

Effects of climate, stock size, and region on recruitment and growth of Pacific halibut

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Abstract

This paper compares long-term changes in Pacific halibut *Hippoglossus stenolepis* recruitment and growth with long-term changes in climate and stock size. It appears that environmental variability—both interdecadal and interannual—is responsible for most of the observed variation in Pacific halibut recruitment. The large changes in growth rates that occurred during the twentieth century appear to have been density-dependent responses to changes in stock size, with virtually no environmental influence. [An abridged version of the paper will be published (Clark and Hare in press).]

Introduction

The productivity of the Pacific halibut stock, like all others, depends on its rates of recruitment and growth, both of which have varied greatly over the last century. The year classes spawned in the 1930s and early 1940s were strong, but thereafter year class strength dropped and remained low until the late 1970s, when it recovered to record levels and has generally remained high. Growth rates have also varied widely, from low levels in the 1920s to a peak around 1970 and then by the 1990s back down to the level of the 1920s. Older fish today weigh only about a third of what fish of the same age did 20 years ago (Clark et al. 1999).

This paper investigates the roles of climate and stock size in these changes. As shown by a number of time series, the climate of the North Pacific has alternated on a decadal scale between two regimes in a pattern named the Pacific Decadal Oscillation (PDO) by Mantua et al. (1997). The two regime types are termed positive and negative because they are opposite in some important features. During positive regimes (1925 through 1946 and 1977 through at least the late 1990s), the Aleutian Low is usually strongly developed, Alaska coastal surface waters are warm, central North Pacific surface waters are cool, and productivity tends to be high in the Alaska Gyre and low in the California Current region. During the last negative regime (1947-1976) all those conditions were usually reversed. Positive regimes clearly enhance the productivity of Pacific salmon *Oncorhynchus spp.* stocks in Alaska (Hare and Francis 1995) and the recruitment of Pacific halibut, which spawn and rear mainly in Alaska waters (Clark et al. 1999).

The identification of regime shifts is based on the analysis of many physical and biological time series (e.g., air and sea surface temperatures, sea level pressure, annual tree rings, salmon catches) because there is a great deal of interannual variation in any one index during a decades-long regime. For our analysis we use the positive/negative regime classification to represent persistent climate type, with shifts in 1925, 1947, and 1977. These regime shifts were identified in independent studies by Hare and Francis (1995), Mantua et al. (1997), and Minobe (1997, 1999).

We also use the annual PDO index described by Mantua et al. (1997) to represent the weather in a given year, which may be what matters most for the Pacific halibut year class spawned in that year. The annual PDO index is the leading principal component of gridded

monthly North Pacific sea surface temperatures in winter (averaged from November of the previous year through March, then standardized over years by subtracting the mean and dividing by the standard deviation).

Recruitment

IPHC has estimates of catch at age by regulatory area dating back to 1935. Before the mid-1990s, however, fishing was light and spotty in Areas 3B and 4, while Areas 2A, 2B, 2C, and 3A have been fully exploited since about 1920. For the fully exploited areas, we have calculated estimates spawning biomass and subsequent recruitment (defined here as abundance at age 6) using standard age-structured methods. We cannot calculate similar estimates for Areas 3B and 4 because the standard methods only reconstruct the exploited part of the stock. We therefore base our analysis here, like all previous halibut studies, on the relationship between spawning biomass and recruitment in Areas 2 and 3A combined.

IPHC analyses of halibut productivity and harvest policy (Quinn et al. 1985; Parma 1991, 1993, 1997; Hare and Clark 2001) have usually assumed one or more kinds of spawner-recruit relationships and then evaluated alternative harvest rates on the basis of simulations. A simple scatterplot of halibut year class strength against spawning biomass shows a dome-shaped relationship, suggesting a Ricker curve:

$$R = \alpha \cdot S \cdot \exp(-\beta \cdot S)$$

where S is spawning biomass, R is subsequent recruitment (here measured as the abundance of age-6 fish 6 years later), and α and β are parameters. In terms of spawner productivity, the relationship is:

$$(R/S) = \alpha \cdot \exp(-\beta \cdot S)$$

or on a logarithmic scale:

$$\log(R/S) = \log(\alpha) - \beta \cdot S$$

If the Ricker curve is accurate for halibut, there should be an inverse linear relationship between the log of spawner productivity and spawning biomass within a given climate regime. A regime shift could alter the value of α or β or both, producing a set of points centered on a different line, with a higher or lower intercept (if α changed) or slope (if β changed) or both. A straightforward plot of the halibut data shows just this sort of pattern (Figure 1), with years during positive PDO regimes mostly grouped around an upper line and years during negative PDO regimes grouped more loosely around an approximately parallel lower line. That is, the regime-specific Ricker model fits suggest that α is higher in positive PDO regimes but that β is the same. Hare (1999) reports fits with different numbers of regime-specific α and β parameters, all of which look similar to Figure 1.

But the data show a number of systematic deviations from the model fits, especially the points from the negative PDO regime (1947-1976), where the 1950s and 1970s are almost all above the line and the 1960s are all below the line. These systematic deviations result from dramatic temporal trends in spawner productivity (Figure 2). Spawner productivity fell steadily

from 1935 to 1947 and rose steadily from 1965 to 1977, both times in the absence of a regime shift or any important change in spawning biomass. It is clear that most of the variation in spawner productivity prior to 1977 resulted from factors that are not even considered when regime-specific Ricker models (i.e., models with separate sets of parameter estimates for each regime) are fitted. Since 1977 spawner productivity has again fallen steadily in the absence of a regime shift. This time the decline has occurred during a period of steadily rising biomass, but in view of the earlier history it is questionable whether biomass had anything to do with it.

Plots of the time series of spawning biomass, PDO values, recruitment, and spawner productivity (Figure 3) suggest an explanation for the trends in spawner productivity. The steady decline in productivity in the 1940s is seen to coincide with a decreasing trend in the PDO, and the increase in the 1970s is seen to coincide with an increasing trend in the PDO. After 1977, spawner productivity declines despite a continuing increase in the PDO, but actual recruitment continues to track the PDO quite well through the peak in 1987-88 and the drop thereafter. Overall there seems to be a better match between the PDO and recruitment than between the PDO and spawner productivity. The important point is that recruitment appears to be strongly influenced by inter-annual variation in the PDO, either instead of or in addition to the decadal variation characterized as regime shifts.

The time series plots suggest considering and comparing two models of recruitment that take account of the apparent influence of the annual PDO value:

Model 1. A regime-specific Ricker model of spawner productivity $\log(R/S)$ with an added annual PDO term:

$$\log(R/S) = \log(\alpha_i) - \beta_i \cdot S + \gamma_i \cdot PDO$$

or equivalently

$$\log(R) = \log(\alpha_i) - \log(S) - \beta_i \cdot S + \gamma_i \cdot PDO$$

where i indexes regime type.

Model 2. A regime-specific linear predictor of recruitment $\log(R)$ based on the annual PDO alone:

$$\log(R) = \delta_i + \gamma_i \cdot PDO$$

As a starting point, the two models were fitted with separate estimates of the intercept parameters α and δ for positive and negative regimes. Single values of the slope parameters β and γ in both models were estimated for all years in the series. Fits of Model 1 and Model 2 are shown in Figure 4a. Neither of the fits matches the trajectory of recruitment very well. The estimates of γ are both small and not significantly different from zero. The predicted recruitments are too high in the 1940s and 1960s, and too low in the 1970s and 1980s.

Values of spawner productivity and recruitment in the 1960s are anomalously low in both Figure 2 and Figure 3. These were years when both spawning stock size and annual PDO values were near average levels, but of the ten smallest year-classes in the entire series, nine were spawned in the 1960s. We do not know why, but we suspect it is not a coincidence that those were the year-classes that as juveniles went through the intensive distant-water trawl fisheries of

the 1960s and early 1970s. While we include estimates of juvenile and adult bycatch in our calculations of year-class strength, the fact is that the estimates of bycatch from that period are not reliable and we may be seriously underestimating the year-classes involved. In order to allow for the low apparent productivity of the 1960s, whatever the reason, we decided to estimate separate intercept parameters in both models for the years 1959-1970, which are the ones that fall below expectations in Figure 4a.

Making that change substantially improves the fit of both models (Fig. 4b). There is still a tendency, however, for both Model 1 and Model 2 to overestimate recruitment in the period before the 1960s and to underestimate it in the years after. To account for the remaining temporal pattern, separate values of the intercept parameters were estimated by regime type for the years before and after the 1960s, meaning that separate estimates were made for the years 1935-1946 (early positive regime), 1947-1958 (early negative regime), 1959-1970 (all in the negative regime), 1971-1976 (recent negative regime), and 1977-1994 (recent positive regime). They all turned out to be significantly different. Other things (spawning stock size and annual PDO values) being equal, years in positive regimes were about 25% more productive than years in negative regimes within each period, and both kinds of regime were about 30% more productive in the period after the 1960s than in the period before the 1960s (Table 1 and Figure 4c).

