred in the following year, prior to entry into salt water.

Plus growth was included in our measurements of first year (M_1) marine growth. First year marine growth was taken from the outer edge of the freshwater (FW) zone to the outer edge of the first marine annulus. The outer edge was defined as the end of the winter band, a sequence of thin, closely-spaced circuli, that is probably laid down overwinter until early spring. Second and subsequent years of marine growth were taken as the distance between the outside edge of adjacent winter bands. In cases where significant resorption of the scale edge was evident, scale readers were instructed not to include scale measurements for the last year of marine growth. Readers were also instructed to qualitatively record the degree of resorption evident, as low, medium, or high.

RESULTS

Early Stuart (Fraser) Sockeye Salmon

The Early Stuart sockeye stock returns to the Fraser River well before other Fraser sockeye stocks (Woodey 1987). By choosing the Early Stuart run for analysis, it is possible to minimize potential difficulties in interpretation of growth variations caused by contamination of the growth characteristics of one stock by other sockeye stocks.

The average length of both sexes of Early Stuart sockeye has varied erratically over time, but until recently has been without trend (Fig. 1). A sharp drop in mean size occurred in the mid-1950s, followed by subsequent recovery. Beginning in the 1990s, another sharp decline in mean size is evident, with mean sizes declining to sizes not seen even in the 1950s. The mean size at return in 1993 was the smallest on record. The recent decline in mean size of Early Stuart sockeye is also seen in most of the other Fraser sockeye stocks.

Age 4_2 and 5_3 mean scale growth rates ±2 standard errors are shown in Figs. 2 and 3, and compared directly in Fig. 4. Age 4_2 mean growth rates were precisely measured in all years but 1959, when only a limited number of scales were collected. Freshwater (FW) growth of age 4_2 Early Stuart sockeye increased until the early 1970s, and then declined. The decline is mirrored in the age 5_2 scale time series, and probably reflects density-dependent in-lake growth. First and third year marine growth rates (M_1 and M_3, respectively) varied without trend since 1951. M_2 scale growth (growth completed entirely in the open ocean) also varied without trend until the late 1980s, when growth declined suddenly.

Both 4_2 and 5_2 sockeye spend one year in freshwater. Age 4_2 sockeye subsequently spend three years in the ocean, and age 5_2 sockeye four. Note that in all graphs, the growth data is plotted relative to the year of capture; thus freshwater growth by 4_2 sockeye caught in year t actually occurred in year t-3, and in year t-4 for 5_2 and 5_3 sockeye, one year earlier. Conversely, the marine growth of 4_2 and 5_3 sockeye (compared below for the Nass River) occurred one year later than that for 5_2 sockeye when comparing scale growth that occurred at the same life history period (Fig. 5). The convention of plotting scale growth versus year of capture in the test fisheries is kept because we are primarily interested in comparing long-term trends in marine growth here, not short term variation between life history groups.

Some interesting differences in the growth patterns of 4_2 and 5_2 sockeye are evident. Freshwater growth of both groups was similar in the 1950s, but was substantially lower for 5_2 fish in the 1980s. In contrast, first year marine growth (M_1) was very similar for both age groups. Second year (M_2) growth was clearly consistently lower for age 5_2 sockeye. Conversely, M_3 scale growth was lower for age 4_2 sockeye, presumably reflecting the fact that this age group only completes part of a growth season before returning to spawn.

Overall, M_1 growth conditions therefore show no evidence of determining whether an Early Stuart sockeye returns at age 4_2 or age 5_2. Instead, the evidence would indicate that either reduced FW or M_2 growth can results in fish returning at age 5_2-- M_2 growth of 5_2 fish was low in the 1950s while FW growth was good, while FW growth was low in the 1980s.

Skeena Sockeye Salmon

Skeena River sockeye have two major life history patterns, with fish returning at ages 4_2 and 5_2. Figs. 6-8 show the variation in average growth rate by life history stage, along with the ±2 standard error bands on the mean. In all but one year when few scales were collected the uncertainty in the annual average growth rate estimates is small, and the overall pattern of change is clear.

For both age groups, freshwater scale growth has increased since the 1960s, while both M_1, M_3, and M_4 scale growth has shown evidence of long-term decline since either 1970 (M_1 growth) or the late 1950s (M_3 and M_4 growth). In contrast, M_2 (open ocean) scale growth has varied without long-term trend. Also, consistent with observation for the Early Stuart sockeye, scale growth of Skeena River 5_2 sockeye is slightly slower than for 4_2 fish in their second (but not first) ocean year. M_3 scale growth is much greater for 5_2 fish, again presumably reflecting the additional growth completed during a full year in the ocean. Overall, there is substantial covariance between the two age groups in their patterns of growth over time.

Nass Sockeye Salmon

Nass River sockeye have three different life history patterns, with fish returning at ages 4_2, 5_2, and 5_3. Figs. 9-11 show the variation in average growth rate by life history stage, along with the ±2 standard error bands on the mean. In most years uncertainty in rates of annual average growth are small, and the overall pattern of change is clear.

Fig. 12 compares the pattern of variation in growth by life history stage over time. First year freshwater scale growth (FW_1) for both 4_2 and 5_2 sockeye is very similar, with substantially more growth achieved than by 5_3 sockeye. However, age 5_3 sockeye spend two full growing seasons in freshwater, and net freshwater growth of 5_3 fish ($FW_1 + FW_2$) is substantially greater than that achieved by 4_2 and 5_2 sockeye.

No long term trends in either FW1 or FW2 freshwater growth are evident for any life history age group. ***Second*** year growth in the ocean (M_2) also shows little long term trend in growth rates, although M_2 growth between 1955-61 appears to have been slightly higher than in subsequent years. In contrast, first year marine (M_1) growth of all life history groups increased substantially through the 1960s, reaching a peak in the late 1970s. Growth then declined. A long-term decline is evident in M_3 growth for age 4_2 and 5_3 sockeye, which return to coastal waters during their third ocean year, but not for age 5_2 fish. Age 5_2 sockeye, which return to the coast during their fourth ocean year, show no evidence of a long-term decline in either M_3 or M_4 growth. As with Early Stuart and Nass River sockeye, the total scale growth achieved during the M_3 period is much higher than for 4_2 and 5_3 fish, presumably the result of being able to stay at sea and feed for a full year, rather than returning to the coastal zone by mid-summer.

Fraser Pink Salmon

Scale growth of Fraser River pink salmon has been reported by Blackbourn and Tasaka (1990) for the period 1958-1988. Fraser River pink salmon exhibit extreme cyclic dominance, and return to spawn only in odd years. Blackbourn and Tasaka examined variation in three measurements: scale growth from the focus to the 10th circuli (approximately the first four months of life, corresponding roughly to the period of the life history spent in coastal waters), scale growth from the 10th circuli to the outside edge of the first annulus (corresponding to first year growth during the pelagic period of the life history), and growth from the first annulus to the scale edge (second year pelagic plus coastal growth).

In some years, significant scale resorption had occurred by capture, and it was not possible to reliably determine second year growth (Fig. 13). "Coastal" growth (focus to the 10th circuli) was remarkably constant over time. Growth during both the second year of life and the offshore period of the first year showed significant variation over time, but with the largest variation and the greatest decline expressed during M_2 growth. The constancy of growth during the first four months of ocean life suggests that Fraser River pink salmon grow in an essentially food unlimited environment during the first year of life in the coastal environment. Fluctuations in food abundance either influence primarily the growth rates of Fraser pink salmon only during the offshore pelagic period, or during their return to the coastal zone as maturing adults.

Skeena Pink Salmon

To examine the possibility that coastal growth of pink salmon fry is essentially constant, we examined the scale growth of Skeena River pink salmon using the same scale measurement criteria as were used for Fraser pink salmon (Fig. 14). Pink salmon scales were collected in a standardized manner for the 18 year period 1955-72. Pink salmon scales apparently were not collected after 1972.

Average scale growth to the 10th circuli was very similar to that of Fraser pink salmon (ca. 370 versus 400 microns, respectively). Unlike Fraser pink salmon, growth to the 10th circuli showed evidence of much more variability. Both growth from the 10th circuli to the end of the first winter (M_1 growth) and second year ocean growth (M_2) also showed evidence of significant annual variation. First year marine scale growth in both Fraser River and Skeena River pink stocks is very similar, but Fraser pink salmon complete more scale growth in their second year than Skeena pink salmon. This is likely a result of the shortened final growing season for the more northerly Skeena population, which returns to spawn several months earlier than the Fraser population.

DISCUSSION

Each stock and species of salmon we have examined to date has shown substantial differences in patterns of marine growth over time. This suggests that there is not a single uniform feeding ground for these stocks, and that stocks are differentially distributed within the Gulf of Alaska. However, each sockeye stock also shows considerable internal similarities in annual growth patterns between life history groups. The dome-shaped change in M_1 growth for all age classes of Nass River sockeye, plus the declining trend in M_3 growth for 4_2 and 5_3 sockeye (which both return in their third ocean year), suggests that declines in overall sockeye growth are related to feeding in the coastal environment, rather than the offshore. These changes suggest different mechanisms are operating between stocks.

McKinnell (1994) also found stock-specific differences between Nass and Skeena River sockeye, with a negative correlation between the abundance of western Alaska sockeye catches and growth of British Columbia sockeye that completed three years of growth in the ocean (age 5_2 sockeye). However, he also concluded that the greatest interaction therefore occurred for older sockeye, which appeared to be geographically centered further west in the Gulf of Alaska than age 4_2 sockeye.

Clarification as to whether or not the greater limitations to sockeye growth occur on or off the continental shelf will require the development of statistical models that allow joint interpretation of the effect of growth variation in all life history periods. This work is currently underway. However, the very dissimilar growth patterns evident for different ocean ages clearly points to the need to not interpret oceanographic effects as having some uniform influence on salmonid growth and oceanic carrying capacity. Rather, there is a clear need to resolve whether density-dependent (carrying capacity) effects are happening primarily on or off the continental shelf, and to establish what life history periods these effects are expressed.

As suggested by Ricker (1964), sockeye returning to spawn at older ages clearly have slower rates of growth than fish that return at younger ages. However, age at maturity appears to be determined during the second year of ocean residence, because the M_1 growth of all age groups was essentially identical for all three sockeye stocks examined. M_2 growth of age 5_2 fish was significantly less than M_3 growth. This suggests that the factors determining whether sockeye return to spawn in their fourth or fifth year of life are largely determined by the amount of growth achieved during their second ocean year, and that age at maturity is not the result of cumulative differences in growth across all years of life.

CONCLUSIONS

The minimum physiological size at which Pacific salmon can sexually mature is not known. However, the trend over the last four decades is towards reduced growth rates and smaller body size in Pacific salmon in all regions of the Pacific Rim. If this trend continues then the decline in growth will eventually result in a shift in age structure towards return at older ages. Such a change will represent substantial lost salmon production, because population productivity is inversely related to the generation length, T.

For example, a shift from a mean age at spawning of age 4_2 for Fraser sockeye to age 5_2 would result in a 20% ($\frac{1/5}{1/4} = \frac{0.20}{0.25} = 0.8$) reduction in sustainable harvest rates. This would imply in the Fraser River that sustainable harvest rates would have to be reduced from their current target level of 74% to ca. 59%. Such a change would require a huge adjustment in commercial fisheries. Additional economic losses would also be incurred because smaller fish yield lower meat yields, and also incur higher processing costs.

