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Non-predation natural mortality of Norway pout (*Trisopterus esmarkii*) in the North Sea

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Based on age disaggregated data on catch rates in bottom trawl surveys, commercial catches, and the number consumed by the North Sea piscivorous predators, new estimates of non-predation natural mortality, M1, are obtained for Norway pout [*Trisopterus esmarkii* (Nilsson)]. Simple log catch ratio analysis and rough maximum likelihood procedures are applied. The analysis focus on the year classes 1977–1981 and 1987–1991, which are represented in the extensive stomach sampling of North Sea piscivorous fish in 1981 and 1991. Although the M1 of Norway pout varied between the two periods, in both periods it increased with age and was very high for age 2 and older fish (0.10 for age 1, 1.74 for age 2, 2.58 for age 3 and 3.05 for age 4 for the 1977–1981 year classes and 0.10 for age 1, 2.03 for age 2, 3.04 for age 3 and 4.39 for age 4 for the 1987–1991 year classes). This difference between the two periods is not significant. Survey data from each quarter of the year show that the main mortality takes place between the 1st and the 2nd quarter of the year, i.e. from before to after spawning, thus pointing at spawning as the main factor.

Keywords: commercial catch, natural mortality, North Sea, Norway pout, numbers consumed, population dynamics, trawl survey, *Trisopterus esmarkii*.

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Introduction

Norway pout [*Trisopterus esmarkii* (Nilsson)] is a small gadoid fish which, in the North Sea, is exposed to a significant fishery for fishmeal and fish oil. The mean annual catch in 1974–1999 was 278 000 t (ICES, 2001). It is a short-lived species, which rarely gets older than 5 years. Norway pout is an important prey for cod (*Gadus morhua*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*) and mackerel (*Scomber scombrus*) in the North Sea (ICES, 1997), and it is included in the ICES North Sea Multi-Species model (MSVPA) (see e.g. Sparre, 1991). Predation mortality (M2) is estimated by the MSVPA based on extensive stomach analysis of the fish predators, their stock numbers and their consumption rates. For the MSVPA model to run, assumptions about other (non-predation) natural mortality (M1) have to be made. This mortality can be caused by disease, spawning stress, growth stress (Ursin, 1963), etc. As for most species in the MSVPA model, M1 is assumed to be 0.2 for all ages of Norway pout.

There are, however, serious uncertainties about appropriate M1 values for Norway pout. Ursin (1963), Raitt (1968), and Bailey and Kunzlic (1984) have indicated that natural mortality (M) of Norway pout increases with age. Ursin (1963) suggested that the increase could result from: "... the irreversibility of growth in length in a seasonally changing environment, causing a marked loss of condition in winter". Raitt (1968) and Bailey and Kunzlic (1984) observed that total mortality, Z, estimated from survey data increases with age. Bailey and Kunzlic (1984) speculated that this could be due to spawning stress.

In the routine stock assessment made by the ICES Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (e.g. ICES, 2001), natural mortality of Norway pout is assumed to be constant over ages. Based on results of the MSVPA

Table 1. Survey indices (N h^{-1}) for Norway pout by age.

