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# COD (*Gadus morhua*) GROWTH BETWEEN 1956 AND 1966 COMPARED TO GROWTH BETWEEN 1978 TO 1985, ON THE SCOTIAN SHELF AND ADJACENT AREAS.

by

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## ABSTRACT

Growth of cod (*Gadus morhua*) was estimated from length increment data compiled from tagging programs conducted on the Scotian Shelf and adjacent areas during two hydrographically distinct periods: (1) 1956 to 1966 and (2) 1978 to 1985. The earlier and later periods were governed by cooler and warmer temperatures respectively. A model developed by Francis (1988) was used to estimate growth parameters $g_\alpha$ and $g_\beta$ , which represented mean annual growth rate at chosen reference lengths $\alpha$ (50 cm) and $\beta$ (70cm) respectively. Individual growth variability was modelled as a function of the expected change in length, which in turn was a function of time at liberty and initial size. The model fit, determined using a maximum likelihood technique, was considered adequate. Residuals were normally distributed, and did not show any pattern with either of the independent variables (time-at-liberty, length-at-release). During both earlier and later periods, mean annual growth at reference length 50cm was greater in the Bay of Fundy than on the Scotian Shelf, where in turn mean annual growth was greater than in Sidney Bight and the Gulf of St. Lawrence. Regional growth differences reflected the regional hydrographic regime. Fifty cm fish tagged in both the Gulf of St. Lawrence and the Central Scotian Shelf did not grow more slowly in the colder (earlier) period than in the warmer (later) period, whereas fish tagged in Sidney Bight and Bay of Fundy did. Differences in growth rate among regions between periods may have been masked by differences in population abundance between the two periods and/or spatial heterogeneity in the temperature field. Based on the geographic distribution of recaptures, fish from the Scotian Shelf migrated shorter distances than did fish from the Gulf of St. Lawrence, Sidney Bight and Bay of Fundy.

## Introduction

Growth is a fundamental process in the dynamics of fish populations. Environmental variability experienced by genetically different individuals leads to variation in growth. Temperature has a major influence on the rate of fish growth (Taylor 1958, Brander, 1994, 1995, Campana et al. 1995); spatial and temporal variability in temperature results in spatial and temporal variability in growth rate.

In this paper, we describe mean annual growth of Northwest Atlantic cod (*Gadus morhua*) using data from tagging (mark-recapture) programs. Length increment data of tagged individuals were used to compare growth rates among four regions between two tagging periods. The four regions are the Southern Gulf of St. Lawrence, Sidney Bight, Central Scotian Shelf and the Bay of Fundy (Fig. 1). The two tagging periods are represented by tagging programs conducted between (1) 1956 and 1966, and (2) 1978 and 1985. We describe the data from tagging programs, and the model used to estimate individual variability and mean annual growth of each population. We show that growth varied among regions and between tagging periods. The regional trend reflected the underlying hydrographic regime, while the temporal trend was equivocal.

## Material and Methods

### *Data*

Tagging data was compiled from a multi-species tagging data base (Marine Fish Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Halifax, Nova Scotia, Canada B2Y 4A2; Table 1). Release groups were selected on the assumption that the fish tagged spawned annually or were resident for most of the year in the area of tagging, and for which the range of release lengths were similar. Individuals for which length-at-release, time at liberty and length-at-recapture were available were used in this analysis. Length-at-release ranged from 28 to 123 cm. The median time-at-liberty ranged from 196 to 561 days. The median distance travelled ranged from 16 to 82 nautical miles (nm). Further details of tagging programs are documented in Stobo and Fowler (in prep).

### *Growth Model and Analysis*

The von Bertalanffy function is commonly used to analyse fisheries growth data; the form used to analyse tagging data is

$$\Delta L = (L_\infty - L_1)(1 - e^{-k\Delta T}) \qquad (1)$$

where
$\Delta L$ = (length-at-recapture)- (length-at-release)
$L_\infty$= asymptotic length

$L_1$= length-at-release
$\Delta T$= time-at-liberty
k=rate at which $L_\infty$ is approached.

The model describes observed growth increments as a function of time-at-liberty and initial length; parameters k and $L_\infty$ are estimated from the data. The von Bertalanffy parameters k and $L_\infty$ are mean estimates of growth rate and asymptotic length respectively. This assumes that the data are representative of the entire growth function in which growth reaches an asymptote. However, asymptotic length is often not well represented in tagging data because there are fewer, older, larger fish or, growth itself may not reach an asymptote (Knight, 1968; Roff, 1980). When using tagging data to estimate growth, $L_\infty$ may not be estimated properly because the model would predict negative growth for fish whose initial length was greater than the asymptotic length (Sainsbury, 1980; Francis, 1988). In effect, k and $L_\infty$, as used in length-at-age analyses, are age-based parameters, and may be inappropriate descriptors of growth estimated from length increment data.

