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The dynamics of population fecundity in Barents Sea capelin

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The number of eggs spawned during the spawning season is presumed to be an important factor in determining future year-class strength and, therefore, there is value in looking for the relationship between recruitment and the size of the spawning stock. Data on abundance, length and age composition, maturity ogives, and individual fish fecundity were used for calculating population fecundity (PF) for Barents Sea capelin, *Mallotus villosus* (Müller), for the period spanning the early 1970s to present, and for evaluating factors affecting PF. These were combined with recruitment data to calculate the optimum size of the spawning stock that would maintain it in a stable condition.

Keywords: absolute fecundity, capelin, females, length and age composition, population fecundity, stock, survival rates.

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Introduction

Population fecundity (PF) has been studied for a variety of fish species: e.g. Baltic Sea herring (*Clupea harengus*) by Anokhina (1969) and Ojaveer (1974); North Sea cod (*Gadus morhua*) by Daan (1975); North Sea haddock (*Melanogrammus aeglefinus*) by Sahrhage and Wagner (1978); Arcto-Norwegian cod, Barents Sea capelin (*Mallotus villosus*) and Atlanto-Scandian herring by Serebryakov *et al*. (1984, 1985, 1990); Northeast Atlantic blue whiting (*Micromesistius poutassou*) and Atlanto-Scandian herring by Belikov *et al*. (1990), Seliverstova (1990), and Serebryakov *et al*. (1990). This paper presents an analysis of data on abundance, maturity ogives, and individual fish fecundity of Barents Sea capelin that have been collected at the Polar Research Institute (PINRO, Murmansk, Russia) over the period 1970–2000. Calculations of annual fecundity by age- and size-class as well as of the total population are presented, and year-class survival indices are computed. Three levels of population fecundity are defined with respect to stock propagation, safe, minimum, and critical.

Material and methods

Data on individual fish fecundity for capelin between 2 and 5+ years old were collected during spring from 1970 to 2000, overall, more than 7000 individual female gonads being processed. Population fecundity and survival rates of capelin up to age 5 were calculated using the method of Serebryakov (1988).

Apart from egg counts, the basic data consist of annual age-disaggregated estimates of stock abundance based on trawl–acoustic surveys carried out jointly by Norway and Russia every autumn since the early 1970s (ICES, 2000). The maturing portion of the population was determined by maturity ogives derived from age samples, and the estimated stock numbers were reduced by the instantaneous total mortality coefficient (Z) from the time of the surveys until the time of spawning. The sex ratio in the spawning stock is assumed to be 1:1. I have retained Serebryakov's (1988) terminology for defining various aspects of fecundity: AIF, absolute individual fecundity; RIF, relative individual fecundity (number of eggs per gramme): PF, total population fecundity; SPF, safe population fecundity; MRPF, minimum required population fecundity; and CriPF, critical population fecundity. PF was computed by summing the contribution of each age-class, a, to obtain the total number of eggs spawned:

$$PF = AIF_a \times N_a \times M_a \times R_a \quad (1)$$

where N_a, M_a, and R_a are abundance, fraction of mature fish, and fraction of females by age-class a respectively.

Table 1. Mean AIF ('000 eggs) and number of fish sampled (n), 1980–2000, by length- and age-class (dashes indicate no data).

