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Changes in productivity and reference points in Div. 3NO Atlantic cod and Div. 3LNO American plaice

by

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Abstract

Population productivity is not constant but rather varies over time. It is determined by recruits per spawner (RPS), the number of recruits produced in a year per ton of spawning stock biomass (SSB) and spawner per recruit (SPR), the cumulative spawner biomass produced by one recruit over its lifespan. This determines the level of fishing that the population can sustain without declining. We examined how the components of productivity have varied for Div. 3NO Atlantic cod and Div. 3LNO American plaice and how this variation has affected fishing mortality reference points. Productivity of both stocks has varied considerably, however periods of high and low productivity did not occur at the same time for the two stocks. The level of RPS played a major role in determining the level of fishing mortality that did not result in population decline. This was the main factor for both species, while for plaice there was also a substantial change in SPR caused by varying proportion mature at age. When productivity was at its lowest, the level of fishing mortality that could be sustained without causing rapid population decline was very low. The results of this study clearly demonstrate that the impacts of changing productivity can be rapid and very large and if fishing mortality reference points are not adjusted accordingly the results can be catastrophic. Fishing mortality reference points that can be updated using only recent data, but that incorporate all components of productivity, need to be developed.

Key words: reference points, fishing mortality, productivity, 3NO cod, 3LNO American plaice

Introduction

The productivity of a fish population determines the level of fishing that can be sustained without a decline in population size. Population productivity and resilience are determined by recruits per spawner (RPS), the number of recruits produced in a year per ton of spawning stock biomass (SSB) and spawner per recruit (SPR), the cumulative spawner biomass produced by one recruit over its lifespan. Together these two quantities determine the equilibrium yield response of the modelled population at different levels of fishing mortality (F) assuming a vector of selectivity at age. RPS is a function of fecundity of the parents and survival rate to the age at which recruitment is estimated. SPR is a function of mortality rate from age of recruitment onwards, growth in terms of weight at age, and maturation at age. These components vary over time and therefore so too does the overall productivity of the population.

Three commonly used fishing mortality reference points are F_{MSY}, $F_{0.1}$ and $F_{40\%SPR}$. $F_{0.1}$ is generally used as a target, $F_{40\%SPR}$ is a limit, while F_{MSY} is used as both depending on the fisheries management jurisdiction. F_{MSY} is the fishing mortality giving the maximum sustainable yield from a population (Schaefer, 1954). Fishing at levels above F_{MSY} will result in a population size that is lower than B_{MSY} the biomass giving maximum sustainable yield (*MSY*). $F_{0.1}$ is determined as the *F* where the slope of the yield per recruit curve is 10% of the slope at the origin. $F_{40\%SPR}$ is the *F* that reduces SPR to 40% of the unfished value. F_{MSY} is determined by all components of productivity and will therefore be affected by changes in any component of the productivity of the population (Morgan et al., 2009; Brooks, 2013). Reference points derived from yield per recruit or spawner per recruit do not include the recruitment component of productivity. Stock productivity is often assumed to be constant when estimating reference points, particularly F_{MSY}, including a stationary functional relationship between spawning stock biomass (SSB) and recruitment (A'mar et al., 2009; Brooks, 2013; Wayte, 2013).

If changes in productivity are short term, then the impact of assuming constant conditions is likely to be small. However, if the components of productivity are influenced by environmental conditions, changes may be prolonged as a result of extended periods of warm and cold ocean conditions (Colbourne et al., 2012). This leads to the possibility of population decline during periods of low productivity if *F* is set at a reference point level based on an assumption of constant, more productive, conditions.

In this study we examine time series of abundance and biological data on these stocks for indications of varying productivity levels, focussing on the warm periods in the 1960s and 2000s and the cold period of early 1990s. We estimate F_{MSY}, $F_{0.1}$, and $F_{40\%SPR}$ using the productivity from these periods and determine which components of productivity (recruitment, weight at age, maturity at age) are responsible for any differences. We also explore the implications of failing to recognize changes in stock productivity by examining the consequences of fishing the populations when they are at one level of productivity at reference points derived from a different level of productivity.

Materials and Methods

Productivity

The 1960s, early 1990s and 2000s represent warm, cold and warm periods respectively on the Grand Bank (Colbourne, 2004; Colbourne et al., 2012). We chose years within these time periods based on anomalies in the North Atlantic Oscillation (NAO), an index of ocean climate on the Grand Bank (Colbourne, 2004), as a basis for comparisons of productivity. The years 1962-1966, 1990-1994, and 2001-2004, were chosen to represent the 1960s, 1990s and 2000s respectively (Fig. 1). These were years with consistently high (cold) or low (warm) NAO. The 2000s were more variable and so there was only a 4 year period with a consistent NAO for which population data were available.

All analyses and data are based on information from the most recent assessment of Div. 3NO cod (Power et al., 2010) and Div. 3LNO American plaice (Rideout et al., 2011). Model estimates of population numbers at age in each year were extracted for each stock. Stock weights at age (for calculating spawning stock biomass, SSB) and catch weights at age (for calculating catch) were based on commercial sampling conducted for these assessments. Maturities at age in these assessments were modelled by cohort based on research vessel data. SSB was calculated as the sum of the product of model estimates of numbers at age (both sexes combined), model estimates of female proportion mature at age, and average beginning of year stock weights at age (both sexes combined). Recruitment was calculated from the assessments as number at age 1 such that

$$r = N_{agerec} \times e^{(m*a)} \qquad (1)$$

Where N_{agerec} is the number of recruits and *a* is 1 for 3NO cod and 4 for 3LNO American plaice and m =0.2 for all years for 3NO cod and for all years except from 1989-1996 for 3LNO American plaice when it was 0.53, as is the case in the assessment, to include an increase in natural and other unaccounted for mortality over that period (Morgan and Brodie, 2001).