We used the methodology developed by Francis (1988) to examine annual mean growth and growth variability from length increment data[1]. Francis (1988) re-expressed the von Bertalanffy parameters, k and $L_\infty$, as two new parameters, $g_\alpha$ and $g_\beta$, which represent mean annual growth at chosen reference lengths $\alpha$ and $\beta$ respectively. Lengths $\alpha$ (50 cm) and $\beta$ (70 cm) were chosen from the data to estimate mean annual growth ($g_\alpha$) and ($g_\beta$) respectively. Francis also modified the von Bertalanffy equation to allow for seasonal variation in growth rates. The von Bertalanffy equation becomes (Equation 2 from Francis 1988):

$$\Delta L = \left(\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1\right)\left(1 - \left[1 + \frac{g_\alpha - g_\beta}{(\alpha - \beta)}\right]^{(\Delta T + (\phi_2 - \phi_1))}\right)$$

where
$\Delta L$ = expected length increment for a fish of length $L_1$ at liberty for $\Delta T$
$\beta$ = length (70 cm)
$\alpha$ = length (50 cm)
$g_\beta$ = mean annual growth at length $\beta$
$g_\alpha$ = mean annual growth at length $\alpha$
$L_1$ = length-at-release
$\Delta T$ = time-at-liberty
$\phi_i = u(\sin(2\pi[T_i - w])/(2\pi)$, for i=1,2;$T_1$=release date, $T_2$=recapture date; w is the time of year of maximal growth rate, u is the range, maximum and minimum growth occurs in ratio of 1 + u: 1-u.

This model was fit to the data using a Maximum Likelihood (ML) technique. The ML method determines the values of unknown parameters that maximize the probability of obtaining

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[1] We used a modified version of the FORTRAN program "Grotag", originally written and provided to us by R.I.C.C. Francis, Fisheries Research Centre, Ministry of Agriculture and Fisheries, P.O. Box 297, Wellington, New Zealand (p, a parameter describing the probability of outliers in the "Grotag" program, was set to 0, and is not included in the ML equation).

the observed data. The ML technique is more general than a least squares method in that it allows for a non-constant variance in the data. The function used in the fitting routine was the log-likelihood function:

$$\lambda = \Sigma_i \log \lambda_i \tag{3}$$

where

$$\lambda_i = \frac{\exp\left[-1/2(\Delta L_i - \mu_i - m)^2 / (\sigma_i^2 + s^2)\right]}{\left[2\pi(\sigma_i^2 + s^2)\right]^{1/2}} \tag{4}$$

where i=1.....n individuals
$\Delta L_i$=observed length increment of ith individual
$\mu_i$= expected length increment
$\sigma_i^2$=growth variability modelled as function of mean expected growth (which is a function of $L_1$ and $\Delta$ T) where $\sigma=v\mu$
$s^2$ = SD of measurement error of length increment
m = mean measurement error of length increment

The goal is to find the parameters ($g_\alpha$,$g_\beta$,v,m,s,u,w) that minimize $\lambda$.

A relevant question in multi-parameter models is to what extent does adding parameters improve the model fit? Quite often, the likelihood ratio test is used to evaluate whether parameters add significant information to a model (e.g., Hampton, 1991; Francis, 1988); an additional parameter is judged appropriate for inclusion in the model if the maximum likelihood is twice more than without its inclusion. Although we relied on the minimization of $\lambda$ to judge the model, the likelihood ratio test was not used strictly because we felt that the (observed) sensitivity of $\lambda$ to small changes in parameter values made this test numerically suspect. Besides the value of $\lambda$, we examined the model fit by the distribution of residuals for normality, and whether there was any relationship between the residuals and either of the independent variables.

Mean annual growth was estimated for four regions in two periods (Table 1). The range of sample sizes and differences in data sets between the two periods (see below) in the present analysis precluded us from making any formal statistical comparisons. We considered it more appropriate to make qualitative comparisons among growth parameters while the other parameters were estimated commonly. In addition, there was prior evidence for regional differences in growth based on analysis of age-length data (Beacham 1982; Brander 1995), whereas differences in seasonal and measurement error would be questionable; such signals are more difficult to detect in tagging data than are differences in growth parameters (R.I.C.C Francis, pers.comm.). Thus, growth parameters $g_\alpha$ and $g_\beta$ were estimated separately for each region/period combination, while growth variability, measurement error and bias and seasonal parameters, (v,s,m,u,w) were estimated jointly for all regions. This allowed us to make qualitative comparisons of growth parameters while others were common to the entire group.

The data sets of each period differed in one respect, the negative growth increments had been edited out and were effectively irretrievable. This would most greatly affect the estimates of measurement error ($\nu$) and measurement bias (m). Thus, the results of common estimates are biased by the later period. We also estimated seasonal parameters in common, thus we cannot be entirely confident of the seasonal parameter estimates since we know that the hydrographic regimes differed between the two periods.

The certainty of parameter estimates was determined using data simulations. For each sample the model generated a set of fitted parameters from which, for each observed $\Delta T$ and $L_1$, a model $\Delta L$ and $\sigma$ could be computed. Simulated data were generated by a Monte-Carlo method in which the predicted $\Delta L$, $\sigma$ for each $\Delta T$, $L_1$ are input into a random number generator which selects a value from a normal distribution with mean $\Delta L$ and SD $\sigma$. The model is then refit to these simulated data, producing new parameter estimates. One thousand simulations were done, allowing for estimation of a SD around a mean parameter value.

To summarize, a maximum likelihood method was used to determine values of the unknown parameters ($g_\alpha$,$g_\beta$,$\nu$,s,m,u,w) for which the probability of obtaining the observed data was maximum. Parameters $g_\alpha$ and $g_\beta$ were estimated separately for each region/period combination, while $\nu$,s,m,u,w were estimated commonly for all data sets. The certainty of the resulting parameter estimates was obtained using a simulation technique.

