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Evidence for Density-Dependent Marine Growth in British Columbia Pink Salmon Populations

by

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ABSTRACT

Data was recently discovered in the Pacific Biological Station's archives that was collected from British Columbia canneries between 1927-42. The data allows extension of the available time series on size of British Columbia pink salmon back to 1927. Size at maturity in the early 1930's was comparable to that of present day pink salmon stocks. Genetic selection for slower growing fish is therefore not the primary cause of the long term declines in the size of pink salmon observed since 1951, when the Dept. of Fisheries and Oceans (DFO) salmon stock assessment (SSA) database was first developed. The consequences of these density-dependent changes in marine growth rates now need to be assessed from three perspectives: *(i)* What are the full economic impacts of the observed declines in size of pink salmon? *(ii)* At what period during the marine life history of pink salmon is growth density-dependent, and how does this density-dependence contribute to determining the economic productivity of salmon stocks when compared with events happening in freshwater? *(iii)* To what degree will further increases in salmon population sizes impair the productivity of Pacific salmon stocks?

INTRODUCTION

Changes in the average size of Pacific salmon occurring between 1951-1974 were reviewed by Ricker (1981), and were recently updated to include data for the 1980's (Ricker *in press*). Ricker's analyses and conclusions were largely based on data derived from Annual Reports on British Columbia Fisheries, which constitute the basis of the Pacific Biological Station's (PBS) Salmon Stock Assessment (SSA) database. In essence, the commercial database is formed by taking the reported landed weights of Pacific salmon in each year since 1951, and dividing by the mean weight of salmon landed in various statistical areas.

Large interannual changes in the average size of all species of Pacific salmon are evident in this database. However, for many of the species, very large long-term declines in size are also evident. British Columbia pink salmon are now 40% smaller in mean weight than was the case in the 1950's, and coho are on average 30% smaller. (All references to size within this paper refer to weight, unless explicitly indicated otherwise). Chinook, chum, and sockeye each show different patterns of growth variation, but little overall change in terminal size between the 1950's and 1990's.

Recent increases in abundance of Pacific salmon have occurred throughout the Pacific Rim. As abundance has increased, the value of salmon per unit landed weight has declined, as has the average mean size of individual fish. Declines in average size exacerbate revenue declines, by reducing meat yields, increasing processing times, and increasing the operating cost of the processing machinery. In addition, the declines in size may also reduce the biological productivity of the individual salmon (e.g. Forbes and Peterman 1994).

DATA AND METHODS

Methods

There are approximately 30 statistical areas reporting data on the mean weight of pink salmon caught in different areas of the coast of British Columbia in any given area. Cluster analysis was used on the 43 yr time series of mean weights extracted from the SSA data base to identify geographical areas within which the variation in mean weights over time were similar. All groups were calculated using hierarchical clustering on the Euclidean distance measures between the time series of mean weights. Mean weight observations from different statistical areas within major clusters were combined directly (without attempting to statistically weight the individual observations) in order to form a single time series of weights for each geographic area identified by the clustering. We base our analysis on these geographic areas.

Preliminary measures of salmon abundance were calculated by summing catches for all statistical areas lying within each geographic cluster. These are used to compare changes in size of seine-caught salmon with the abundance of a stock-grouping in order to detect evidence of density-dependent growth. Seine data is used preferentially here, as it is the least size-selective of the three commercial salmon fishing gears. Analysis of between-stock or between-species density-dependent effects on growth have not yet been carried out.

In a number of cases, escapement data for adjacent river systems was also included in order to obtain an index of recruitment, rather than indexing abundance solely on the total catch for the aggregate area. We distinguish between these two measures in the graphs subsequently shown by referring to them as catch and recruitment. It should be recognized that neither measure currently takes into account catches of the relevant stocks made in areas outside those composing each cluster, not stocks that spawn in regions not directly adjacent to the geographic clusters.

Data

1927-58

Ricker (see references) has commented extensively on the changes in size of salmon that have occurred since 1951, when the modern catch reporting system began. As part of a larger study to examine the reasons for the changes in Pacific salmon sizes, we searched the PBS archives for size data for earlier periods. To date, we have found two new sources.

British Columbia Packers collected values on the average number of pink and chum salmon required to make a 48 lb case of canned product for the years 1927-43. This data was apparently sent from B.C. packers to W. Hoar around 1947 when Hoar was preparing FRB Bulletin No. 90 (Hoar 1951), and was archived without comment in the PBS archives (Archive No. CP-1/30.) The data are reported as annual production rates for each of 41 canneries widely distributed up and down the coast of British Columbia. For this report, we averaged the values reported for all canneries within a major geographic area (Skeena, Nass, Bella Coola, Fraser, west coast Vancouver Island, etc.).

We converted the fish per case data into estimates of mean weight of pink salmon using the conversion factors reported in Marshall and Quinn (1988) for canneries operating in southeast Alaska at roughly the same time period. The regression estimates of the round-to-canned conversion factor for pink salmon in southeast Alaska was 0.637. Marshall and Quinn state that their conversion estimate was not statistically different from other values reported in the literature for pink salmon.

To date, we have not yet compared the conversion factors values published by Marshall and Quinn with other estimates that may exist for British Columbia. The conversion constants used here are likely to significantly affect only the mean level of the overall time series, not the trend to *increasing* mean weight through the 1930's and 40's. We view it as unlikely that changes in the conversion factors over time would be large enough to significantly alter the conclusion (*see below*) that the long-term decline in mean size of pink salmon is not caused by genetic selection, as Ricker (1981) originally suggested, but is instead caused by density-dependent marine growth.

For the period 1944-58, Godfrey (1959) reported on the average weight of fish required to produce a 48 lb case of pink salmon. The original data were reported in aggregate by the Fisheries Association of B.C. for five major sub-areas of the coast: Queen Charlotte Islands, Northern, Central, Southern, and west coast Vancouver Island. We found the original mean weight data for pink salmon in the PBS archive of Godfrey's files (Archive #CP/1/1). Together with the mean weight data from B.C. Packers, this provides us with new time series that extend from 1927-1958, or into the "modern" period of catch reporting.

1951-93

Annual landed weight and numbers of pink salmon caught in each statistical area in British Columbia between 1952-93 were selected from the PBS salmon stock assessment (SSA) catch database. Mean weights were calculated by dividing the landed weights by the number of pieces. Mean weights were not calculated for statistical areas reporting less than less than 3000 lbs total landed weight.

Starting in 1967, catch information from sale slips was entered directly into the SSA catch database. Prior to 1967 the data for the SSA catch database (1952-66) was based on the Annual Reports of British Columbia Catch Statistics. Sales slip information was broken down by species, gear, and statistical area for each month of the fishing season. Pink salmon catches were reported as both landed weights (rounded to the nearest hundred pounds) and pieces. Seine and gillnet catches were reported as whole weights and troll weights were reported as dressed. Troll dressed weights were converted to whole weights by multiplying by 1.18.

During preliminary examination, approximately half the statistical areas reporting between 1952-62 the average weights and total catches (in numbers) extracted from the SSA catch database were found to be inaccurate. From 1952-55 the SSA catch database used a constant average weight for chum, pink, and coho salmon in many statistical areas. These statistical areas turned out to be those areas where only landed weights were reported and the number of pieces was not provided in the annual B.C. Catch Statistics publications (Areas 1, 2E, 2W, 5, 14, 15, 16, 17, 18, 19, 24, 22, 25, 26, 27, 28). The average weights used were in fact calculated from the total B.C. commercial landings between 1963-67.

The number of salmon caught in those statistical areas lacking direct information was estimated by dividing the reported catch weight by the mean weights of salmon caught in 1963-67 in order to estimate the number of pieces. As the mean weight of Pacific salmon shows large inter-annual variability, as well as long-term trends, the SSA database provides misleading estimates of the numbers of fish caught in those area-time combinations.

The SSA does not include data for 1951, although the Annual (and monthly) B.C. Catch Statistics begin in this year. We extracted the average weights of pink salmon in 1951 from the preliminary B.C. Catch Statistics reports for statistical areas 2W, 14, 15, 16, 19, 22, and 28. We used the average weights from Ricker's published reports for the remaining areas.

To calculate the mean weight and numbers of salmon caught in later years, we relied on Ricker's published data, and supplemented these statistics with calculations from the B.C. Catch Statistics where necessary. (When asked, Dr Ricker could not recall how he calculated his published mean weight values; however, Ricker's mean weight estimates match those in the B.C. Catch Statistics exactly for those years and statistical areas where both data sets exist). We substituted Ricker's published average weights for pink salmon in statistical areas 1, 2E, 5, 17, 18, 24, 25, 26, and 27 from 1952 to 1955 and calculated average weights for statistical areas 2W, 14, 15, 16, 19, 22, and 28 from the monthly reports of B.C. Catch Statistics (after manually aggregating to an annual basis), because these reports included both the number of pieces and the landing weights by statistical area for all major fisheries, unlike the annual reports on which the SSA is based. We then divided these average weights into the reported landed weights to obtain improved estimates of catch in pieces.

RESULTS

Changes in Size of Pink Salmon, 1951-1993

Odd-Year Stocks

Fig. 1 shows the clusters formed for the odd year pink salmon time series (1951-93). Although slight differences in ranking within clusters is evident, the major clusters formed are almost identical for all three gears. Odd year time series break cleanly into two groups: south and north coast.

The coast-wide trend to smaller size for seine-caught pink salmon is shown clearly in Fig. 2, and is in clear contrast to the trend to increasing pink salmon abundance (Fig. 3). Fig. 4 contrasts the changes in average size of British Columbia pink salmon with their recruitment. A pronounced trend to smaller body size at higher recruitment levels is evident.

Breaking the British Columbia provincial data into the two major geographic clusters gives similar results. The mean size of north and central B.C. pink salmon declined relatively steadily over time, while recruitment increased (Fig. 5). When mean weight is contrasted with recruitment to the north and central coast regions, a negative density-dependent relationship is again evident (Fig. 6). The density-dependent relationship is similar when mean weight is compared with total recruitment for all areas combined (Fig. 7).

The decline in mean size for south coast odd year pink salmon (i.e. Fraser river stocks) is very similar to the north coast case, except that the mean size of the fish is slightly larger than in the north-central coast (Fig. 8). Again, a density-dependent relationship between size and abundance is evident (Fig. 9), with the relationship slightly tighter when recruitment to the entire province is considered (Fig. 10).

Even-Year Stocks

Fig. 11 shows the cluster analysis for even year pink salmon stocks. Catches of pink salmon in even years are negligible in southern parts of the province, because of the lack of even year runs to the Fraser river. The clustering is somewhat less clear-cut for the even year runs, and could be interpreted as either one cluster containing upper Georgia Strait, central, and northern districts, or one cluster encompassing only the central and north coast regions. We show examples using both clusters.

Fig. 12 shows the trend in mean size and recruitment for even year pink salmon taking the upper Georgia Strait, central, and northern districts of B.C. as one geographic cluster. Although recruitment shows a relatively pronounced decline over time, recruitment has been more irregular. Catch and escapement estimates for this region (Fig. 13) show that the two measures have tended to covary over much of the available record, and mean size shows evidence of a negative density-dependent relationship with recruitment (Fig. 14), but not as strong as for the odd year runs. Figs. 15 and 16 show that a similar relationship is evident when only data from the central and north coast regions is considered. Both even and odd year pink salmon runs therefore show evidence of density dependent growth in all regions of the province

Changes in Size of Pink Salmon, 1927-1993

Although the evidence for density-dependent marine growth of pink salmon appears to be quite good, the change in size since 1951 has been essentially linear, so a linear trend in any other independent variable over the same time period would provide a similar explanation for the changes in pink salmon size.

Ricker (1981) has argued that the decline is probably due to genetic selection against rapid growth by size-selective fishing gear. The last period of high salmon abundance was in the 1930's. When the B.C. Packer's cannery data for 1927-1943 is plotted along with the Fisheries Association of B.C. data for 1944-57 and the SSA data for 1951 forwards, clear evidence emerges that pink salmon in most regions of the coast were substantially *smaller* in years prior to 1951 (Figs. 17-20). With the exception of data from canneries located on the west coast of Vancouver Island, the evidence points to a long-term cycle in the size of odd year pink salmon, with maximum size being attained in the early 1950's. A similar cycle in the size of even year pink salmon is also evident (Figs. 21-25).