This type of calculation will apply equally anywhere in the Pacific Rim where salmon size is declining. It also implies that changes in growth should have major impacts on salmon fisheries. Further scientific studies to establish the reasons for the trend towards reduced growth now seen around the Pacific Rim should be seen as an important priority for future co-operative international research.

ACKNOWLEDGEMENTS

I thank Ms Judy MacArthur and Ms Barb Campbell for their meticulous work on the scale measurements, and their assistance in tabulating and graphing the data. Dr Jim Woodey (Pacific Salmon Commission) kindly provided scale samples for the Early Stuart sockeye run, and advice on the run timing period during which to choose these samples.

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Ricker, W.E. 1964. Ocean growth and mortality of pink and chum salmon. J. Fish. Res. Bd. Canada 21:905-931

Woodey, J.C. 1987. In-season management of Fraser River sockeye salmon (*Oncorhynchus nerka*): meeting multiple objectives, p.367-374. *In* H.D. Smith, L. Margolis, and C.C. Wood [eds] Sockeye salmon population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96

FIGURE CAPTIONS

Fig. 1. Standard length of age 4_2 early Stuart sockeye. An equal sex ratio was assumed in the calculation.

Fig. 2. Early Stuart age 4_2 growth patterns.

Fig. 3. Early Stuart age 5_2 growth patterns.

Fig. 4. Comparison of early Stuart growth patterns for age 4_2 and 5_2 sockeye.

Fig. 5. Comparison of sockeye life history patterns.

Fig. 6a. Skeena River age 4_2 growth patterns.

Fig. 6b. Skeena River age 4_2 growth patterns (concluded).

Fig. 7a. Skeena River age 5_2 growth patterns.

Fig. 7b. Skeena River age 5_2 growth patterns (concluded).

Fig. 8a. Comparison of Skeena River growth patterns.

Fig. 8b. Comparison of Skeena River growth patterns (concluded).

Fig. 9. Nass River age 4_2 sockeye growth patterns.

Fig. 10a. Nass River age 5_2 sockeye growth patterns.

Fig. 10b. Nass River age 5_2 sockeye growth patterns (concluded).

Fig. 11a. Nass River age 5_3 sockeye growth patterns.

Fig. 11b. Nass River age 5_3 sockeye growth patterns (concluded).

Fig. 12a. Comparison of Nass River sockeye growth patterns.

Fig. 12b. Comparison of Nass River sockeye growth patterns (concluded).

Fig. 13. Fraser River pink salmon scale growth. Note that data is plotted relative to fry year, one year prior to adult return. (◆: Growth to 10th circuli (C_{10}) ; ■: M_1-C_{10}; ●: M_2 growth)

Fig. 14. Skeena River pink salmon scale growth. Data is plotted relative to return year.

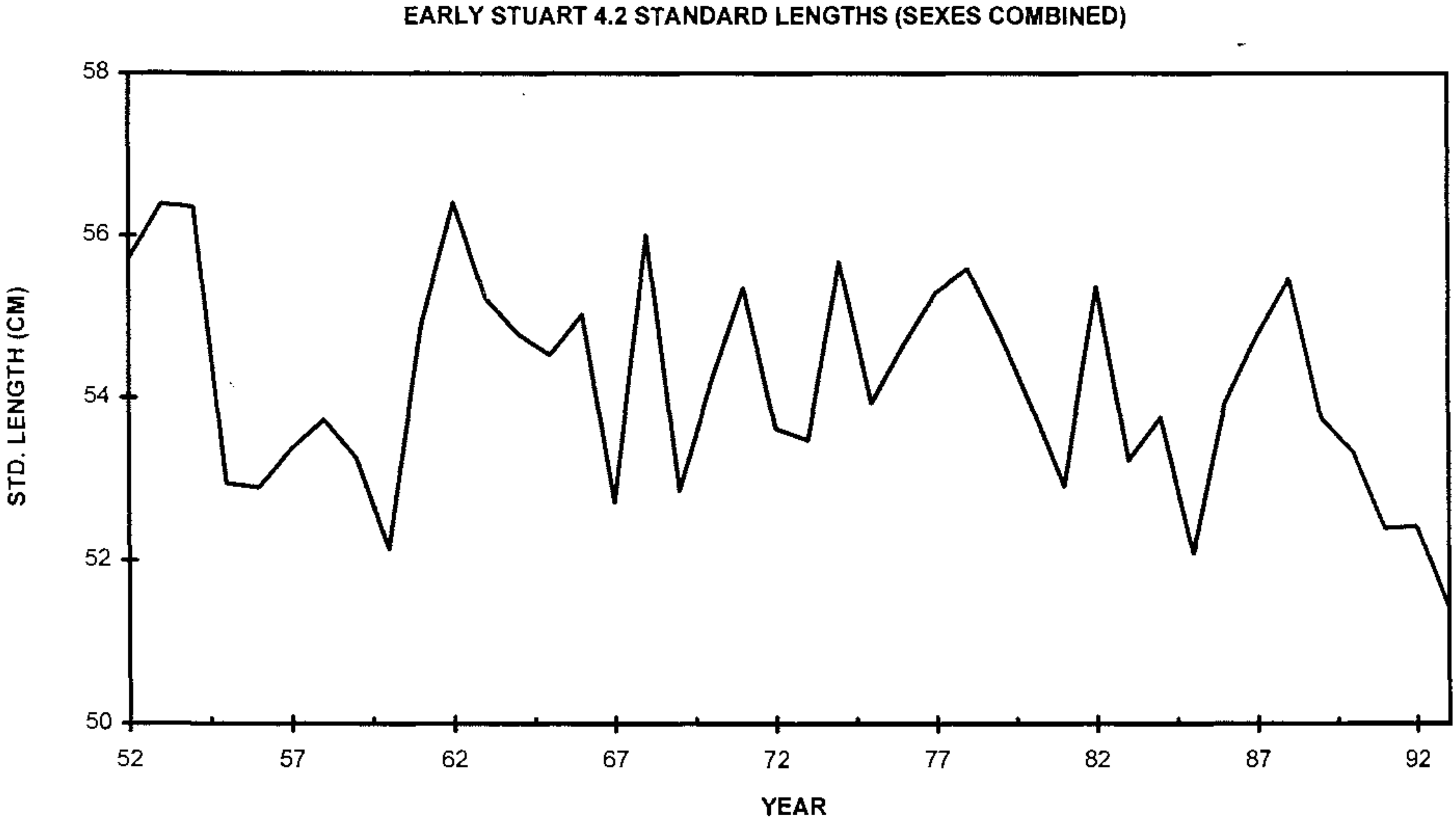
EARLY STUART 4.2 STANDARD LENGTHS (SEXES COMBINED)
STD. LENGTH (CM)
58
56
54
52
50
52
57
62
67
72
77
82
87
92
YEAR

Fig. 1.

EARLY STUART 4.2 SOCKEYE

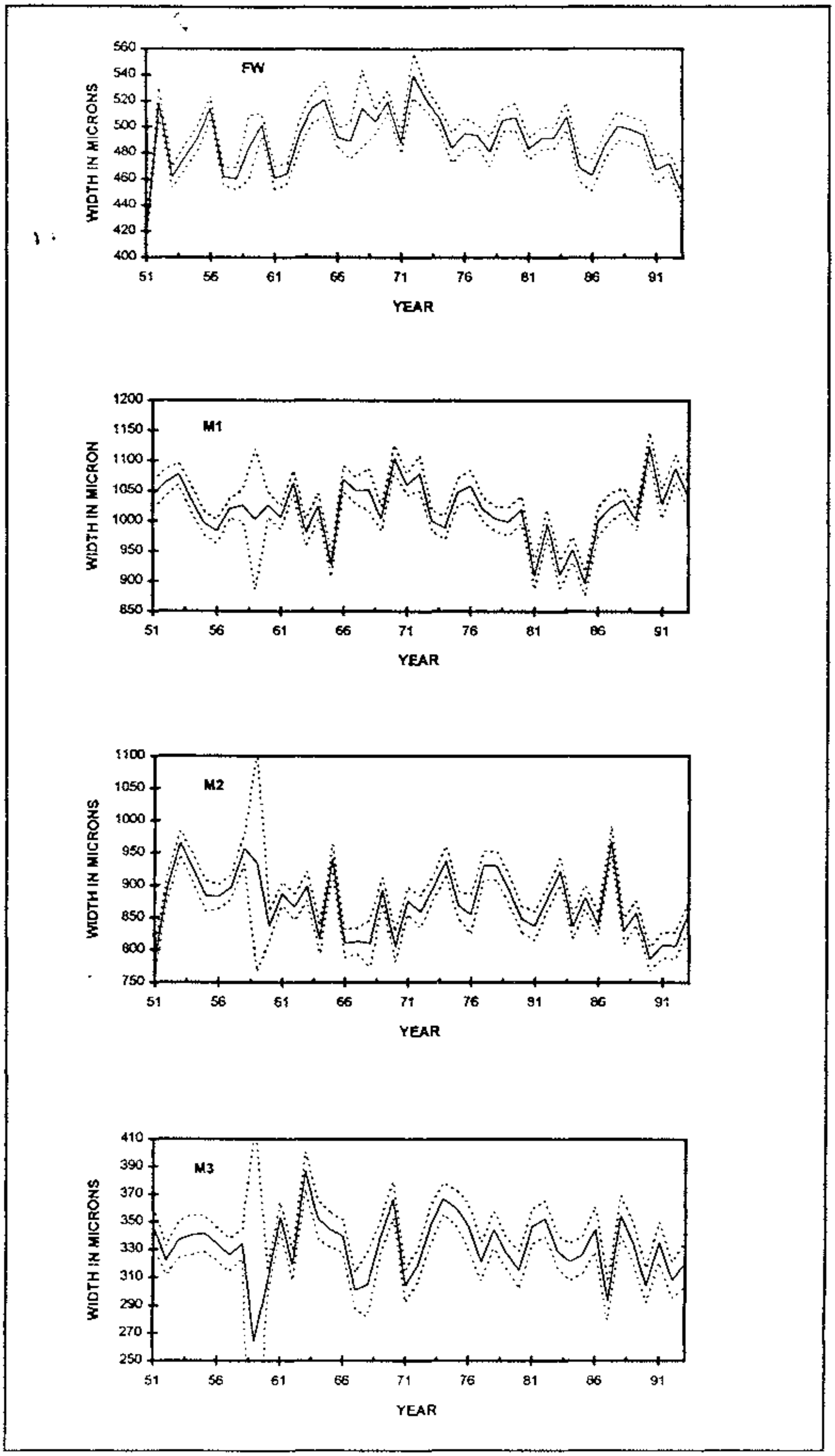

Fig. 2.