	IBTS 1st quarter					EGFS August				SGFS August			
Year/age	1	2	3	4	5	0	1	2	3	0	1	2	3
1974	11 921	8100	776.0	1.0	0.1	—	—	—	—	—	—	—	—
1975	4 827	1808	20.7	11.0	0.5	—	—	—	—	—	—	—	—
1976	4 066	303	13.8	0.0	0.0	—	—	—	—	—	—	—	—
1977	6 095	256	53.8	0.0	0.0	—	—	—	—	—	—	—	—
1978	1 480	551	46.9	0.3	0.0	—	—	—	—	—	—	—	—
1979	2 558	307	73.4	0.0	0.0	—	—	—	—	—	—	—	—
1980	3 275	552	29.1	4.1	0.0	—	—	—	—	—	1928	346	12
1981	1 092	377	14.9	0.2	0.0	—	—	—	—	—	185	127	9
1982	4 437	256	57.3	1.2	0.0	6594	2609	39	77.0	8	991	44	22
1983	2 326	628	8.0	3.4	0.1	6067	1558	114	0.4	13	490	91	1
1984	3 957	812	56.3	0.9	0.2	457	3605	359	14.0	2	615	69	9
1985	2 117	1423	72.9	3.2	0.0	362	1201	307	0.0	5	636	173	5
1986	2 051	385	20.0	1.1	0.0	285	717	150	80.0	38	389	54	9
1987	3 173	485	62.9	3.2	0.3	8	552	122	0.9	7	338	23	1
1988	124	724	12.9	2.1	0.6	165	102	134	21.0	14	38	209	4
1989	2 015	252	171.6	2.7	0.2	1530	1274	621	20.0	2	382	21	14
1990	1 271	758	40.4	2.7	0.0	2692	917	158	23.0	58	206	51	2
1991	2 497	677	129.0	0.0	0.0	1509	683	399	6.0	10	732	42	6
1992	5 121	902	33.0	4.7	0.0	2885	6193	1069	157.0	12	1715	221	24
1993	2 681	2644	259.0	6.0	0.0	—	—	—	—	2	580	329	20
1994	1 868	375	67.0	2.9	0.2	—	—	—	—	136	387	106	6
1995	5 941	785	77.0	8.6	0.0	—	—	—	—	37	2438	234	21
1996	912	2635	234.0	4.7	0.1	—	—	—	—	127	412	321	8
1997	9 752	1474	670.0	2.9	0.0	—	—	—	—	1	2154	130	32
1998	1 006	5343	300.0	73.8	0.1	—	—	—	—	—	—	—	—
1999	3 527	597	667.0	4.0	0.3	—	—	—	—	—	—	—	—

model, natural mortality is set to 1.6 annually, for all age groups.

This paper tries to resolve the problem of appropriate M1 values by analysing, (1) catch rate indices from research vessel trawl surveys, (2) catch in commercial fisheries and (3) the number of Norway pout consumed by the predators in the North Sea. All data series are disaggregated by age.

Materials

Standard abundance indices of Norway pout (Table 1) from the International Bottom Trawl Survey (IBTS) in the North Sea, Skagerrak and Kattegat (see e.g. ICES, 1999) in February each year are used to calculate total mortality (Z). Beginning in 1974 the IBTS spatial coverage of the Norway pout distribution area is good and fairly constant over time (Anon., 1999). The IBTS covers mainly depths less than 200 m in the North Sea and less than 250 m in the Skagerrak. According to Poulsen (1968) very few Norway pout are caught at depths greater than 200 m in the North Sea and Skagerrak on shrimp trawl surveys. Albert (1994) found Norway pout at depths greater than 200 m, but very few at depths greater than 300 m.

The IBTS index expresses the mean catch (N h^{-1}) within a standard area (ICES, 1999). The area comprises 93 statistical rectangles (1° Longitude × 0.5° Latitude) and covers most of the geographical distribution of the Norway pout stock in the North Sea and Skagerrak. The area with depths less than 300 m not covered by the index area is about 15% of the index area, and the index area is thus assumed to cover the main part of the stock distribution. Between 274 and 527 trawl hauls have been made annually and since 1978 almost all fish were caught using the GOV trawl (Anon., 1999). The data used in the present analyses are taken from the ICES IBTS database.

Data from Scottish and English ground fish surveys were also used. The Scottish Ground Fish Survey (SGFS) is conducted in the third quarter of the year and covers the period 1980–2001. Scotland changed from the Aberdeen trawl to the IBTS GOV trawl in 1998 and therefore no data from 1998 and onwards have been included in order to avoid intercalibration problems. The English Ground Fish Survey (EGFS) is also conducted in the third quarter of the year and covers the period 1982–2001. England changed from a Granton trawl used until 1992, to the IBTS GOV trawl. Again to avoid intercalibration problems no data from later than 1992 were considered. The number of statistical

Table 2. Commercial catch in numbers ('000) at age and in weight ('000 t).

