Northwest Atlantic Fisheries Organization

Serial No. N1035 NAFO SCR Doc. 85/77

SCIENTIFIC COUNCIL MEETING - JUNE 1985

Age Specific M and its Effect on VPA: Div. 4VWX Silver Hake

by

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INTRODUCTION

The silver hake (Merluccius bilinearis) stock from the Scotian Shelf (NAFO Division 4VWX) has posed some interesting contradictions for fisheries managers in recent years. Quota allocation for this stock began with the 200 mile extension of jurisdiction in 1977. The mean annual catch prior to this time was approximately 100,000 tonnes - the mean catch since that time has been approximately 50,000 tonnes. Contrary to expectations the mean population numbers (taken from the latest assessment Waldron and Harris, 1984) for the latter period have dropped from 2.3 billion fish to 1.9 billion fish, a drop of 20% in the population with a 50% reduction in the catch.

Variation in recruitment in this stock is not extreme with only a factor of 4 separating the biggest and smallest year classes at age 1. The reproductive strategy of these fish may be a contributing factor; that is, their serial spawning capability with a protracted spawning season lasting from May until September. A second possible factor may be the high rate of cannibalism acting as a density dependent control mechanism. Schaefer (1960) pointed out that silver hake cannibalism could be a limiting factor upon their own population numbers and more recently Lleonart et al. (1985) discussed the effects on management advice of incorporating such information into virtual population analysis (VPA) modelling.

A serious constraint with VPA is the necessity (for most stocks) of assigning one natural mortality rate for all age groups and all years of the analysis. In an attempt to understand the effect of using age-specific natural mortality we have chosen to investigate the effects of the specialized form of predation, that is cannibalism. Swan and Clay (1979) and Clay et al (1984) presented feeding data collected specifically to test the effects of age specific natural mortality due to predation on and by the Scotian shelf hake stock.

THE MODEL

The standard VPA model was modified to allow the natural mortality to be divided between the 'known' cannibalism mortality and the 'unknown' residual mortality; the later due to predation, disease, senesence, etc. In an attempt to use a varying non-fishing mortality that more realistically reflects a fish population's true 'natural' rate, we have partitioned the natural mortality into 2 components - an age-specific predation (cannibalism) rate and the remaining 'undefined' or residual natural mortality rate, assumed to be a constant.

The changes required in the VPA to accomodate this partitioning of the usual natural mortality are as follows:

First, several assumptions were made:

1) all age classes of fish up to and including a maximum age of prey are susceptible to cannibalism, (in this example ages 1 to 3 are the prey),
2) all age classes greater than the minimum age of the predators are considered to be predators, (in this example ages 2 to 10 are the predators), and
3) a matrix of the number of fish of age i eaten annually by fish of age j is available, this matrix is considered to be time independent (Table 1).

Secondly, the analysis follows a format similar to that of the usual virtual population analysis:

1) for each year proceeding backwards:
   - the fishing mortality rate (F) for the previous year is calculated for all age classes greater than the oldest prey,
   -the population for the current year is then determined for these ages,
   -the total number of fish of each prey age eaten in the current year is calculated,
   -the total defined mortality rates are found for the prey ages similar to finding the F in the VPA, ie: by solving the equation:

$$(\#\ \text{defined deaths}) = \left(\frac{\text{defined rate}}{Z}\right) \times (\text{population}) \times (1-e^{-Z})$$

2) this rate is partitioned into its cannibalism and fishing portions in the same ratio as the total numbers dying due to cannibalism and fishing,
3) the population in the current year for each of these prey ages is then calculated.

The algorithms used are presented in Appendix I. The cannibalism mortality is age specific; the remainding non-fishing mortality is assumed to be age independent. Several individuals have suggested the inclusion of predation mortality as a variable component of natural mortality in VPA (Pope, 1979; Helgason and Gislason, 1979; Pope and Knight, 1982). However, the major draw back in applying this in practice is the complexity of multispecies interactions. Studying the same effect with a specialized form of predation mortality - cannibalism - allows a single species VPA to mimic the 'real' multi-species world. This adapted VPA we have referred to as VPAC.

INPUT DATA

The starting VPA input parameters for this initial trial were taken from the 1984 assessment of the 4VWX silver hake stock (Waldron and Harris, 1984) and the cannibalism parameters (Table 1) were modified from those presented in Clay et al. (1984).

