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Natural Mortality Rates of Adult Pacific Herring (*Clupea pallasi*) from Southern British Columbia

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ABSTRACT

Data for over 904,000 Pacific herring (*Clupea pallasi*) seined or gillnetted in British Columbia between 1951 and 1998 was used to estimate age- and year-specific adult natural mortality rates. Apparent sampling bias precluded using data for all stocks before 1980 and for northern British Columbian stocks since then. For the southern (West Coast Vancouver Island, Strait of Georgia) stocks, the instantaneous natural mortality rate (M) for adult herring is an increasing exponential function of age. Surplus energy requirements for gonad recrudescence and overwintering appear to cause the death of adult herring. It was found that, based on an experiment using a hypothetical herring population and assessment model or regression estimates of M, the escapement model overestimates survival, relative to the age structured model and the predictive regression, for West Coast Vancouver Island herring; the three mortality estimates generate similar abundance trajectories for Strait of Georgia herring. It is suggested that the described sampling bias be considered by herring stock assessment models.

RÉSUMÉ

Des données relatives à plus 904 000 harengs du Pacifique (*Clupea pallasi*) capturés à la senne ou au filet maillant en Colombie-Britannique entre 1951 et 1998 ont été utilisées pour estimer les taux de mortalité naturelle des adultes spécifiques à l’âge et à l’année. Un biais d’échantillonnage interdisait d’utiliser les données pour tous les stocks avant 1980 et pour les stocks du nord de la Colombie-Britannique après cette date. Dans le cas des stocks du sud (côte ouest de l’île de Vancouver, détroit de Géorgie), le taux de mortalité naturelle instantané (M) des harengs adultes est une fonction exponentielle de l’âge. Les besoins énergétiques supplémentaires pour la croissance des gonades et l’hivernage semblent expliquer la mortalité chez les adultes. Il à été trouvé, qu'à partir d’une expérience fondée sur une population de hareng théorique et un modèle d’évaluation, ou des estimations de M par régression, le modèle des échappées surestimait la survie par rapport au modèle structuré par âges et aux régressions de prévision pour le hareng de la côte ouest de l’île de Vancouver, les trois estimations de mortalité donnant des courbes d’abondance similaires pour le hareng du détroit de Géorgie. Il est donc proposé que le biais d’échantillonnage décrit soit considéré pour les modèles d’évaluation des stocks de hareng.

INTRODUCTION

Vetter (1988) is an excellent review of the current state of natural mortality estimation for fish stocks, even though it was published over a decade ago. He began by describing the three general approaches taken. These are analysis of catch curves, correlations of M (instantaneous natural mortality rate) with various life history parameters (eg. GSI, Gunderson and Dygert (1988); Pauly (1980), size (McGurk 1993)) and predation models. Vetter also makes a number of good comments pertaining to sampling bias. Perhaps his greatest contribution is the point he makes about how the existing estimates of M are used unrealistically in fish population models. In all cases, M is assumed to be constant through the whole adult life history, or at least during the phases(s) when these stocks are exploited. According to McGurk (1993), it is commonly accepted that M decreases with dry mass. Yet stock assessment models persist in using a single estimate of M for all adult fish, and in some instances all ages of fish, over time. Vetter stated that the true rates of natural mortality, and their variability, are still very poorly known even though the great stocks of commercial fish in temperate regions have been subjected to continuous exploitation for decades. Because M appears to vary widely within fish stocks, and because the results from fishery models can be sensitive to large variations in M, one must conclude that assuming constancy without proof can have serious consequences for fisheries management (Vetter 1988). Vetter extends this by stating that fish population models have been shown to be sensitive to input values of M and that the sensitivity is also affected by the interactions of M and the values chosen for other parameters in the models.

This state of affairs, however, is not a consequence of a lack of effort. It is an unfortunate irony that information such as M is needed to manage stocks after exploitation has begun. As stated by Ricker (1949), studies of unexploited populations are prized rarities in the fisheries literature. In terms of natural mortality however, Ricker's statement could be extended to mean that instances are rare when M and F (instantaneous fishing mortality) can be determined, in other words, total mortality can actually be decomposed into its two components.

It appears that the sampling activities associated with herring fishing in British Columbia may provide one of these rare opportunities. Biological samples of the commercial catch have always been taken. A roe fishery has operated since 1972. In 1975, Fisheries and Oceans Canada began hiring test fishing vessels to collect samples of prespawning aggregations before fisheries began. This programme became more dedicated in 1980 when test fishing vessels were excluded from the fishery and used to sample prespawning herring schools before, during and after the fisheries, in some cases until spawning. In addition, spawn surveys are conducted to estimate spawning biomass (Schweigert et al. 1999). Therefore since 1980, the commercial catch has been sampled, prefishery schools of herring have been sampled in a relatively unbiased manner, and spawn surveys have provided estimates of spawner biomass. As shown below, these data allow the estimation of the number of fish in the stock-specific prefishery biomass, the number of fish removed by fishing and the number of fish which survived the fishery to spawn, and ultimately, to potentially return the following spring to spawn. Therefore, total mortality can be segregated into fishing and natural mortality on a stock-, age- and year-specific basis. The aim of this study was to take advantage of this sampling to estimate natural mortality rates in adult Pacific herring and then try to determine why they vary. If this was successful then adult natural mortality rate could be predicted on a biological basis. In addition, the estimates of natural mortality could be compared with those currently assumed for herring stock assessment.

MATERIALS AND METHODS

British Columbian stocks of Pacific herring have been sampled intermittently since 1913 (Taylor 1964) and continuously since 1951, except between 1968 and 1972 when fisheries were closed coastwide. In all instances, at least standard length (mm) and total mass (g) were measured and recorded and scales were taken from below the left pectoral fin for subsequent aging. Before 1972, herring were fished for reduction and the only regular sampling was that of the commercial catch. The spring roe fishery began in 1972 and, in 1975, seiners were hired to provide some samples of the herring schools before the commercial fishery began. In 1980, a dedicated test fishing programme began. Seiners were hired to, among other activities, collect samples from herring schools throughout the potential fishing area over the last several weeks before the fishery. In some areas, sampling continued after the fishery and in some instances until after spawning began. Samples of 100 fish were taken from each test seine set, and repeatedly from the commercial seine and gillnet catch by port samplers as catch was offloaded.

Spawning biomass is estimated annually for each major stock as part of the stock assessment process. The spawn survey procedure is described in Schweigert et al. (1999). Briefly, SCUBA divers survey transects of spawns. Egg deposition for each sampling quadrat is estimated from a predictive equation. Total eggs deposited in a major stock assessment region is translated into spawning biomass using an assumed 50:50 sex ratio and a relative fecundity of 200 eggs x g^{-1} wet female mass.

I estimated the number of fish-at-age caught in the commercial fishery and the number of spawners-at-age for the five major stocks (Fig. 1) for all years between 1951 and 1998, except for 1968-72 when no biological samples were collected. Number of fish-at-age caught by commercial gear type (seine, gillnet) was estimated as the number of fish-at-age in the total mass of samples for each commercial gear multiplied by the ratios of seine catch or gillnet catch to total sample mass for the respective sample source. The number of fish-at-age in the prefishery biomass was estimated as the number of fish-at-age in the total mass of test fishing samples for the prefishery period multiplied by the ratio of commercial catch plus spawning biomass to total sample mass. Number of spawners-at-age was estimated as the number of fish-at-age not caught during the commerical fisheries. Tanasichuk (1997a) has shown that, for B. C. stocks, there is no effect of sampling time on the age composition of samples collected by test seiners from prespawning aggregations. The instantaneous natural mortality rate was estimated as:

$$-\log_e((N_{\text{seined, } i+1,\, j+1} + N_{\text{gillnetted, } i+1,\, j+1} + N_{\text{spawned, } i+1,\, j+1})/N_{\text{spawned},i,j}),$$

where N is number of fish, i is year and j is age. I considered estimates of M for age 4 and older fish only. British Columbian herring recruit to the adult biomass at age 2 but mostly by age 3. Therefore, estimates of number of age 2 fish would be biased downward consequently deflating the estimate of M for age 3 herring.

I tested for the effects of age, size and environmental conditions on M using age, mean size-at-age estimates (mean mass- and length-at-age for the springs before and after the period when natural mortality would occur) and sea surface temperature and salinity measurements for Amphitrite Point lighthouse. Temperature and salinity have been measured daily there since 1935. Amphitrite Point is used conventionally as the time series for temperature and salinity for the west coast of Vancouver Island. This is where the West Coast Vancouver Island stock summers. The summer feeding areas for the other major British Columbian stocks (Strait of Georgia, Central Coast, North Coast, Queen Charlotte Islands) are not known confidently. The data were adjusted to reflect temperature and salinity at 50 m depth where adult herring feed over summer (Tanasichuk 1997b). Relationships were tested using multiple regression analysis. The temperature and salinity values tested were for monthly and consecutive 2- through 8-month intervals over the period of potential feeding season (March – October) and includes the period when adult herring would interact with potential predators (Pacific hake (*Merluccius productus*) and spiny dogfish (*Squalus acanthias*) (Tanasichuk et al. 1991)). I did not test for an effect of fish abundance on M. Most herring join the adult biomass as age 3 fish. The first estimate of the abundance of these fish can only be made in the spring following their first year spent exposed to the same mortality conditions as the other adults. Therefore, the initial number of adult herring is unknown.

Statistical analyses followed the procedures outlined in Sokal and Rohlf (1981). These included partial correlation analyses and tests of the significance in the improvement in R^2 for multiple regression analyses. I used SYSTAT (1994) calculate predictive equations for M.

RESULTS

Sampling bias

Before I began examining the effects of size and environmental characteristics on mortality, I scrutinised the data, looking for potential sampling bias.

I excluded all reduction fishery samples because virtually all were collected too early. Figures 2 through 6 show the relationship between the sampling and spawning periods for the major stocks for 1951-98. Most sampling during the reduction period was done between October and December. The reduction fishery characteristically took place then because the oil content of herring was high. Fish are thought to be migrating from summer feeding to overwintering and spawning areas during this period. Therefore, it is likely that the reduction fishery operated as an interception fishery rather than a terminal fishery as the roe fishery does. Consequently, fish cannot be assigned confidently to a particular stock. As indicated in Table 1, the difference between the last day that samples were collected and the first day that spawning began was significantly ($p<0.05$) greater than zero for all stocks except the Strait of Georgia. I examined the Strait of Georgia in more detail by plotting the cumulative proportion of fish sampled with respect to sampling date. There were only two years when samples were collected within one week of the beginning of spawning. These samples accounted for less than 5% of the total fish sampled in those years. Fish sampled after spawning never accounted for more than 12% of the fish sampled in a year; in all instances these samples were collected at least 50 days after spawning ended.

It appears that sampling during the roe fishery period (1975-98) may not reflect the true spawning population for all major stocks either. Fig. 7 shows the relationship between the end of test seiner sampling and the spawning period. The only stocks which appear to be sampled through most of the spawning period are the southern B. C. stocks, that is the West Coast Vancouver Island and Strait of Georgia populations.

I suggest that sampling bias is disclosed by the catch curves. Plots of apparent survival rate (S) for the major stocks, where $S=e^{-Z}$ and Z is the instantaneous total mortality rate, are presented in Figs. 8 through 12. These figures can be considered summaries of year-class specific catch curves. If the right limb of the catch curve does not descend between consecutive ages for a year-class then S is greater than 1. In general, catch curves for the northern stocks do not decline consistently until about age 7. For the southern stocks, catch curves begin declining consistently after age 3 as of 1980, when the dedicated test fishing programme began. Hay (1985) developed B. C. herring maturity ogives based on egg diameters measured over the winter before spawning. He concluded that B. C. herring mature mostly at age 3. One should expect then that an unbiased catch curve for a British Columbian herring year-class would show a descending right limb beginning at age 4, as is the case for southern B. C. herring as of 1980.