Year	Age 0	1	2	3	4	Weight
1974	6 565 750	25 647 060	821 700	174 830	690	735.8
1975	10 856 250	20 091 580	2 919 240	16 630	640	559.7
1976	6 183 000	21 035 390	2 143 130	166 770	510	435.4
1977	1 715 690	19 868 160	2 413 650	91 210	2 510	389.9
1978	1 529 650	7 896 880	3 129 160	322 520	3 930	270.1
1979	1 886 960	15 189 410	2 182 570	264 710	4 120	329.2
1980	684 950	19 839 730	4 363 080	115 360	7 210	482.7
1981	37 003 370	5 705 490	3 589 540	174 730	8 080	238.5
1982	1 245 270	18 654 330	1 202 010	310 030	0	395.3
1983	3 117 380	16 154 400	4 485 510	48 760	2 120	451.4
1984	2 232 100	13 793 570	4 956 070	420 160	0	393.0
1985	684 420	7 512 340	2 475 540	224 400	714	205.1
1986	5 571 530	3 633 200	1 440 140	81 120	3 010	178.4
1987	234 700	7 540 110	865 010	17 430	1 010	149.3
1988	3 886 670	1 158 680	1 428 740	20 100	0	109.5
1989	5 012 250	5 827 040	540 410	29 630	0	172.5
1990	1 013 000	5 772 000	1 457 000	49 000	10 000	151.6
1991	4 219 620	4 704 170	2 141 420	152 290	6 000	192.9
1992	1 833 230	11 319 480	2 035 240	140 710	3 000	299.8
1993	1 271 130	4 952 680	2 528 550	93 660	170	184.2
1994	4 885 090	4 524 270	1 430 790	156 000	0	182.3
1995	2 392 040	11 789 850	602 180	43 330	0	241.0
1996	3 241 550	2 788 630	2 308 020	88 640	0	166.2
1997	451 120	5 782 810	1 035 400	337 390	0	169.7
1998	432 520	1 404 180	1 538 760	83 050	28 400	79.8

rectangles covered at the SGFS is 86 and at the EGFS 73. Both surveys cover the entire North Sea, but Skagerrak is not covered. Normally one haul is made in each rectangle (Cotter, 2001). The data are taken from ICES (2000).

Commercial catch (numbers-at-age per year) from 1974–1998 were taken from ICES routine assessment work (ICES, 2000) (Table 2).

The number of Norway pout consumed by the piscivorous predators in the North Sea (Table 3) was calculated from the MSVPA model based on the Key-run of ICES (1997). The basis for the calculation is the stomach content of the predators, the numbers of the predators and the prey, and the consumption rates of the predators. The stock numbers are integrated parts of the MSVPA calculations and consequently use the assumed M1 values. These are, however, what we in the present paper try to estimate. To avoid circularity in the logic, we estimated the numbers of Norway pout consumed in the years where predator stomachs were sampled (1981 and 1991). For these years the estimates of numbers predated are basically a simple multiplication of predator numbers, consumption rates and fraction of Norway pout in the stomach.

Table 3. Number ('000) of Norway pout consumed by age according to the MSVPA.

Year	Age 0	1	2	3
1974	199 606 469	94 982 799	1 972 306	212 529
1975	353 421 137	75 619 550	5 435 707	11 867
1976	189 202 594	116 344 116	5 391 641	197 327
1977	87 953 305	76 936 061	7 665 342	80 035
1978	128 218 549	38 356 893	6 813 697	414 319
1979	158 546 416	58 334 339	3 027 496	217 896
1980	131 129 669	75 898 765	5 963 956	59 692
1981	228 789 151	35 741 200	10 129 841	219 985
1982	209 840 717	86 164 145	1 907 051	261 172
1983	172 921 338	65 912 278	7 645 556	48 961
1984	208 592 270	52 908 393	7 721 441	292 568
1985	143 569 361	46 539 874	5 568 713	127 141
1986	233 472 637	30 435 654	2 124 384	93 138
1987	207 134 563	37 614 512	1 709 526	50 981
1988	221 679 199	12 590 380	3 386 310	4 573
1989	196 586 439	30 914 165	1 279 065	75 583
1990	250 028 184	29 143 276	3 672 968	40 490
1991	238 651 609	29 841 369	2 730 734	236 719
1992	177 709 628	46 854 308	2 864 390	64 680
1993	236 576 148	28 083 447	6 528 422	146 458
1994	261 622 328	24 921 411	2 771 157	189 176
1995	223 786 325	58 949 185	2 777 046	87 225

In order to calculate stock biomass from stock numbers at 1 January mean values of weight at age in quarter 1 and in quarter 4 the previous year were used. Data were taken from ICES (2000).

Methods

Two methods were used to estimate M1. First, individual time series of data, i.e. the survey data, the commercial catch data and the number consumed, were used to calculate total mortality by Baranov (1918)'s catch equation. Secondly, a simple model is used to estimate fishing mortality (F), other mortality (M1), and predation mortality (M2) by maximum likelihood fitting of the IBTS survey indices, commercial catches and numbers consumed, to the model.