## Results and Discussion

### *Model Fit*

The final model fit was selected as above. Residuals were normally distributed reflecting a good model fit (Fig.2). The residuals did not show a trend with either of the independent variables: time-at-liberty (Fig. 3) and length-at-release (Fig. 4). The results of the simulations show that the data are adequate for estimating all of the parameters of the model (Tables 2 and 3).

### *Parameters estimated in common for all nine regions*

#### (i) Growth variability

The measurement error s was estimated as 3 cm, the mean measurement error m was estimated as 0.76 cm ,whereas $\nu$ was estimated as 0.51 (Table 2). The standard deviation (SD) of the mean expected $\Delta L$ ($\mu$) was modelled as $\pm(\sigma+s+m)$, where $\sigma=\nu\mu$. Sources of measurement error will vary among release groups, and among species. A possible source of error in the present analysis may be the different sources of measuring upon recapture (fishery observers, plant workers, fishers, fishery officials), as well as the change in reporting rate between the two periods.

(ii) Seasonality

Seasonal parameter estimates w = 0.41 and u = 0.56 indicate that maximal growth occurs in May and is 3.5 times faster than minimal growth that occurs in November. The timing of maximal growth may reflect growth after spawning. Rijnsdorp (1990) found that the growing period of plaice (*Pleuronectes platessa*) begins after spawning. Fish may preferentially allocate energy to reproduction as spawning time approaches, and to somatic growth at other times, which would result in seasonal variation in growth. Spawning times among regions analysed herein range from January to October (Brander and Hurley, 1992; Brander, 1994; Serchuk et al., 1994 ); however there is much variation within regions among years.

Regional and inter-annual differences in seasonal growth would contribute to error in estimating seasonal parameters. As well, common estimates of seasonal parameters were influenced by those release groups with larger sample sizes. Since the seasonal parameter estimates represent a composite (regional and temporal) seasonal pattern, they are best used in the growth model (eq'n 2-4) for estimation of regional growth patterns, and not for describing a regional/seasonal growth patterns.

*Growth Parameters estimated separately for each region*

During both earlier and later periods, mean annual growth at reference length 50cm was greater in the Bay of Fundy than on the Scotian Shelf, where in turn mean annual growth was greater than in Sidney Bight and the Gulf of St. Lawrence. The regional/temporal patterns of mean annual growth were not as evident for fish of 70 cm (Fig. 5).

Regional growth differences reflected the regional hydrographic regime. Fish tagged in both the Gulf of St. Lawrence and the Central Scotian Shelf did not grow more slowly in the colder (earlier) period than in the warmer (later) period, whereas fish tagged in Sidney Bight and Bay of Fundy did. Differences in growth rate among regions between periods may have been masked by differences in population abundance between the two periods.

The simulation results show that the data were adequate to estimate the model parameters. Thus, if the model was a true representation of growth, then the parameter estimates reflect accurately growth of each region (Fig. 6).

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Table 1. Summary information of data from tagging programs conducted by Department of Fisheries and Oceans, Canada, on the Scotian Shelf and adjacent areas: (A) Region, region code, Northwest Atlantic Fishery Organization (NAFO) fishery division-year/month of release; N=number of recaptures used in analysis. (B) Region (by code), mean and range of length-at-release, median time-at-liberty, median distance travelled.

(A)

| Region | Code | NAFO Div.- Year /Month of Release | N |
|---|---|---|---|
| Earlier Period: | | | |
| Southeastern Gulf | GSL1 | Tf -56/5; 57/7,8; 58/5; Tg -56/5; Tk -56/6 | 258 |
| Sidney Bight | SB1 | VNa -60/2;62/4 | 113 |
| Middle Bank | CSS1 | Whj -59/3,9; 60/3 | 115 |
| Bay of Fundy | BF1 | Xs-66/5 | 44 |
| Later Period: | | | |
| Southeastern Gulf | GSL2 | Tg -79/9; 80/5,11,12; 81/4 | 802 |
| Sidney Bight | SB2 | VNa -80/9,10 | 468 |
| Middle Bank | CSS2 | We -78/10,11 | 757 |
| Bay of Fundy | BF2 | Xs-85/7,11 | 58 |

(B)

| Region | Length-at-release (cm) | | Time-at-Liberty (d) | Distance travelled (nm) |
|---|---|---|---|---|
| | Mean | Range | Median | Median |
| Earlier Period: | | | | |
| GSL1 | 70 | 38-101 | 380 | 48 |
| SB1 | 57 | 47-80 | 334 | 60 |
| CSS1 | 60 | 43-82 | 275 | 16 |
| BF1 | 55 | 34-98 | 411 | 16 |
| Later Period: | | | | |
| GSL2 | 47 | 28-123 | 561 | 82 |
| SB2 | 54 | 31-110 | 493 | 24 |
| CSS2 | 50 | 36-68 | 211 | 13 |
| BF2 | 56 | 38-78 | 196 | 29 |

Table 2. Model estimates and mean and SD of 1000 simulations of v,s,m,u, and w for 8 region/periods combined (n=2616).

