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Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1800s

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The exploitation history of North Sea plaice is reconstructed from the late 1800s to 1993 using data on catch per unit of e ort, total international landings, size and age composition of landings, and growth rate. Available data indicate that fishing mortality was already high in the 1890s (F=0.4) and increased to a record high in the late 1920s and early 1930s (F=0.8). After World War II, fishing mortality was reduced, but from the 1960s onwards it increased steadily to a level of F=0.6 in the early 1990s. Indices of catch per unit of e ort during the last quarter of the 19th century are concurrent with the expansion of the fisheries. Stock biomass was at a low level in the 1930s but increased between the 1960s and 1980s owing to increased recruitment and improved growth. Landings were fairly stable around 55 000 t until the mid-1950s when they increased almost threefold to a record level of 170 000 t in 1989. The causes of these changes are discussed. It is suggested that changes in both growth rate and exploitation rate in young fish have been important.

Key words: plaice, North Sea, exploitation, discards, recruitment history.

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Introduction

Throughout the century, plaice has been an important target species of the mixed demersal fisheries in the North Sea. Having been stable around 55 000 t until the mid-1940s, landings increased to a record level of 170 000 t in 1989, but subsequently declined to 110 000 t in 1994 (ICES, 1995). This prompts the question as to whether these changes in yield were a consequence of changes in exploitation as predicted by classical yield per recruit theory (Beverton and Holt, 1957). Alternative explanations, however, are also tenable, since changes in both recruitment and growth have been reported (Bannister, 1978; Rijnsdorp and van Beek, 1991; Rijnsdorp and van Leeuwen, 1992, 1994). The causes of these changes and their relation to the shift within the North Sea ecosystem from pelagic to demersal species are still obscure (Andersen and Ursin, 1978; Daan, 1978; Hempel, 1978).

In this paper we attempt to reconstruct the population dynamics of North Sea plaice since the late 19th century. An understanding of the response of plaice to exploitation may help to unravel the e ects of fishing from those due to changes in the natural environment. From a management point of view, it is important to investigate the e ects of reduced exploitation of small plaice on yield.

The basis for embarking on a reconstruction of mortality rates and stock biomass is formed by published information as well as archived data: (1) catch per unit of e ort; (2) age composition of commercial catches; (3) size compositions of commercial catches and landings; (4) growth rates.

The history of the fishery

Until the mid-19th century, North Sea plaice were primarily fished by sailing smacks deploying small-beam trawls. Since then, fishing fleets and areas fished have expanded considerably. Towards the end of the century, steam trawlers gradually replaced sailing vessels and motor cutters were introduced in the early 1900s (Thursby-Pelham, 1939; Schmidt, 1942). Motorized propulsion allowed replacement of beam trawls by otter trawls, which have a wider net opening at increased towing speed. After World War I, bobbin ropes and

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tickler chains came into use, which allowed trawling of previously unfished grounds, and the introduction of the Vigneron-Dahl sweeps between 1923 and 1929 increased the e ciency of the nets by a further 25% (Thursby-Pelham, 1939). In Denmark, an important seine fishery by cutters developed in the 1920s. After World War II, steam trawlers were replaced by motor trawlers, and since the early 1960s otter trawls have been gradually replaced by large-beam trawls.

The development and expansion of the fishery and the concurrent decline in catch rates prompted the first biological studies (Wimpenny, 1953; Cushing, 1982). When collection of international fisheries statistics started in 1906, total international landings of plaice had stabilized at around 50 000 t. This level was maintained until the 1950s, with the exception of the period during the two world wars. Comprehensive statistics are not available for years before 1906, but catch data reported by some countries suggest that total plaice landings between 1892 and 1905 would have been at least 50 000 t. During both war-time periods (1914–1918; 1940–1945), landings were reduced due to restricted fishing activities, but extremely good catches were made in the first year thereafter, followed by a gradual decline to pre-war levels (Borley, 1923; Bannister, 1978). From the early 1950s, landings increased to record high levels of more than 150 000 t by the early 1980s, followed by a sharp decline to about 110 000 t by 1994.

The traditional mixed demersal fisheries have undoubtedly caught substantial quantities of undersized plaice, because intensive fishing also occurred in the shallow coastal waters of the eastern North Sea where the important nursery areas are situated. Although there have been national regulations, no legal minimum mesh sizes or minimum landing sizes were internationally agreed before 1937. Mesh sizes in use at the turn of the century were about 7 cm in o shore fleets and 4–5 cm in the coastal fisheries (Garstang, 1905; Schmidt, 1937). Given a selection factor for plaice of 2.2 (van Beek *et al.*, 1983), the 50% retention length is 10 and 15 cm for mesh sizes of 5 and 7 cm, respectively. Undersized plaice were either discarded or landed for the fish meal industry. However, landings for fish meal have never been included in the o cial statistics. Fishing for juvenile plaice increased in the early 1930s because of declining catches for human consumption (Anon., 1933; Schmidt, 1942). Fishing for industrial purposes, the shrimp fishery, continued until the 1950s (Boddeke, 1989).

International agreement upon minimum mesh size (70 mm) and landing size (23 cm) was reached in 1937 (Wimpenny, 1953), but regulations were not imposed until after World War II. Legal minimum mesh size was increased to 80 mm in the 1980s. In 1989, almost 75 years after the first o cial recommendation to this extent (Heincke, 1913), a protected area was established along the eastern coast, where the majority of the pre-recruits are found (ICES, 1987, 1994). This “plaice box” coincides to a large extent with the mine fields, which e ectively restricted fishing in the German Bight in the post-war years up to the 1960s.

Historically, discard rates have varied in response to market conditions and changes in minimum landing size, but quantitative data are sparse. Baerends (1947) estimated that the contribution of undersized plaice to the total catch by weight increased from 8% during 1903–1927 to 14% in the late 1930s. These estimates are low compared with reported discard percentages of 66% by weight and 83% by number in the German catches during the early 1930s (Lundbeck, 1934a). Discards in the Dutch beam-trawl fishery in the late 1980s (accounting for about 60% of the total international landings) were estimated to be 23% by weight and 50% by number (van Beek, 1990), survival being negligible (van Beek *et al.*, 1990).

Material and Methods

Landings and catch per unit of e ort

International landings (Table 1) for 1892–1906 provide minimum estimates, being based on main fishing countries only (Kyle, 1905), but from 1906 onwards landings reported by country in *Bulletins Statistiques* are fairly complete. Catch per unit of e ort (c.p.u.e.) data for di erent time periods and fleets, encompassing all years between 1875 and 1993 except for the war periods (Table 2), have been selected based on criteria of length of the series and area covered. The available time series have been standardized by setting the c.p.u.e. index to 1 in series A and B in both 1892 and 1893, and using the period of overlap with other series for calculating correction factors.