To avoid possible long-term trends when estimating total mortality by Baranov's catch equation, separate analysis have been performed on the year classes 1977–1981 represented in the stomach data from 1981, and on the year classes 1987–1991 represented in the stomach data from 1991. Within each of the two periods the year class data have been averaged before analysis. This makes it more difficult to calculate confidence intervals of estimated parameters, but has the advantage of increasing the signal to noise ratio. This approach is especially important for the survey data where individual yearly abundance indices are quite variable with large positive correlation between adjacent age groups in a given year (Cotter, 2001).

While the above procedures give independent estimates of Z for each time series, the aim in the maximum likelihood model is to estimate M1 for age 2, 3 and 4 as consistent as possible with all three data series; IBTS survey indices, commercial catches and numbers consumed.

The model is a forward calculation procedure, which starts with an input stock number of age 1, N_1, and successively calculates N_2, N_3, etc. The parameters, F, M1 and M2 by age are estimated by the model on the basis of formulas relating these parameters to (1) the IBTS indices, (2) commercial catches, and (3) numbers consumed.

Catch at age in numbers (C) is assumed to be log normal distributed with mean

$$E[C(a,y)] = avN(a,y) * F(a,y),$$

where avN(a,y) is the mean number of fish of age a present in year y, assuming the Baranov's catch equation.

The numbers consumed (D) are treated in a similar way, with F replaced by M2.

The IBTS indices ($N\ h^{-1}$) are also assumed to be log normal distributed with mean

$$E[IBTS(a,y)] = q * N(a,y),$$

where q is the catchability of the IBTS survey, and N(a,y) is the number of fish at the beginning of year y.

For each of the two time periods the five year-classes are merged in order to reduce the noise in the data. This implicitly assumes that F, M1 and M2 at age are constant within each of the two time periods.

It is assumed that M1 on age 1 is 0.1, and that F and q are constant for age 1 and older fish for each of the two time periods. This assumption is justified by the following points: (1) that the spatial distribution of Norway pout of age 1 does not differ much from that of older fish, (2) that the mesh size in the GOV trawl is 10 mm (knot to knot) with a 100% selection for Norway pout greater than 9 cm (Anon., 1998), which means that almost all Norway pout of age 1 or older entering the trawl will be caught, and (3) that Norway pout of age 2 and older rarely are longer than 20 cm, i.e. not much bigger than those of age 1 and therefore can be expected to have approximately the same catchability.

The data on number consumed at age 4 and older are unfortunately only available as a part of an age 3+-group. However, as the stock number of age 4 and older are very low compared to age 3 as judged from all available information, the number of age 3+ consumed can be assumed to be representing only age 3. Also due to the lack of information on age 4 fish consumed it is assumed that the ratio between number caught and number consumed is equal to that of age 3.

The IBTS standard area for Norway pout is 284 000 km^2. The swept area of a 1 h haul is 4 nm times a trawl wing spread of 20 m, i.e. 0.15 km^2. The IBTS catchability is measured as the percentage caught by the trawl in the swept area, assuming that the entire stock is distributed in the standard area.

A maximum likelihood estimates are obtained by minimizing the following function:

$$\Sigma(\ln(C) - \ln(E[C]))^2 + \Sigma(\ln(D) - \ln(E[D]))^2 + \Sigma(\ln(qN) - \ln(E[IBTS]))^2$$

which is the sum of the squared differences between observed and expected values of the survey catch rates, the commercial catches, and the numbers consumed, all log-transformed. The variances of the log-transformed data are assumed to be constant except for age 4 in the commercial catches and age 5 in the IBTS data, which are assumed to have a low precision and are down-weighted by an arbitrary factor of 10.

The parameters estimated are N_1, F at age 1–4 (constant by age), M1 at age 2–4 (variable by age) and the IBTS catchability (constant by age), in total 6 parameters. M2 can be calculated from F based on the proportion of numbers caught to numbers predated. The observations are (1) the mean IBTS indices for the year classes 1977–1981/1987–1991 at age 1, 2, 3, 4 and 5 (5 observations), (2) the mean commercial catch of the

Table 4. Z estimated by time series. Y.c. = year class. 1q = first quarter of the year, 3q = third quarter of the year.

