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On distributional responses of North Atlantic fish to climate change

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Changes in fish distribution and climate in the North Atlantic have been observed for millennia by seafaring peoples, chronicled in many historical anecdotes, and recently studied systematically. For temperate to Arctic North Atlantic fish, a literature compendium of limits of temperature, salinity, and depth during feeding and spawning was used to investigate factors that influence distribution. Latitude and depth were negatively correlated with species number and density. Peak numbers of species feed at 0–4°C, but spawn at 2–7°C and salinities of 32.5–33.5. Principal components of feeding depths and temperatures suggested four groups of species: (i) small pelagics characterized by shallow habitat and cooler temperatures; (ii) most groundfish in deeper and warmer waters; (iii) warm-water large pelagics; and (iv) deepwater species. Spawning temperatures, salinities, depths, and timing produced groupings consistent with feeding components for pelagics, but differing for distant migrants such as tunas. Principal components (PCA) of spawning characteristics explained 56% of the variance in species resilience (doubling time), while PCA of feeding characteristics explained only 23%. We infer that the small pelagics capelin (*Mallotus villosus*) and herring (*Clupea harengus*) react strongly and quickly to climate change because of their physiological limits and potential for fast population growth. Verification comes from Icelandic and Greenland waters, which warmed considerably during 1920–1940, and where capelin, herring, cod (*Gadus morhua*), and other species shifted north very quickly.

Keywords: capelin, climate change, distribution, migration, North Atlantic.

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Introduction

Since time immemorial, seafaring peoples have observed variations in the distributions and migrations of marine animals in association with climate. In terms of their essentially Lagrangian view, there were good and bad days, months, years, and decades. Not all species varied in the same way, and some species varied more than others. Groups of species having similar responses have been identified both from anecdotes and recent systematic study (Murawski, 1993). The earliest reported historical events have ample anecdotes, but lack data or systematic investigation (e.g. Prowse, 1895). In the recent past, however, a major warming event in Icelandic and Greenland waters between 1920 and 1940 was extensively documented (e.g. Sæmundsson, 1932; Ahlmann, 1948; Lysgaard, 1948).

Early works in marine zoogeography addressed some of the historical queries about the comings and goings of fish by explaining the distribution patterns of species and their dynamics in terms of species physiology and ecology. An essential element of this work was to explain how distribution patterns developed over much longer time scales. The seminal works of Ekman (1953) and Briggs (1974) provide rich descriptions of variations in fish distribution and migration in relation to physical factors of the environment, especially sea temperature, salinity, depth, bathymetry, and currents, on both geological and contemporary scales. Similar dynamics are also well known in marine invertebrates (e.g. Petuch, 2004). These works suggest that climate has a dominant influence on the long-term ($\gg$1000 years) distribution and migration patterns of marine fish and invertebrates, and provide comprehensive treatments of how these patterns developed in the world's oceans over geological time scales.

Reports on shorter-term changes in the distribution and migration of many marine phyla, species, and stocks are numerous in the literature. Many works have investigated warming and cooling periods, and describe northward advances of species during warm periods or, alternatively, southward contractions during cold periods. There can be no doubt that the main commercial species of the North Atlantic, including Atlantic cod (*Gadus morhua*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), haddock (*Melanogrammus aeglefinus*), and capelin (*Mallotus villosus*) are subject to north–south movements in response to climate (Ekman, 1953). Cushing (1982) summarized some better known examples, such as North Sea species changes, the effects of cold winters in northwest Europe in the 20th century, and northward movements of many species in the North Atlantic in the warm period of the 1920s to 1940s.

The reality of climate change in the 21st century has refocused concerns about the potential effects of environmental change on the fish populations of the North Atlantic (e.g. Murawski, 1993; Drinkwater, 2002; Godø, 2003). In addition to the stresses on fish stocks imposed by overfishing (Sinclair and Murawski, 1997), climate change may have particular impacts on the North Atlantic, because of a dependence on north–south oceanic heat transfer (Pflaumann *et al.*, 2003). A key question is, how changes in sea temperatures, salinities, and currents may affect both the fish and the fisheries (McGinn, 2002). There is also the likelihood that environmental effects and overfishing can interact (e.g. Rose and Kulka, 1999), and that recent depletions whose primary cause is recruitment overfishing have been amplified and prolonged by changes in climate (e.g. Cushing, 1982; Rose *et al.*, 2000; Drinkwater, 2002).

All fish have limits in terms of the sea temperatures and salinities that they inhabit, and these limits may change with age and be very different during feeding and spawning (Ekman, 1953). Whether broad or narrow, these limits form the large-scale boundaries of the distribution of species. Within these boundaries, the specifics of stock structure and life cycles have developed as adaptations to the scales and patterns of currents and seasonal variations in temperature, salinity, and the availability of food (Robichaud and Rose, 2004). In the North Atlantic, there are many variations in such life cycles. For example, some fish spawn only in warm subtropical waters but migrate into colder North Atlantic waters to feed (e.g. bluefin tuna, *Thunnus thynnus*). Other species spawn and carry out their full life cycle within fairly constant physical conditions and locations (e.g. some of the eelpouts, Zoarcidae). Still others may spawn in relatively warm waters, spend part of the juvenile cycle in cool waters, then move to very cold waters as adults to feed (e.g. capelin). There are many variants with many spatial and temporal overlaps. All contribute to and influence what we call "ecosystems".

In this paper, I pose several questions. What factors influence the distribution of species in the temperate to Subarctic regions of the North Atlantic? Can the different responses of species be quantified? Do groups of species respond similarly to and differently from other groups? To address these questions, I examined the feeding and spawning limits of North Atlantic fish for which data were available. As a qualitative test of the outcomes of this broad-scale analysis, I examine historically documented changes in distribution and migration patterns that occurred during the warming period of 1920–1940 in Iceland and Greenland.

