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## **An examination of the possible effect of spawning stock characteristics on recruitment in 4 Newfoundland groundfish stocks**

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## **Abstract**

Several characteristics of the spawning stock biomass of 3LNO American plaice, 2J3KL cod, 3NO cod and 3Ps cod were explored for variability and for relationships with the residuals from Beverton-Holt stock-recruit models. Weighted mean age of the SSB, proportion of first time spawners and proportion female all show substantial variation over the time period. The residuals from the stock-recruit relationship show a tendency to increase with mean age of the SSB for 3LNO American plaice and 2J3KL cod, indicating that recruitment is over estimated when mean age is low. The residuals tend to increase with proportion of first time spawners for 3NO cod and perhaps 3LNO American plaice and 3Ps cod, indicating that recruitment is over estimated when the proportion of first time spawners is low. For 3LNO American plaice, 3NO cod and 3Ps cod there is a tendency for the residuals from the Beverton-Holt fits to increase as proportion female increases indicating that recruitment is under estimated when proportion female is high.

## **Résumé**

Plusieurs caractéristiques de la biomasse du stock reproducteur de la plie canadienne 3LNO et de la morue 2J3KL, 3NO et 3Ps ont été étudiées pour la variabilité et les relations avec les résidus des modèles stock-recrutement Beverton-Holt. L'âge moyen pondéré de la biomasse du stock reproducteur, la proportion des nouveaux reproducteurs et la proportion des femelles présentent tous des variations importantes au cours de la période. Les résidus de la relation stock-recrutement présentent une tendance à accroître avec l'âge moyen de la biomasse du stock reproducteur pour la plie canadienne 3LNO et la morue 2J3KL cod, ce qui indique que le recrutement est surestimé lorsque l'âge moyen est faible. Les résidus tendent à augmenter avec la proportion des nouveaux reproducteurs pour la morue 3NO et peut-être pour la plie canadienne 3LNO et la morue 3Ps, ce qui indique que le recrutement est surestimé lorsque la proportion des nouveaux reproducteurs est faible. Pour la plie canadienne 3LNO, la morue 3NO et 3Ps, il existe une tendance pour les résidus du modèle Beverton-Holt à augmenter à mesure que la proportion des femelles s'accroît, ce qui indique que le recrutement est sous-estimé lorsque la proportion des femelles est élevée.

## Introduction

The relationship between spawning stock biomass (SSB) and recruitment is an essential element in the understanding of the population dynamics of fish stocks. The stock-recruit relationship underlies the definition of reference points for the precautionary approach. However, for most marine fish stocks the stock-recruit relationship remains poorly defined with large variability around the predicted relationship.

In most stock-recruit relationships SSB is calculated as the sum of the biomass at age multiplied by maturity at age (often the female maturity at age). This assumes that a given SSB will produce the same number of recruits regardless of the characteristics of the fish comprising the spawning stock. There is growing evidence that not all SSBs are created equal. First time spawners produce eggs of poorer quality than repeat spawners (Solemdal *et al.* 1995;Kjesbu *et al.* 1996;Trippel 1998). Wigley (1999a) showed an improvement in the stock-recruit relationship for Georges Bank haddock (*Melanogrammus aeglefinus*) once first time spawners were removed. Fish in poor condition can have reduced fecundity and/or reproductive success or they can fail to spawn at all (Burton and Idler 1984;Kjesbu *et al.* 1991;Burton *et al.* 1997;Marshall *et al.* 1998;Marteinsdottir and Steinarsson 1998). The age composition of the SSB has also been found to be an important determinant of recruitment (Lambert 1990;Marteinsdottir and Thorarinsson 1998).

This paper examines the stock-recruit relationships of four Newfoundland groundfish stocks, 3LNO American plaice (*Hippoglossoides platessoides*), 2J3KL cod (*Gadus morhua*), 3NO cod and 3Ps cod. We then determine if there is variability in age composition, proportion of first time spawners and proportion of mature females for these stocks. Finally we explore the possibility of relationships between these characteristics of the SSB and the residuals from the stock-recruit relationships.

## Materials and Methods

Population numbers and weights at age were taken from SPA's for the four stocks (Table 1). The formulations of the SPAs varied among stocks.

For 3LNO American plaice, the most recent SPA (Morgan *et al.* 1999) was used. The ADAPT applied to total catch and calibrated with Canadian RV survey spring 1985-1998 indices was applied to estimate terminal numbers  $N_{a,y}$   
where  $a = 6$  to 15,  $y = 1999$

and Catchabilities

$q_a$  where  $a = 5$  to 14 for the Canadian Research Vessel survey spring

The following structure was imposed:

- (i) natural mortality was assumed to be 0.2 except 0.6 on all ages from 1989-96
- (ii) fishing mortality at ages 15-17 was set as the average of ages 12-14
- (iii) no "plus" age class;

(iv) no error in the catch numbers-at-age.

Input data were:

Catch numbers at age

$C_{a,y}$  where  $a = 5$  to  $17$  and  $y = 1975$  to  $1998$ ,

Canadian Spring Research Vessel survey estimates of abundance at age (Campelen or Campelen equivalent values)

$RV_{a,y}$  where  $a = 5$  to  $14$  and  $y = 1985$  to  $1998$

The objective function that was minimized is

$$SS = \sum_{a,y} (\log(RV_{a,y}) - \log(q_a N_{a,y}))^2$$

where  $a$ =age 5 to 14,  $y$ = year of survey. The results of this model were added to the results for the 1960-1974 time period from a previous model (Brodie et al. 1993).

For 2J3KL cod, the last accepted SPA is found in Bishop et al. (1993). Subsequent assessments (e.g. Bishop et al. 1994) found that there was an unacceptable pattern in the residuals and the model was not used to provide quantitative estimates of stock size after the 1993 assessment. Shelton and Lilly (In Press) explored alternative approaches of reducing the residual pattern in the model fit. The pattern can be removed by allowing survey catchability to change in the late 1980s and early 1990s or by allowing for increased unaccounted for deaths in the early 1990s through unreported catches and/or natural mortality in excess of the assumed value of 0.2. In the analyses that follow, we assume the latter explanation holds because there is no corroborating evidence of changes in survey catchability. To account for missing fish the following formulation of the basic population model was used:

$$N_{a+1,y+1} = ((N_{a,y} e^{(-M/2)}) - C'_{a,y}) e^{(-M/2)},$$

where  $C'_{a,y}$  is a matrix of parameters representing missing fish to be estimated (these fish are removed mid-year),  $N_{a,y}$  is the number alive at the beginning of age  $a$  and the beginning of year  $y$ ,  $M$  is the annual instantaneous rate of natural mortality, assumed to be 0.2,  $a = 2$  to  $13$  and  $y = 1962$  to  $1994$ . It is not feasible to estimate the entire catch matrix. Instead, through trial and error, a block of cells ( $a = 3$  to  $10$  and  $y = 1991$  to  $1993$ ) was chosen so as to provide the smallest departure from the assumptions required in order to allow a reasonably consistent interpretation of survey and catch data in the SPA. The remaining catch matrix remained unaltered from that used in past assessments. Research vessel survey mean numbers per tow at age,  $RV_{a,y}$  from the fall groundfish bottom trawl survey for  $a = 2$  to  $13$  and  $y = 1978$  to  $1994$  (original Engel data) were used to calibrate the model using the ADAPT framework (Gavaris 1988). The objective function sums of squares,  $SS$ , that was minimized is

$$SS = \sum_{a,y} (\log(RV_{a,y}) - \log(q_a N_{a,y}))^2,$$

where  $q_a$  is a vector of catchability parameters to be estimated. The vector of survivors in the last year,  $N_{a,1994}$  were also treated as parameters that must be estimated. A constraint was placed on the fishing mortality on the oldest age,  $F_{13,y}$  so that

$$F_{13,y} = (F_{9,y} + F_{10,y} + F_{11,y} + F_{12,y}) / 4,$$

where  $F_{a,y} = -\log\left(\frac{(N_{a,y} \exp^{(-M/2)} - C_{a,y})}{(N_{a,y} \exp^{(-M/2)})}\right)$ .

For 3NO cod, the most recent SPA (Stansbury et al. 1999) was used. The ADAPT applied to total catch and calibrated with Canadian RV survey spring 1984-1998, Canadian RV survey fall 1990-98 and Canadian juvenile flatfish survey 1989-94 indices was applied to estimate terminal numbers  $N_{a,t}$ .

where  $a = 3$  to  $12$ ,  $t = 1999$  and  $a = 12, t = 95$  to  $98$

and Catchabilities

- $q1_a$  where  $i = 2$  to  $10$  for the Canadian Research Vessel survey spring
- $q2_a$  where  $i = 2$  to  $10$  for the Canadian Research Vessel survey fall
- $q3_a$  where  $i = 2$  to  $10$  for the Juvenile Research Vessel survey.

The following structure was imposed:

- (i) natural mortality was assumed to be 0.2;
- (ii) fishing mortality on the oldest age (12) set equal to the average F for ages 6 to 9 for years 1959-1995.
- (iii) no “plus” age class;
- (iv) no error in the catch numbers-at-age.

Input data were:

Catch numbers at age

$C_{a,t}$  where  $a = 2$  to  $12$  and  $t = 1959$  to  $1998$ ,

Canadian Research Vessel survey estimates of mean numbers per tow-at-age (Campelen or Campelen equivalent values)

$RV1_{a,t}$  where  $a = 2$  to  $10$  and  $t = 1984$  to  $1998$ , spring

$RV2_{a,t}$  where  $a = 2$  to  $10$  and  $t = 1990$  to  $1998$ , fall

and Canadian juvenile Research Vessel survey estimates of mean numbers per tow-at-age (Yankee 41.5 shrimp trawl in August – September)

$RV3_{a,t}$  where  $a = 2$  to  $10$  and  $t = 1989$  to  $1994$ .

The objective function that was minimized is

$$SS = \sum_{s,a,t} (\ln(RV_{s,at}) - \ln(q_{s,a} N_{a,t}))^2$$

where  $s =$  Survey 1 to 3,  $a =$  age 2 to 10,  $t =$  year of survey.

The SPA estimates from the most recent assessment (Bratley et al. 1999) were used for 3Ps cod. QLSPA (Cadigan 1998) was adopted as the SPA approach in this assessment. The cohort model was run over ages 2-14 for 1959-1999(May). The commercial catch at age 14 in 1959 was taken to be 1000 tonnes. Population numbers at age 14 were derived using constraints on the fishing mortalities. For 1959-1993 F at age 14 was estimated as  $\gamma_1$  times the average F at ages 11-13. The  $\gamma_1$  parameter was estimated. This parameter was constrained to

be equal in all years between 1959 and 1993 for simplicity, and because the gear composition was relatively stable prior to the fishing moratorium in 1993. After 1993 the gear composition changed substantially, with gillnets being the dominant gear used in 3Ps. F constraints could not be used to derive numbers at age 14 in 1994-97 because the catches at age 14 were zero in these years. This problem was overcome by approximating 1993 population numbers at ages 10-13 using F constraints, and then projecting these numbers forward to age 14 in 1994-1997. The F-constraints were of the form  $F_a = \gamma_a \text{ave}(F_{a-1:a-3})$  that is, F's at ages 10-13 in 1993 were estimated as an unknown parameter times the average F at the previous three ages. F's at age 14 in 1998 and 1999 were estimated as unknown parameters times the average F at ages 11-13. Different  $\gamma$  parameters in 1998 and 1999 were estimated than in 1959-1993 because of the known change in the gear composition of the commercial fishery. In the end seven  $\gamma$  parameters were estimated to give the population numbers at age 14 throughout 1959-1999. Age 2 Engel indices were given no weight in estimation. Catchabilities at ages 13 and 14 were assumed to be equal, but different in the winter and spring. Catchability for the Engel and Campelen gears at ages 13-14 were also assumed to be different. Sentinel gillnet indices for age= 3 to 10 and year=1995 to 1998 were used and assumed to be proportional to numbers at age.