Data source/Age	0	1	2	3	4
IBTS 1q, y.c 1977–1981	—	1.92	2.55	2.92	3.39
Commercial catch, y.c. 1977–1981	—	1.45	2.69	4.58	
Numbers consumed, y.c. 1977–1981	0.91	2.33	3.48	—	—
IBTS 1q, y.c 1987–1991	—	0.75	2.29	3.17	4.30
SGFS 3q, y.c. 1987–1991	—	1.53	2.44	—	—
Commercial catch, y.c. 1987–1991	—	1.20	2.69	4.17	
Numbers consumed, y.c. 1987–1991	2.01	2.17	3.23	—	—
IBTS 1q, entire period 1974–1999	—	1.02	2.13	3.13	3.99
EGFS 3q, entire period 1982–1992	—	1.70	2.29	—	—
SGFS 3q, entire period 1980–1997	—	1.73	2.54	—	—
Commercial catch	—	1.53	2.78	4.41	—
Numbers consumed	1.35	2.45	3.45	—	—

same year classes at age 1, 2, 3, and 4 (4 observations) and (3) the mean number consumed of the same year classes at age 1, 2, and 3 (3 observations), in total 12 observations. The IBTS survey data were the only survey data included in the modelling, because these data cover both time periods and because the IBTS data are expected to be more precise than the EGFS and SFGS data due to better spatial coverage and to a significant higher number of annual trawl hauls. The model was run separately for each of the two time periods.

Confidence intervals of the parameters are obtained by the bootstrap method (see e.g. Haddon, 2001).

Results

Table 4 shows Z by age, calculated from the various time series. In the surveys, the catch rates of 0 group Norway pout are relatively low, probably due to the fact that 0 group Norway pout in the 3rd quarter of the year are small and some can escape through the meshes. Furthermore, a large fraction of the 0 groups is probably still semi-pelagic at that time and will not be caught by the bottom trawl. Norway pout recruit to the commercial fishery as 0-groups at the end of the year and the total annual catch of them is therefore low. 1-group Norway pout can be regarded as fully recruited to the fishery already from the start of the year. Therefore, the only time series, which might produce realistic Z values for age 0 fish are the numbers consumed.

Z of 0 groups based on numbers consumed was 0.91 for the year classes 1977–1981 and 2.01 for year classes 1987–1991. For age 1 Z was between 1.45 and 2.33 for the year classes 1977–1981, while Z for the year classes 1987–1991, was between 0.75 and 2.17. Z of age 2 increased by about 1.0 for all data series compared to Z for age 1. For ages 3 and 4 Z increased further compared to Z for age 2. The increase varied between 0.37 and 2.01.

The EGFS and the SGFS gave generally slightly higher Z values for age 1 and age 2. These surveys are conducted in the 3rd quarter and thus represent fish half a year older than the IBTS data.

Generally, Z calculated from numbers consumed was higher than for the other time series for age 1 and older fish and Z from the commercial catches slightly higher than Z from the surveys.

Table 5 shows the results of the maximum likelihood model runs for each of the two periods.

The model estimates of M1 is 1.74 for age 2, 2.58 for age 3 and 3.05 for age 4 for the year classes 1977–1981. For the year classes 1987–1991 the comparable estimates are 2.03, 3.04 and 4.19. Total mortality, Z, estimated for the two period matches quite well Z estimated from the IBTS survey (Table 4). Fishing mortality on age 1 and older fish is estimated to be 0.29 in the first and 0.10 in the second period. Predation mortality decreases by increasing age, as well as from the first to the second period. For age 1 from 1.27 to 0.50, for age 2 from 0.53 to 0.19, for age 3 from 0.24 to 0.11. Due to the model structure predation mortality on age 4 is equal to that of age 3. Catchability on the IBTS survey is estimated to 4.0% in the first period and 4.9% in the second. Stock biomass of Norway pout was estimated to 1.36 million t in the first period and to 1.71 million t in the second period.

The Coefficient of Variation (C.V.) of the observations was 20% in the first period and 8% in the second. As the observations used in the models are the mean over 5 year data points this compares roughly to CVs of 45% and 18%, respectively, of individual observations. These C.V.s are model dependent and therefore likely to be under-estimates of the real uncertainty. The confidence intervals of the estimated parameters for the two periods overlap for all parameters except for fishing mortality (F).

Table 5. Maximum likelihood estimation based on IBTS cpue indices, commercial catch in numbers, and numbers eaten. Bold type represents parameters estimated. Intervals given in brackets are 95%-confidence limits obtained by bootstrapping.