	Length-class (cm)																Age-class									
	11		12		13		14		15		16		17		18		1		2		3		4		5	
Year	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n	AIF	n
1980	—	—	7.7	1	8.9	71	11.4	103	14.2	58	15.1	6	20.9	1	—	—	—	—	9.7	8	11.5	217	12.0	15	—	—
1981	—	—	—	—	7.0	9	9.0	76	11.0	84	14.8	38	17.4	12	17.7	1	—	—	9.4	7	11.1	154	11.6	58	11.2	1
1982	—	—	5.5	3	6.4	37	8.0	114	11.1	132	13.6	65	17.0	18	18.5	1	—	—	9.1	108	10.6	215	12.2	46	12.7	1
1983	—	—	6.1	1	7.3	9	9.7	20	11.8	25	13.6	4	14.3	1	—	—	—	—	9.4	23	11.1	35	12.7	2	—	—
1984	—	—	6.7	1	6.9	16	8.1	37	11.0	15	13.7	12	—	—	—	—	—	—	8.6	20	9.3	59	12.1	2	—	—
1985	—	—	6.3	2	6.5	16	9.2	24	12.8	16	14.6	11	18.3	3	21.3	1	—	—	11.5	12	10.4	54	11.7	7	—	—
1986	—	—	5.9	9	6.9	132	8.7	101	10.3	32	12.9	3	—	—	—	—	—	—	7.8	87	7.9	177	10.3	11	13.6	2
1987	—	—	5.3	12	6.2	59	8.0	34	10.2	3	—	—	—	—	—	—	4.8	2	6.5	54	7.0	43	7.7	9	—	—
1988	—	—	6.7	6	8.1	39	9.6	77	11.2	10	—	—	—	—	—	—	6.3	4	9.1	119	10.7	9	—	—	—	—
1989	—	—	—	—	7.6	19	9.6	51	12.3	26	15.3	3	—	—	—	—	7.3	1	10.1	84	10.5	14	—	—	—	—
1990	—	—	7.4	4	8.6	29	10.8	46	12.3	45	13.5	11	21.6	2	—	—	7.7	4	10.3	66	11.9	58	13.9	8	11.7	1
1991	7.7	1	5.7	1	8.1	11	8.9	49	11.4	66	14.6	22	17.6	5	—	—	9.7	2	9.9	98	11.9	38	14.6	16	14.3	1
1992	—	—	5.0	5	6.4	30	8.3	60	11.5	68	14	17	16.7	1	—	—	—	—	8.6	93	10.9	81	11.3	7	—	—
1993	—	—	6.4	33	6.8	91	8.2	102	10.7	51	12.9	10	—	—	—	—	8.2	2	7.3	77	8.4	201	11.2	7	—	—
1994	3.5	1	4.4	5	5.6	41	7.0	104	8.2	61	8.2	16	—	—	—	—	—	—	5.7	61	7.5	145	8.0	21	8.7	1
1995	—	—	5.9	13	7.4	38	8.7	33	10.8	11	—	—	—	—	—	—	6.6	18	7.7	38	9.0	33	10.3	6	—	—
1996	—	—	6.2	11	8.5	54	10.3	110	11.8	69	14.2	22	8.1	1	—	—	8.7	64	10.8	117	11.4	82	12.3	4	—	—
1997	—	—	8.1	6	8.2	53	9.9	60	12.3	67	16.5	57	19.3	12	—	—	8.0	3	9.9	53	11.9	140	14.2	48	16.5	11
1998	—	—	7.7	10	9.1	73	12.1	120	14.4	63	17.2	28	20.9	7	—	—	—	—	7.7	28	11.5	163	14.3	88	17.8	22
1999	—	—	7.9	1	—	—	10.2	41	12.0	172	14.3	89	16.8	15	18. 9	2	8.1	2	11.6	116	12.7	143	14.3	50	17.3	9
2000	—	—	—	—	7.9	7	10.2	60	12.7	77	15.8	87	18.9	40	—	—	9.1	1	11.0	61	13.5	115	16.0	81	18.6	13
1980–1989	—	—	5.9	35	7.2	407	9.2	637	11.6	401	14.1	142	17.3	35	19.2	3	6.0	7	8.8	522	10.2	977	11.5	150	12.8	4
1990–2000	5.6	2	6.4	89	7.7	427	9.5	785	11.5	750	14.0	359	18.3	83	18.9	2	8.2	96	9.3	808	10.6	1199	13.6	336	17.1	58

Table 2. Mean AIF, RIF, length, weight, and age of capelin females sampled by year, 1970–2000 (n is the sample size, and dashes indicate no data).

Year	AIF ('000 eggs)	RIF (eggs g^{-1})	Length (cm)	Weight (g)	Age (years)	n
1970*	14.3	—	15.4	21.4	4.2	151
1971*	11.3	—	14.7	18.6	3.9	325
1972*	13.1	—	14.9	18.5	4.1	123
1973*	9.9	—	14.9	19.8	4.4	376
1974*	14.2	—	14.8	21.2	4.0	613
1975*	12.4	—	14.8	19.2	4.0	196
1976*	12.5	—	14.5	18.1	3.9	351
1977*	12.9	—	14.8	20.0	4.3	557
1978*	13.4	—	15.1	20.8	4.0	414
1979*	12.5	—	14.5	18.7	4.0	509
1980	11.4	701	14.0	16.3	4.0	240
1981	11.2	534	14.9	20.9	4.2	220
1982	10.4	535	14.8	19.4	3.8	370
1983	10.5	610	14.5	17.2	3.7	60
1984	9.2	568	14.3	16.2	3.8	81
1985	10.7	608	14.5	17.5	3.9	73
1986	8.0	572	13.6	14.4	3.7	277
1987	6.7	578	13.3	11.7	3.5	108
1988	9.2	646	13.7	14.2	3.0	132
1989	10.1	591	14.1	17.1	3.1	99
1990	11.1	651	14.3	17.0	3.5	137
1991	10.9	595	14.6	18.3	3.5	155
1992	9.7	552	14.4	17.5	3.5	181
1993	8.2	577	13.7	14.1	3.7	287
1994	7.1	480	14.2	14.8	3.8	228
1995	8.1	601	13.4	13.5	3.3	95
1996	10.5	639	14.1	16.4	3.1	267
1997	12.1	607	14.6	19.9	4.0	255
1998	12.4	578	15.2	21.8	4.3	301
1999	12.7	587	15.2	21.6	3.8	320
2000	13.9	658	15.1	21.1	4.1	271
1970–1979	12.7	—	14.8	19.7	4.1	3615
1980–1989	9.9	588	14.2	16.9	3.7	1660
1990–2000	10.6	584	14.5	17.8	3.7	2497