EARLY STUART 5.2 SOCKEYE

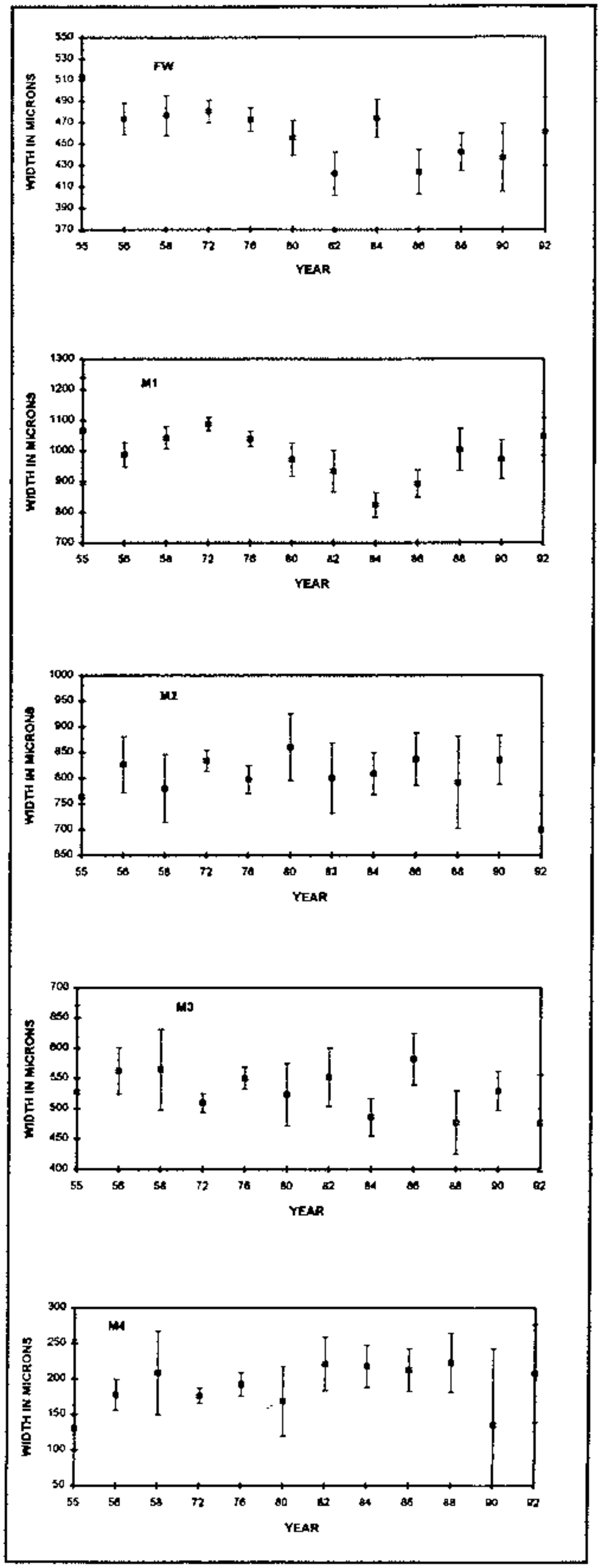

Fig. 3.

EARLY STUART 4.2, 5.2 SOCKEYE

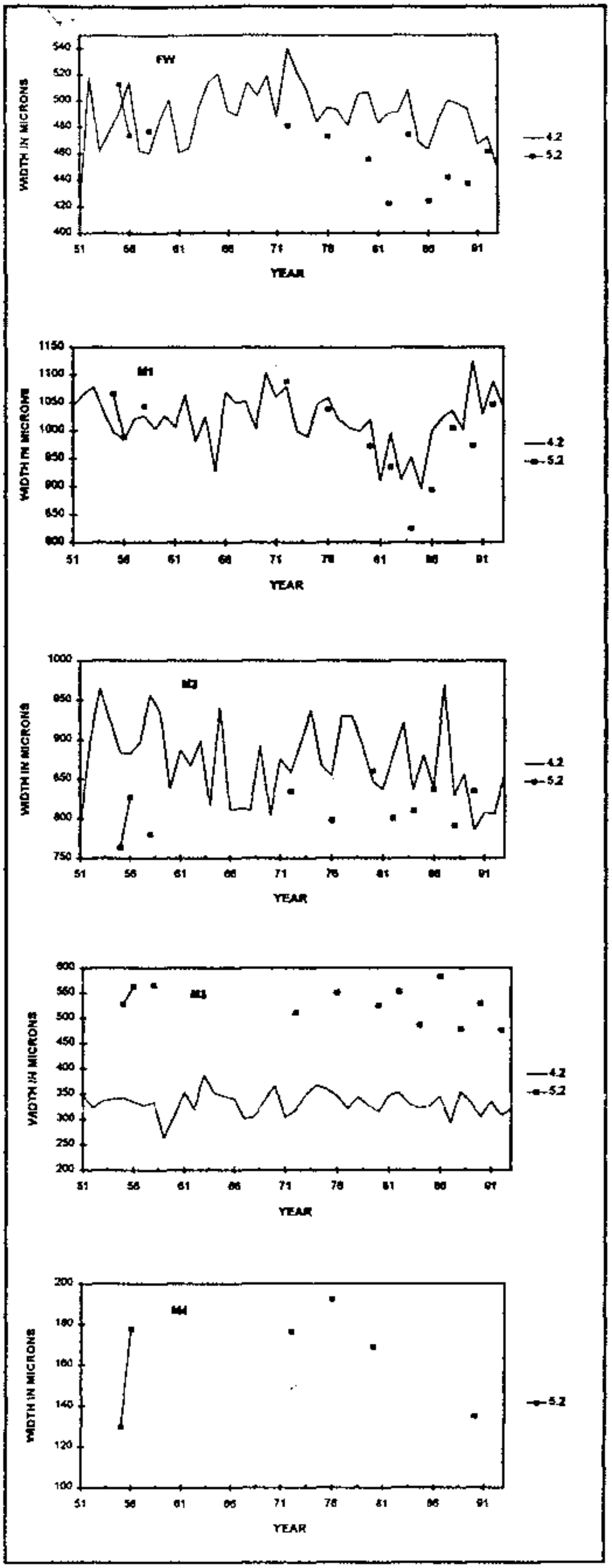

Fig. 4.

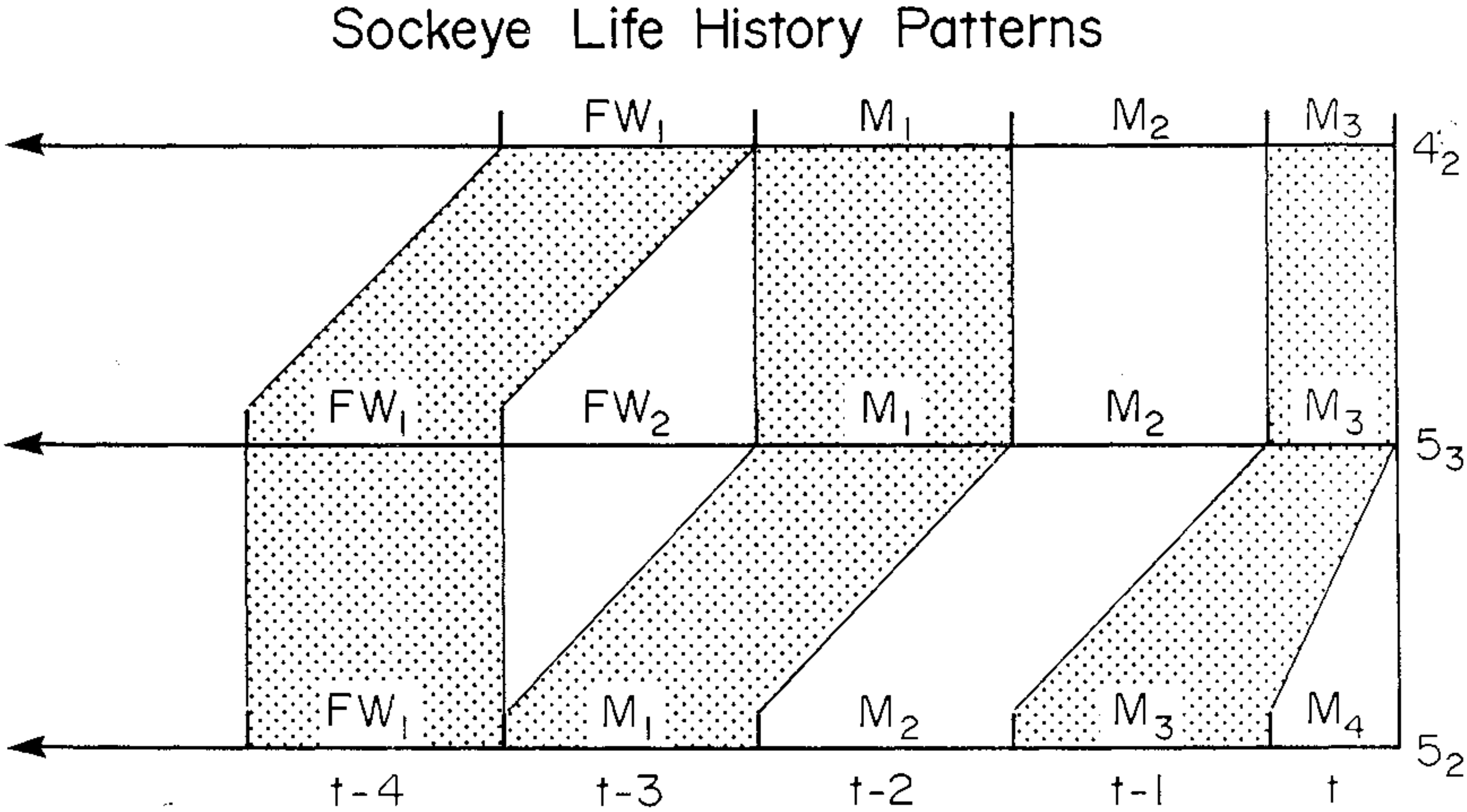
Sockeye Life History Patterns
FW_1
M_1
M_2
M_3
4_2
FW_1
FW_2
M_1
M_2
M_3
5_3
FW_1
M_1
M_2
M_3
M_4
5_2
t-4
t-3
t-2
t-1
t

Fig. 5.