Indices of total international e ort by year were calculated by dividing total international landings by the combined c.p.u.e. series. Average catchability was estimated by dividing estimates of fishing mortality from Virtual Population Analysis (VPA) by the total e ort for the period of overlap. Fishing mortalities were then calculated for all years based on total e ort and average catchability.

Length distributions of catches and landings

Size compositions of plaice catches vary among areas and between seasons (Garstang, 1909; Heincke, 1913; Wimpenny, 1953) and therefore are not directly representative of the total population. Nevertheless, a reliable index with which to study long-term variations may be obtained from samples collected during the first quarter of the year when adults are congregated on the spawning grounds in the southern North Sea (de Veen, 1964; Rijnsdorp, 1989). When first-quarter data were

Table 1. Total international landings of North Sea plaice, 1892–1994, average fishing mortality rate of age groups 4–8 from VPA [F(4–8)u] and fishing mortality rate based upon c.p.u.e. [F(c.p.u.e.)].

Year	Landings (t)	F(4–8)u	F (c.p.u.e.)	Year	Landings (t)	F(4–8)u	F (c.p.u.e.)
1892	43 339	—	—	1944	44 859	—	—
1893	52 711	—	0.30	1945	52 581	—	—
1894	53 379	—	0.34	1946	107 903	—	0.28
1895	46 380	—	0.41	1947	89 835	0.41	0.33
1896	44 950	—	0.38	1948	91 440	0.40	0.38
1897	45 775	—	0.45	1949	87 905	0.36	0.36
1898	44 426	—	0.60	1950	73 525	0.30	0.40
1899	50 533	—	0.37	1951	69 946	0.28	0.33
1900	51 005	—	0.59	1952	74 394	0.29	0.34
1901	58 702	—	0.49	1953	83 042	0.32	0.32
1902	83 958	—	0.51	1954	69 897	0.26	0.28
1903	56 741	—	0.53	1955	66 059	0.25	0.25
1904	56 561	—	0.55	1956	66 889	0.22	0.26
1905	55 235	—	0.54	1957	70 563	0.23	0.31
1906	50 677	—	0.69	1958	73 354	0.26	0.31
1907	58 192	—	0.71	1959	79 300	0.27	0.30
1908	53 189	—	0.65	1960	87 541	0.31	0.33
1909	54 928	—	0.66	1961	85 984	0.30	0.28
1910	52 705	—	0.66	1962	87 472	0.30	0.34
1911	56 774	—	0.66	1963	107 118	0.35	0.31
1912	57 231	—	0.71	1964	110 540	0.35	0.32
1913	53 925	—	0.79	1965	97 143	0.33	0.30
1914	45 770	—	0.70	1966	101 834	0.33	0.25
1915	29 534	—	—	1967	108 819	0.31	0.25
1916	27 319	—	—	1968	111 534	0.27	0.30
1917	27 173	—	—	1969	121 651	0.28	0.38
1918	44 578	—	—	1970	130 342	0.43	0.35
1919	55 488	—	0.38	1971	113 944	0.36	0.34
1920	60 430	—	0.50	1972	122 843	0.39	0.36
1921	48 586	—	0.51	1973	130 429	0.42	0.43
1922	54 493	—	0.64	1974	112 540	0.43	0.50
1923	46 756	—	0.72	1975	108 536	0.46	0.53
1924	50 037	—	0.65	1976	113 670	0.36	0.50
1925	60 679	—	0.76	1977	119 188	0.39	0.48
1926	61 631	—	0.78	1978	113 984	0.38	0.41
1927	61 017	—	0.73	1979	145 347	0.54	0.38
1928	69 698	—	0.90	1980	139 951	0.45	0.36
1929	71 107	0.90	0.86	1981	139 747	0.46	0.33
1930	66 793	0.92	0.88	1982	154 547	0.48	0.40
1931	56 643	0.78	0.83	1983	144 038	0.49	0.44
1932	55 353	0.75	0.83	1984	156 147	0.45	0.48
1933	58 761	0.59	0.84	1985	159 838	0.44	0.47
1934	56 688	0.72	0.78	1986	165 347	0.52	0.44
1935	51 591	0.74	0.78	1987	153 670	0.57	0.47
1936	51 438	0.91	0.66	1988	154 475	0.53	0.57
1937	51 951	0.73	0.66	1989	169 643	0.47	0.54
1938	50 322	—	0.67	1990	156 207	0.46	0.63
1939	—	—	—	1991	147 478	0.54	0.64
1940	25 687	—	—	1992	124 712	0.52	0.74
1941	35 473	—	—	1993	115 230	0.52	0.77
1942	50 072	—	—	1994	111 060	0.54	0.79
1943	67 142	—	—				

lacking, annual data pooled for the total North Sea have been used. Because discards are not reflected in market samples, it is important to distinguish between size compositions of catches and landings.

The earliest information available (by 1 cm) stems from extensive trawling surveys carried out by RV "Huxley" in the period 1905–1908 (Anon., 1907, 1912), and from German and English market samples taken

Table 2. Time series of c.p.u.e. index and c.p.u.e. by fleet: A – Four English trawling smacks (cwt yr^{-1}; Wimpenny, 1953); B – German steam trawl (0.5 kg d^{-1}; Herwig, 1906); C – English 1st class steam trawl (cwt d absence^{-1}; Thursby-Pelham, 1939); D – English sailing vessels (cwt d absence^{-1}; Thursby-Pelham, 1939); E – English 1st class steam trawl (cwt 100 h^{-1}; Wimpenny, 1953); F – English 1st class steam trawl (G2+G3; Jan/Feb; cwt 100 h^{-1}; Simpson, 1959); G – English motor trawl (corr.; Bannister, 1977); H – English motor trawl (corr.; ICES, 1980); I – Dutch beam trawl (t.HP d^{-1}; RIVO unpubl).