*Data updated from Galkin and Kovalev (1975).

SR_a represents the percentage surviving from the initial number of eggs spawned until the year-class had reached age a. As an integrated index of environmental conditions during early ontogenesis, SR can be used for calculating population fecundity, generating year-classes of predefined abundance levels under different survival rates. On the basis of data on abundance of the spawning stock, SR_2-values and year-class strength of two-year-olds, three levels of PF and associated biomass were established.

- A safe population fecundity (SPF) ensures strong year-classes ($>300 \times 10^9$) even with average survival up to age 2 during early ontogenesis ($0.05\% > SR_2 > 0.02\%$).
- The minimum required population fecundity (MRPF) corresponds to the level that generates strong year-classes under favourable conditions for survival, but produces average year-classes ($100 \times 10^9 < N_2 < 300 \times 10^9$) with average survival.
- The critical population fecundity (CriPF) is the level that generates a strong year-class under only the best possible conditions for survival (1989: $SR_2 = 0.72\%$). In other words, a decline of PF below CriPF excludes the possibility that a strong year-class will appear.

Results

Individual fecundity

Mean AIF by size-class, age-class, and year are given in Table 1, and Table 2 lists estimates of mean AIF, RIF, length, weight, and age of the samples processed. AIF varied within a wide range, averaging 10 000–12 000 eggs. Minimum fecundity was 1876 eggs in a 3-year-old

Table 3. Mean AIF of capelin (thousand eggs) and number of fish sampled (n) belonging to strong (abundance index >500: 1979–1981, 1983, 1989) and poor (abundance index <100: 1970, 1978, 1987, 1992–1995) year–classes by age.

	Strong		Poor	
Age	AIF	n	AIF	n
2	9.7	2	6.6	19
3	8.6	331	9.9	288
4	9.5	426	12.7	1002
5	11.0	56	14.1	129
6	13.6	2	17.5	32
Mean	9.2	817	12.4	1500

female of 13.4 cm and 14.8 g, while maximum fecundity was 34 146 eggs in a 4-year-old female of 17.2 cm and 31.5 g. Mean values were high in the 1970s, and low during the 1980s and early 1990s. In the most recent years, AIF, as well as other biological parameters, have returned to the level of the 1970s.

During the period of investigation, the capelin population has twice been in a state of depletion, during the years 1986–1990 and 1993–1998. At the beginning of both periods the population was characterized not only by low abundance and reduced average age, but also by a drastic decrease in mean AIF, reaching minima of 6700 eggs in 1987 and 7100 eggs in 1994. This decline cannot be explained just by variations in the length and age structure of the population, because AIF also decreased in fish of the same size and age (Table 1). Furthermore, RIF in 1994 was the lowest on record for the entire period.

When data are grouped by year-class strength, based on abundance indices, AIF of all age-classes proved to be generally higher (average 35%) for poor year-classes than for strong ones, except for the poorly represented age 2 (Table 3).

Population fecundity and survival

The total number of eggs released by all females during the spawning season (PF) depends mainly on the abundance of mature fish. However, deviations in PF from direct measures of female spawning-stock biomass (SSB) show that variations in the length and age composition may influence AIF to such a degree that they have a marked effect on the PF (Figure 1). PF and SSB were highest in 1976 and 1980 respectively.

