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History of the North Atlantic cod stocks

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During the last decades, all cod stocks of the North Atlantic have been exposed to gradually rising fishing pressures due in part to improvements in technology that result in increasingly efficient fishing practices. At the same time, all stocks have experiences changing environmental conditions, which, together with increasing fishing pressures, are thought to be responsible for the historical fluctuations in stock abundances and structures. Stock sizes, and the age and size structures of stocks have consequently been depleted. Such drastic changes in population sizes have raised concerns about potential (selective) changes in genetic composition and loss in genetic diversity. Today many of the stocks are heavily overfished and some are considered to have reached the stage of recruitment overfishing. In this paper, we review the state of knowledge concerning the genetic composition as well as trends in landings, fishing mortality, stocks size, stock composition and recruitment among all major cod stocks in the North Atlantic.

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Introduction

Of all fish in the North Atlantic, cod has supported the greatest commercial fishery of the last centuries. Through centuries, or since the 15-16th century, cod has been caught in great numbers in the Barents sea, Icelandic waters, on the banks between Nova Scotia and Labrador and in the waters of the coast of Maine and Massachusetts. (Cushing, 1988; Jonsson, 1994; Oiestad, 1994; Serchuk, et al., 1994; de La Villemarqué, 1994). The majority of the cod fishery at these locations was operated by Basque, French and English fishermen but also Dutch as well as locals (Palmadottir, 1989; Cushing, 1988). The cod were either salted or dried for local consumption or exported to foreign markets (Jonsson, 1994; Cushing, 1988).

During the early centuries, the cod fishery was operated with hook and line from open boats, initially rowboats, and later sailboats (Jonsson, 1994; Lilly and Carscadden, 2002). It was not until the end of the 18th and beginning of the 19th century that motors were installed into the sea vessels (Jonsson, 1994). Since then, immense improvements have taken place involving new technology in all areas important for fishing, re ships, gears, navigation, and fish detection. Consequently, all commercially important fish stocks including most cod stocks in the North Atlantic have endured dramatic changes in fishing pressures as well as fishing efficiency due to the technological advances. Subsequently during last century, stock sizes underwent significant long term changes characterised by an increase during the post war period, followed by a steady decline since the 1970s (Jakobsson, 1992; de La Villemarqué, 1994; Oiestad, 1994; Garrod and Schumacher, 1994; Hylen, 2002). At the same time, the cod stocks were subjected to large climate changes and many stocks were directly influenced by the “Great Salinity Anomaly” that circulated the North Atlantic in 1970s and 1980s (Jakobsson, 1992).