Female maturity data were collected during research vessel surveys from 1960-95 (Table 1). Stratified random surveys were used where possible (1978-94 2J3KL cod, 1971-95 3LNO American plaice and 3NO cod, 1972-95 3Ps cod). Data from earlier years came from surveys that were conducted mainly as line transects. The coverage of a stock area would generally not be as complete as the stratified random surveys. For 3LNO American plaice and 3NO cod, spring survey information was used. For 2J3KL cod, data came from the fall. For 3Ps cod the timing of the surveys varied from February to June but most of the data came from the spring. For the period of the stratified random surveys, observed proportion mature at age was calculated according to the method of Morgan and Hoenig (1997) to account for the length stratified method of sampling. Prior to this, only data from the aged fish was used without weighting by the length frequencies. This should not have a large impact on the model estimates (Morgan and Hoenig 1997).

Maturities were modelled by cohort using the following generalized linear model with a logit link function and binomial error (McCullagh and Nelder, 1983; SAS Inst. Inc., 1993):

$$pmat = \log\left(\frac{u}{1-u}\right)$$

where:  $pmat$ = proportion mature at age or length

$$u = \tau + \delta_j v_i + \beta_j$$

$\tau$  = intercept

$v_i$  = age  $i$

$\delta_j$  = combined age\*cohort effect for cohort  $j$

$\beta_j$  = cohort effect

Before a cohort was included in the model it was first tested separately to ensure that there were sufficient data to which to fit a model. Only cohorts with both a significant slope and a significant intercept were included in the overall model. For 2J3KL cod the 1961, 63, 68 and 70 cohorts were excluded, and for 3Ps cod the 1963 cohort was excluded. For excluded cohorts the average of the two adjacent cohorts was used in the calculation of SSB. Age at 50% maturity was calculated for each cohort to examine the maturity data for trends.

Maturities are generally incorrectly modelled by year rather than by cohort as done here. The form of the model used in these analyses allows the cohorts to mature earlier or later as well as at a faster or slower rate. Modelling the maturities in this way also allows the production of a longer time series of maturity data and allows the proper calculation of the proportion of first time spawners in each year.

Spawning stock biomass was calculated in the standard manner as

$$\sum_{a=b}^n B_a P_a$$

where:

$B_a$  is the biomass at age from the SPA

$P_a$  is the female proportion mature at age

$b$  and  $n$  are the first and last age included in the SPA

The time series of SSB and recruitment were plotted along with trends in recruits/SSB.

Three characteristics of SSB were examined; the weighted mean age of the SSB, the proportion of first time spawners and the proportion of females in the mature population. The weighted mean age of the SSB (referred to hereafter as mean age) was calculated as:

$$\frac{\sum_{a=b}^n B_a P_a a}{SSB}$$

where  $a$ =age and the other terms are as defined above. The proportion of first time spawners in the spawning stock biomass was calculated by determining for each cohort in each year the proportion of first time spawners. For example if 10% of the fish at age 4 of a cohort are mature and in the next year 20% of the age 5 fish of that cohort are mature then one-half of the age 5 fish in that year are first time spawners. Then for each year the proportion of

first time spawners in the SSB was:  $\frac{\sum_{a=b}^n B_a P_a Pfirst_a}{SSB}$  where  $Pfirst_a$  is the proportion of first

time spawners at age and the other terms are as defined above. The proportion female in the mature population was calculated from the stratified random survey data. Survey estimates of the mature population numbers at age by sex were produced and from these, estimates of the proportion of the mature survey population that was female was calculated. Time series of these three characteristics were plotted for each stock.

For each stock we fit a Beverton-Holt stock-recruit model using maximum likelihood fitting as described in Myers et al. (1995) and as applied in Shelton and Healey (1999). The residuals from these fits were then plotted against the characteristics of the SSB to look for relationships.

## Results

Age at 50% maturity for the females from the four stocks is shown in Figure 1. There has been a substantial decrease in  $A_{50}$  over the time period for all four stocks but the extent of the decline and the time period varied among stocks. The decline began earliest in 3LNO American plaice, starting at least with the cohorts of the early 1970's. 3NO cod has shown a smaller decrease in  $A_{50}$  than 2J3KL or 3Ps cod. Similar declines are seen for these stocks when the maturities are calculated annually (Brodie et al., 1994; Bratney et al., 1999; Lilly et al., 1999; Stansbury et al., 1999).

Trends in recruitment and SSB are shown in Figure 2. For all stocks recruitment has declined in recent years and SSB is low for all but 3Ps cod. The most recent time period has seen below average recruits/SSB ( $r/s$ ) for all stocks (Fig. 3). For 3LNO American plaice  $r/s$  was below average during the mid-1960's and from 1985-92. For 2J3KL cod  $r/s$  was below average in the late 1960's and early 1970's and has been below average since 1983 except for the 1986 and 1987 year classes. An examination of the  $r/s$  plot for the SPA for 2J3KL cod without the correction for missing fish shows a very similar pattern except that the 1986 and 1987 year classes are below average. 3NO cod exhibits perhaps the most persistent 'recruitment dilemma' with  $r/s$  having been below average since 1981. 3Ps cod has been more variable in recent years but has also had below average  $r/s$  since 1983 except for the 1989 and 1994 year classes. All of the stocks show other periods of below average  $r/s$  but this is particularly clear for 3LNO American plaice and 2J3KL cod.

Figure 4 shows the Beverton-Holt fits to the data for the 4 stocks. The model provides the poorest description of the data for 3NO cod. For all stocks it would appear that we have been on the ascending limb of the relationship for the duration of the time series. In other words, the compensatory period was traversed during stock declines before the commencement of commercial catch at age data series. The time series of residuals from these relationships show much the same pattern as the plots of  $r/s$  (Fig. 5).

Weighted mean age of the SSB, proportion of first time spawners and proportion female all show substantial variation over the time period (Fig. 6-8). Mean age has declined substantially in 3LNO American plaice, 2J3KL cod and 3Ps cod as a result of a decrease in the abundance of older age classes and maturity at a younger age. 3NO cod has not shown the same trend probably because of such an extended period of lack of recruitment to the SSB. The proportion of first time spawners has shown an increase in recent years in all stocks but has only reached very high levels in 2J3KL cod. The proportion female is available for only part of the time series. For all stocks the proportion of the mature population which is female is generally greater than 0.5. After a period of decrease there has been a large increase in the proportion



female in 3LNO American plaice and 3NO cod in recent years but the proportion female remained below average for these 2 stocks until the last 2 to 3 years of the time series.

Scatter matrices for recruitment, SSB and the characteristics of the SSB are given in Figures 9-12 and show that these are not necessarily independent. For all stocks the proportion of first time spawners generally decreases as mean age increases and shows some tendency to decrease as SSB increases. For all but 3NO cod mean age increases as SSB increases. The proportion female tends to decrease as SSB increases.

The residuals from the Beverton-Holt fits for each stock were plotted against mean age, proportion of first time spawners and proportion female. The residuals show a tendency to increase with mean age of the SSB for 3LNO American plaice and 2J3KL cod, indicating that recruitment is over estimated when mean age is low (Fig. 13). However the opposite pattern was seen for 3NO cod. The residuals tend to increase with proportion first time spawners for 3NO cod and perhaps 3LNO American plaice and 3Ps cod, indicating that recruitment is over estimated when the proportion of first time spawners is low (Fig. 14). For 3LNO American plaice, 3NO and 3Ps cod there is a tendency for the residuals from the Beverton-Holt fits to increase as proportion female increases indicating that recruitment is under estimated when proportion female is high (Fig. 15).

## **Discussion**

Weighted mean age of the SSB seemed to explain some of the pattern in the residuals from the Beverton-Holt stock-recruit relationships for 3LNO American plaice and perhaps 2J3KL cod. For these stocks there was a tendency for recruitment to be over estimated when mean age was low. Age composition of the SSB has previously been shown to be important to recruitment (Lambert 1990; Marteinsdottir and Thorarinnsson 1998). An SSB composed of older fish or a broader age range of fish may result in a longer time span of spawning (Hutchings and Myers 1993; Trippel and Morgan 1994). Older, larger fish also produce more viable eggs and larvae (Solemdal et al. 1995; Kjesbu et al. 1996; Trippel 1998; Marteinsdottir and Steinarsson 1998). This should mean that for a given weight of SSB, a spawning stock composed of fish of a lower mean age will, on average, produce fewer recruits. In this study, one stock (3NO cod) showed the opposite pattern and as yet there is no explanation for this.

Proportion of first time spawners in the SSB showed a positive relationship with the residuals from the fitted stock-recruit relationship for 3NO cod and perhaps 3LNO American plaice and 3Ps cod. The increase in residuals as proportion of first time spawners increased indicates that SSB's with a higher proportion of first time spawners produce more recruits than expected. This is a surprising result given studies that have shown that repeat spawners are more successful than first time spawners (Trippel, 1998; Solemdal et al., 1995).

The proportion of the mature population that was female seemed to have the strongest relationship with the residuals from the stock-recruit fit, showing a positive relationship for 3 of 4 stocks (3LNO American plaice, 3NO and 3Ps cod). Currently SSB's do not take the proportion female into account. If the proportion female varies then when it is greater than

average our estimate of SSB will be an under estimate and observed recruitment will be higher than expected because of this under estimate of SSB. (This assumes that there are always a sufficient number of males to fertilize the females). This appears to be the case for these three stocks. A variable sex ratio in the mature portion of the SSB has also been found for northeast Arctic cod (Marshall et al. 1998;Jakobsen and Ajiad 1999).

All characteristics of the SSB showed some relationship with the residuals from the stock-recruit fits. However none showed a consistent relationship across all stocks. This may indicate that the important factors vary with population. It is also not clear what the functional relationship of these characteristics should be to recruitment. As well, the correlation of these characteristics with each other and with SSB complicate any exploration of effects or attempts to ascribe functional relationships. For all stocks the proportion of first time spawners generally decreases as mean age increases and shows some tendency to decrease as SSB increases. For all but 3NO cod mean age increased as SSB increased. These relationships are probably related to the decrease in the abundance of older repeat spawning age classes as SSB decreases and maturation at a younger age as population size declines. The proportion female tended to increase as SSB decreased possibly indicating differential mortality on the sexes, a phenomenon described for northeast Arctic cod (Jakobsen and Ajiad, 1999). Such covariance of characteristics of the SSB make it difficult to treat them as separate factors.