Natural mortality

Some estimates of M must be biased because they were < 0. Figs. 13 and 14 show scatterplots of M against total mass and age for age 4 and older fish from the Strait of Georgia and West Coast Vancouver Island stocks respectively. For the Strait, 22 of the 152 observations had $M<0$; three of these were isolated events, seven cases were for older fish (age>6) when sample sizes would be small ($n<10$), and 12 were from 1982, 1989 and 1992 which suggests biased sampling in those years or the year before. For the West Coast of Vancouver Island stock, 29 of the 152 observations had $M<0$; 20 instances were from older fish and the remainder from the sampling years 1989, 1992, 1995 and 1996. Sources of bias for the data used in this analysis potentially include errors in age composition, catch and spawning biomass. The question is are the data biased enough to generate untrue results? It is unknown how biased each estimate of M might be. Therefore, I could only eliminate instances where $M<0$, and then continue with the analyses to see if the results I got were biologically reasonable.

I found that adult natural mortality rate was an exponential function of fish age. Results of partial correlation analyses showed that natural mortality was more closely related to fish age than to size (Table 2). Results of multiple regression analyses showed that, for the West Coast Vancouver Island stock, for which the summer feeding area is most confidently known, sea temperature or salinity did not account for a significant ($p>0.05$) increase in the explained variation of M. Therefore, there was no variable that I tested which would generate interannual variation in adult M. I calculated weighted regression (SYSTAT 1994) of M against age (A), using 1/A as the weighting factor, because the variance of M increased with age. Coefficient of determination (R^2) suggested that the data fit an exponential function better than a linear or power function. I used that parameter estimates and their standard errors to compare the stock-specific regressions of M on age. I found no significant differences ($p>0.05$) in slope or intercept. The pooled weighted regression equation was:

$M=0.14e^{0.18*A}$, $p<0.0001$, $n=235$, adjusted $R^2=0.46$.

Both parameter estimates were significantly different ($p<0.05$) from 0. Residuals for the regression are shown in Fig. 15. One data pair had a studentised residual $>|2|$ and a leverage coefficent $>4/n$, which Sokal and Rohlf (1981) would define as a significant outlier.

DISCUSSION

The results of this study, showing that variations in adult natural mortality rates of stocks of Pacific herring are an increasing exponential function of fish age, are a natural extension of studies examining natural mortality in fishes. Beverton and Holt (1959) were the first to relate M to the biology of fishes. Their work was built upon by others (eg. Hoening 1983, Pauly 1980, Peterson and Wroblewski 1984) who developed predictive relationships between M and life history parameters over a number of species. McGurk (1993) was to first to examine factors affecting M within species, that is, among various stocks of herring. There are several concerns common to all these studies. First, all the above studies estimated one value of M for each population. There was no considerations of interannual variability or variation due to age or life history stage (eg. juvenile) effects. Second, all previous mortality studies assumed that the samples providing these estimates were unbiased. I have tested for a number of forms of bias in this study and have excluded samples which do not confidently reflect the populations being studied. The results I present describe age-specific adult natural mortality for 26 year classes in each of two Pacific herring populations.

It appears that, as suggested by Vetter (1988) and Cushing (1975), and implied by Beverton and Holt (1959), that the mortality rate of a cohort of fish is a parabolic rather than some smooth negative function of age. Mortality rates are very high during egg and larval stages, likely decline as fish grow beyond the size taken by most predators, and then begin to increase with age likely due to the increasing energetic demands of gonad recrudescence and overwintering as discussed below. I explain the difference between my results and those which show a decrease in M with age (size) as a consequence of the conceptual differences discussed above and examining a different part of the mortality curve than McGurk (1993) did. He focussed on the differences in M between the very early and adult life histories. This then would be a time when M would be expected to decrease with size. I concentrated on the adult phase completely and examined variations in adults over time rather than using point estimates for a given stock.

I suggest that most adult herring natural mortality is due mainly to senescence because age influences M. Woodhead (1979) discussed senescence in fish in detail. He described the few examples of captive fish deteriorating and dying with increased age, and refers to Cushing (1975) as an example of fish reaching a critical age after which senescent mortality takes place. Woodhead also presents the common observation that stored material is mobilised for gonad recrudescence and that this supports the concept of reproductive stress. This stress is considered a source of age-related changes which contributes to the reduced efficiency of metabolic function, that is, Pauly's (1980) physiological mortality. Woodhead (1979) states that although the data are not extensive, they imply that the increased energy requirements of reproduction in older individuals might well contribute to unstable homeostasis and so predispose them to death. This may be particularly important if the fish cease to feed during maturation or during years when little food is available. Newsome and Leduc (1975) concluded that female yellow perch (*Perca flavescens*) may die over winter when ovarian development depletes lipid reserves below a critical level.

I suggest that the trajectories of ripe GSI (Ware and Tanasichuk 1989) and surplus energy (Fig. 16) for Pacific herring are artifacts of physiological mortality. If this in fact is true, then the fish that would succumb to this type of mortality would not be alive to be sampled. This is likened to Ricker's (1979) comment/warning that all sampling of older fish from fish populations may be biased by age-specific mortality. There is evidence supporting the suggestion that reproduction alone exerts a progressively greater strain on Pacific herring. Ware and Tanasichuk (1989) present a figure which shows the relationship between ripe gonosomatic index (GSI) and fish weight. GSI increases linearly with size to about 130 g in males and 145 g total mass at spawning in females. Beyond these sizes, GSI begins increasing at a slower rate, suggesting a progressively greater inability to satisfy reproductive demands. In addition, I have constructed a surplus energy schedule (Table 3) following Ware (1985). Reproductive demands account for progressively more of the total surplus energy. Partial correlation analyses of the covariation of surplus energy with age and somatic mass showed that age had no effect on surplus energy allocation with the effect of somatic mass held constant. This could suggest that herring face a phenological maximum; otherwise, the relationship between ripe GSI and mass should continue to increase linearly. Based on the presence of some fish larger than 130 g for males and 145 g for females, there would seem to be no physical constraint imposed by a herring's body. An important consideration to re-iterate and remember, is that what could well be sampled in older herring is the left tail of the distribution of fish-at-age which are the survivors of the concurrent metabolic demands of gonad development and overwinter starvation.

I tested the influence of the M's from the assessment models, and from the predictive regression, on the abundance trajectory of a hypothetical herring population. The experiment began with a herring population with 10000, 5000, 2500 and 1250 age 4 through 7 year old fish respectively. There was no recruitment. Table 4 provides the estimates of M used in the experiment. Fig. 17 shows that, using estimates of M for the West Coast Vancouver Island stock, the numbers of fish estimated using the M's from the age-structured model and the regression were very similar. However, the abundances estimated from the M's derived from the survival rates used by the escapement model were substantially greater. Population size was 1.4, 1.8 and 2.3 times greater than the mean abundances estimated using the other two estimates of M for years 2 through 4 respectively. In contrast, abundance estimates based on model values of M for the Strait of Georgia, and the predictive regression, were similar. The results of this experiment suggest that the stock-specific, and age- and year- independent estimates of M from the age-structured model are realistic for the two stocks examined. This is not the case for the escapement model estimates. It appears that the M's derived from the age-specific survival rates used by the escapement model are reasonable for the Strait of Georgia only.

Unfortunately, it appears that the predictive regression cannot be extended to the three northern stocks. There is evidence that the surplus energy schedule should apply to B. C. herring in general. Tanasichuk and Ware (1987) reported that mass-specific ripe ovarian mass was independent of stock and year. Considering that the surplus energy required for reproduction determines the surplus energy schedule, then one would not expect age-specific surplus energy allocation to be different among B. C. herring stocks. Unpublished results confirm that in fact the surplus energy schedules are similar among all major B. C. herring stocks. However, Pacific cod (*Gadus macrocephalus*) may be a significant predator of adult herring in Queen Charlotte Sound and Hecate Strait (J. Fargo, Pacific Biological Station, Nanaimo, B. C., *pers. comm.*). Therefore, the northen herring stocks could be exposed to natural mortality in addition to that caused by surplus energy demands.

I suggest that the the data I used suffer minimally from the sampling biases that Vetter (1988) expressed concern about. I tested for sampling bias and eliminated instances where $M<0$. I suggest that because catch is so closely monitored and well sampled, that number of fish-at-age taken commercially is well estimated. The question remains however regarding the accuracy of the prefishery biomass estimates themselves. There are unquantified errors associated with the spawn surveys and some question about how well spawning populations are sampled in some areas. Catch curves suggest, in instances where sampling is unbiased, that annual biomass estimates are reasonable relative to each other because year-class size declines realistically over time. This would imply that the spawning biomass estimates are accurate, at least in a relative sense. The results presented here relating to sampling bias have important implications for herring stock assessments. They show that sampling is biased for all stocks before 1980, and for the northern herring stocks since. These biases have to be considered when biologically realistic models of British Columbian herring populations are being developed.

There is an apparent inconsistency in my discussion of the effects of sampling time on sample age composition. I reported (Tanasichuk 1997a) that there was no effect of sampling time on the age composition of samples collected by test seiners, yet I express concern about the relationship between sampling time and spawning time. I suggest that the seiners do sample the fish in accessible prespawning aggregations well but that, in the instances of the northern stocks especially, not all spawning fish are in the sampling area at the time of sampling. Ware and Tanasichuk (1989) reported that larger (older) fish spawn earlier. Therefore sampling could concentrate on the earlier, older spawning fish in the northern stocks. This bias cannot be investigated further until sampling regimes would be changed to cover the entire spawning season. This type of sampling bias seems to be the simpliest explanation for the apparently unrealistic catch curves, and consequently suspicious survival estimates, for northern B. C. herring stocks.

In summary, this study has shown that adult natural morality rates in southern stocks of Pacific herring vary as a function of fish age. There were no environmental effects, or effects of size-at-age variation, which would generate a significant interannual variability. As stated by Vetter (1988), all current stock assessment models depend on a non-biologically based estimate of M, whether it be a model parameter that is fitted with many others during a modelling exercise, or a dogmatic estimate which has become entrenched. This is another instance where effort should be expended to learn more fish biology rather than deal with the mathematical nuances related to the exercise of fish population model-building.

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Table 1. Mean annual difference between last day of sampling and first day of spawning for the major B. C. herring stocks during the reduction fishing period, 1951-68. Positive values indicated sampling ending before spawning began.

Stock	Mean difference	2 x S.E.
Queen Charlotte Islands	20	9.2
North Coast	45	15.2
Central Coast	18	10.1
Strait of Georgia	-34	53.6
West Coast Vancouver Island	26	19.0

Table 2. Partial correlation coefficients for relationships between age- and year-specific M and age and M and age- and year-specific estimates of mean length (L) and mass (W) for the spring preceding (p) and following (f) the period when natural mortality would have occurred . MA_W indicates a test of the effect of age on M with the effect of mass held constant. X – p<0.05. XX – p<0.01.

Test	Strait of Georgia	West Coast Vancouver Island
MW_p_A	0.03	-0.18
MA_W_p	0.26^{xx}	0.40^{xx}
ML_p_A	-0.06	-0.10
MA_L_p	0.19^{xx}	0.31^{xx}
MW_f_A	-0.11	-0.15
MA_W_f	0.21^{xx}	0.39^{xx}
ML_f_A	-0.08	0.07
MA_L_f	-0.23^{xx}	-0.83^{xx}

Table 3. Surplus energy schedule for West Coast Vancouver Island herring.

