EFFECTS OF DIFFERENT HARVESTING STRATEGIES ON THE MACKEREL ICEFISH *CHAMPSOCEPHALUS GUNNARI* AROUND SOUTH GEORGIA

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Abstract

The effects of a number of harvesting strategies on the mackerel icefish (*Champsocephalus gunnari*) have been simulated for a period of 30 years. These were:

- different levels of constant fishing mortality ($F_{0.1}$, F_{max}, $2xF_{max}$);
- harvesting constantly at 50% $F_{0.1}$ with F increasing three or five years after a good recruitment;
- pulse fishing at an interval of three years with no fishing in between; and
- changes in net selectivity resulting in a shift in partial recruitment.

For the projections, recruitment was assumed to follow the historical pattern.

Pulse fishing proved to be the least preferable harvesting alternative. In the absence of regular recruit surveys constant fishing at $F_{0.1}$ is most likely to be the most profitable and least risky harvesting strategy at present. The establishment of a regular recruit survey would offer the possibility of adjusting constant levels of fishing mortality to the strength of the incoming year class. An increase of F, however, should not occur earlier than four years after a good recruitment. A forward shift in partial recruitment values would not alter yield significantly when fishing at $F_{0.1}$ and F_{max} but would lead to a higher spawning stock biomass.

Резюме

Было выполнено математическое моделирование воздействия различных промысловых стратегий на антарктическую ледяную рыбу (*Champsocephalus gunnari*) на протяжении 30 лет. Рассматривались следующие стратегии:

- различные постоянные уровни промысловой смертности ($F_{0.1}$, F_{max}, $2xF_{max}$);
- промысел на постоянном уровне в 50% $F_{0.1}$ при повышении F через 3 года или 5 лет после вступления в запас многочисленного пополнения;
- пульсирующий промысел с интервалом в 3 года при отсутствии промысла в промежутках;

- изменение селективности сетей и связанное с этим изменение частичного пополнения.

При моделировании пополнение было принято за обычное.

Пульсирующий промысел является менее предпочтительным вариантом промысловой стратегии. Вероятно, что в отсутствие регулярных съемок пополнения промысел на постоянном уровне $F_{0.1}$ в настоящее время будет наиболее выгодной и наименее рискованной промысловой стратегией. Регулярное проведение съемок пополнения предоставит возможность регулировать постоянные уровни промысловой смертности в соответствии с мощностью вступающего в пополнение годового класса. Тем не менее, F не должно повышаться ранее, чем через четыре года после многочисленного пополнения. Сдвиг вперед значений частичного пополнения не изменит объема вылова при $F_{0.1}$ и F_{max}, в значительной мере, но приведет к увеличению биомассы нерестующего запаса.

Résumé

Les effets sur le poisson des glaces (*Champsocephalus gunnari*) d'un certain nombre de stratégies d'exploitation ont été simulés pour une période de 30 ans. Ces stratégies sont:

- des niveaux différents de mortalité par pêche constante ($F_{0.1}$, F_{max}, 2 x F_{max});
- une exploitation constante à 50% de $F_{0.1}$ avec une augmentation de F, trois ou cinq ans après un bon recrutement;
- une pêche par à-coups à intervalles de trois ans, sans aucune pêche dans l'intervalle;
- des changements de sélectivité des filets ayant pour résultat un changement du recrutement partiel.

Pour les prévisions, le recrutement était censé suivre le modèle historique.

La pêche par à-coups s'est avérée la solution la moins souhaitable. Faute de campagnes d'évaluation régulières des recrues, il est probable que la pêche constante à $F_{0.1}$ soit la stratégie d'exploitation la plus profitable et la moins hasardeuse à présent. L'établissement d'une campagne régulière d'évaluation des recrues offrirait la possibilité d'ajuster les niveaux constants de mortalité par pêche à l'importance de la nouvelle classe d'âge. Une augmentation de F, cependant, ne devrait avoir lieu qu'un minimum de 4 ans après un bon recrutement. Une augmentation des valeurs de recrutement partiel ne changerait pas de beaucoup le rendement de pêche à $F_{0.1}$ et F_{max}, mais entraînerait une augmentation de la biomasse du stock reproducteur.

1. INTRODUCTION

Since 1976/77 the Antarctic icefish *Champsocephalus gunnari* has become the dominant species in the fishery around South Georgia. Catches were highest at about 93 000 tonnes, 210 000 tonnes and 105 000 tonnes in 1976/77, 1982/83 to 1983/84 and 1986/87 to 1987/88 respectively. During 1976/77 when the fishery was at its first peak 4 and 5 year old fish were the major component of the catch. Stock size is now strongly dependent on the strength of the incoming cohort and the fishery is currently based on age classes 2 and 3 of which age class 2 is not yet fully recruited.

Recruitment is the most important factor determining the size of the population. However, no regular recruit surveys (e.g. on age class 1) have been carried out to estimate the strength of the incoming year class. Advice on the total allowable catch (TAC) in the following season is largely dependent on the abundance estimate of age class 2 derived from Virtual Population Analysis (VPA). Historical recruitment has varied by a factor of up to 19 between seasons. Short-term catch predictions based on mean recruitment values are thus only of limited value (Kock and Köster, 1989).

In its Report of the Seventh Meeting, CCAMLR requested its Scientific Committee to provide advice on management options and their consequences for heavily exploited fish stocks. Such advice should consider, *inter alia*: the likely trajectories of catch and spawning stock biomass under different patterns of fishing mortality including:

- different constant levels of F including $F_{0.1}$; and
- a complete ban, or a low value of F for a short period followed by a higher level.

The Commission further noted that its decisions in respect to fisheries management would be facilitated by alternative management recommendations and their consequences for each of the fisheries requiring management. This should include, beside TACs for the current season, a forecast for catch levels in the following season based upon realistic assumptions about fishing mortality and recruitment (CCAMLR, 1988a, p. 26-27).

In the following we have tried to demonstrate the effect of some of the harvesting strategies mentioned above in the stock of *C. gunnari* around South Georgia. The effects of factors such as stock size, spawning stock size and environment on the size of the recruiting year class are presently not known. We have therefore used the historical recruitment pattern for our simulations. Hennemuth et al. (1987) used a probabilistic model based on recruitment series of 18 fish stocks from various parts of the world in their analysis of South Georgia fish stocks.