Methods

The literature was searched for data on fish species of the temperate to Subarctic North Atlantic (Table 1). In all, 141 species were examined. The list is not comprehensive since data were not available for all known species. Variables recorded for each species both during feeding and spawning periods of adults were minimum and maximum temperature of occurrence in the wild, minimum and maximum salinity, minimum and maximum depth, spawning start and end months, and a measure of species resilience [population doubling time, categorized from literature values of "r", the intrinsic rate of increase, as very short (1 year), short (to 3 years), medium (to 9 years), or long (>9 years)]. All variables were available for only a subset of the total species. In cases where literature values for the measured variables differed, judgements were made to determine which values to use. For some species, especially those that are poorly described, values may not be strictly comparable, because it was evident that some workers described where fish were most often found, while others described the full limits of even minor distribution. In general, feeding limits describe the range where most feeding occurs, but spawning limits are full limits beyond which little or no spawning has been observed. No account has been taken of the success of the spawning. In cases where data were thought not to be reliable, they were not used. Principal component analyses were used to describe associations among the variables measured, and then to identify groups of species with similar variable loadings. These analyses did not include species that were poorly known because insufficient data were available.

Surface air temperature data were extracted from the NASA database available through the Goddard Institute for Space Studies, New York for Norway, Iceland, Greenland, and Newfoundland (http://www.giss.nasa.gov/data/update/gistemp/station_data/).

Results

The number of species declined exponentially with increasing latitude from approximately 400 at 25°N to 50 at 60°N (Figure 1a). Mean water temperature also declined with increasing latitude (Figure 1b). Hence, there is a general positive association between average temperature and the number of species.

Table 1. Summary of environmental limits to distributions of temperate to Subarctic North Atlantic fish, population resilience, and references. Ranges are where fish are typically found or concentrated (some fish may, at times, be found outside these ranges). D(m) = depth range; T(C) = feeding temperature range in °C; Sp(mo) = spawning months; SpD(m) = spawning depth range; SpT(C) = spawning temperatures; SpS(psu) = spawning salinity; and Dy = index of population resilience. Species listed alphabetically by family (not shown), then scientific name.

	Common name	Scientific name	D(m)	T(C)	Sp(mo)	SpD(m)	SpT(C)	SpS(ppt)	Dy	Reference
1	Shortnose sturgeon	*Acipenser brevirostrum*		10	5 to 9				14	Jones *et al.*, 1978
2	Atlantic sturgeon	*Acipenser oxyrhynchus*	to 46						14	Page and Burr, 1991
3	Arctic alligatorfish	*Aspidophoroides olriki*	7 to 520	−1.9 to 2.5				33 to 35	—	Andriashev, 1986a; Scott and Scott, 1988
4	Northern alligatorfish	*Agonus decagonus*	to 930	−1.7 to 4.4	6				—	Andriashev, 1986a; Scott and Scott, 1988
5	Alligatorfish	*Aspidophoroides monopterygius*	18 to 332	−1.1 to 2.5	11 to 1				—	Bigelow and Schroeder, 1953a; Scott and Scott, 1988
6	Lancetfish	*Alepisaurus ferox*	0 to 1 830						—	Post, 1984
7	Hairfin smoothhead	*Bathytroctes homopterus*	560 to 1 690						9	Markle and Sazanov, 1990
8	Bluntsnout smoothhead	*Xenodermichthys copei*	100 to 2 650		9 to 11				3	Markle and Quéro, 1984; Markle, 1986
9	Sandlance	*Ammodytes americanus*			12 to 1				9	Collette and Nauen, 1983; Scott and Scott, 1988
10	Northern sandlance	*Ammodytes dubius*	to 200	0 to 15	12 to 1			30 to 36	3	Collette and Nauen, 1983; Robins and Ray, 1986; Scott and Scott, 1988
11	Striped wolffish	*Anarhichas lupus*	50 to 500	−0.4 to 4	9	50 to 500	−0.4 to 4	34 to 35	9	Bigelow and Schroeder, 1953a; Scott and Scott, 1988; Barsukov, 1996
12	Broadhead wolffish	*Anarhichas denticulatus*	150 to 600	1.6 to 4		150 to 600	1.6 to 4	34 to 35	9	Barsukov, 1959; Scott and Scott, 1988
13	Spotted wolffish	*Anarhichas minor*	25 to 600		11 to 12	100 to 700	3.1 to 4	34 to 35	9	Barsukov, 1959; Scott and Scott, 1988
14	American eel	*Anguilla rostrata*	400 to 2 900		2 to 7				—	Bigelow and Schroeder, 1953a; Snelgrove and Haedrich, 1985; Scott and Scott, 1988
15	Summer flounder	*Paralichthys dentatus*	to 200		11 to 3				3	Bigelow and Schroeder, 1953a
16	4spot flounder	*Paralichthys oblongus*	to 300		5 to 6				9	Bigelow and Schroeder, 1953a; Robins and Ray, 1986; Scott and Scott, 1988
17	Windowpane	*Scophthalmus aquosus*	to 80		4 to 6				3	Bigelow and Schroeder, 1953a; Scott and Scott, 1988
18	Shad	*Alosa sapidissima*	to 250	13 to 18	5 to 7				9	Scott and Crossman, 1973; Whitehead, 1985; Scott and Scott, 1988
19	Herring	*Clupea harengus*	1 to 200	1 to 18	1 to 10	5 to 50	2 to 14	25.5 to 29	1	Svetovidov, 1952; Whitehead, 1985
20	Alewife	*Alosa pseudoharengus*	56 to 110	3 to 17	4 to 5				3	Whitehead, 1985; Scott and Scott, 1988
21	Sprat	*Sprattus sprattus*	10 to 150	15 to 20			7 to 10	35+	—	Svetovidov, 1952; Whitehead, 1985
22	Shorthorn sculpin	*Myoxocephalus scorpius*	to 110		11 to 2				3	Bigelow and Schroeder, 1953a; Fedorov, 1986; Scott and Scott, 1988
23	Mailed sculpin	*Troglops nybelini*	135 to 930		6 to 8				9	Scott and Scott, 1988
24	Ribbed sculpin	*Troglops pingelii*	5 to 745		9 to 11				9	Fedorov and Nelson, 1986; Pietsch, 1993
25	Hookear sculpin	*Artediellus atlanticus*	35 to 900	−1.7 to 4	5 to 11				—	Bigelow and Schroeder, 1953a; Fedorov, 1986; Scott and Scott, 1988
26	Staghorn sculpin	*Gymnocanthus tricuspis*	to 240	−1.8 to 5	11 to 2			32 to 35	3	Fedorov and Nelson, 1986; Robins and Ray, 1986; Scott and Scott, 1988