	C.p.u.e. index	A	B	C	D	E	F	G
1867	5.94	998	—	—	—	—	—	—
1875	3.27	549	—	—	—	—	—	—
1876	3.58	601	—	—	—	—	—	—
1877	2.51	421	—	—	—	—	—	—
1878	1.51	254	—	—	—	—	—	—
1879	1.77	298	—	—	—	—	—	—
1880	1.73	291	—	—	—	—	—	—
1881	1.44	242	—	—	—	—	—	—
1882	2.29	385	—	—	—	—	—	—
1883	2.02	340	—	—	—	—	—	—
1884	1.93	325	—	—	—	—	—	—
1885	1.67	280	—	—	—	—	—	—
1886	1.49	250	—	—	—	—	—	—
1887	1.32	221	—	—	—	—	—	—
1888	1.16	195	—	—	—	—	—	—
1889	1.05	177	—	—	—	—	—	—
1890	1.22	205	—	—	—	—	—	—
1891	1.21	203	—	—	—	—	—	—
1892	1.00	168	—	—	—	—	—	—
1893	1.00	—	1.5	—	—	—	—	—
1894	0.90	—	1.7	—	—	—	—	—
1895	0.65	—	2.0	—	—	—	—	—
1896	0.68	—	1.9	—	—	—	—	—
1897	0.59	—	2.2	—	—	—	—	—
1898	0.42	—	3.0	—	—	—	—	—
1899	0.79	—	1.8	—	—	—	—	—
1900	0.50	—	2.9	—	—	—	—	—
1901	0.69	—	2.4	—	—	—	—	—
1902	0.95	—	2.5	—	—	—	—	—
1903	0.61	—	2.6	—	—	—	—	—
1904	0.59	—	2.7	—	—	—	—	—
1905	0.58	—	2.7	—	—	—	—	—
1906	0.42	—	3.4	2.1	1.2	—	—	—
1907	0.49	—	—	2.4	1.2	—	—	—
1908	0.42	—	—	2.4	1.4	—	—	—
1909	0.46	—	—	2.3	1.5	—	—	—
1910	0.40	—	—	2.3	1.5	—	—	—
1911	0.42	—	—	2.5	1.7	—	—	—
1912	0.40	—	—	2.3	1.6	—	—	—
1913	0.37	—	—	2.1	1.4	—	20.5	—
1919	0.72	—	—	4.5	2.5	—	—	—
1920	0.56	—	—	3.4	2.0	—	54.2	—
1921	0.44	—	—	2.5	1.7	—	44.0	—
1922	0.40	—	—	2.2	1.5	—	43.2	—
1923	0.33	—	—	1.9	1.2	—	22.8	—
1924	0.39	—	—	2.1	1.3	13.7	33.2	—
1925	0.40	—	—	2.3	1.4	17.2	29.5	—
1926	0.40	—	—	2.5	1.3	17.4	26.6	—
1927	0.40	—	—	2.5	1.4	17.8	33.3	—
1928	0.40	—	—	2.5	1.2	18.0	28.8	—
1929	0.40	—	—	2.6	1.2	18.8	34.2	—
1930	0.39	—	—	2.5	1.0	18.2	30.6	—
1931	0.39	—	—	2.6	0.9	18.1	20.9	—
1932	0.37	—	—	2.5	0.8	17.5	22.1	16.1

Table 2 Continued on next page.

Table 2. *Continued from previous page.*

	C.p.u.e. index	C	D	E	F	G	H	I
1933	0.39	2.6	0.8	17.9	24.6	16.7	—	—
1934	0.40	2.6	0.8	17.9	30.6	16.9	—	—
1935	0.38	2.6	0.8	17.6	20.4	16.8	—	—
1936	0.40	2.9	1.0	18.7	26.7	18.2	—	—
1937	0.40	2.9	1.0	19.2	27.5	18.7	—	—
1938	0.39	—	—	18.4	27.6	17.5	—	—
1946	1.32	—	—	76.5	125.9	75.5	—	—
1947	1.02	—	—	54.1	64.7	58.2	—	—
1948	0.88	—	—	44.3	60.1	51.6	—	—
1949	0.62	—	—	—	53.3	35.8	—	—
1950	0.47	—	—	—	40.2	27.2	—	—
1951	0.57	—	—	—	43.3	32.7	—	—
1952	0.55	—	—	—	47.1	31.5	—	—
1953	0.58	—	—	—	65.1	33.5	—	—
1954	0.65	—	—	—	54.5	37.3	—	—
1955	0.66	—	—	—	59.6	38.2	—	—
1956	0.63	—	—	—	56.3	36.1	—	—
1957	0.58	—	—	—	—	33.7	—	—
1958	0.59	—	—	—	—	34.1	—	—
1959	0.67	—	—	—	—	38.9	—	—
1960	0.73	—	—	—	—	42.3	3.9	—
1961	0.70	—	—	—	—	40.1	4.6	—
1962	0.73	—	—	—	—	42.0	3.8	—
1963	0.89	—	—	—	—	51.5	5.1	—
1964	0.86	—	—	—	—	49.5	5.0	—
1965	0.69	—	—	—	—	39.9	4.7	—
1966	0.63	—	—	—	—	36.3	6.0	—
1967	0.44	—	—	—	—	25.6	6.4	—
1968	0.52	—	—	—	—	30.2	5.5	—
1969	0.70	—	—	—	—	40.5	5.1	130.4
1970	0.84	—	—	—	—	48.2	5.5	161.7
1971	0.71	—	—	—	—	41.0	5.2	136.9
1972	0.78	—	—	—	—	—	—	149.1
1973	0.70	—	—	—	—	—	4.4	134.1
1974	0.55	—	—	—	—	—	3.2	104.3
1975	0.48	—	—	—	—	—	2.9	92.3
1976	0.54	—	—	—	—	—	3.3	103.3
1977	0.61	—	—	—	—	—	3.4	116.2
1978	0.64	—	—	—	—	—	—	122.2
1979	0.88	—	—	—	—	—	—	167.0
1980	0.91	—	—	—	—	—	—	172.9
1981	0.97	—	—	—	—	—	—	185.3
1982	0.90	—	—	—	—	—	—	170.7
1983	0.76	—	—	—	—	—	—	144.1
1984	0.75	—	—	—	—	—	—	143.9
1985	0.79	—	—	—	—	—	—	151.1
1986	0.87	—	—	—	—	—	—	165.3
1987	0.75	—	—	—	—	—	—	144.0
1988	0.63	—	—	—	—	—	—	119.4
1989	0.72	—	—	—	—	—	—	137.9
1990	0.58	—	—	—	—	—	—	109.9
1991	0.54	—	—	—	—	—	—	102.2
1992	0.39	—	—	—	—	—	—	74.5
1993	0.34	—	—	—	—	—	—	65.7
1994	0.33	—	—	—	—	—	—	62.0

during 1904–1905 (Herwig, 1906) and 1905–1908 (Heincke, 1913), respectively. The Huxley data represent information on catches, since length compositions were obtained during experimental fishing operations with di erent commercial gears at stations distributed throughout the North Sea and English Channel and throughout the year. The monthly English market data are representative of the major fishing grounds of the

English fleet in the southern and western North Sea, while the annual German data are representative of the eastern North Sea.

Length distributions of market samples of German landings in the early 1930s (March–October) by cutters and steam trawlers mainly fishing in the eastern North Sea were reported by Lundbeck (1937). Separate data on landings and catches are available for 1930–1932 (Lundbeck, 1934a). Summary sheets of extensive market measurements of the English landings in 1932, 1934, and 1936 (Thursby-Pelham, 1939) have been recovered in Lowestoft, but the original sampling information is missing.

For the period after World War II, length distributions by 5 cm class are available from English market samples. First-quarter data for Dutch landings were analysed for four 3-year periods (1959–1961, 1969–1971, 1979–1981, 1989–1991). English and Dutch data are considered to be representative of the main spawning areas in the southern and south-eastern North Sea. Recent length distribution data on catches are taken from van Beek (1990).