The difference between periods may reflect a real difference in stock performance due to unknown factors that are not considered in this analysis, or it may be an artifact of unknown trends or biases in the estimates of spawning biomass and recruitment. The early estimates are based on data and methods that differ in some respects from recent assessment data and methods, so it would not be surprising if there were some purely technical difference in the level of the estimates for the two periods.

While the regime effect is significant, leaving it out of the models does not greatly affect the fits. When only three intercept parameters are estimated (one for each of the periods 1935-1958, 1959-1970, and 1971-1994), the fits are nearly indistinguishable from the 5-intercept fits (Fig. 4d). What happens is that the estimate of the coefficient γ on the annual PDO value increases from 0.12 to 0.18. Evidently there is a tradeoff between the regime-specific intercept estimates and the coefficient on the annual PDO, which is not surprising. While the fits appear very similar, this 3-intercept model fit is not as close and is inferior to the 5-intercept model when judged by the Akaike Information Criterion (Wei 1990, p. 153).

We experimented with models that had lagging and/or leading PDO terms in addition to the PDO value in the year of spawning. For example, a centered three-year series would appear in Model 2 as:

$$\log(R_t) = \delta + \gamma_{-1} \cdot PDO_{t-1} + \gamma_0 \cdot PDO_t + \gamma_{+1} \cdot PDO_{t+1}$$

The logic of this sort of model is that conditions in the year of spawning might be affected somehow by the previous few years (lagging PDO terms) or that year-class strength might be affected by conditions not just in the year of spawning but also in the first few years of life (leading PDO terms). None of these models substantially improved on the fits obtained with the single PDO value in the year of spawning, and the estimates of the coefficients were generally small and not significantly different from zero. The coefficients on leading PDO terms were consistently positive, suggesting that there may be some small continuing effect of the PDO on juveniles even though it is not statistically significant. The coefficients on lagging terms were not consistent as to sign, suggesting there really is no effect.

We computed separate estimates of β and γ for each PDO regime and for each of the three periods considered in Figure 4d. The estimates of β did not differ significantly in any case. The estimates of γ did not differ among the three periods, but they differed between regimes, with a significantly lower estimate for the negative regime (about 0.05 vs 0.15). But the difference was only marginally significant, and allowing γ to vary by regime hardly changed the fits, so for simplicity and consistency we are inclined to ignore the difference.

On the basis of our analysis, we conclude that the 5-intercept forms of Model 1 and Model 2 shown in Fig. 4c fit the data as well as any of the more complicated models. While quite parsimonious, they track the general pattern of the data series quite well, and there are no large systematic patterns in the residuals although there are some short runs of high and low values.

Remarkably, the fits of Model 1 and Model 2 are nearly the same, both as a statistical matter and as a practical matter. Although the coefficient on spawning biomass (β) in Model 1 is significant, this model fits no better (in fact a little less well) than Model 2, which does not use information on spawning biomass at all. The Akaike Information Criterion and the Schwartz' Bayesian Criterion (Wei 1990, p. 153) are two measures of goodness of fit that are commonly used to choose between models that have different parameter sets. By both of these criteria (and the older root mean squared error criterion), Model 2 is superior to Model 1 in all cases, albeit by only a small margin.

The estimates of γ and the predicted recruitments are nearly the same for the two models because most of the spawning biomass values in the historical series are between 100 and 200 million pounds, and in that range the fitted Ricker curves are at their peak and therefore vary little. Figure 5 shows recruitment predictions under Model 1 for the range of observed spawning biomass levels and PDO values, using parameter estimates calculated for the most recent period 1971-1994. Only at the highest observed spawning stock sizes does the estimated spawner-recruit relationship have much effect on the recruitment predictions. The fit in this region reflects the coincidence of an increasing biomass and decreasing spawner productivity at high stock sizes in the 1980s and 1990s, which may well be no more than a coincidence. Even if the effect is real, it amounts to only about a 20% reduction from the maximum. Meanwhile the combined effects of regime type and the annual PDO account for nearly the whole range of variation in recruitment.

Regional differences in recruitment and spawner productivity were investigated by fitting the 5-intercept forms of Model 1 and Model 2 to data from each of the areas 2AB, 2C, and 3A separately (Figure 6). Fitting a Ricker model to a subset of the stock is questionable because it is not known to what extent the recruits to each area are the progeny of the spawners from that area. They may be, or they may simply be part of a mixed coastwide dispersion. It turns out that the area-specific fits in Areas 2AB, 2C, and 3A are similar to the combined fits in that Model 2 (PDO only) provides just as good a fit as Model 1, so the question of reproductive independence can be largely ignored.

The area-specific fits do show quite different contrasts between periods. In Area 2AB the parameter estimates indicate that, other things being equal, recruitment and productivity were 20-25% lower in recent years (since 1970) than in the early period (before 1959). In Area 3A, other things being equal, recruitment and productivity were about 100% *higher* in the recent period. Area 2C is intermediate, with relatively little variation in recruitment apart from the run of low values during the 1960s.

The contrast between areas in this respect suggests that there is some real (unknown) difference between the early and recent periods rather than just some technical difference

resulting from features of the assessment data and methods. The latter differ among periods but not among areas, so a purely technical difference would be expected to be the same in all areas.

Growth

In principle growth is simple to estimate, but there are some features of the Pacific halibut stock, fishery, and data that complicate the task. Females grow faster than males, and the fish are eviscerated at sea on commercial vessels, so commercial size samples are affected by unknown variations in sex ratio that would contribute to variations in average size at age. The commercial data are also complicated by the effect of changes in the minimum size limit and a long period (1962-1990) when the fish in commercial samples were not actually measured.

The IPHC does have survey and other research samples from Areas 2B and 3A going back to the 1920s that contain measured sizes of females and males, and we base our analysis here on those females, but the research data contain some large gaps. They are also surprisingly noisy, with the average weight increments of females of a given year class in a given area in successive years showing a great deal of variability, so that trends in growth over time are not easily discerned from a simple plot of year-to-year differences.

The general patterns are clear. The average weight at age 8 increased through the middle of the twentieth century, reached a maximum around 1970 (several years before the regime shift of 1977), and since then has decreased to approximately the level seen in the 1920s (Figure 7). A similar increase followed by a return to the level of the 1920s is seen among older fish, but the peak occurs a few years later as the effect of the decrease in size at age 8 propagates through the age spectrum. In Area 3A there was a dramatic drop in size at age between 1989 and 1992. It appears that growth was close to nil among most age groups in that period. (There are no data for the years 1990 and 1991.)

To estimate trends in growth, we fitted a simple model to the historical weight-at-age data, consisting of two time series: mean weight at age 8 in each year, and weight increment among older fish in each year. The predicted weight of a given year class at a given age was then its weight at age 8 plus the estimated weight increments in each year thereafter. This is basically a linear model of growth in weight with a time-varying intercept and slope. We excluded fish younger than age 8 from the model fit because the average size of younger fish in setline catches is greatly affected by setline selectivity. At ages 8 and 9 the weight increment in setline catches is lower than at ages 10+, so the model included a fitted coefficient for each of those ages to scale down the annual increment estimated for older fish.

To smooth the data and fill the gaps, each time series (weight at age 8 and annual weight increment) was modeled as a broken-stick function, i.e. a set of points joined by straight lines. Parameter values were estimated for each of the years 1920, 1930, 1950, 1960, 1972, 1980, 1988, 1989, 1992, and 2000, and values for the other years filled in by linear interpolation. The years chosen as break points are just the decadal years with a few exceptions: 1940 was left out because of the lack of data from the 1940s, 1972 was used instead of 1970 because that is when the weight at age 8 peaked, and 1988/1989/1992 were used instead of 1990 to allow for the possibility of one or more abrupt changes at that time.

The fitted values do provide a good description of the trends (gray lines in Figure 7). The overall form of the fitted time series of weight at age 8 and annual weight increment are very similar to each other and very similar between Area 2B and 3A (Figure 8). The path followed between 1920 and 1950 is not well determined owing to large gaps in the data series, but the estimated path after 1950 is well supported. The abrupt collapse of growth rates in Area 3A in

1989 shows up clearly, but thereafter growth recovers to a level that while low and declining is back in line with a more gradual long-term trend. The 1989-1992 event therefore appears to have been an episode apart from the long-term processes affecting growth. Because the long-term trends are so similar in Areas 2B and 3A, it is reasonable to run a single smoother through the estimated series to represent coastwide trends in growth (gray lines in Figure 8).

The estimated time series of weight at age 8 shows a strong negative correlation with smoothed abundance at age 8, representing average year class strength during the early years of life (Figure 9, middle left). It shows no consistent relationship with either smoothed spawning biomass (Figure 9, upper left) or the smoothed annual PDO index (Figure 9, lower left). For the latter comparisons, the time series of smoothed spawning biomass and smoothed PDO were lagged 4 years to represent average conditions during the first 8 years of life.