2. MATERIAL AND METHODS

Simulations of catch and spawning stock biomass (SSB) under different potential harvesting regimes reflecting the Commission's requests were performed for a period of 30 years (1988/89 to 2017/18) using the ICES Standard Prediction Program (Anon., 1981). Input data such as the preliminary catch and the actual stock size in 1988/89, partial recruitment to fishing mortality values, estimates of natural mortality, maturity ogives and weight-at-age values were those used by Kock and Köster (1989) for their short-term projections (Table 1). Future recruitment was assumed to follow the historical pattern as has been derived from Virtual Population Analysis for the period 1971/72 to 1984/85 (Figure 1) (Kock and Köster, 1989). Growth, maturity, natural mortality and partial recruitment had been assumed not to change over the 30 years.

The first harvesting option included different levels of constant fishing mortality at $F_{0.1}$ (0.252), F_{max} (0.596) and $2xF_{max}$ (1.192) (Kock and Köster, 1989) throughout the whole period (1 a, b, c).

The second option was harvesting constantly at 50% $F_{0.1}$, with an increase of F three years after a good recruitment of age class 1 (> 900 x 10^6 individuals) had been observed. The increase in fishing mortality was adjusted not to exceed the cumulative values of $F_{0.1}$ (7.308), F_{max} (17.284) and $2xF_{max}$ (34.569) for the 30 year period (2 a, b, c).

The third option differed from the second option by a delay in the increase of F to five years after a good recruitment (3 a, b, c).

The fourth option simulated the effects of pulse fishing at an interval of three years without any harvesting in between (4 a, b, c).

Mesh size regulations as a means of protecting juvenile fish and first spawners of *C. gunnari* is under debate in CCAMLR at present (CCAMLR, 1988b; Kock, 1989). A change in net selectivity either by an increase of mesh size and/or the introduction of different mesh types (e.g. square meshes) is likely to occur. This would result in a change in the exploitation pattern. We have therefore simulated the effect of decreased partial recruitment of the youngest age classes by shifting the age-specific mortalities from the VPA one year forward. Partial recruitment values were recalculated for a reference F averaged over age classes 4 to 8 (Table 2). In order to keep results easier to understand we have only presented results for $F_{0.1}$ (recalculated option 1a) and F_{max} (recalculated option 1b) here.

3. RESULTS

Catch and spawning stock biomass projections for different harvesting strategies are presented in Figures 2 to 15. Key results for each projection are given in Table 2. These are: the cumulative catch over the 30 year period; the average spawning stock biomass with corresponding coefficients of variation (CV); and the number of years with a spawning stock biomass of less than 100 000 tonnes, of less than the 1988/89 level of 53 400 tonnes and of less than the lowest spawning stock biomass recorded of 24 800 tonnes.

3.1 Variation of Catch and Spawning Stock Biomass Estimated for Different Harvesting Strategies at Constant Levels of F

Cumulative catch is lowest when harvesting is carried out constantly at 50% $F_{0.1}$ with an increase of F three years after a good recruitment (option 2) (Table 3). Cumulative catch is highest at the same level of F but with an increase of F five years subsequent to a good recruitment (Table 3). Pulse fishing at an interval of three years (option 4) resulted in a cumulative catch higher than that for option 2, but lower than that obtained when fishing constantly at $F_{0.1}$ and F_{max} (option 1) (Table 3).

The lowest average spawning stock biomass is observed at a cumulative F of 7.308 for option 3. Both other levels of F for the same option, however, result in the highest average spawning stock biomass (Table 3). The high coefficients of variation within option 3 a, b, c are due to an increase in spawning stock biomass up to 290 000 tonnes when fishing at 50% of $F_{0.1}$ until five years after a good recruitment. After the increase of F to a level of 0.735, however, spawning stock biomass drops substantially to less than 125 000 tonnes (Figure 4). At a cumulative level of F of 17.286 spawning stock biomass will decrease to less than 100 000 tonnes in 16 of the 30 years. In five out of the 30 years it would even fall below the 1988/89 level (Figure 8). At a cumulative level of F of 34.569 spawning stock biomass would be less than the 1988/89 level in even 10 out of 30 years. This would include two years with spawning stock biomass below the lowest observed level of 24 800 tonnes (Figure 12).

The highest spawning stock biomass is achieved when fishing is carried out constantly at $F_{0.1}$ (option 1a). Both other levels of F within option 1, F_{max} and $2xF_{max}$, lead to the lowest average spawning stock biomass (Table 3). In contrast to option 3, the coefficients of variation in option 1 are considerably lower. At a cumulative F of 17.286 (option 1b) spawning stock biomass is expected to fall below 100 000 tonnes in 12 years out of 30 including five years when spawning stock biomass will fall below the 1988/89 level (Figure 6). At a cumulative F of 34.569 (option 1c) spawning stock biomass will fall below the 1988/89 level in eight out of 30 years including two years below the lowest spawning stock size observed (Figure 10).

Fishing constantly at 50% $F_{0.1}$, with an increase in F three years after a good recruitment (option 2) and pulse fishing (option 4), result in average levels of spawning stock biomass with the lowest coefficients of variations for option 2 compared to relatively high CVs for option 4 (Table 3). Consequently, option 2 leads to the lowest number of extreme spawning stock biomass estimates. At a cumulative level of F of 17.286, for example, spawning stock biomass would never fall below the 1988/89 level (Figure 7). At the same level of F, pulse fishing (option 4) would result in a spawning stock biomass to be less than the 1988/89 level in four out of the 30 years including one year with a spawning stock size below the lowest observed value (Figure 9).

3.2 Variation of Catch and Spawning Stock Size Estimated for Different Levels of F

The cumulative catch is 904 000 to 922 000 tonnes at $F_{0.1}$ (options 1a, 2a, 3a, 4a; Table 3), 1 039 000 to 1 160 000 tonnes at F_{max} (options 1b, 2b, 3b, 4b; Table 3) and 1 044 000 to 1 175 000 tonnes at $2xF_{max}$ (options 1c, 2c, 3c, 4c; Table 3) respectively. Under constant mortality policies (option 1) fishing at F_{max} gives a higher catch than $F_{0.1}$ and $2xF_{max}$ (1 074 000, 922 000 and 1 073 000 tonnes). However, if fishing mortality varies from year to year within the same cumulative total, the picture changes. The highest fishing mortality ($2xF_{max}$) will then give the highest catches, especially if fishing is timed to increase five years after good recruitment.

The corresponding average spawning stock biomass is 168 000 to 172 000 tonnes at $F_{0.1}$, 105 000 to 125 000 tonnes at F_{max} and 69 000 tonnes at $2xF_{max}$ respectively (Table 3). Average spawning stock biomass is thus 26 to 39% at F_{max} and 36 to 60% at $2xF_{max}$ lower than spawning stock size at $F_{0.1}$.

3.3 Variation of Catch and Spawning Stock Biomass for Different Sets of Partial Recruitment Values

Variation of catch and spawning stock biomass due to changes in partial recruitment (= net selectivity, option 5) for harvesting at $F_{0.1}$ and F_{max} constantly are shown in Figures 14 and 15.