Total instantaneous mortality rates (Z) for fully recruited size classes were estimated from the slopes of the regression of ln numbers with size, taking into account only the size range beyond the length at peak numbers. Beverton and Holt (1956) showed that:

$$Z=K \times (L_{bar} - L_{peak})/(L_{\infty} - L_{bar})$$

where L_{peak}=length at the peak, L_{bar}=mean size of fish $>L_{peak}$, and K and L_{∞} represent von Bertalan y growth parameters. To evaluate the exploitation pattern, estimates of Z by 5-cm size class were obtained by multiplying the slope by size class with the annual length increment by size class.

Age composition of landings

Annual age composition data for commercial landings in the 1930s are available for England (Thursby-Pelham, 1939) and for Germany (Lundbeck, 1932, 1934a,b, 1935; Schmidt, 1936, 1937, 1938, 1939). Together, these two countries accounted for about 50% of the total landings. No distinction has been made between males and females. The English data were previously analysed by Beverton and Holt (1957), Gulland (1968), and Bannister (1978). Mean weight-at-age was calculated as the ratio of catch weight over catch number per 100 fishing hours, which resulted in slightly di erent values from those presented by Beverton and Holt (1957). No weight-at-age data were available for German landings. Representative catch weights by age group were therefore estimated by multiplying German catch numbers by English average weights, adjusted for the resultant discrepancy between thus calculated landings and reported landings. Mean catch weights in German landings appear to have been on average 30% lower than in English landings, reflecting the more inshore fishing grounds.

The international age composition was calculated by (1) raising German data to total landings of the German, Dutch, and Danish fleets, (2) adding the raised data to the English data, and (3) then raising the sum to total international landings. Mean weights-at-age in the international landings were calculated from the estimated total weights and numbers landed by age group. Sum of product (SOP) discrepancies was $< \pm 1\%$, except in 1928 (+15%).

Age compositions of landings are available for males and females separately from 1947 onwards. Until 1956, only English data are available, corresponding to about 25% of total international landings. The number of countries that introduced a market sampling programme increased rapidly thereafter and since 1957 about 90% of plaice landings have been sampled for age composition and weight-at-age (ICES, 1995). SOP discrepancies are generally <5%.

Population analysis

Mortality rates and population numbers were estimated by VPA for two separate periods, 1929–1938 and 1947–1993. Terminal fishing mortalities were estimated by Extended Survivor Analysis (Darby and Flatman, 1994). The 1929–1938 VPA was tuned using both commercial and research vessel survey age-specified c.p.u.e. data. Fishing mortality on the oldest age group was fixed at 0.4 times the average fishing mortality rate of the five previous age groups in order to match the exploitation pattern indicated by the length distribution analysis (see below). Details are given in Rijnsdorp (1995). Tuning of the 1947–1993 VPA followed that of ICES (1995).

The instantaneous natural mortality rate was set at M=0.10, intermediate to the estimated values of M=0.08 for females and M=0.14 for males (Beverton, 1964). Unweighted average fishing mortalities were calculated for age groups 4 to 8 [F(4–8)u]. These age groups are fully recruited and dominate the landings in most years.

Growth

Estimates of growth rates (derived from otolith back calculations) of female plaice by size class are available for 1930–1992 (Rijnsdorp and van Leeuwen, 1992, 1994). Annual length increments in 10-year periods and 5-cm size classes are given in Table 3.

Reliable estimates of von Bertalan y growth parameters during specific periods are di cult to obtain because spatial distribution of plaice is a function of size

Table 3. Mean, standard deviation, and number of observations of annual growth increments (cm) of female plaice for 10-yr periods since 1925 obtained by back-calculation of otoliths (from Rijnsdorp and van Leeuwen, 1994).

Size class (cm)		1925–1934	1935–1944	1945–1949	1950–1954	1955–1964	1965–1974	1975–1984	1985–1994
25–29	Mean	5.60	4.81	5.27	4.35	4.99	5.64	5.97	5.60
	S.D.	1.52	1.56	1.68	2.06	1.53	1.51	1.58	1.64
	n	4	32	40	102	383	361	244	306
30–34	Mean	5.73	4.29	3.49	3.78	4.01	4.02	4.53	4.26
	S.D.	1.79	1.41	1.52	1.80	1.60	1.40	1.56	1.50
	n	3	29	35	110	407	473	320	343
35–39	Mean	2.76	2.97	2.24	2.55	2.55	2.54	2.99	3.19
	S.D.	—	1.17	1.39	1.29	1.34	1.13	1.23	1.41
	n	1	28	33	98	400	657	407	380
40–44	Mean	2.90	2.06	1.50	1.86	1.79	1.80	2.05	2.50
	S.D.	0.47	1.04	0.98	1.32	1.07	0.93	0.92	1.20
	n	3	26	50	79	351	500	397	337
45–49	Mean	—	1.34	0.84	1.23	1.26	1.23	1.52	1.82
	S.D.	—	0.63	0.58	0.97	0.67	0.70	0.64	0.84
	n	0	9	106	66	269	298	189	205
>50	Mean	—	0.40	0.61	0.48	0.67	0.76	1.21	1.29
	S.D.	—	0.04	0.46	0.42	0.48	0.47	0.79	0.74
	n	0	4	104	96	265	259	80	100

(Garstang, 1909; Heincke, 1913; Wimpenny, 1953; Rijnsdorp and van Leeuwen, 1992) and estimates of older age may be biased (van Leeuwen and Groeneveld, 1988). Rijnsdorp and van Leeuwen (1992, 1994, 1996) indicate that growth rates of fully recruited size classes (>25 cm) have been fairly constant, except for a temporary decrease following World War II and an increase since 1975. Hence, the parameter estimates of $K=0.095$ and $L_{\infty}=68.5$ cm for the 1930s (Bannister, 1978) were assumed to be representative for the entire period.

Cohort simulation

A length-based cohort simulation was carried out to explore the e ect of changes in growth, exploitation pattern, and discard practices between the 1930s and 1990s on equilibrium yield and spawning stock biomass. The population comprised 5-cm length classes between 10 and 60 cm. Decay of population numbers at length was calculated according to

$$N_{i+1}=N_i \exp(-Zt_i)$$

where t_i is time (year) a fish stays in size class i and defined as $t_i=5\ dL^{-1}$. dL is the annual length increment (cm yr^{-1}). Total mortality was estimated from the observed decline in numbers at length and back-calculated growth rate. The exploitation pattern was smoothed by averaging the available series by period and taking a running mean over three size classes. Finally, the exploitation pattern was extrapolated to the smaller sizes under the assumption of gradual recruitment to the fisheries from size class 10–15 cm onwards. Numbers caught were divided into discards and landings according to discard ogives from Lundbeck (1934a) and van Beek (1990). Weight (kg) of size class i was calculated according to $W_i=L_i^3 \times 10^{-5}$. Spawning stock biomass was calculated using a constant maturity ogive (25%, 50%, 75%, and 100% mature in size classes 20–24.9, 25–29.9, 30–34.9, and 35–39.9 cm, respectively).