The estimated time series of annual weight increment at ages 10+ similarly shows no relationship with the current PDO but a strong negative correlation with spawning biomass and numerical abundance at ages 10+ (Figure 9, graphs on right). The two measures of adult abundance are themselves highly correlated, but it appears that there is a more consistent relationship with abundance in number than with abundance in biomass.

Discussion

Our general conclusions are that environmental variability is responsible for most of the observed variation in Pacific halibut recruitment while density dependence is probably responsible for most of the observed variation in growth rates.

Our analysis shows that Pacific halibut recruitment is strongly influenced by climatic regime and weather in the year of spawning. The regime effect was known in a general way before (Clark et al. 1999), but Ricker models with regime-specific parameters did not fit the data well. In this paper we have shown that good fits can be achieved by adding the annual PDO index as a covariate and allowing for (unexplained) differences among the periods before, during, and after the 1960s.

Although spawning biomass is a significant covariate of recruitment, models with and without a spawning biomass term produce virtually the same predictions of recruitment, meaning that over the range of spawning biomass levels present in the historical data, recruitment is not much affected by spawning stock size. At some sufficiently low level, spawning biomass would presumably limit recruitment, but it seems unlikely that spawning biomass will ever fall that low under the present management regime. The lowest values in the data—in the 1970s—resulted from a combination of unfavorable environmental conditions, high bycatch, and heavy directed fishing in the 1960s. The present IPHC management strategy is to apply a constant, moderate rate of fishing mortality, chosen in part to maintain spawning biomass above the historical minimum. Even a long run of environmentally unfavorable years and the resulting low recruitments would not be expected to lead to spawning biomass levels as low as those reached in the 1970s (Clark et al. 1999).

The overwhelming importance of environmental conditions in the year of spawning suggests that most of the regulation of year class strength occurs in that year and depends either on variable transport of eggs and larvae to nursery grounds by ocean currents, or on planktonic production that varies strongly with climate and weather. The response of the Gulf of Alaska zooplankton community to ocean climate variability has been documented in several studies. Observed changes have included a doubling of total zooplankton biomass following the 1976-77 regime shift (Brodeur and Ware 1992; Brodeur et al. 1996); an earlier and narrower

developmental period for *Neocalanus plumchrus*, a dominant copepod species, in response to warmer surface waters (Mackas et al. 1998); and extreme changes in zooplankton community composition (Mackas et al. 2001).

It thus appears that Pacific halibut recruitment is directly responding to an interannual modulation of regime changes with recruitment essentially established within the first year of life. Pacific salmon are generally thought to be most impacted by changes in the plankton community (Beamish and Bouillon 1993; Hare et al. 1999), but the 6-month planktonic residency of age-0 Pacific halibut exposes them to essentially the same environment as juvenile Pacific salmon. Higher on the food chain, community structure is more persistent and the effects of both weather and climate on species abundance appear to be more gradual (Francis et al. 1998; Anderson and Piatt 1999).

There is no explanation in our analysis for the decline in average recruitment that occurred in the southern areas (2A and 2B) and the large increase that occurred in the north (Area 3A) during the twentieth century. This was a period when, quite apart from regime shifts, average sea surface temperatures increased, particularly during the last quarter of the century (IPCC 2001). It is possible that there has been a northward shift in the center of abundance.

The long-term rise and fall of growth rates had also been recognized in a general way before (Clark et al. 1999), but it was not until we actually fitted a model and estimated complete time series of weight at age 8 and annual weight increment thereafter, that we were able to discern that growth rates are closely related to abundance and unrelated to environmental conditions (at least as measured by the annual PDO index).

It is not clear how Pacific halibut density affects growth, but it has been widely observed that flatfish growth rates tend to increase under exploitation (Rijnsdorp 1994). Before 1910, the Pacific halibut fishery was small scale and artisanal, but it added larger vessels and expanded rapidly over the next two decades. Fishing effort tripled between 1910 and 1930, and commercial catch rates fell by 70-90% between 1915 and 1930 (Thompson and Freeman 1930; Thompson and Bell 1934). Pacific halibut were certainly very abundant before 1920 and the stocks were rapidly depleted thereafter, so the small sizes at age in the first samples from the 1920s followed by an increase in growth rates is consistent with the notion of density dependent growth, as is the recent decline.

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Table 1. Summary of the 5-intercept recruitment model fits (Fig. 4c). Three measures of goodness of fit are shown. With $y_i, i=1, \dots, n$ denoting the observations, \hat{y}_i the model predictions, p the number of parameters in the model, $ssq = \sum (\hat{y}_i - y_i)^2$, and $s^2 = ssq/n$, they are:

$$\text{RMSE} = \text{root mean squared error} = \sqrt{ssq/(n-p)}.$$

$$\text{AIC} = \text{Akaike Information Criterion} = \text{constant} + 2n \cdot \log(s) + 2p.$$

$$\text{SBC} = \text{Schwartz' Bayesian Criterion} = \text{constant} + 2n \cdot \log(s) + p \cdot \log(n).$$

Only the variable part of the AIC and SBC are shown. For all three measures, a lower value indicates a better fit.

Model 1				Model 2			
Term	Years	Value	SD	Term	Years	Value	SD
$\log(\alpha_1)$	1935-1946	-2.27	0.10	δ_1	1935-1946	1.71	0.06
$\log(\alpha_2)$	1947-1958	-2.53	0.13	δ_2	1947-1958	1.46	0.07
$\log(\alpha_3)$	1959-1970	-2.93	0.10	δ_3	1959-1970	1.07	0.06
$\log(\alpha_4)$	1971-1976	-2.18	0.10	δ_4	1971-1976	1.72	0.09
$\log(\alpha_5)$	1977-1994	-1.95	0.14	δ_5	1977-1994	1.92	0.05
β	1935-1994	0.0067	0.0006	no β			
γ	1935-1994	0.12	0.03	γ	1935-1994	0.12	0.03
RMSE		0.199				0.195	
AIC		-187				-191	
SBC		-173				-178	

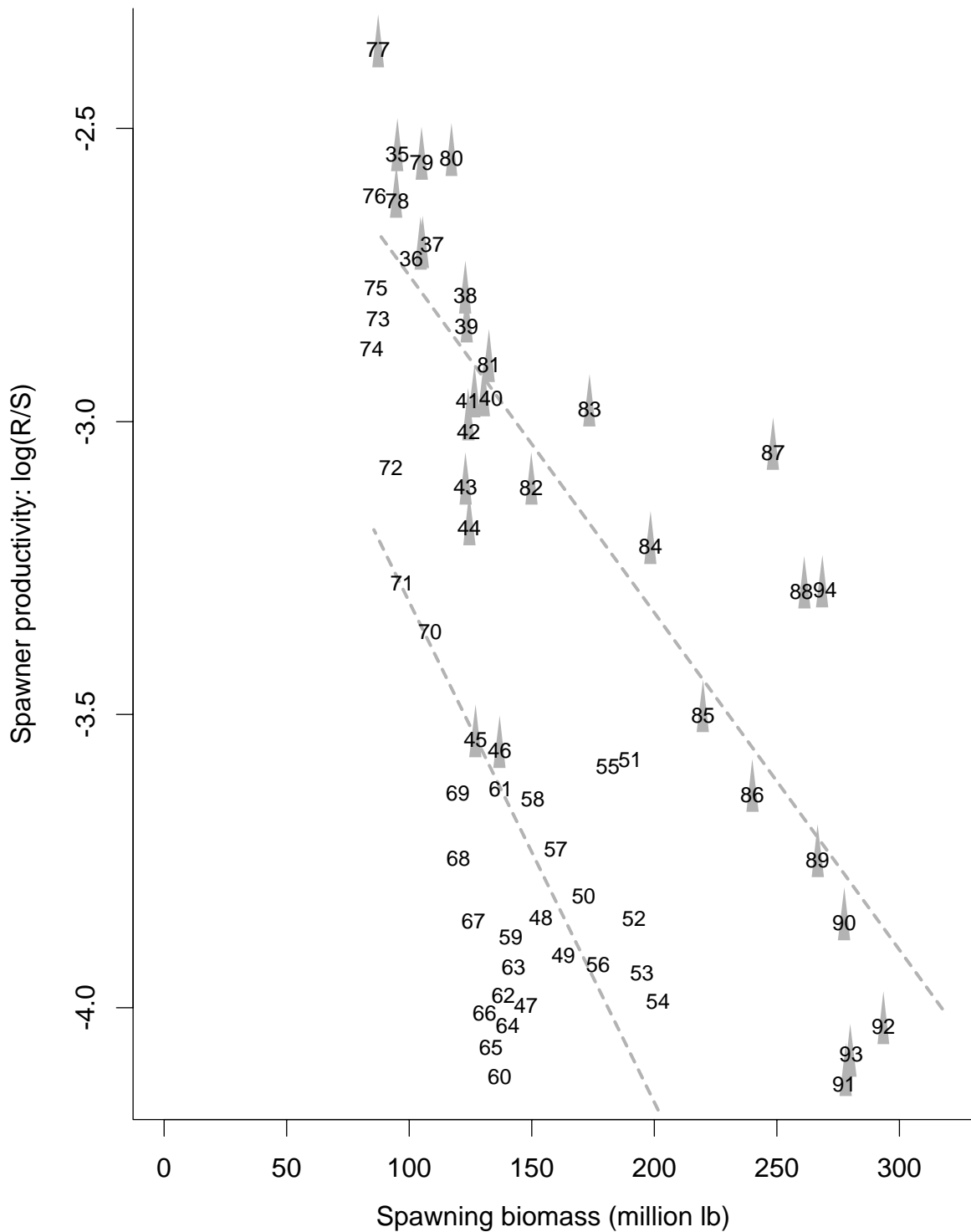


Figure 1. Productivity of halibut spawners vs spawning biomass. The numbers plotted are the year of spawning; i.e., the “85” point shows refers to spawning biomass in 1985 and resulting recruitment at age 6 in 1991. The gray triangles indicate years falling within a positive PDO regime (1925-1946 and 1977-present). Numbers are for IPHC Areas 2 and 3A combined.