ESTIMATION OF PARAMETERS

Traditional techniques of 'tuning' a VPA may not be applicable when working with age specific values of M. However, despite this fact, we have attempted to follow past practices in order to compare the resulting populations from the 1984 assessment and our VPAC.

The partial recruitment (PR) was derived by iteration, using the 1984 PR as a starting point with a terminal F of 0.2. The average PR of 1978 to 1981 inclusive was then used for the VPAC. A fully recruited age of 5 was used, although it may be higher.

The residual natural mortality (referred to as M') was selected by tuning the VPA at 6 levels of M' (Figure 1). The M' chosen was 0.15, by coincidence the same as the value of the terminal F for the 1983 catch. The population numbers were very different in both absolute values and age composition from the

1984 assessment. Despite these differences, the goodness of fits (R2) for the various 'tuning' relationships were similar to that achieved by Waldron and Harris (1984). The choice of terminal F was made as the point at which a levelling-off was observed in the value of R2. The M' was selected as the level at which the R2 for the chosen terminal F begins to decline, ie. M'=0.15. These are not presented as the best possible estimates, however they should be reasonably good indicators of relative population parameters.

ASSESSMENT RESULTS

The population numbers (Table 2) from the VPAC are very different from those of the 1984 VPA (Table 3). The total VPAC population for the years prior to 1977 are about 4 times higher than those derived from the 1984 VPA, totals after 1977 are approximately 8 times higher.The percent composition of the VPAC population (Table 4) shows over 60% by numbers are age 1 fish while the VPA population has generally less than 50% at age 1.

The fishing mortalities from the VPAC (Table 5) follow the same pattern as those from the VPA (Table 3), however they appear slightly higher. This creates some doubt as to the validity of the low terminal F used. (For this reason, only the data from 1970 to 1980 -the stable portion of the matrix- for the VPAC are presented in the tables.)

The data on the cannibalism rates and numbers (Table 6) indicate the magnitude of this form of mortality and the variability of 'total' natural mortality between age groups. The cannibalism level in most years approaches 50% of the age 1 fish. The total mortality (Z) calculated within cohort from the VPAC population numbers shows low initial Z's increasing to a peak at age 3, thereafter decreasing to age 9 (Table 7).

DISCUSSION

Such high rates of natural mortality in the first 3 years of life by those hake over 2 years of age leads to the unmistakable conclusion that if the older fish are under-exploited, they will have a detrimental effect on hake recruitment. A management scheme based on mesh regulations, aimed at placing heavier fishing mortalities on the cannibal age groups, will have a greater effect than placing catch and or effort restrictions upon a fishery exploiting mainly the cannibalized age groups. Likewise, restrictions in overall fishing mortality will be unlikely to lead to higher population levels and eventual higher yields as the increased numbers of older fish will themselves harvest any expected increase.

Although data are only presented on cannibalism mortality, it is known that the hake do prey upon other species such as haddock, red hake, sand lance, etc. With the population numbers indicated here, it can be calculated that even low rates of predation would result in very great absolute numbers of prey being removed. It can therefore be seen that a reduction in numbers of older (3+) silver hake would increase total production of silver hake, albeit requiring more effort, and possibly permit a more rapid recovery and higher standing stocks of other species in the area.

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Table 1. Matrix of cannibalism in the NAFO Division 4VWX silver hake stock (modified after Clay et al. 1984).

		PREDATOR										
		1	2	3	4	5	6	7	8	9	10+	age
	PREY											
	1	0	1.5	2.5	2.5	13	13	13	15	0	0	
age	2	0	0	0	2	16	21	21	23	69	0	
	3	0	0	0	0	7	11	15	18	49	49	

Table 2. Catch and population numbers (000's) from VPAC with M' = 0.15 and a terminal F = 0.15.