Weight at age, maturity at age, RPS, SPR at F=0 and G_0 (average annual percentage SSB growth rate at low stock size in the absence of fishing) were examined to determine how they differed among The 1960s, the 1990s, the 2000s and average conditions. For each period, average weights, maturities and recruits per spawner were calculated. Variation in recruitment was expressed as RPS as this metric accounts for some of the influence of SSB on recruitment without assuming a specific form of a stock recruit relationship, other than a constant recruitment rate during each period.

SPR at F=0 was calculated as

$$SPR = \sum_{a=1}^{A} N_a W_a P_a \qquad (2)$$

Where N_a is the number at age starting with one recruit, W_a is the weight at age and P_a is the proportion mature at age. N_a is incremented as in equations 3 and 5 below but with F=0 and A is the terminal age in the assessment.

Potential annual percentage SSB growth rate (G_0) reflects the combined impact of RPS and SPR on the productivity of the stock at F=0. It was calculated as

$$G_0 = average\left(\frac{SSB_t - SSB_{t-1}}{SSB_{t-1}}\right) * 100 \qquad (3)$$

when the stock is below the break point of the hockey stick stock recruit curve and has a stable age composition.

Fishing mortality reference points

Projections of stock size were carried out to equilibrium over a range of fishing mortality values to determine the fishing mortality giving maximum sustainable yield (F_{MSY}). This reference point is affected by changing recruitment rate, weight and maturity at age. Population numbers at age were projected as:

$$N_{a+1,y+1} = N_{a,y} \times e^{-(m+F_{a,y})} \qquad (4)$$

where $N_{a,y}$ is the number alive at age a and the beginning of year y, m is the annual instantaneous rate of natural mortality and $F_{a,y}$ is the fishing mortality on age a in year y, obtained from:

$$F_{a,y} = K_a F_y \qquad (5)$$

where K_a is the selectivity or partial recruitment value at age a and F_y is the fully recruited fishing mortality in year y. For 3NO cod, a = 2 to 12 with no plus group. For 3LNO plaice, a = 5 to 15, where age 15 is a plus group, which was updated in the simulation by applying:

$$N_{15,y+1} = N_{14,y} e^{-(m+F_{14,y})} + N_{15,y} e^{-(m+F_{15,y})} \qquad (6)$$

Catch was calculated in each year as:

$$\sum_{a=1}^{n} C_{a,y} \times Cw_{a,y} \qquad (7)$$

Where $Cw_{a,y}$ is the catch weight at age a in year y and $C_{a,y}$ is the catch number at age a in year y calculated as:

$$C_{a,y} = N_{a,y} \times (1 - e^{-(m+F_{a,y})} \times (\frac{F_{a,y}}{(m+F_{a,y})})) \qquad (8)$$

Recruitment was calculated using a segmented regression (hockey stick)

$$R = \begin{cases} \alpha SSB \text{ if } SSB < \beta \\ \alpha\beta \text{ if } SSB \geq \beta \end{cases} \qquad (9)$$

Where R is recruitment, α is RPS and β is the maximum observed SSB.

All projections applied the same partial recruitment vector calculated from the matrix of fishing mortality at age for each stock. Natural mortality was (0.2) for all cases. Weight at age and proportion mature at age averaged over each time period and over the whole time series were used in separate analyses together with the average RPS calculated over the corresponding period.

The yield per recruit reference point $F_{0.1}$ was calculated for each period using equations 4, 5, 7 and 8 above, starting with 1 recruit and applying a range of F values, to produce a curve of yield across F. For American plaice the population was extended to age 30 to approximate the plus group in the assessment. $F_{0.1}$ is determined as the F where the slope of the yield per recruit curve is 10% of the slope at the origin. This reference point is affected by variation in weight at age but not by RPS or maturity at age. Average weight at age in each time period and the overall average were used to examine how $F_{0.1}$ varied across period.

The F that gave 40% of the SPR at F=0 ($F_{40\%SPR}$) was determined by solving for the value of F giving this amount of SPR depletion per recruit using equations 2, 4 and 6 above. This reference point is affected by changing weight and maturity at age but not recruitment rate.

The impact of fishing at these reference points under varying productivity was examined. Populations were projected to equilibrium at F_{MSY} determined for the 1960s, 1990s and 2000s and the weights, maturities and RPS from the corresponding period. The response of the population was compared over 20 year projections from equilibrium at the 3 F reference points (F_{MSY}, $F_{0.1}$, $F_{40\%SPR}$) derived from the period being examined and from average conditions.

Results

Productivity

Proportion mature at age for both stocks was lowest in the 1960s and highest recently, although the variation was much greater for plaice than for cod (Figure 2). Weight at age for older fish was markedly reduced during the 1960s compared to the other periods for both stocks. For cod, ages 7-12 had lower weight at age in the 1960s, while for plaice it was ages 11-15 that had lower weight.