SKEENA 4.2 SOCKEYE

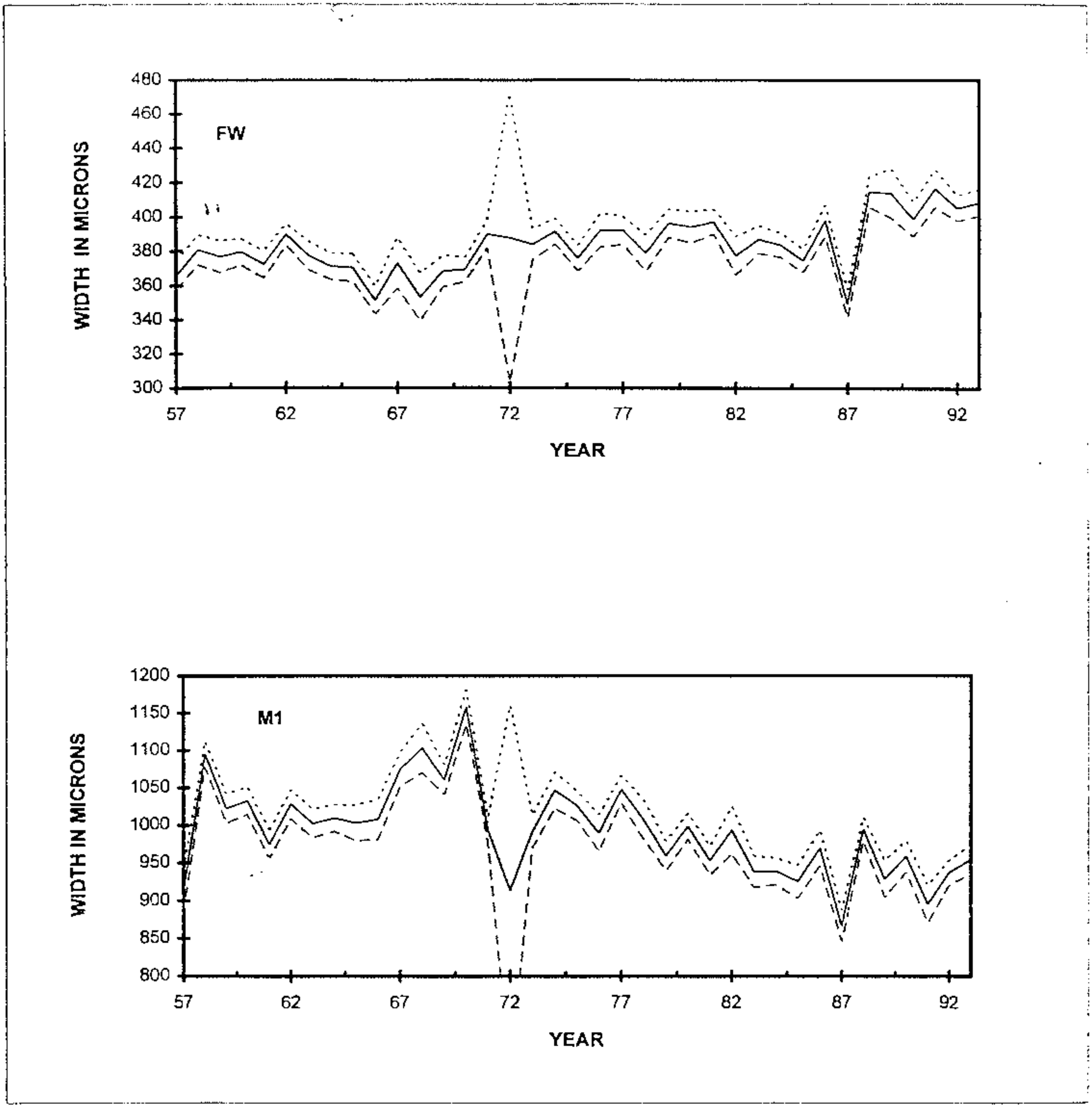

Fig. 6a.

SKEENA 4.2 SOCKEYE

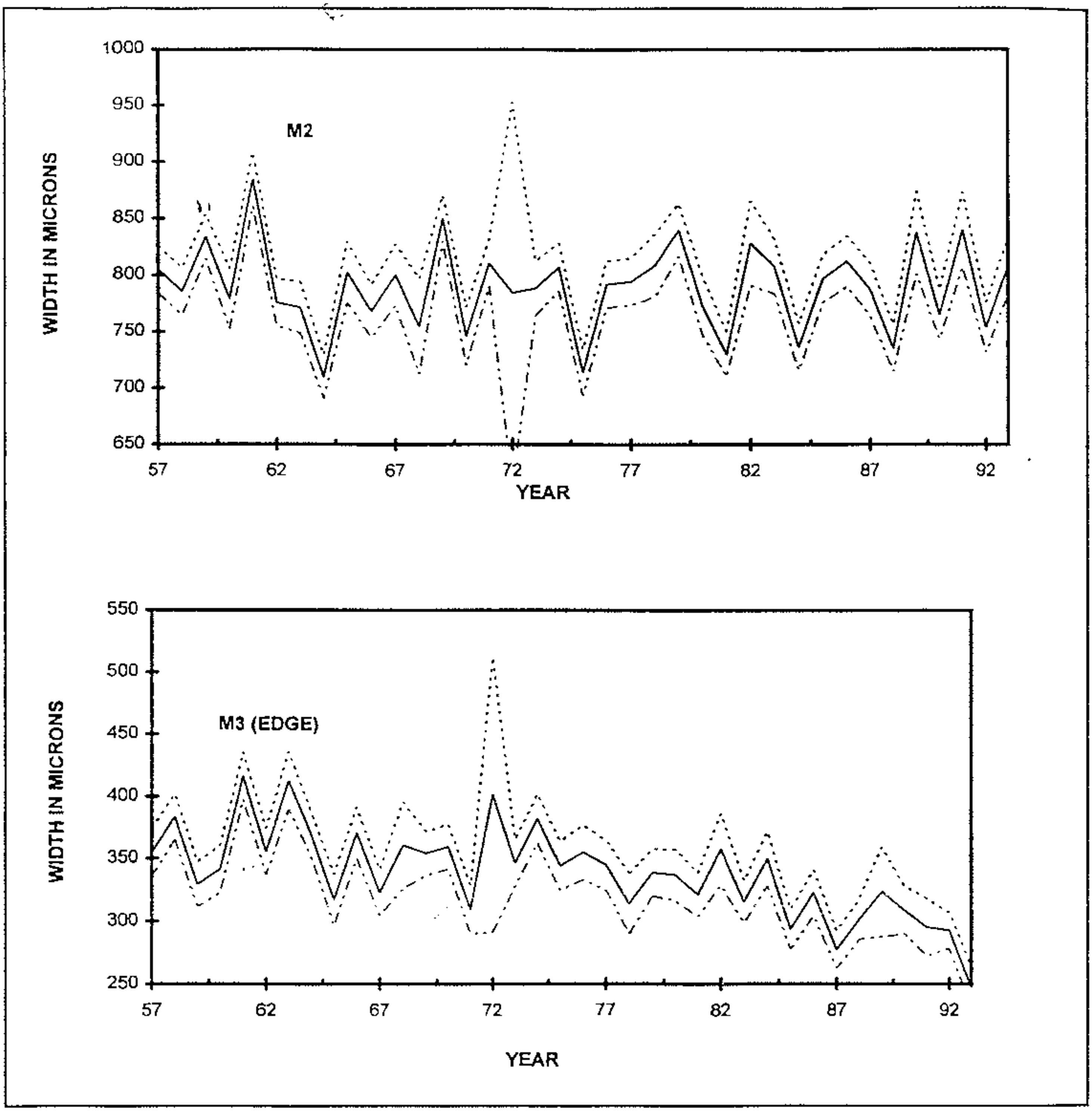

Fig. 6b.

SKEENA 5.2 SOCKEYE

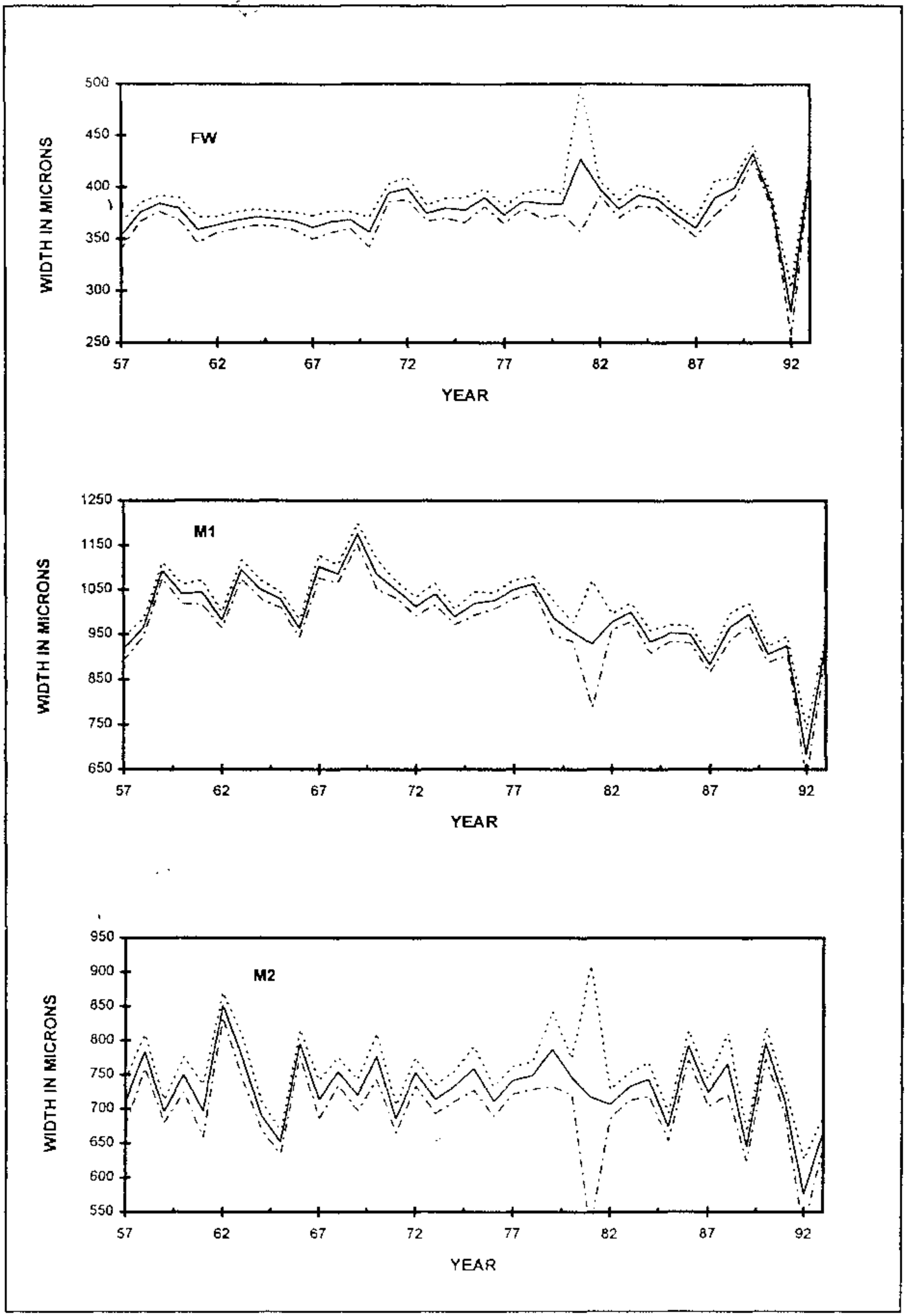

Fig. 7a.