| Common Estimates | Model | Simulations |
|---|---|---|
| | | Mean (SD) |
| Growth variability (v) | 0.51 | 0.50 (0.05) |
| S.D. of Measurement Error (s) | 3.01 | 3.93 (0.29) |
| Measurement Bias (m) | 0.76 | 0.38 (0.17) |
| Seasonal: | | |
| -Period of maximum growth (w) | 0.41 | 0.38 (0.09) |
| -Extent of growth u(1+u:1-u) | 0.56 | 0.36 (0.17) |

Table 3. Separate estimates of $g_\alpha$ and $g_\beta$ (mean annual growth rate at 50 cm and at 70 cm respectively) and mean and SD of 1000 simulations for each region/period combination.

| Study | $g_\alpha$ | | $g_\beta$ | |
|---|---|---|---|---|
| | Model | Simulations | Model | Simulations |
| Earlier Period: | | | | |
| GSL1 | 5.63 | 5.64 (0.04) | 4.52 | 4.55(0.08) |
| SB1 | 2.99 | 2.99 (0.13) | 2.77 | 2.80(0.12) |
| CSS1 | 9.6 | 9.59 (0.04) | 8.19 | 8.19(0.06) |
| BF1 | 11.07 | 11.08 (0.13) | 8.17 | 8.14(0.15) |
| Later Period: | | | | |
| GSL2 | 3.17 | 3.18 (0.04) | 2.37 | 2.38(0.05) |
| SB2 | 4.56 | 4.56 (0.03) | 3.79 | 3.77(0.06) |
| CSS2 | 6.58 | 6.59 (0.02) | 3.26 | 3.26(0.01) |
| BF2 | 15.34 | 15.33 (0.13) | 7.59 | 7.58(0.17) |

Fig. 1. Location of Tagging Programs conducted between 1956 and 1966 (Region Code 1: GSL1, SB1, CSS1, BF1) and between 1978 to 1985 (Region code 2: GSL2, SB2, CSS2, BF2). Region codes are as follows: GSL- Gulf of St. Lawrence; SB- Sidney Bight; CCS- Central Scotian Shelf; BF- Western Bay of Fundy. Contours: solid=100m, dotted=200m, dashed=300m.

Fig. 2. Distribution of residuals from fit of von Bertalanffy model (Equations 1-3) (n=2616).

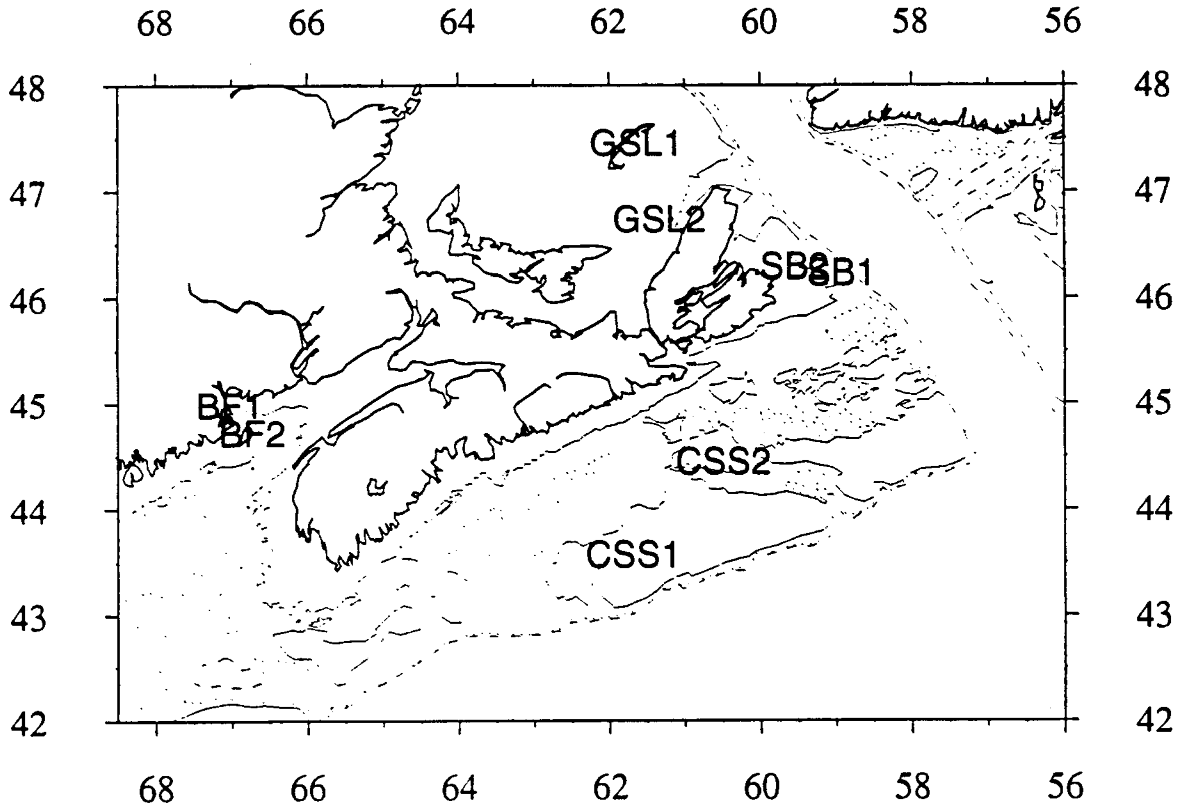
Fig. 3. Distribution of residuals from fit of von Bertalanffy model against length-at-release (n=2616).