Both 3NO cod and 3LNO plaice have exhibited substantial variation in RPS (Figure 3). The timing of this variation and the association between RPS and SSB was not the same for the two populations although there were extended periods when RPS was below average for both stocks. There was a very long period of low productivity of 24 years from 1981-2004 for cod and two periods of low RPS from 1961-1971 and 1979-1988 of 11 and 10 years respectively for plaice. During the 1960s both SSB and RPS were high for cod while SSB was high and RPS low for plaice (Table 1). In the 1990s period SSB and RPS were low for cod with low SSB and high RPS for plaice. In recent years (the 2000s), there has been mainly low RPS at low SSB for American plaice and high RPS and low SSB for cod. Average RPS was much higher for plaice than for cod.

Average SPR for plaice was an order of magnitude lower than for cod (Figure 3). For both populations there has been a general increase in SPR since the beginning of the series but this increase is much greater for plaice.

The differing RPS resulted in very different levels of recruitment when applied as α in a hockey stick S-R model (Figure 4). The much larger RPS for plaice results in much greater recruitment than for cod. The highest level of recruitment for plaice was during the 1990s period while for cod it is during the 1960s. Maximum recruitment for cod in the 1960s was 16 times that of the 1990s period. For plaice, maximum recruitment during the 1990s period was 3.5 times that of the 1960s.

The potential annual percent growth in the SSB (G_0) was very low for cod during the 1990s period (Table 1), at just over 1%. In comparison during the 1960s G_0 for cod was 33%. The highest G_0 for plaice was during the 1990s period, although G_0 was also elevated during the 2000s.

Overall, the 1960s appears to have been a high productivity period for cod with high RPS and very high G_0, although SPR was below average because of the lower weights and maturity at age. The cold 1990's were a period of very low productivity for cod despite a higher SPR. For plaice the 1960s was a low productivity period, with low RPS, SPR and consequently low G_0. The 1990s period was one of high productivity for plaice (Table 1).

Reference points

The estimated F_{MSY} differed substantially for both plaice and cod across periods, by 80 and 95% respectively (Table 2). The variation in $F_{0.1}$ and $F_{40\%SPR}$ was much less. $F_{40\%SPR}$ was much lower for plaice than for cod but varied more (28% vs 5%) reflecting large changes in maturity at age in plaice. During low productivity periods, F_{MSY} was very low for both cod and plaice. Both $F_{0.1}$ and $F_{40\%SPR}$ were much higher than F_{MSY} during the low productivity, the 1990s, for cod. But for plaice, while $F_{0.1}$ was much higher than F_{MSY} during the low productivity period of the 1960s, $F_{40\%SPR}$ was similar to F_{MSY}.

For cod, fishing under low productivity conditions (the 1990s) with reference points derived under average conditions has a very detrimental effect on SSB, causing a steep decline (Figure 5). Both $F_{0.1}$ and $F_{40\%SPR}$ derived from conditions during the 1990s also cause a steep decline in SSB under these low productivity conditions. During the conditions of the 2000s, the F_{MSY} estimated using average conditions also causes the SSB to decline over the projection period. For plaice the 1960s was the low productivity period. Average F_{MSY} and $F_{0.1}$ both result in population decline under the conditions of the 1960s period, while average $F_{40\%SPR}$ allows the SSB to grow (Figure 6). The $F_{0.1}$ estimated using the weight at age from the 1960s also results in a decrease in SSB.

Discussion

There was twice as much plaice SSB than cod SSB on the Grand Bank at the start of the series in the 1960s. Compared to cod, plaice is more resilient in terms of producing recruits from SSB than in terms of producing SSB from a recruit. Average RPS is four times higher for plaice than cod, whereas average SPR is an order of magnitude higher for cod than plaice. In combination, RPS and SPR result in a G_0 value for cod that is twice as high as plaice, indicating that higher recovery rates could be expected from the depleted cod stock compared to the depleted plaice stock. The fact that neither stock has recovered above their respective SSB limit reference points since moratoria were applied to directed fishing in the early 1990s, indicates that all, or nearly all, the surplus production under prevailing productivity conditions has been removed through bycatch mortality (Shelton and Morgan, 2005). Matching the target fishing mortality rate to specific dynamics of the stock and the prevailing productivity conditions is an important consideration in terms of sustainable fisheries management. The combined effect of RPS and SPR on productivity, reflected by G_0, shows that productivity for cod was much higher during warm periods and higher during the 1990s conditions for plaice.

Productivity of both cod and plaice has varied substantially over time. This had a large impact on the level of fishing mortality based reference points, particularly F_{MSY}. When productivity was at its lowest, F_{MSY} was very low. Low or even negative (i.e. population decline) productivity has been found in other stocks, sometimes lasting for extended periods of time (Shelton et al., 2006; Swain and Chouinard, 2008; Lambert, 2011). That different assumptions about productivity can lead to different estimates of fishing mortality reference points has been demonstrated previously (Beddington and May, 1977; Morgan et al., 2009; Brooks, 2013; Cervino et al., 2013). The results of this study clearly demonstrate that the impacts of changing productivity can be rapid and very large, and if fishing mortality reference points are not adjusted accordingly the results can be catastrophic.

The variation in F_{MSY} under changing productivity conditions was greater than that of $F_{0.1}$ and $F_{40\%SPR}$. This is a result of the importance of changing RPS in both populations. The relative importance of the components of productivity leading to the variation in F_{MSY} was not the same in the two populations. In both stocks, the major source of variation was change in RPS, but for plaice there was also a substantial change in SPR caused by varying proportion mature at age, which caused greater variation in $F_{40\%SPR}$ for plaice compared to cod. Changes in weight at age seemed to be of less importance than changes in maturity in both stocks. Changes in weight at age occurred mainly at older ages and would have a reduced impact on stock productivity under higher levels of F.