Population numbers estimated by VPA for 1929–1938 and for the post-World War II period do not include discards and will therefore be biased downward for age groups subjected to discarding. To explore the e ect of discards mortality on the bias in the recruitment estimate, the cohort simulation was extended by a reconstruction of the population numbers based on the simulated numbers landed in each size class and the corresponding partial fishing mortality rates, starting at the largest size class.

Results

According to the separate VPAs carried out for the periods 1947–1992 and 1929–1938, fishing mortality (F) in the 1930s was considerably higher ($F \sim 0.80$) than in the post-war period (Fig. 1). Immediately after World War II, F first declined from about 0.40 to about 0.25 in the late 1950s, followed by a steady increase to about 0.60 in the 1990s.

The exploitation pattern is essentially dome-shaped, but the age of maximum exploitation has changed considerably (Fig. 2). In the 1930s, F peaked at age 7–8, whereas the exploitation pattern became much more flat-topped in the immediate post-war years with a slight

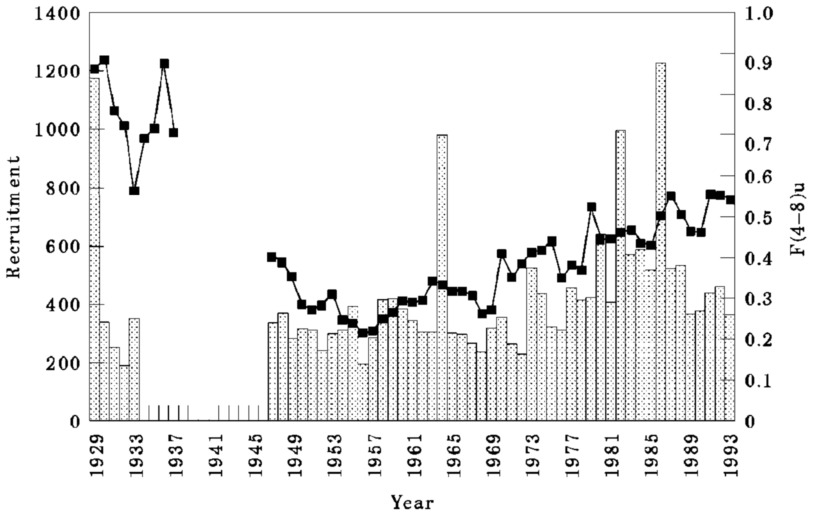

Figure 1. Time trend in unweighted average annual fishing mortality rate of age group 4 to 8 [F(4–8)u] and of recruitment (number*10^{-6} at 1 year of age) estimated by VPA (sexes combined). Bars represent recruitment: ■ = F(4–8)u.

peak at age 4–5. The peak shifted to ages 3–5 during 1975–1984 and back to ages 4–6 in 1985–1994.

The time series of recruitment indicates four exceptionally strong year classes (1928, 1963, 1981, and 1985; Fig. 1). Otherwise, year-to-year variations were relatively small, although average recruitment appears to have varied periodically. Recruitment was relatively low in the 1930s and 1950s and relatively high in the 1970s and 1980s.

Total stock biomass of age group 1 and older (TSB) varied between 200 000 t and 400 000 t in the 1930s, and between 300 000 t and 650 000 t since World War II (Fig. 3). The three peaks are coincident with the recruitment of strong year classes. In contrast to TSB, total abundance did not di er much between the pre-war and post-war period.

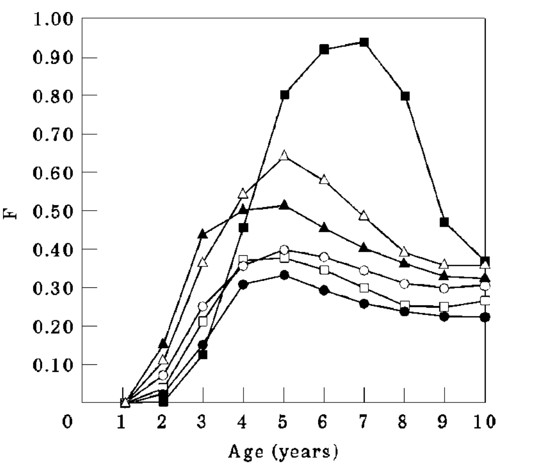

Figure 2. Exploitation pattern by time period as estimated by VPA. ■ = 1929–1938; □ = 1947–1954; ● = 1955–1964; ○ = 1965 1974; ▲ = 1975 1984; △ = 1985 1994.

Time series of c.p.u.e.

Standardized c.p.u.e. data indicate that by the turn of the century catch rates had stabilized at a substantially reduced level compared with those in the 1870s and 1880s (Fig. 4). Throughout the 20th century, c.p.u.e. was fairly stable, except for small peaks immediately following the war years. Catch rates increased slightly between 1960 and 1980, but decreased again in the late 1980s.

The time series of average fishing mortality rate was extrapolated backwards using the relationship between indices of international fishing e ort and the F(4–8)u estimated from VPA. Within each series catchability varied without significant trend, but mean catchabilities (Table 4) indicate some di erences between the 1930s

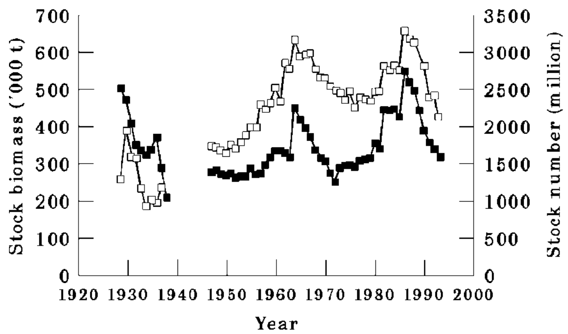

Figure 3. Time series of stock biomass (B in '000 t) and stock numbers (N in millions) of age group 1 and older from VPA. □ = B; ■ = N.

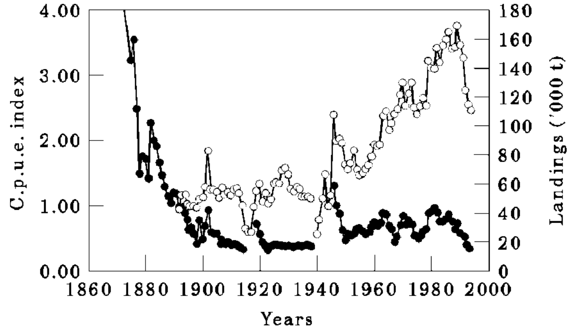

Figure 4. Time trends of international landings (○, in '000 t) and combined c.p.u.e. index (●).

Table 4. Catchability coe cients (g) by fleet before and after World War II used to estimate fishing morality (F) from the index of total international e ort (f) according to F=q × f (series no. refers to Table 2).