Age	Total mass (g)	Gonadal mass (g)	Somatic mass (g)	Delta somatic mass (g)	Surplus energy (g)	Prop. surplus energy as gonad
Females						
2	72	17	55			
				21	38	0.45
3	101	25	76			
				18	43	0.58
4	128	34	94			
				16	50	0.68
5	152	42	110			
				12	54	0.78
6	170	48	122			
				8	56	0.86
7	182	52	130			
				5	57	0.91
8	190	55	135			
				3	58	0.95
9	195	57	138			
				2	59	0.97
10	201	61	140			
Males						
2	64	10	54			
				21	31	0.32
3	91	16	75			
				17	33	0.48
4	114	22	92			
				16	38	0.58
5	137	29	108			
				11	40	0.73
6	152	33	119			
				7	40	0.83
7	164	38	126			
				5	43	0.88
8	170	39	131			
				5	44	0.89
9	178	42	136			
				4	46	0.91
10	183	43	140			

Table 4. Comparison of survival rates (S) as of the 1999 forecasts estimated using the M – age regressions (Reg) and from the escapement (ESM) and age-structured stock assessment (ASM) models.

	S					
	Reg	ESM	ASM	Reg	ESM	ASM
Age	Strait of Georgia			West Coast Vancouver Island		
4	0.75	0.81	0.55	0.75	1.05	0.65
5	0.71	0.67	0.55	0.71	0.87	0.65
6	0.66	0.58	0.55	0.66	0.80	0.65
7	0.61	0.55	0.55	0.61	0.73	0.65

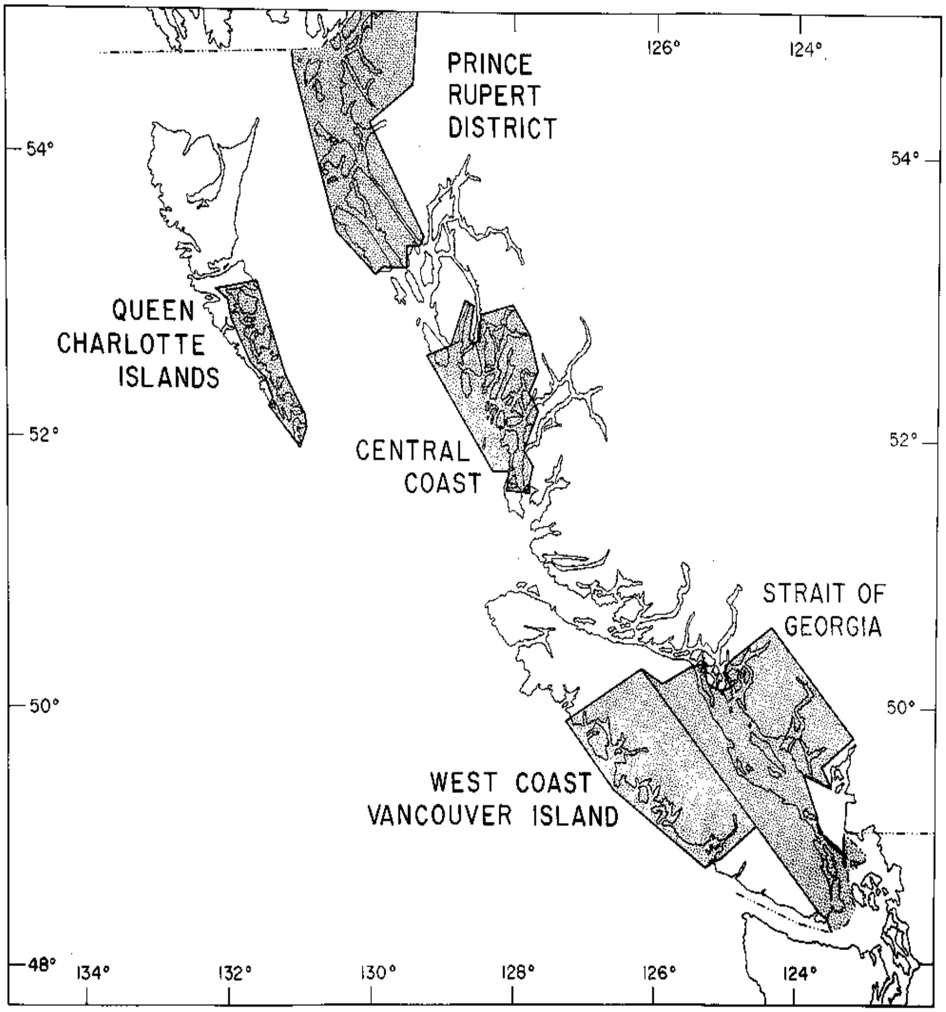

Fig. 1. British Columbian coast showing major herring stocks (from Schweigert et al. 1999). Prince Rupert District is synonymous with North Coast and includes herring which spawn in Port Simpson/Big Bay or Kitkatla.

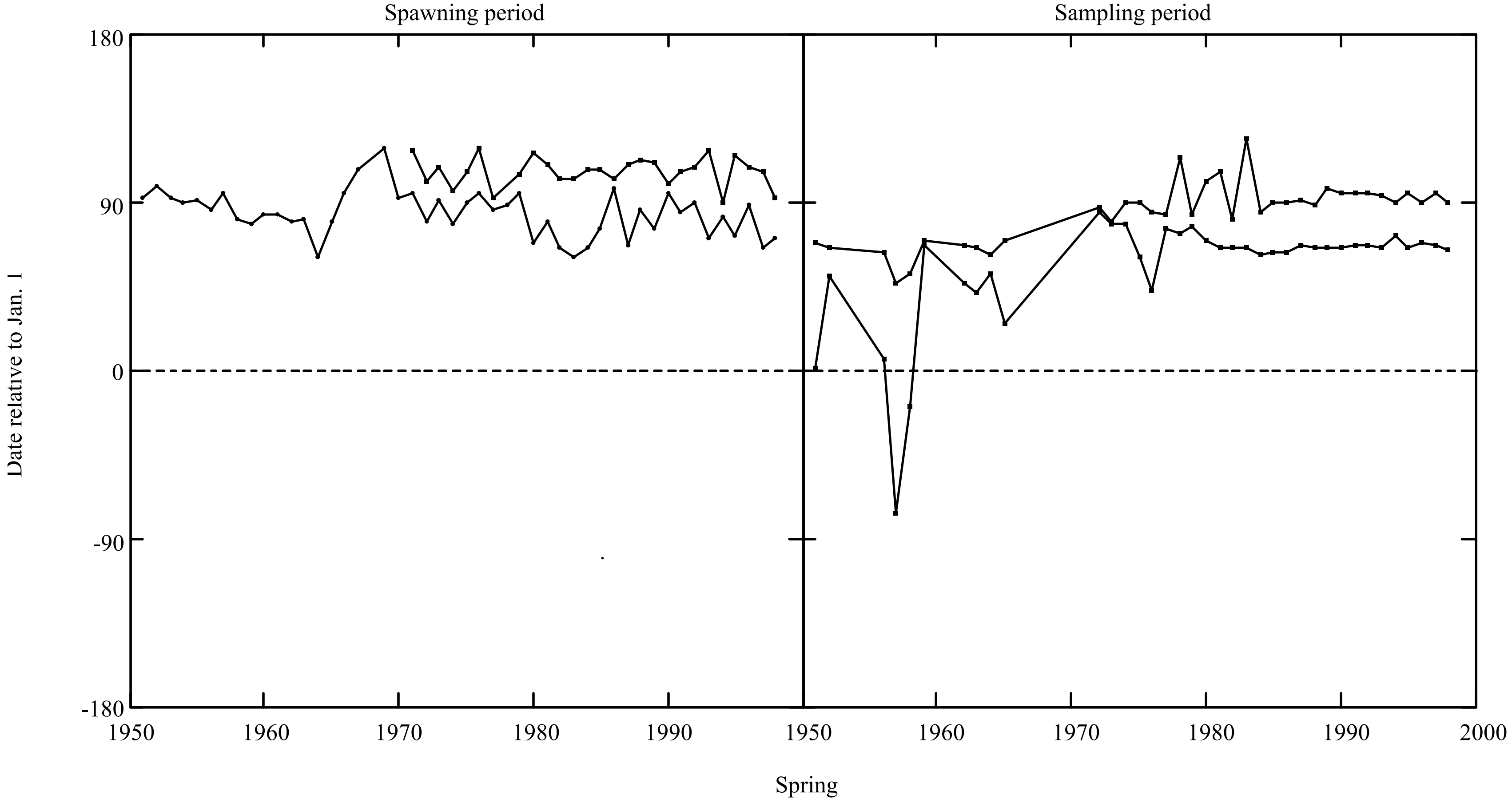

Fig. 2. Relationship between spawning and sampling periods for lower east coast Queen Charlotte Island herring.

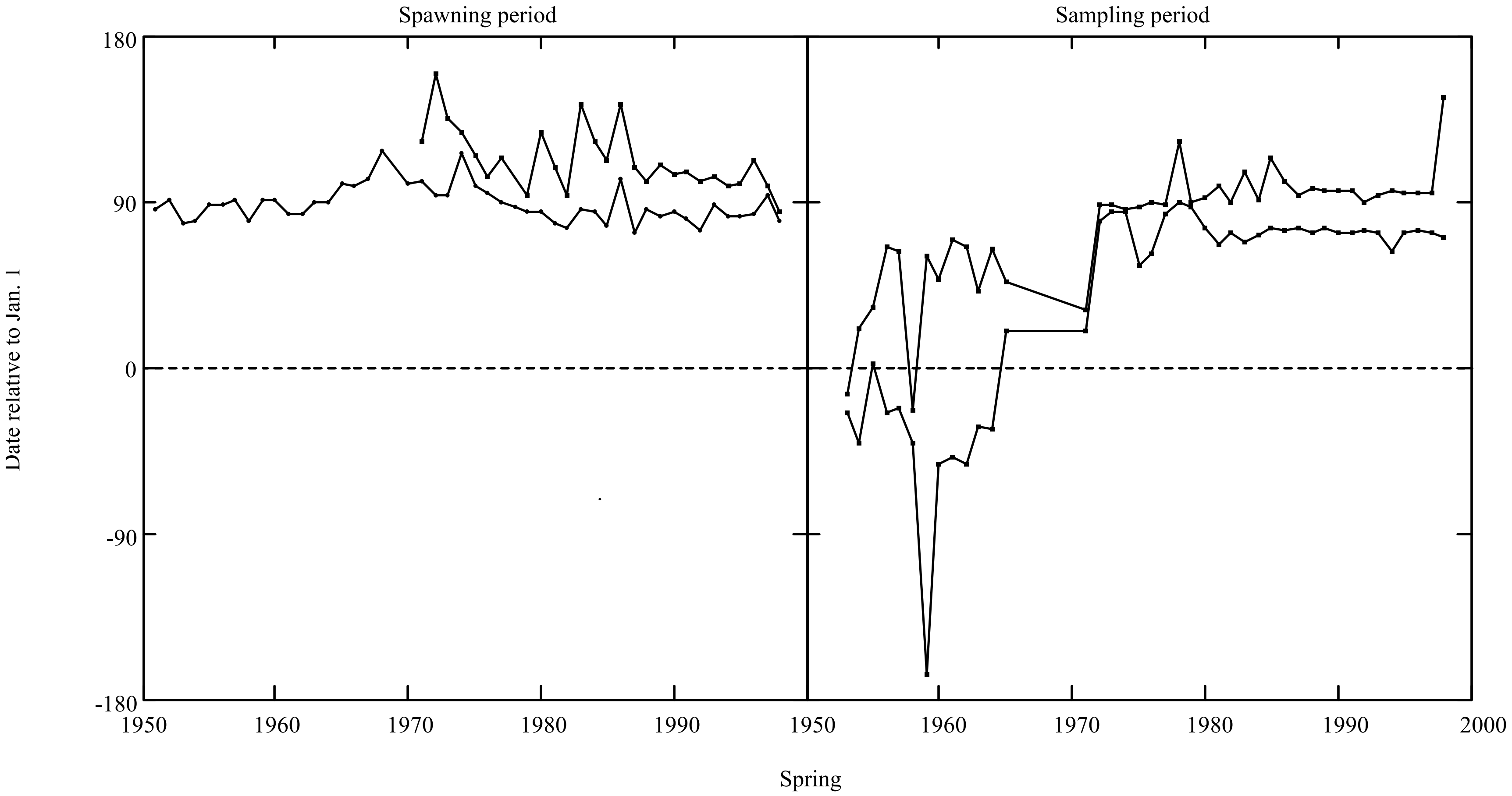

Fig. 3. Relationship between spawning and sampling periods for North Coast herring.