SKEENA 5.2 SOCKEYE

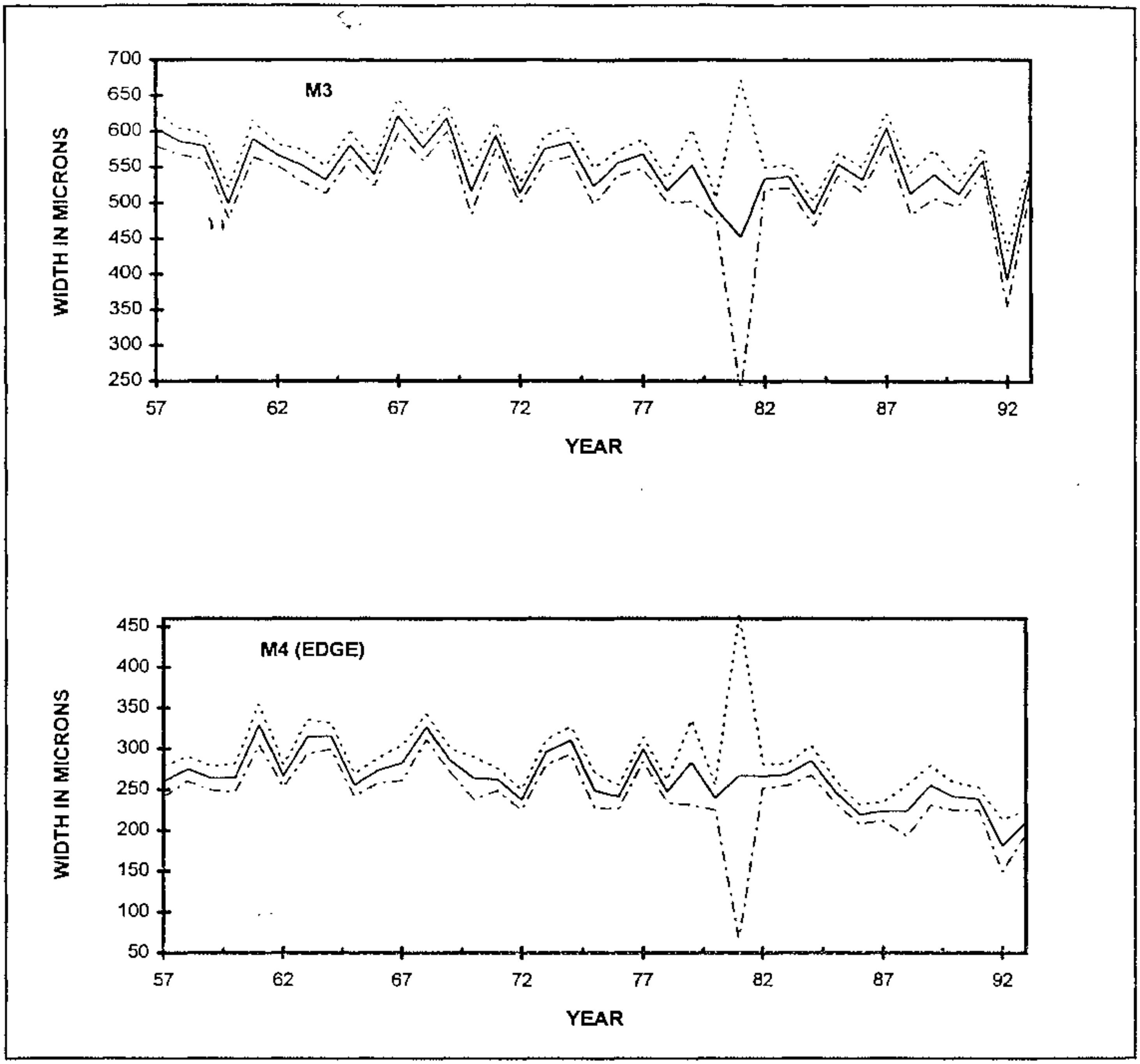

Fig. 7b.

SKEENA 4.2, 5.2 SOCKEYE

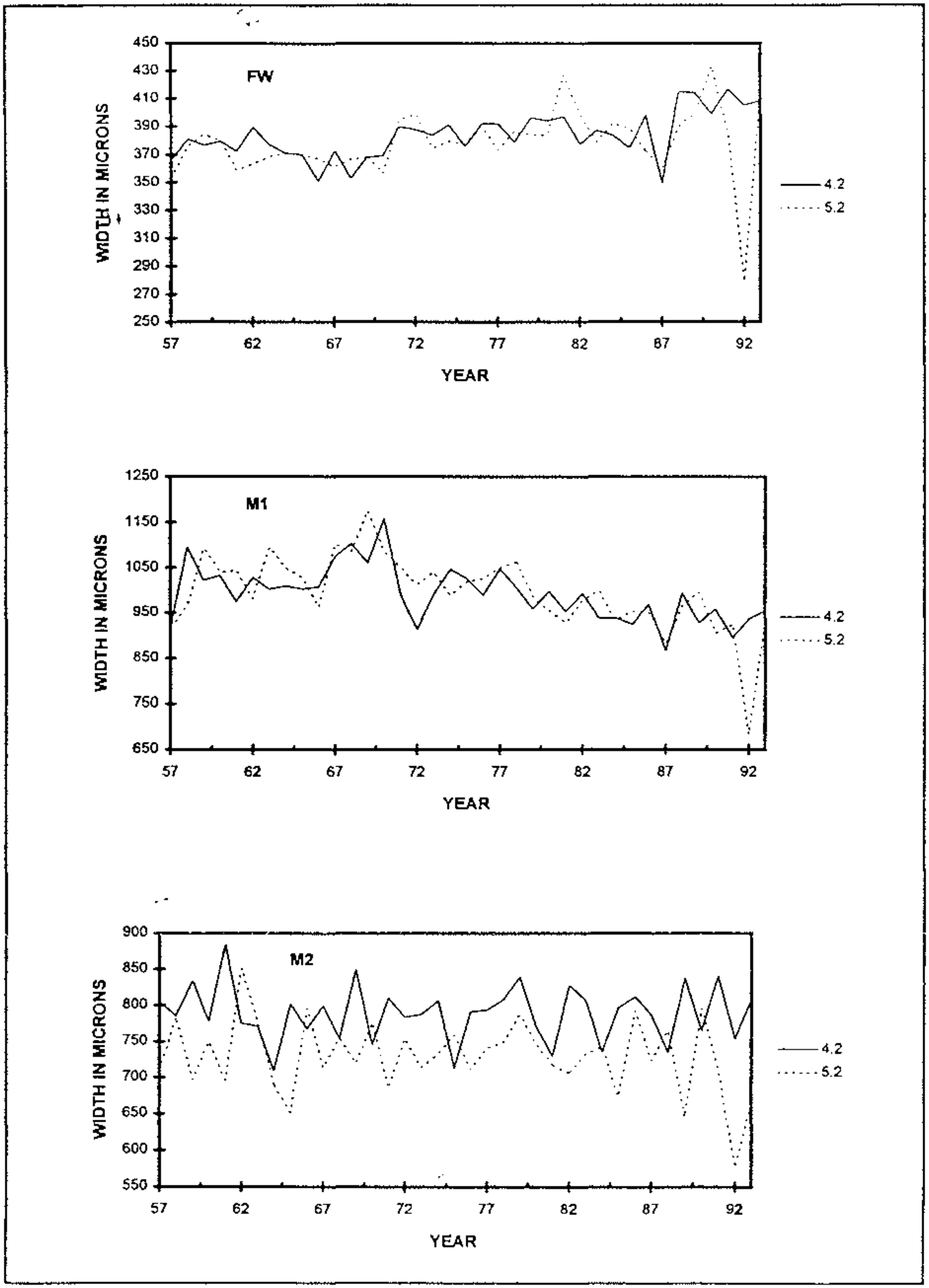

Fig. 8a.

SKEENA 4.2, 5.2 SOCKEYE

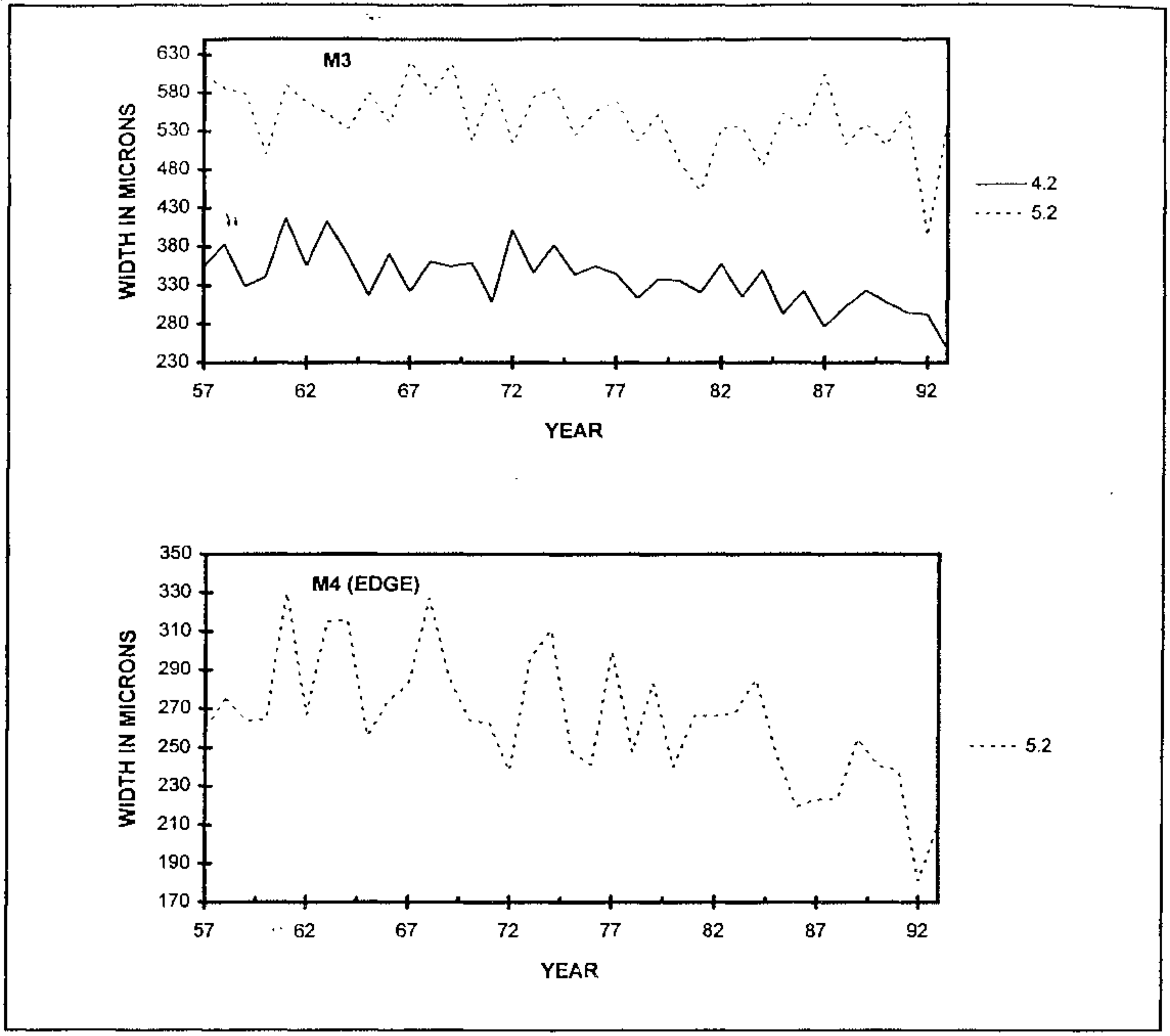

Fig. 8b.