	Age 1	Age 2	Age 3	Age 4	Age 5
Model using the year classes 1977–1981					
F	**0.29** **(0.17–0.41)**	0.29	0.29	0.29	
M1	0.10	**1.74** **(0.96–2.52)**	**2.58** **(2.22–2.94)**	**3.05** **(1.51–4.59)**	
M2	1.27	0.53	0.24	0.24	
Z	1.66	2.56	3.10	3.58	
IBTS catchability (% of fish in swept area caught)	**4.0%** **(2.5%–5.5%)**	4.0%	4.0%	4.0%	4.0%
Stock numbers (millions)	**119 000** **(92 000–146 000)**	22 628	1 748	78	2
Stock biomass ('000 t) by age at 1st January	774	509	72	4.5	0.1
Stock biomass	Total = 1.36 mill. t				
	Statistic: C.V. of individual years observations 45%				
Model using the year classes 1987–1991					
F	**0.10** **(0.07–0.12)**	0.10	0.10	0.10	
M1	0.10	**2.03** **(1.76–2.31)**	**3.04** **(2.76–3.32)**	**4.19** **(3.88–4.48)**	
M2	0.50	0.19	0.11	0.11	
Z	0.69	2.32	3.25	4.39	
IBTS catchability (% of fish in swept area caught)	**4.9%** **(3.1%–6.6%)**	4.9%	4.9%	4.9%	4.9%
Stock numbers (millions)	**86 000** **(63 000–109 000)**	43 077	4 259	165	2
Stock biomass ('000 t) by age at 1st January	559	969	175	9.4	0.1
Stock biomass	Total = 1.71 mill. t				
	Statistic: C.V. of individual years observations 18%				

Table 6. Model sensitivity analysis. (a) Sensitivity to errors in estimated numbers consumed. (b) Sensitivity to assumed M1 of age 1.

	Data basis	M1 age 2	M1 age 3	M1 age 4	Stock biomass
(a)					
Predation ***under***-estimated by a factor of 2	Model using year classes 1977–1981	1.85	2.75	3.21	2.56 mill. t
Predation ***over***-estimated by a factor of 2		1.47	2.17	2.68	0.73 mill. t
Predation ***under***-estimated by a factor of 2	Model using year classes 1987–1991	2.06	3.07	4.22	3.07 mill. t
Predation ***over***-estimated by a factor of 2		2.00	3.00	4.14	1.00 mill. t
M1 of age 1					
(b)					
0.05	Model using year classes 1977–1981	1.72	2.56	3.04	1.31 mill. t
0.2		1.79	2.61	3.09	1.45 mill. t
0.05	Model using year classes 1987–1991	2.02	3.03	4.17	1.59 mill. t
0.2		2.09	3.08	4.23	2.08 mill. t

Sensitivity analyses were performed to test the dependence of the estimated M1 values to uncertainties in numbers consumed. Due to e.g. large uncertainties in consumption rates used in the MSVPA for the North Sea, the numbers consumed even when averaged over 5 year classes, are expected to be estimated with large uncertainties. Model runs with numbers consumed halved and doubled were made for each of the two time periods. In the first time period M1 on age 2 decreased from 1.74 (Table 5) to 1.47 (Table 6a) when the number consumed was halved, and increased to 1.85 when the number was doubled. For age 3 the values were 2.58, 2.17, and 2.75, respectively, and for age 4 3.05, 2.68, and 3.21, respectively. In the second period the changes were much smaller. In general, the estimates of M1 were moderately sensitive to uncertainties in numbers consumed, but all values were still very high, between 1.47 and 4.22. The biomass estimates of the model runs are included in Table 6a to show that some parameters estimated or calculated were indeed very sensitive to the uncertainty in numbers consumed. The biomass estimates varied by a factor of 3 in both periods, and gave unrealistic high values of around 3 million t when the doubling of numbers consumed were used. Fishing mortality and predation mortality varied to the same extent as these are closely linked to the estimated biomass.

The model's sensitivity to the assumption of M1=0.10 for age 1 was also tested. Model runs with this value halved and doubled were made for each of the two time periods. The estimated M1 values for age 2 and older were insensitive to this perturbation (Table 6b). The biomass estimates were moderately sensitive and gave values between 1.31 and 2.08 million t.

The down weighing of age 4 in the commercial catches and age 5 in the IBTS data by a factor of 10 was tested on the 1987–1991 data set by varying this factor between 5 and 20. This gave less than 2% variations in the parameter estimates.