27	Grubby sculpin	*Myoxocephalus aeneus*	to 130	0 to 21	2 to 4				—	Robins and Ray, 1986; Scott and Scott, 1988
28	Moustache sculpin	*Triglops murrayi*	10 to 300	0 to 12	9 to 2				9	Fahay, 1983; Pietsch, 1993
29	Longhorn sculpin	*Myoxocephalus octodemspinosus*	50 to 100	0.5 to 19					—	Scott and Scott, 1988; Page and Burr, 1991
30	Arctic sculpin	*Cottunculus microps*	170 to 1 000	1 to 4	6 to 7			35 to 35.4	—	Fedorov and Nelson, 1986; Scott and Scott, 1988
31	Sea raven	*Hemitripterus americanus*	to 180		11 to 2				—	Bigelow and Schroeder, 1953a; Robins and Ray, 1986; Scott and Scott, 1988
32	Wrymouth	*Cryptacanthodes maculatus*	to 110		12 to 2				—	Scott and Scott, 1988
33	Lumpfish	*Cyclopterus lumpus*	50 to 400		3		4		9	Stein, 1986a; Scott and Scott, 1988
34	Scotian seasnail	*Careproctus ranula*	95 to 253						—	Coad, 1995
35	Leathernfin lumpsucker	*Eumicrotremus derjugini*	50 to 274	−2 to 0					9	Stein, 1986a; Scott and Scott, 1988
36	Spiny lumpsucker	*Eumicrotremus spinosus*	60 to 930	−1.8 to 3					—	Stein, 1986b; Scott and Scott, 1988
37	Seasnail	*Careproctus reinhardi*	150 to 1 200	2 to 4					—	Scott and Scott, 1988
38	4beard rockling	*Enchelyopus cimbrius*	20 to 650		6 to 9				3	Cohen *et al.*, 1990
39	Greenland cod	*Gadus ogac*	to 200		2 to 5				3	Cohen *et al.*, 1990
40	3beard rockling	*Gaidropsarus ensis*	450 to 1 450						—	Snelgrove and Haedrich, 1985
41	Haddock	*Melanogrammus aeglefinus*	80 to 300	4 to 8	1 to 7	80 to 150	6 to 7	35 to 35.2	3	Bigelow and Schroeder, 1953a; Ekman, 1953; Hodder, 1965; Leim and Scott, 1966; Scott and Scott, 1988; Cohen *et al.*, 1990; Sambilay, 1990
42	Silver hake	*Merluccius bilinearis*	55 to 914		6 to 9				3	Scott and Scott, 1988; Cohen *et al.*, 1990
43	Atlantic tomcod	*Microgadus tomcod*	to 10		11 to 2		2 to 9	1 to 30	3	Bigelow and Schroeder, 1953a; Scott and Scott, 1988; Cohen *et al.*, 1990
44	Blue whiting	*Micromesistius poutassou*	150 to 3 000		3 to 5				3	Miller, 1966; Scott and Scott, 1988; Cohen *et al.*, 1990
45	European ling	*Molva molva*	100 to 1 000		3 to 7	100 to 200	7+		9	Svetovidov, 1986; Cohen *et al.*, 1990
46	Pollock	*Pollachius virens*	to 200	3 to 10	11 to 2	100 to 200	7 to 8	35.2+	3	Ekman, 1953; Scott and Scott, 1988; Cohen *et al.*, 1990
47	Squirrel hake	*Urophycis chuss*	37 to 364		3 to 8				3	Bigelow and Schroeder, 1953a; Scott and Scott, 1988; Cohen *et al.*, 1990
48	Atlantic cod	*Gadus morhua*	10 to 500	−1 to 10	3 to 7	40 to 350	−0.5 to 6	33 to 35	3	Svetovidov, 1948; Rose and Leggett, 1988; Heessen and Daan, 1994; Rose, unpublished
49	Arctic cod	*Boreogadus saida*	100 to 700	−1 to 4	12 to 3	100 to 300	−1 to 2	34 to 35	3	Scott and Scott, 1988; Cohen *et al.*, 1990
51	Cusk	*Brosme brosme*	70 to 370	2 to 12	5 to 8	200 to 1 000	6 to 9	32 to 34	9	Damas, 1909; Scott and Scott, 1988
52	Longfinned hake	*Phycis chesteri*	90 to 1 400	3.5 to 6.5	10 to 3				–	Scott and Scott, 1988; Cohen *et al.*, 1990
53	Spotted hake	*Urophycis regia*	to 420	5 to 11	12 to 2				–	Scott and Scott, 1988; Cohen *et al.*, 1990
54	Mud hake	*Urophycis tenuis*	200 to 1 000	5 to 11	7 to 9				9	Scott and Scott, 1988; Cohen *et al.*, 1990
55	Blackspot stickleback	*Gasterosteus wheatlandi*			5 to 6				3	Scott and Scott, 1988
56	4spine stickleback	*Apeltes quadracus*		4 to 20	5 to 7				1	Scott and Scott, 1988; Robins *et al.*, 1991

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Table 1 (*continued*)