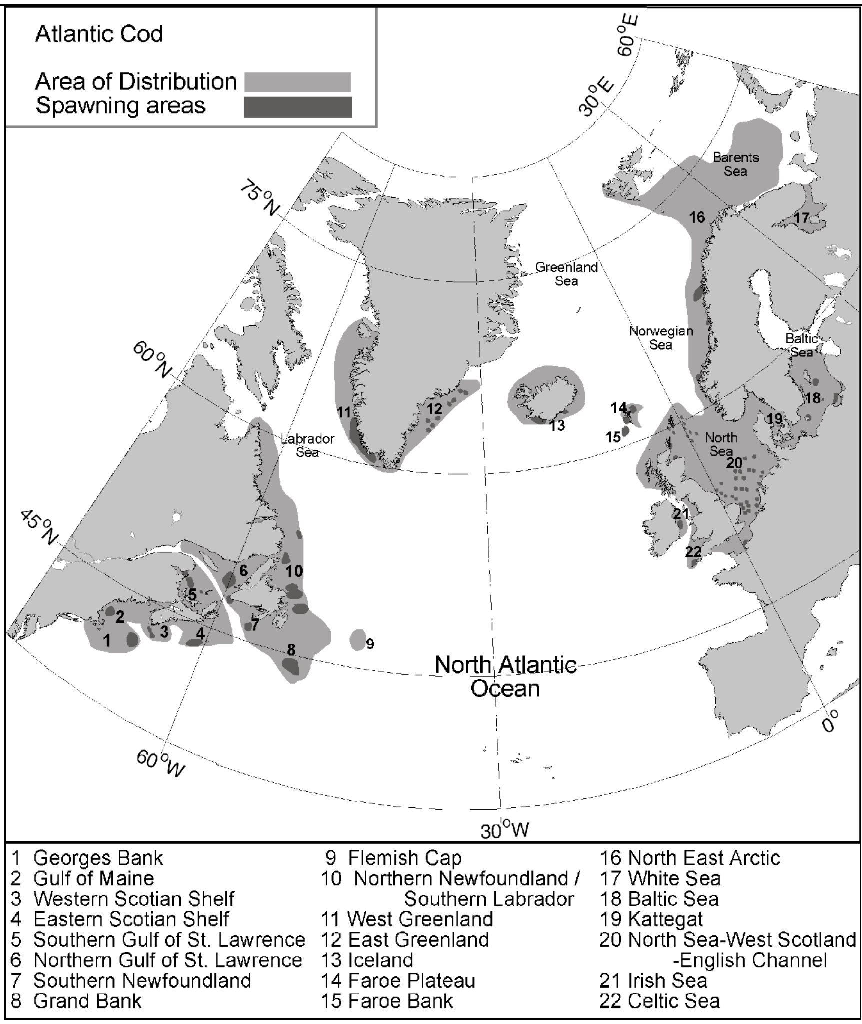

Figure 1. Geographical distribution and location spawning areas of all major cod stocks in the North Atlantic (from Brander and Drinkwater, in prep). Please note that stocks are discussed in a reversed numerical order in the text, i.e. Barents Sea = 22; and George Bank a= 1

Distribution and stock discreteness

Cod are distributed on the shelf and upper slopes of the continent around the fringes of the North Atlantic, from Barents Sea in the East and northern Labrador – Greenland in the west, south to the Celtic sea in the East and Massachuset – New Jersey in the West (Figure 1; Lilly and Carscadden, 2002). Cod reside mostly within 500 m depth but have been found at depths to at least 850 m (Lilly and Carscadden, 2002).

More than forty years of genetic research have been focussing on assessing the discreteness of cod stocks/populations. Knowledge of stock structure is of paramount importance for fisheries management in order to assure that discrete stocks are managed separately to avoid overexploitation and possible extinction of small and/or slow growing populations in a mixed fishery. During this long succession of research on cod genetics, methodologies have changed dramatically from the studies of haemoglobin alleles in the 1960´s to direct studies of DNA during the current genetics and genomics revolution. Along this long line of research a lot of cohesive knowledge cod population structure has been gained and the understanding of population structure range among the very best described for any species of marine fishes.

It is well established that there is large genetic differentiation between cod populations from the north-eastern and north-western Atlantic Ocean respectively (see Mork et al. 1985; Pogson et al. 1995; Bentzen et al. 1996). Also within the two major geographical groups, ample evidence of genetically discrete populations has been gathered.
Within the NW Atlantic genetic differentiation at continental shelf scales have been observed (see Ruzzante et al. 1998) for most of the major populations (NE Newfoundland Shelf, Grand Banks, Flemish Cap, Scotian Shelf, Georges Bank). Even on a smaller geographical scale population structure has been suggested. For example Ruzzante et al. (2000) found evidence of multiple stocks in and around the Gulf of St. Lawrence.

In the NE Atlantic, genetic methods have revealed significant differentiation among the major cod stocks (NE Arctic, North Sea and Baltic Sea; see Nielsen et al. 2001). Also in the NE Atlantic genetic evidence has been gathered, strongly suggesting genetic differentiation on a much smaller scale. For example Fevolden and Pogson (1997), found large genetic differences between NE Arctic and Norwegian coastal cod. This pattern has been supported recently by the studies of Sarvas (unpublished) employing another class of genetic markers (microsatellites). These studies suggested that even on a microgeographical scale within the Norwegian coastal cod stock (among fiords) significant genetic differentiation can be found. This is in line with the studies of (Knutsen et al. 2003; see also Hutchinson et al. 2001) who found evidence of isolated fiord populations on the Skagerrak coast of Norway. There is also evidence that isolation among populations is not necessarily discrete, but populations can be connected by a hybrid zone; with a gradual transition between putative populations. This has for instance been shown to be the case for the isolation between North Sea and Baltic cod (Nielsen et al. 2003).

Mid-Atlantic “island” cod populations from Iceland and the Faeroe Islands (bank and plateau) are also genetically different from other “continental” populations (Nielsen et al. unpublished). For Iceland there is evidence of distinct populations in the North and in the South (Imsland et al. 2004 and Pampouli pers. com.) and the bank and plateau populations of the Faeroe Islands also show evidence of genetic isolation.