For harvesting at $F_{0.1}$ the cumulative catch will be reduced by 4% to 886 000 tonnes if partial recruitment is shifted by one year forward from the present stage. Average spawning stock biomass, however, will increase by 19% to 206 000 tonnes (Table 3). For fishing at F_{max} the cumulative catch will increase by 2% to 1 094 000 tonnes and spawning stock biomass will be raised by 38% to 145 600 tonnes (Table 3). The coefficient of variation will slightly increase after the change in partial recruitment. Spawning stock biomass, however, will be continuously higher throughout the 30 year period (Figures 14 and 15). Consequently, fishing at F_{max} will never reduce spawning stock biomass below the 1988/89 level.

4. DISCUSSION

With the exception of fishing, it is the size of the recruiting year class that effects the future stock size of *C. gunnari* around South Georgia far more than changes in growth, maturity or natural mortality (Hennemuth et al., 1987; Kock and Köster, 1989). Maturity and weight-at-age had not changed significantly in the course of the fishery (Kock, 1989; Kock and Köster, 1989). For this reason we assumed for our projections of future catches and spawning stock size that growth, maturity and natural mortality would not change over time. Partial recruitment values have been assumed to remain constant as well. However, as partial recruitment values are likely to change over a 30 year period of time due to alterations in the fishery, we have investigated that effect in a separate set of simulations by shifting partial recruitment values one year forward.

The aim of our simulations has not been to model or predict future recruitment, but to assess the effect of different harvesting strategies on a stock with highly fluctuating recruitment. Historical recruitment derived from VPA analysis has followed a cyclic pattern (Kock and Köster, 1989) which seemed to be largely independent of spawning stock size. We have therefore assumed that future recruitment will follow the historical pattern instead of applying randomly fluctuating recruitment values estimated from a probabilistic model to our data (see Hennemuth et al., 1987). It is obvious that this should have affected our results, as yield from a series of good year classes should be higher that from a single one. On the other hand a series of poor year classes would likely result in a reduction of spawning stock biomass below the level derived from randomly fluctuating recruitment values.

Article II, 3a of the Convention for the Conservation of Antarctic Marine Living Resources states that "Any harvesting [....] shall be conducted in accordance [....] with the following principles of conservation:

> prevention of decrease in the size of any harvested population to levels below those which ensure its stable recruitment. For this purpose its size should not be allowed to fall below a level close to that which ensures the greatest net annual increment." (CCAMLR, 1988).

No stock-recruitment relationship seems to be apparent in *C. gunnari* around South Georgia. It is likely, however, that a larger and relatively stable spawning stock would minimize the risk of recruitment failure, in particular since spawning stock sizes derived from VPA analysis tend to overestimate the number of fish actually spawning (Kock, 1989). We have used estimates of average spawning stock biomass, their corresponding coefficients of variations and the number of years when spawning stock size was below a certain level (see Table 3) as a measure of overall level of spawning stock biomass and spawning stock 'stability'.

Of all the options studied, fishing at constant $F_{0.1}$ (option 1a) would result in the second largest cumulative catch and a high and relatively stable spawning stock. Fishing at higher levels of constant F (F_{max} and $2xF_{max}$, options 1 b, c) would produce average cumulative yields and an average stability relative to the other options.

Harvesting at a low constant level of F (50% $F_{0.1}$) and an increase of F three years after a good recruitment (option 2) would result in the lowest cumulative yield of all options, the highest stability of the spawning stock and an average spawning stock size relative to the other options.

Fishing at a constant level of F of 50% $F_{0.1}$ and an increase of F five years after a good recruitment (option 3) would result in the highest cumulative catch of all options coupled with a relatively low stability of the spawning stock.

Pulse fishing (option 4) would produce an average cumulative yield with the lowest stability of all options. Spawning stock size would be at an average level.

Throughout all options fishing at F_{max} would produce a cumulative yield 15 to 19% (= 4 500 to 6 000 tonnes per year) higher and an average spawning stock biomass 26 to 39% lower compared to fishing at $F_{0.1}$. Harvesting at $2xF_{max}$ would increase cumulative yield by 16 to 22% (= 4 700 to 6 600 tonnes per year) and reduce average spawning stock biomass by 36 to 60% compared to fishing at $F_{0.1}$. Stability of the spawning stock would decrease with increasing cumulative F.

Shifting of partial recruitment values one year forward as a result of changes in net selectivity would produce a reduction in cumulative catch by 4% and an increase in spawning stock biomass by 19% relative to the present values when fishing at $F_{0.1}$. If harvesting is maintained at F=0.596 (the present value of F_{max}) then shifting partial recruitment values one year forward will increase cumulative yield by 2% and spawning stock size by 38% relative to the present partial recruitment values.

No regular fishery-independent recruitment surveys have been carried out around South Georgia so far. Information on age class 1 is only available from the VPA and is known to have a high degree of uncertainty, at least for the most recent years in the VPA.

In the absence of any reliable prediction of the strength of the incoming cohort from fishery-independent sources (surveys, recruitment models) the application of a harvesting strategy with a constant low F (50% $F_{0.1}$) and an increase of F three years after a good recruitment (option 2) seems to have little meaning at present.

Abundance estimates of age class 1 from the VPA four years after recruitment (to establish a TAC for five years after a good recruitment) are likely to be more reliable than after two years. This seems to favour option 3. However, this estimate is still entirely based on fishery-dependent information. Any false prognosis would further destabilize the spawning stock which is already less stable than predicted for options 1 and 2.

Pulse fishing had been mentioned as one potential alternative strategy in harvesting Antarctic finfish (Gulland, 1983). Pulse fishing at a three year interval (option 4) would destabilize the spawning stock most, but would only produce average cumulative yields.

In the present state, fishing at a constant level of F is likely to be the most meaningful and least risky harvesting strategy for *C. gunnari* around South Georgia. The most appropriate level of F seems to be $F_{0.1}$. Fishing at F_{max} would produce an annual catch which is only 3 000 tonnes higher relative to fishing at $F_{0.1}$ but an average spawning stock biomass which is 39% less than at the $F_{0.1}$ level. Spawning stock biomass would fall five times below the 1988/89 level, which may bear additional risks for recruitment failure. Fishing at a high spawning stock biomass would be more renumerative (in catch-per-unit-effort) than on a low spawning stock biomass.

A cautious increase of F beyond the level of $F_{0.1}$, however, seems to be feasible if net selectivity experiments are able to demonstrate that an increase in mesh size and/or the introduction of new mesh types would lead to the forward shift in partial recruitment values assumed in our simulations.