	Common name	Scientific name	D(m)	T(C)	Sp(mo)	SpD(m)	SpT(C)	SpS(ppt)	Dy	Reference
57	3spine stickleback	*Gasterosteus aculeatus*	1 to 100	4 to 20	4 to 9				—	Arnoult, 1986; Scott and Scott, 1988
58	9spine stickleback	*Pungitius pungitius*		10 to 20					3	Kottelat, 1997
59	Cunner	*Tautogolabrus adspersus*	to 10	5 to 6	6 to 8				3	Fahay, 1983; Robins and Ray, 1986; Scott and Scott, 1988
60	Northern seasnail	*Liparis liparis liparis*	1 to 300		1 to 4				3	Bigelow and Schroeder, 1953a; Stein and Able, 1986; Scott and Scott, 1988
61	Blacksnout seasnail	*Paraliparis copei*	200 to 1 000		4 to 8				9	Able *et al.*, 1986; Stein and Able, 1986; Scott and Scott, 1988
62	Atlantic seasnail	*Liparis atlanticus*	to 1 200	7 to 14.5	1 to 6				3	Snelgrove and Haedrich, 1985; Scott and Scott, 1988
63	Roughnose grenadier	*Trachyrhynchus murrayi*	400 to 2 000	2 to 5					14	Scott and Scott, 1988
64	Straptailed grenadier	*Chalinura occidentalis*	140 to 1 945						14	Cohen *et al.*, 1990
65	Longnose grenadier	*Coelorhynchus carminatus*	200 to 500						9	Cohen *et al.*, 1990
66	Rock grenadier	*Coryphaenoides rupestris*	400 to 1 000						9	Scott and Scott, 1988; Cohen *et al.*, 1990
67	Marlin spike	*Macrourus bairdii*	183 to 732		7 to 11				3	Bigelow and Schroeder, 1953a; Scott and Scott, 1988; Cohen *et al.*, 1990
68	Grenadier	*Macrourus holotrachys*	300 to 1 400						—	Cohen *et al.*, 1990
69	Rough head grenadier	*Macrourus berglax*	100 to 1 000	1 to 4	12 to 3				14	Scott and Scott, 1988; Cohen *et al.*, 1990
70	Glacier lanternfish	*Benthosema glaciale*	0 to 800	4 to 16	3 to 9				3	Bauchot, 1987; Scott and Scott, 1988
71	Lanternfish	*Ceratoscopelus maderensis*	51 to 700		3 to 9				3	Hulley, 1984
72	Headlight lanternfish	*Diaphus effulgens*	40 to 700						9	Hulley, 1984
73	Speckled lanternfish	*Lampadena speculigera*	60 to 950						9	Hulley, 1984
74	Coco lanternfish	*Gonichthys cocco*	400 to 1 000		3 to 6				3	Hulley, 1984
75	Jewel lanternfish	*Lampanyctus crocodilus*	150 to 1 000		3 to 8				14	Hulley, 1984
76	Metallic lanternfish	*Myctophum affine*	0 to 600						3	Hulley, 1984
77	Spotted lanternfish	*Myctophum punctatum*	125 to 750		2 to 4				3	Hulley, 1984; Scott and Scott, 1988
78	Lancet fish	*Notoscopellus castaneus*	to 1 000						9	Hulley, 1984
79	Pearly lanternfish	*Notoscopelus margaritifer*	to 1 000						3	Hulley, 1984
80	Rainbow smelt	*Osmerus mordax*	to 150	7.2 to 15.6	3 to 5				3	Scott and Crossman, 1973
81	NW Atlantic Capelin	*Mallotus villosus*	1 to 400	−1 to 2	6 to 7	0 to 20	3.5 to 10	14 to 33	3	Nakashima and Wheeler, 2002
82	NE Atlantic Capelin	*Mallotus villosus*	10 to 250	−1 to 2	3 to 4	10 to 100	1.5 to 6.5	32 to 34.6	3	Loeng *et al.*, 1983; Vilhjálmsson, 1994
83	Icelandic Capelin	*Mallotus villosus*	10 to 400	−1 to 2	3 to 4	10 to 150	2 to 7	35+	3	Vilhjálmsson, 1994
84	Greenland Capelin	*Mallotus villosus*	1 to 600	−1 to 2	4 to 7	0 to 10	1.9 to 8.5	15 to 33	3	Hansen, 1943; Friis-Rodel and Kanneworff, 2002
86	Duckhead barracudina	*Paralepis brevis*	50 to 2 000		3 to 6				9	Post, 1990; Ambrose, 1996
87	Ribbon barracudina	*Paralepis rissoi*	200 to 2 000						9	Post, 1990
88	Gunnel	*Pholis gunnellus*	46 to 100		10 to 4				3	Bigelow and Schroeder, 1953a; Makushok, 1986; Scott and Scott, 1988
89	Smooth flounder	*Liopsetta putnami*			2 to 4				—	Scott and Scott, 1988
90	Winter flounder	*Pseudopleuronectes americanus*	2 to 150	−2 to 15	3 to 6	10 to 50	−1 to 2	32 to 35	3	Scott and Scott, 1988; Murdy *et al.*, 1997