In summation, there is a vast amount of data, which very strongly indicate that cod is structured at many geographical levels often associated with the occurrence of oceanic circulation systems and environmental gradients. The future challenge for cod population genetics will be to investigate the temporal stability and biological meaning of the suggested microgeographical population structure; i.e. are the patterns of discrete populations we observe ephemeral or do they really represent different evolutionary trajectories of cod adapted to their local environment?

Stock size and landings among the North Atlantic cod stocks

A total of 22 cod stocks have been routinely assessed in North Atlantic by ICES and NAFO (Figure 1; Table 1). In addition to those listed in Table 1, five other fishing stocks have been historically recognized. These include: Coastal cod, Norway; East Greenland; Faroe Bank and Bay of Fundi-Scotian Shelf (4X). Assessment information on stock size and structure exist back to 1946 for the Northeast Arctic, 1950 for the Icelandic cod stock, and the 1960s-1970s for most of the other stocks. All of these stocks are distinctly different with respect to size (Table 1) as well as structure, growth and other population dynamic characteristics (see Brander and Drinkwater, in prep). During the recent assessment periods, only 5 stocks, Northeast Arctic, North Sea, East Baltic, Icelandic and Northern cod, have attained the size of one million tonnes (Table 1). Most of the stocks have been considerably smaller or below 100-140 thousand tonnes, on the average, including the Irish Sea, Celtic Sea, West of Scotland, West Baltic, Faroe Plateou, George Bank and the Grand Bank. In terms of spawning stock biomass, only three stocks, North Arctic cod, Icelandic cod and Northern cod, have attained a size close to or above 1 million tonnes (Table 1). Most stocks (Celtic, Irish Sea, W-Scotland, Faroe and W-Baltic, Grand Bank and George Bank) have been characterised by a considerably smaller spawning stock, or only 11-60 thousand tonnes on the average while the size of the E-Baltic and North Sea spawning stocks were at an intermediate levels of approximately 130-300 tt on the average and a maximum size of 250 (North Sea) and 700 tt (East Baltic).

Like stock sizes, catches have also varied distinctly among the stocks (Table 1). Within the recent assessment time period, the greatest landings have been obtained from the largest stocks with maximum landings reaching as high as 1343, 810, 585 and 545 tt from the Northeast Arctic, Northern cod, North Sea and the Icelandic stock, respectively. Additionally, high landings have also been obtained from the East Baltic (max 392 tt) and Grand Bank (max 227 tt). For the remaining stocks, maximum landings have ranged from 15-60 tt (Table 1).

In all of the stocks, fishing pressures increased gradually throughout the 1950s-1990s. As a result, fishing mortality varied annually however in a gradually increasing manner, reaching levels of 0.8-1.8 during the last quarter of the 19' century. In most stocks, fishing pressures declined in the beginning of the 20' century, although regrettably, in many stocks the enforcing of lowering fishing mortality was due to drastically declining stock levels (e.g., North Sea, Irish Cod, W-Scotland, East Baltic, Northern Cod, Grand Bank and George Bank).

Table 1. Information on stock status, landings, stock size, recruitment, age groups and time periods used in assessment of the major cod stocks in the North Atlantic.

	NAC[1]	W-BALT[2]	E-BALT[3]	KAT[4]	NS[5]	CE[6]	IR[7]	WSCOT[8]	FAROE PLAT[9]	ICE[10]	GREENL[11]
Present status	ISBL	OSBL	OSBL	OSBL	OSBL	OSBL	OSBL	OSBL	ISBL	ISBL	Collapsed
Fishing status[21]	Open	Open/Open[22]	Open	Closed/Open	Closed/Open	Open	Closed/Open	Closed/?	Open	Open	Closed
Years of Assessment	1946-2003	1970-2003	1966-2003	1971-2003	1963-2003	1971-2003	1968-2003	1978-2003	1961-2003	1955-2003	1924-2003
Mean landings	660	38	168	11	245	9	8	14	25	352	128
Range landings	212-1343	17-54	45-392	2-22	66-580	3-19	1.8-15	1.3-28	6-40	169-545	0.7-478
Mean Total Biomass	2026	72	459	20	579	17	19	31	93	1091	1197
Range Tot. biomass	739-4168	27-116	136-1057	3-45	164-1146	9-34	6-30	9-54	29-155	536-2282	0.2-4129
Mean SSB	371	33	292	15	139	11	11	21	64	320	
Range SSB	57-1165	9-57	95-697	3-37	37-253	6-24	2-21	6-40	21-117	121-932	0.1-3200
Mean R	579	104	304	13	612	4	6	16	17	181	
Range R	53-1819	18-286	83-829	0.1-37	88-2517	0.345-16	0.4-1.8	1.3-92	4-48	63-350	0.1-620
Age groups	3-13+	1-7+	2-8+	1-8+	1-11+	1-7+	0-7+	1-7+	1-9	3-14+	3-11+