During periods of low productivity, RPS was very low for both populations. $F_{0.1}$ does not respond to changes in RPS and it was much higher than F_{MSY} under these conditions. $F_{40\%SPR}$ was also higher than F_{MSY} during low productivity for cod, but not for plaice. This may be related to the timing of the low productivity periods. $F_{40\%SPR}$ incorporates maturity at age. The lowest productivity period for cod was the 1990s, by which time proportion mature at age had already increased in this population. The lowest productivity period for plaice was the 1960s which was prior to any increase in proportion mature at age.

The length of the low productivity periods observed here in both populations was long enough to result in substantial population decline and even collapse, if the populations were to be fished at fishing mortality reference points based on average conditions. The level of constant fishing mortality that would ensure that the populations would not decline under low productivity conditions would be so low as to result in a large loss in yield if applied to all time periods, implying that target fishing mortality should be adjusted between low and higher productivity periods. We propose that this be done by applying recent average data in the computation of fishing mortality target and limit reference points.

In practice, it is usually YPR and SPR type reference points that are updated using recent data, while F_{MSY} is usually estimated based on long term data. YPR and SPR based reference points do not incorporate recruitment and our study demonstrated that RPS can be so low as to make YPR and SPR based reference points dangerously high during periods of low productivity. Fishing mortality reference points that can be updated using only recent data, but that incorporate all components of productivity, need to be developed. One possible approach is to calculate F_{MSY} using recent average RPS and a hockey stick stock recruit relationship as done in this study. Another potential approach is to compute G_0 based on recent RPS and SPR and to apportion a fraction of that to the fishery and a fraction to population growth, the relative proportion depending on whether or not the population is depleted or healthy.

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Table 1. Average spawning stock biomass (SSB, '000 tons), recruits per spawner (RPS), spawner per recruit (SPR), percentage potential annual growth rate in in SSB (G_0) and fishing mortality for the selected periods used in the estimation of reference points.

cod	SSB	RPS	SPR	G_0	F
1960s	92.3	2.74	4.52	32.97	0.280
1990s	18.6	0.17	6.45	1.08	0.756
2000s	7.6	0.49	6.64	14.49	0.287
Average	43.2	1.17	5.95	24.14	0.387
American plaice					
1960s	179	2.43	0.48	4.16	0.122
1990s	34.4	8.50	0.87	18.99	0.752
2000s	21.03	3.34	0.93	11.81	0.269
Average	94.2	4.43	0.59	11.67	0.328

Table 2. Estimated F_{MSY}, $F_{0.1}$ and $F_{40\%SPR}$ for different time periods for Div. 3NO cod and Div. 3LNO American plaice.

	cod			American plaice		
Period	FMSY	F0.1	F40%SPR	FMSY	F0.1	F40%SPR
1960s	0.33	0.21	0.12	0.08	0.19	0.05
1990s	0.02	0.18	0.12	0.33	0.16	0.06
2000s	0.25	0.20	0.12	0.48	0.16	0.07
Average	0.30	0.20	0.12	0.37	0.17	0.06