NASS 4.2 SOCKEYE

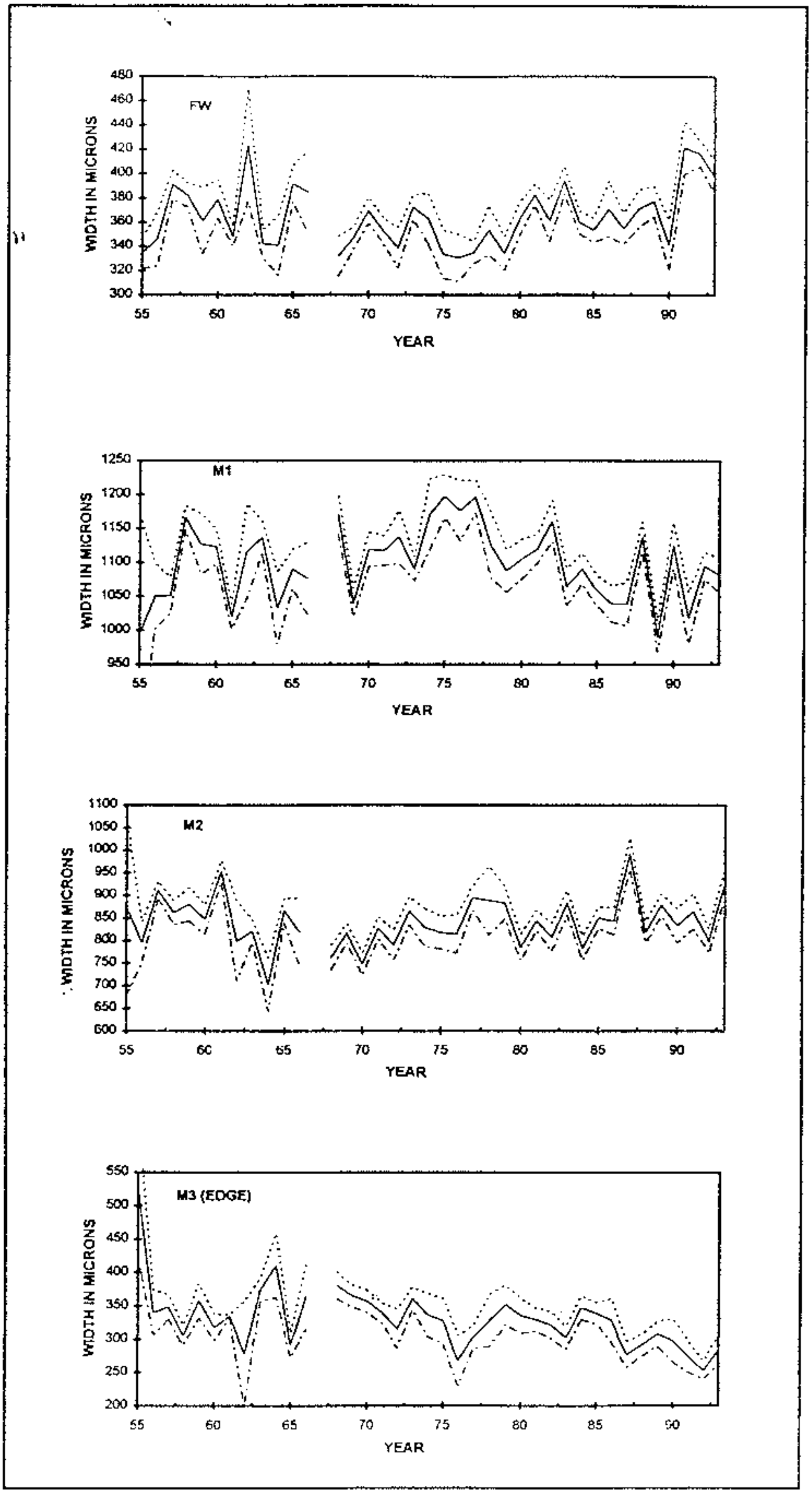

Fig. 9.

NASS 5.2 SOCKEYE

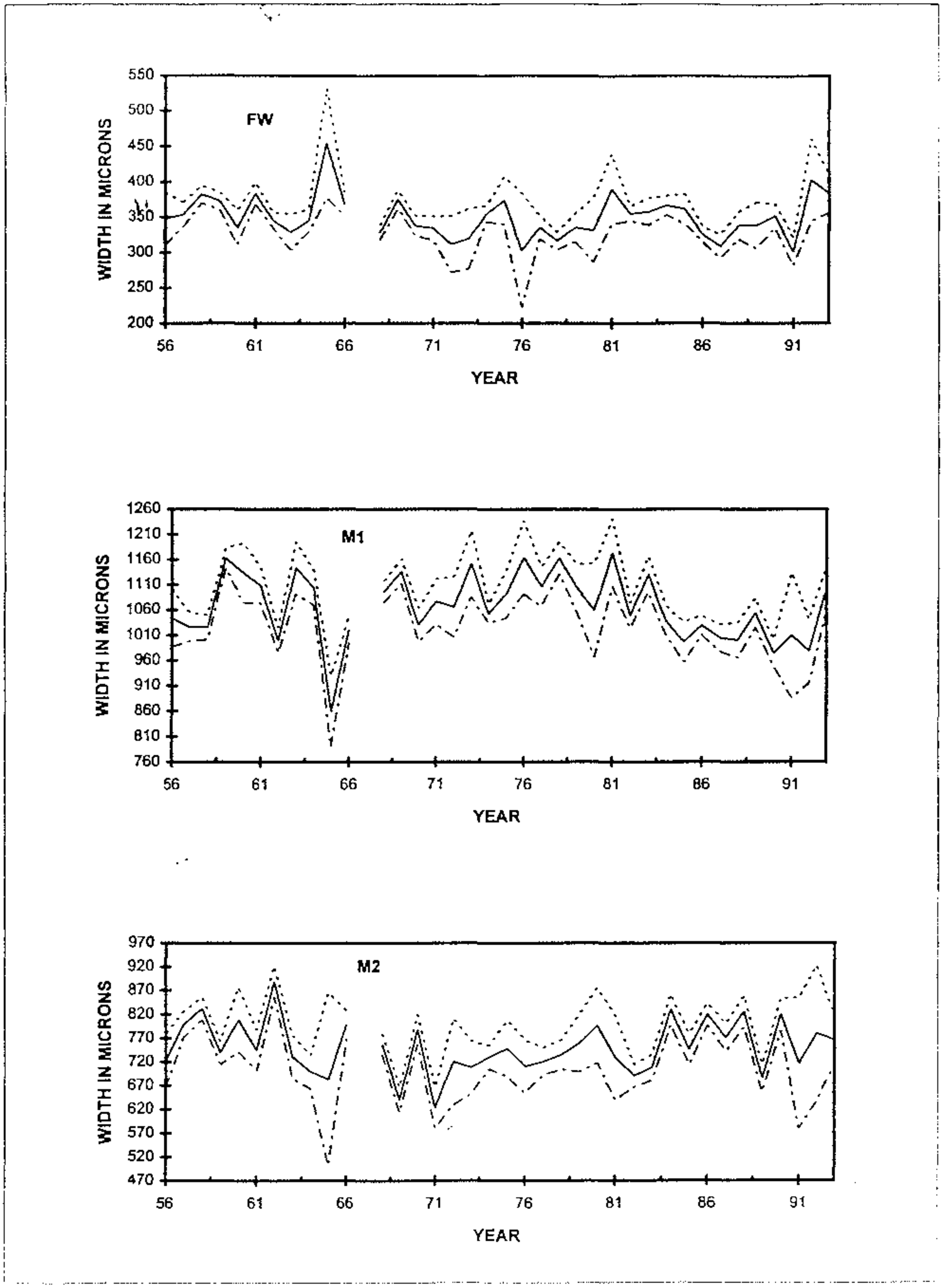

Fig. 10a.

NASS 5.2 SOCKEYE

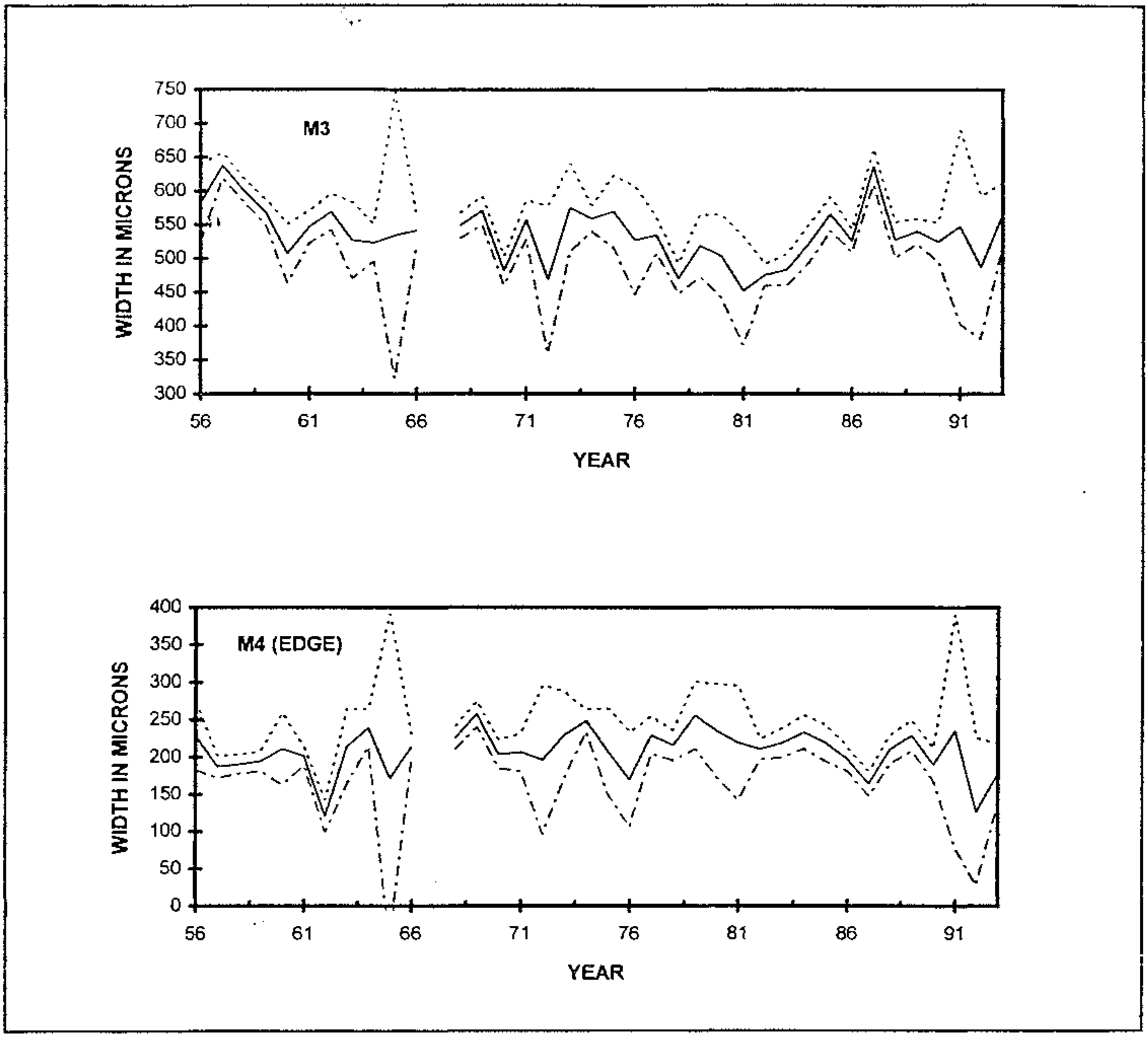

Fig. 10b.