OSBL = Outside safe biological limits (or below biomass referenc points (Kattegat, Celtic, Irish,
ISBL = Inside safe biological limits

Table 1 continued

	Northern[12] cod	Flemish [13]Cap	Grand[14] Bank	St. Pierre[15] Bank	South St-Lawrence [16]	North St-Lawrence [17]	N-Scotian Shelf[18] 4vsw	Gulf of Main[19]	George Bank[20]
Present stock status	Collapsed	Collapsed	Collapsed	Collapsed	OSBL	Collapsed	Collapsed	ISBL	OSBL
Fishing status	Closed 1992 Reopened 2004	Closed 1999	Closed 1994	Closed 1993	Reopened 1998	Closed 1995	Closed 1993	Open	Open
Years of Assessment	1962-1993	1972-2001	1959-2002	1959-2003	1971-2003	1974-2003	1970-2003	1982-2001	1978-2002
Mean landings	268	16	49	41	41	56	39	8	29
Range landings	0.3-810	3-57	0.17-227	0.6-80	1-69	0.1-106	0.1-80	1.6-17	8-57
Mean Total Biomass	1001	30	131		206	270		25	73
Range Tot. biomass	100-3000	2-113	6-395	65-250	92-473	36-603		15-42	25-135
Mean SSB	444	11	49		151	143	51	16	53
Range SSB	33-1552	2-40	4-125	45-125	63-354	13-379	5-161	11-24	17-92
Mean R	300	20	53		108	84	106	12	15
Range R	23-1196	0.03-113	0.4-252	11-80	30-322	10-206	9-332	0.5-100	1.5-46
Age groups	3-15+	1-8	1-12	3-14	3-15	3-13	3-	1-7	1-10+

1) ICES 2004a
2-4) ICES 2004b
5) ICES 2004c
6) ICES 2004d
7-8) ICES 2005
9) ICES 2004e
10) ICES 2004e
11) West Greenland, offshore and inshore combined; Wieland and Storr-Paulsen 2004; Buch, et al., 1994; ICES 2004e
12) Lilly et al., 1998; Smedbol et al., 2002
13) Cervino and Vázquez, 2004
14) Healey et al., 2003
15) Brattey et al., 2003
16) Chouinard, et al. 2003
17) Fréchet et al., 2003
18) Clark and Hinze, 2003; Fanninig et al, 2003
19) Mayo and Col 2002
20) O'Brien et al., 2002
21) (status as adviced by ICES/current action)
22) The absence of separate TAC for the eastern and western Baltic stocks limits the ability to restrict fishing acitivity by TAC (ICES 2004b)

Historical changes in stock structures and genetic diversity

In chorus with increasing fishing pressures and declining stock levels, the size and age diversity of the cod stocks have been eroded resulting in lower proportion of old and large individuals within most of the stocks (Figures 2-4, Table 2). As a shift in age and size distributions towards smaller and younger size and age classes will affect reproductive performance of the stocks (Marteinsdottir and Begg, 2002; Marshall, et al. 2004 and references therein), recruitment potentials have are also been impacted (Marteinsdottir and Thorarinsson, 1998; Ottersen et al., in press; Cardinale and Arrhenius, 2000). In the Icelandic cod stock, low recruitment levels were explained by declines in age diversity (Mareinsdottir and Thorarinsson, 1998). In the Northeast Arctic cod stock, Ottersen et al, (in press, 1994) demonstrated that due to changes is age composition, the stock is now less resilient to adverse climate conditions.