These analyses depend on population estimates from SPAs. Each model has a different formulation and like all SPAs are subject to errors in catch at age. The likelihood of misreported/unreported catch may vary across stocks and across time within a stock leading to errors in population numbers and so SSB and recruitment. This may obscure some of the underlying stock-recruit relationships. Note that the 2J3KL SPA fit requires, as one alternative, a substantial increase in unreported deaths, probably primarily due to fishing activity (dumping, discarding and under-reporting). As well, the 3LNO American plaice SPA includes a change in natural mortality for a portion of the time period.

Condition of the fish is an important characteristic of the SSB which has not been examined in these analyses. Part of the reason is that it is difficult to estimate yearly average condition because of possible within-year variation in condition cycles and because surveys are not always conducted at the appropriate time relative to the condition cycle of the fish. Fish in poor condition are thought to be spawners of lesser quality than those in good condition (Burton and Idler 1984;Kjesbu et al. 1991;Burton et al. 1997;Marshall et al. 1998;Marteinsdottir and Steinarsson 1998). This factor will therefore likely affect recruitment and will likely interact with the characteristics of the SSB examined here. All of these factors deserve further study as does the appropriate means of dealing with the effect of SSB characteristics on recruitment. There are at least two possible approaches; one is to alter the measure of SSB and the other is to include the effects in a stock-recruit model. Which approach is more appropriate is not apparent at this time.

## References

- Bishop, C.A., Murphy, E.F., Davis, M.B., Baird, J.W. and Rose, G.A. 1993. An assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR. Doc. 93/86, 51pp.
- Bishop, C.A., Anderson, J., Dalley, E., Davis, M.B., Murphy, E.F., Rose, G.A., Stansbury, D.E., Taggart, C., Winters, G. and Methven D. 1994. An assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR Doc. 94/40, 50pp.
- Brattey, J., Cadigan, N.G., Lilly, G.R., Murphy, E.F., Shelton, P.A., and Stansbury, D.E. 1999. An assessment of the cod stock in NAFO Subdivision 3Ps in October 1999. Canadian Stock Assessment Secretariat Res. Doc. 99/161, xxp.
- Brodie, W.B., Morgan, M.J., and Power, D. 1994. An assessment of the American plaice stock in Divisions 3LNO. NAFO SCR Doc., 94/55, 43pp.
- Brodie, W.B., Power, D., and Morgan, M.J. 1993. An assessment of the American plaice stock in NAFO Divisions 3LNO. NAFO SCR Doc., 93/91, 60pp.
- Burton, M.P. and Idler, D.R. 1984. The reproductive cycle in winter flounder, *Pseudopleuronectes americanus* (Walbaum). Can. J. Zool. **62**: 2563-2567.
- Burton, M.P.M., Penney, R.M., and Biddiscombe, S. 1997. Time course of gametogenesis in Northwest Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 122-131.
- Cadigan, N. 1998. Semi-parametric inferences about fish stock size using sequential population analysis (SPA) and quasi-likelihood theory. DFO Can. Stock Assess. Sec. Res. Doc. 98/25.
- Hutchings, J.A. and Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2468-2474.
- Jakobsen, T. and Ajiad, A. 1999. Management implications of sexual difference in maturation and spawning mortality of northeast Arctic cod. J. Northw. Atl. Fish. Sci. **25**: 125-131.
- Kjesbu, O.S., Klungsoyr, J., Kryvi, H., Whitthames, P.R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. **48**: 2333-2343.
- Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **53**: 610-620.
- Lambert, T.C. 1990. The effect of population structure on recruitment in herring. J. Cons. int. Explor. Mer. **47**: 249-255.

- Lilly, G.R., Shelton, P.A., Brattey, J., Cadigan, N., Murphy, E.F., and Stansbury, D.E. 1999. An assessment of the cod stock in NAFO Divisions 2J+3KL. Canadian Stock Assessment Secretariat Res. Doc. 99/42, 165pp.
- Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, O. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Can. J. Fish. Aquat. Sci.* **55**: 1766-1783.
- Marteinsdottir, G. and Steinarsson, A. 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *J. Fish Biol.* **52**: 1241-1258.
- Marteinsdottir, G. and Thorarinsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Can. J. Fish. Aquat. Sci.* **55**: 1372-1377.
- McCullagh, P. and Nelder, J.A. 1983. Generalized linear models. Chapman and Hall, London, 261 pp.
- Morgan, M.J. and Hoenig, J.M. 1997. Estimating maturity-at-age from length stratified sampling. *J. Northw. Atl. Fish. Sci.* **21**: 51-63.
- Morgan, M.J., Brodie, W.B., and Bowering, W.R. 1999. An assessment of American plaice in NAFO Divisions 3LNO. NAFO SCR Doc. 99/40, 55pp.
- Myers, R.A., Bridson, J., and Barrowman, N.J. 1995. Summary of worldwide stock and recruitment data. *Can. Tech. Rep. Fish. Aquat. Sci.* No.2024.
- SAS Institute Inc. 1993. SAS technical report P-243, SAS/STAT software: the genmod procedure, release 6.09. SAS Institute Inc., Cary, NC.
- Shelton, P.A. and Healey, B.P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Can. J. Fish. Aquat. Sci.* **56**: 1521-1524.
- Shelton, P.A. and Lilly, G.R. In Press. Interpreting the collapse of the northern cod stock from survey and catch data. *Can. J. Fish. Aquat. Sci.*
- Solemdal, P., Kjesbu, O.S., and Fonn, M. 1995. Egg mortality in recruit- and repeat-spawning cod - an experimental study. *ICES C.M.* **G:35**: 14pp.
- Stansbury, D.E., Shelton, P.A., Murphy, E.F., and Brattey, J. 1999. An assessment of the cod stock in NAFO Divisions 3NO. NAFO SCR Doc. 99/62, 47pp.
- Trippel, E.A. 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. *Trans. Amer. Fish. Soc.* **127**: 339-359.

Trippel,E.A. and Morgan,M.J. 1994. Age-specific paternal influences on reproductive success of Atlantic cod (*Gadus morhua* L.) of the Grand Banks, Newfoundland. ICES mar. Sci. Symp. **198**: 414-422.

Wigley,S.E. 1999a. Effects of first-time spawners on stock-recruitment relationships for two groundfish species. J. Northw. Atl. Fish. Sci **25**: 215-218.

Table 1. Details of data used.

Stock	Period of SPA	Age range of SPA	Tuning series	Catch at age	Age at recruitment	Last SSB used	Maturity data
3LNO A. plaice	1960-98	5-17	Spring 1985-98	5-17, 1975-98 <sup>1</sup>	5	1998	3L:65,67,69-82,84-95 3N:60-65,67-82,84-95 3O:61-65,68,73,75-82,84-95
2J3KL cod	1962-94	2-13	Fall 1978-94	2-13, 1962-94	2	1992	2J:63-64,71,76-94 3K:63-64,71,77-94 3L:65-67,69,72,76-77,81-94
3NO cod	1959-98	2-12	Spring 1984-98 Fall 1990-98 Juvenile 1989-94	2-12, 1959-98	3	1995	3N:60-62,65-82,84-95 3O:60-66,67,73-82,84-95
3Ps cod	1959-99	2-14	Winter-Spring 1983-99 Sentinel gillnet 1995-98	2-14, 1959-99	3	1995	3Ps:60,62-65,67,69,72-95

<sup>1</sup> 1960-74 are from SPA run in 1993

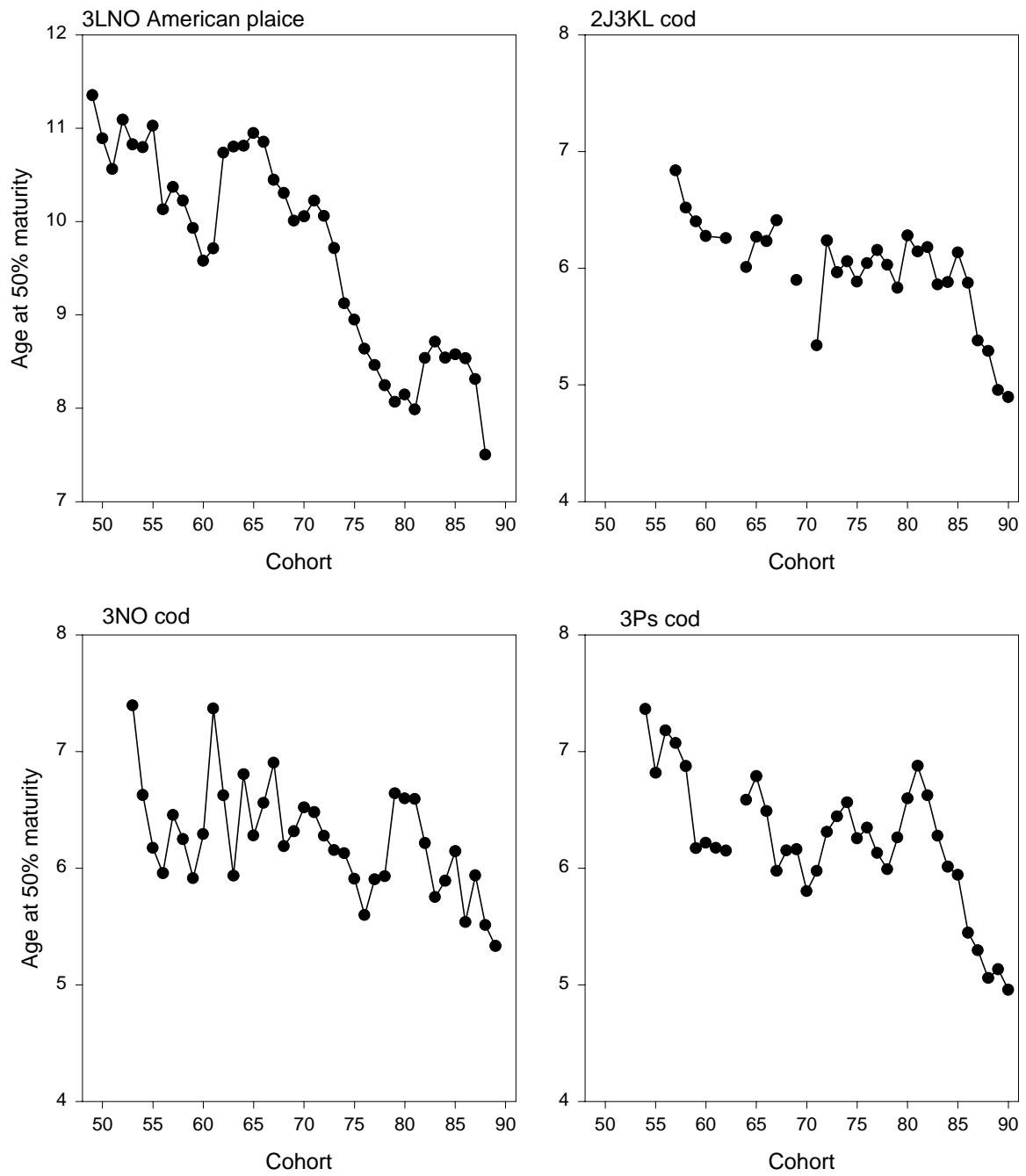


Figure 1. Age at 50% maturity for females from 4 Newfoundland groundfish stocks.