91	Greenland halibut	*Reinhardtius hippoglossoides*	300 to 2 000	0 to 4	2 to 4	500 to 2 000	0 to 4	34 to 35	9	Nielsen, 1986; Scott and Scott, 1988
92	American plaice	*Hippoglossoides platessoides*	70 to 300	−0.5 to 2.5	4 to 6	50 to 250	−0.5 to 2.5	34 to 35	3	Scott and Scott, 1988; Bowering and Brodie, 1991; Cooper and Chapleau, 1998
93	Witch flounder	*Glyptocephalus cynoglossus*	45 to 1 460	2 to 6	3 to 8				9	Bigelow and Schroeder, 1953a; Fedorov and Nelson, 1986; Scott and Scott, 1988
94	Atlantic halibut	*Hippoglossus hippoglossus*	50 to 2 000	2.5+	2 to 4	>180	4.5 to 7	33.8 to 35.0	14	Nielsen, 1986; Scott and Scott, 1988
95	Yellowtail flounder	*Limanda ferruginea*	30 to 100	3 to 5	5 to 7				1	Bigelow and Schroeder, 1953b; Scott and Scott, 1988; Bowering and Brodie, 1991; Scarratt, 1996; Cooper and Chapleau, 1998
96	Jensen's skate	*Raja jenseni*	366 to 2 196						9	McEachran and Dunn, 1998
97	Soft skate	*Raja mollis*	450 to 1 568						–	Stehmann, 1990
98	Smooth skate	*Raja senta*	46 to 914					32.6 to 35.4	9	Bigelow and Schroeder, 1953b; Pietsch, 1993
99	Spinytailed skate	*Raja spinicauda*	140 to 800	−1.5 to 3.3	6 to 7				9	Krefft, 1956; Scott and Scott, 1988; McEachran and Dunn, 1998
100	Barndoor skate	*Raja laevis*	to 430	0 to 20	12 to 3				9	Scott and Scott, 1988; McEachran and Dunn, 1998
101	Round skate	*Raja fyllae*	170 to 2 050	1 to 7					–	McEachran and Dunn, 1998
102	Eyed skate	*Raja ocellata*	to 100	1 to 10	1 to 12				–	Scott and Scott, 1988
103	Thorny skate	*Raja radiata*	18 to 996	−1.4 to 14					9	Scott and Scott, 1988
104	Little skate	*Raja erinacea*	to 90	1.2 to 21	1 to 12				9	Scott and Scott, 1988
105	Brook charr	*Salvelinus fontinalis*	1 to 27	0 to 26	10 to 11	0.1 to 1	4 to 20	20 to 25	3	Scott and Crossman, 1973; Page and Burr, 1991
106	Atlantic salmon	*Salmo salar*	1 to 10	4 to 10	10 to 11				3	Scott and Scott, 1988; Page and Burr, 1991; Reddin and Friedland, 1993
107	Arctic charr	*Salvelinus alpinus*	1 to 30	4 to 16	9 to 12	1 to 4.5	4		9	Svetovidov, 1984; Scott and Scott, 1988
108	Atlantic saury	*Scomberesox saurus*	to 30	8.2 to 24	12 to 3		16.8 to 23.7		3	Scott and Scott, 1988; Wisher, 1990
109	Bluefin tuna	*Thunnus thynnus*	1 to 200	2.8 to 29	5 to 6	1 to 50	25 to 29	34 to 36	9	Scott and Scott, 1988; Gunn and Block, 2001
110	Atlantic mackerel	*Scomber scombrus*	1 to 200	9 to 12	3 to 7	10 to 200	10 to 11	34 to 36	3	Collette and Nauen, 1983; Lockwood, 1988; Scott and Scott, 1988
111	Frigate mackerel	*Auxis thazard*	to 50	20 to 27					1	Collette and Aadland, 1996
112	Deepwater redfish	*Sebastes mentella*	300 to 1 000		3 to 7				14	Hureau and Litvinenko, 1986; Scott and Scott, 1988; St-Pierre and de Lafontaine, 1995
113	Acadian redfish	*Sebastes fasciatus*	70 to 500	−1 to 10					9	Robins and Ray, 1986; Scott and Scott, 1988
114	Rosefish	*Sebastes marinus*	100 to 1 000	3 to 7	4 to 5	50 to 700	3 to 7	33 to 35	9	Hureau and Litvinenko, 1986; Scott and Scott, 1988
115	Arctic shanny	*Stichaeus punctatus*	1 to 100		2 to 3				3	Eschmeyer *et al.*, 1983; Scott and Scott, 1988

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Table 1 (*continued*)

	Common name	Scientific name	D(m)	T(C)	Sp(mo)	SpD(m)	SpT(C)	SpS(ppt)	Dy	Reference
116	Radiated shanny	*Ulvaria subbifurcata*			3 to 8				3	Scott and Scott, 1988
117	Blenny	*Chirolophis ascanii*	20 to 280						14	Makushok, 1986
118	Greenland blenny	*Lumpenus fabricii*	to 175	−1.6 to 13	7				14	Allen and Smith, 1988; Scott and Scott, 1988
119	Snakeblenny	*Lumpenus lampretaeformis*	50 to 200		9 to 11				3	Scott and Scott, 1988; Muus and Nielsen, 1999
120	Daubed shanny	*Leptoclinus maculatus*	15 to 400	−1.4 to 0.5	12 to 2				9	Eschmeyer *et al.*, 1983; Scott and Scott, 1988
121	Fourlined snakeblenny	*Eumesogrammus praecisus*	5 to 240						9	Robins and Ray, 1986
122	Sars eelpout	*Lycenchelys sarsii*	150 to 600						9	Anderson, 1994
123	Jimmy Durante eelpout	*Lycenchelys verrillii*	46 to 1 100						14	Scott and Scott, 1988
124	Atlantic eelpout	*Lycodes atlanticus*	630 to 1 920						14	Anderson, 1994
125	Polar eelpout	*Lycodes turneri*	20 to 125						14	Anderson, 1994
126	Polar eelpout	*Lycodes polaris*	to 300		9 to 11				14	Scott and Scott, 1988
127	Fish doctor	*Gymnelis viridis*	2 to 320	−1.9 to 4	6 to 9				9	Scott and Scott, 1988; Anderson, 1994
128	Frigid eelpout	*Lycodes frigidus*	475 to 2 438	−2 to −1		1 000 to 2 500	−2 to −1	35 to 35.5	14	Muus *et al.*, 1990
129	Newfoundland eelpout	*Lycodes lavalaei*	57 to 535	−1.2 to 2.52	6 to 9				14	Scott and Scott, 1988
130	Reticulated eelpout	*Lycodes reticulatus*	100 to 380	−1 to 4					14	Anderson, 1994
131	Esmark's eelpout	*Lycodes esmarki*	250 to 800	−0.4 to 5					14	Snelgrove and Haedrich, 1985; Andriashev, 1986b
132	Ocean pout	*Macrozoarces americanus*	0 to 180	0 to 16.7	8				9	Scott and Scott, 1988; Anderson, 1994
133	Vahl's eelpout	*Lycodes vahlii*	100 to 600	1 to 4.5					14	Scott and Scott, 1988
134	Atlantic soft pout	*Melanostigma gelatinosum*	276 to 366	3 to 5.18	7 to 9			33.4 to 34.7	14	Scott and Scott, 1988
135	Piked dogfish	*Squalus acanthias*	0 to 1 460	7 to 15					–	Compagno, 1984
136	Sea lamprey	*Petromyzon marinus*	1 to 650	5 to 20	3 to 8		15		9	Hardisty and Potter, 1971; Hardisty, 1986
137	Agassiz' slickhead	*Alepocephalus agassizii*	600 to 2 500						9	Markle and Sazanov, 1990
138	Baird's smoothhead	*Alepocephalus bairdii*	365 to 1 700						9	Markle and Quéro, 1984
139	Arctic skate	*Raja hyperborea*	300 to 2 500				0		9	Bigelow and Schroeder, 1953a; McEachran and Dunn, 1998
140	Stout eelblenny	*Lumpenus medius*	10 to 300	below 0					3	Eschmeyer *et al.*, 1983; Fahay, 1983
141	Blue hake	*Antimora rostrata*	350 to 3 000						3	Cohen *et al.*, 1990
142	Greater argentine	*Argentina silus*	140 to 1 440	7 to 10	4 to 7				9	Makushok, 1986
143	Arctic hookear sculpin	*Artedielus uncinatus*	13 to 350		6 to 8				3	Cohen, 1984
144	Simony's frostfish	*Benthodesmus simonyu*	200 to 900						9	Van Guelpen, 1986
145	Black dogfish	*Centroscyllium fabricii*	180 to 1 660	1 to 4.5					9	Compagno, 1984