Reduction in population sizes induced by fishing or environmental changes can have various consequences for cod populations. Reduction in the "effective population size, N_e" (in popular terms, N_e can be said to be the part of the population that actually produces offspring that lives to reproduce again each generation), reduces the levels of genetic variation within populations and can lead to inbreeding. General conservation genetic rules of thumb says that effective populations should range between 500 and 5000 (Frankham 2002) to be sufficient to secure the evolutionary potential of an isolated population. Classical marine fish populations have generally been considered safe in this context. Even when fished down to a historical minimum census number (N) often counts millions of remaining individuals in the populations. However, recently this conventional wisdom has been challenged by a number of studies demonstrating that the effective population sizes can be much smaller than census sizes. Estimates of N_e /N ratios as small as 10^{-5} has been suggested (example in Hauser et al. 2002), meaning that effective population sizes for numerous marine species could range in the hundreds. Three studies have been conducted in cod where the specific aim was to study potential loss of genetic variability over time. Ruzzante *et al*. (2001), observed stability in the genetic structure for Newfoundland cod employing DNA from historical otolith collections, and no evidence of losses of genetic variation, despite the fact that the population today is only 1% of its former size. In contrast Hutchinson et al. 2003 found a loss of genetic variability and very low effective population sizes in cod from the North Sea area. They estimated the effective population size of cod at Flamborough Head in the North Sea to be 69 between 1954 and 1960, and 121 between 1960 and 1970, respectively. A very recent study by Poulsen et al. (accepted) again challenges these findings of low effective population size of North Sea cod from the Moray Firth and Baltic Sea cod from the Bornholm Basin. They found that effective populations most likely ranged in the thousands and found no evidence of loss of genetic variation. In summation there is at present very much debate regarding estimation of effective population sizes in marine fishes and accordingly the loss of genetic variability associated with population declines.

Table 2. Rate of change (average of first 5 years – last 5 years; as formulated by Hutchings and Baum, 2005) in catch, stock biomass, spawning stock biomass, recruitment, proportion 6 or 10+ and age diversity (H) among cod stocks in the North Atlantic.

Stock	Years of landings/ demographic properties	Rate of change (%) in landings and demographic properties					
		Landings	Biomass	SSB	R	Prop old (10+ or 6+)	Age Diversity (H)
NAC	1946-2003 1946-2003	-41	-59	-57	-53	-96	-23
E-Baltic	1966-2003 1966-2003	-50	-48	-45	-44	77	13
W-Baltic	1970-2003 1970-2003	-32	-56	-51	-71	-0.2	-14
Kattegat	1971-2003 1971-2003	-77	-87	-86	-88	-58	-18
North Sea	1963-2003 1963-2003	-50	-63	-74	-61	-67	-17
W-Scotl	1966-2003 1978-2003	-85	-79	-77	-81	125	3
Irish Sea	1968-2003 1968-2003	-59	-67	-74	-71	-89	-63
Celtic Sea	1971-2003 1971-2003	85	36	19	99	-64	-19
Faroes	1961-2003 1961-2003	29	23	4	-2	1	0
Iceland	1955-2003 1955-2003	-54	-64	-79	-25	-94	-14
W-Greenl	1924-2003 1982-2003	-79	-99	-98	na	na	Na
Northern cod 1)	1959-1993 1962-1993	-70	Na	-62	-95	-97	Na
Flemish Cap	1959-1998 1972-2001	-84	-95	-87	-98	na	na
Grand Bank	1953-1994 1959-2002	-82	-95	-90	-99	136[1)]	0.9
S-St.Lawrence	1964-1995 1974-2003	-91	-33	30	-61	na	Na
N-St.Lawrence	1965-1995 1971-2002	-76	-78	-78	-86	-81	-43
N-Scotian shelf	1958-1993 1970-2002	-52	Na	-75	-81	-72	na
Gulf Main	1960-2001 1982-2001	-67	-34	-21	-47	-48	Na
George Bank	1960-2001 1978-2001	-49	-73	-72	-79	-74	-4.1

1) Grand Bank, 9+: Increase in proportion of 10+ in recent years due to the strong year classes from 1989-1990 and lower recruitment compare to the earlier years.

Stock status and recovery

Of the 22 cod stocks in the North Atlantic that are presently assessed (Table 1), only four (NAC, ICE, FAROE and Gulf of Main) are considered to be inside safe biological limits. Of those that are considered to be outside safe biological limits, 7 stocks are currently collapsed. For all of these stocks the management advice has been to close the fishery and today, most of these are closed to all directed commercial fishery.