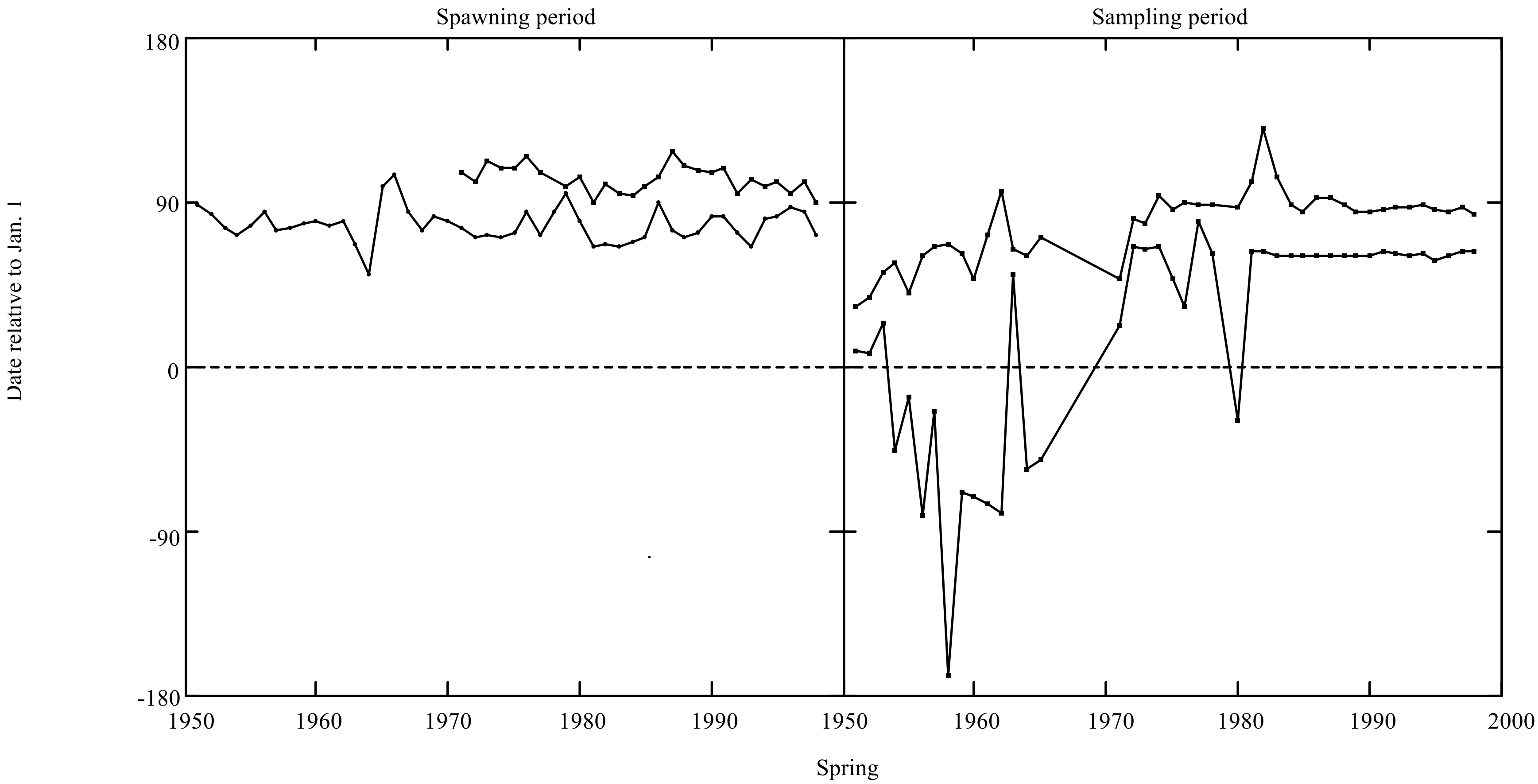

Fig. 4. Relationship between spawning and sampling periods for Central Coast herring.

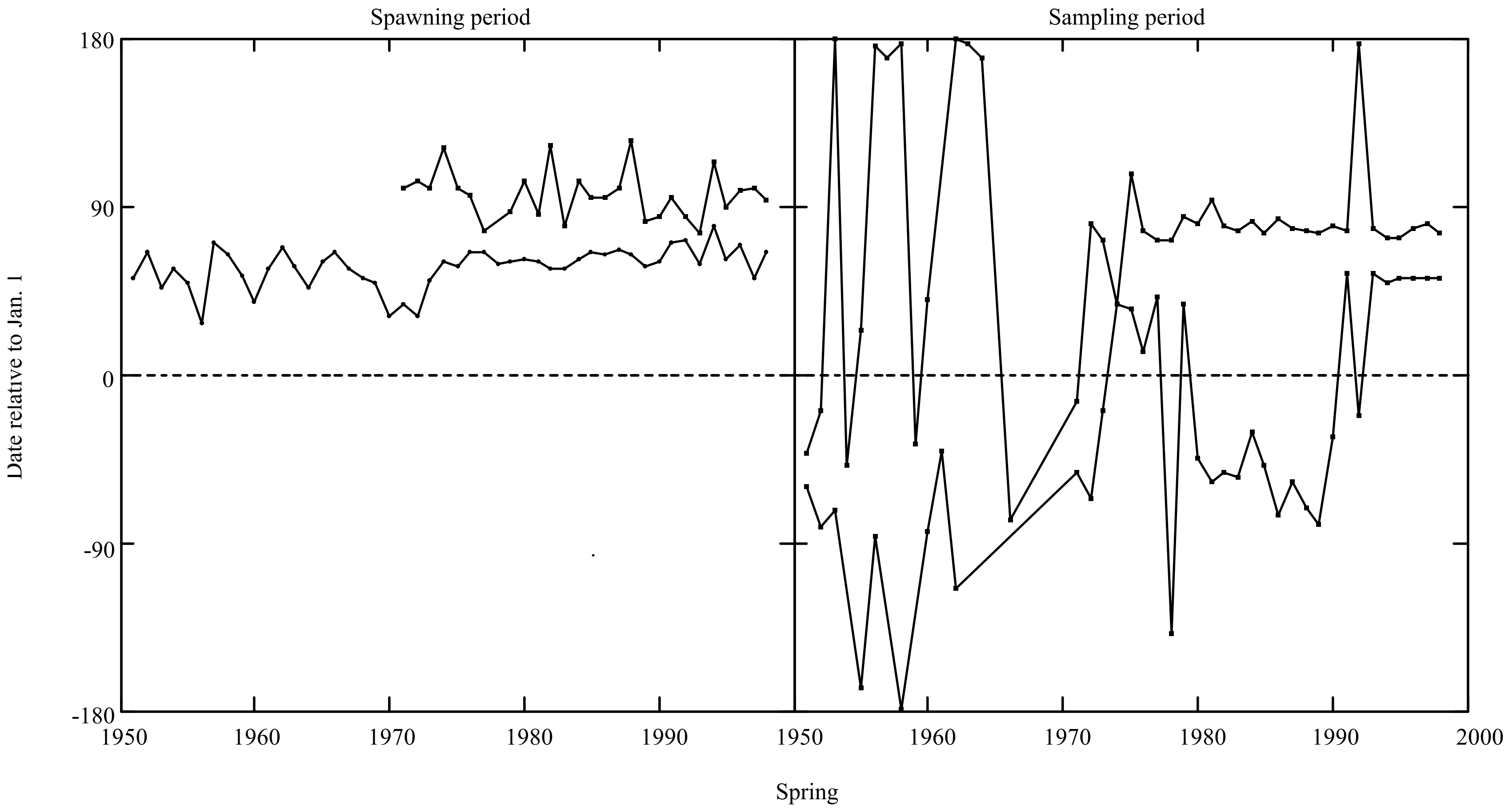

Fig. 5. Relationship between spawning and sampling periods for Strait of Georgia herring.

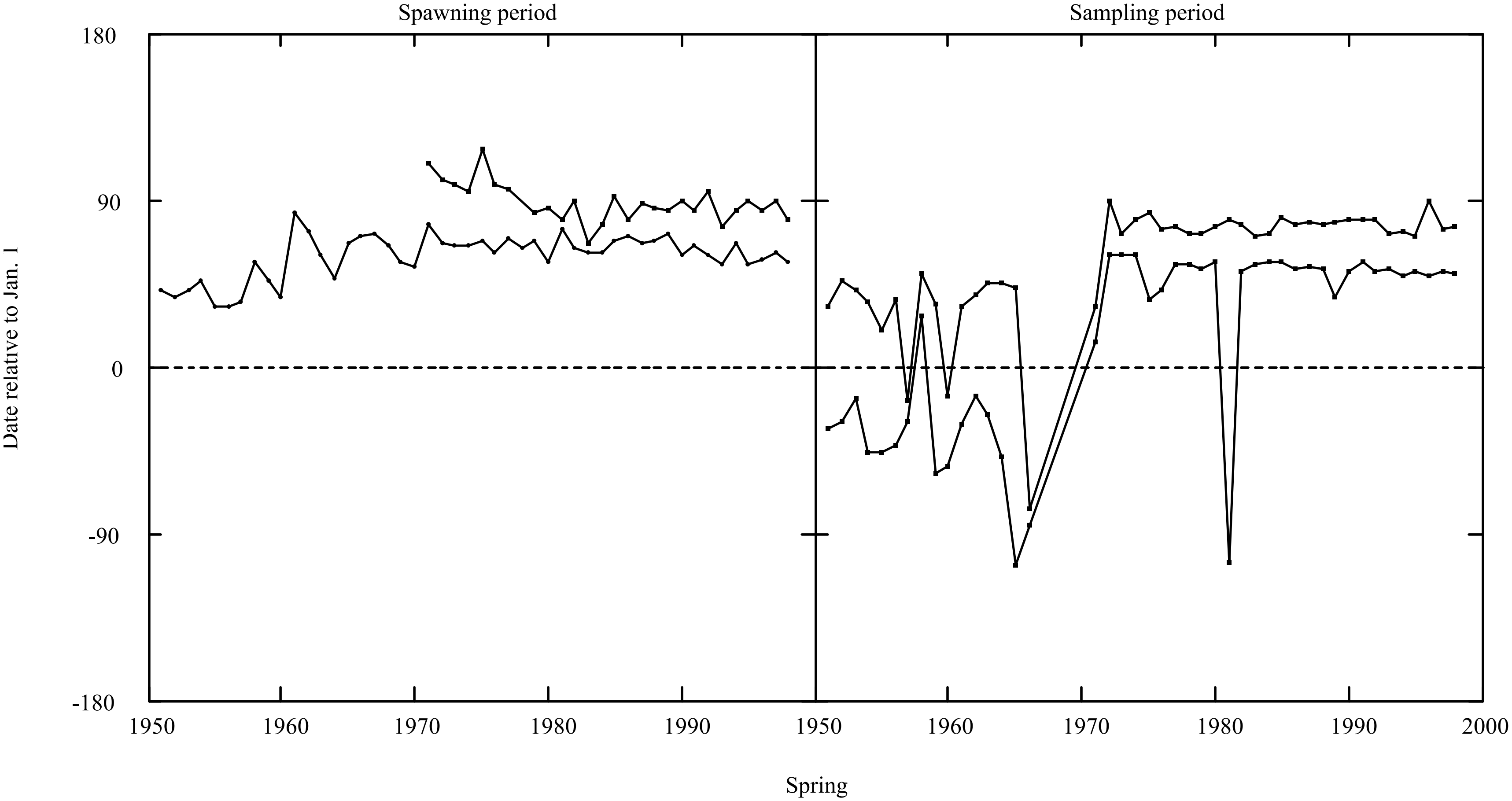

Fig. 6. Relationship between spawning and sampling periods for west coast Vancouver Island herring.