In the 1970s, with a consistently high PF and apparently under favourable conditions for survival, year-classes were relatively strong (Figure 1). In the 1980s, survival (and therefore also recruitment) declined, followed by a stock collapse. The associated reduction in the size and age structure of the stock resulted in a lower average individual female fecundity. PF decreased to an all-time minimum in 1987, but apparently extremely high rates of survival in 1988 and 1989 were instrumental in initiating a rapid stock recovery. Although PF fluctuations during the 1990s were similar to those observed in the 1980s, the PF during the past two decades failed to reach the high values of the 1970s.

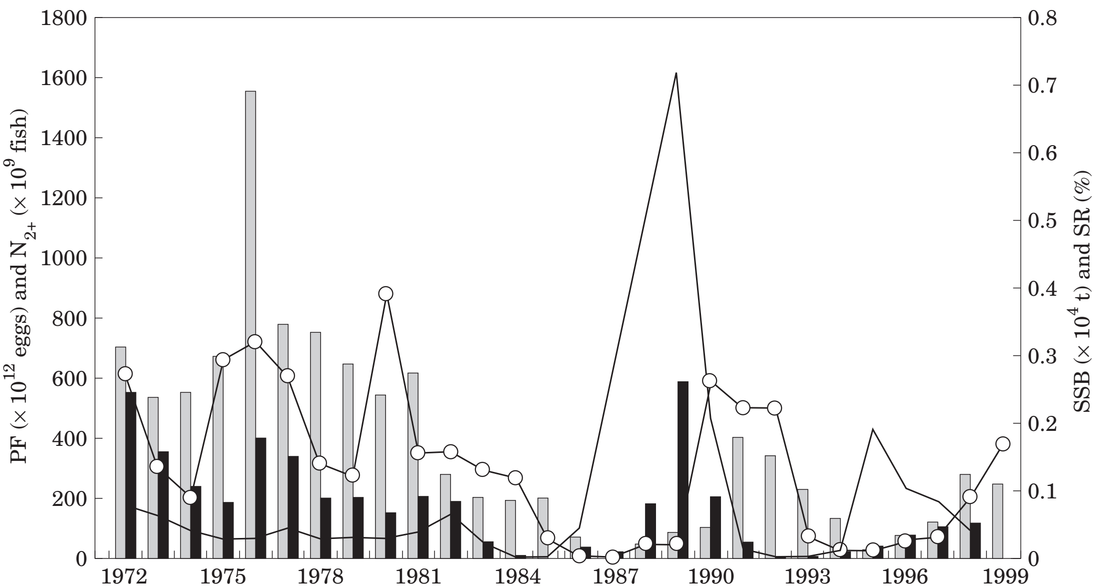

Figure 1. Population fecundity (PF, $\times 10^{12}$ eggs, grey columns), spawning stock (SSB, $\times 10^4$, open circles), abundance (N_{2+}, $\times 10^9$, dark columns), and survival rates (SR, %, solid line) of 2-year-old capelin, 1972–1999.

Table 4. Contribution by age-class to population fecundity (eggs × 10^{12}), 1972–2000 (dashes indicate no data).

Year	Age-class 2	3	4	5	6	7	Total
1972	—	52	404	207	17	—	679
1973	—	15	265	230	21	—	530
1974	—	50	315	182	2	—	549
1975	—	50	508	106	3	—	668
1976	—	151	933	464	3	—	1551
1977	—	66	350	298	50	8	772
1978	—	68	427	223	30	1	749
1979	—	70	447	115	9	1	642
Mean		66	456	227	17	3	770
%	8.6	59.4	29.4	2.2	0.4	100	
1980	—	43	454	41	1	—	539
1981	—	25	397	178	8	—	606
1982	—	55	153	68	3	—	277
1983	—	42	139	13	0	—	194
1984	—	12	149	24	0	—	185
1985	—	4	139	50	3	—	195
1986	—	12	43	8	—	—	63
1987	—	3	4	1	—	—	8
1988	2	32	6	0	—	—	40
1989	0	42	30	8	—	—	81
Mean	1	26	151	38	2		219
%	0.6	11.9	69.2	17.3	1.0		100
1990	1	61	31	2	0	—	95
1991	1	156	128	98	15	—	398
1992	—	180	143	17	—	—	339
1993	1	15	199	11	—	—	226
1994	—	33	81	14	1	—	128
1995	4	5	9	3	—	—	20
1996	17	24	27	1	—	—	69
1997	1	16	55	37	10	—	118
1998	—	63	101	68	46	—	277
1999	1	141	64	31	8	—	246
2000	1	67	147	126	38	—	379
Mean	3	69	89	37	17		216
%	1.4	32.1	41.5	17.2	7.8		100

The contribution of females of different age to the population fecundity has varied over the period (Table 4). In the 1970s, most eggs were spawned by 4- and 5-year-old fish. Between 1988 and 1992 and again in 1999, 3- and 4-year-old capelin played the key role in population reproduction. Since 1988, 2-year-old females have also contributed to reproductive output.