Even though some stocks have been closed for fishing over a decade, recovery has been slow. Recent reports have demonstrated that recovery may be delayed or prevented by changes in dominance structure where cod have been replace by smaller fish species resulting a restructuring of the total food web by a cascading effects (Frank et al., 2005). Additionally, genetic changes associated with population collapse (as described elsewhere in this paper) may act in concert with environmental and ecosystem changes to explain the unexpected slow recovery of cod populations. Reductions in genetic variability *per se* impair the ability to respond to environmental changes in general. Also, selective changes of the genetic composition caused by fishing may shift the life-history characteristics of the population away from optimal trait value under natural selection. To return to the “natural” trait optimum might take a considerable number of generations. For example, model based calculations suggest that age at maturity for cod can take centuries to revert to the natural state even under a scenario of little contemporary fishing (Dieckman pers. com.).

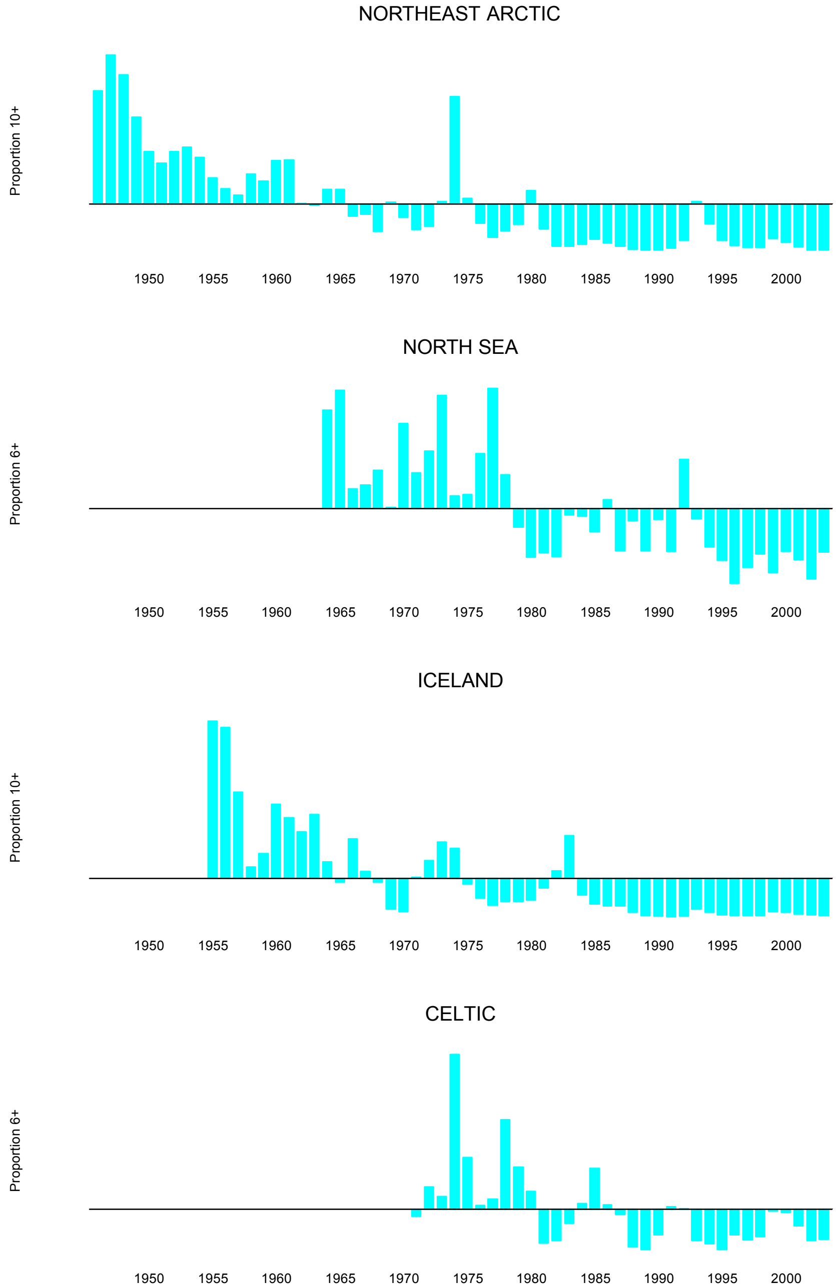

Figure 2. Deviations from the mean of the proportion of cod ten years and older in the Northeast Arctic and Icelandic spawning stocks (ICES 2004a,e) and six years and older in the North Sea and Celtic spawning stocks (ICES 2994c,d).