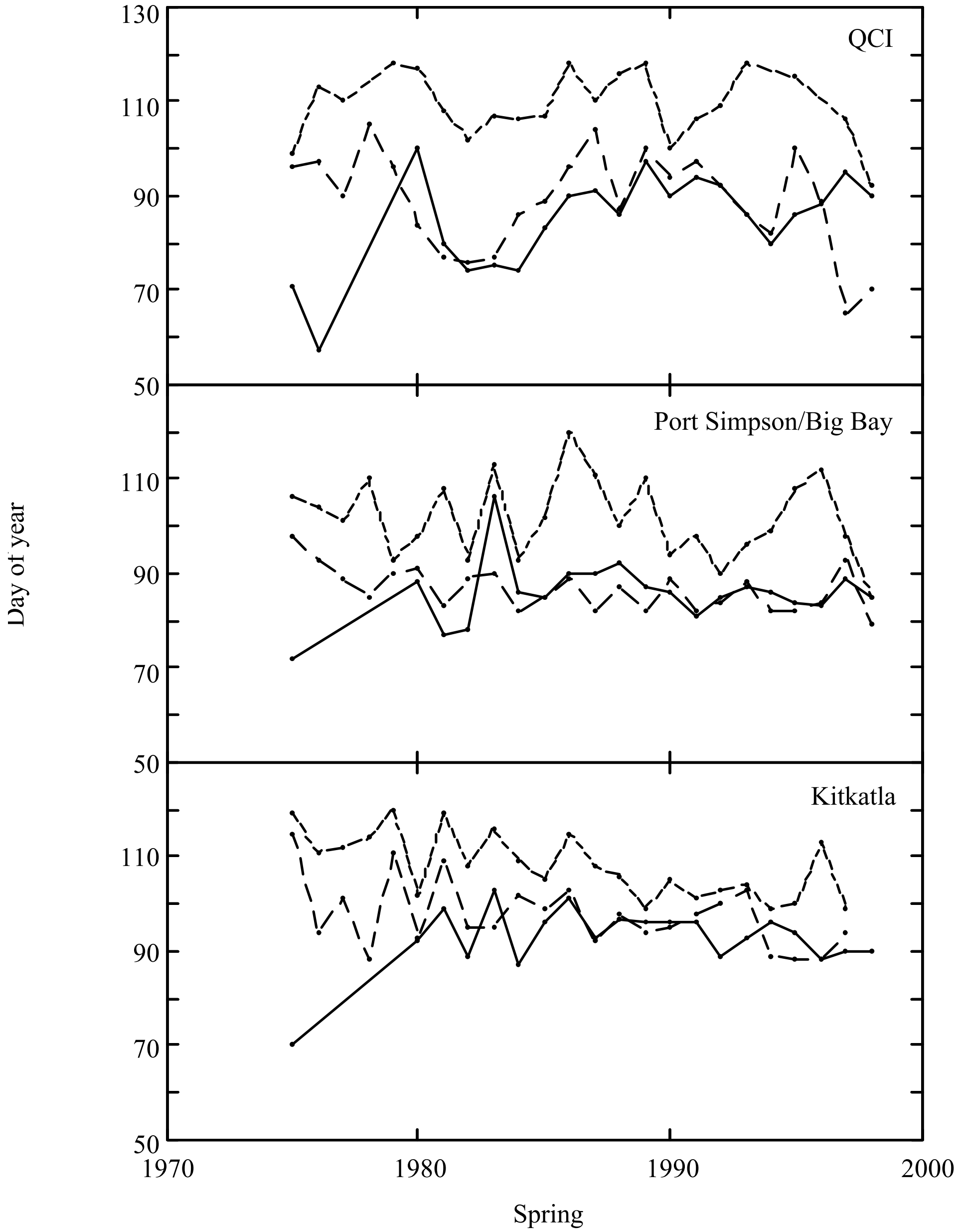

Fig. 7. Relationship between date sampling ends (solid line), date spawning begins (long-dashed line) and date spawning ends (short-dashed line).

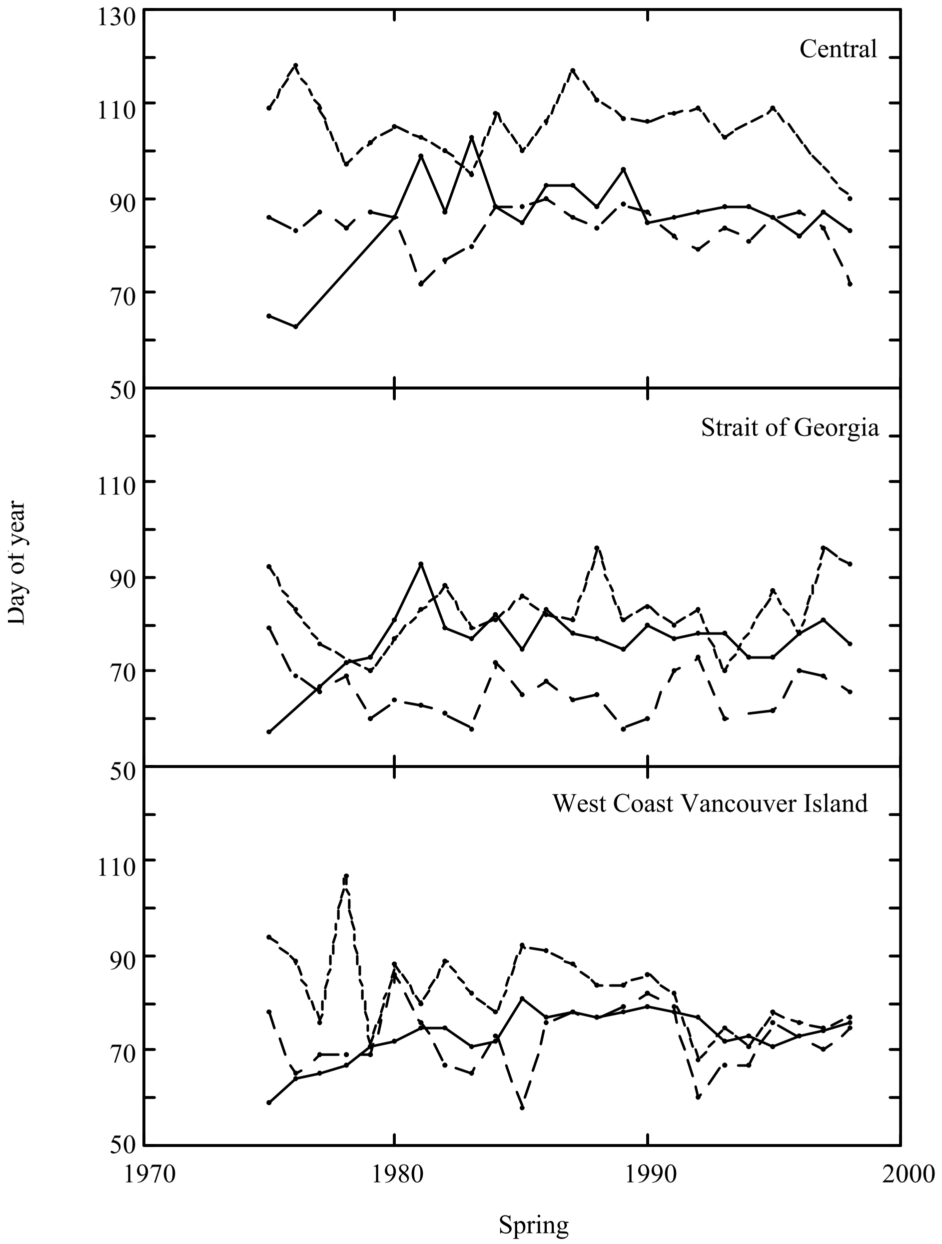
130
110
90
70
50
Central
Strait of Georgia
West Coast Vancouver Island
Day of year
1970
1980
1990
2000
Spring

Fig. 7 cont.