Fig. 4. Distribution of residuals from fit of von Bertalanffy model against time-at-liberty (n=2616).

Fig. 5. Mean annual growth of each region /period combination at reference length 50 cm (A-left hand plot) and 70 cm (B-right-hand plot).GSL- Gulf of St. Lawrence; SB- Sidney Bight; CCS- Central Scotian Shelf; BF- Western Bay of Fundy. Suffixs 1 and 2 refer to Earlier and Later Period respectively.

Fig. 6. Box and whisker plots of simulation results of parameters $g_\alpha$ and $g_\beta$ for each region. GSL- Gulf of St. Lawrence; SB- Sidney Bight; CCS- Central Scotian Shelf; BF- Western Bay of Fundy. Suffixs 1 and 2 refer to Earlier and Later Period respectively.

Figure 1


68
66
64
62
60
58
56
48
47
46
45
44
43
42
GSL1
GSL2
SB2
SB1
BF1
BF2
CSS2
CSS1

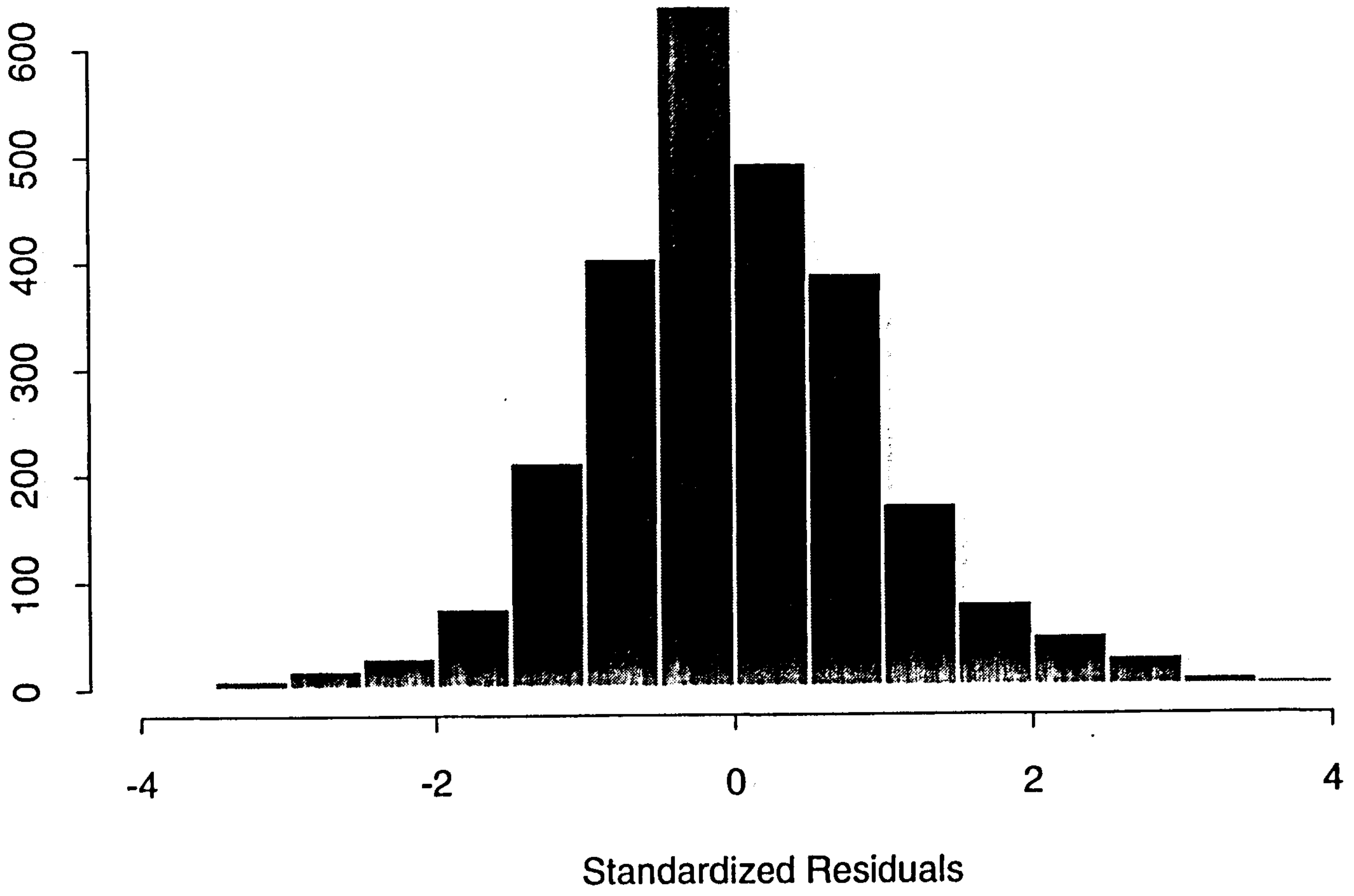
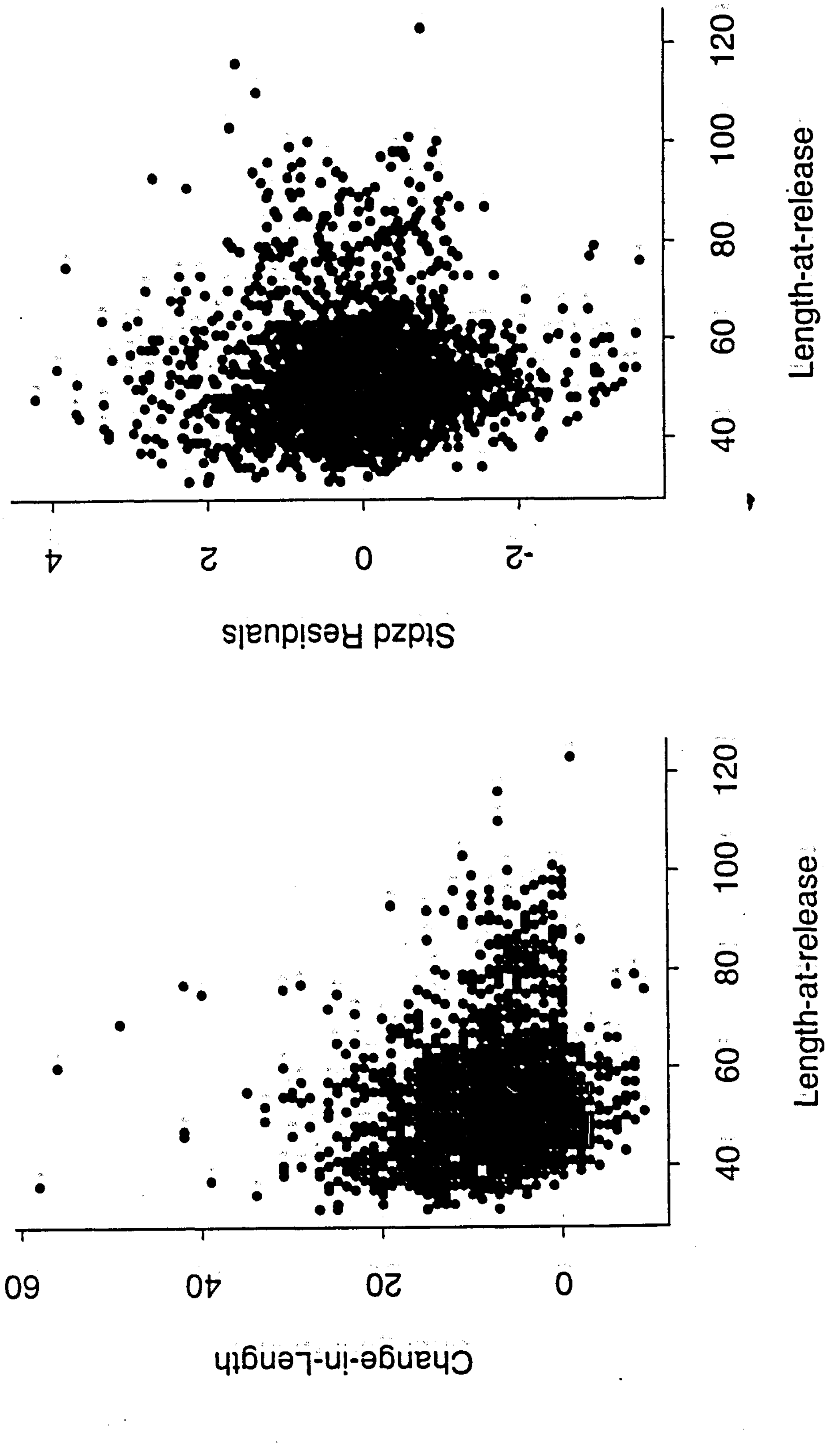