Thus, although abundance data for the period prior to 1951 is poor, it is clear that the two periods of slowest pink salmon growth both occurred at times of high salmon abundances, and the period of fastest growth coincides with the period of lowest abundance on record. Ricker's argument that genetic selection was the probable cause of the long term decline in size is therefore unlikely to be correct, although genetic selection for slower growth is undoubtedly occurring.

DISCUSSION

Size-selective harvesting of pink salmon has been suggested by Ricker et al. (1978) as the cause of the long-term decline in mean size of Pacific salmon in British Columbia. The results from the current study clearly show that the mean size of pink salmon *increased* from 1927 to the early 1950s, and that 60 years ago pink salmon were as small as currently observed.

We have shown that there is good evidence for a strong relationship between pink salmon abundance and growth in most regions of the Pacific coast. This result suggests that detailed comparison of growth changes using the information recorded in scale collections is likely to provide information useful in disentangling the effects of oceanographic changes on growth from the effects of the abundance of different species and stocks of salmon on somatic growth rates.

The relationships between abundance and growth that we have shown here are statistically much better identified than are the relationships between abundance and pre-recruit survival for the same stocks. The possibility therefore needs to be taken seriously that the major variable ***amenable to manipulation by management*** is not survival, but rather growth. This possibility needs further study.

CONCLUSIONS

The consequences of the density-dependent changes in marine growth rates for pink salmon now need to be assessed from three perspectives: *(i)* At what period during the marine life history of pink salmon is growth density-dependent, and how does this density-dependence contribute to determining the economic productivity of salmon stocks when compared with events happening in freshwater? *(ii)* What are the full economic impacts of the observed declines in size of pink salmon? and *(iii)* To what degree will further increases in salmon population sizes impair the productivity of pink salmon stocks?

These questions are of equal relevance to all species of Pacific salmon. However, the preliminary evidence that we report here is particularly surprising, because it suggests that even pink salmon may have the potential to graze down their food supply in open ocean areas. It is important to carefully test this idea, in order to better evaluate at what point the carrying capacity of the North Pacific Ocean might be limiting pink salmon production.

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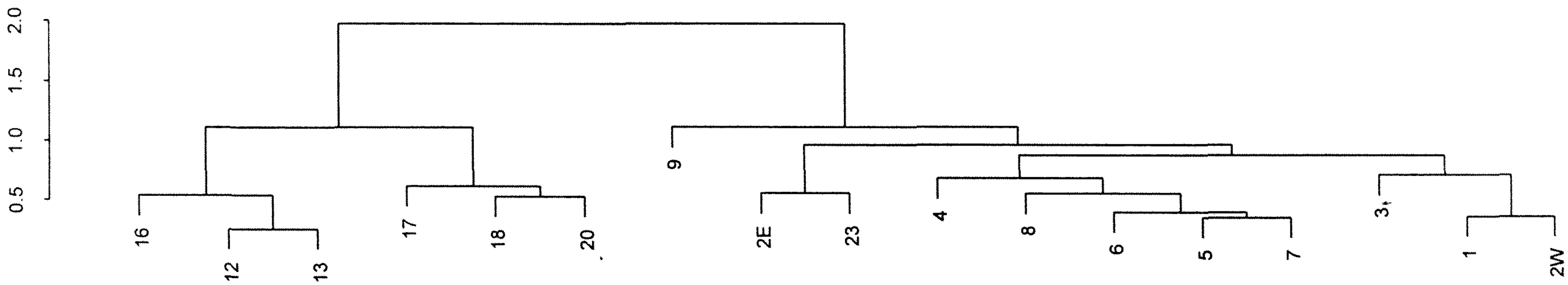
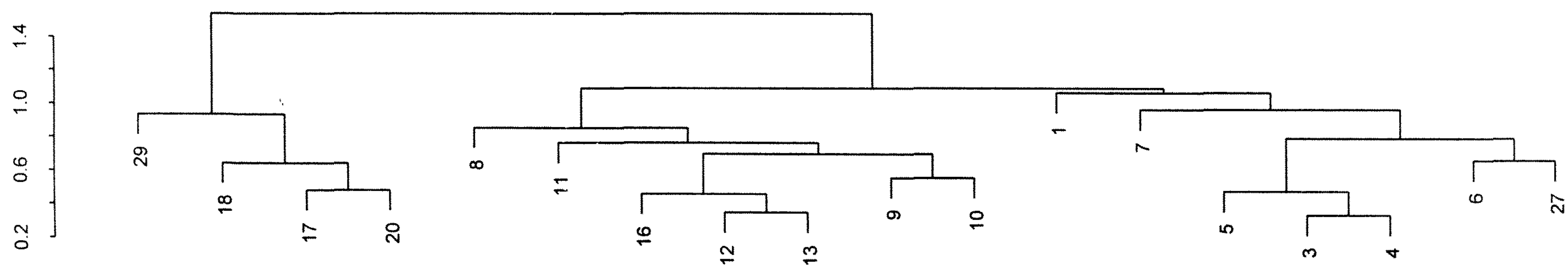
Fig. 1