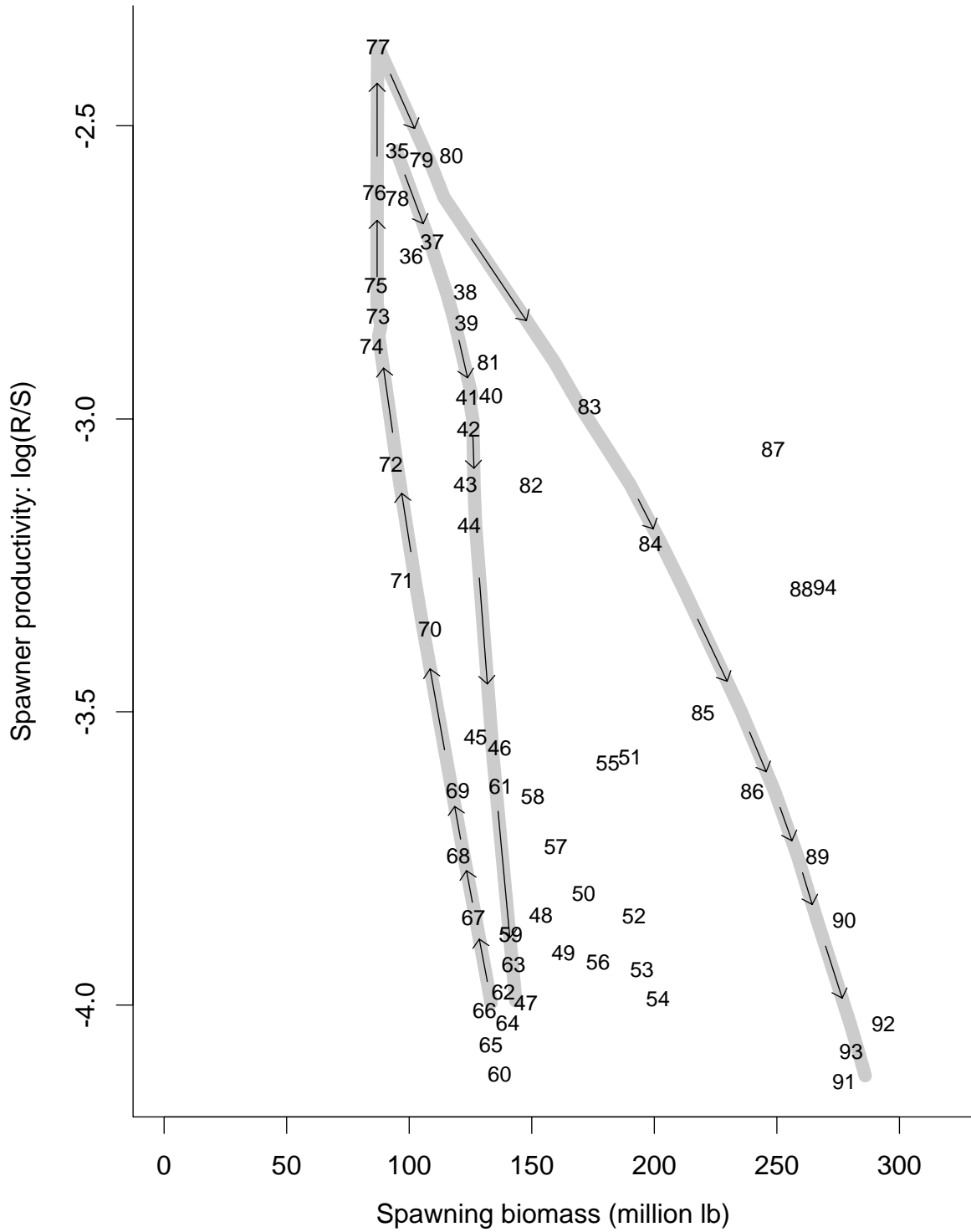


Figure 2. The same estimates of spawning biomass and spawner productivity plotted in Figure 1, but with temporal trends indicated.

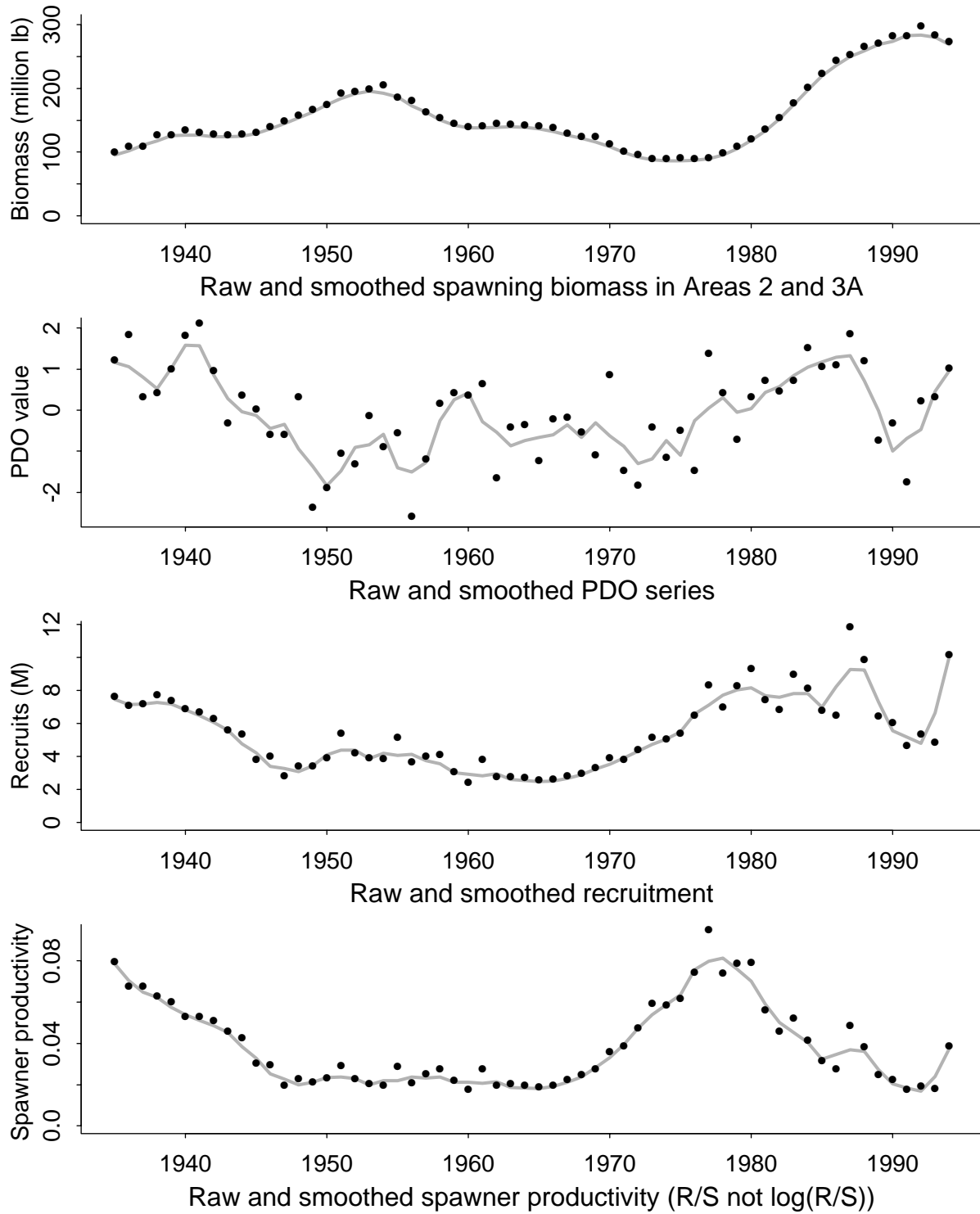


Figure 3. Time series of spawning biomass, PDO, recruitment, and spawner productivity in Areas 2 and 3A combined, 1935-1994.