Figure 2

Figure 3


Stdzd Residuals
4
2
0
-2
40
60
80
100
120
Length-at-release
Change-in-Length
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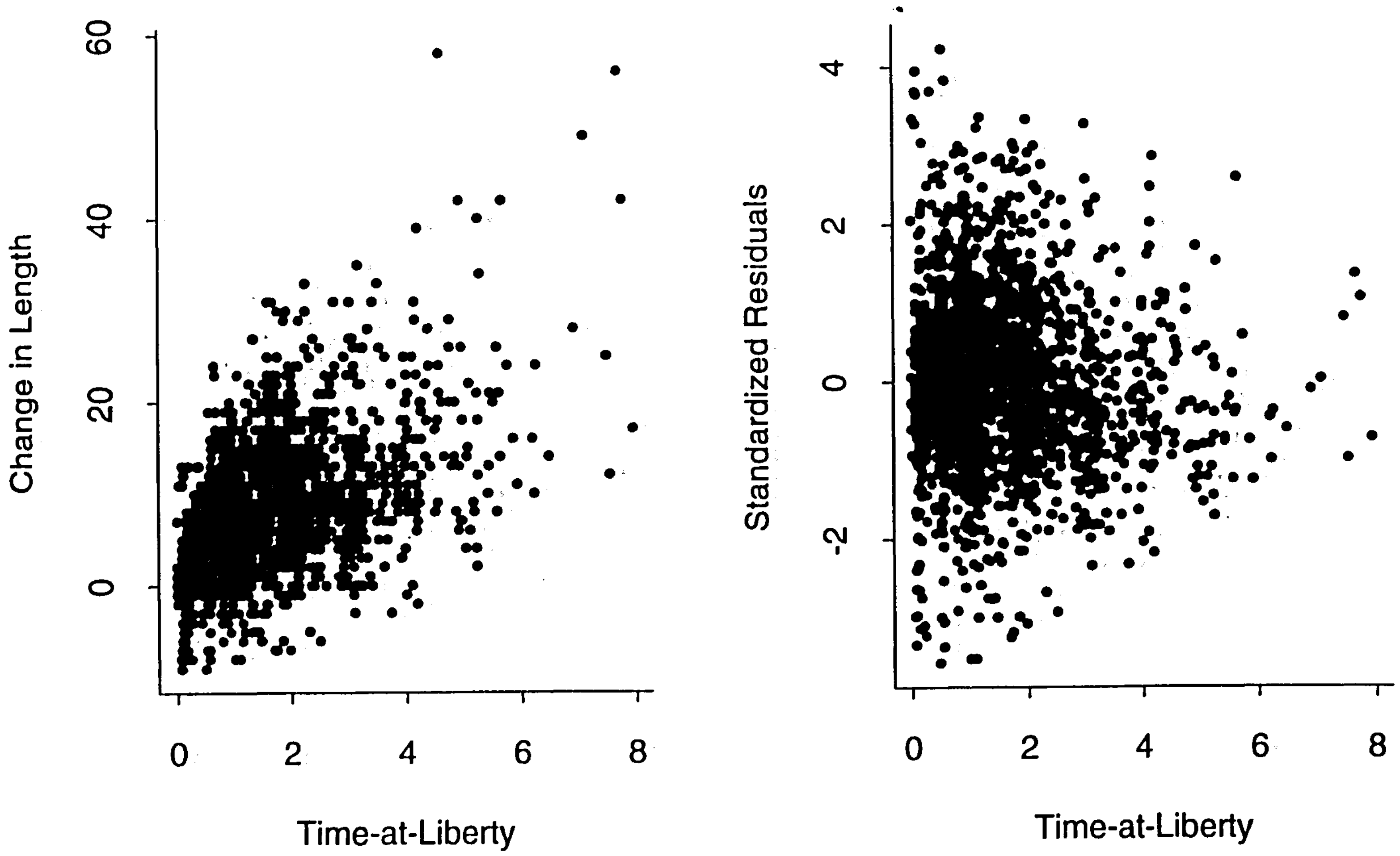
20
0
40
60
80
100
120
Length-at-release


Change in Length
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0
2
4
6
8
Time-at-Liberty
Standardized Residuals
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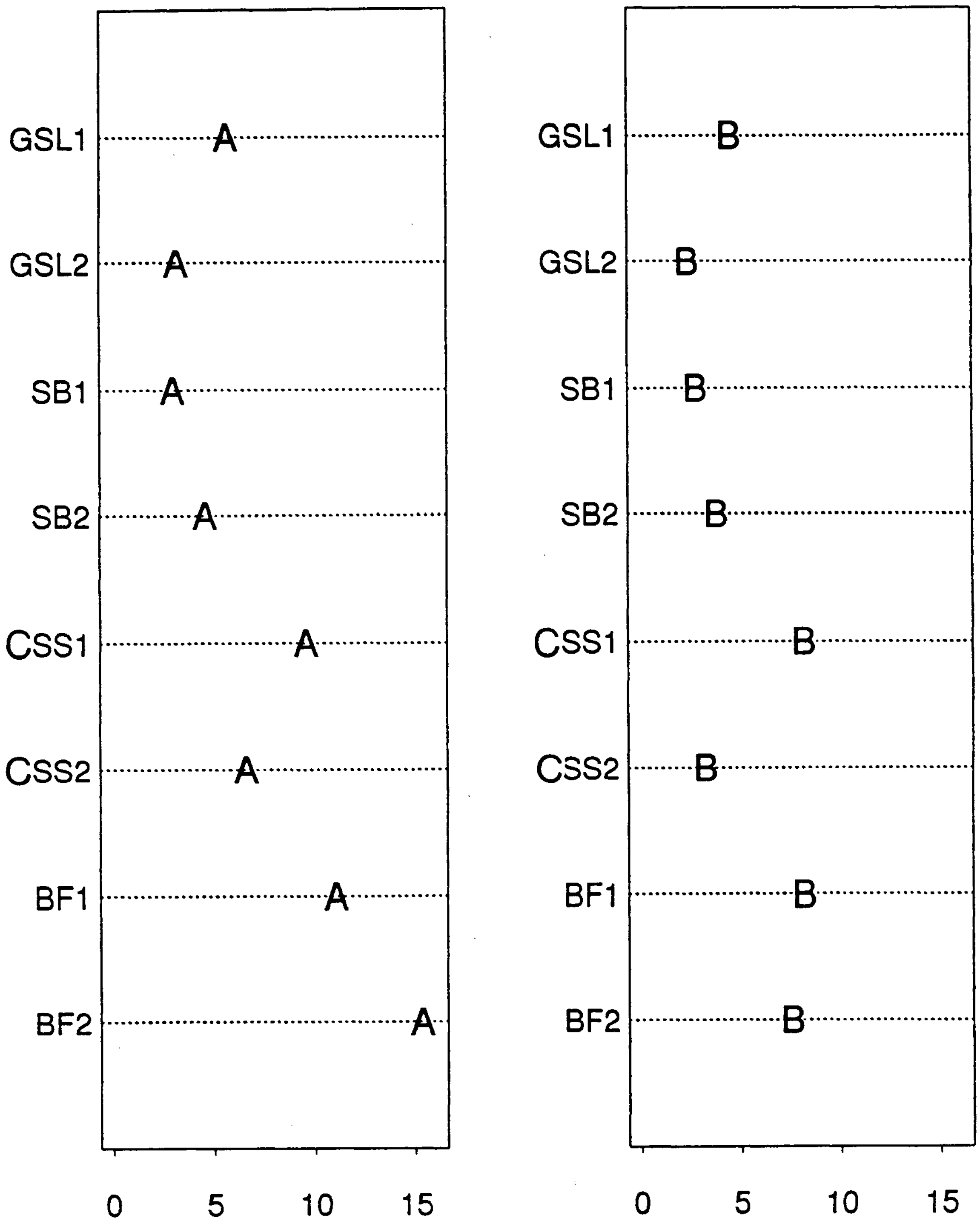
0
2
4
6
8
Time-at-Liberty