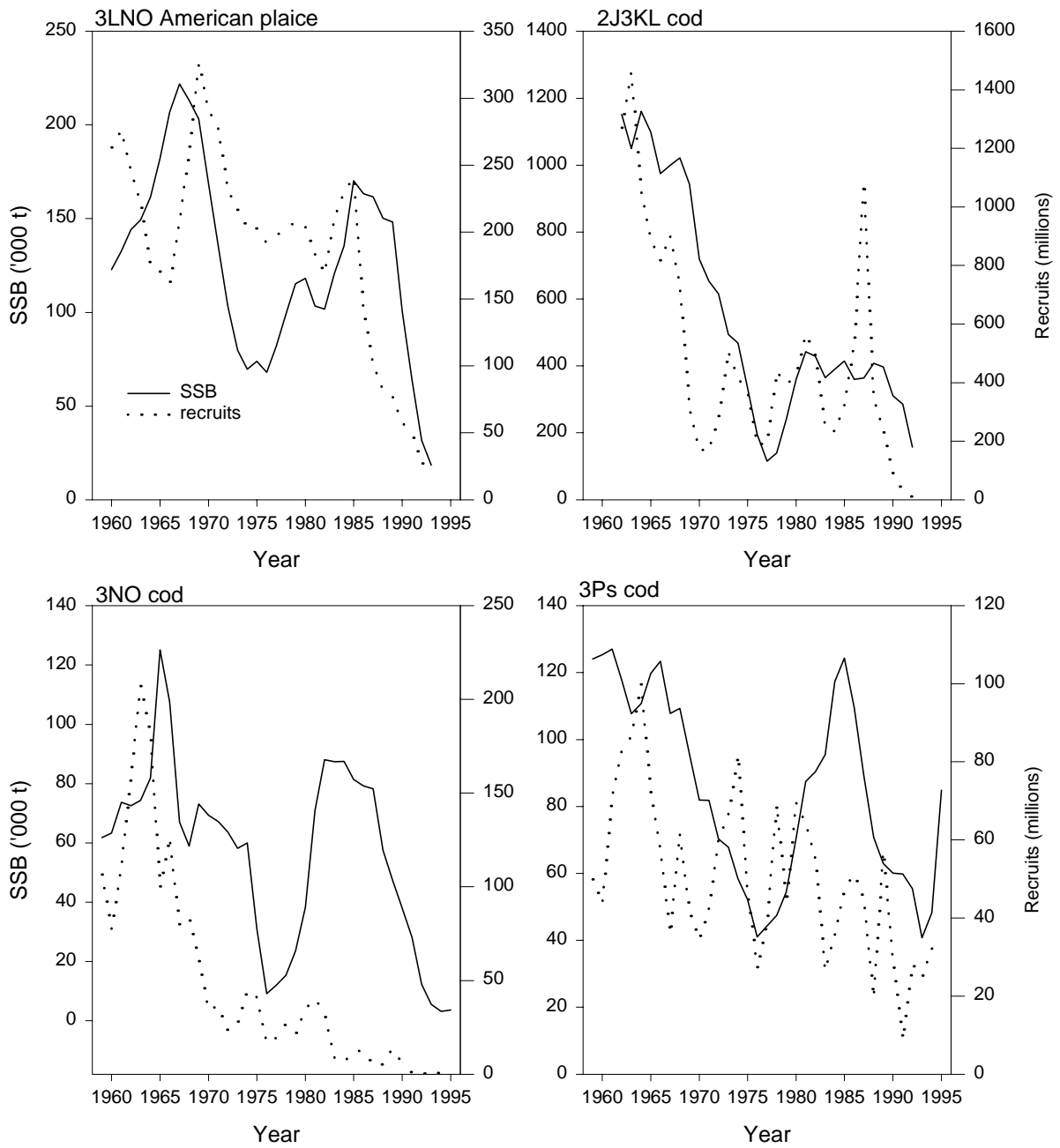


Figure 2. SSB ('000 t) and recruitment (millions of recruits see Table 1 for ages) for 4 Newfoundland groundfish stocks.



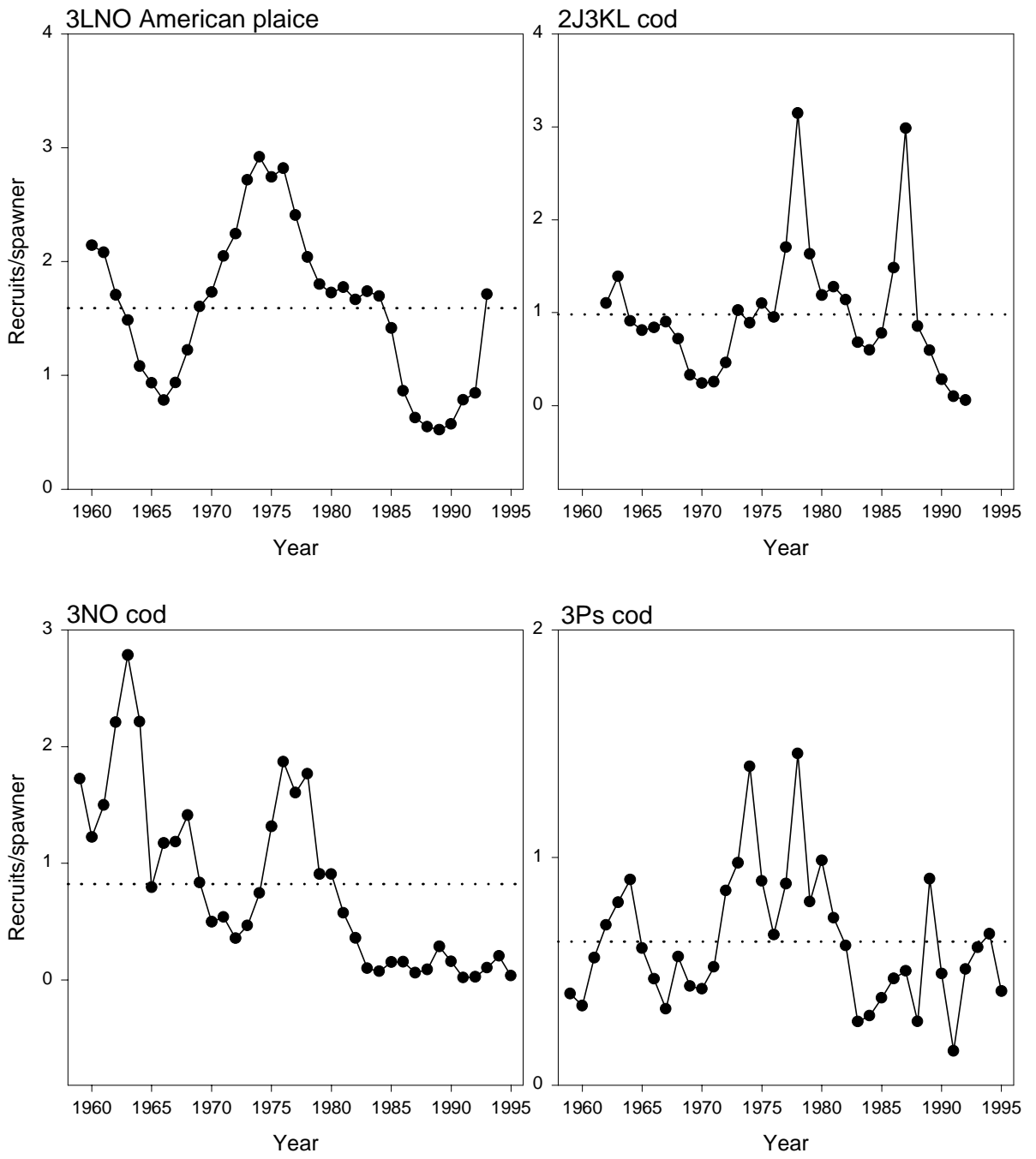


Figure 3. Recruits/spawner for 4 Newfoundland groundfish stocks. The dotted line shows the average.

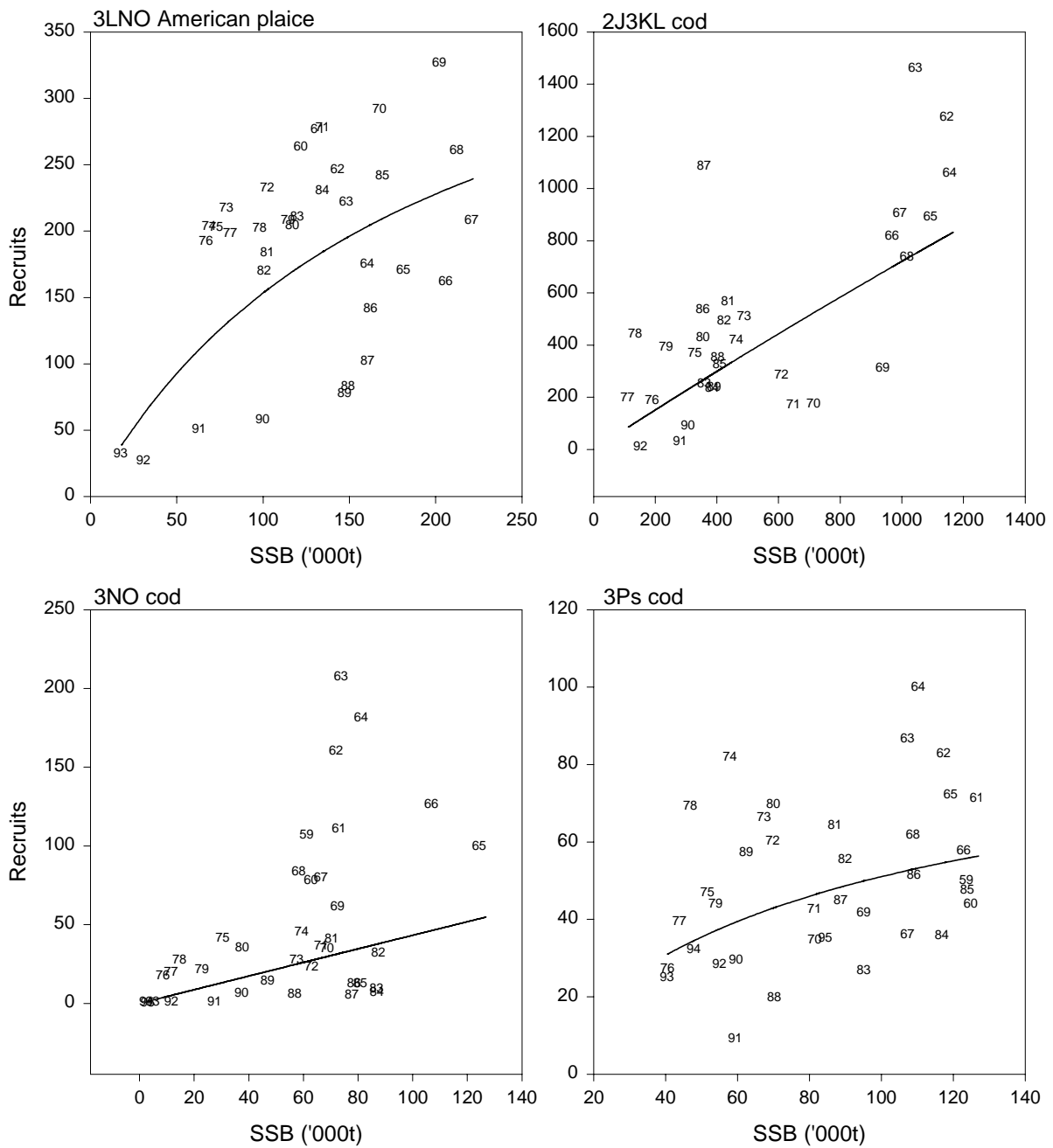


Figure 4. Predicted recruitment (line) from the Beverton-Holt stock recruit relationship as well as observed recruitment for 4 Newfoundland groundfish stocks. The numbers represent the cohorts.