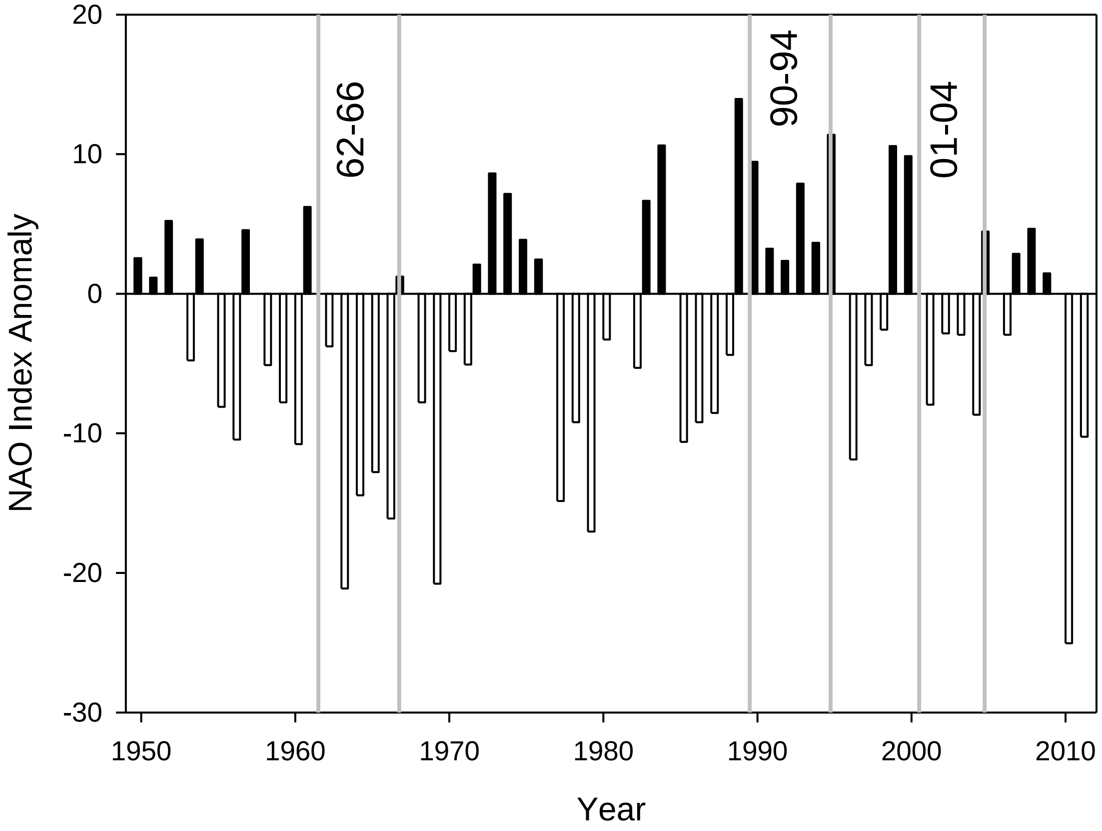

Figure 1. Rogers North Atlantic Oscillation (NAO) anomaly (millibars of pressure) relative to the 1981 to 2010 average. The years chosen to represent the 1960s (1962-1966), 1990s (1990-1994) and 2000s (2001-2004) are indicated.

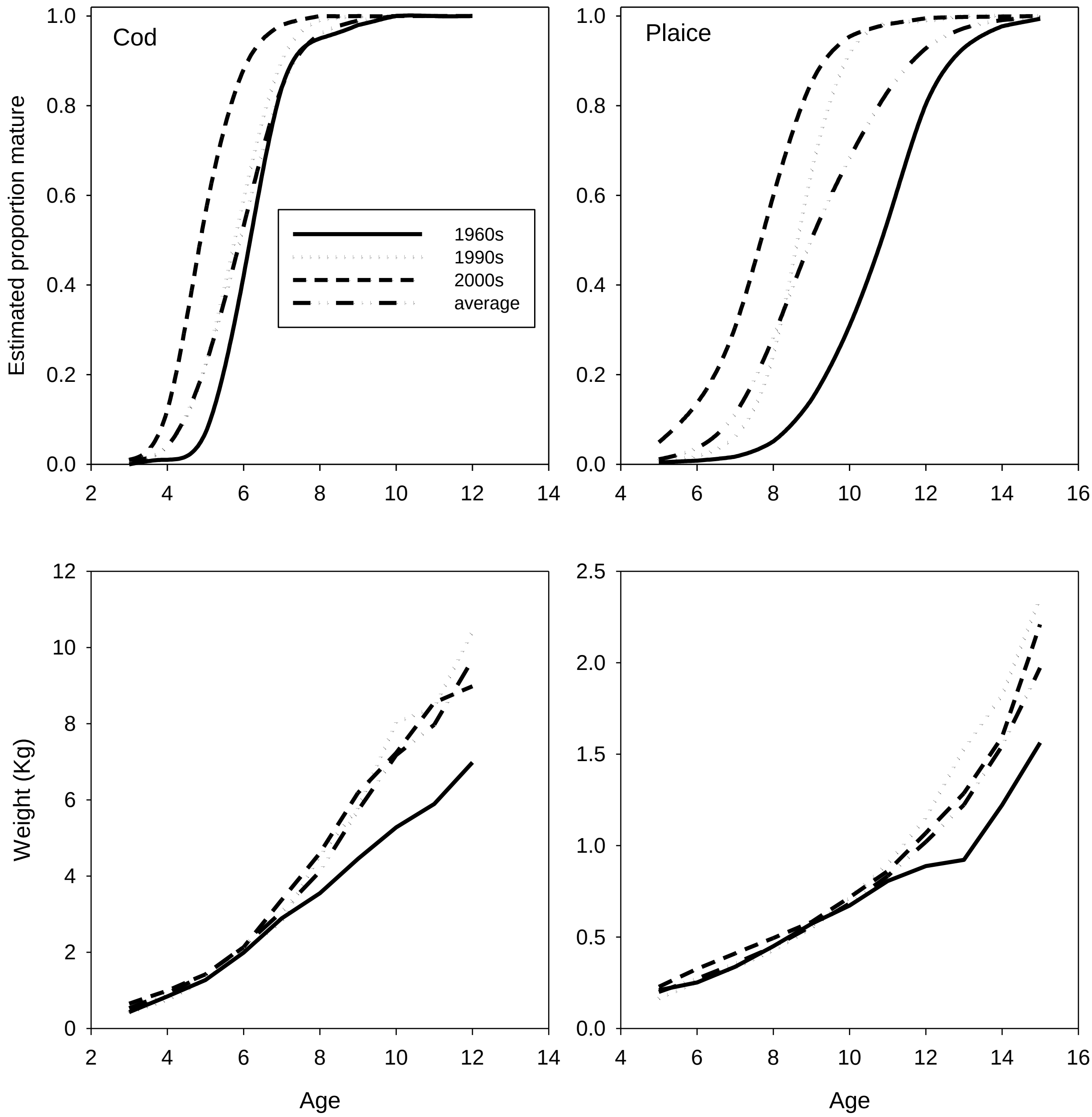

Figure 2. Average estimated proportion mature at age and weight at age for Div. 3NO cod and Div. 3LNO American plaice from each of three time periods and for the entire time series.