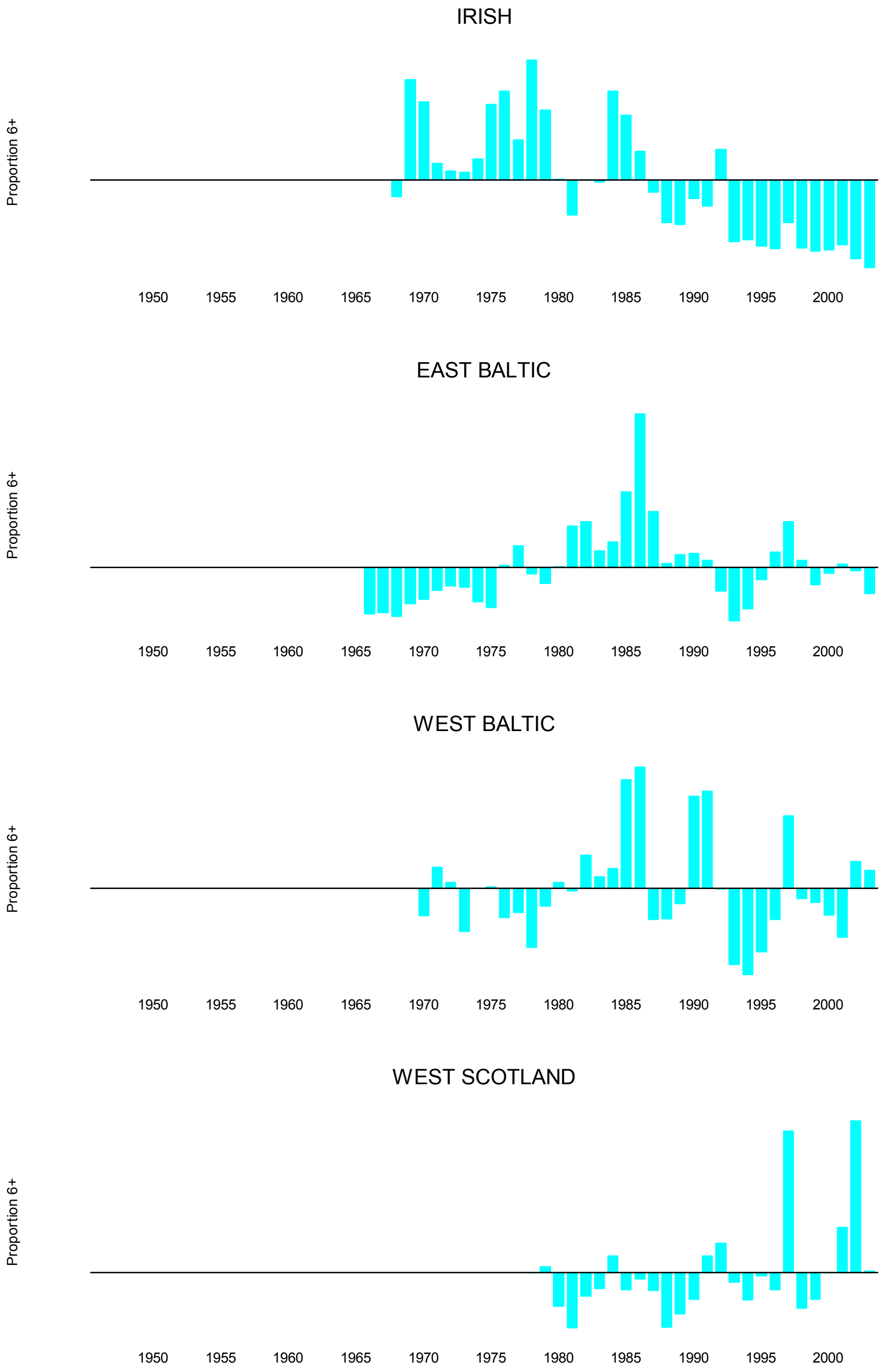

Figure 3. Deviations from the mean of proportion of cod six years and older in the Irish, East and West Baltic and West Scotland spawning stocks (ICESd,b; ICES 2005)