Discussion

All the above time series and model runs give a consistent picture of a very high total mortality and one, which is increasing by age. Whether this can be an artefact is discussed below. Two possibilities could be:

(1) That catchability decreases with age for all three data series. Catchability in the IBTS survey could decrease with age if Norway pout becomes more pelagic with age. However, according to Albert (1994) Norway pout distributed close to the bottom (at most 1.2–1.5 m above) during day and at night up to 10 m above the bottom. Albert (1994) based his judgement on echo sounder traces. This also fits well with Raitt (1968) who stated, that available evidence suggests that Norway pout normally inhabit a zone just clear of the sea-bed. Raitt (1968) based his statement partly on stomach content data, which showed that Norway pout consumed food from that part of the water column. As most hauls at the IBTS are made during day and the net opening is around 4 m most part of the stock should be caught by the trawl, although the very low catchability estimated to be 4–5% (Table 5) indicates that avoidance is strong and this could be age dependent. However, even if Norway pout become more pelagic with age or better to avoid the trawl gear, the predators should have no problems in finding them and probably likewise the commercial fishermen.

(2) That old Norway pout migrate out of the area. The only possibility seems to be that Norway pout migrate out to the north and northwest because, according to Albert (1994) they are not found in the Norwegian Deep. Some spawning is known to take place in the North Sea, but whether this is the main spawning area is not well known. However, large numbers of old Norway pout have never been found anywhere outside the North Sea and, at least in the Faeroe Islands waters, very few Norway pout of age 3 and older are found (Jakup Reinert, Fisheries Laboratory of the Faroes, personal comm.). In light of the high mobility of the commercial fishing fleet and its ability to find commercial interesting aggregations of fish when such exists, and the large biomass of old Norway pout that would have to move to account for the estimated increase in Z, it seems unlikely that old Norway pout have migrated out of the area to any significant extent. Thus, it can be concluded that the observed increase in Z from age 1 onwards most probably is real.

As Z is the sum of F, M1 and M2 the question becomes which of these parameters is increasing with age.

Is F increasing? Fishing mortality on the age 1 and older is probably quite independent of age, as all age groups are distributed in almost the same area and they are only slightly different in size. The mesh size used in the commercial fishery for Norway pout is typically 16 mm stretched mesh and that will not allow many Norway pout of age 1 or older to escape. It can, however, not *a priori* be ruled out as a possibility that old Norway pout might be better to avoid being caught by being better swimmers, more "experienced", etc. However, an increase in Z as a function of F for older fish would be an explanation if the converse were true. Furthermore, if F is the only reason for the increase in Z, F must be higher than the difference between Z of age 2 and Z of age 1, i.e. about 1 for age 2 and even higher for age 3. Such high F values are unrealistic. Lastly, if F really increases with age, then the older ages in the commercial catches should be over-represented compared to the younger age groups and the real Z must then be even much higher than estimated from the commercial data. The Z values calculated from the commercial catch data should then be smaller than Z values calculated from the survey data, which is not the case (Table 4). Thus, it can be ruled out that increase in F by age is the main explanation for increases in Z by age. Thus natural mortality (M) must increase with age.

Predation mortality (M2) generally decreases with age (e.g. Sparholt 1994) and the high Z values from the time series of numbers consumed supports this feature, because it indicates that old fish are under-represented compared to the other two data series. Because M=M1+M2 it can be concluded that it must be the residual or non-predation natural mortality (M1) which increases with age.

The result of the model runs support this conclusion. Both model runs estimate non-predation natural mortality to increase significantly with age.

Predation mortality of age 1 decreases from 1.27 for the year classes 1977–1981 to 0.50 for the year classes 1987–1991. This took place with the decrease in biomass of the three main predators of 1 group Norway pout, mature cod, whiting and saithe, from spawning stock biomass of 925 000 t in 1981 to 451 000 t in 1991 (ICES, 2001).

Fishing mortality is estimated to be 0.29 in the first period, but only 0.10 in the second period. The mean annual landings in weight were 351 000 t in 1977–1985 where the year classes 1977–1981 were fished and 187 000 t in 1987–1995 where the year classes 1987–1991 were fished. The drop in F seems consistent with the commercial landings in weight. Furthermore, according to a Danish effort data series form 1982–1998 (ICES, 1995, 2000), effort decreased from 9276 (arbitrary scale) in 1982–1985 to 3561 in 1987–1995. If 1982–1985 is representative for the entire period 1977–1985, there is a fairly good agreement between effort data and the estimated F.