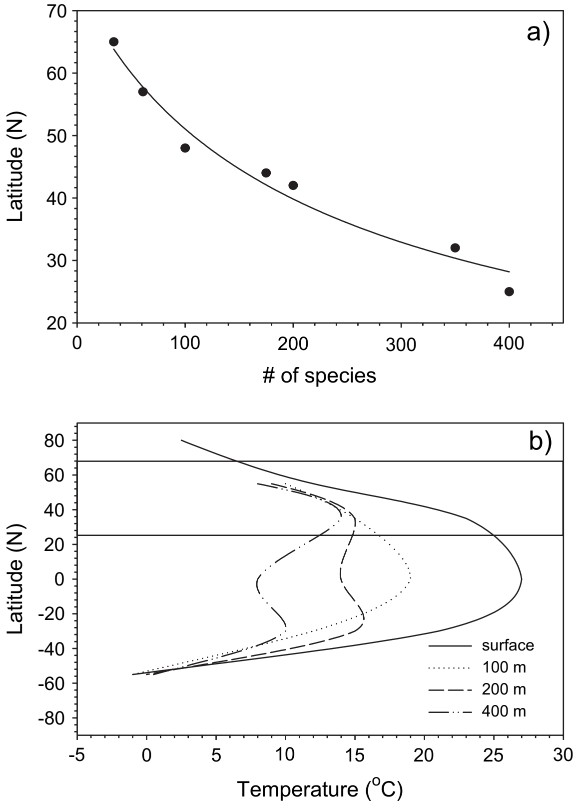

Figure 1. (a) Number of species with latitude in the North Atlantic. Data from Briggs (1974), Moyle and Cech (2004). (b) Temperatures in mid-Atlantic over latitude, inner box shows range of latitudes of data in (a). Data from Ekman (1953).

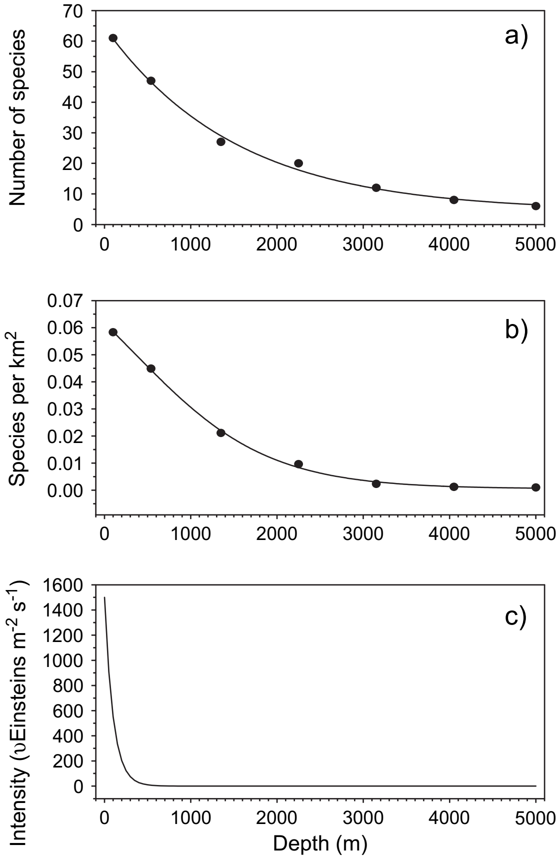

Figure 2. Mean number (a) and density (b) of species with depth in the North Atlantic. Data from Challenger Cruise, 1860 (summarized by Norman and Greenwood, 1963), and present data investigation. Areas for density from Emery and Uchupi (1984). Lines fitted are exponential declines. Also, light intensity (c) with depth according to Beer's Law with surface intensity of 1500 μEinsteins m^{-2} s^{-1}, and attenuation coefficient of 0.01.

The number of species declined exponentially with depth, from approximately 60 in shallow shelf waters to very few in waters >2000 m deep (Figure 2a). The same trend is evident in both the present literature-based survey and in original data from the Challenger cruise from 1872 to 1876. A similar trend is evident in species density, which takes into account the total areas of the depth zones (Figure 2b). Increasing depth is also associated with declines in light (Figure 2c). However, species number and density declined with depth at a much slower rate than did light intensity.

Minimum and maximum temperatures were available for 90 species. These ranged from near −2 to 25°C (Table 1). However, the majority of species had minimum or maximum temperatures between 3 and 4°C, and the ogives were steepest in this region (Figure 3a). Spawning temperatures were somewhat higher (Figure 3b). The temperature range that included the most feeding species was approximately 0−4°C (Figure 3c). For spawning, the temperature range of 2−7°C included the most species. The salinity range that included the most spawning species was approximately 32.5−33.5 (Figure 4).

In all, 43 species had data available on depth and temperature range and time of feeding (approximated as the non-spawning time in months) (Table 1). Principal components of these factors indicated that the species fell into four overlapping groups (Figure 5). The first principal component was loaded most heavily by depth, the second by temperature, and the third by feeding time (Table 2a). The four groups can be characterized as cold-water pelagic species, warm-water pelagics, cool-water shallow-depth demersals, and deeper water demersal species.