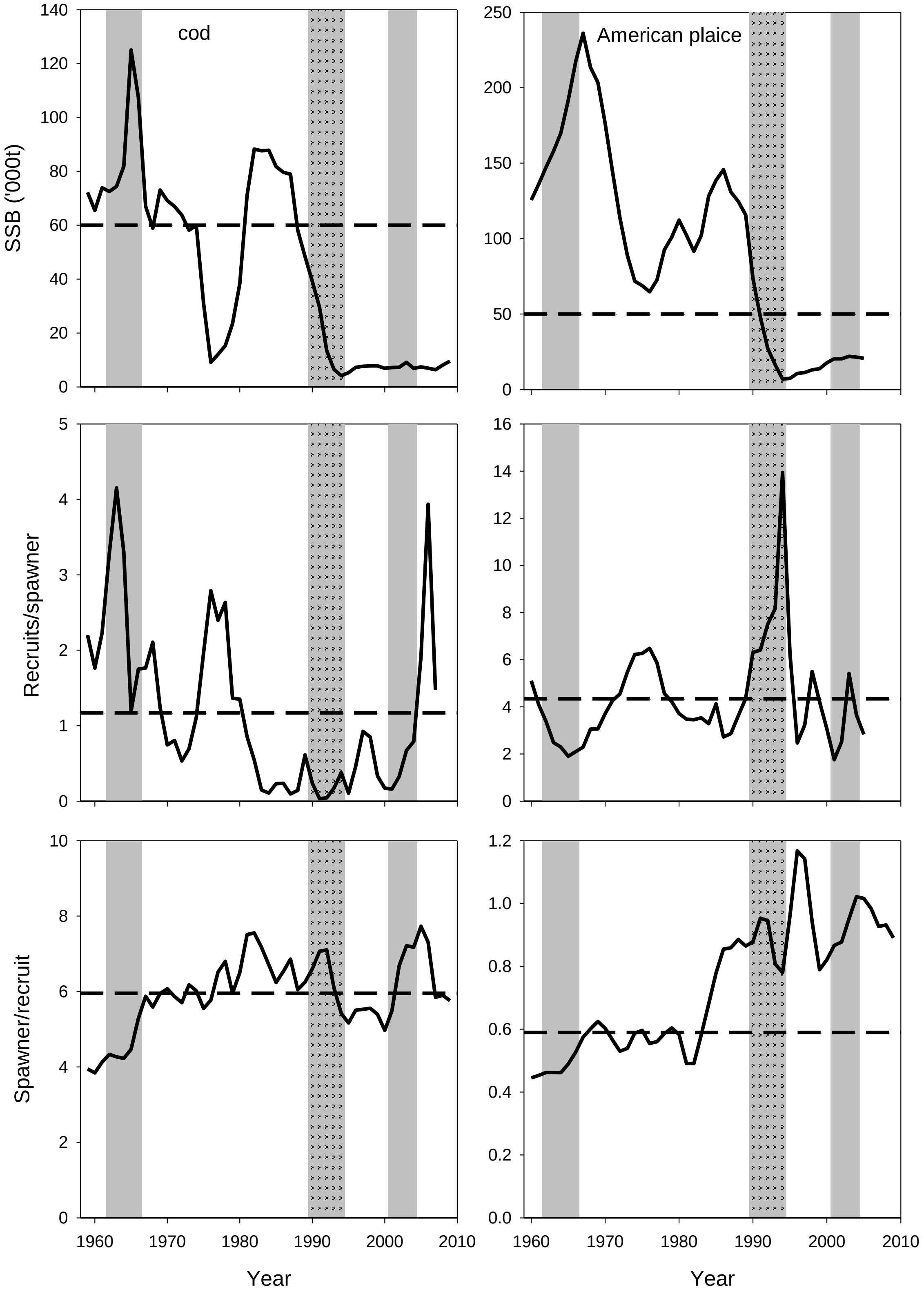

Figure 3. Spawning stock biomass ('000t), recruits per spawner, and spawner per recruit for Div. 3NO cod and Div. 3LNO American plaice. Blim and average SPR and RPS are also shown. The gray areas indicate the warm periods of 1960s and 2000s and the gray with stiple the cold period of 1990s used in this study.