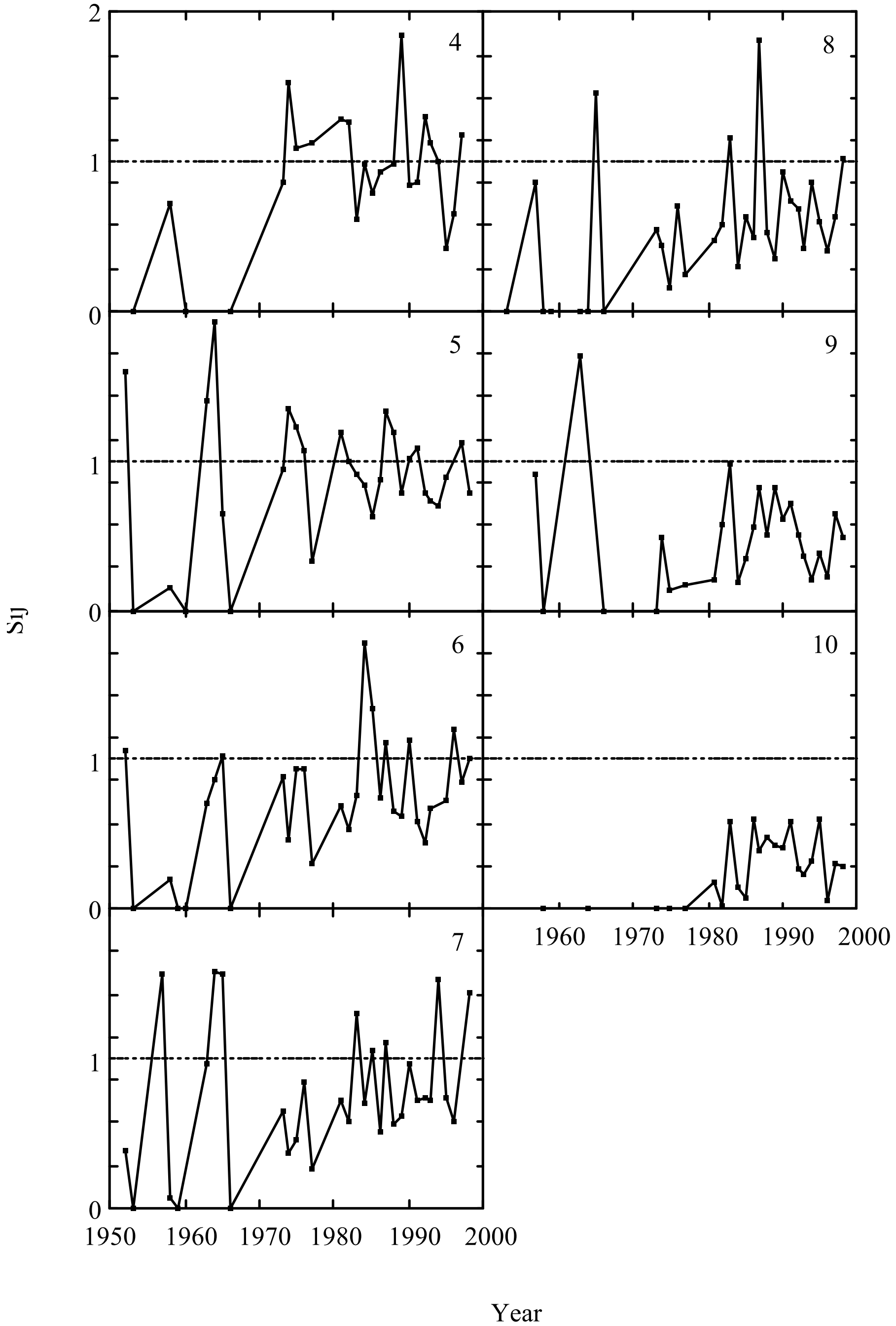

Fig. 8. Estimates of apparent survival rate (S_{ij}) for Queen Charlotte Islands herring. Dotted line is S=1. Label is year of life; eg. 4 is for the period from spawning as age 3 in year x to the prefishery biomass as age 4 in year x+1.

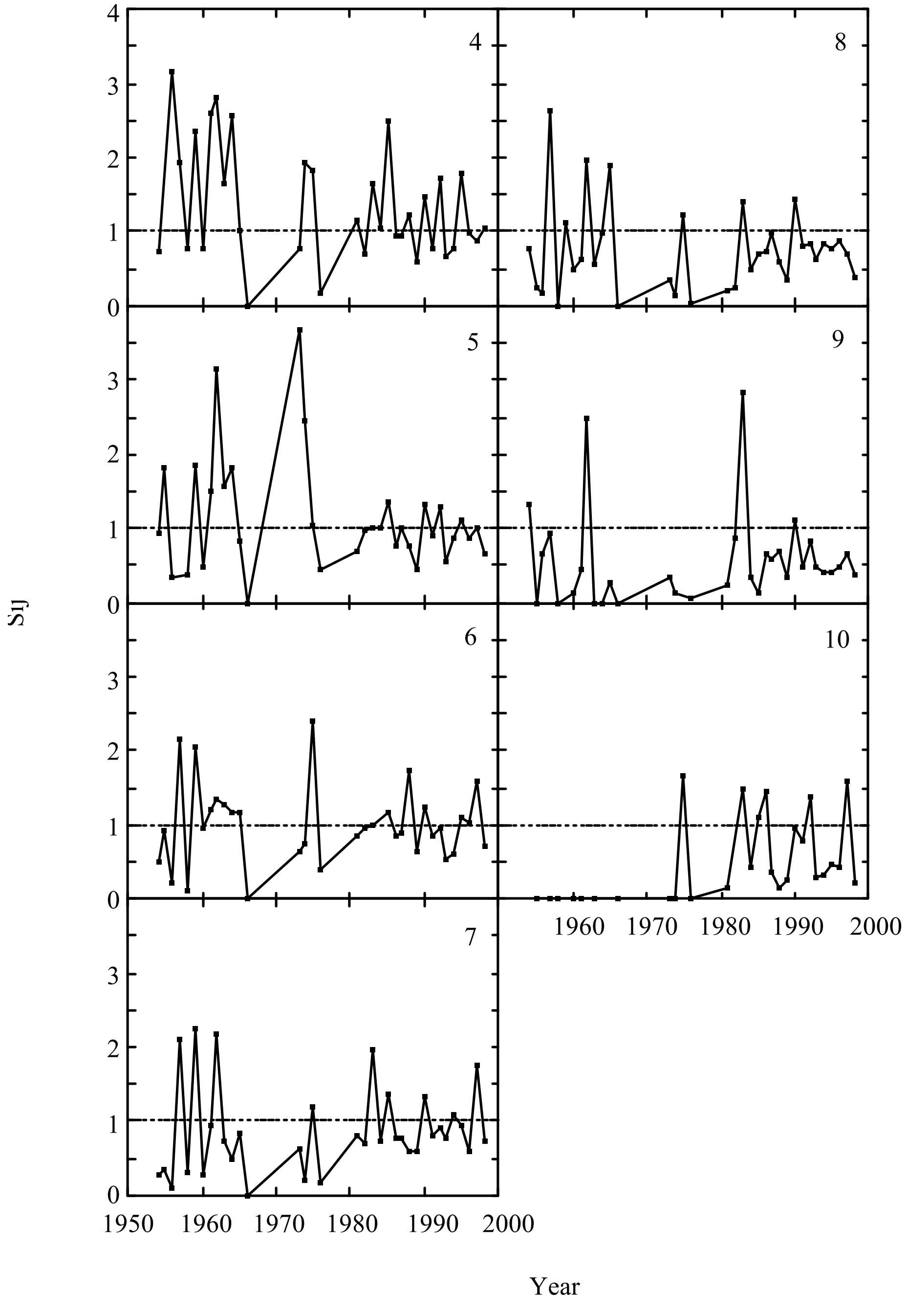

Fig. 9. Estimates of apparent survival rate (S_{ij}) for North Coast herring.

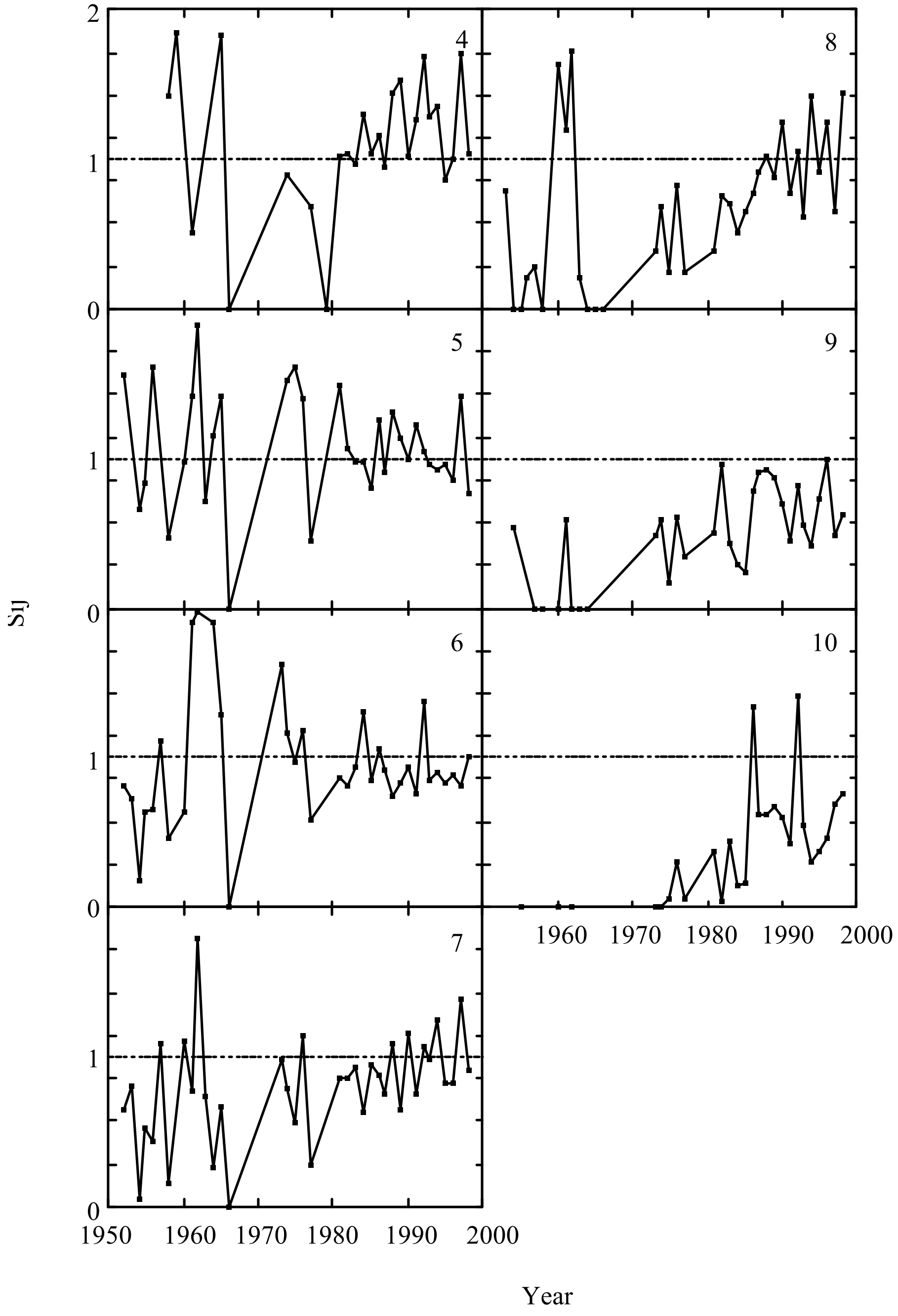

Fig. 10. Estimates of apparent survival rate (S_{ij}) for Central Coast herring.