NASS 5.3 SOCKEYE

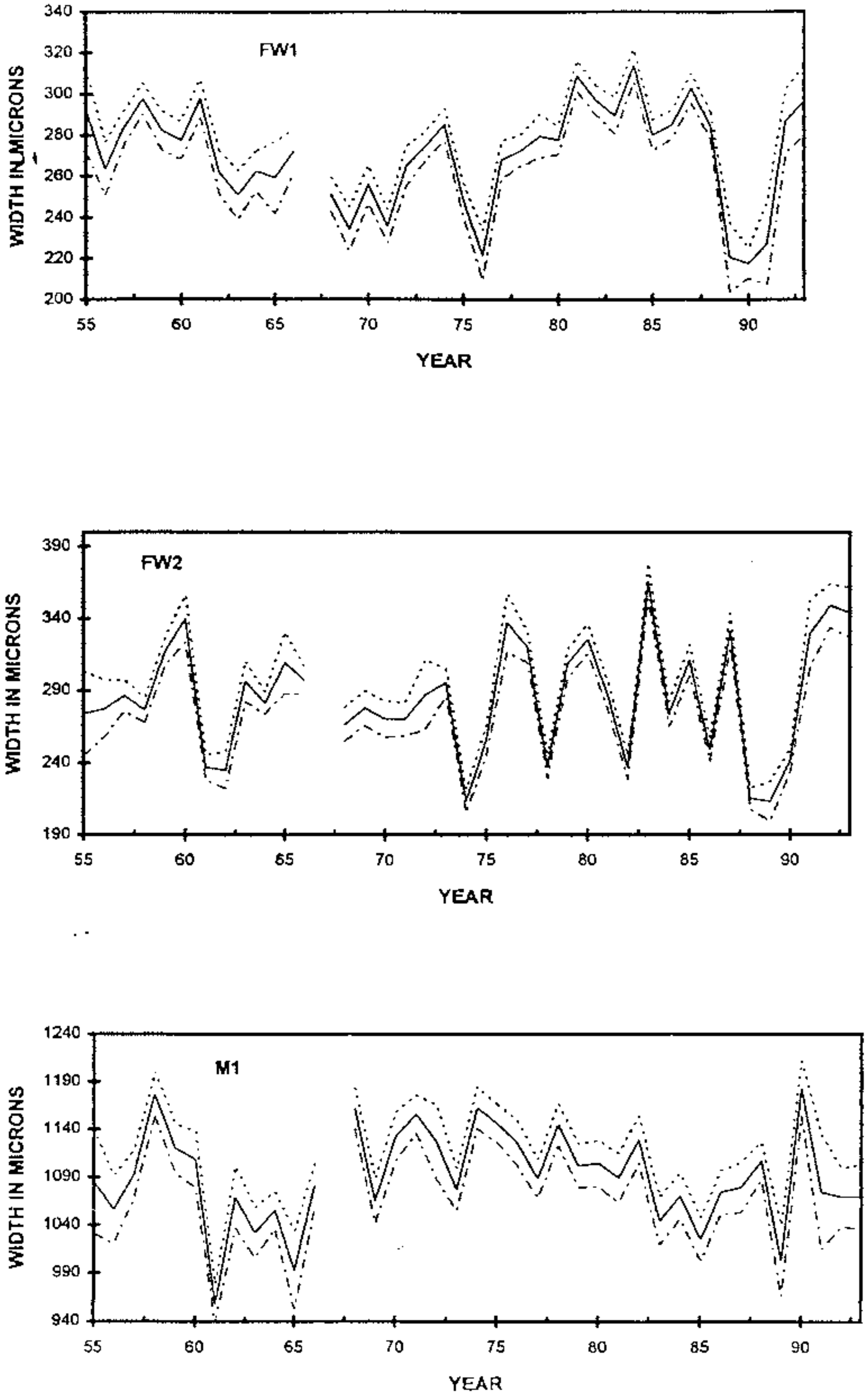

Fig. 11a.

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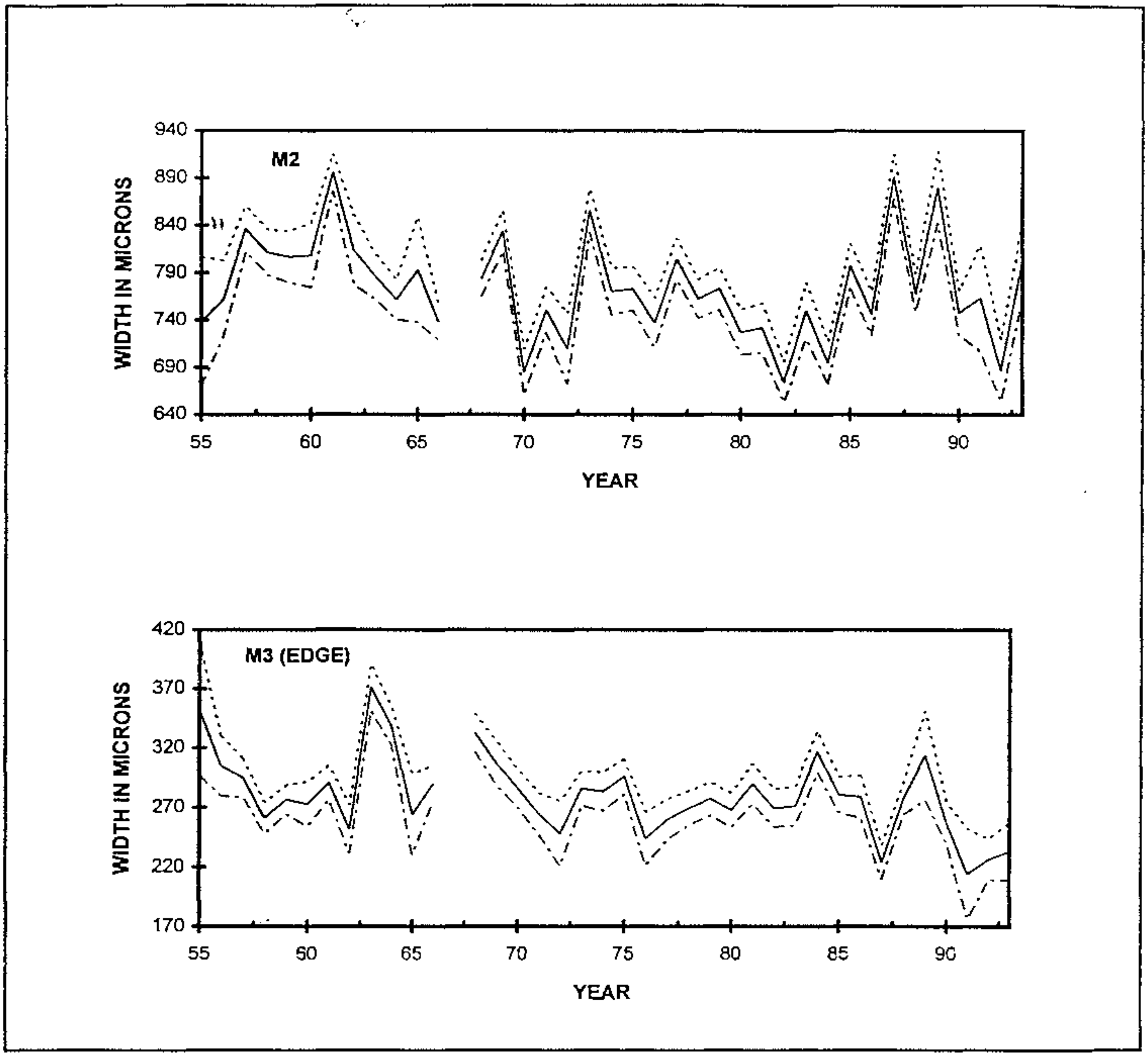

Fig. 11b.

NASS 4.2, 5.2, 5.3 SOCKEYE

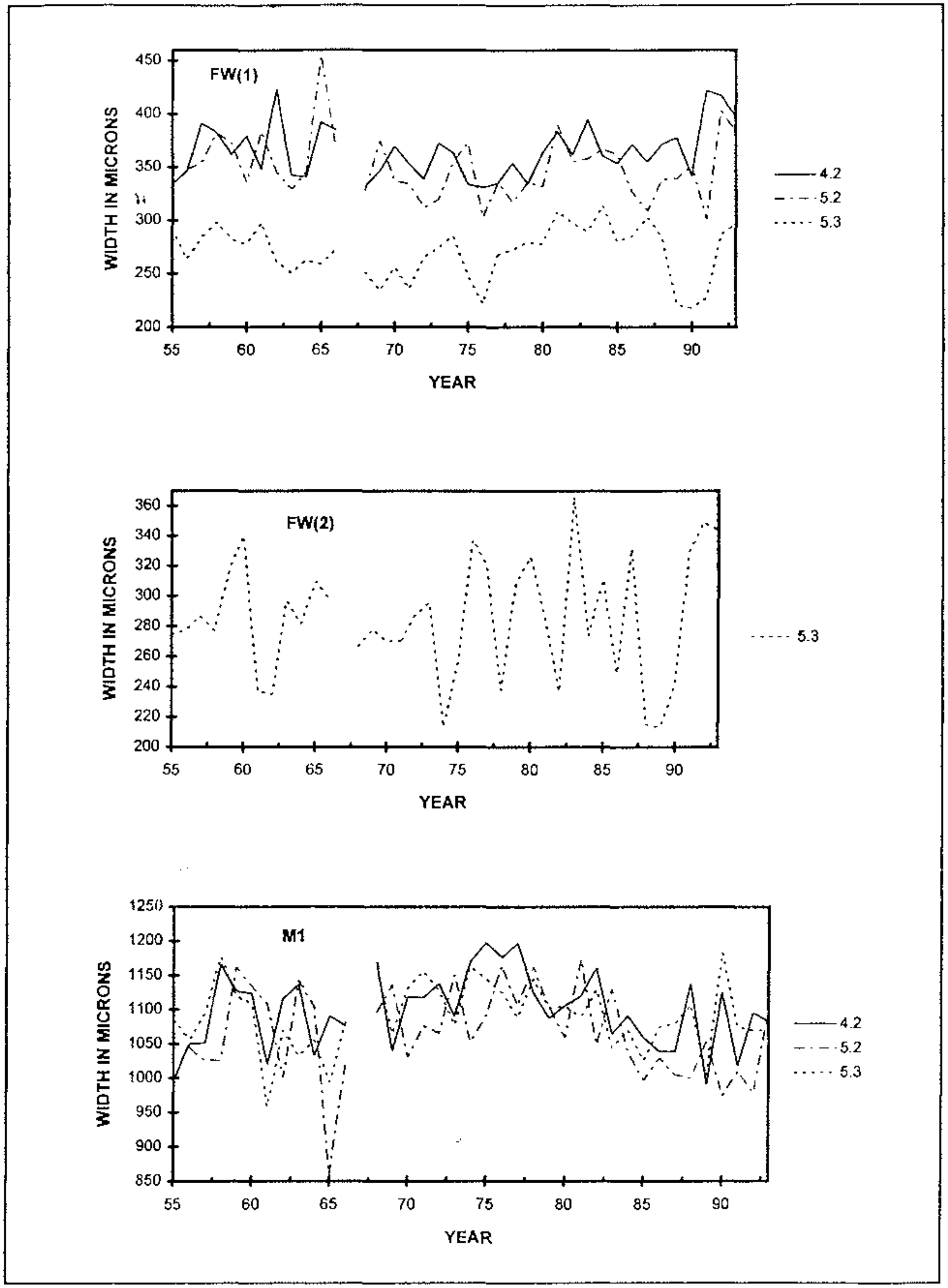

Fig. 12a.