Catch numbers in thousands for 4VWX Silver Hake
DATE = 11/6/85

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE :											
1 :	187298.	221256.	382196.	245891.	101313.	144748.	153442.	2145.	28940.	9665.	6243.
2 :	748021.	413228.	464110.	1481377.	390645.	365100.	381420.	43838.	91526.	48332.	60302.
3 :	216246.	176319.	72079.	96683.	150973.	52712.	72374.	78784.	90457.	69045.	81642.
4 :	59832.	75316.	48267.	106563.	7105.	60662.	31276.	29767.	43232.	46538.	35725.
5 :	20695.	22200.	17957.	96839.	9804.	38554.	5578.	7029.	19602.	29650.	15223.
6 :	9636.	1891.	7508.	19650.	3250.	4791.	2667.	2017.	8657.	16960.	6151.
7 :	3608.	5177.	1168.	15187.	93.	310.	513.	486.	3248.	5078.	1674.
8 :	1988.	1343.	440.	5469.	109.	362.	104.	567.	2025.	1764.	342.
9 :	1114.	2077.	611.	483.	60.	359.	389.	525.	423.	1150.	89.
10 :	680.	1914.	2015.	817.	77.	998.	81.	1.	648.	488.	43.
1+ :	1249118.	920721.	996351.	2068959.	663429.	668596.	647844.	165159.	288758.	228670.	207434.
2+ :	1061820.	699465.	614155.	1823068.	562116.	523848.	494402.	163014.	259818.	219005.	201191.
3+ :	313799.	286237.	150045.	341691.	171471.	158748.	112982.	119176.	168292.	170673.	140889.
4+ :	97553.	109918.	77966.	245008.	20498.	106036.	40608.	40392.	77835.	101628.	59247.

Population numbers in thousands of 4VWX Silver Hake
DATE = 11/6/85

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE :											
1 :	11338691.	9620044.	9114077.	5971660.	4705241.	4871988.	5337793.	5539784.	4883953.	4581039.	5672297.
2 :	5303462.	4656108.	3748144.	3875434.	2015641.	1926617.	2160877.	2257853.	2222224.	1702518.	1930021.
3 :	1771310.	1855884.	1109826.	833534.	924216.	611115.	626716.	914524.	917492.	695901.	688543.
4 :	128769.	131905.	179923.	135825.	66250.	84320.	63743.	83569.	95474.	86192.	79193.
5 :	41128.	55844.	44521.	110313.	20167.	50446.	17309.	26140.	44503.	42431.	31504.
6 :	19706.	16399.	27629.	21792.	7693.	8352.	8377.	9755.	16011.	20278.	9483.
7 :	11078.	8111.	12365.	16852.	1102.	3632.	2799.	4751.	6533.	5841.	2113.
8 :	20850.	6208.	2248.	9561.	859.	862.	2839.	1935.	3640.	2640.	448.
9 :	7245.	16106.	4103.	1529.	3218.	638.	409.	2347.	1143.	1276.	662.
10 :	3300.	5206.	11941.	2966.	870.	2714.	220.	6.	1535.	594.	65.
1+ :	18645539.	16371815.	14254776.	10979466.	7745256.	7560684.	8221084.	8840665.	8192508.	7138710.	8414330.
2+ :	7306848.	6751771.	5140700.	5007806.	3040015.	2688696.	2883291.	3300882.	3308555.	2557672.	2742033.
3+ :	2003386.	2095663.	1392556.	1132372.	1024374.	762079.	722414.	1043029.	1086331.	855154.	812011.
4+ :	232076.	239778.	282730.	298837.	100159.	150965.	95698.	128504.	168839.	159253.	123468.

Table 3. Population numbers (000's) and fishing mortalities of silver hake from 1984 VPA (Waldron and Harris, 1984).

SILVER HAKE POPULATION NUMBERS (000) AT TF=.25 AND M=.4

	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
1	1711006	1689321	3807998	1435711	1366446	1492339	901581	719373	866332	1010972	705900	685618	1878611	374654
2	1772299	995308	954788	2245392	763723	833941	882831	480424	480477	557406	669816	468080	458320	1243248
3	518837	593324	340865	275549	353240	204058	268428	288594	286767	248873	334469	399914	297907	265394
4	193181	175803	257414	170865	107384	116985	94336	121790	130639	120376	111403	158264	178825	145788
5	74083	81568	58427	133916	31299	66227	30458	38202	57868	53264	43592	45952	75104	67024
6	27490	33053	36986	24885	15168	13141	14102	15914	19977	23243	12396	17003	19375	22782
7	12433	10728	20633	18787	1737	7554	4975	7301	9047	6568	2539	3427	6958	5913
8	33697	5441	3124	12890	1094	1089	4811	2918	4502	3490	529	396	1749	2442
9	13006	20975	2575	1741	4289	645	439	3139	1501	1424	946	88	160	354
10	3269	7815	12390	1238	778	2826	149	7	1683	670	83	561	12	11
1+	4359301	3613336	5495199	4320975	2645157	2738804	2202110	1677663	1858793	2026286	1881673	1779300	2917020	2127611
2+	2648296	1924015	1687202	2885263	1278711	1246465	1300529	958290	992461	1015314	1175773	1093683	1038409	1752957
3+	875996	928707	732414	639871	514989	412524	417698	477866	511984	457908	505957	625603	580089	509709
4+	357159	335383	391549	364322	161749	208467	149270	189272	225217	209035	171488	225689	282183	244315
5+	163978	159580	134135	193457	54365	91482	54934	67482	94578	88659	60085	67425	103358	98527