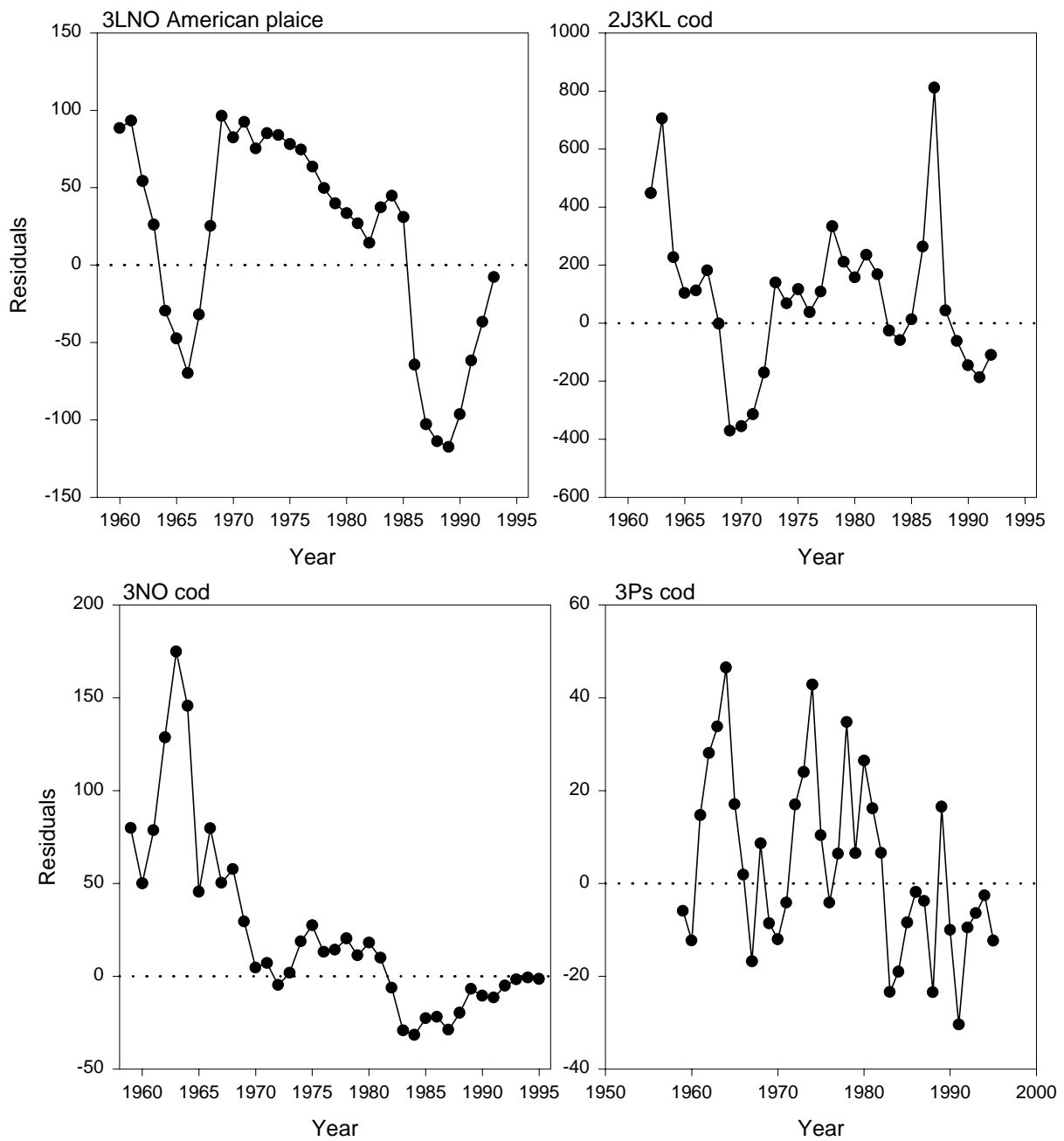


Figure 5. Residuals from Beverton-Holt stock recruit relationships for 4 Newfoundland groundfish stocks.

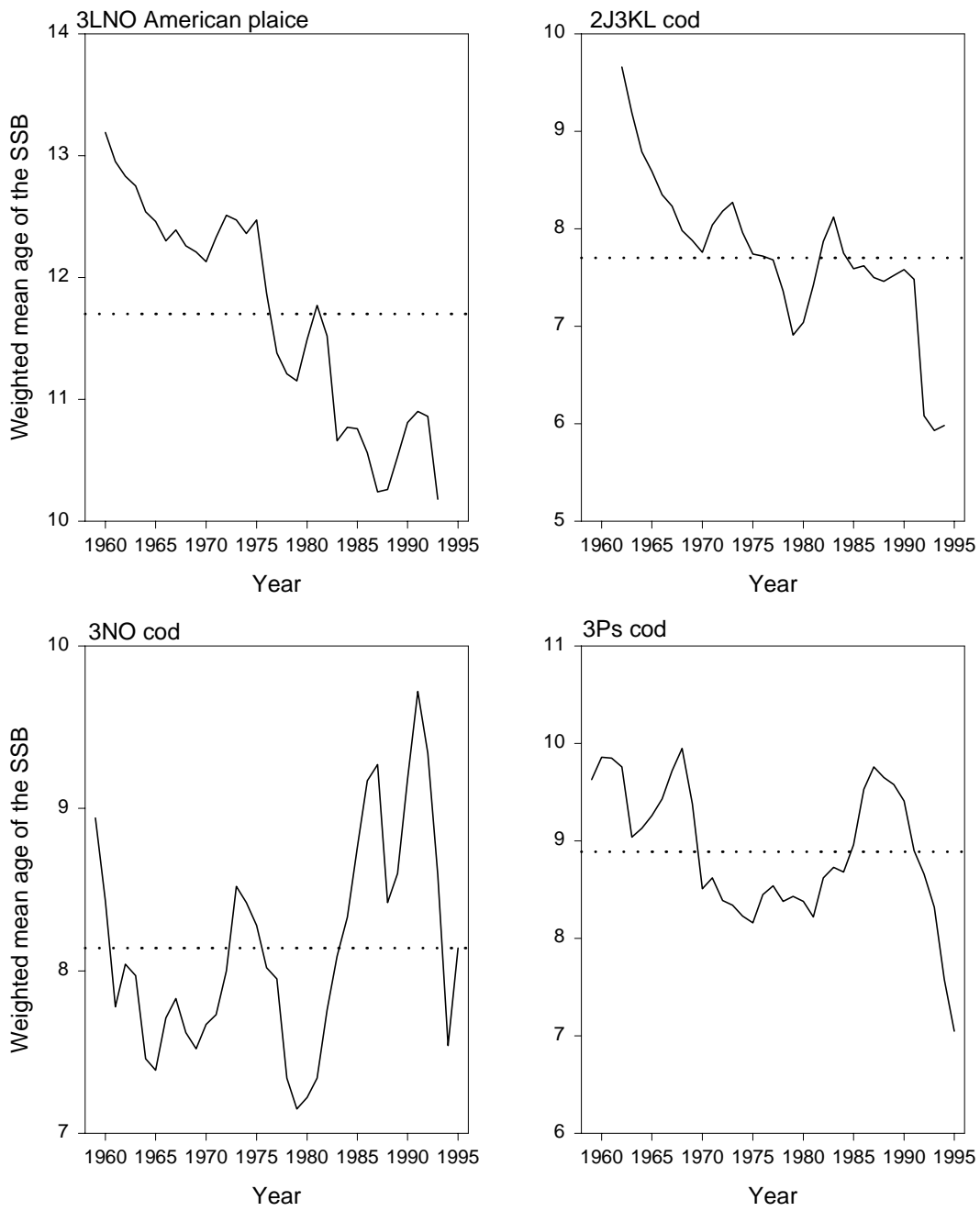


Figure 6. Weighted mean age of the SSB for 4 Newfoundland groundfish stocks. The dotted line shows the average.

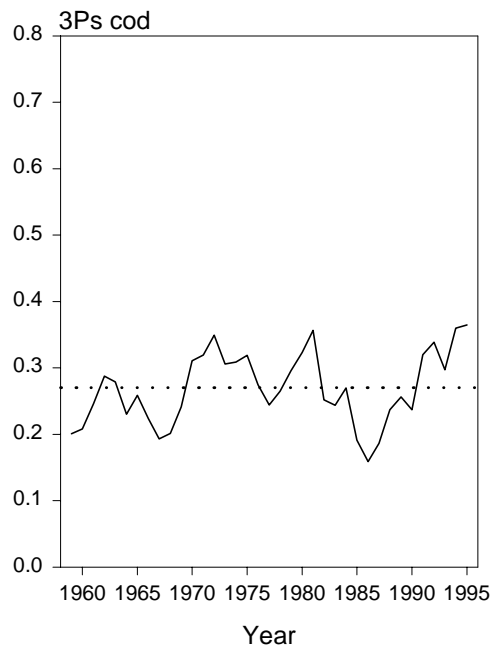
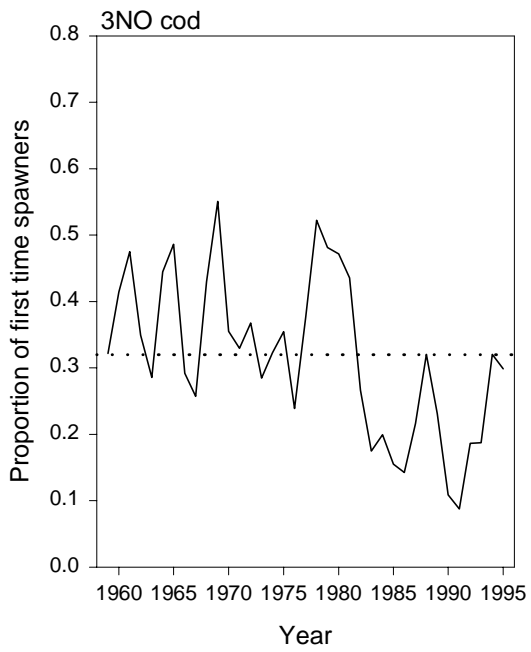
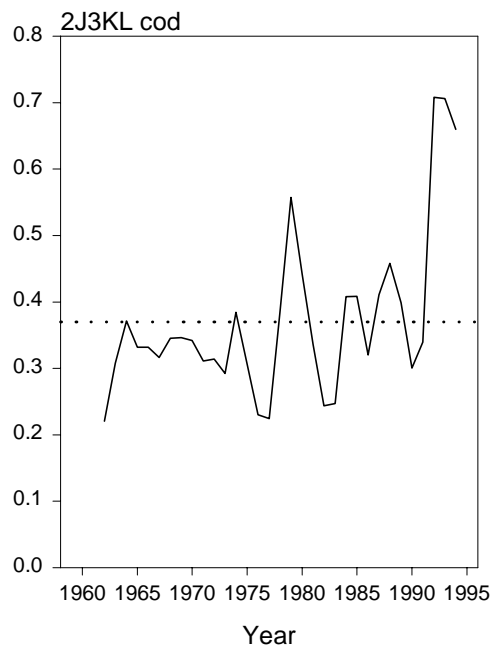
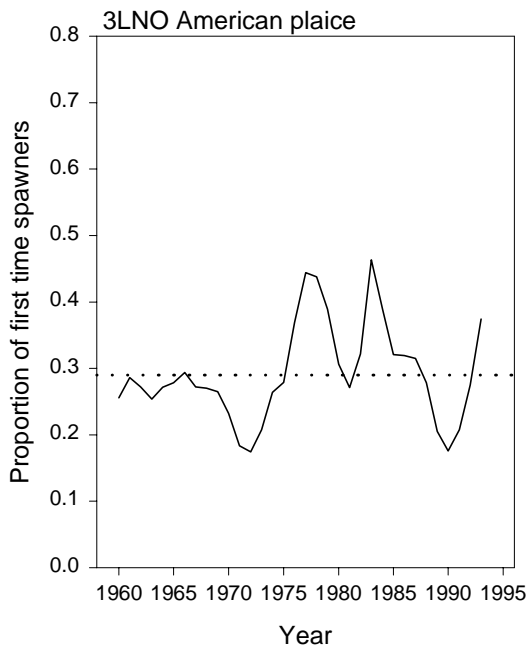