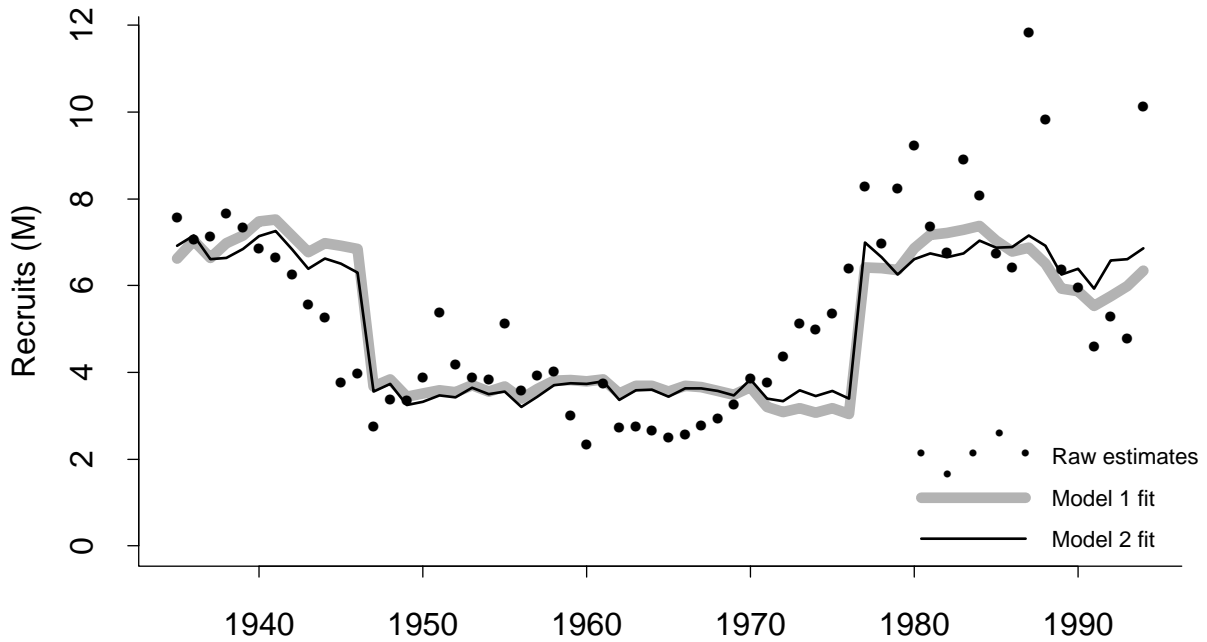


Figure 4a. 2-intercept fits: positive regimes (1935-1946, 1977-1994) and negative regime (1947-1976). Model 1 is the regime-specific Ricker with an added annual PDO term. Model 2 has only an intercept and the PDO term.

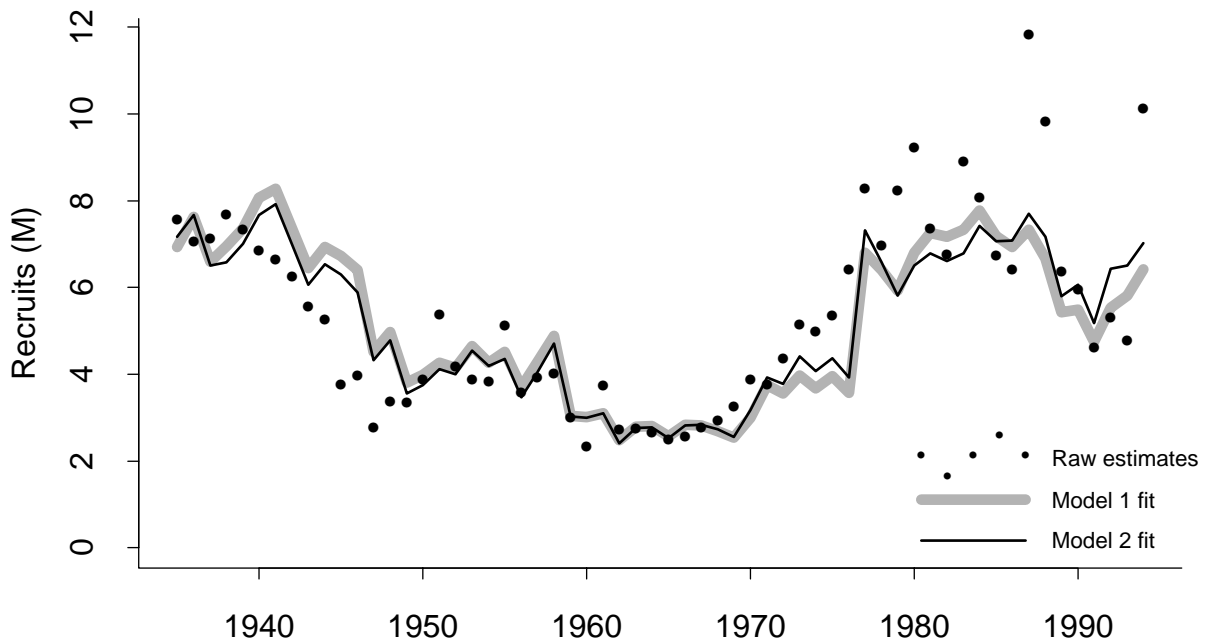


Figure 4b. 3-intercept fits: positive regimes(1935-1946, 1977-1994), the 1960s (1959-1970), remaining negative regime years before and after the 1960s (1947-1958, 1971-76).

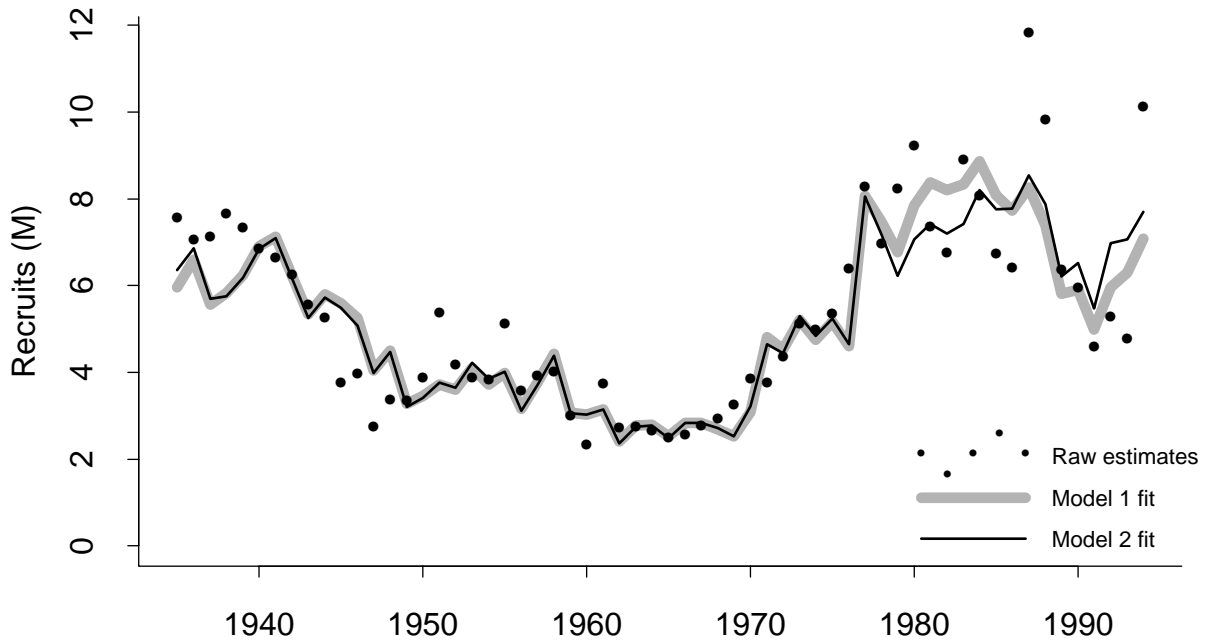


Figure 4c. 5-intercept fits: early positive regime (1935-1946), early negative regime (1947-1958), the 1960s (1959-1970), recent negative regime (1971-1976), recent positive regime (1977-1994).