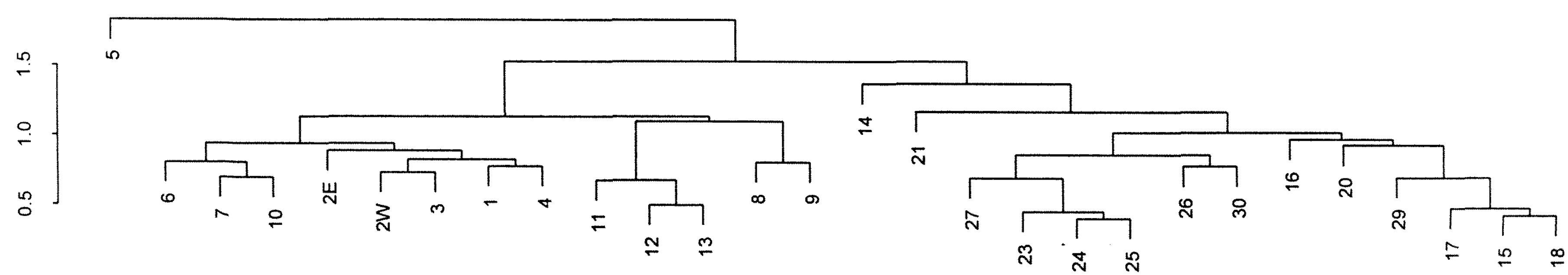
MEAN ODD-YEAR PINK SALMON WEIGHTS BY STATISTICAL AREA, 1951-93



SEINE CAUGHT ODD-YEAR PINK SALMON



GILLNET CAUGHT ODD-YEAR PINK SALMON



TROLL CAUGHT ODD-YEAR PINK SALMON

Fig. 2

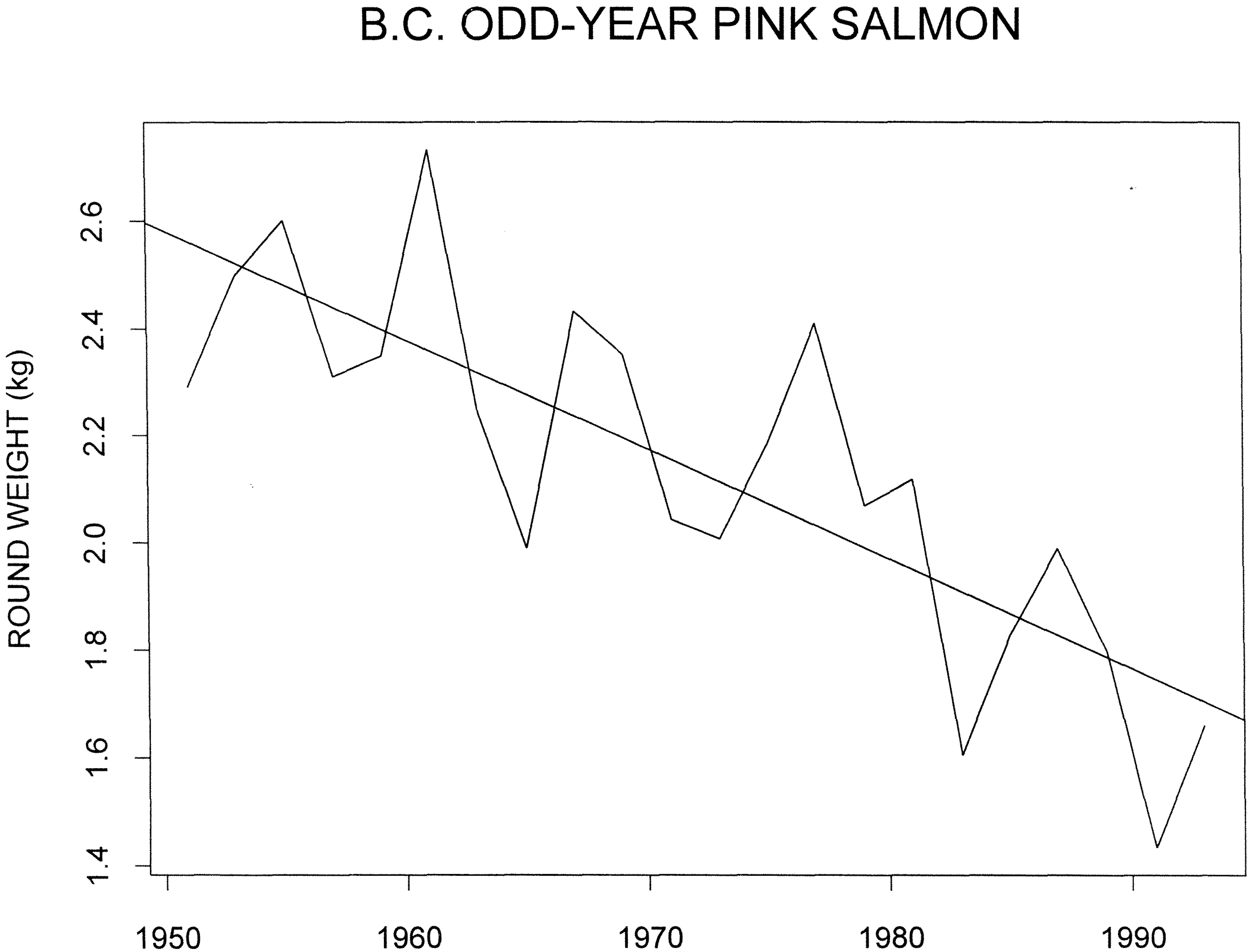

B.C. ODD-YEAR PINK SALMON
ROUND WEIGHT (kg)
1.4
1.6
1.8
2.0
2.2
2.4
2.6
1950
1960
1970
1980
1990

Fig. 3

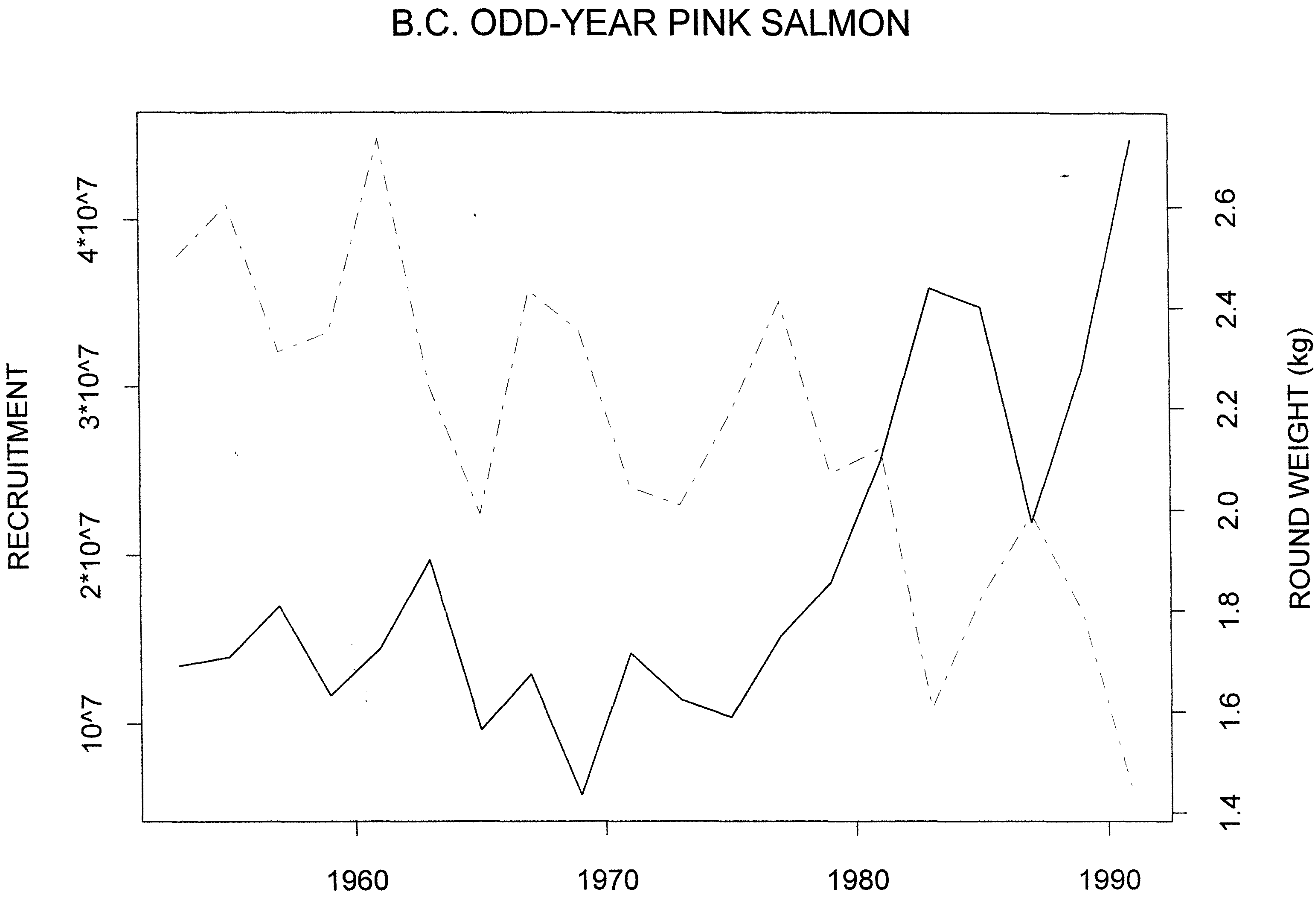

B.C. ODD-YEAR PINK SALMON
RECRUITMENT
10^7
2*10^7
3*10^7
4*10^7
ROUND WEIGHT (kg)
1.4
1.6
1.8
2.0
2.2
2.4
2.6
1960
1970
1980
1990