Figure 7. Proportion of first time spawners in the spawning stock biomass for 4 Newfoundland groundfish stocks. The dotted line shows the average.

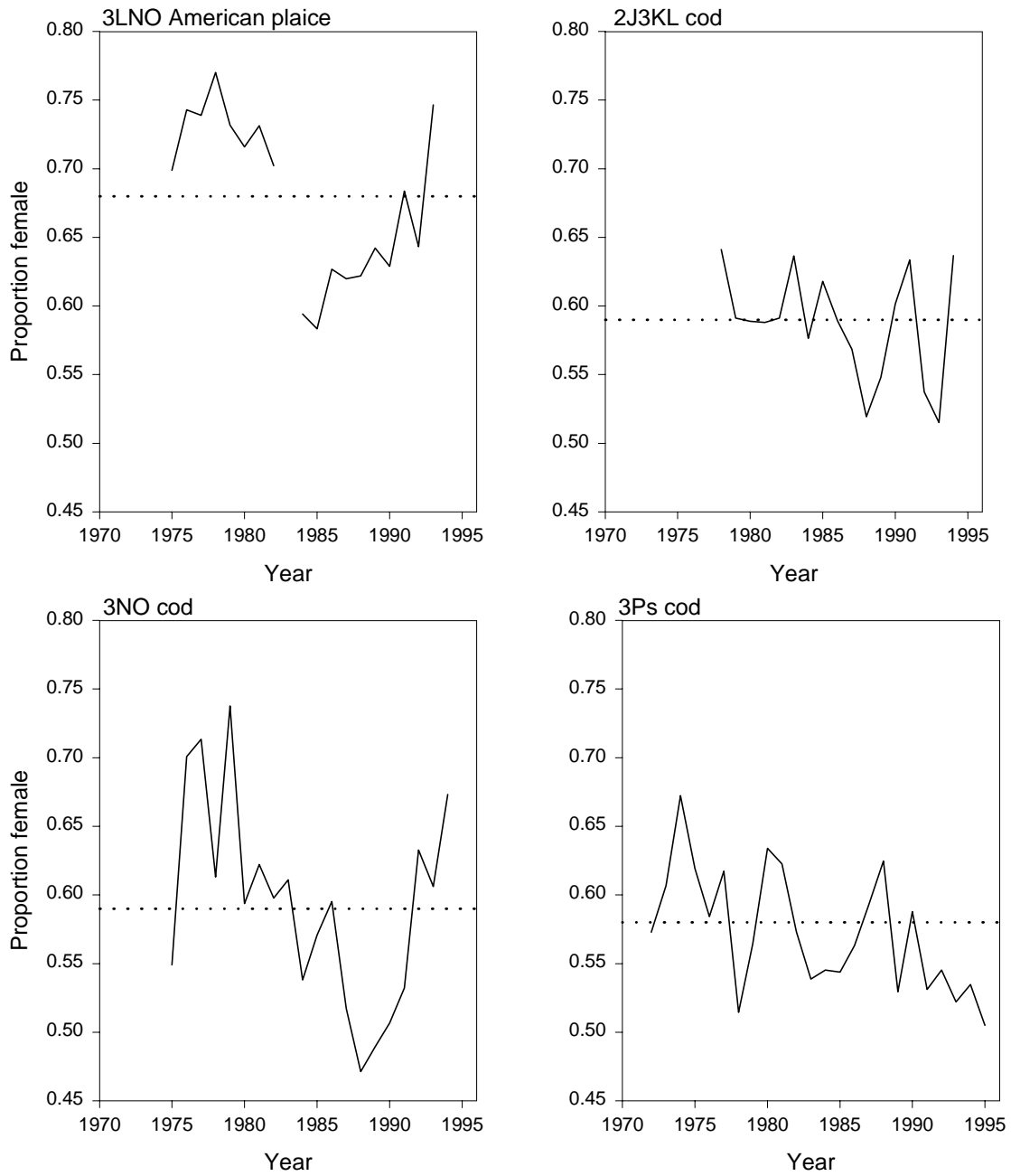


Figure 8. Proportion of the mature fish (by number) that are female as determined from rv surveys for 4 Newfoundland groundfish stocks. The dotted line shows the average.

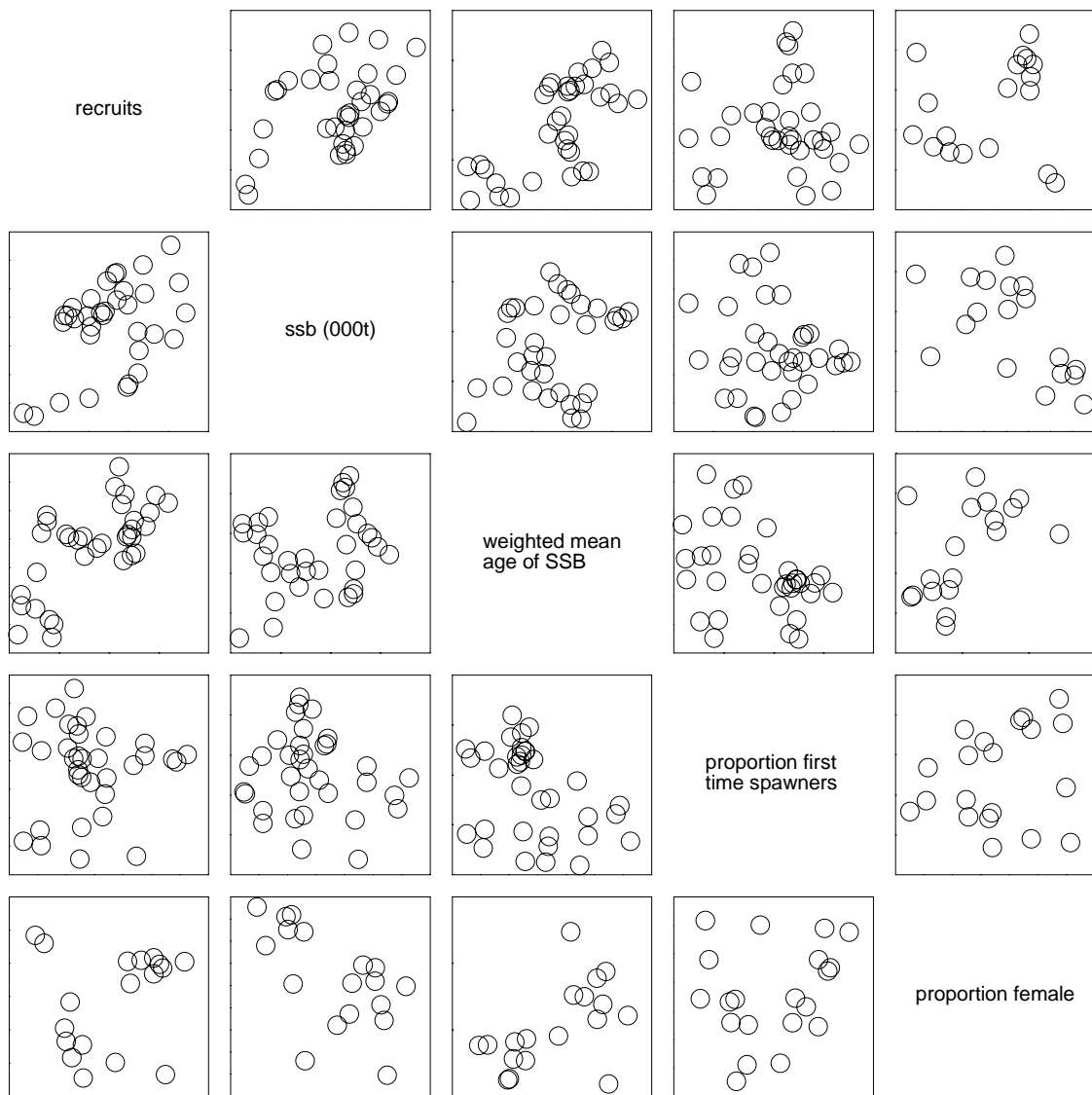


Figure 9. Scatter matrix of relationship between recruitment and various characteristics of the SSB for 3LNO American plaice