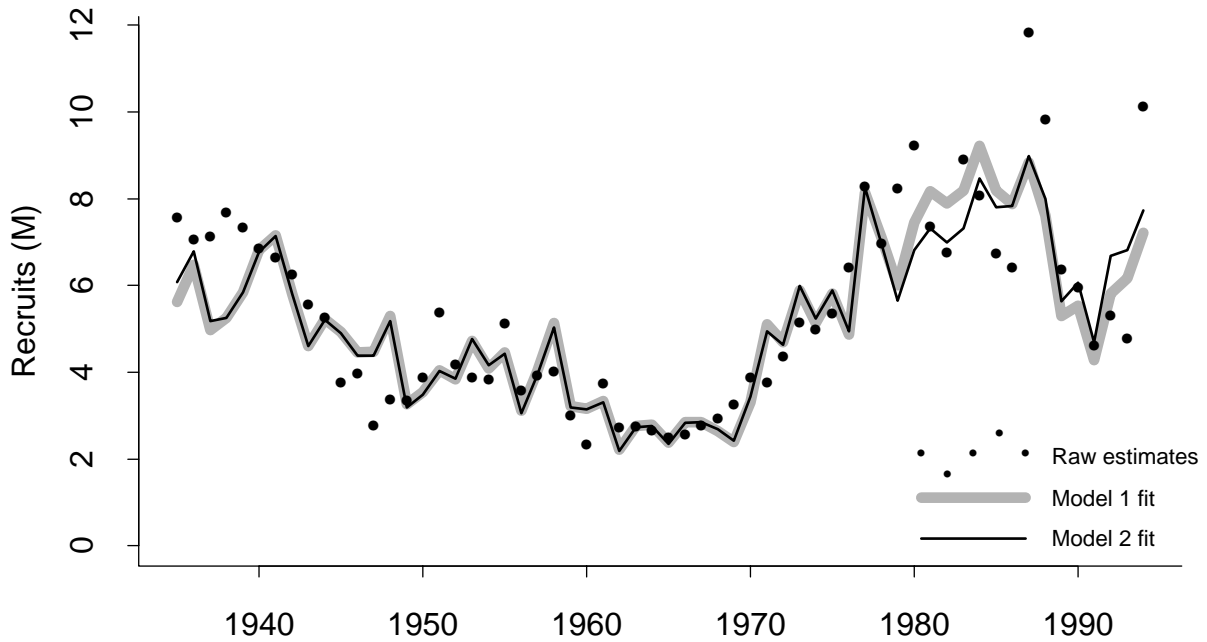


Figure 4d. 3-intercept fits by period not regime: early period (1935-1958), the 1960s (1959-1970), recent period (1971-1994).

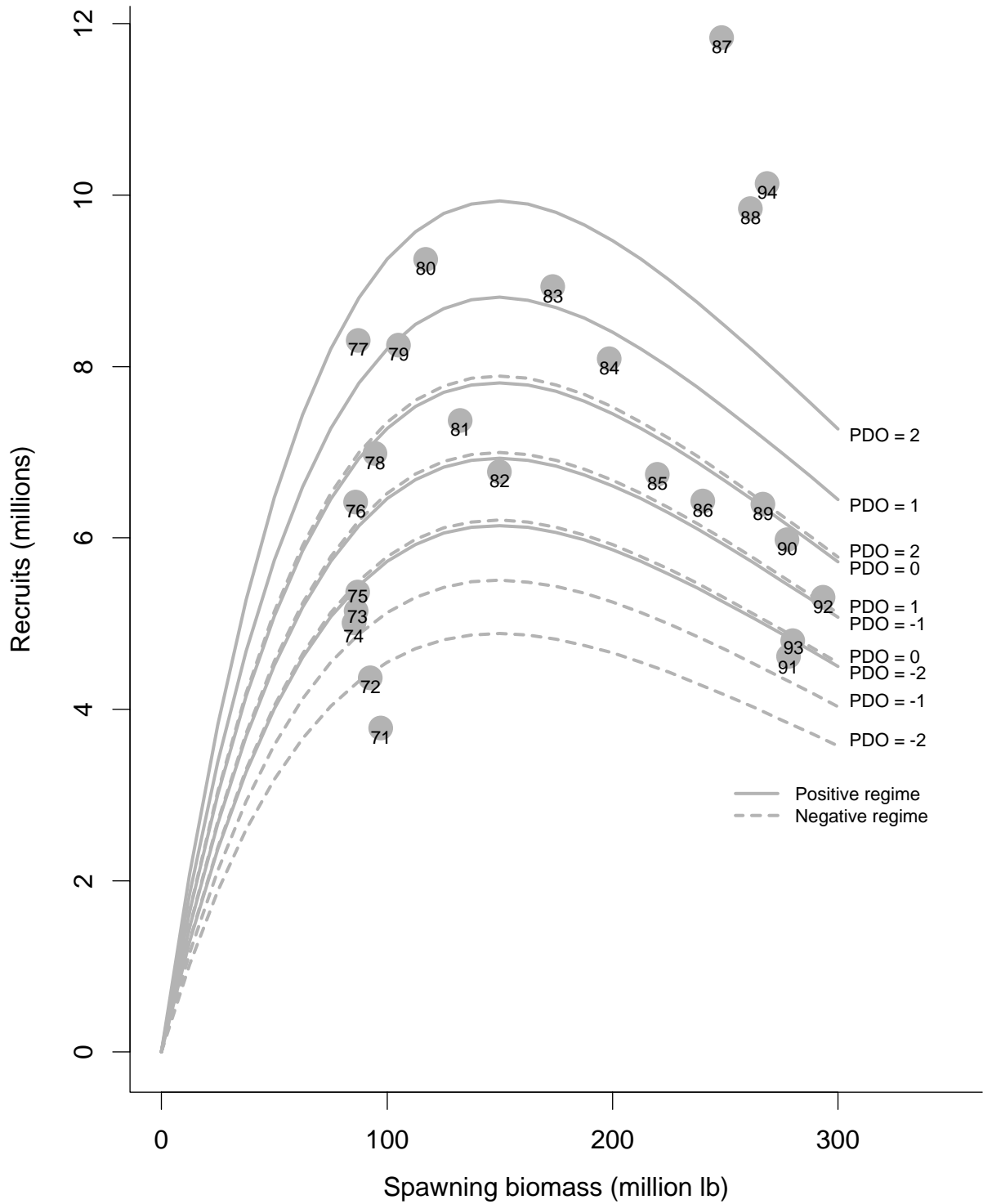


Figure 5. The fitted regime-specific Ricker curves (Model 1) FOR Areas 2 and 3A combined, plotted for the range of values of the PDO. The parameter estimates apply to the years 1971-1994.

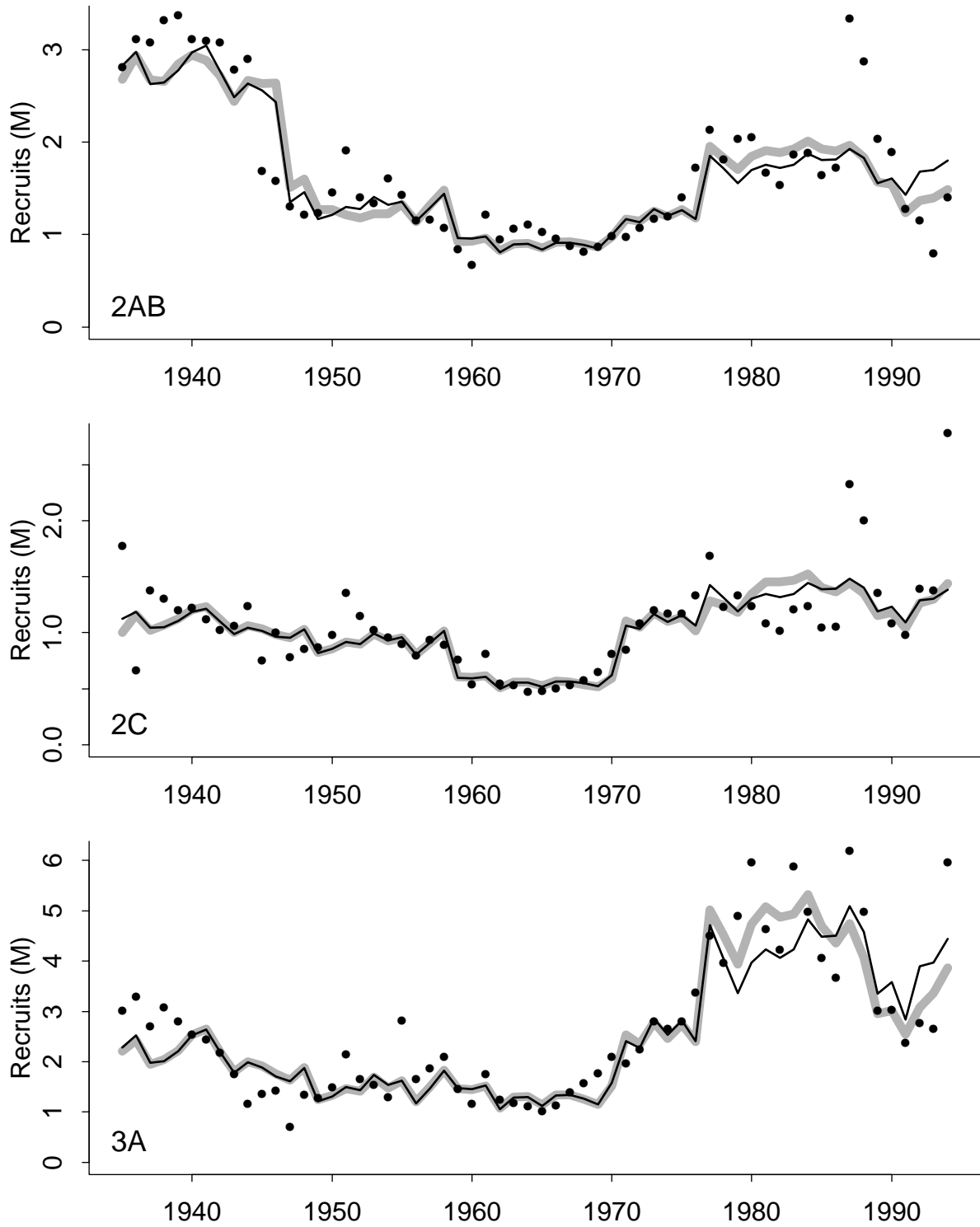


Figure 6. Regional fits of the 5-intercept forms of Model 1 (gray line) and Model 2 (black line).