After regular fishery-independent recruitment surveys have been established to predict the strength of the incoming cohort, an adjustment of F values to the recruitment of good (or poor) year classes (options 2 and 3) should also be practicable. Fishing mortality should be increased later than three years after a good recruitment (option 3). An increase after only three years (option 2) would not produce a higher yield. As the higher yield in option 3 is coupled with a higher instability of the spawning stock, F should only be increased moderately.

The intention of our paper is to provide a starting point for discussing alternative strategies. However, it should be kept in mind that additional risks exist when converting fishing mortality into TAC. Estimates of stock size are usually derived from research vessel surveys which do have a considerable variability. TACs may therefore miss the target F by a substantial margin.

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Table 1: List of input values for yield and stock projection of *Champsocephalus gunnari* in Subarea 48.3.

The reference F is the mean F for the age-group range from 3 to 7.

Assumed catch in 1988/89 = 23 000 tonnes

Data are listed in the following units:

Number of fish:	numbers x 10^3
Weight by age-group in the catch:	g x 10^3
Weight by age-group in the stock:	g x 10^3

Age	Stock Size	Partial Recruitment	Natural Mortality	Maturity Ogive	Weight in the Catch	Weight in the Stock
1	558816	0.0342	0.3500	0.0000	0.034	0.034
2	385993	0.2591	0.3500	0.7750	0.086	0.086
3	38636	0.7719	0.3500	0.8070	0.153	0.153
4	32682	0.9980	0.3500	1.0000	0.243	0.243
5	25915	1.0568	0.3500	1.0000	0.337	0.337
6	11744	1.0987	0.3500	1.0000	0.482	0.482
7	2202	1.0746	0.3500	1.0000	0.632	0.632
8	210	1.0000	0.3500	1.0000	0.805	0.805
9	43	1.0000	0.3500	1.0000	1.142	1.142

Table 2: Set of partial recruitment values reflecting a change in mesh selectivity in the fishery on *Champsocephalus gunnari* in Subarea 48.3.

Age	Partial Recruitment
1	0.0002
2	0.0364
3	0.2690
4	0.7928
5	1.0143
6	1.0943
7	1.0995
8	1.0709
9+	1.0000

Table 3: Simulated harvesting strategies of *Champsocephalus gunnari* in Subarea 48.3, total catch during the 30 year period of projection, average spawning stock biomass (SSB) and corresponding coefficients of variation (CV) as well as numbers of years with SSB below 100 000 tonnes, below the 1988/89 level of 53 400 tonnes and below the lowest value on record of 24 800 tonnes.

Option	Harvesting Strategy	Cumulative F	Total Catch (tonnes)	SSB	CV	Number of Years with SSB Below:		
						100 000 tonnes	1988/89 level	Lowest Level
1a	Constant fishing at $F_{0.1}$ (0.252)	7.308	922 041	172 749	0.404	6	0	0
2a	Constant fishing at 50% $F_{0.1}$, increased F(0.735) three years after good recruitment	7.308	903 726	170 426	0.344	6	0	0
3a	Constant fishing at 50% $F_{0.1}$, increased F(0.735) five years after good recruitment	7.308	977 841	167 999	0.415	6	0	0
4a	Pulse fishing (F=0.812) with a period of three years	7.308	912 045	170 428	0.435	7	1	0
1b	Constant fishing at F_{max} (0.596)	17.284	1 074 106	105 564	0.418	12	5	0
2b	Constant fishing at 50% $F_{0.1}$, increased F(2.398) three years after good recruitment	17.286	1 039 179	116 482	0.390	12	0	0
3b	Constant fishing at 50% $F_{0.1}$, increased F(2.398) five years after good recruitment	17.286	1 159 527	125 223	0.617	16	5	0

Table 3 (continued)

Option	Harvesting Strategy	Cumulative F	Total Catch (tonnes)	SSB	CV	Number of Years with SSB Below:		
						100 000 tonnes	1988/89 level	Lowest Level
4b	Pulse fishing (F=1.92) with a period at three years	17.280	1 073 940	110 521	0.533	17	4	1
1c	Constant fishing at 2xF_{max}	34.569	1 073 067	69 716	0.461	26	8	2
2c	Constant fishing at 50% three years after good recruitment	34.569	1 044 465	86 567	0.499	21	6	2
3c	Constant fishing at 50% $F_{0.1}$, increased F(4.321) five years after good recruitment	34.569	1 175 421	106 911	0.744	19	10	2
4c	Pulse fishing (F=3.841) with a period of three years	34.569	1 109 625	82 749	0.636	22	9	3
5a	Constant fishing at $F_{0.1}$, changed mesh selectivity	7.308	885 610	206 036	0.412	6	0	0
5b	Constant fishing at F_{max} changed mesh selectivity	17.184	1 094 016	145 580	0.427	10	0	0

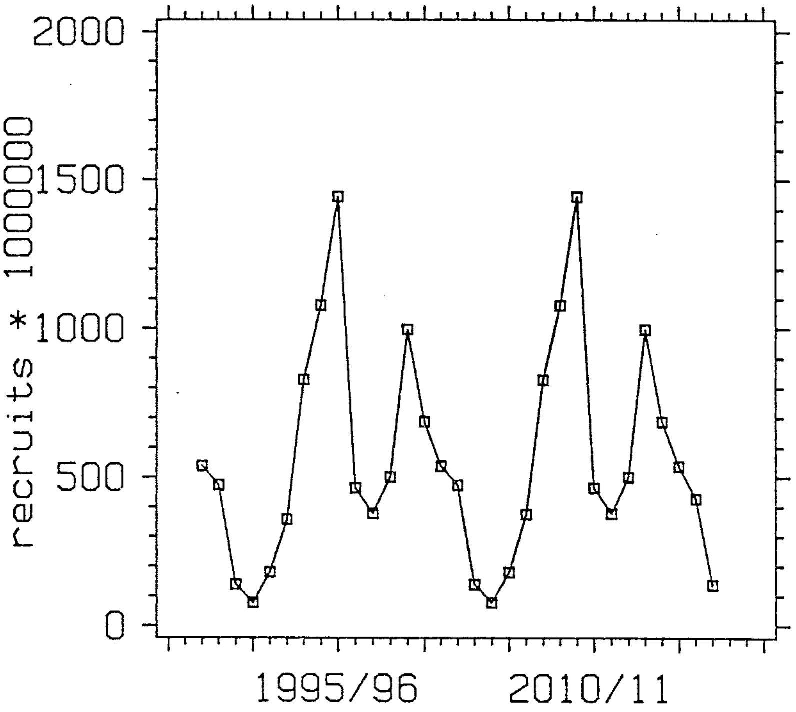


Figure 1: Historical pattern of recruitment in *Champsocephalus gunnari* around South Georgia (from Kock and Köster, 1989) used for the 30 year period of projection.