Fig. 4

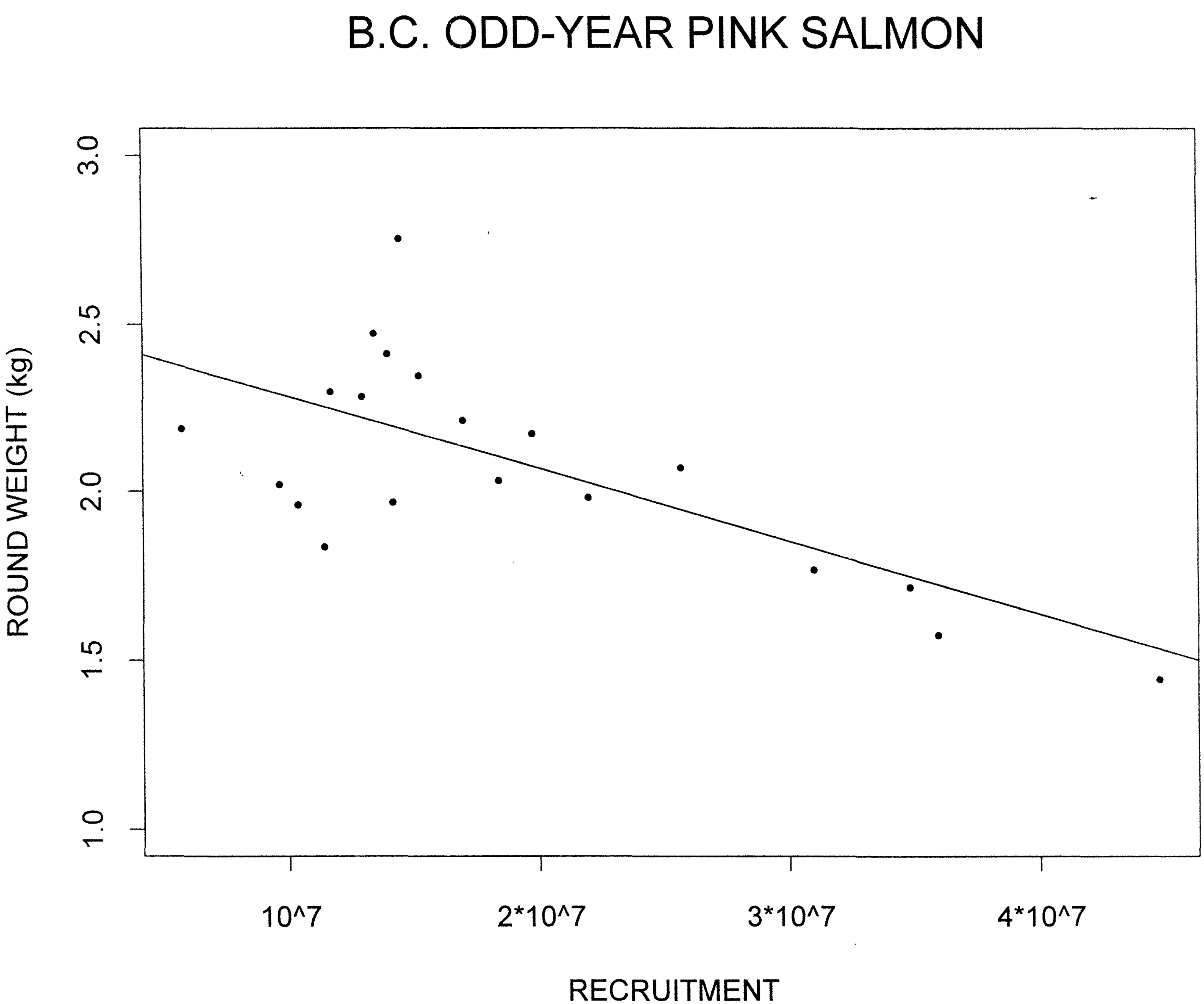

B.C. ODD-YEAR PINK SALMON
ROUND WEIGHT (kg)
1.0
1.5
2.0
2.5
3.0
10^7
2*10^7
3*10^7
4*10^7
RECRUITMENT

Fig. 5

ODD-YEAR PINK SALMON - CENTRAL AND NORTHERN DISTRICTS

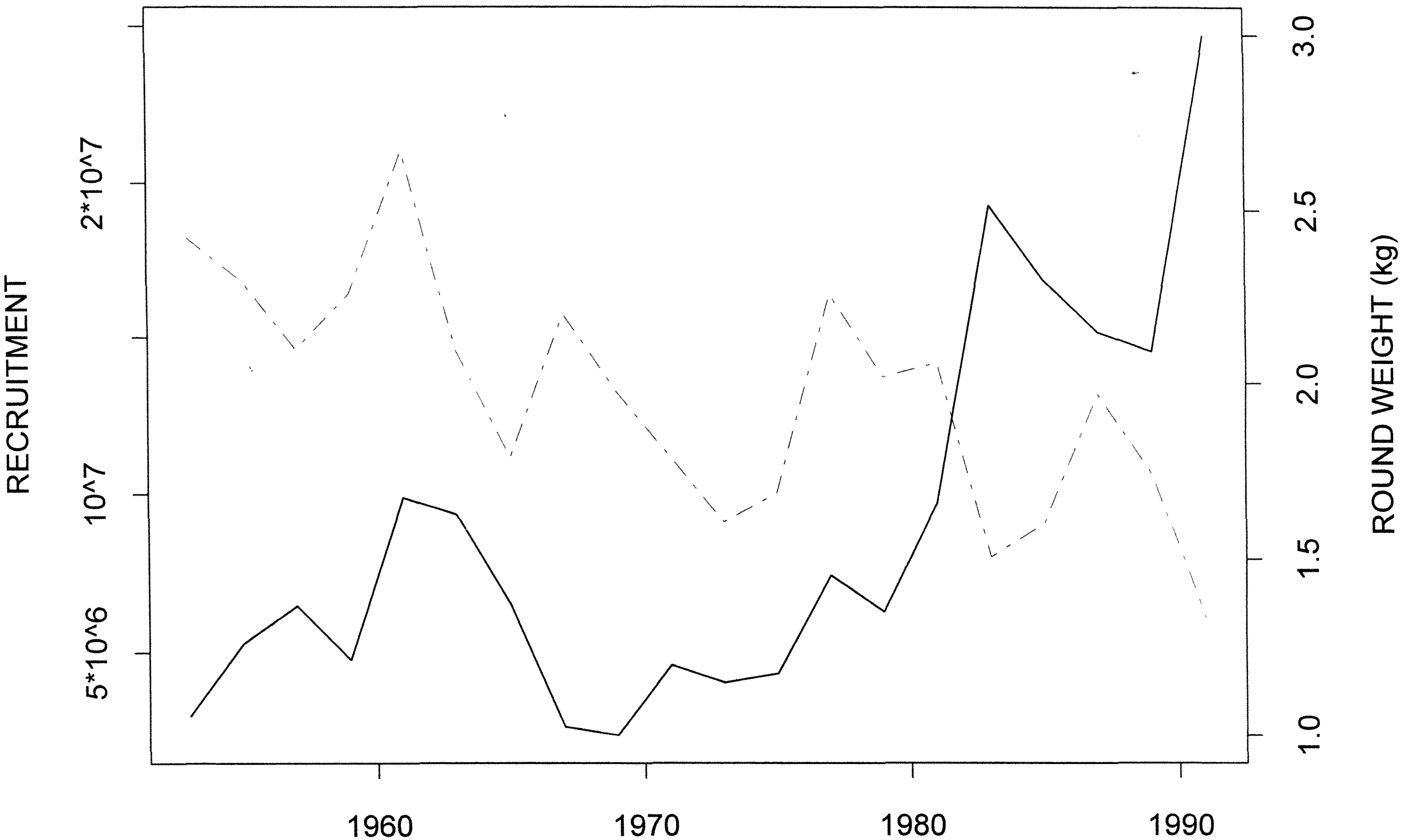


Fig. 8

ODD-YEAR PINK SALMON, CENTRAL & NORTHERN DISTRICTS

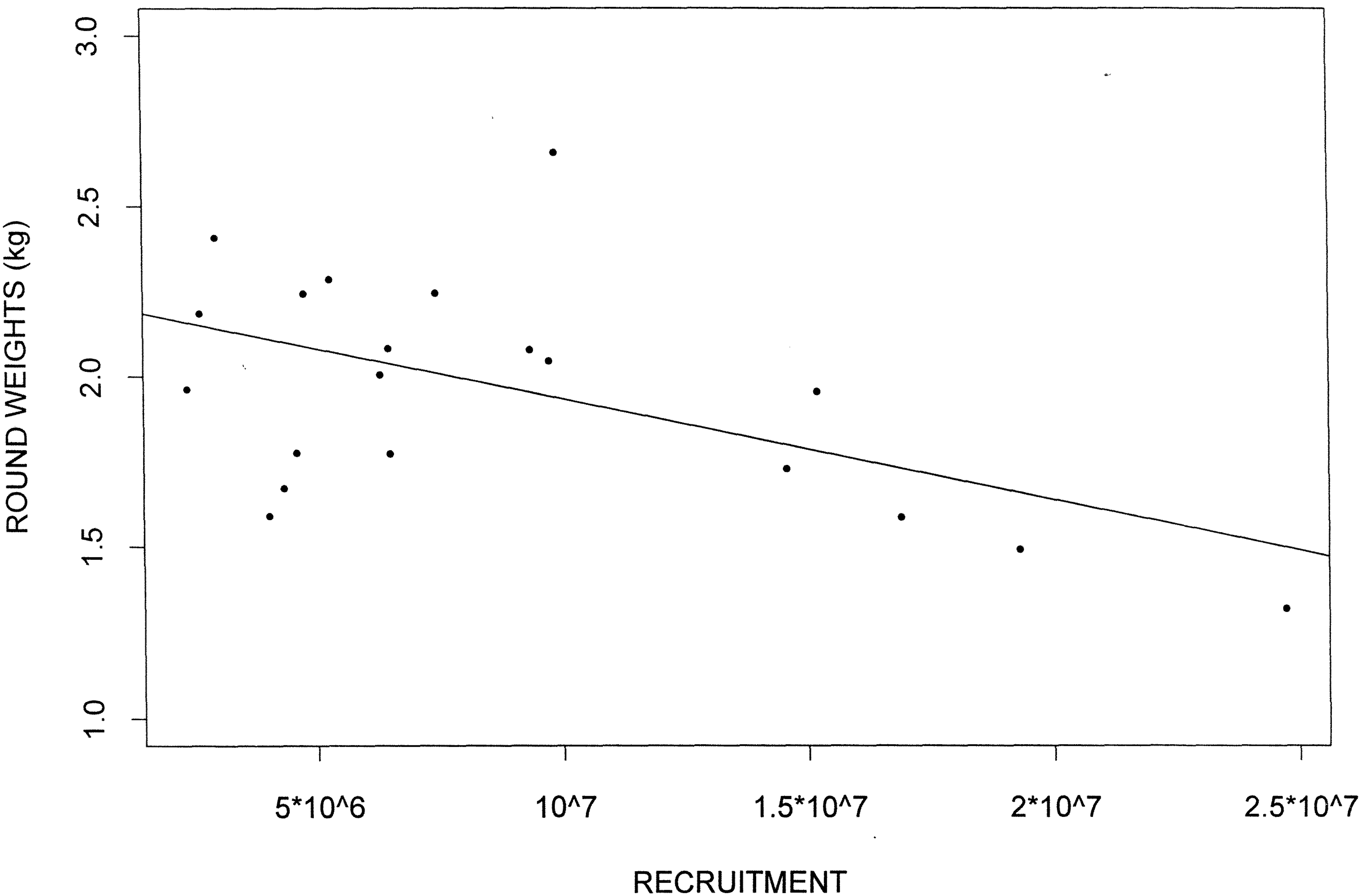


Fig. 7

ODD-YEAR PINK SALMON, CENTRAL & NORTHERN DISTRICTS

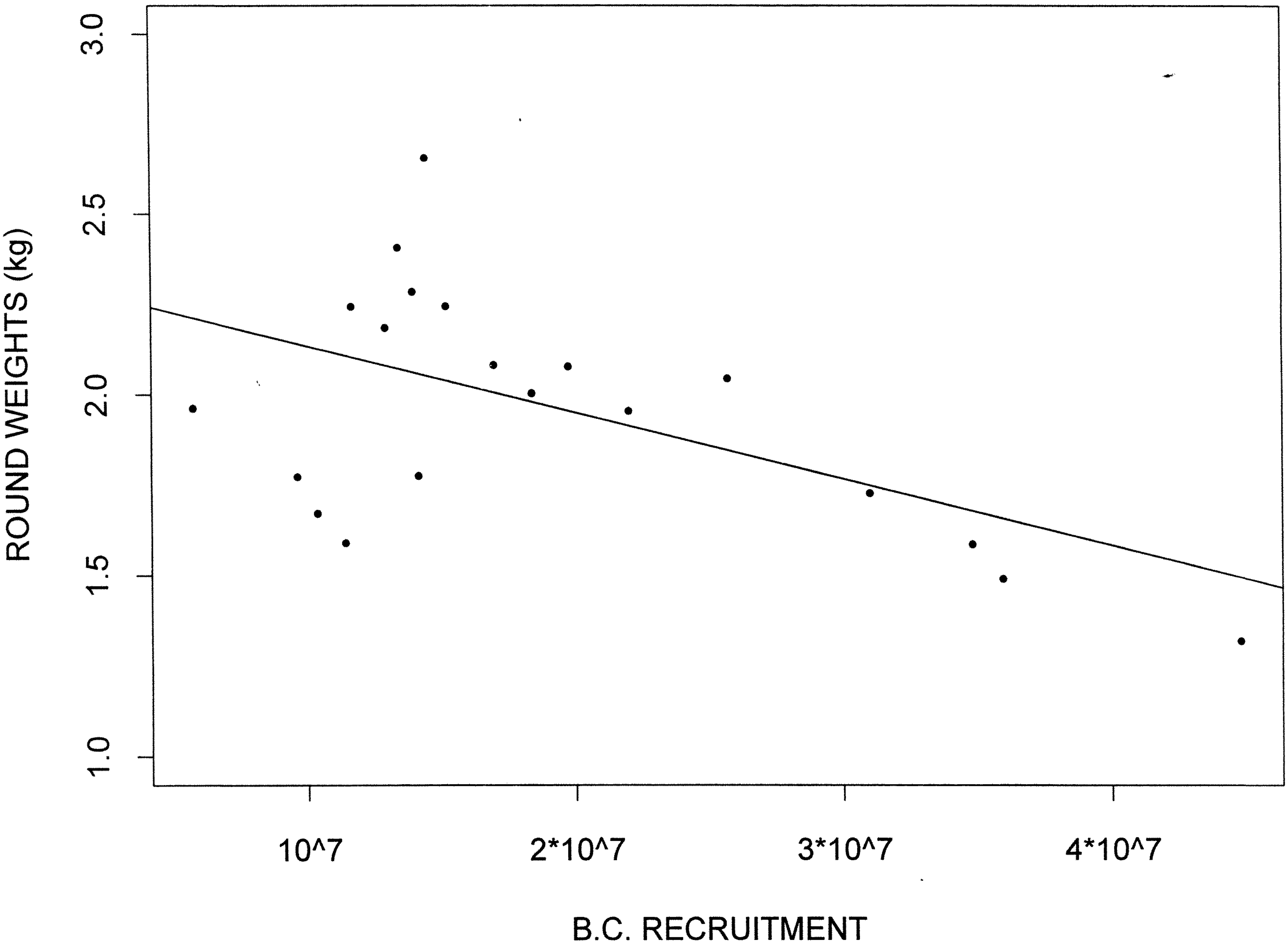


Fig. 8