Series no.	1929–1938	1947–1993
C	0.364	—
D	0.127	—
E	0.152	0.152
G	0.237	0.146
F	0.358	0.216
H	—	0.147
I	—	0.453

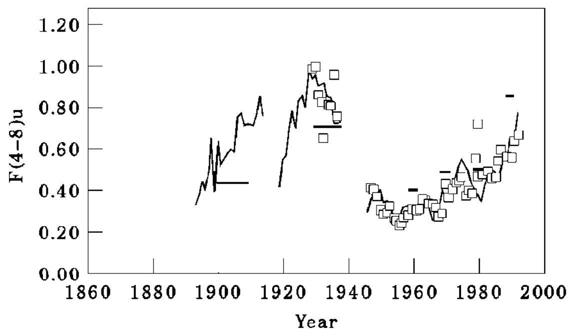

Figure 5. Trends in fishing mortality rate extrapolated from the e ort data (thin line) compared to estimates from VPA (open squares) and length distribution analyses (heavy lines).

and the post-war period. Estimated F almost doubled between 1893 and 1914 (Fig. 5). For the period of overlap, the VPA and c.p.u.e. time series are, of course, interdependent.

Length distributions

Comparison of size-frequency distributions across periods indicates three main di erences (Fig. 6). First, large plaice of 60–70 cm regularly occurred in the landings during the first half of this century, but have been less common in later periods. Second, the peak in the distributions shifted from about 25 cm before 1940 to around 35 cm in the 1960s and 1970s and then back to 30 cm in the late 1980s. Third, the right-hand slope of the distributions has clearly steepened from 1900 onwards, implying an increase in mortality (Fig. 5). Concurrent with the changes in size composition, the proportion of (slower growing) males in the larger size range has markedly declined (Fig. 7).

The estimated mortality rates of the fully recruited size classes are given in Table 5A. However, because the peaks in the size distribution vary with time, estimated mortalities refer to di erent size ranges and are therefore not strictly comparable. Introduction of a constant range (L_{peak}=30.5 cm) reduced the mortality estimates in most cases but did not change the overall pattern (Table 5B). Comparison of the corresponding estimates of fishing mortality (after subtraction of M=0.1) with estimates from VPA and c.p.u.e. appears to confirm the general pattern observed over the entire period.

Inspection of the length distributions (Fig. 6) suggests that slopes vary between size classes and therefore mortality rates were estimated for each 5-cm size class separately (Table 5C). The corresponding fishery mortalities clearly show dome-shaped curves peaking at intermediate size classes of 25–35 cm (Fig. 8). The dome has flattened in the most recent period 1975–1994.

Cohort simulation

The length-based cohort simulation was based on smoothed exploitation patterns (Fig. 8), which resulted in simulated discard percentages in weight of 57% and 32% in the 1930s and 1980s, respectively. Details are presented in Table 6. Because of the uncertainty about discard rates in the 1930s, the results are only tentative. The simulation results show that yield and spawning-stock biomass in recent years at constant recruitment should have increased by factors of 2 and 4, respectively (Table 7A). These improvements are due to the combined e ect of a reduction in discard rate and enhanced growth.

The relative contribution of each of these two factors was estimated by repeating the analysis with the high growth rate in the 1930s and the low growth rate in the 1980s (Table 7B). The results indicate that changes in growth and exploitation patterns contributed 40% and 60% to the increase in yield, respectively, and 20% and 80% to the increase in spawning-stock biomass, respectively.

Reconstructed recruitment as estimated from the landings, only indicates that the bias, ignoring discards, may be up to 50–70% (Table 8A).

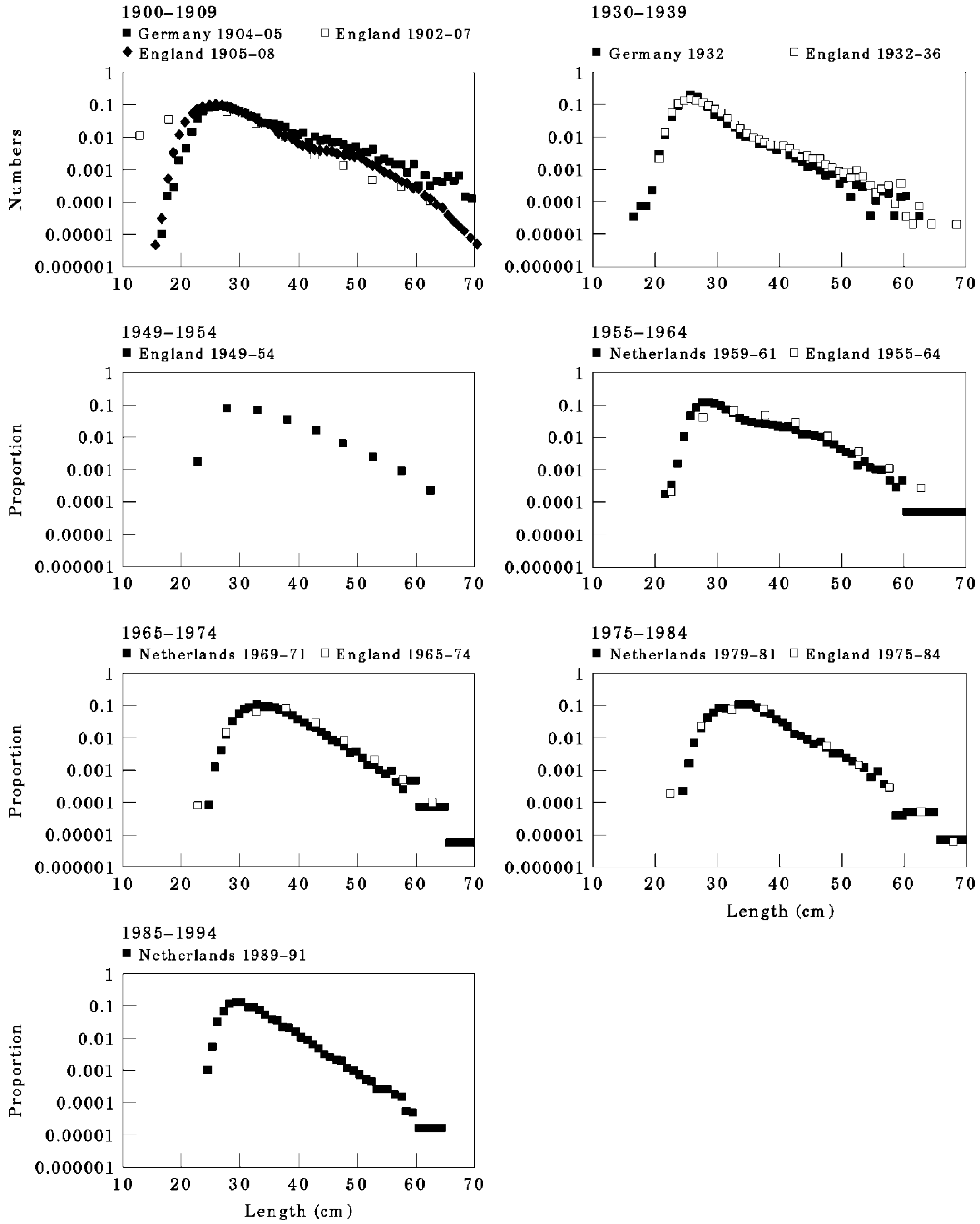

Figure 6. Length compositions of landings and catches by period.