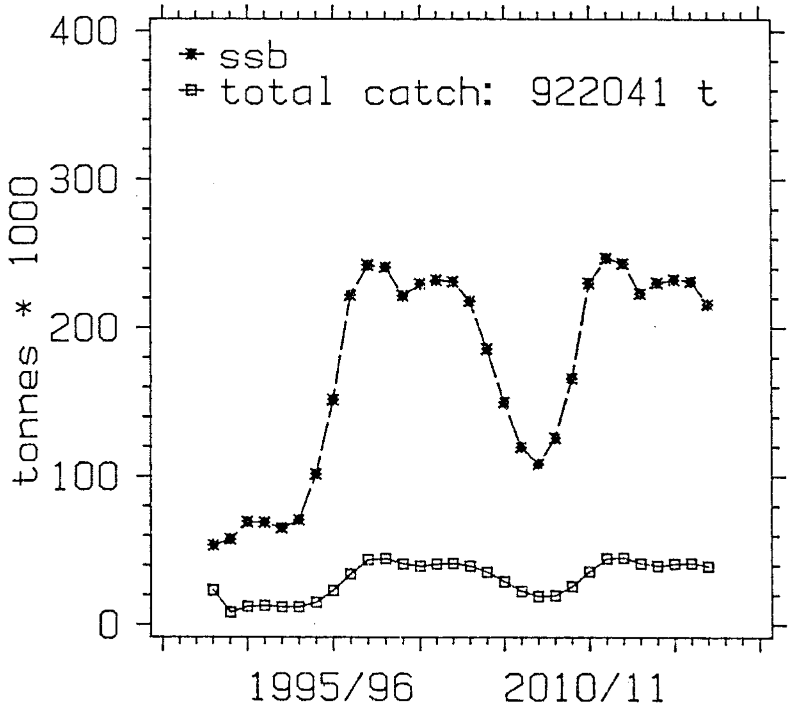


Figure 2: Catch and spawning stock biomass when fishing constantly at $F_{0.1}$ (0.252) (option 1a, Table 3).

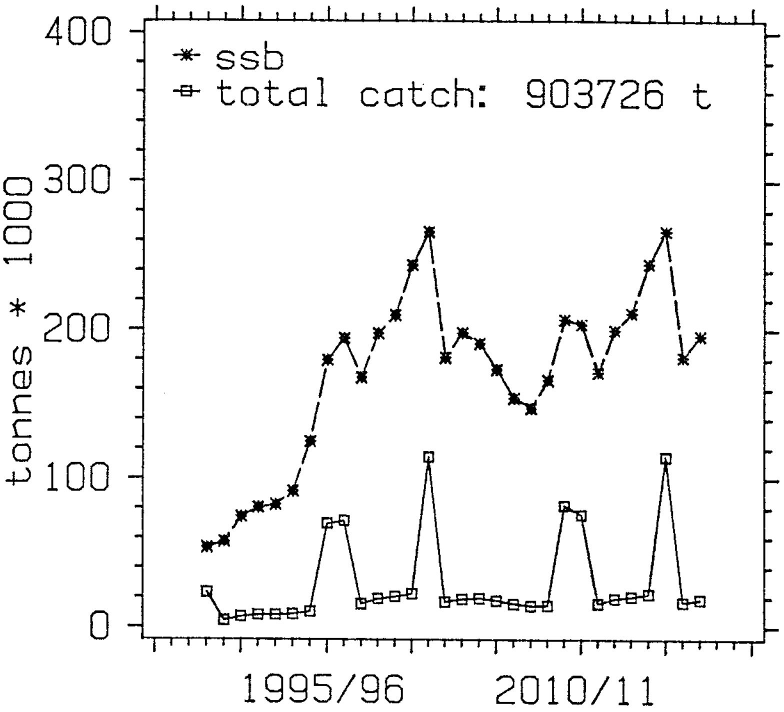


Figure 3: Catch and spawning stock biomass when fishing constantly at 50% $F_{0.1}$, with an increased F (0.735) three years after a good recruitment (> 900 x 10^6 individuals) (option 2a, Table 3).

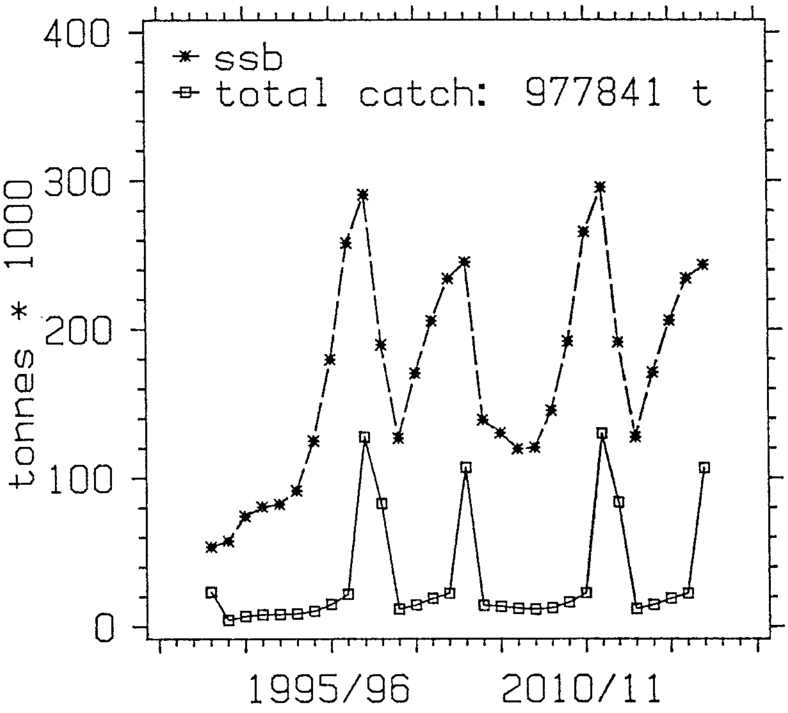
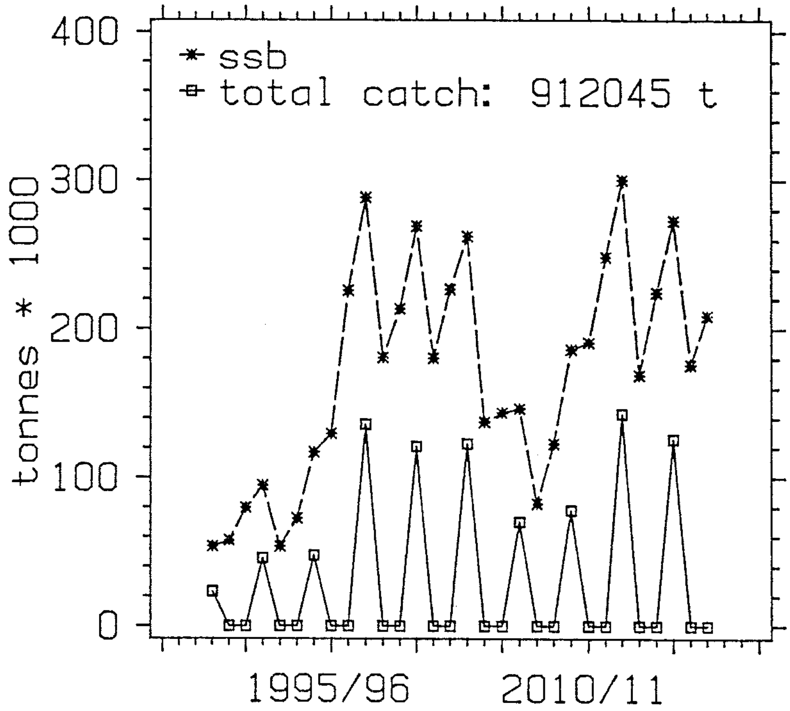