FISHING MORTALITY AT AGE

	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
1	0.14	0.17	0.13	0.23	0.09	0.12	0.23	0.00	0.04	0.01	0.01	0.00	0.01	0.01
2	0.69	0.67	0.84	1.45	0.92	0.73	0.72	0.12	0.26	0.11	0.12	0.05	0.15	0.08
3	0.68	0.44	0.29	0.54	0.71	0.37	0.39	0.39	0.47	0.40	0.35	0.40	0.31	0.25
4	0.46	0.70	0.25	1.30	0.08	0.95	0.50	0.34	0.50	0.62	0.49	0.35	0.58	0.25
5	0.41	0.39	0.45	1.78	0.47	1.15	0.25	0.25	0.51	1.06	0.54	0.46	0.79	0.25
6	0.54	0.07	0.28	2.26	0.30	0.57	0.26	0.16	0.71	1.81	0.89	0.49	0.79	0.25
7	0.43	0.83	0.07	2.44	0.07	0.05	0.13	0.08	0.55	2.12	1.46	0.27	0.65	0.25
8	0.07	0.35	0.18	0.70	0.13	0.51	0.03	0.26	0.75	0.91	1.40	0.51	1.20	0.25
9	0.11	0.13	0.33	0.41	0.02	1.06	3.71	0.22	0.41	2.44	0.12	1.63	2.29	0.25
10	0.29	0.34	0.22	1.45	0.13	0.55	1.03	0.18	0.61	1.82	0.96	0.72	1.21	0.25

Table 4. Percent composition of catch and population numbers (Table 2) from VPAC.

Percentage Composition: Catch - Numbers 4VWX Silver Hake

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE:											
1 :	0.1499	0.2403	0.3836	0.1188	0.1527	0.2165	0.2369	0.0129	0.1002	0.0422	0.0301
2 :	0.5988	0.4488	0.4658	0.7160	0.5888	0.5461	0.5898	0.2654	0.3170	0.2114	0.2907
3 :	0.1731	0.1915	0.0723	0.0467	0.2276	0.0788	0.1117	0.4770	0.3133	0.3019	0.3936
4 :	0.0479	0.0818	0.0484	0.0515	0.0107	0.0907	0.0482	0.1802	0.1497	0.2035	0.1722
5 :	0.0165	0.0241	0.0180	0.0468	0.0147	0.0576	0.0086	0.0425	0.0678	0.1297	0.0733
6 :	0.0077	0.0020	0.0075	0.0094	0.0048	0.0071	0.0041	0.0122	0.0299	0.0741	0.0296
7 :	0.0028	0.0056	0.0011	0.0073	0.0001	0.0004	0.0007	0.0029	0.0112	0.0222	0.0080
8 :	0.0015	0.0014	0.0004	0.0026	0.0001	0.0005	0.0001	0.0034	0.0070	0.0077	0.0016
9 :	0.0008	0.0022	0.0006	0.0002	0.0000	0.0005	0.0006	0.0031	0.0014	0.0050	0.0004
10 :	0.0005	0.0020	0.0020	0.0003	0.0001	0.0014	0.0001	0.0000	0.0022	0.0021	0.0002