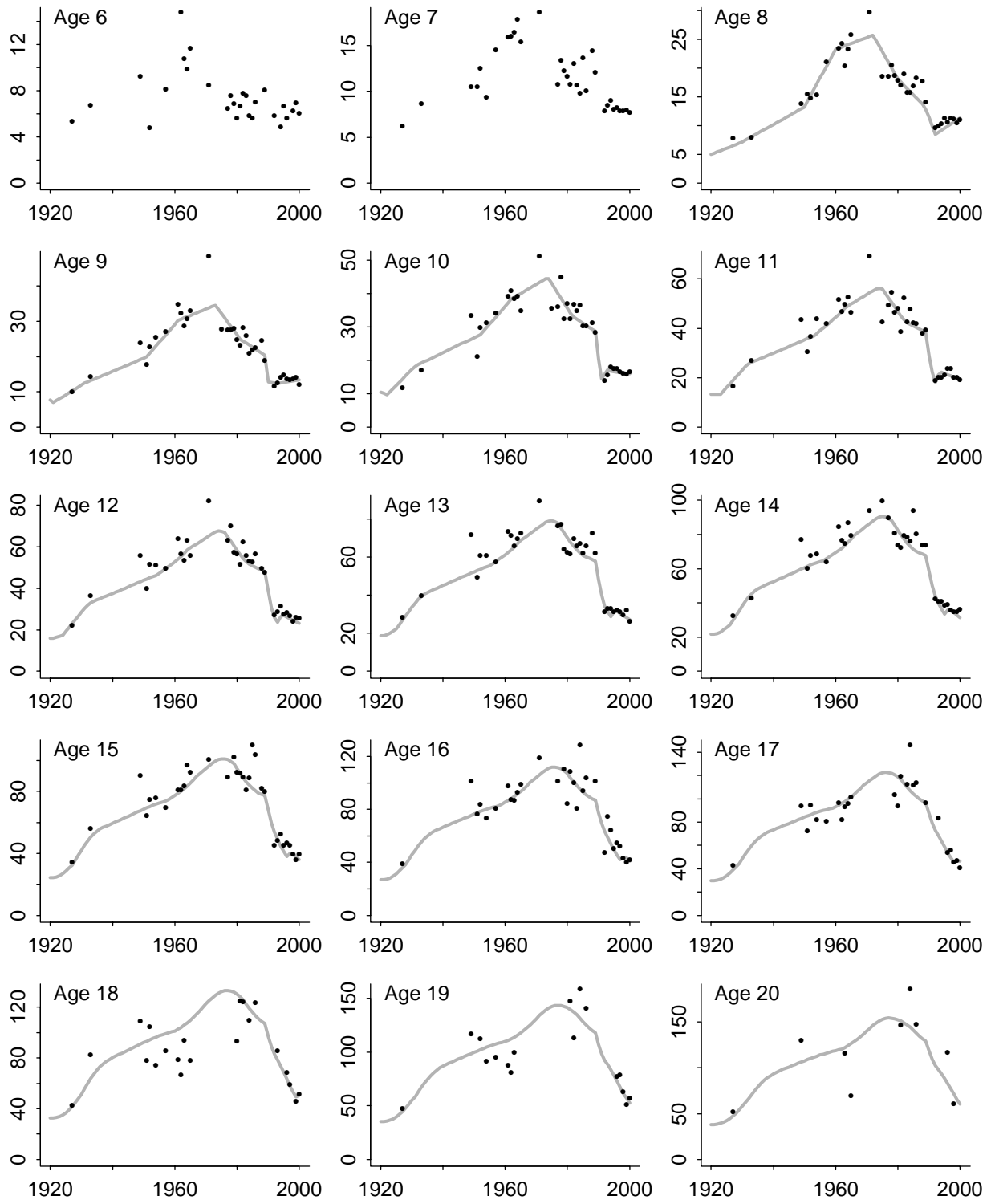


Figure 7a. Long-term trends in weight at age (net pounds) of females caught on IPHC setline charters in Area 3A. The gray line is the fit of a simple model.

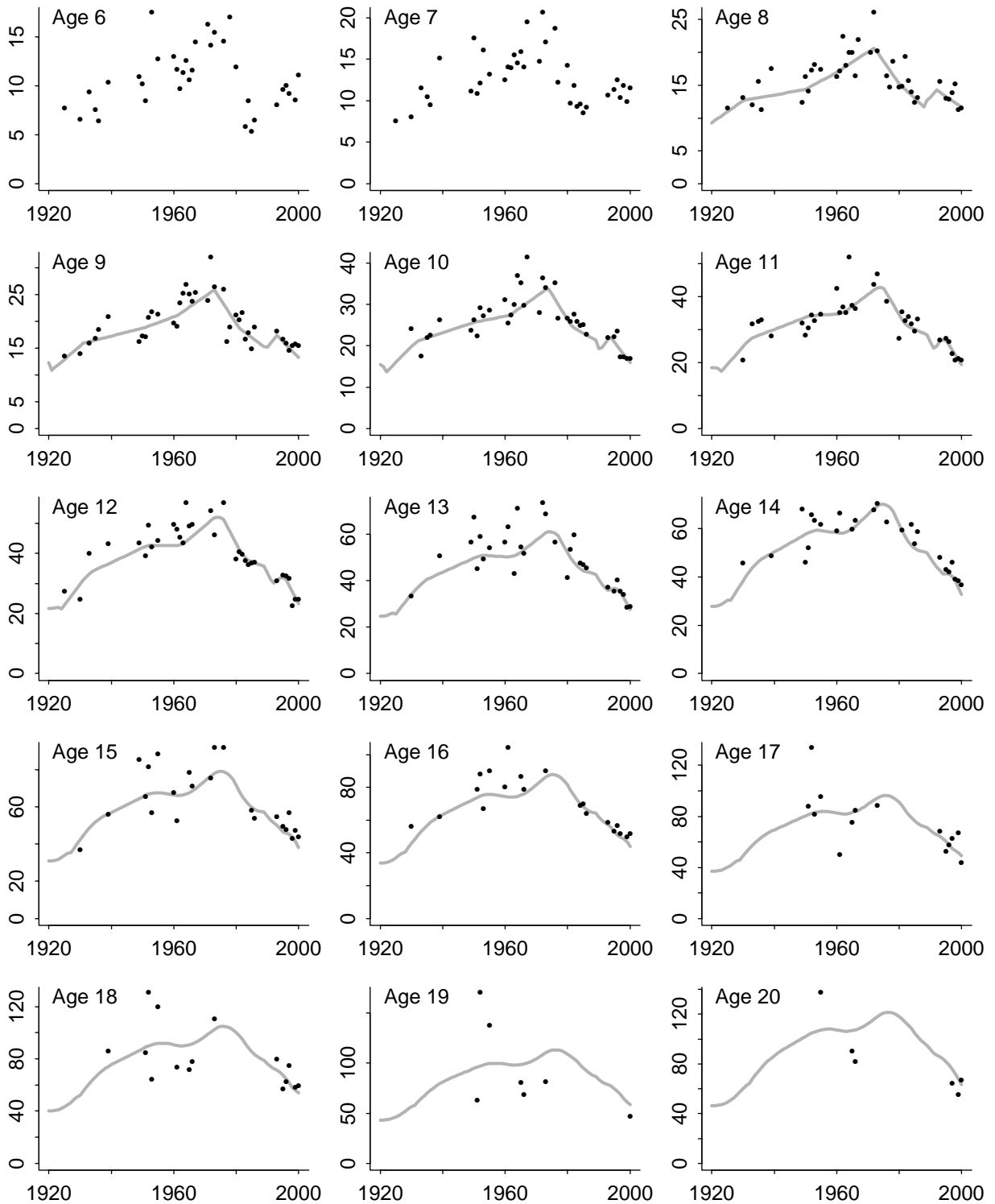


Figure 7b. Long-term trends in weight at age (net pounds) of females caught on IPHC setline charters in Area 2B. The gray line is the fit of a simple model.