Principal components of spawning characteristics (spawning temperatures, depths, salinities, and timing) were estimated for 17 species (with four capelin stocks) for which data were available (Figure 6). The first component was most heavily loaded by salinity, with species requiring fresher water separating from others (Table 2b). The second component was loaded most heavily by depth, and the third by temperature. A group of low salinity shallow-water spawners composed of capelin and herring was clearly isolated from other groups. A more diffuse group of

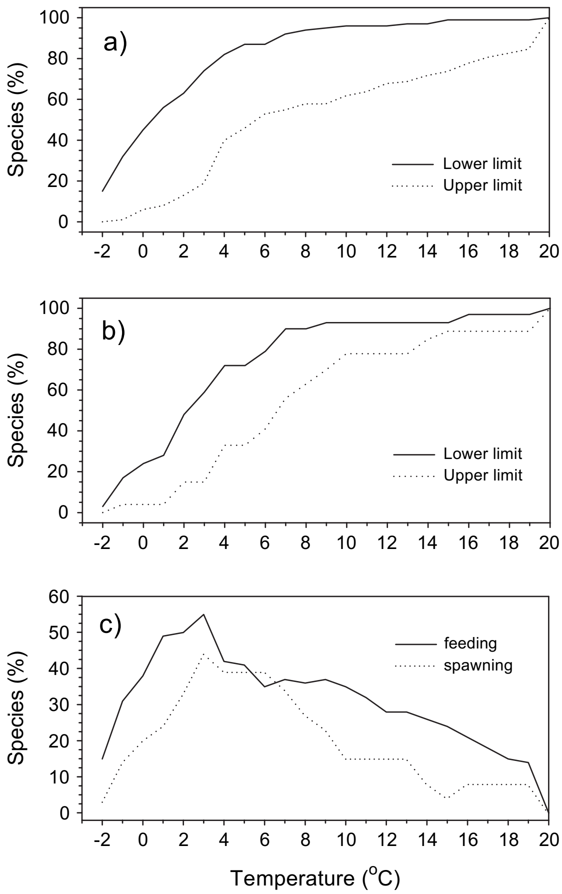

Figure 3. The upper and lower limits of temperatures for species distributions (a) and spawning (b) in the North Atlantic, expressed as a cumulative percentage, and the percentage of species not limited by temperature over the range of temperatures (c).

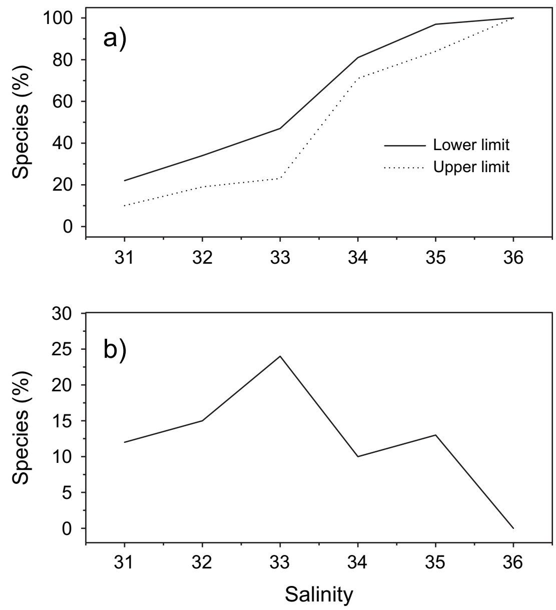

Figure 4. The upper and lower limits of salinities for species spawning (a) in the North Atlantic, expressed as a cumulative percentage, and the percentage of species whose spawning is not limited by salinity over the range of salinities (b).

groundfish and some warmer-water pelagics included the most species. Northeast Atlantic and Icelandic capelin were grouped with the groundfish, although at the fringes of the group, and not with herring (*Clupea harengus*) and Northwest Atlantic and Greenland capelin. Greenland halibut (*Reinhardtius hippoglossoides*) was widely separated from the main groupings largely because of their deepwater habitat.

The principal components of feeding habitat and spawning requirements were related to species resilience (Table 3). Resilience was indexed by the estimated doubling time of the population (Table 1). The first component, which was heavily loaded by depth distribution, indicates that pelagic species have faster doubling times and are likely to react quickly to changes in the environment when feeding. The spawning distribution model was more complex, with the first component of distribution (loaded heavily by salinity), unimportant, but the second and third components loaded by depth and temperature, respectively, highly significant. This confirms that pelagic species are more likely to respond substantially to changes in the environment, evidently because of their shallow-water spawning habits, and can do so more quickly because of faster doubling times.

The 1920–1940 warming event

From approximately 1920 to 1940, North Atlantic Waters from Greenland to Norway warmed significantly, by as much as 3–4°C (Tåning, 1948). Although the causes of this event are not well understood, there is no doubt of its authenticity or widespread occurrence in temperature records (Figure 7).

The predictions of the principal components analyses were generally supported by changes in fish distribution documented during the warming event. Species expected to react quickly, such as capelin, and to a lesser extent Atlantic herring and cod (*Gadus morhua*), expanded their ranges northwards. Some southern migrants became more numerous, and other resident species increased their densities, although evidence of distribution change is lacking. Species expected not to change distribution, such as Greenland halibut, did not, but may have increased in density in some areas. Tåning (1948) summarized earlier accounts and identified several types of changes: (i) species typically found farther south were more frequently observed in Greenland waters (e.g. tuna; Atlantic skipper or saury, *Scomberesox saury*; mackerel; and others), (ii) local species extended their distributions northwards

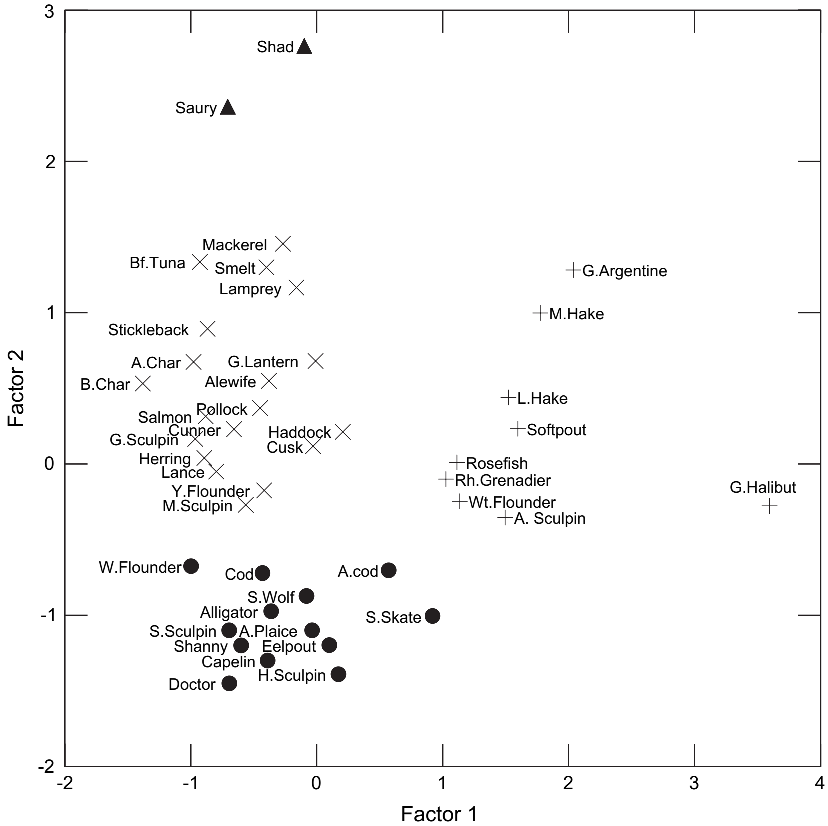

Figure 5. Principal components 1 and 2 for feeding distributions of North Atlantic fish. Component weightings are given in Table 2a. Groupings done visually.