Percentage Composition: Population - Numbers 4VWX Silver Hake

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE:											
1 :	0.6081	0.5876	0.6394	0.5439	0.6075	0.6444	0.6493	0.6266	0.5961	0.6417	0.6741
2 :	0.2844	0.2844	0.2629	0.3530	0.2602	0.2548	0.2628	0.2554	0.2713	0.2385	0.2294
3 :	0.0950	0.1134	0.0778	0.0759	0.1193	0.0808	0.0762	0.1034	0.1120	0.0974	0.0818
4 :	0.0069	0.0080	0.0126	0.0123	0.0085	0.0111	0.0077	0.0094	0.0116	0.0120	0.0094
5 :	0.0022	0.0034	0.0031	0.0100	0.0026	0.0066	0.0021	0.0029	0.0054	0.0059	0.0037
6 :	0.0010	0.0010	0.0019	0.0019	0.0009	0.0011	0.0010	0.0011	0.0019	0.0028	0.0011
7 :	0.0005	0.0004	0.0008	0.0015	0.0001	0.0004	0.0003	0.0005	0.0007	0.0008	0.0002
8 :	0.0011	0.0003	0.0001	0.0008	0.0001	0.0001	0.0003	0.0002	0.0004	0.0003	0.0000
9 :	0.0003	0.0009	0.0002	0.0001	0.0004	0.0000	0.0000	0.0002	0.0001	0.0001	0.0000
10 :	0.0001	0.0003	0.0008	0.0002	0.0001	0.0003	0.0000	0.0000	0.0001	0.0000	0.0000

Table 5. Fishing mortality from VPAC.

Fishing Mortality of 4VWX Silver Hake
DATE = 11/6/85

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE :											
1 :	0.024	0.035	0.062	0.067	0.032	0.043	0.042	0.000	0.009	0.003	0.001
2 :	0.228	0.167	0.239	0.720	0.332	0.315	0.263	0.029	0.069	0.043	0.044
3 :	0.343	0.246	0.155	0.319	0.430	0.218	0.268	0.217	0.257	0.243	0.251
4 :	0.685	0.936	0.339	1.757	0.123	1.433	0.741	0.480	0.661	0.856	0.657
5 :	0.769	0.554	0.564	2.513	0.732	1.645	0.423	0.340	0.636	1.348	0.725
6 :	0.738	0.132	0.344	2.834	0.601	0.943	0.417	0.251	0.858	2.111	1.167
7 :	0.429	1.133	0.107	2.827	0.095	0.096	0.219	0.117	0.756	2.417	1.803
8 :	0.108	0.264	0.236	0.939	0.147	0.595	0.040	0.377	0.898	1.234	1.639
9 :	0.181	0.149	0.174	0.413	0.020	0.914	4.085	0.275	0.505	2.823	0.156
10 :	0.250	0.500	0.200	0.350	0.100	0.500	0.500	0.200	0.600	2.000	1.200
MEAN :	0.376	0.412	0.242	1.274	0.261	0.670	0.700	0.229	0.525	1.308	0.764
MEAN/POP:	0.120	0.107	0.122	0.373	0.161	0.154	0.125	0.036	0.067	0.063	0.042

Table 6. Cannibalism levels from VPAC of NAFO Division 4VWX silver hake.

Cannibalism numbers in thousands of Silver Hake
DATE = 11/6/85

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE :											
1 :	5369059.	4716212.	3937562.	3163761.	2210530.	2066150.	2389547.	2770627.	2699663.	2181316.	2524826.
2 :	2207045.	2762098.	2159686.	1161022.	837346.	761176.	647511.	1073260.	1237607.	797634.	740206.
3 :	1328483.	1391913.	832369.	625151.	636305.	458336.	430336.	685893.	688119.	505098.	439019.
1+ :	8904587.	8870223.	6929618.	4949933.	3684181.	3285662.	3467395.	4529780.	4625390.	3484048.	3704051.
2+ :	3535528.	4154012.	2992056.	1786172.	1473651.	1219512.	1077847.	1759153.	1925727.	1302732.	1179226.
3+ :	1328483.	1391913.	832369.	625151.	636305.	458336.	430336.	685893.	688119.	505098.	439019.

Cannibalism Mortality of 4VWX Silver Hake

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE :											
1 :	0.715	0.757	0.643	0.869	0.710	0.620	0.668	0.763	0.894	0.711	0.646
2 :	0.672	1.117	1.114	0.564	0.711	0.658	0.447	0.721	0.941	0.712	0.542
3 :	2.105	1.938	1.795	2.063	1.814	1.893	1.596	1.892	1.958	1.780	1.352
MEAN :	1.164	1.271	1.184	1.165	1.079	1.057	0.904	1.125	1.264	1.068	0.847
MEAN/POP:	0.836	0.997	0.861	0.851	0.844	0.734	0.680	0.871	1.029	0.818	0.680