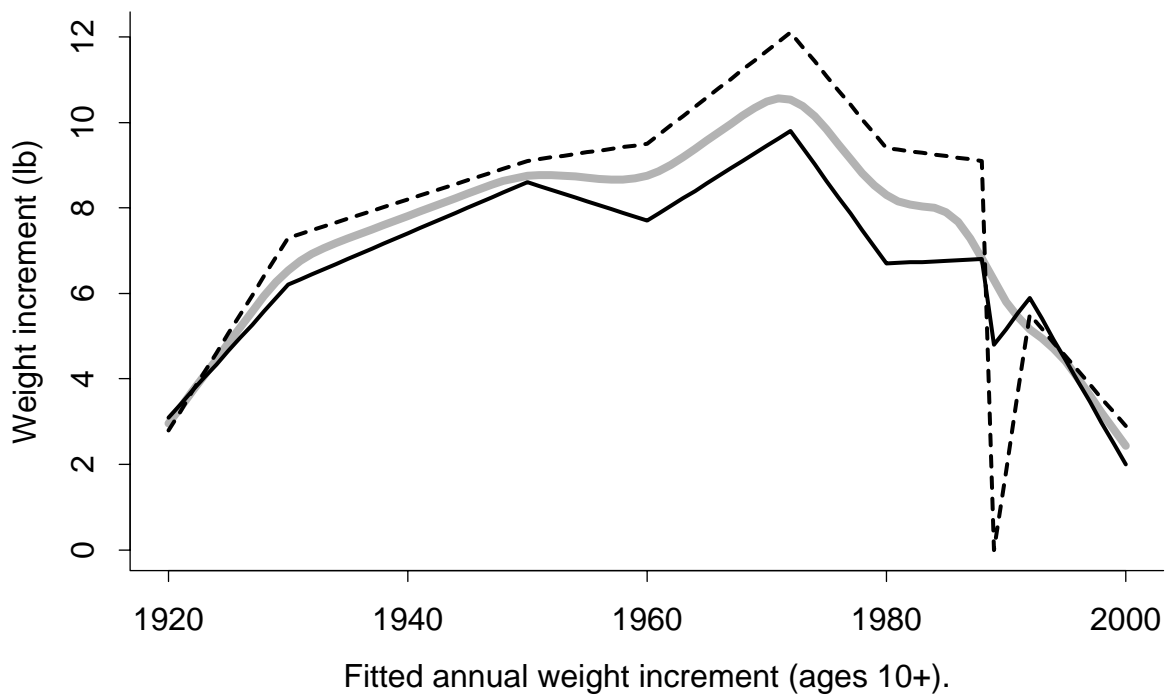
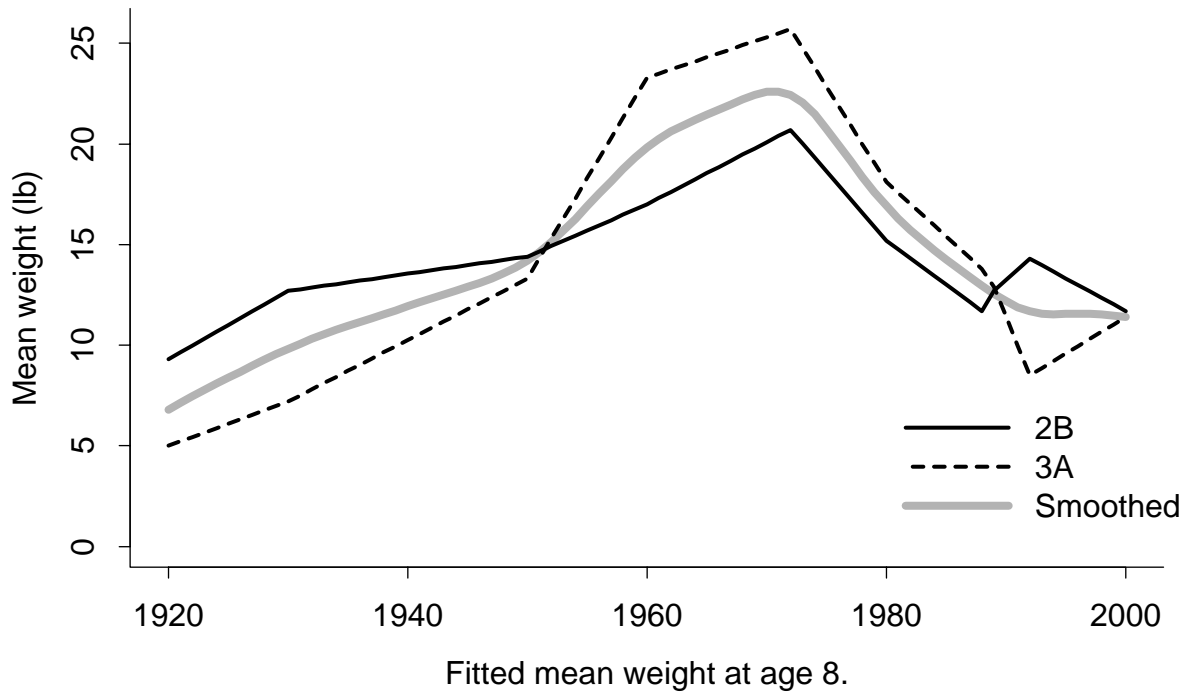


Figure 8. Model estimates of long-term trends in weight of females at age 8 (upper graph) and annual weight increment among older fish (lower graph).

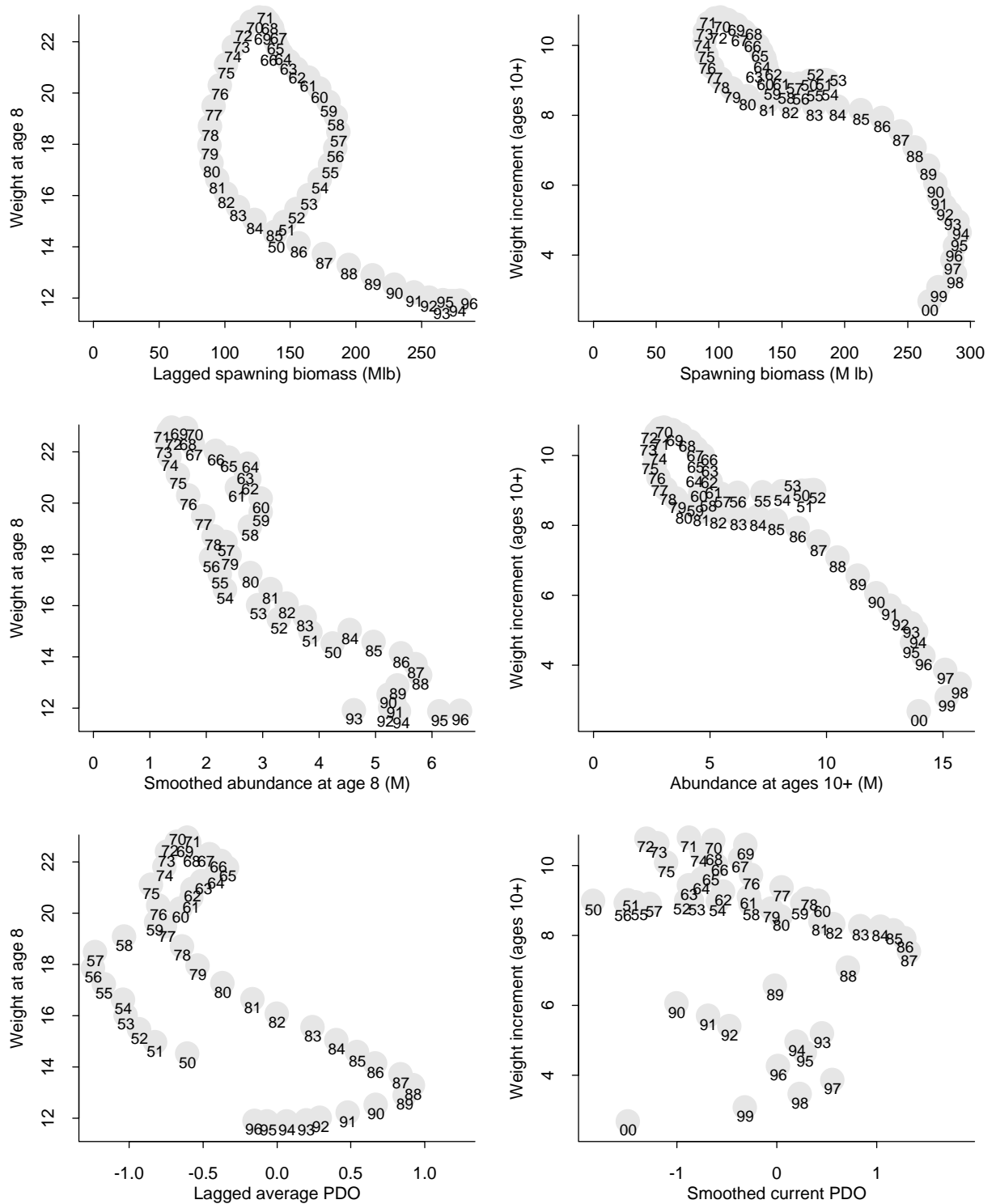


Figure 9. Model estimates of weight at age 8 (graphs on left) and annual weight increment among older fish (graphs on right) plotted against spawning biomass (upper graphs), numerical abundance (middle graphs), and annual PDO value (bottom graphs). Plotted numbers are years.