ODD-YEAR PINK SALMON - SOUTHERN DISTRICT

Fig. 9

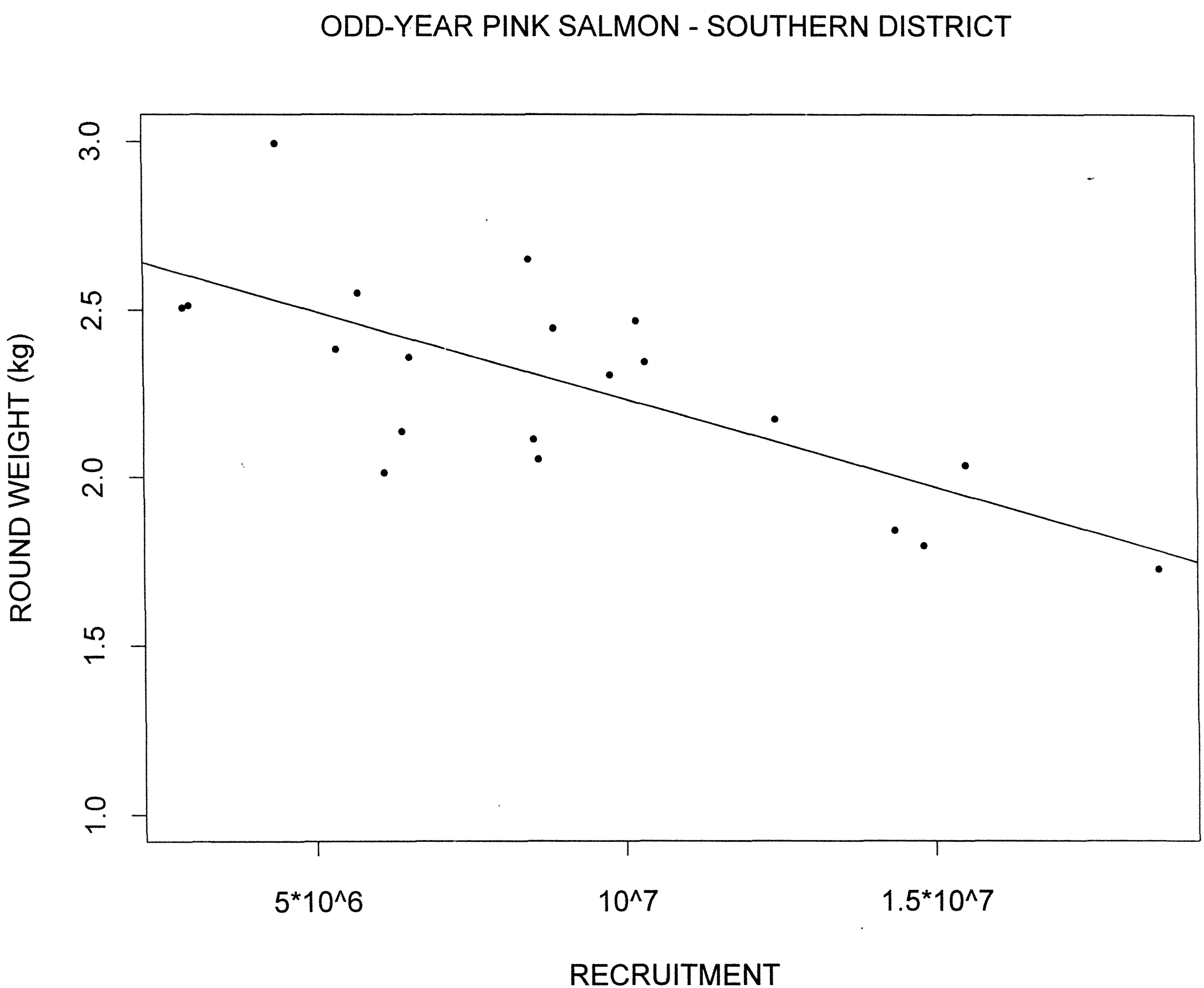

ODD-YEAR PINK SALMON - SOUTHERN DISTRICT
ROUND WEIGHT (kg)
1.0
1.5
2.0
2.5
3.0
5*10^6
10^7
1.5*10^7
RECRUITMENT

Fig. 10

ODD-YEAR PINK SALMON, SOUTHERN DISTRICT

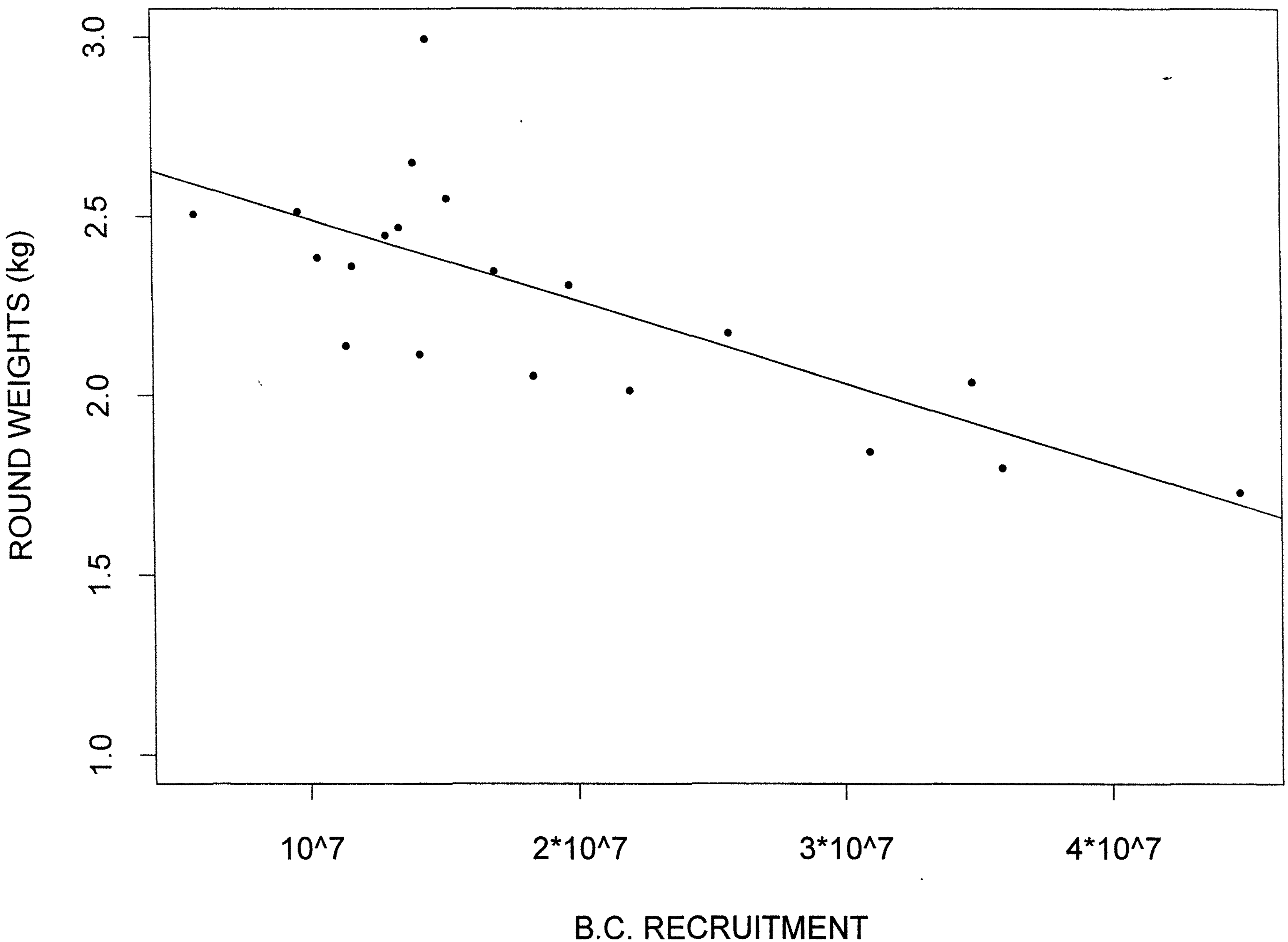
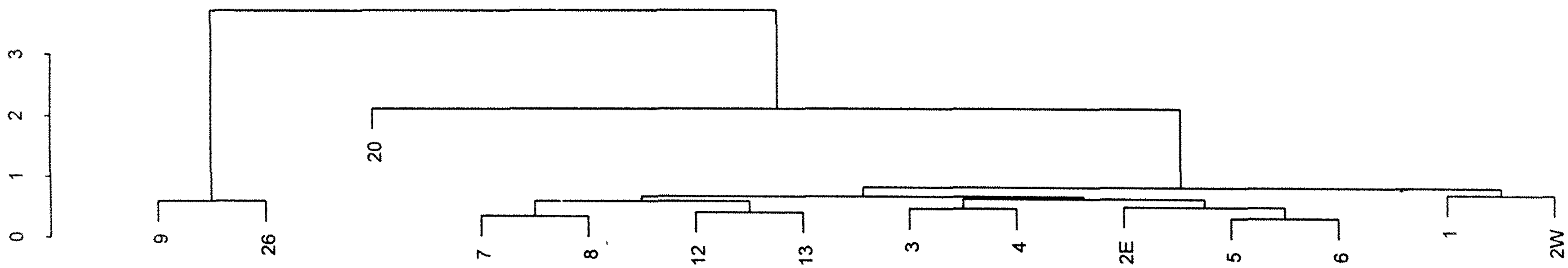
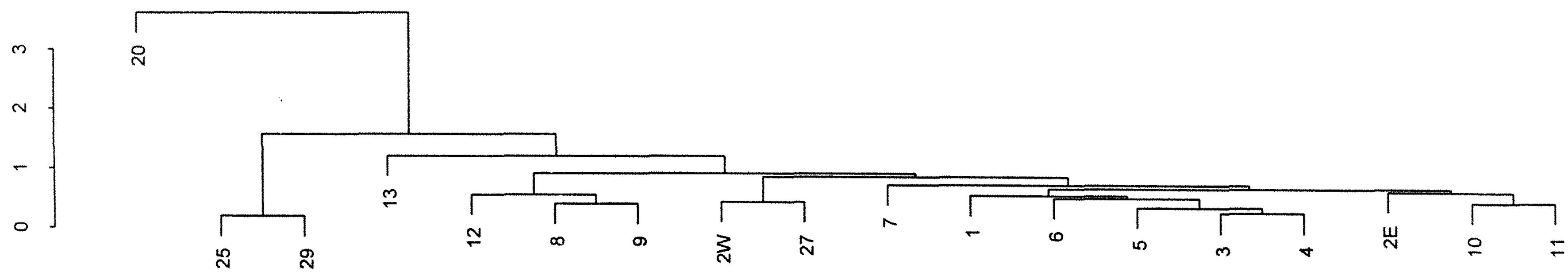


Fig. 11

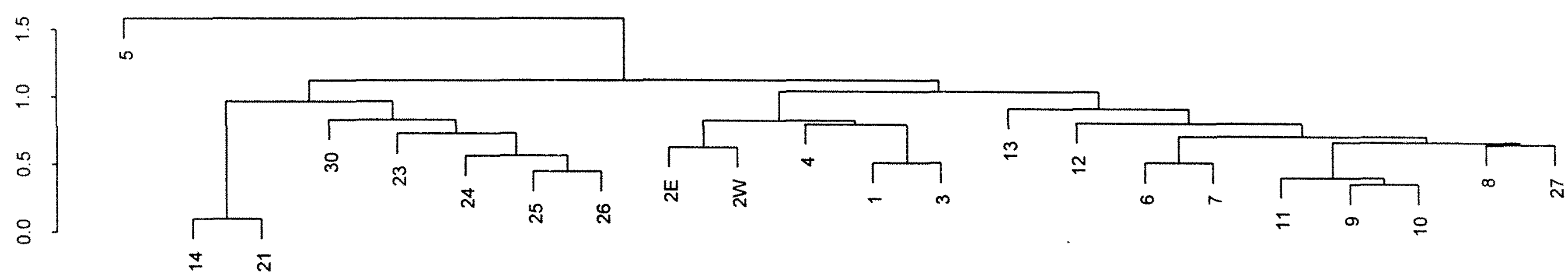
MEAN EVEN-YEAR SALMON WEIGHTS BY STATISTICAL AREA, 1952-92