Cannibalism Biomass in Tonnes of 4VWX Silver Hake
DATE = 11/6/85

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE :											
1 :	322144.	188648.	220503.	142369.	139263.	138432.	150541.	171779.	132284.	133060.	103518.
2 :	278088.	353549.	257003.	148611.	108018.	117982.	95832.	157769.	136137.	122836.	104369.
3 :	221857.	261680.	173965.	135033.	129806.	111376.	105863.	144038.	119733.	101020.	93511.
1+ :	822088.	803877.	651471.	426013.	377087.	367790.	352236.	473586.	388153.	356915.	301398.
2+ :	499944.	615228.	430968.	283643.	237824.	229358.	201694.	301807.	255870.	223855.	197880.
3+ :	221857.	261680.	173965.	135033.	129806.	111376.	105863.	144038.	119733.	101020.	93511.

Table 7. Total mortality of NAFO Division 4VWX silver hake calculated within cohorts from population numbers from VPAC (Table 2).

Total Mortality of 4VWX Silver Hake

DATE = 11/6/85

YEAR :	70	71	72	73	74	75	76	77	78	79	80
AGE :											
1 :	0.89	0.94	0.86	1.09	0.89	0.81	0.86	0.91	1.05	0.86	0.80
2 :	1.05	1.43	1.50	1.43	1.19	1.12	0.86	0.90	1.16	0.91	0.74
3 :	2.60	2.33	2.10	2.53	2.39	2.26	2.01	2.26	2.37	2.17	1.75
4 :	0.84	1.09	0.49	1.91	0.27	1.58	0.89	0.63	0.81	1.01	0.81
5 :	0.92	0.70	0.71	2.66	0.88	1.80	0.57	0.49	0.79	1.50	0.88
6 :	0.89	0.28	0.49	2.98	0.75	1.09	0.57	0.40	1.01	2.26	1.32
7 :	0.58	1.28	0.26	2.98	0.25	0.25	0.37	0.27	0.91	2.57	1.95
8 :	0.26	0.41	0.39	1.09	0.30	0.75	0.19	0.53	1.05	1.38	1.79
9 :	0.33	0.30	0.32	0.56	0.17	1.06	4.22	0.42	0.65	2.98	0.31
MEAN :	0.93	0.98	0.79	1.92	0.79	1.19	1.17	0.76	1.09	1.74	1.15