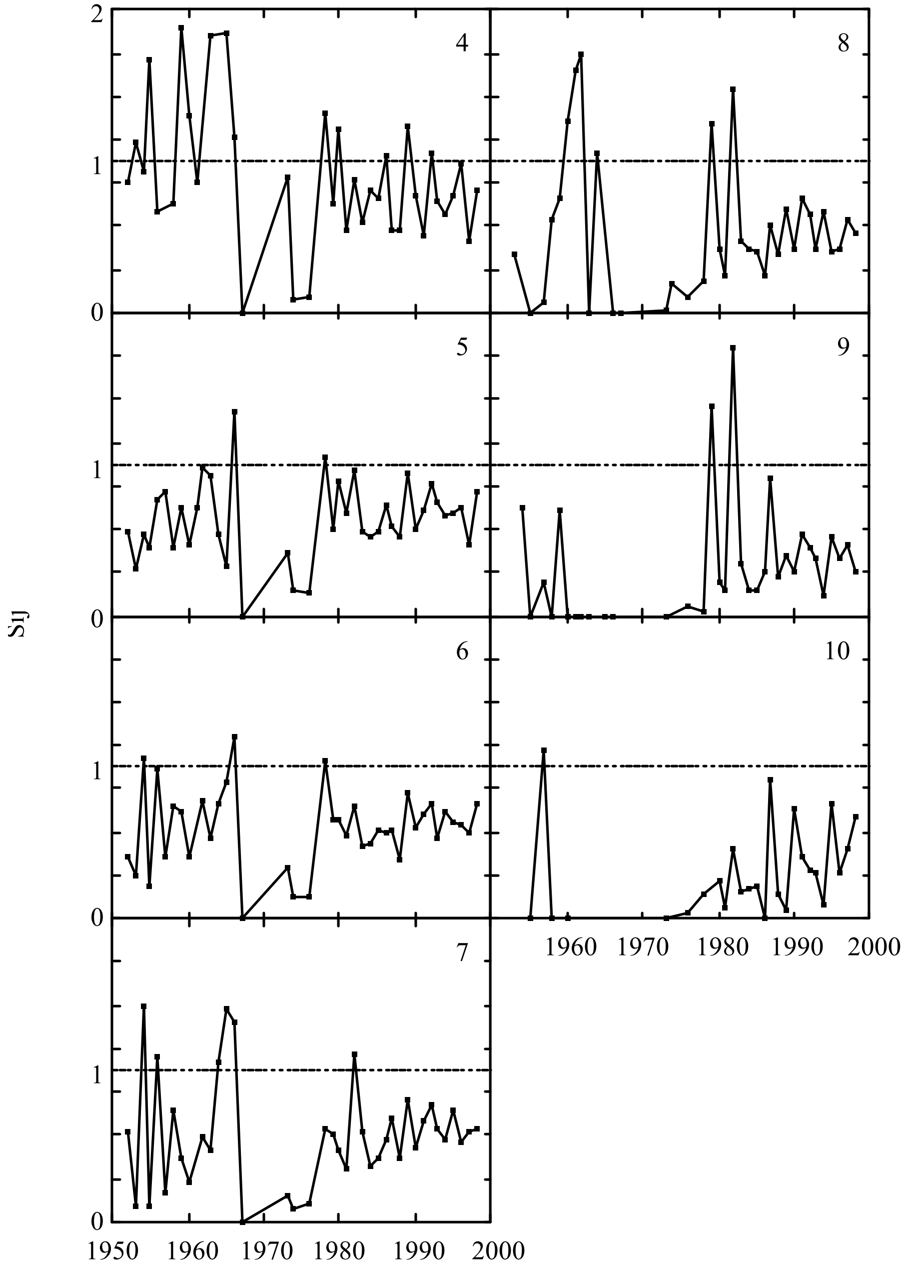

Fig. 11. Estimates of apparent survival rate (S_{ij}) for Strait of Georgia herring.

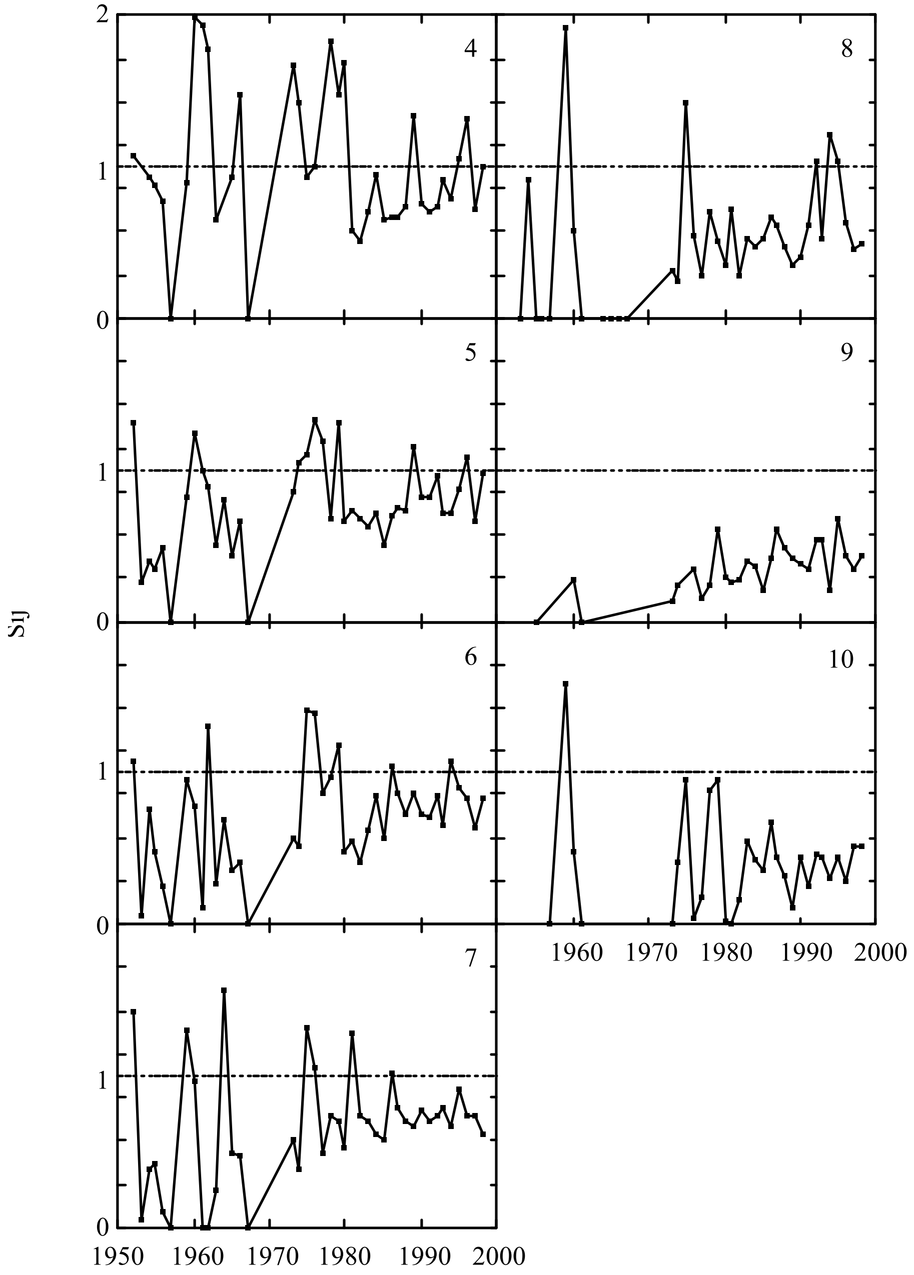

Fig. 12. Estimates of apparent survival rate (S_{ij}) for West Coast Vancouver Island herring.

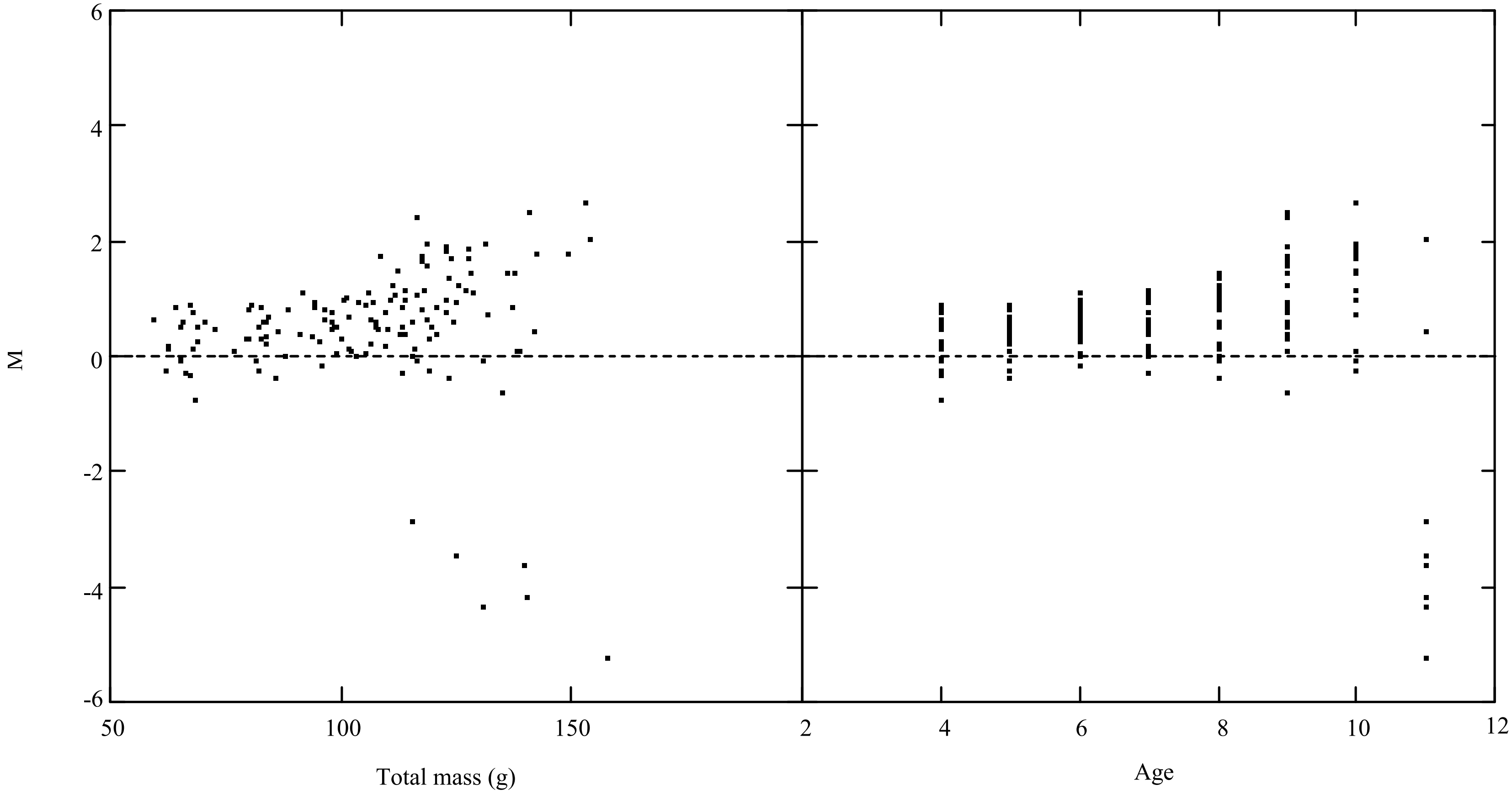

Fig. 13. Scatterplot of M against initial mass and age for Strait of Georgia herring.