Discussion

The most reliable estimate of the status of the stock comes from the recent VPA, which is updated annually (ICES, 1995), and forms the biological basis for the management advice. VPAs for the earlier periods are less certain because of less complete data. Nevertheless, mortality estimates based on two largely independent methods (VPA and c.p.u.e.) and one totally independent method (length distributions) all indicate the same trends (Fig. 5), suggesting that the overall picture is fairly reliable.

Exploitation patterns estimated by analysis of age and length distributions were both dome-shaped. This

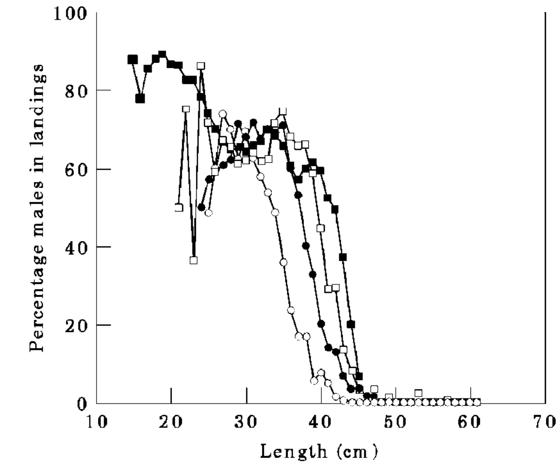

Figure 7. Sex ratio by size class and period. ■ = 1911; □ = 1959–1961; ● = 1979–1981; ○ = 1989–1991.

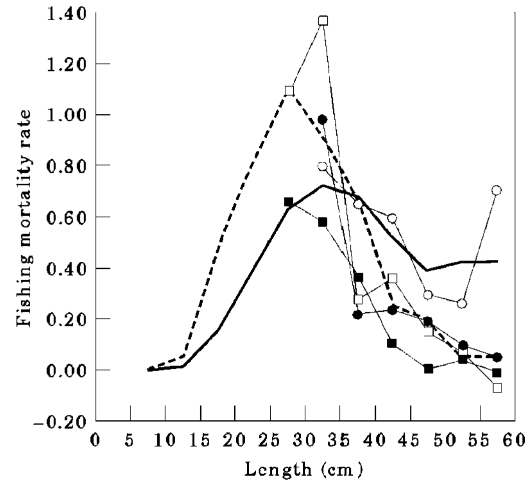

Figure 8. Estimated fishing mortality rates by 5-cm size class by period. Curves A (bold dashed) and B (bold solid) represent smoothed exploitation patterns for 1930–1939 and 1975–1994, respectively, extrapolated to smaller size classes (see text).

finding, however, is not surprising, because the VPA was constrained by terminal F-values set at 0.4 times the average F-values for the previous five age groups in order to match the results obtained from the length distributions. VPA resulted in higher estimates of fishing mortality of older fish than the length-structured analysis for larger fish. This may be an artefact due to insu cient resolution in the age structure of the landings and inaccuracies in age determination. Since the fishery in the 1930s employed relatively small-meshed gear compared with the post-war fishery, a decline in catch

Table 5. Estimates of total mortality (*Z*) based on length distributions (see text). A – Analysis based on true L_{peak} in the length distribution. B – Analysis with L_{peak} fixed at a constant value of 30.5 cm. C – Analysis by 5-cm size class.

	Data sets									
Period	04–05[1]	05–08[2]	07–08[3]	32–36[4]	1930s[5]	1930s[6]	59–61[7]	69-71[7]	79–81[7]	89–91[7]
A										
L_{peak}	26.5	24.5	19.5	23.5	25.5	18.5	27.5	32.5	35.5	29.5
L_{bar}	33.18	30.00	23.62	27.97	28.33	21.96	33.61	36.99	38.80	33.16
Z	0.502	0.666	1.034	0.862	1.346	1.277	0.542	0.666	0.854	0.918
B										
L_{peak}	30.5	30.5	30.5	30.5	30.5	30.5	30.5	30.5	30.5	30.5
L_{bar}	37.36	35.55	35.56	34.67	34.37	31.95	36.64	35.86	35.77	33.97
Z	0.432	0.619	0.618	0.770	0.838	2.400	0.493	0.578	0.591	0.945
C										
20–24 cm	—	—	1.18	—	—	1.40	—	—	—	—
25–29 cm	0.35	0.56	1.37	0.80	1.58	1.60	—	—	—	—
30–34 cm	0.63	0.82	0.59	1.41	1.31	1.74	1.08	—	—	0.90
35–39 cm	0.52	0.56	0.32	0.35	0.40	—	0.09	0.55	0.77	0.74
40–44 cm	0.16	0.13	0.32	0.37	0.55	—	0.26	0.41	0.62	0.77
45–49 cm	0.09	0.10	0.12	0.23	0.26	—	0.30	0.29	0.31	0.49
50–54 cm	0.09	0.12	0.20	0.10	0.26	—	0.19	0.20	0.37	0.34
55–59 cm	0.05	0.13	—	− 0.01	0.07	—	0.20	0.10	1.03	0.59

[1]German market samples (Herwig, 1908).
[2]English first quarter market samples (Heincke, 1913).
[3]"Huxley" research vessel data (Anon., 1912).
[4]English landings (MAFF Fish Lab. Lowestoft, unpubl.).
[5]German landings (Lundbeck, 1936).
[6]German catches (Lundbeck, 1934a).
[7]Dutch landings (RIVO, unpubl.).

Table 6. Length-based cohort simulation for observed growth, exploitation pattern, and discard pattern in the 1930s (A) and 1980s (B). Columns indicate mean length (L_i) of class (i), time it takes to grow through each size class (dt_i), growth rate (dl_i), percentage discards ($\%D_i$), fishing mortality rate (F_i), population numbers (N_i), population weight (W_i), number discarded (ND_i), number landed (NL_i), and population numbers (N_{vpa}) estimated from the numbers landed and partial fishing mortality rate $[(1-\%D) \times F_i]$ of the landings. Simulation starts with $N_0=1$ in the smallest size class and calculates decay in numbers from the fishing mortality rate according to $N_{i+1}=N_i \exp(-Z_i \times dt_i)$.