The biomass estimates of 1.36 and 1.71 million t of Norway pout at 1 January, seem to be of the right order of magnitude as the total amounts consumed were 1.9 and 1.8 million t in 1981 and 1991 (ICES, 1997). The commercial catch was 239 000 t in 1981 and 193 000 t in 1991. It might seem peculiar that the sum of the catch and the amount consumed is higher than the stock biomass, but this can be attributed to individual fish growth during the year and to recruitment.

The catchability of Norway pout on the IBTS survey is estimated to be between 4.0% and 4.9% of the fish present in the swept area. Sparholt (1990), found similarly a low catchability of Norway pout.

The estimated C.V. of the IBTS data, the commercial catches and the numbers consumed was 20% for the first period. This seems as a high uncertainty for the commercial catch data, but might be reasonable for the IBTS data (Cotter, 2001). For the numbers consumed it is difficult to say but as argued above the uncertainty might be larger than 20%. It was specifically tested whether an error of a factor of 2 in both directions of the numbers consumed would give very different estimates of M1 for ages 2 and older. This was not the case as the deviations in M1 were between 1% and 16% for all ages.

It can be concluded that the non-predation or residual natural mortality, M1, of Norway pout increases with age and gets very high on age 2 and older fish.

It can further be concluded that it has been possible to estimate M1 in a way that is consistent with all the information and knowledge currently available on Norway pout.

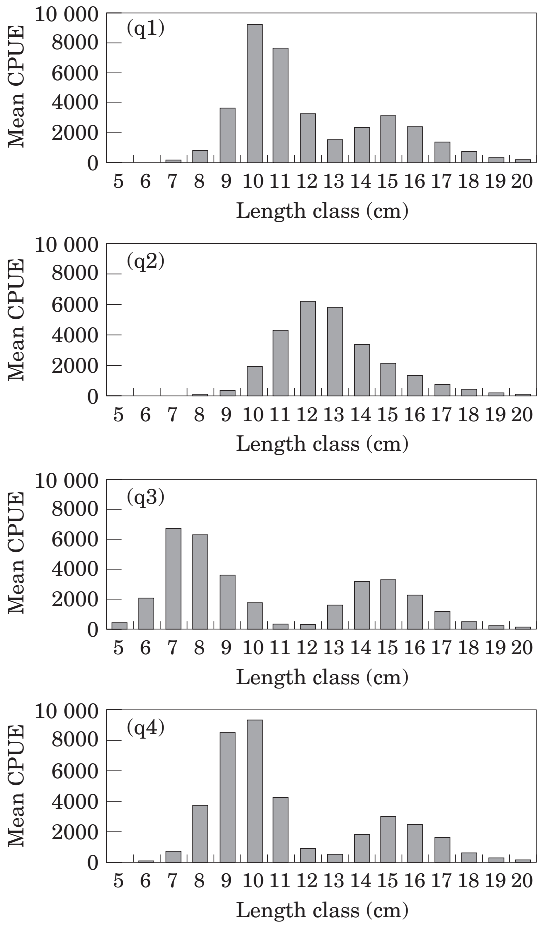

Figure 1. Mean IBTS CPUE (in numbers per hour) per length class and quarter of the year in 1991–1996.

The slightly higher values of M1 of age 2 and older estimated for the second period than for the first period is difficult to explain and is not significant. For the time being mean M1 values for the two periods considered here are recommended for use in the MSVPA and other models, where M1 values are needed.

Norway pout length distribution data for each of the 4 quarters of the year are available for 1991–1996 from the IBTS survey (Figure 1), and these data indicate that the mortality mainly takes place between the 1st and the 2nd quarter of the year, i.e. from before to after spawning. This points at spawning as the main reason for this mortality. Spawning mortality is well known for capelin (*Mallotus villosus*), another North Atlantic fish species. According to Burton and Flynn (1998) and Huse (1998) almost all male capelin dies after spawning. Tanasichuk (2000) finds that surplus energy requirements for gonad recrudescence appear to cause the death of adult Pacific herring (*Clupea pallasi*). To the knowledge of the present authors there are no direct records of evidence of multiple spawning in individual Norway pout. It would be interesting to investigate whether histological analyses of the gonads of North Sea Norway pout can support or reject the spawning mortality hypothesis. For capelin, Bakke and Bjørke (1973) report dead fish in demersal trawling on the spawning grounds, but this has never been recorded for North Sea Norway pout. Demersal trawling for dead North Sea Norway pout at the spawning grounds could also be considered in order to evaluate the hypothesis.

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