SEINE CAUGHT EVEN-YEAR PINK SALMON



GILLNET CAUGHT EVEN-YEAR PINK SALMON



TROLL CAUGHT EVEN-YEAR PINK SALMON

Fig. 12

EVEN-YEAR PINK SALMON, UPPER GEORGIA STRAIT,CENTRAL, AND NORTHERN DISTRICTS

EVEN-YEAR PINK SALMON, UPPER GEORGIA STRAIT,CENTRAL, AND NORTHERN DISTRICTS

EVEN-YEAR PINK SALMON, UPPER GEORGIA STRAIT,CENTRAL, AND NORTHERN DISTRICTS

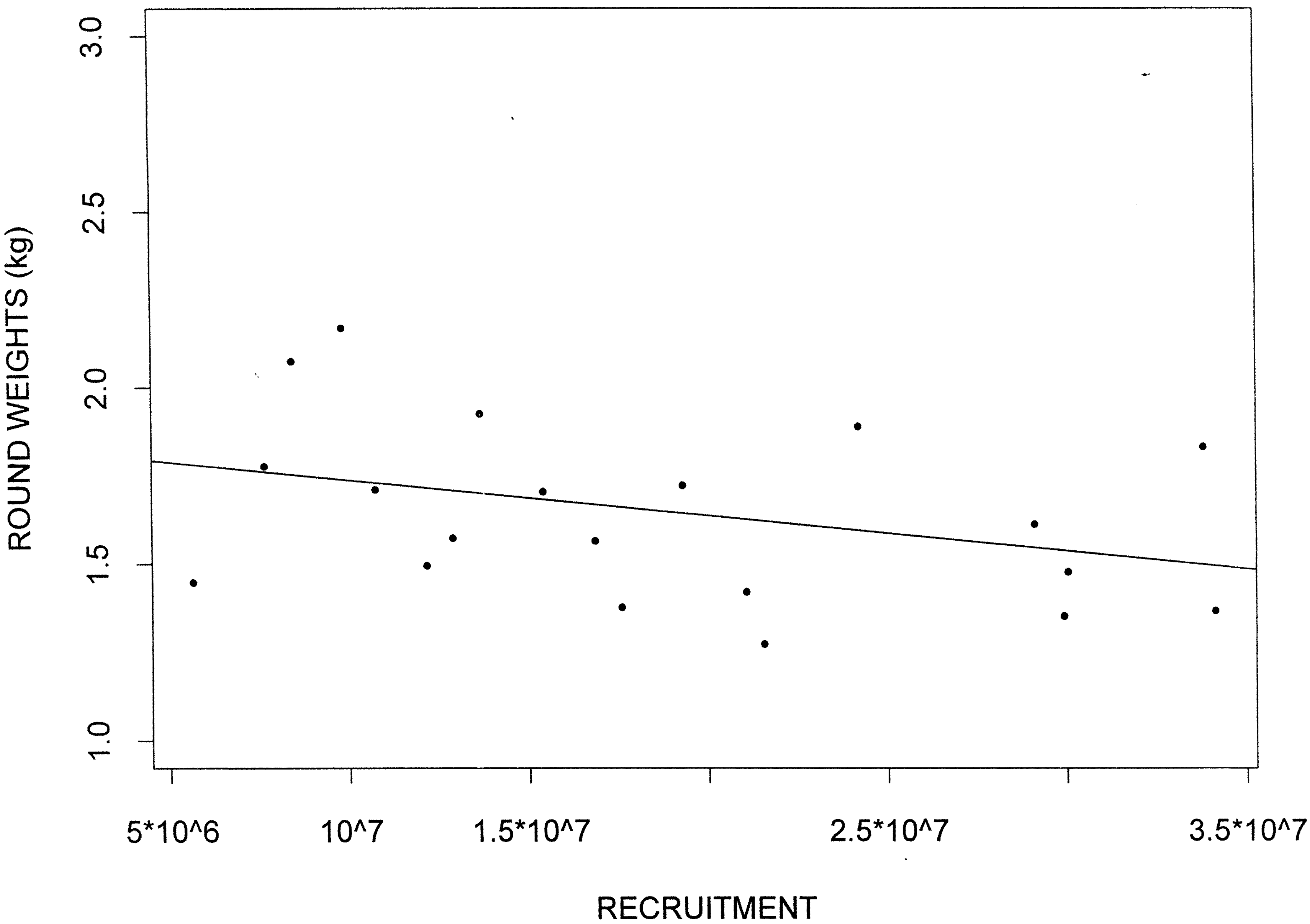
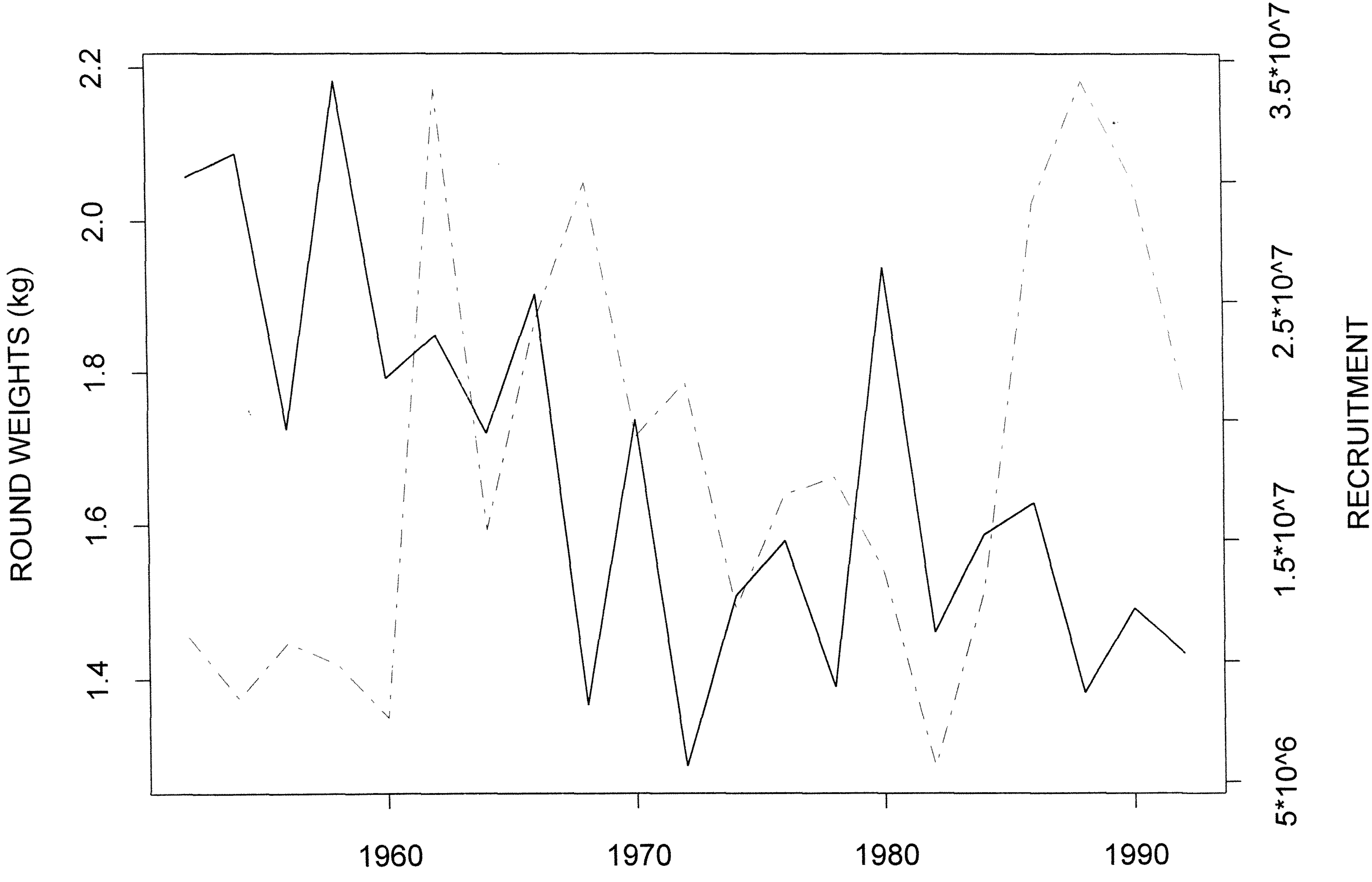
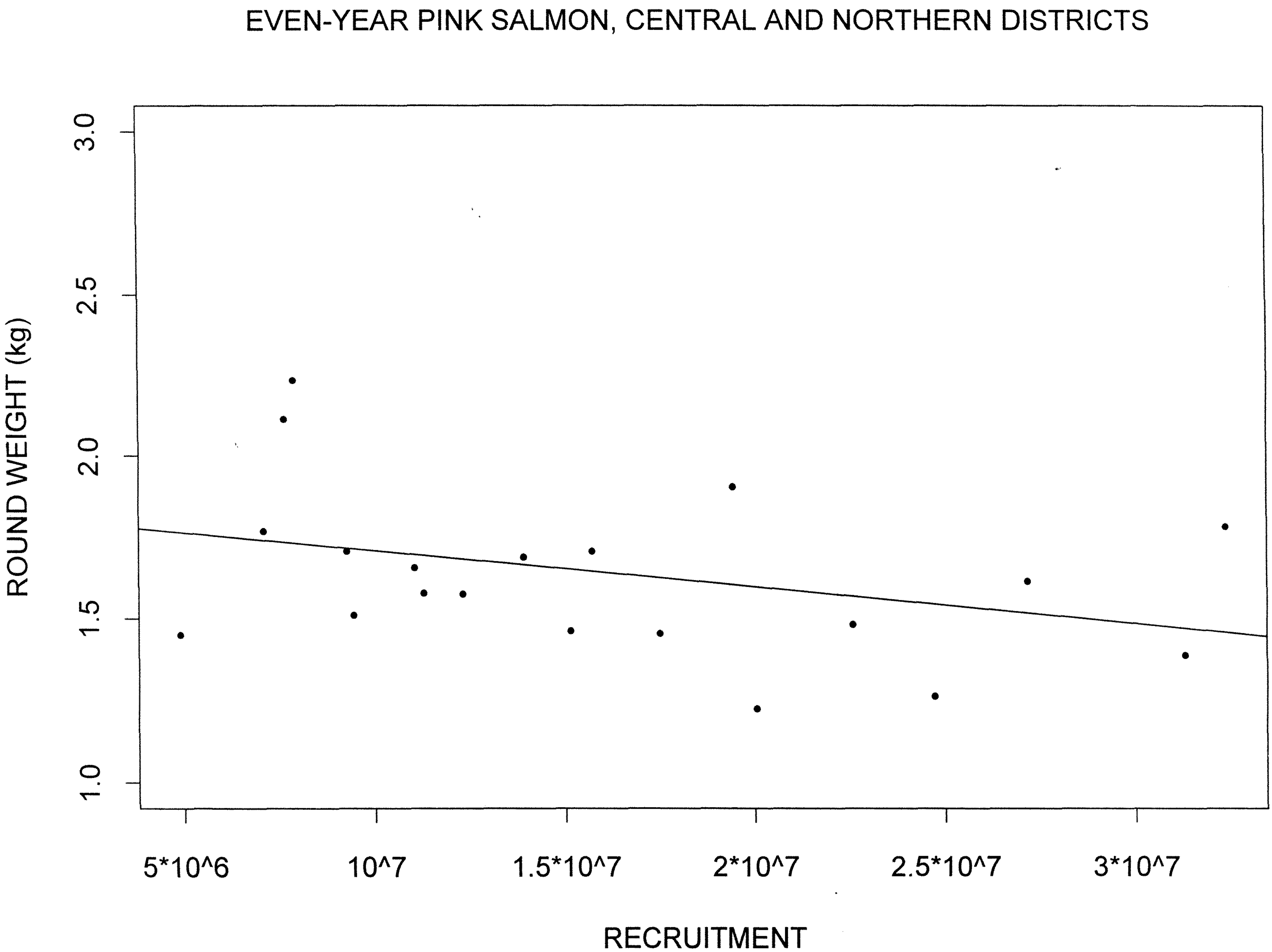