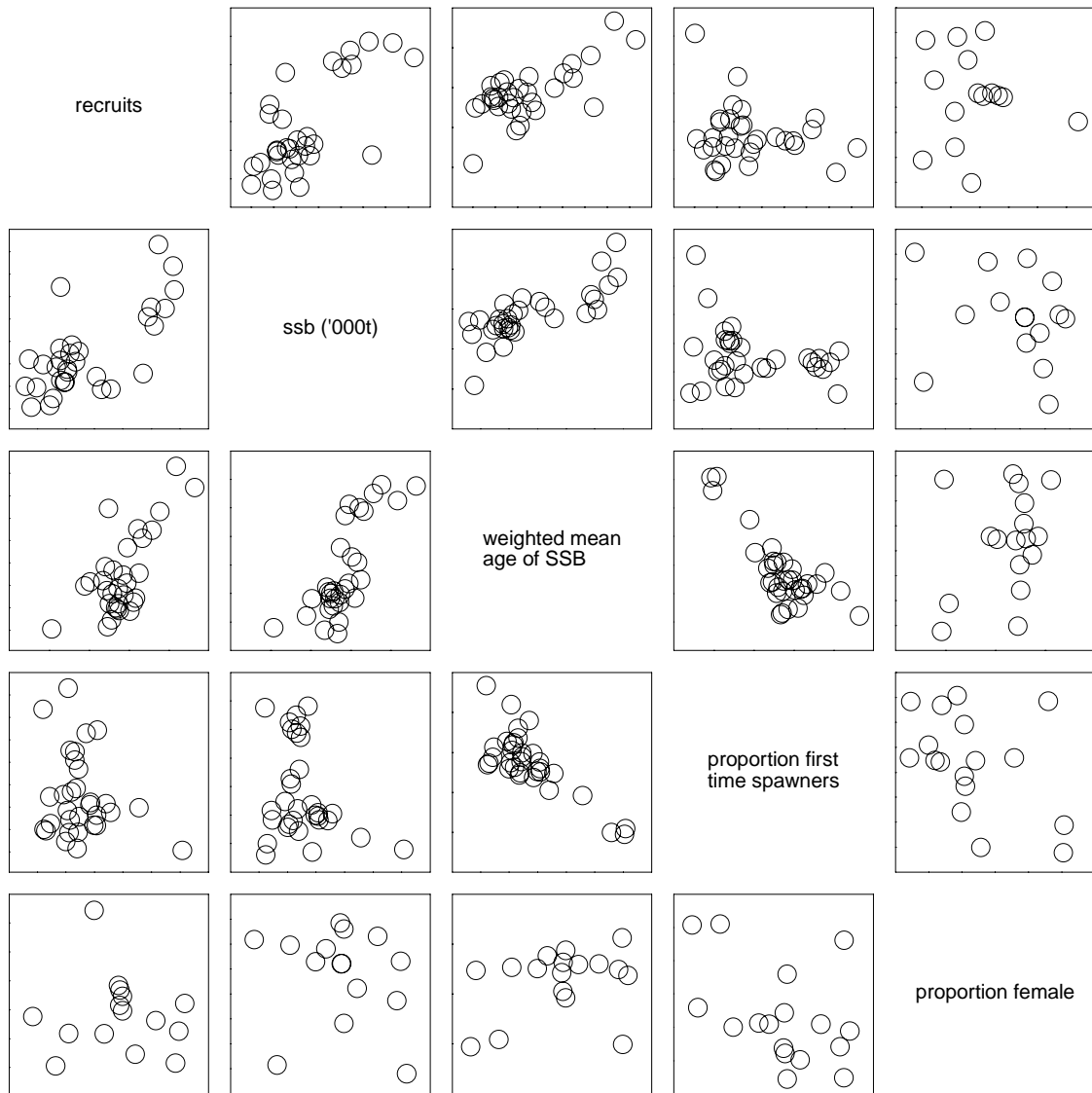


Figure 10. Scatter matrix of relationship between recruitment and various characteristics of the SSB for 2J3KL cod.



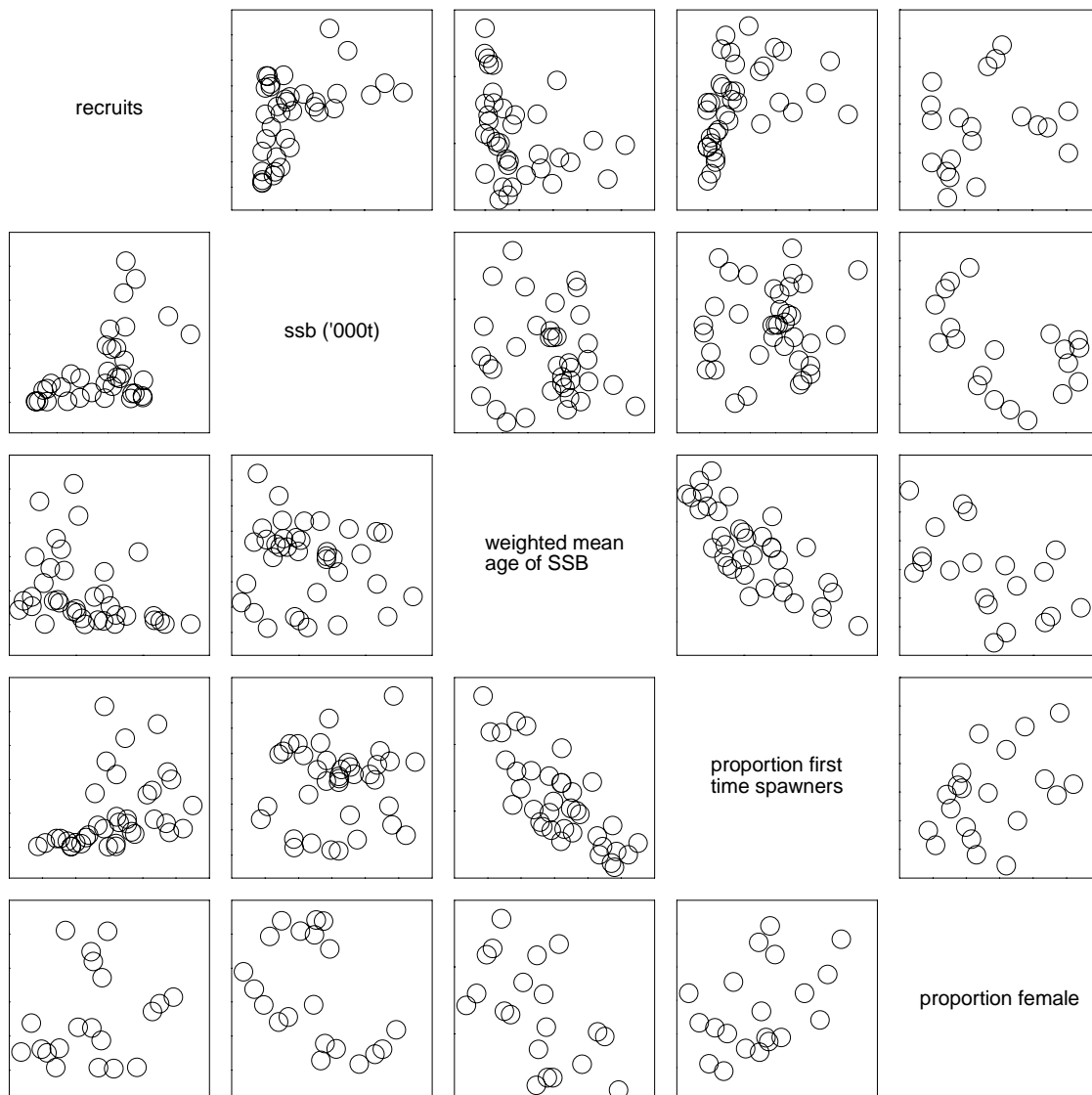


Figure 11. Scatter matrix of relationships between recruitment and various characteristics of the SSB for 3NO cod.

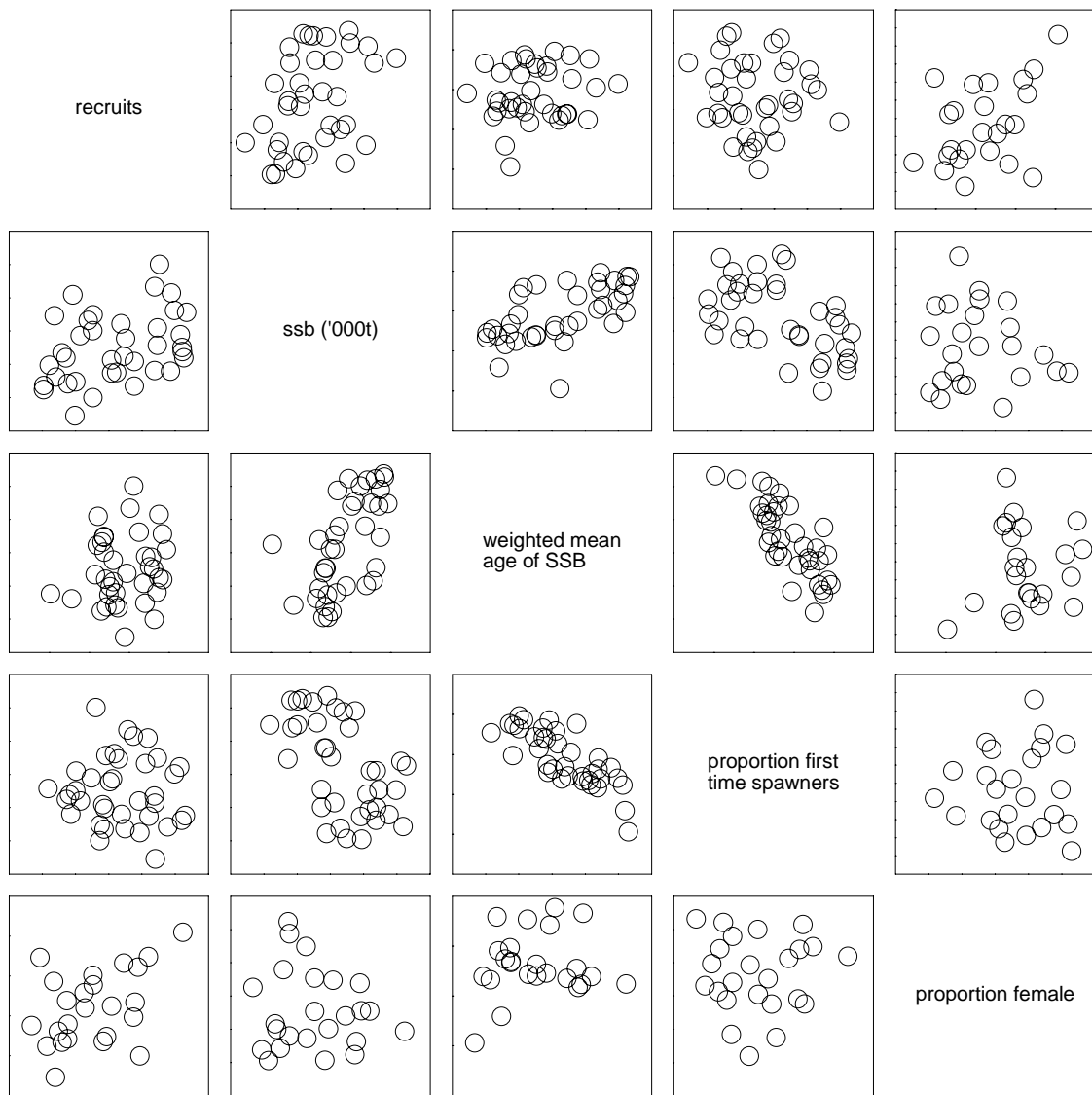


Figure 12. Scatter matrix of relationships between recruitment and various characteristics of the SSB for 3Ps cod.