Figure 4

Figure 5



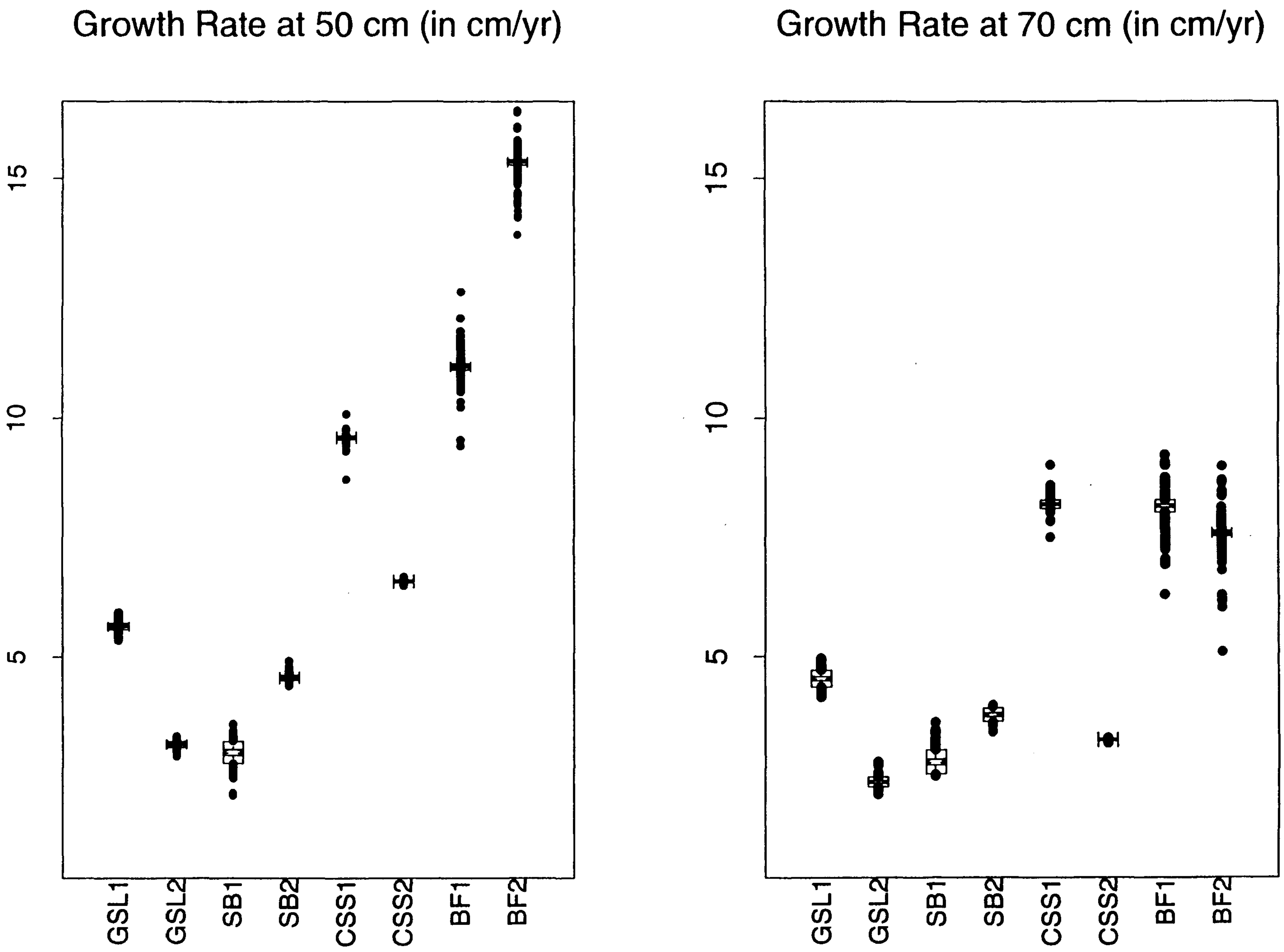

Growth Rate at 50 cm (in cm/yr)
Growth Rate at 70 cm (in cm/yr)
5
10
15
5
10
15
GSL1
GSL2
SB1
SB2
CSS1
CSS2
BF1
BF2
GSL1
GSL2
SB1
SB2
CSS1
CSS2
BF1
BF2

Figure 6