The strong year-class of 1972 was the most productive of the entire period. Females of that year-class spawned 1312×10^{12} eggs during the seasons 1975–1979. The lowest contribution by any year-class was just 17×10^{12} eggs, produced by the poor year-class of 1983. The greatest difference over the period 1970–2000 period is, therefore, in the order of approximately 80 to 1 (Table 4).

With the exception of the 1989 year-class, all strong year-classes (abundance of 2-year-olds $>300 \times 10^9$ fish) between 1972 and 1999 resulted from high PFs with good or average survival (Figure 1). The strong 1989 year-class resulted from a low PF, apparently owing to extremely good survival. Year-classes of medium strength (abundance of 2-year-olds of $100\text{–}300 \times 10^9$ fish) generally resulted from a high PF and good or average survival. Exceptions were the year-classes of 1988 and 1990, when PF was low but survival was excellent. Poor year-classes (abundance of 2-year-olds $<100 \times 10^9$ fish) coincide with poor survival and/or few spawned eggs.

Estimated SR_2s varied throughout the study period, from 0.72 in 1989 to 0.001 in 1985. Maximum SR was recorded during periods in the 1980s and 1990s when the fishery was closed to rebuild the stock. However, even under these favourable conditions for survival, only one strong year-class appeared, other year-classes from these periods being average or poor, probably a direct consequence of the low PF.

On the basis of SR values, the safe egg production level (SPF) is estimated to be around 750×10^{12} eggs, roughly corresponding to a female SSB of 3 000 000 t, which should ensure the appearance of a strong year-class even with average survival. This PF was only exceeded in 1976 and 1977, and in both cases a strong year-class emerged with average survival. The minimum required PF (MRPF), defined as the PF level at which natural fluctuations of the ambient environment are reflected in year-class abundance, was estimated to be about 325×10^{12} eggs (SSB: 1 000 000 t). When PF is at the critical level (CriPF) and the stock is in a state of severe depression, strong year-classes only appear when survival is excellent (as in 1989), but there is no guarantee of the formation of medium year-classes under average ambient conditions. CriPF is estimated to be about 50×10^{12} eggs (SSB: 200 000 t).

Table 5 provides data on population fecundity and survival rates for capelin aged between 1 and 5 years. Conditions of life vary between years and depend on a complex of biotic and abiotic factors. SR, being an integral indicator of these conditions, is also subject to considerable fluctuation. I shall not go into a detailed description of the factors affecting capelin survival. However, SR clearly increased considerably in the years when the fishery was halted. Thus, the closure of the capelin fishery in 1986 was immediately reflected in the survival rate. Already in 1987, SR started to increase, reaching a maximum in 1989. After the fishery was resumed in 1991, SR dropped to the lowest value for the entire period. Poor survival resulted in recruitment failure and a massive stock decline, which again led to closure of the fishery. During this second depression, stock recovery was slower than in the 1980s. In 1994 (the first year of the fishing ban), the stock did not

Table 5. Numbers surviving (N × 10^9) and survival rates (SR, %) of capelin from egg (PF × 10^{12}) to subsequent ages (numbers at age from October surveys; + signifies presence, but not at the number of decimals used; dashes indicate no data).