Figure 4: Catch and spawning stock biomass with an increased F (0.735) five years after a good recruitment (> 900 x 10^6 individuals) (option 3a, Table 3).



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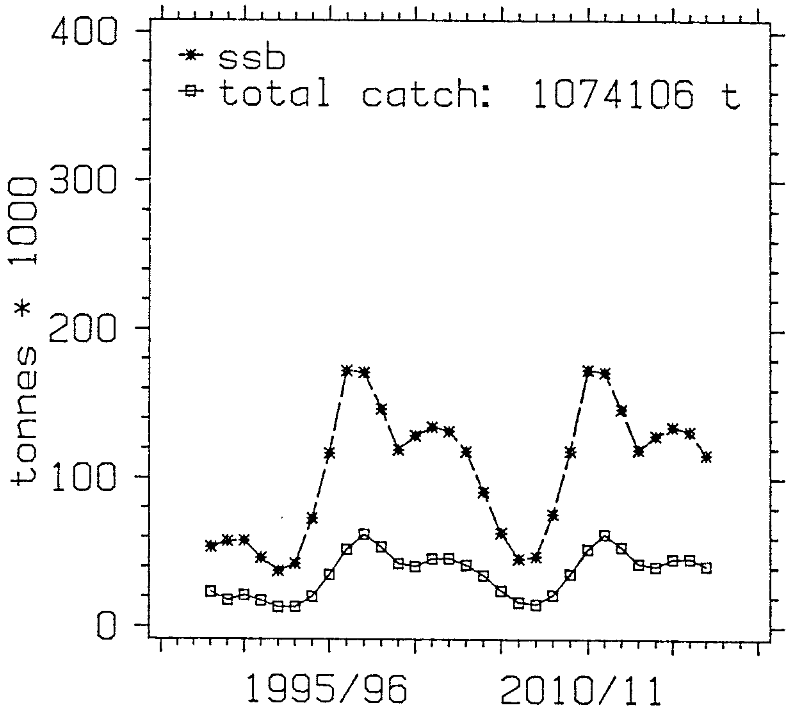

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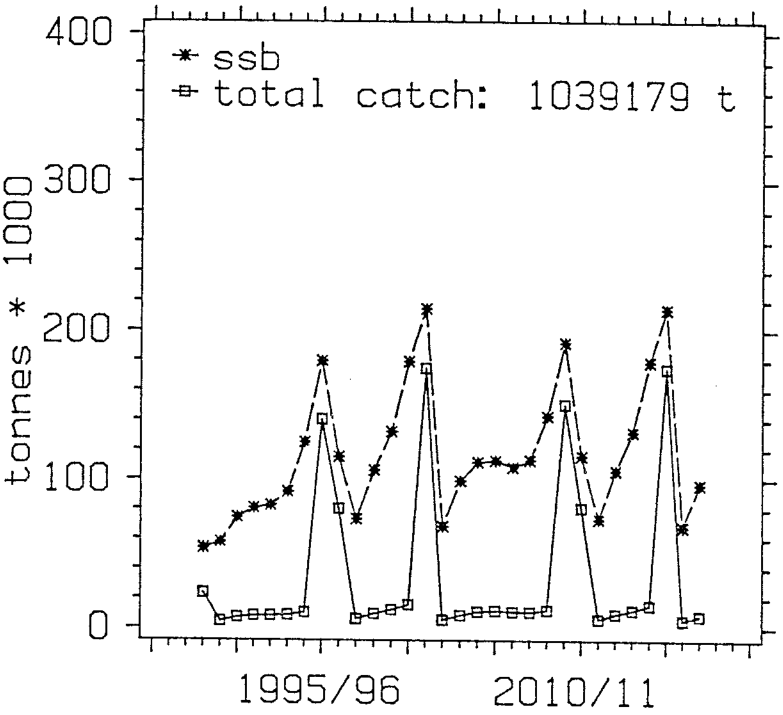

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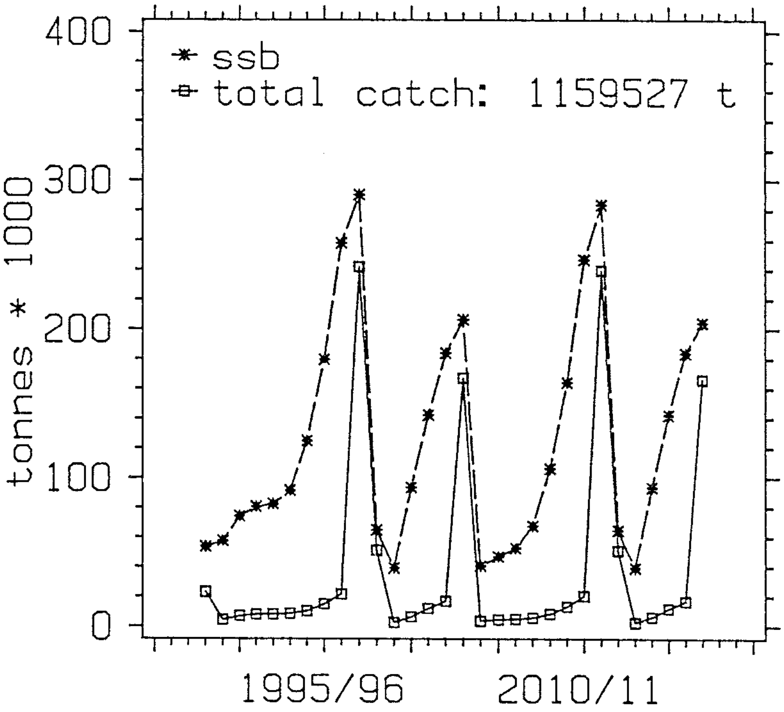