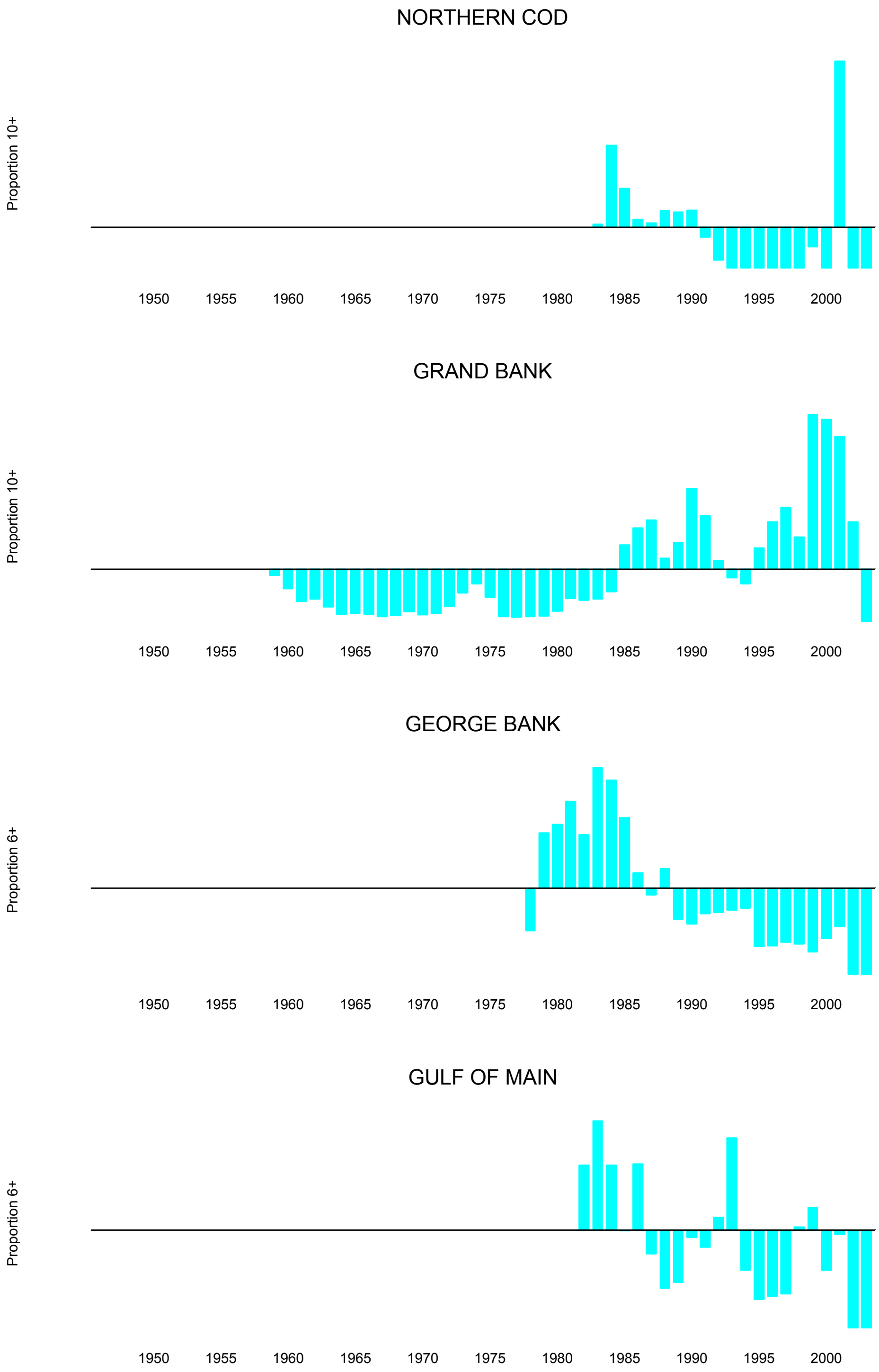

Figure 4. Deviations from the mean of proportion of cod ten years and older in the Northern and Grand Bank spawning stocks (Lilly et al., 1998; Smedbol et al., 2002; Healey et al., 2003) and six years and older in the George Bank and Gulf of Main spawning stocks (Mayo and Col 2002, O'Brien et al., 2002)

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