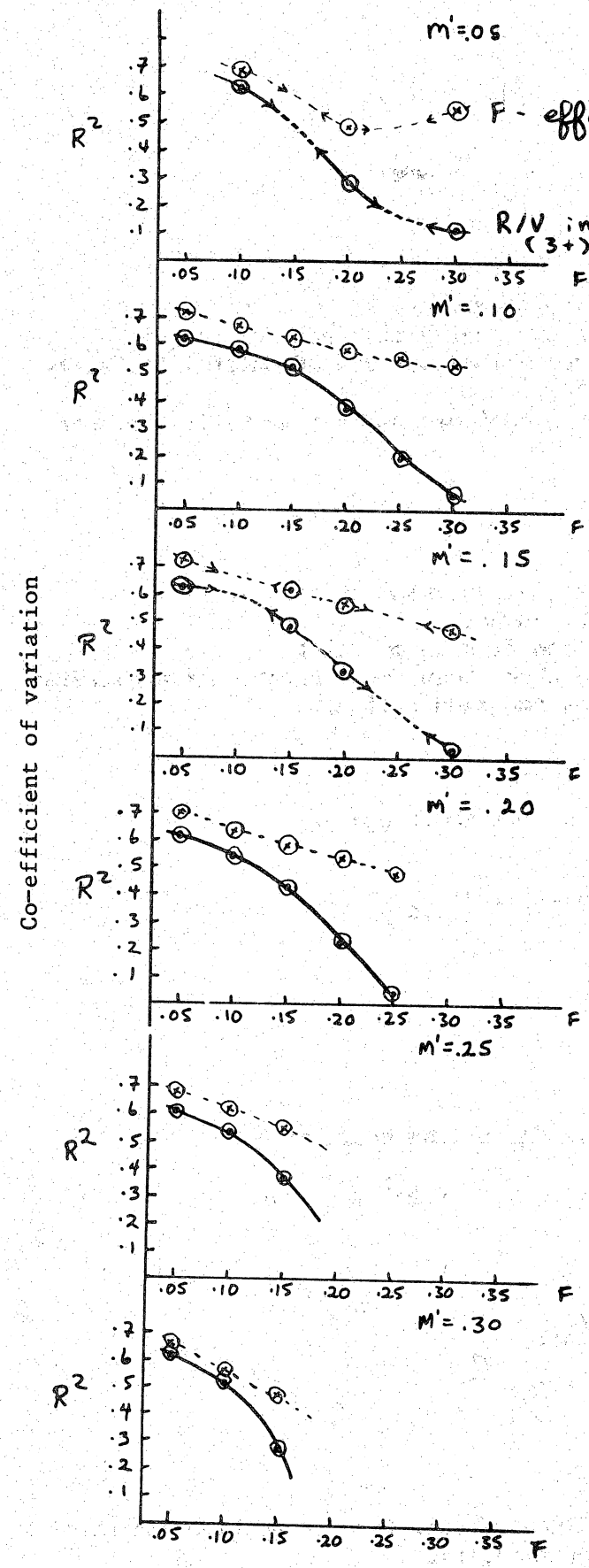

Figure 1. Tuning relationships (F-effort and R/V-VPAC population numbers at 3+) for VPAC on 4VWX silver hake.

Appendix I.

VPA variables

F = instantaneous rate of fishing mortality
M = instantaneous rate of natural mortality (all components)
P = instantaneous rate of the defined portion of natural mortality, predation (cannibalism *)
U = instantaneous rate of the undefined natural mortality ie. other than predation

$M = U + P$
$Z = F + M = F + U + P$

N = population (numbers) at the beginning of the year
N' = population (numbers) at mid-year
C = catch = numbers dying from fishing mortality
U' = numbers dying naturally other than from predation (cannibalism)
P' = number dying from predation (cannibalism)

E_{ij} = # prey of age i eaten by a fish at age j.

$$N_{i+1,t+1} = N_{i,t} - (C_{i,t} + U'_{i,t} + P'_{i,t})$$

where i = age class
t = year

VPA Algorithm

$F_{i,t}$ is found by iteratively solving the equation

$$C_{i,t} = \frac{F_{i,t}}{Z_{i,t}} \times N_{i+1,t+1} \times (e^{Z_{i,t}} - 1)$$

then
$$N_{i,t} = \frac{C_{i,t} \times Z_{i,t}}{F_{i,t} \times (1 - e^{-Z_{i,t}})}$$

* Throughout this documentation, the general term 'predation' is used in this specific example to refer to cannibalism.

VPA (with cannibalism) Algorithm

For all fish aged greater than the oldest prey:

$F_{i,t}$ is found by iteratively solving the equation

$$C_{i,t} = \frac{F_{i,t}}{Z_{i,t}} \times N_{i+1,t+1} \times (e^{Z_{i,t}} - 1)$$

$N_{i,t}$ is found by solving the equation

$$N_{i,t} = \frac{C_{i,t} \times Z_{i,t}}{F_{i,t} \times (1 - e^{-Z_{i,t}})}$$

The mid-year population is calculated

$$N'_{i,t} = N_{i,t}\, e^{(-Z_{i,t}/2)}$$

For all fish of age less than or equal to the oldest prey :

$$P'_{i,t} = \sum_{j} N'_{j,t} \times E_{i,j}$$

The total defined mortality rates are found by iteratively solving the equation:

$$(C_{i,t} + P'_{i,t}) = \frac{(F_{i,t} + P_{i,t})}{Z_{i,t}} \times N_{i+1,t+1} \times (e^{Z_{i,t}} - 1)$$

Then:

$$F_{i,t} = \frac{C_{i,t} \times Z_{i,t}}{N_{i+1,t+1} \times (e^{Z_{i,t}} - 1)} \quad ; \quad P_{i,t} = \frac{P'_{i,t} \times Z_{i,t}}{N_{i+1,t+1} \times (e^{Z_{i,t}} - 1)}$$

$N_{i,t}$ is calculated from the equation

$$N_{i,t} = \frac{(C_{i,t} + P'_{i,t}) \times Z_{i,t}}{(F_{i,t} + P_{i,t}) \times (1 - e^{-Z_{i,t}})}$$

For age classes greater than or equal to the youngest predator, the mid-year population is calculated.

$$N'_{i,t} = N_{i,t} \times e^{-Z_{i,t}/2}$$