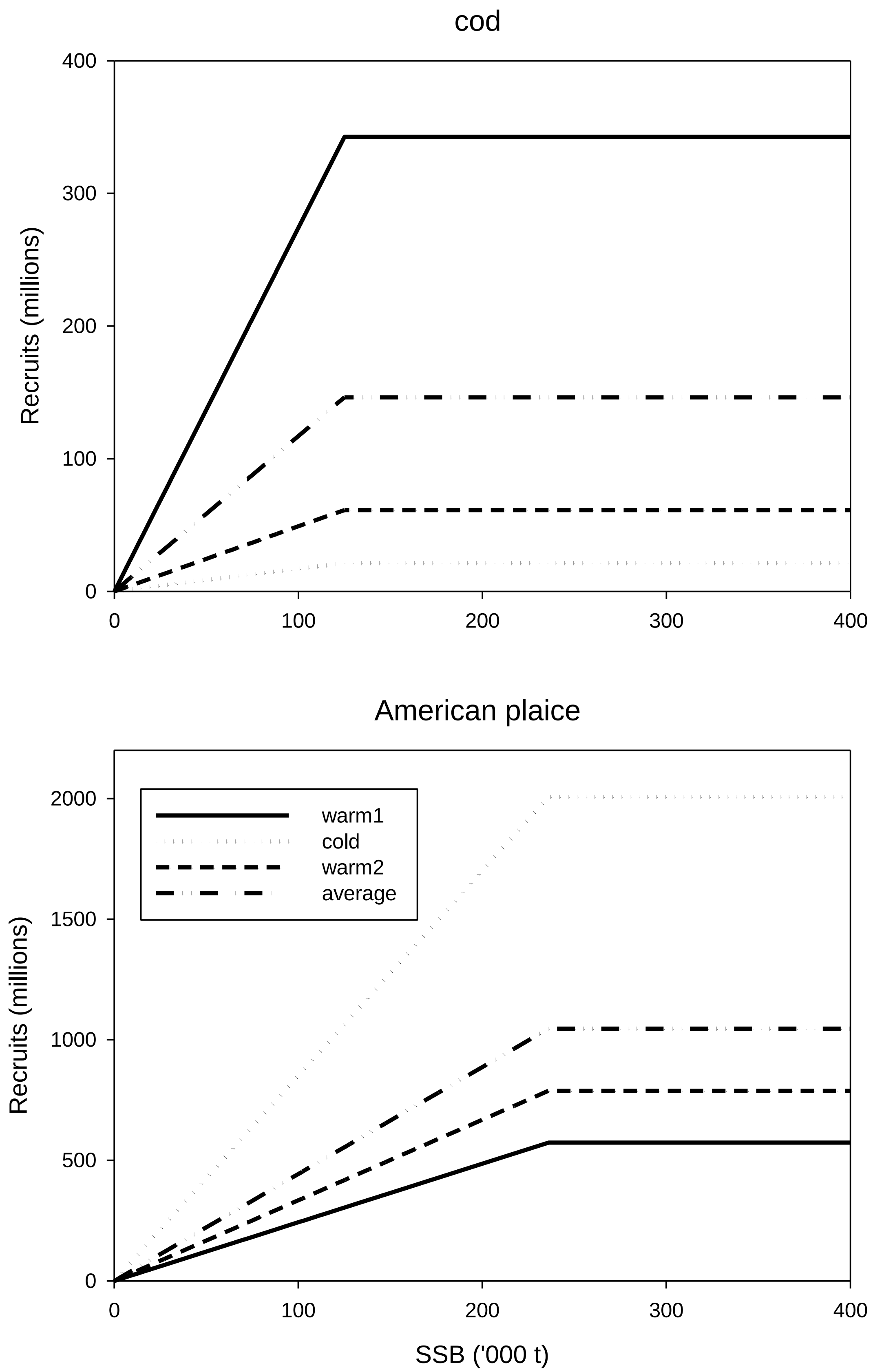

Figure 4. Stock recruit relationships for Div. 3NO cod and Div. 3LNO American plaice based on the assumption of a segmented regression with a slope equal to the RPS for each period and a plateau at that RPS times the maximum observed SSB.