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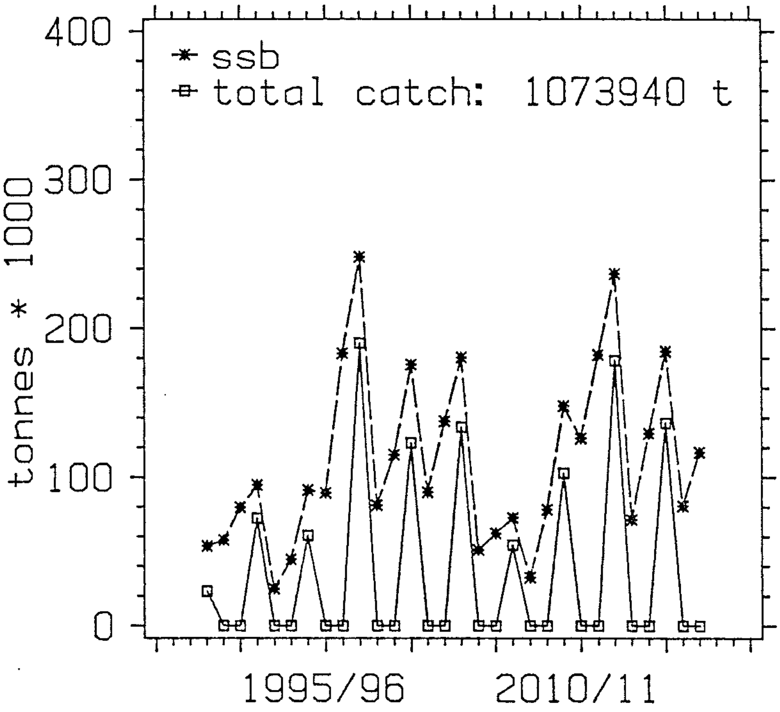

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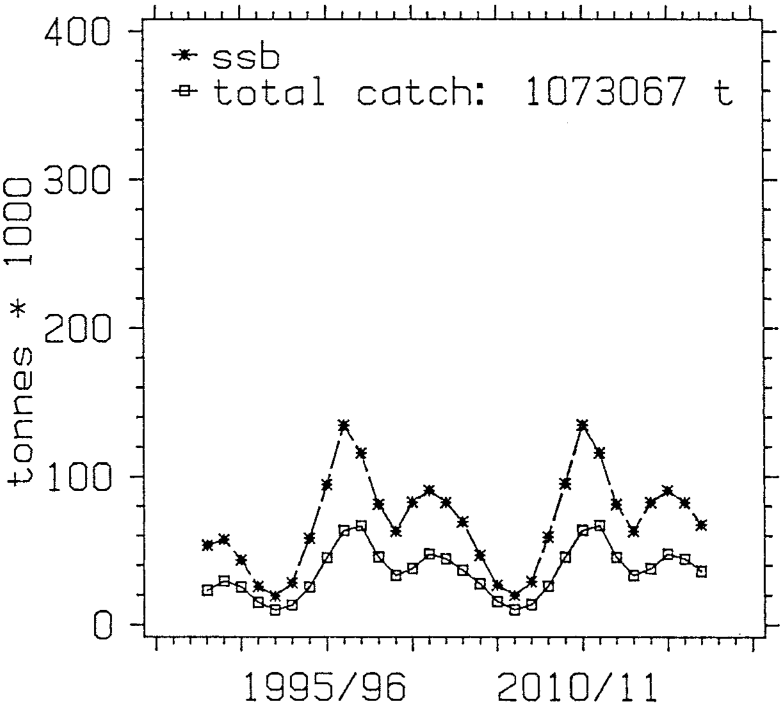

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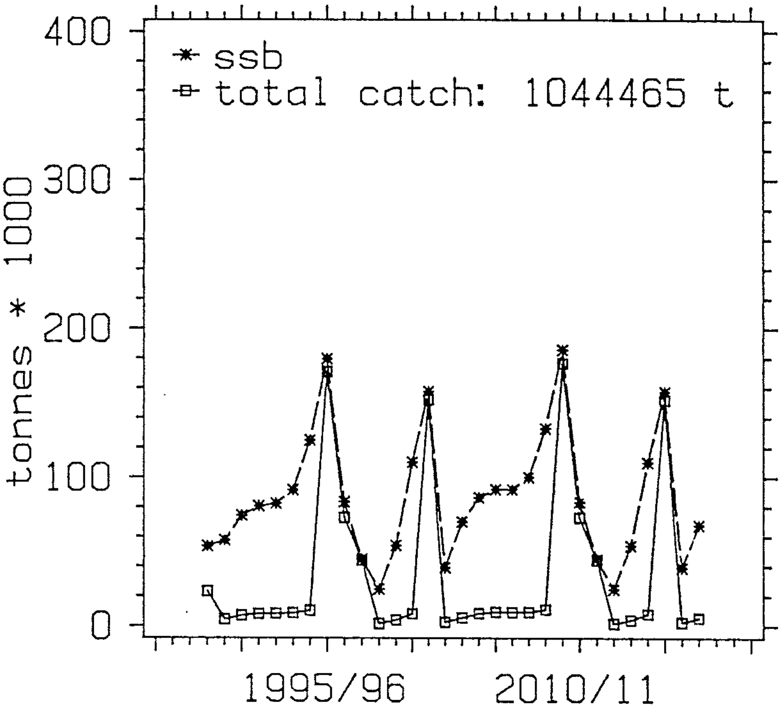