L_i cm	dt_i yr^{-1}	dl_i cm yr^{-1}	$\%D_i$	F_i yr^{-1}	N_i	W_i kg	ND_i	NL_i	N_{vpa}
A 1930s									
12.5	0.9	5.6	1.00	0.05	1.000	0.02	0.041	0.000	0.368
17.5	1.0	5.1	0.95	0.47	0.874	0.05	0.296	0.015	0.336
22.5	0.9	5.4	0.65	0.82	0.496	0.11	0.165	0.089	0.298
27.5	1.0	5.0	0.01	1.11	0.210	0.20	0.001	0.133	0.207
32.5	1.0	4.8	0.00	0.91	0.063	0.34	0.000	0.037	0.063
37.5	1.3	3.8	0.00	0.67	0.021	0.52	0.000	0.012	0.021
42.5	2.0	2.5	0.00	0.26	0.008	0.76	0.000	0.003	0.008
47.5	3.8	1.3	0.00	0.20	0.004	1.07	0.000	0.002	0.004
52.5	8.0	0.6	0.00	0.05	0.001	1.44	0.000	0.000	0.001
57.5	16.0	0.3	0.00	0.05	0.000	1.90	0.000	0.000	0.000
B 1980s									
12.5	0.6	8.9	1.00	0.01	1.000	0.02	0.005	0.000	0.537
17.5	0.6	8.0	1.00	0.15	0.940	0.05	0.084	0.000	0.507
22.5	0.7	7.0	1.00	0.39	0.802	0.11	0.190	0.000	0.477
27.5	0.9	5.8	0.41	0.63	0.564	0.20	0.093	0.134	0.444
32.5	1.1	4.4	0.02	0.73	0.300	0.34	0.003	0.157	0.295
37.5	1.6	3.1	0.00	0.68	0.117	0.52	0.000	0.073	0.117
42.5	2.2	2.3	0.00	0.52	0.033	0.76	0.000	0.020	0.033
47.5	3.0	1.7	0.00	0.38	0.008	1.07	0.000	0.005	0.008
52.5	4.0	1.3	0.00	0.42	0.002	1.44	0.000	0.001	0.002
57.5	8.0	0.6	0.00	0.42	0.000	1.90	0.000	0.000	0.000

Table 7. Results of the length-based cohort simulation for the 1930s and 1980s, including yield (landings), spawning-stock biomass (SSB), total biomass (TSB), the percentage discards in numbers and weights, and the mean fishing mortality weighted over the catch numbers (F). The yield (Y/R*) and spawning-stock biomass (SSB/R*) are expressed per reconstructed recruit ($R^*=N_{vpa}$ of size class 1 in Table 6): A with observed growth rates and exploitation patterns in both periods; B with high 1980s growth rates applied to the 1930s, and low 1930s growth rates applied to the 1980s.

	Landings kg	SSB kg	TSB kg	Discards		F yr^{-1}	Y/R* kg	SSB/R* kg	R*
				nr	kg				
A									
1930s	0.063	0.043	0.213	63%	36%	0.74	0.204	0.139	0.307
1980s	0.145	0.165	0.482	49%	24%	0.58	0.269	0.307	0.537
B									
1930s	0.096	0.068	0.290	51%	26%	0.81	0.192	0.137	0.498
1980s	0.111	0.134	0.401	58%	30%	0.56	0.248	0.298	0.449

e ciency, and thus a decline in fishing mortality, with size of the fish is not unlikely, but needs further study. Comparison of the maximum fishing mortalities shows that in recent years the length distribution analysis generally gave higher estimates than VPA. This result may be due to the fact that recruitment to the fisheries is size-dependent rather than age-dependent.

The results of the cohort simulation rely heavily on the assumed exploitation patterns and discard rates. For the 1930s, the simulated discard rate lies between the estimates of Baerends (1947) and Lundbeck (1934a). The German fleet data cannot be considered representative for the English fleets because of di erences in fishing grounds between these two. However, the Baerends' estimate for the Dutch fleet is very low compared with recent estimates and there are several reasons why the amount of discards should have decreased after World War II. First, the occurrence of mine fields in the coastal waters of the German Bight restricted fishing in the nursery areas for at least two decades and the introduction of a 12-mile zone has reduced exploitation of the smaller sizes. In addition, industrial landings of small plaice by shrimpers were forbidden in the 1950s. Although these catches were not discarded, they have a similar e ect on the assessment, because they were not reported. On the other hand, the introduction of a legal minimum mesh size and minimum landing size as well as changing market demands must have led to changes in discard practices and the size distribution involved. These factors together are presumably responsible for the observed shifts in peaks of the length compositions (Fig. 6).

The cohort simulation suggests that the change in exploitation rate and exploitation pattern has considerably enhanced the equilibrium yield and spawning-stock biomass, and this would explain the increase in landings and total stock biomass observed since World War II. The simulation further showed that 40% for the increase in yield may be due to the increase in growth rate. At a higher growth rate, plaice will recruit to the fishery at a younger age. This results in a reduction of the cumulative discard and natural mortality during the pre-recruit phase. Because recruitment is estimated in the VPA from the cumulative landings only, the estimated e ects of the changes in exploitation and growth on the yield per recruit and spawning-stock biomass per recruit are smaller than on total yield and total spawning-stock biomass (Table 7).

The important conclusion from the cohort simulation is that time series of recruitment estimates from VPA may be very much a ected by changes in discard practices, if discards are not incorporated in the analysis, and the e ects will be confounded with changes in growth. Consequently, there is much more uncertainty about the estimated long-term trend in recruitment than in fishing mortality (Fig. 1).

The notion that recruitment estimates are sensitive to discarding implies that scatter plots of spawning stock and recruitment might give rather misleading representations of the "true" relationship. Since the current spawning-stock biomass of North Sea plaice is at a historically low level since 1963, and there are serious concerns that recruitment may become reduced (ICES, 1995), it is of great importance to establish whether the older data can be used to provide an estimate of the minimum level of spawning-stock biomass below which recruitment has been impaired. However, given the uncertainty about discarding and its e ect on recruitment estimates, this problem cannot be resolved at present and a critical evaluation of discarding practices throughout the century is required.

The analysis confirms earlier studies (Beverton and Holt, 1957; Gulland, 1968) that North Sea plaice was very heavily exploited in the 1930s, although Bannister (1978) arrived at lower estimates of fishing mortality. The present lack of large plaice as compared with the 1930s, despite lower overall fishing mortality rates, may be explained by the change from a strongly dome-shaped exploitation pattern prior to World War II to a rather flat pattern with higher mortalities on larger fish in recent decades (Fig. 8). The high F on younger age groups in the 1930s, which was mainly exerted in the coastal waters of the eastern North Sea, must have restricted recruitment to the o shore spawning areas. Since the 1930s the importance of the German Bight spawning population has increased (Buckmann, 1961; Harding *et al.*, 1978; Heessen and Rijnsdorp, 1991) and so has the c.p.u.e. (Cushing, 1982), which is consistent with the estimated reduction in fishing mortality in the coastal waters since World War II.

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