Year	PF	N_1	SR_1	N_2	SR_2	N_3	SR_3	N_4	SR_4	N_5	SR_5
1972	679	529	0.078	547	0.081	296	0.074	77	0.011	7	+
1973	530	305	0.057	348	0.066	163	0.031	40	0.008	1	+
1974	549	190	0.035	233	0.042	99	0.018	9	0.002	+	+
1975	668	211	0.032	175	0.026	76	0.011	5	0.001	+	+
1976	1551	359	0.023	392	0.025	114	0.007	33	0.002	+	+
1977	772	84	0.011	333	0.043	155	0.020	14	0.002	0	0.000
1978	749	12	0.002	196	0.026	48	0.006	2	+	0	0.000
1979	642	270	0.042	195	0.030	57	0.009	+	+	0	0.000
1980	539	403	0.075	148	0.027	38	0.007	3	0.001	0	0.000
1981	606	528	0.087	200	0.033	48	0.008	1	+	0	0.000
1982	277	515	0.186	187	0.067	21	0.007	0	+	0	0.000
1983	194	155	0.080	48	0.025	3	0.002	0	+	0	0.000
1984	185	39	0.021	5	0.003	+	+	0	0.000	0	0.000
1985	196	6	0.003	2	0.001	+	+	+	+	0	0.000
1986	63	38	0.059	29	0.045	3	0.004	+	+	0	0.000
1987	8	21	0.272	18	0.230	16	0.210	1	0.015	0	0.000
1988	40	189	0.477	178	0.448	33	0.083	1	0.003	0	0.000
1989	81	700	0.866	580	0.717	129	0.159	2	0.003	0	0.000
1990	95	402	0.425	196	0.208	17	0.018	+	+	0	0.000
1991	398	351	0.088	53	0.013	4	0.001	+	+	0	0.000
1992	339	2	0.001	3	0.001	2	0.000	+	+	0	0.000
1993	226	40	0.009	8	0.004	2	0.001	+	+	+	+
1994	128	7	0.006	12	0.009	2	0.001	1	+	0	0.000
1995	20	82	0.405	39	0.193	11	0.052	1	0.004	+	+
1996	69	99	0.144	73	0.106	27	0.039	1	0.001	—	—
1997	118	179	0.152	102	0.086	34	0.029	—	—	—	—
1998	277	156	0.056	111	0.040	—	—	—	—	—	—
1999	246	449	0.183	—	—	—	—	—	—	—	—
2000	379	—									
Mean	366	225	0.138	163	0.096	54	0.030	8	0.002	1	+

respond immediately, and survival rates did not reach an above-average level until 1995 (Table 5).

Discussion

Under favourable conditions for survival, a high PF automatically means the appearance of a strong year-class. However, average survival, even at a high PF, does not ensure the formation of strong year-classes. For instance, average survival and a high PF (539 × 10^{12} eggs) in 1980 generated only an average year-class, while a similar PF generated a strong year-class under prevailing favourable conditions for survival in 1973. Furthermore, when survival was poor, not even a single average year-class appeared, irrespective of whether PF was high or low.

An analysis of fecundity data in relation to year-class strength indicates that the AIF of poor year-classes is higher than that of strong ones. Apparently, this is a typical natural response during periods of low stock abundance, which may be associated with improved feeding opportunity owing to less competition. However, it should be borne in mind that, in situations when acoustic surveys record extremely low abundance of the adult stock, deviations from the "true" state of the stock tend to be exaggerated in relation to a normal situation. Furthermore, experience has shown that, under such conditions, stock size is more likely to be under- than overestimated. While the extremely high SR_2s in 1987, 1988, 1989, and 1995 may thus be classified as "overshots", they should nevertheless be accepted as indications of the general trends observed.

In my opinion, the decline in fecundity during the period of stock depletion can be explained as follows.

(1) Any fishery removes primarily the fastest-growing part of the population, and recruitment consequently becomes increasingly dependent on slow-growing fish, which leads to reduced population fecundity. This effect is accentuated if growth rates are reduced even further by adverse abiotic factors.
(2) Heavy fishing pressure in the late 1970s and early 1980s radically altered the age and size structure of the stock, and the contribution of subsequent age-classes to the population fecundity changed

accordingly. Thus, the contribution of age-class 3 to population fecundity increased from an average of about 10% during the years 1972–1986 to about 50% during the years 1987–1992 (Table 4). Younger and smaller spawners result in a severe overall fecundity decline (Luka *et al*., 1991).

The best rates of survival were recorded in years when the fishery was banned, indicating the negative impact of fishing on stock development. When the stock is stable and the spawning stock varies around or exceeds the minimum abundance level required (MRPF), year-class strength is determined by survival. It is only in years when stock abundance is low that PF becomes the principal factor contributing, in combination with favourable survival, to the formation of strong year-classes. These aspects are captured in the estimated values for SPF, MRPF, and CriPRF that may be used as broad guidelines for managing the fishery:

SPF – 750×10^{12} eggs (SSB, 3 000 000 t);

MRPF – 325×10^{12} eggs (SSB, 1 000 000 t);

CPF – 50×10^{12} eggs (SSB, 200 000 t).

For management purposes, stock size should probably exceed MRPF to maintain the multi-age structure of a stock and to preserve natural fluctuations in stock abundance. This by itself should help ensure that the SSB does not fall to a critical level.

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