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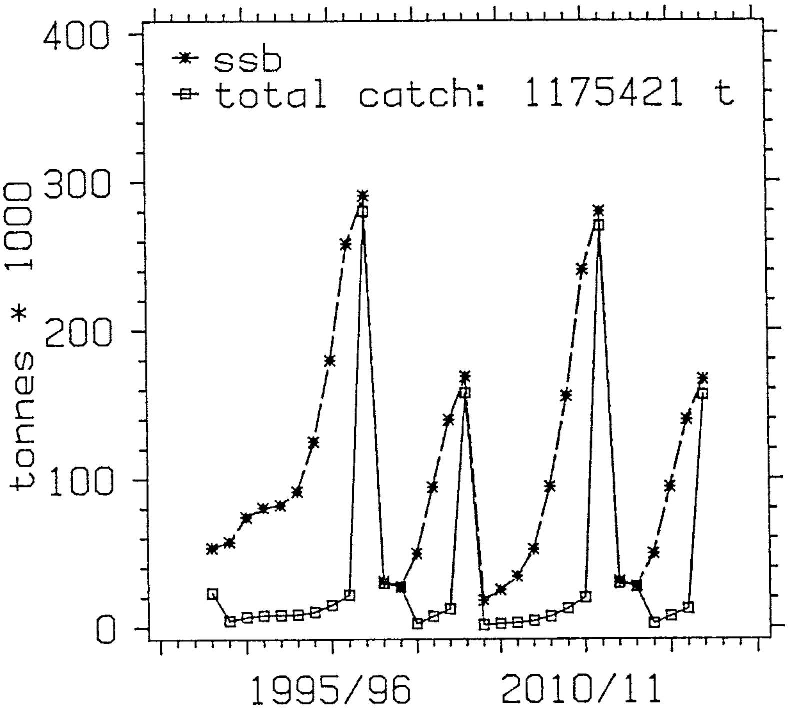

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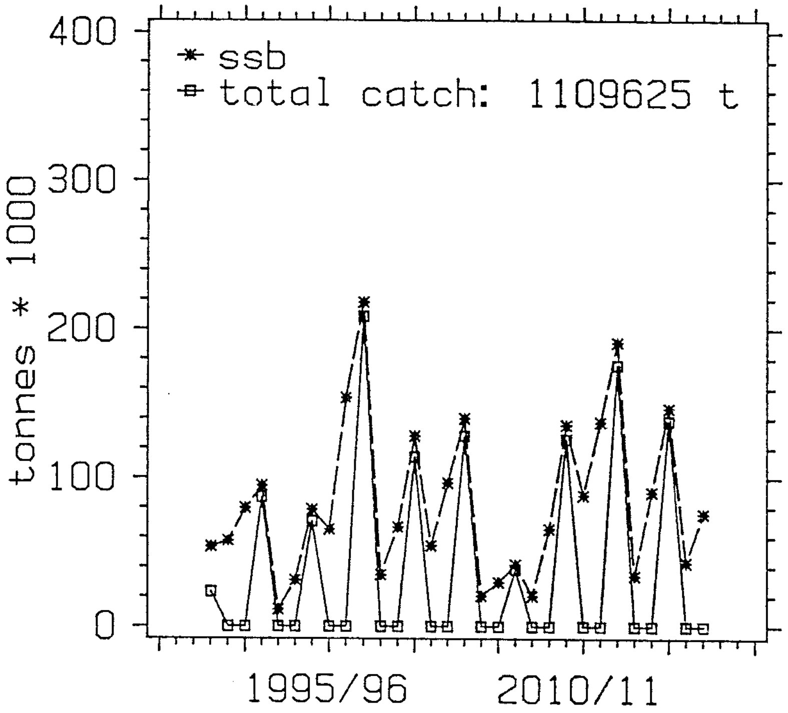

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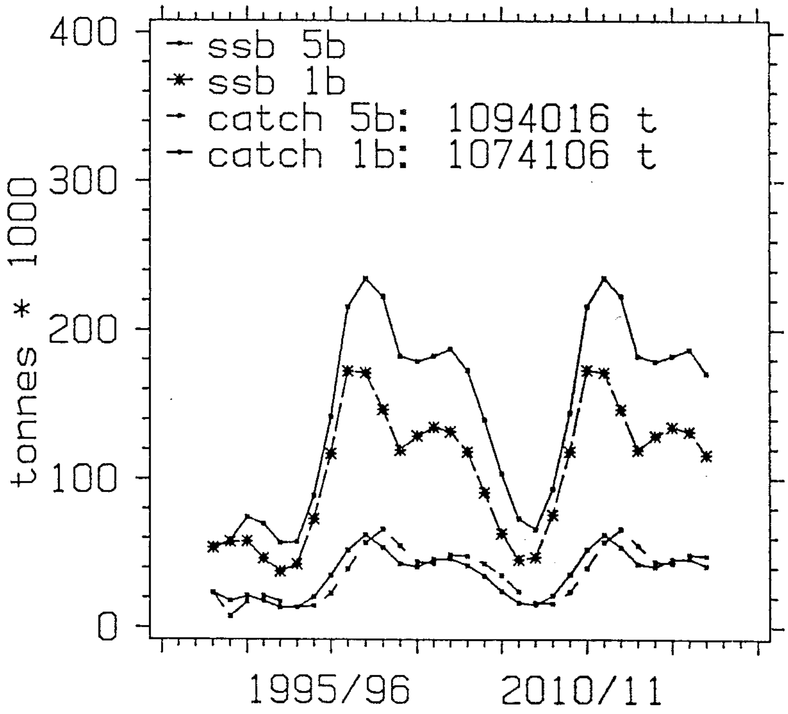

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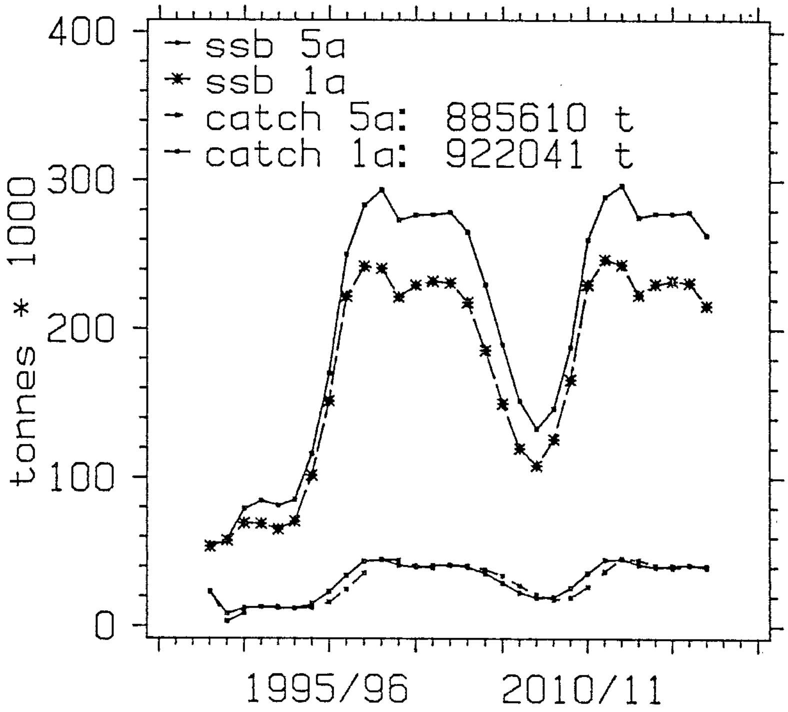

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