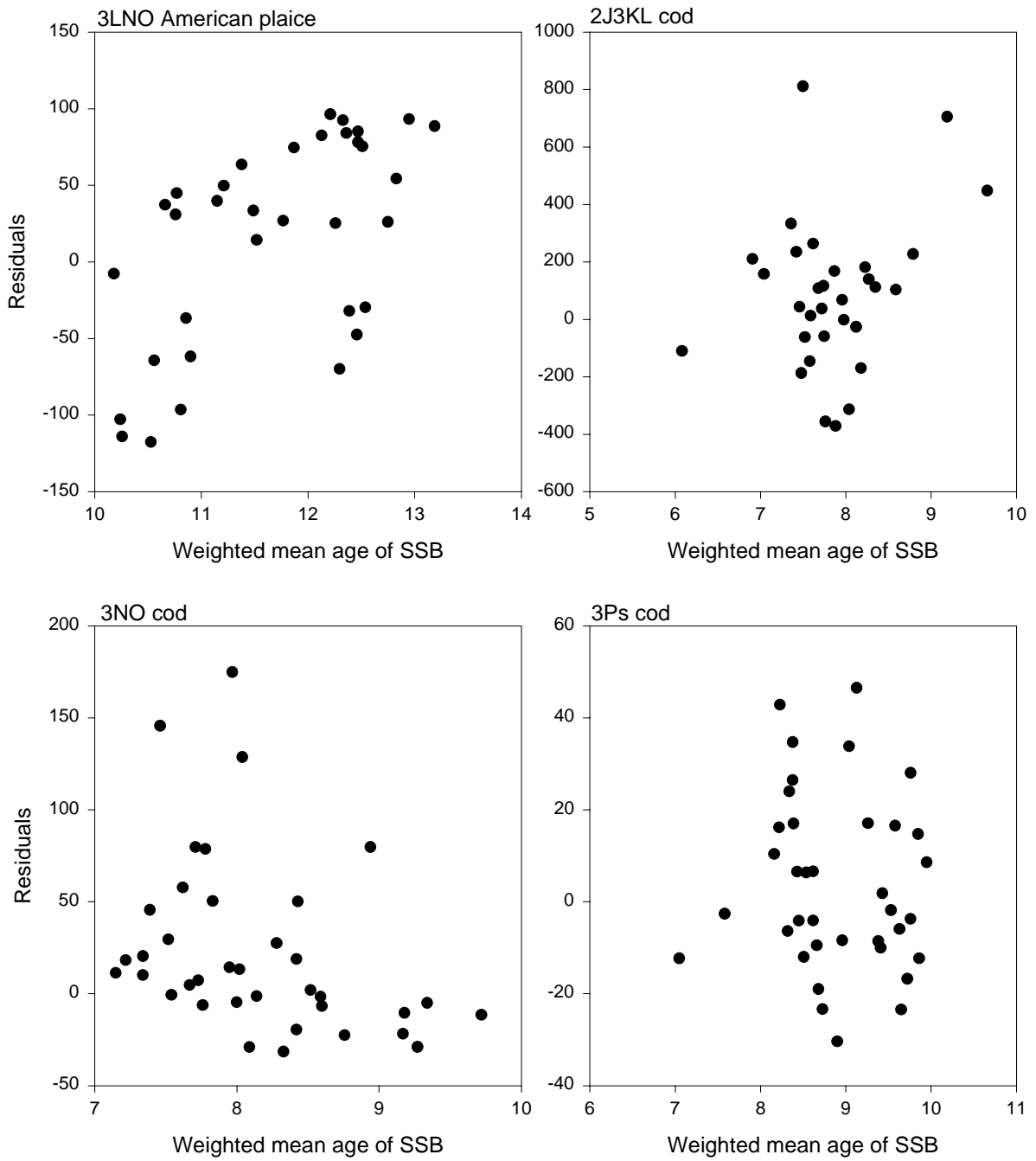


Figure 13. Residuals from Beverton-Holt stock recruit relationships vs weighted mean age of the SSB for 4 Newfoundland groundfish stocks.

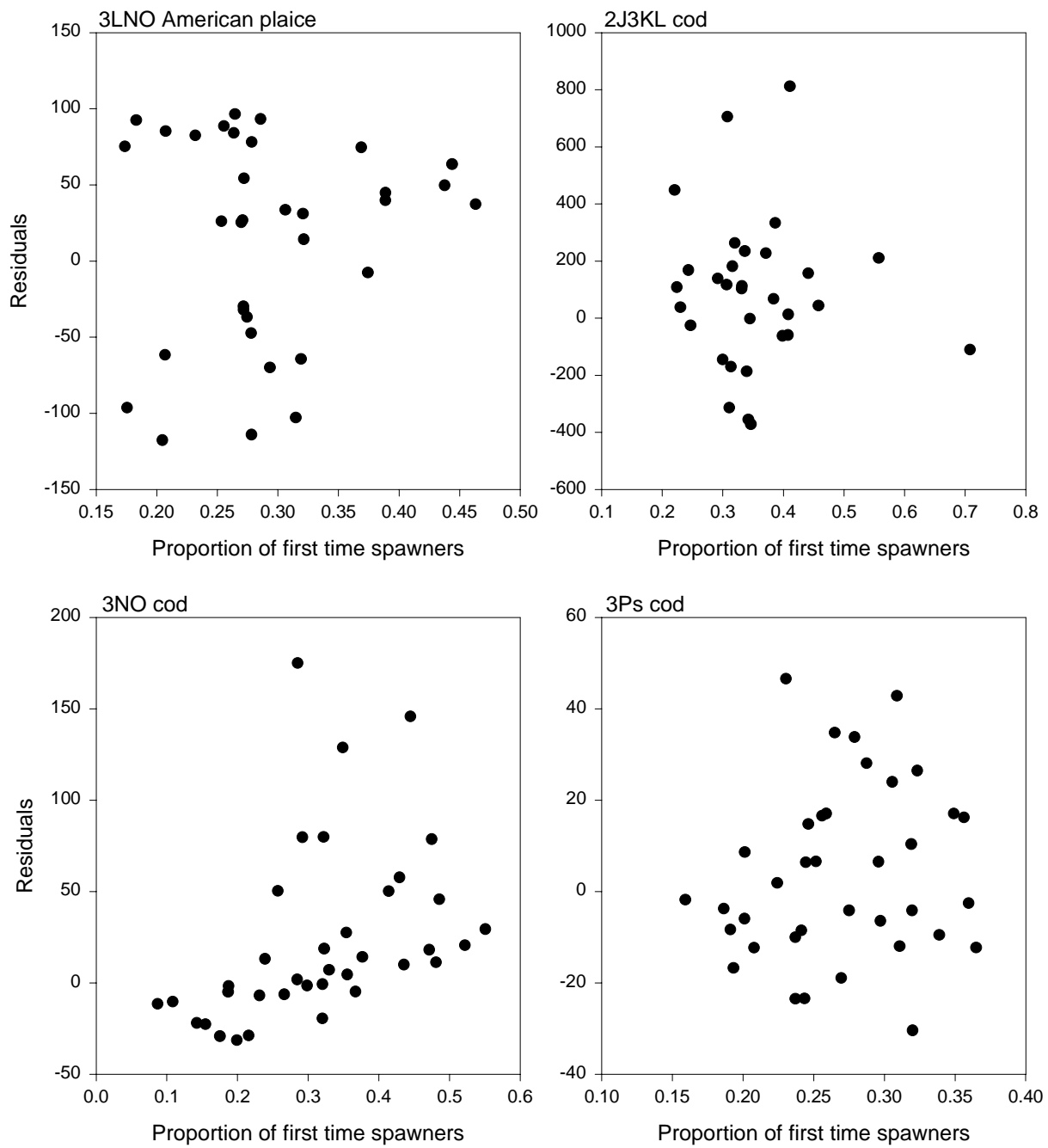


Figure 14. Residuals from Beverton-Holt stock recruit relationship vs proportion of first time spawners in the SSB for 4 Newfoundland groundfish stocks.

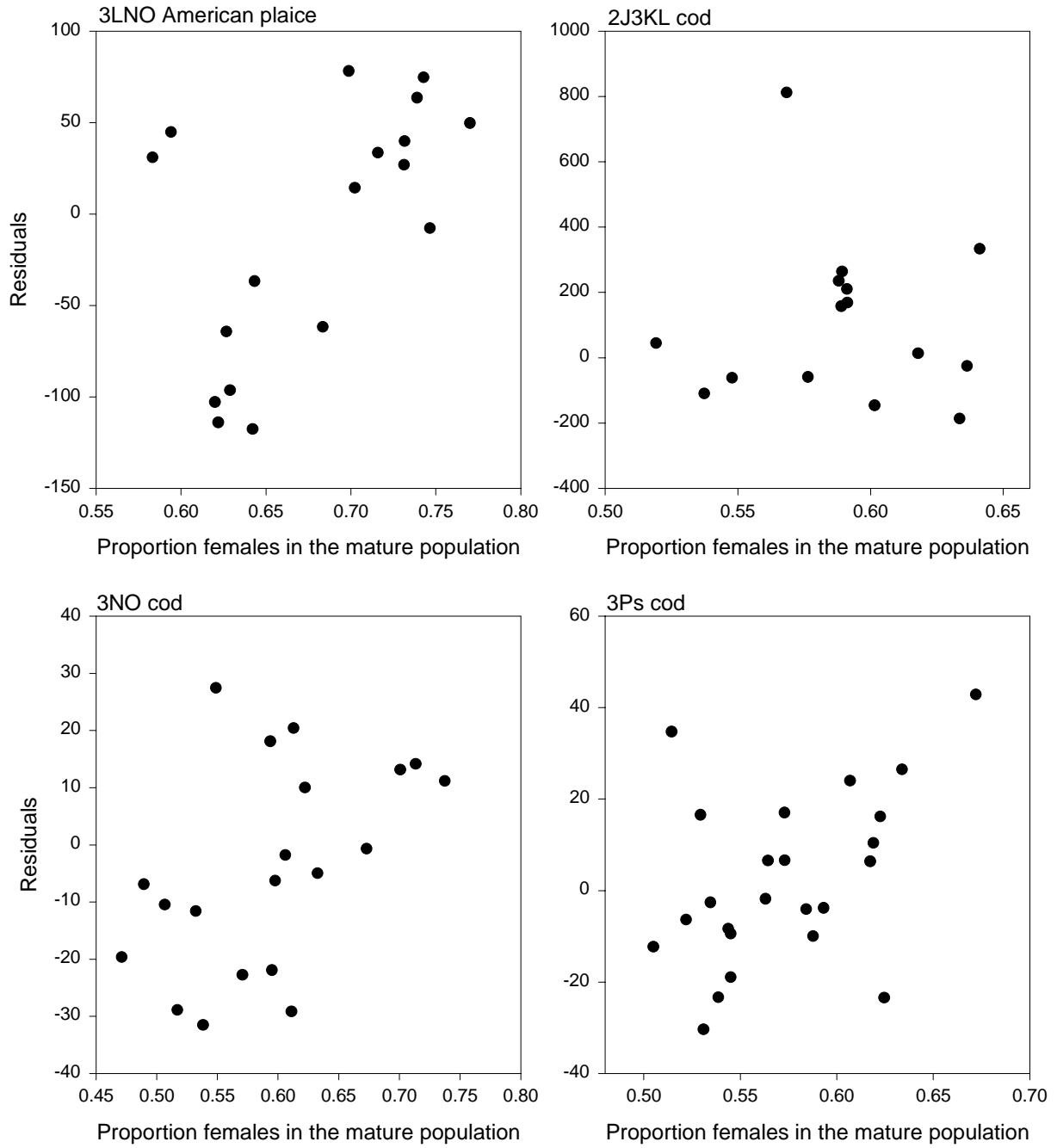


Figure 15. Residuals from the Beverton-Holt stock recruit relationship vs the proportion of the mature fish (by number) that are female as determined from rv surveys for 4 Newfoundland groundfish stocks.