NASS 4.2, 5.2, 5.3 SOCKEYE

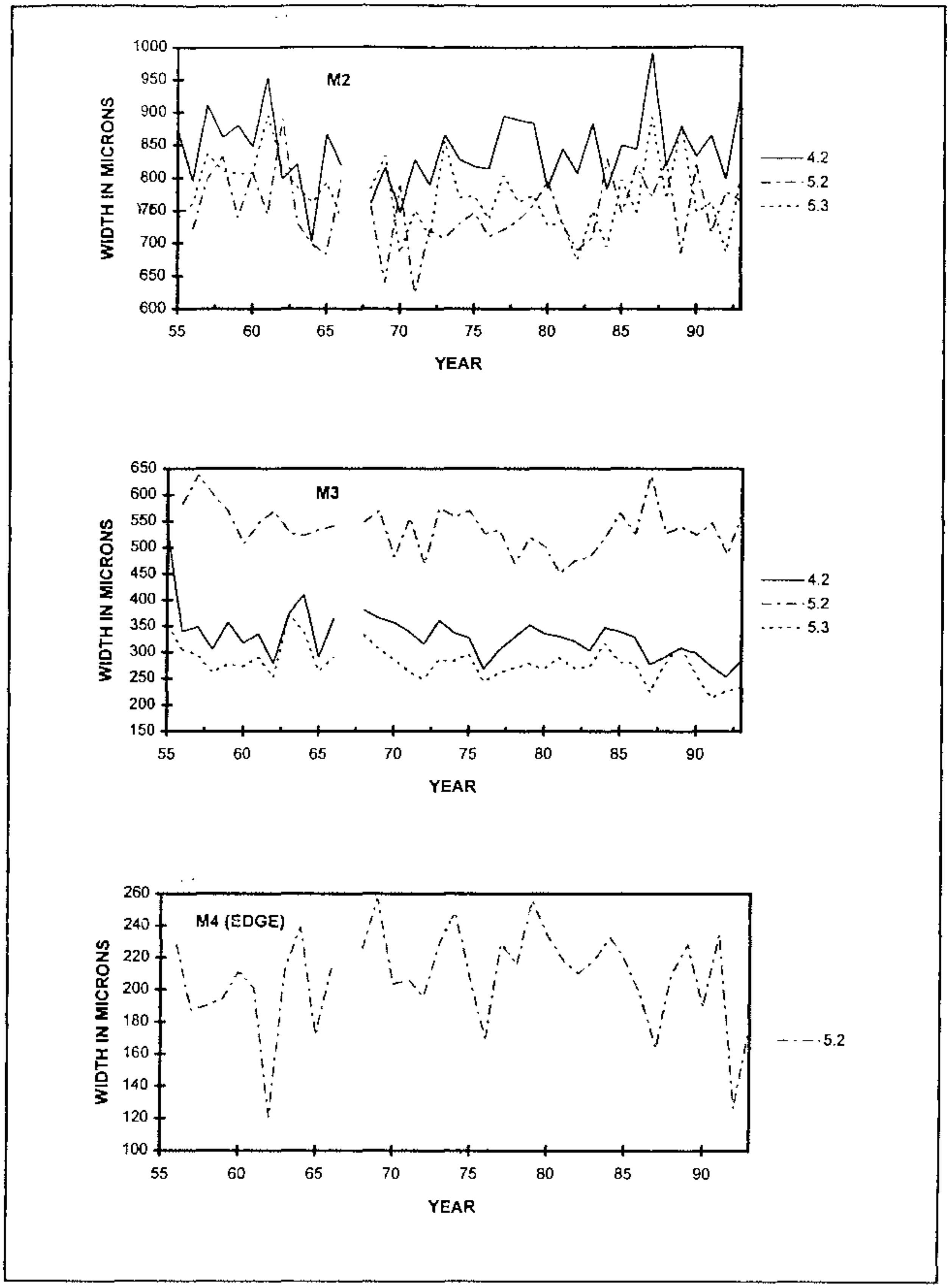

Fig. 12b.

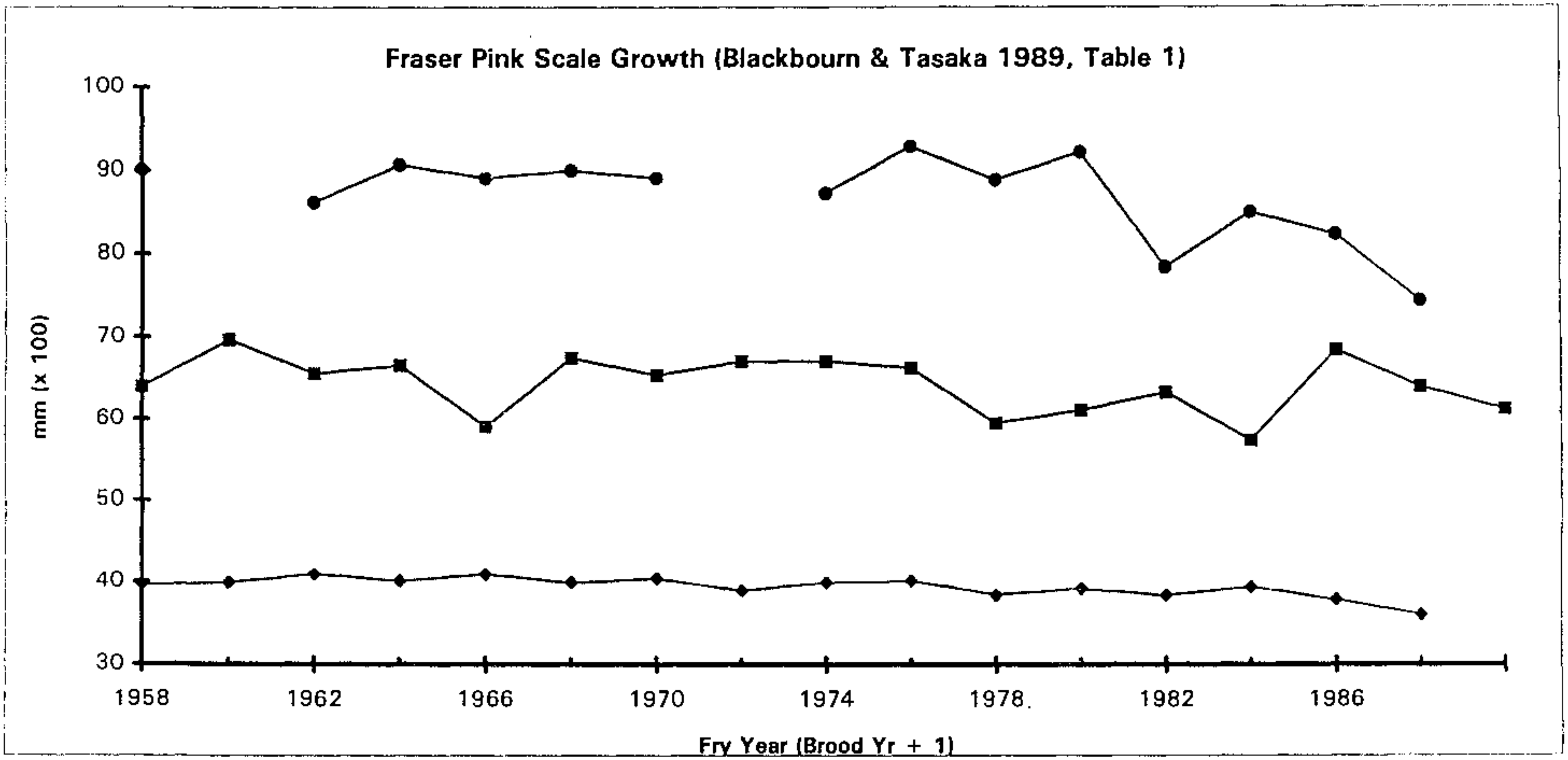
Fraser Pink Scale Growth (Blackbourn & Tasaka 1989, Table 1)
mm (x 100)
100
90
80
70
60
50
40
30
1958
1962
1966
1970
1974
1978
1982
1986
Fry Year (Brood Yr + 1)

Fig. 13.

SKEENA PINK AREA 4

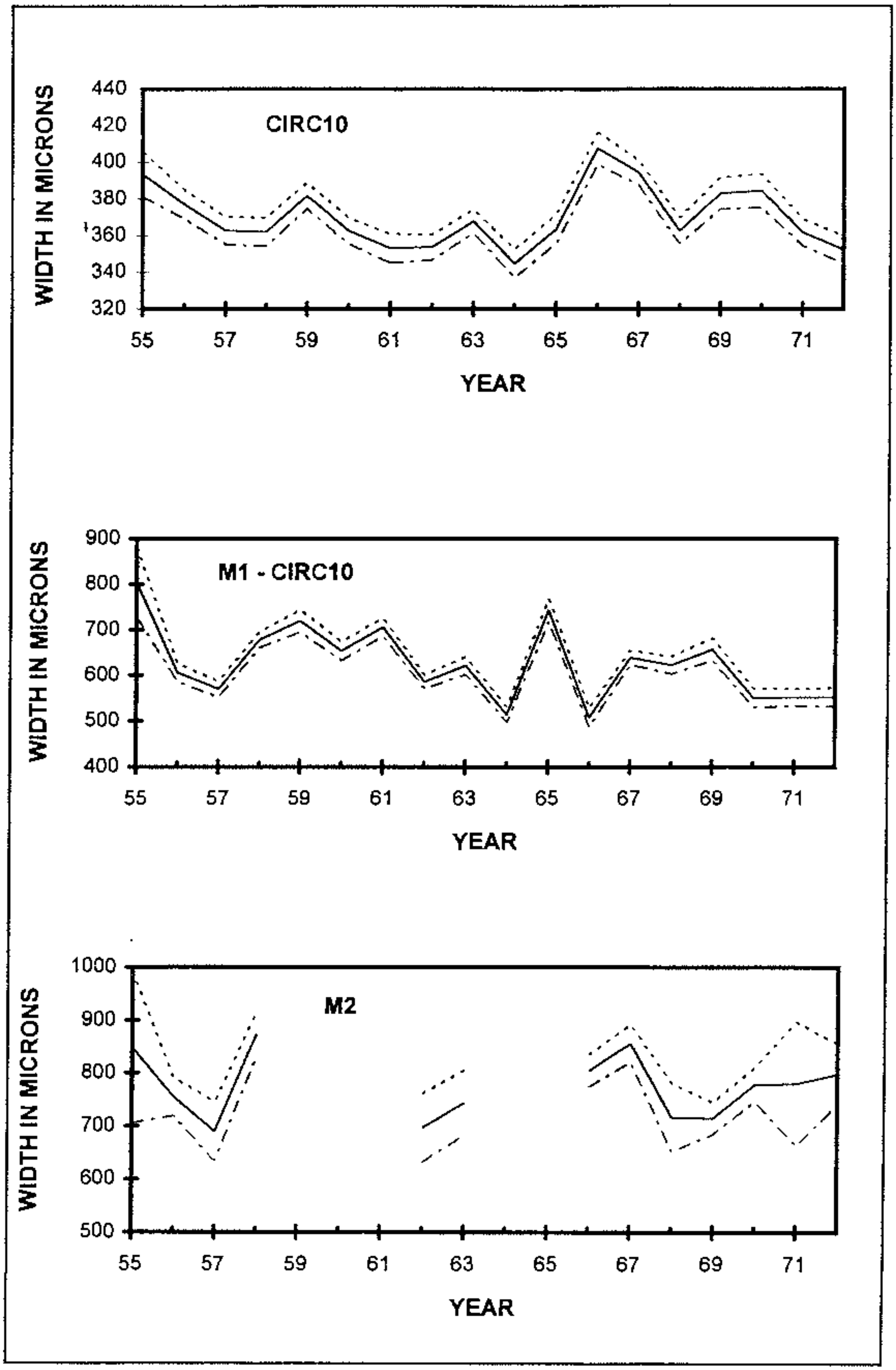

Fig. 14.