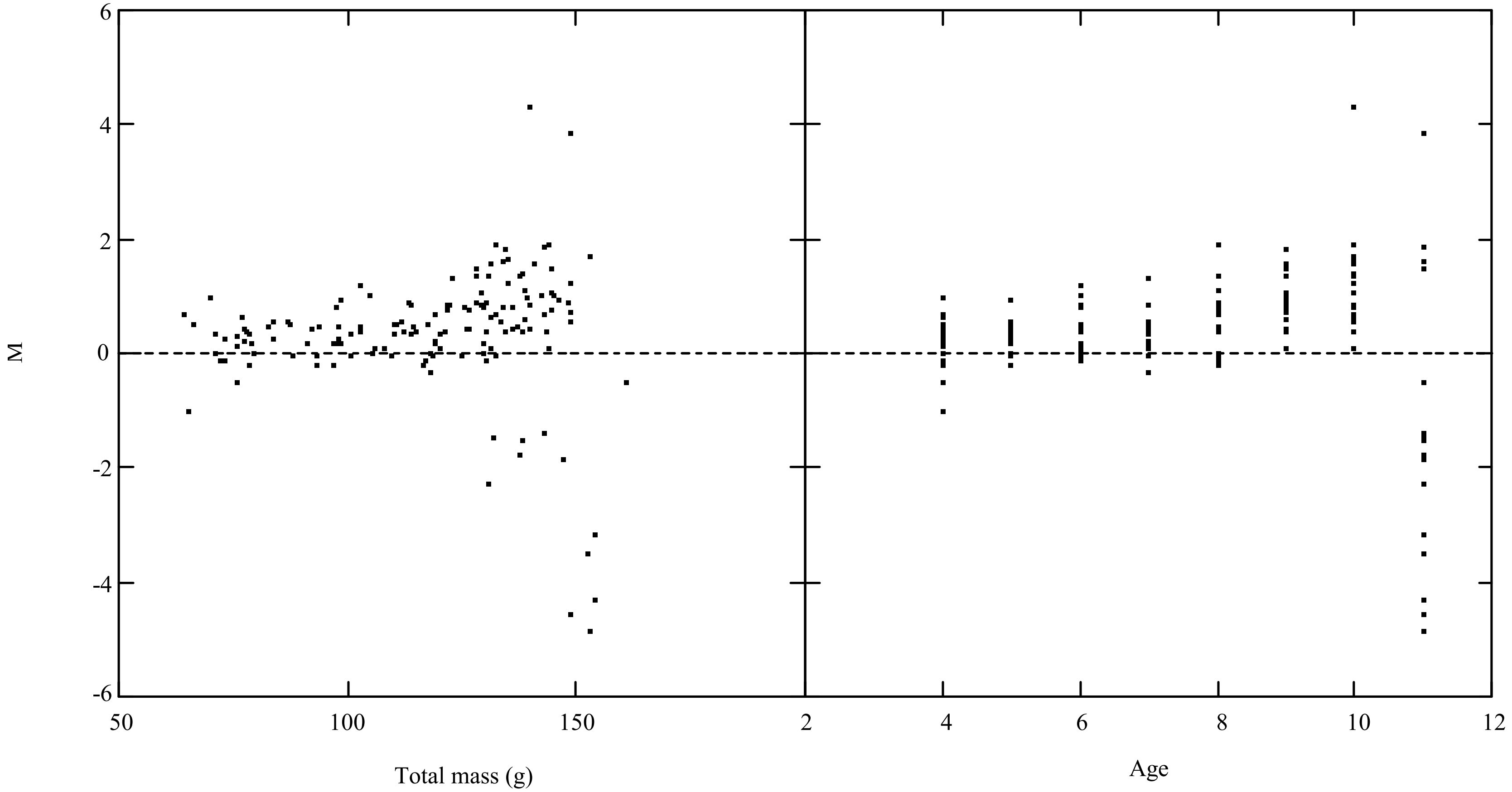

Fig. 14. Scatterplot of M against initial mass and age for West Coast Vancouver Island herring.

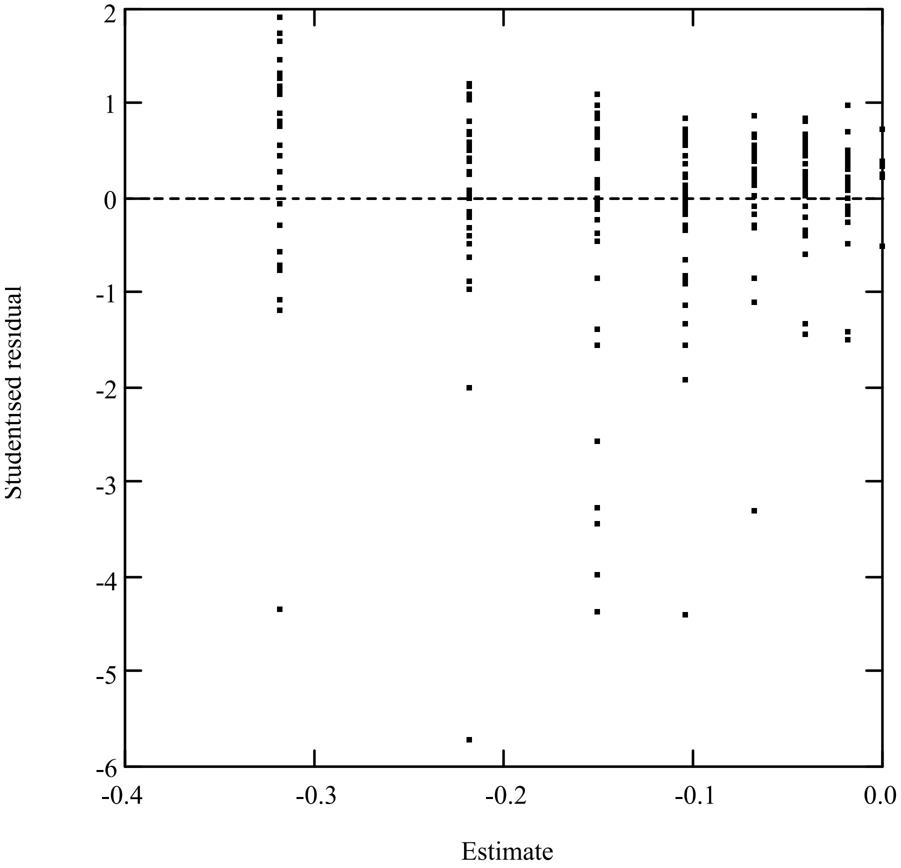

Fig. 15. Residual plot for $M=0.14e^{(0.18*age)}$.

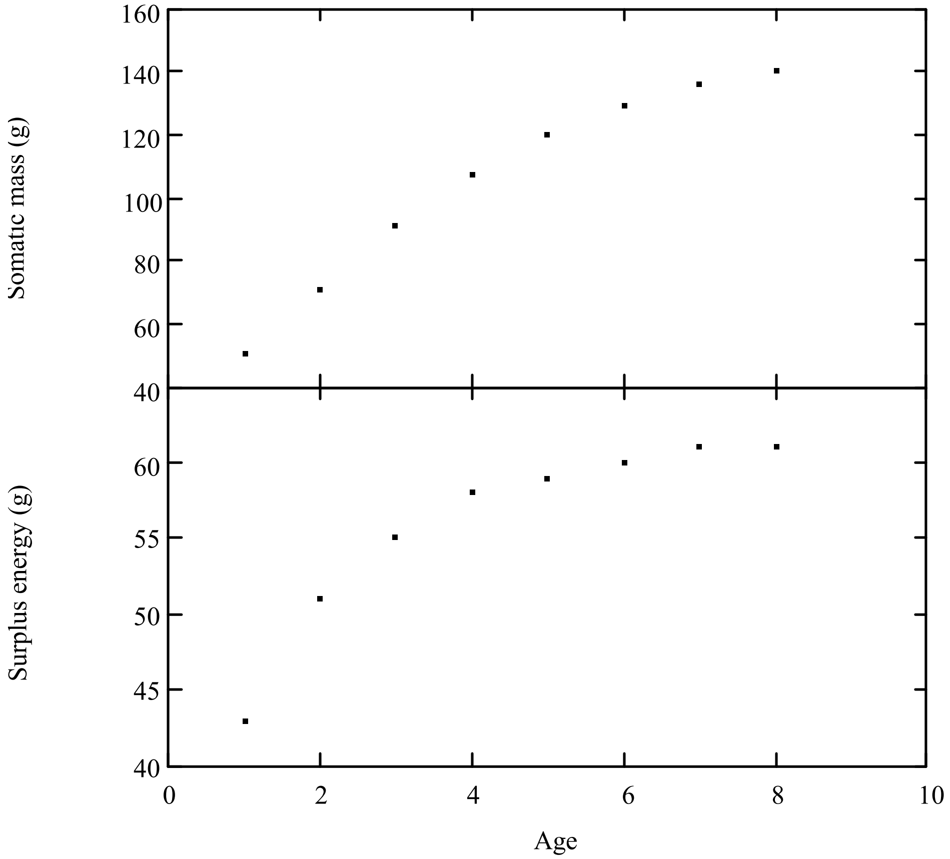

Fig. 16. Somatic mass and surplus energy versus age for West Coast Vancouver Island female herring.

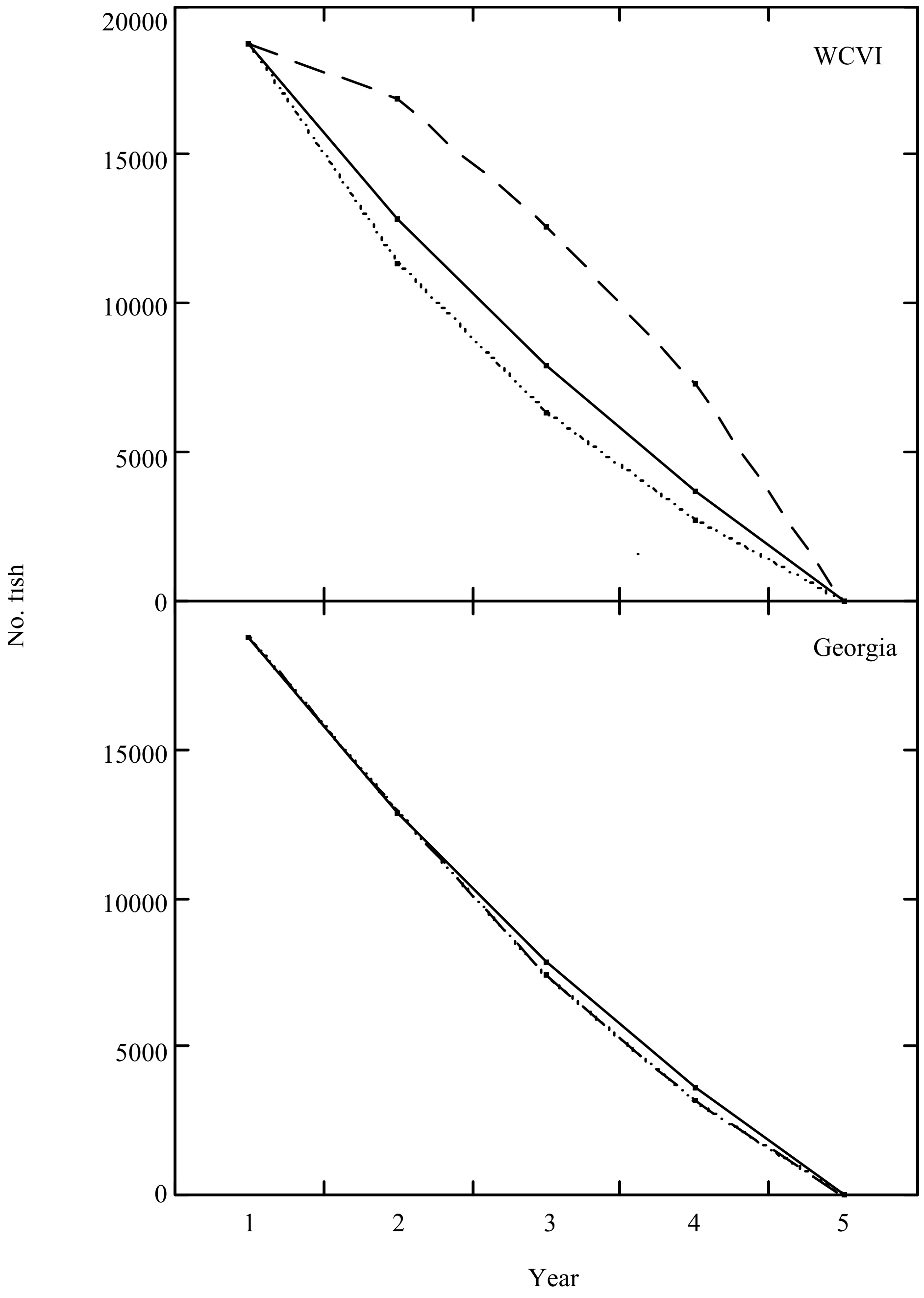

Fig. 17. Abundance trajectories for a hypothetical herring population. Lines represent abundance trends based on M estimated by the predictive regression (solid line), age-structured model (short-dashed line) and used by the escapement model (long-dashed line).