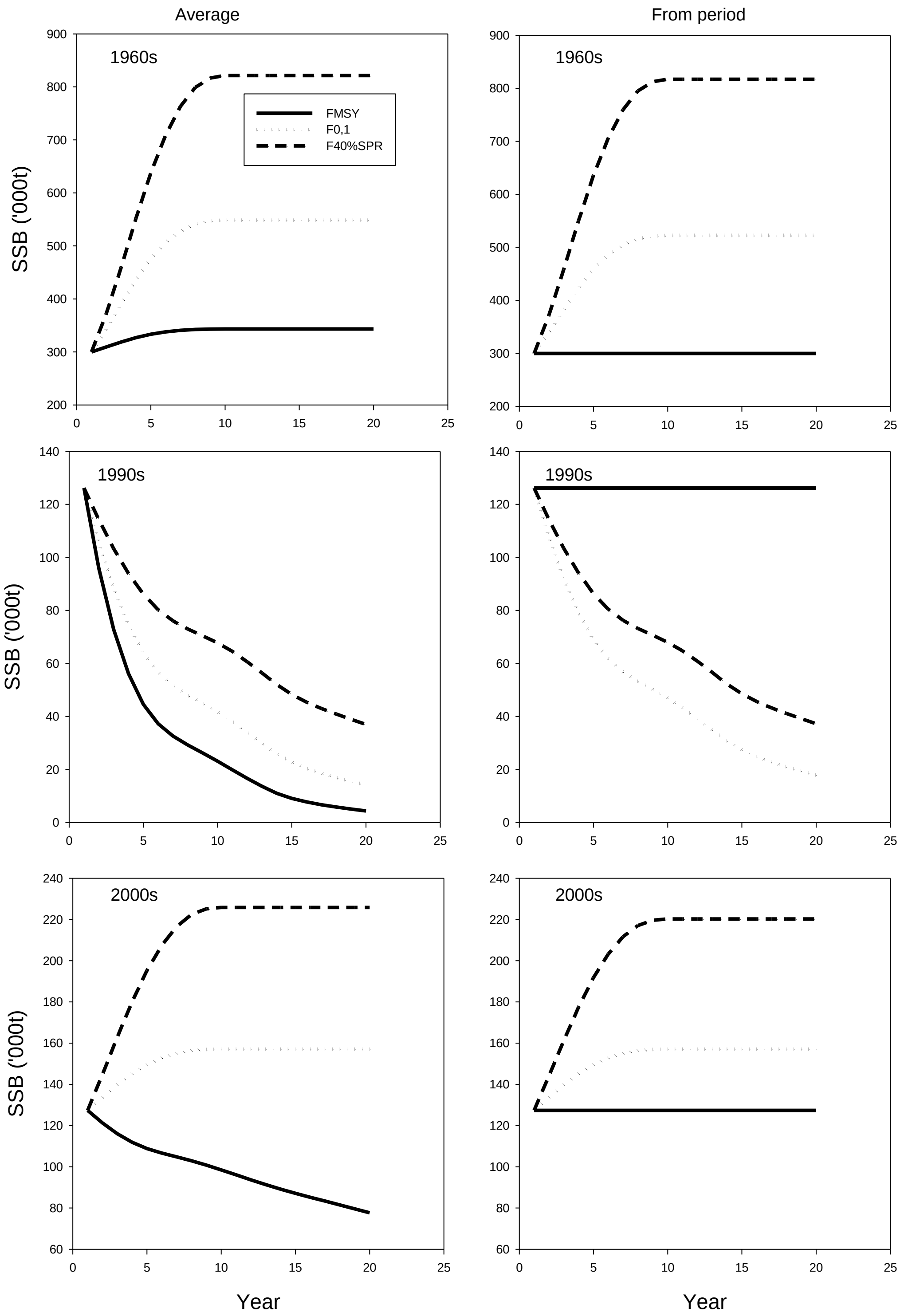

Figure 5. Spawning stock biomass (SSB '000 t) resulting from projections of population size of Div. 3NO cod. Projections start with equilibrium population size calculated using productivity parameters and F_{MSY} specific to each period. Panels on the left use F_{MSY}, $F_{0.1}$ and $F_{40\%SPR}$ derived under average conditions while those on the right use those reference points derived from the conditions applicable to the particular period.

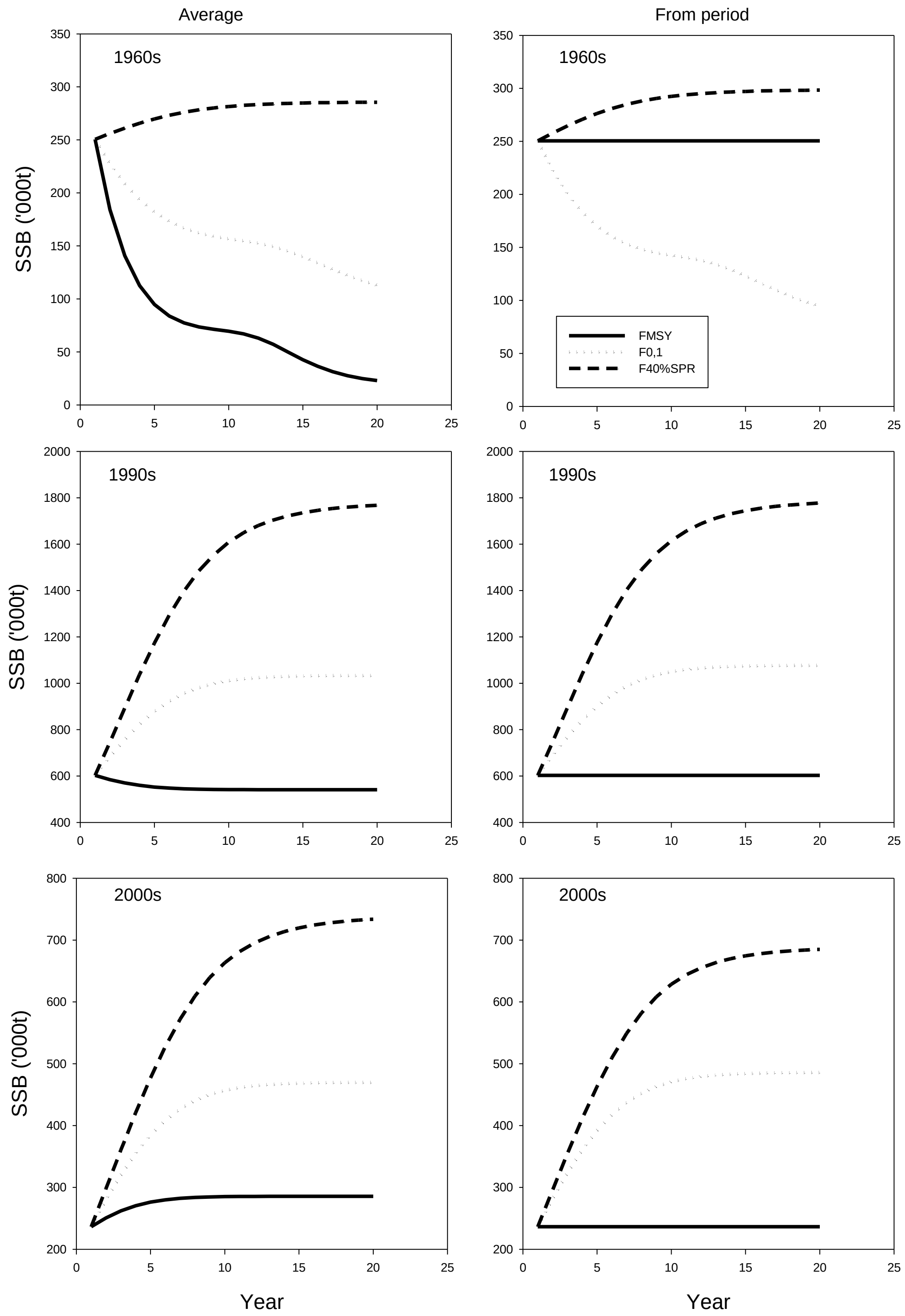

Figure 6. Spawning stock biomass (SSB '000 t) resulting from projections of population size of Div. 3LNO American plaice. Projections start with equilibrium population size calculated using productivity parameters and F_{MSY} specific to each period. Panels on the left use F_{MSY}, $F_{0.1}$ and $F_{40\%SPR}$ derived under average conditions while those on the right use those reference points derived from the conditions applicable to the particular period.