Fig. 15

EVEN-YEAR PINK SALMON - CENTRAL & NORTHERN DISTRICTS




EVEN-YEAR PINK SALMON, CENTRAL AND NORTHERN DISTRICTS
ROUND WEIGHT (kg)
1.0
1.5
2.0
2.5
3.0
5*10^6
10^7
1.5*10^7
2*10^7
2.5*10^7
3*10^7
RECRUITMENT

B.C. SOUTHERN DISTRICT ODD-YEAR PINK SALMON

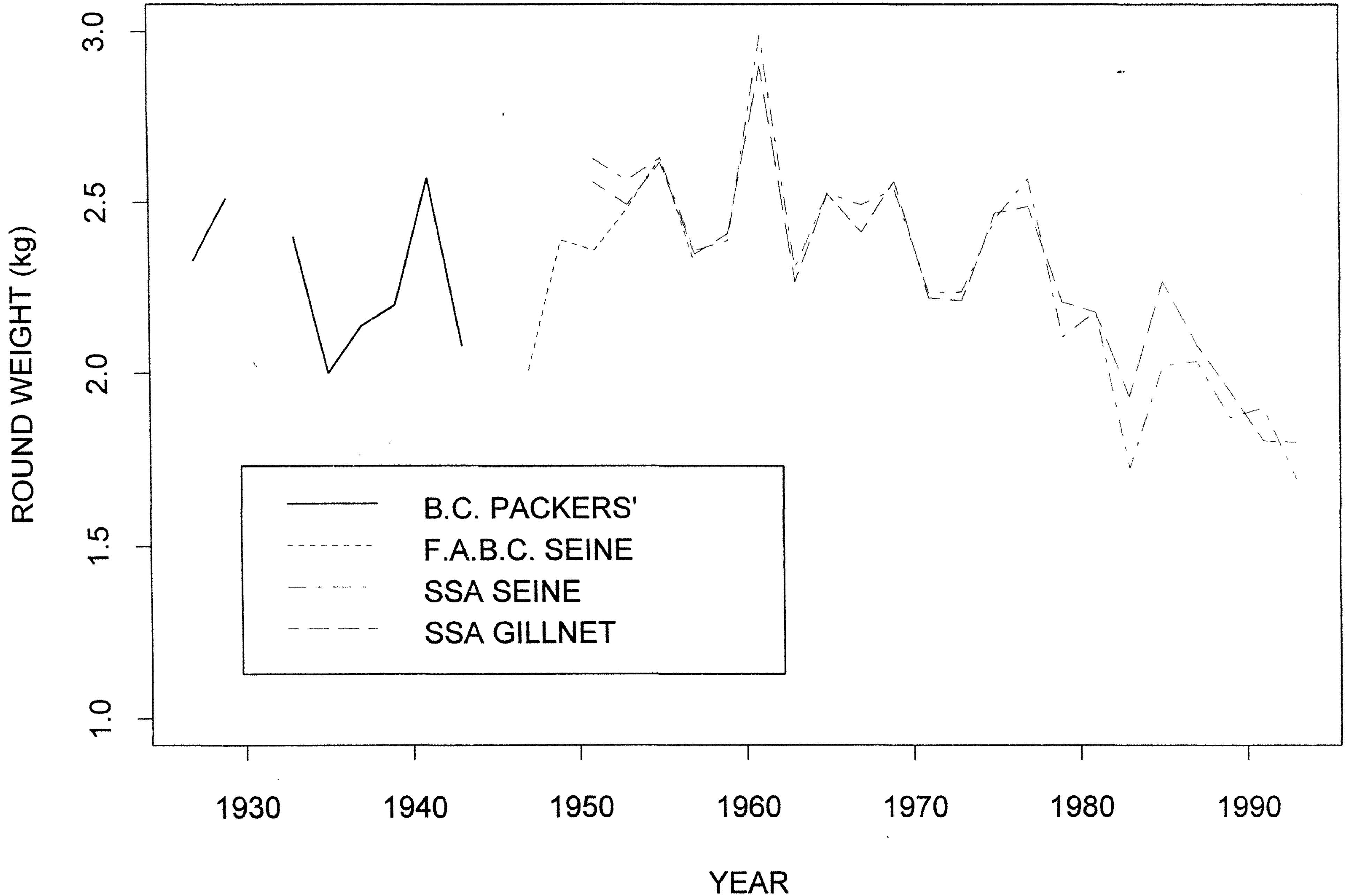


Fig. 18

WEST COAST VANCOUVER IS. ODD-YEAR PINK SALMON

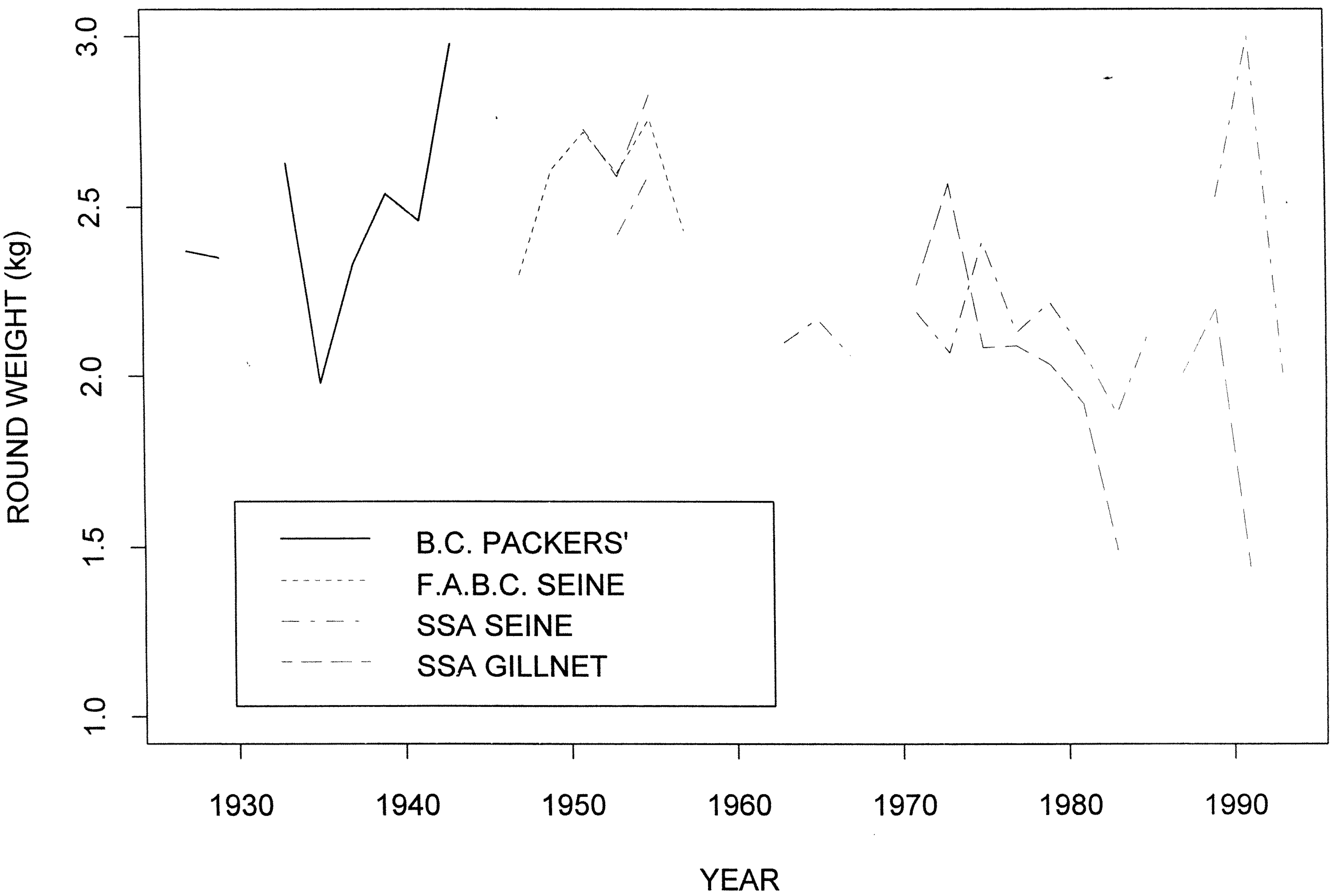


Fig. 19

B.C. CENTRAL DISTRICT ODD-YEAR PINK SALMON

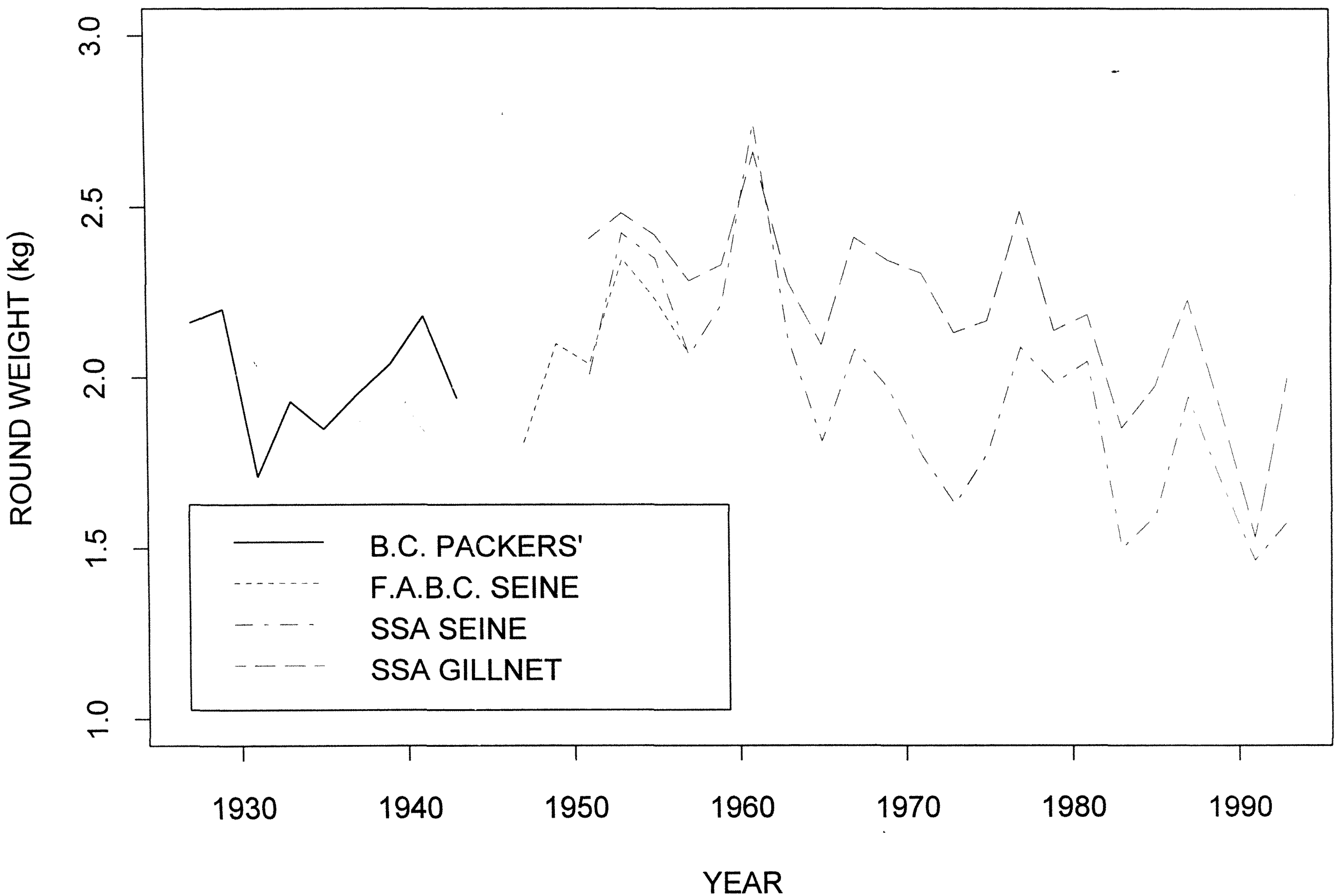
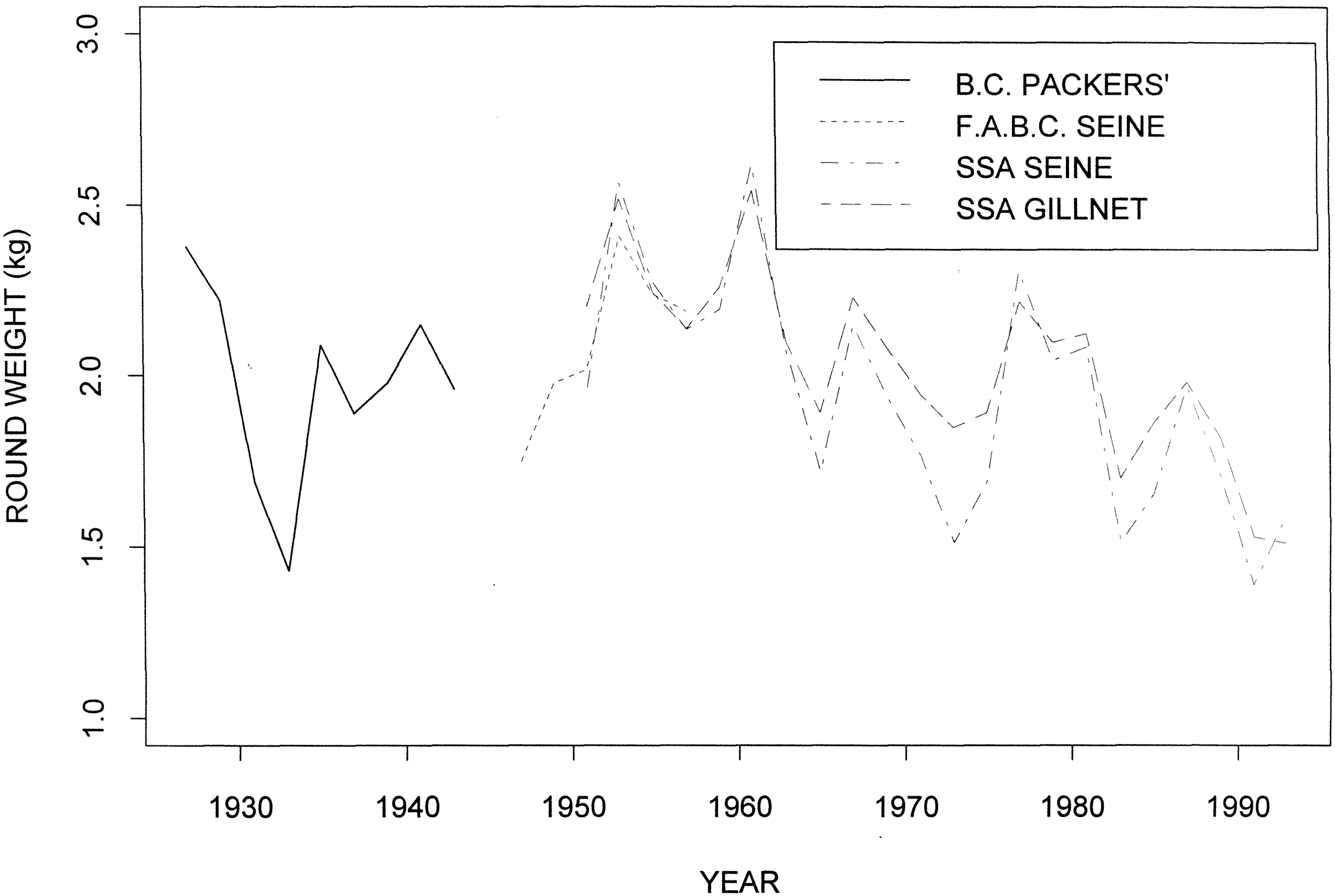


Fig. 20

B.C. NORTHERN DISTRICT ODD-YEAR PINK SALMON



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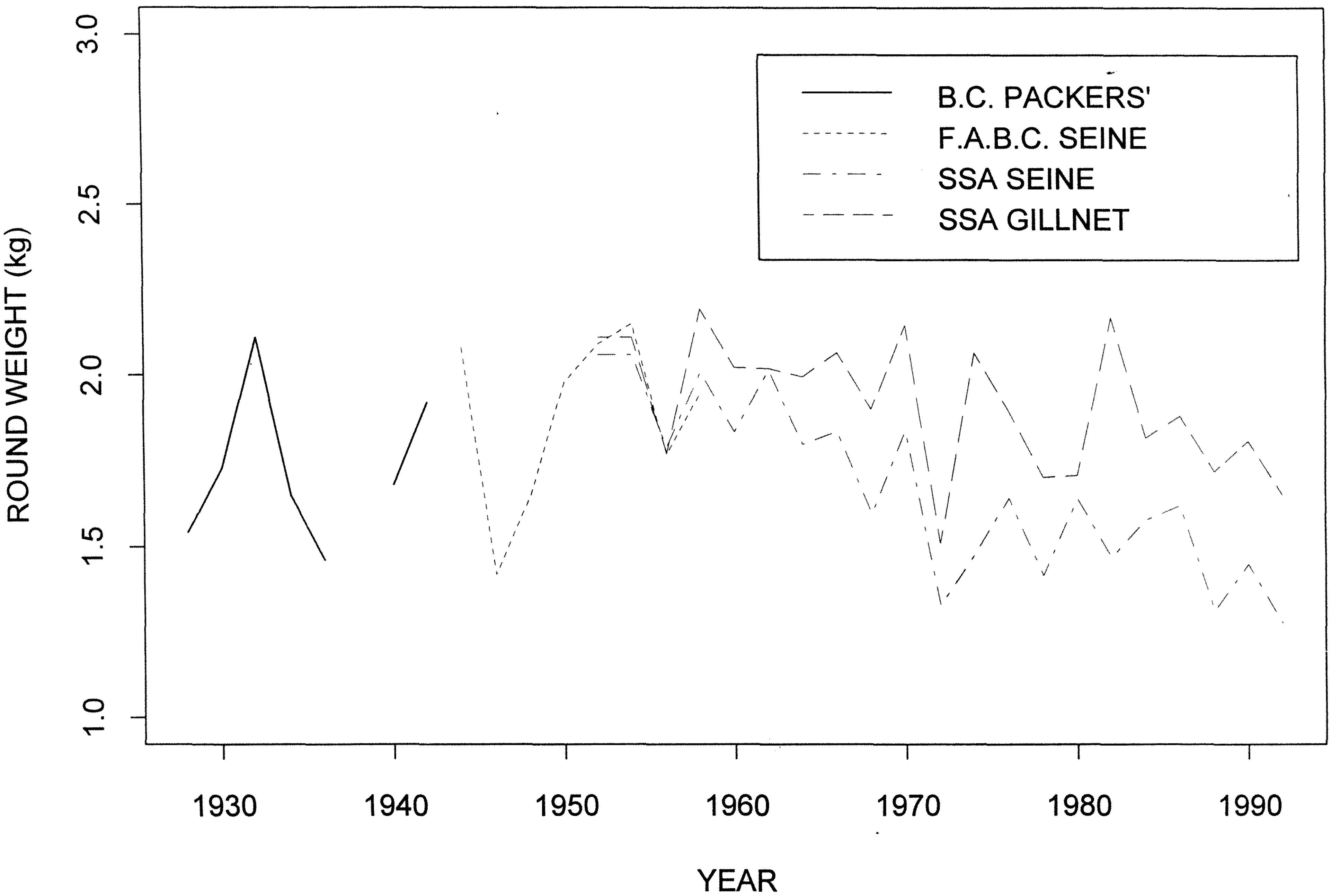
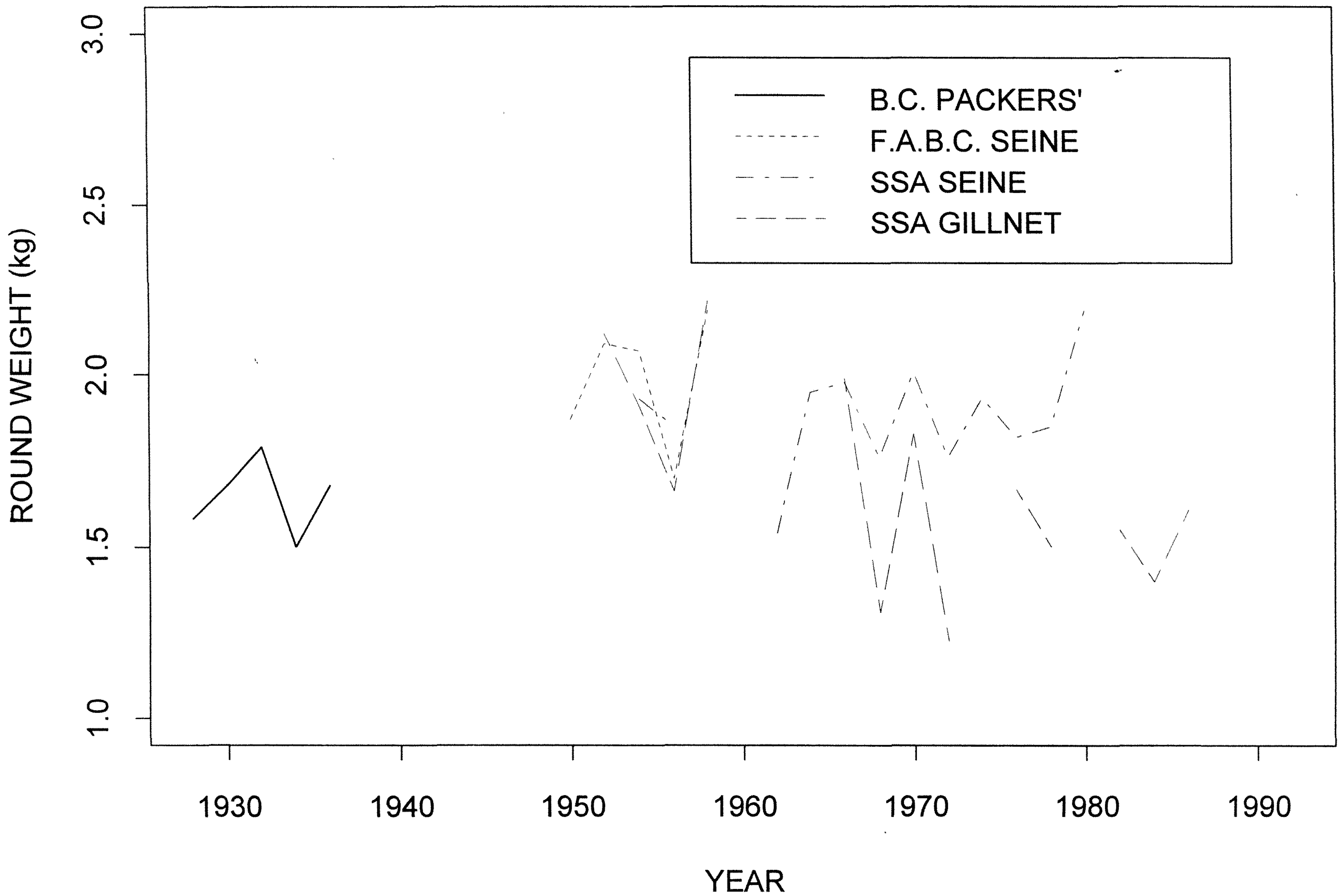


WEST COAST VANCOUVER IS. EVEN-YEAR PINK SALMON



B.C. CENTRAL DISTRICT EVEN-YEAR PINK SALMON

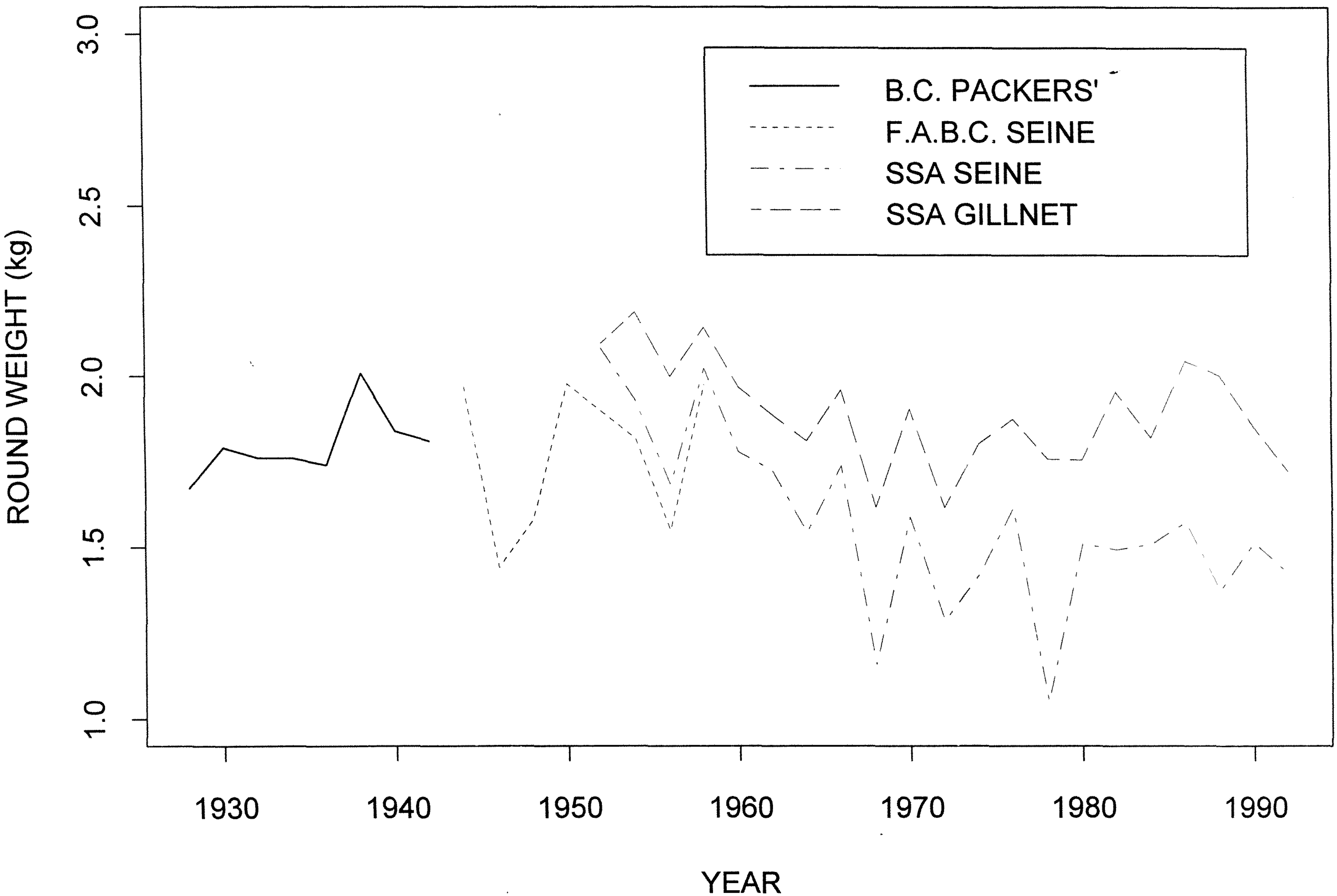
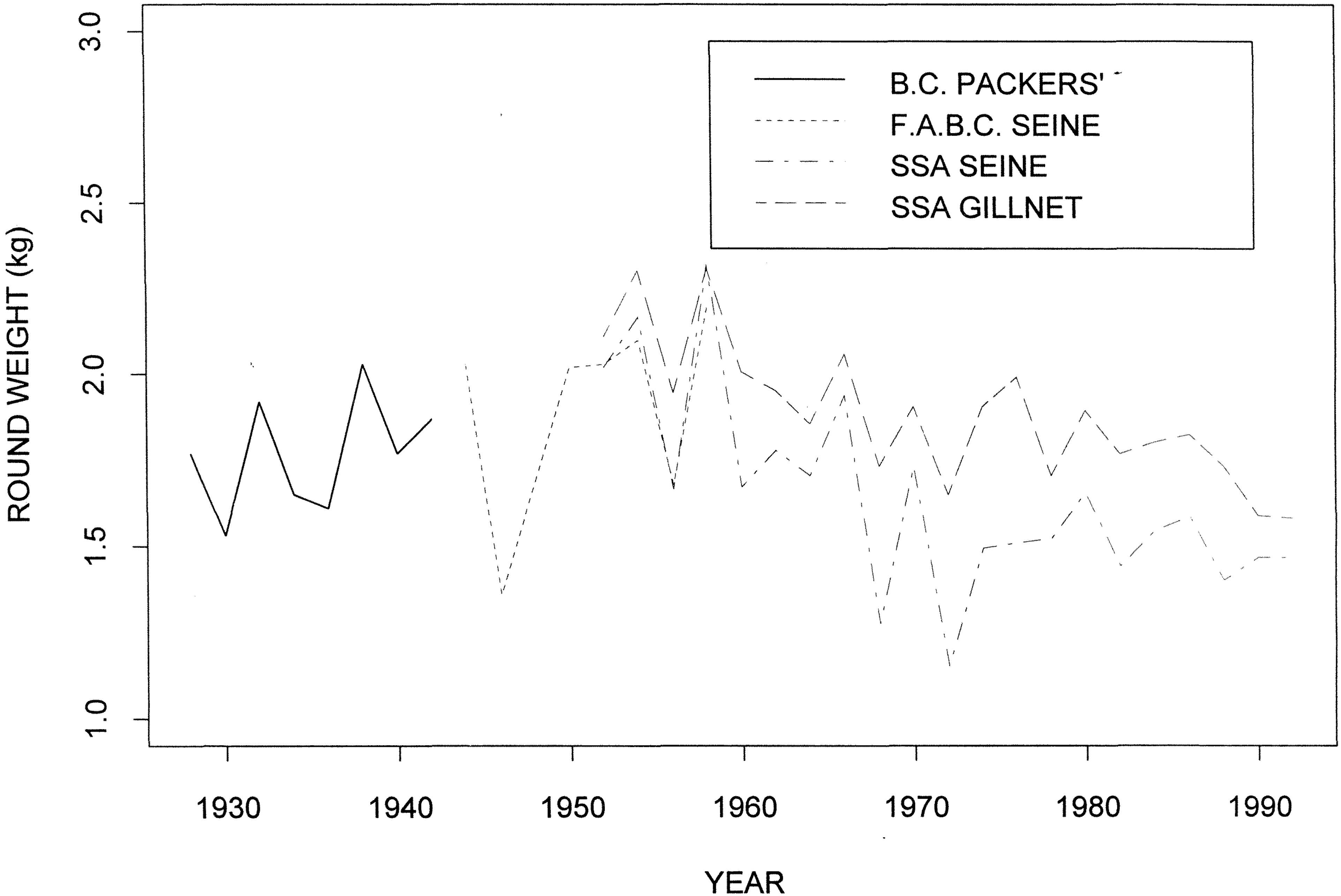


Fig. 24

B.C. NORTHERN DISTRICT EVEN-YEAR PINK SALMON



QUEEN CHARLOTTE IS. EVEN-YEAR PINK SALMON