Table 2. Rotated component matrices for analyses of general features of location (a) and spawning (b) for North Atlantic species. Principal components with a varimax rotation of the Kaiser type were used (SPSS Inc software). Feeding and spawning starts and ends are months. The rotations converged in five iterations.

Variable	Component 1	Component 2	Component 3
(a)			
Minimum depth	0.9	−0.004	0.002
Maximum depth	0.893	−0.119	0.004
Low temperature	0.008	0.919	0.007
High temperature	−0.417	0.744	0.13
Feeding start	−0.106	−0.005	−0.826
Feeding end	−0.006	0.108	0.816
(b)			
Minimum depth	0.155	0.954	−0.118
Maximum depth	0.132	0.97	−0.125
Low temperature	0.19	−0.101	0.959
High temperature	−0.264	−0.18	0.93
Low salinity	0.759	0.271	0.002
High salinity	0.917	0.007	−0.007
Spawning start	−0.162	−0.005	−0.008
Spawning end	−0.758	0.002	0.147

(e.g. Atlantic cod, capelin, and herring), (iii) local species increased in density (many commercial species including Atlantic cod and herring; salmon, *Salmo salar*; haddock, *Melanogrammus aeglefinus*), (iv) spawning grounds changed (e.g. capelin; herring; redfish, *Sebastes* spp.), (v) local species decreased in density where waters became too warm, but increased in colder areas (e.g. capelin, Greenland halibut). Similar events occurred in Icelandic waters at the same time (Sæmundsson, 1932; Fridriksson, 1948).

From the present analyses, species in the top left of Figure 5 are warm-water species that would be expected to be new arrivals to Greenland and Iceland waters in a warm period. These include Atlantic saury, mackerel, and tuna, as observed (Tåning, 1948). Local species that would be expected to shift north are found in the lower left of Figure 5, and include Atlantic cod, capelin, and several other species not mentioned by Tåning (1948). Changes in spawning grounds are expected from species in the lower left of Figure 6, which includes herring, capelin, and perhaps cod but not redfish (*Sebastes* spp.), which is consistent with the observations reported by Tåning (1948).

This warming event, which so influenced Greenland and Iceland as well as Norwegian waters and the Barents Sea,

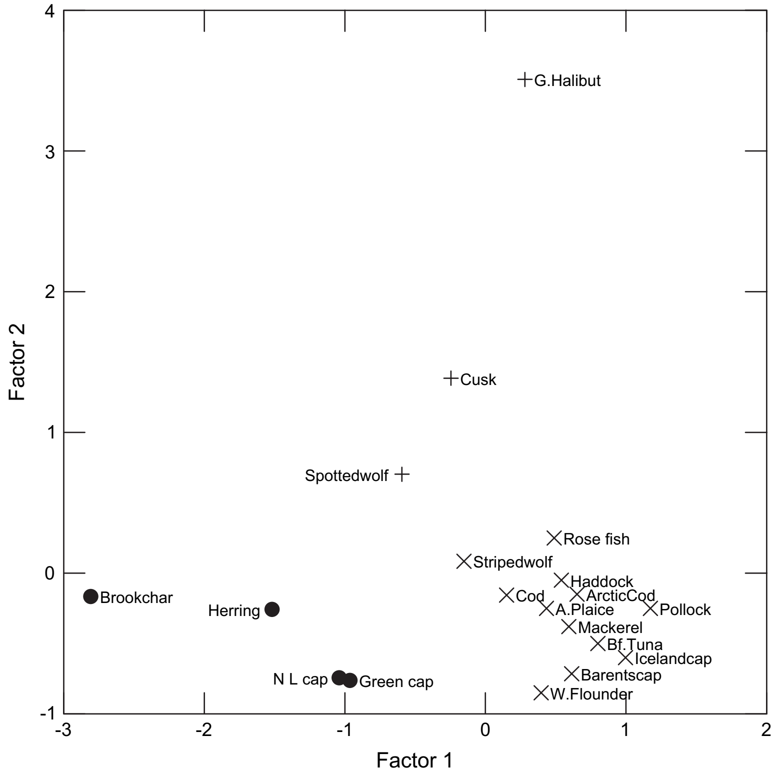

Figure 6. Principal components 1 and 2 for spawning distributions of North Atlantic fish. Component weightings are given in Table 2b. Groupings done visually.

Table 3. Summary of statistics of models relating principal components of the feeding (a) and spawning (b) distribution data to doubling time of the species (from Table 1).

Source	Type III SS	d.f.	Mean square	F	p
(a) Feeding distribution*					
Corrected model	163.472	3	54.5	4.9	0.006
Intercept	1 365.4	1	1 365.4	123.8	0.000
FAC1	157.0	1	157.0	14.2	0.001
FAC2	2.8	1	2.8	0.3	0.620
FAC3	5.7	1	5.7	0.5	0.477
Error	397.0	36	11.0		
Total	1 902.5	40			
Corrected total	560.4	39			
(b) Spawning distribution†					
Corrected Model	92.3	3	30.8	9.1	0.001
Intercept	378.3	1	378.5	112.2	0.000
SPFAC1	0.9	1	0.9	0.3	0.610
SPFAC2	70.2	1	70.2	20.8	0.000
SPFAC3	21.1	1	21.1	6.3	0.024
Error	54.0	16	3.4		
Total	524.7	20			
Corrected total	146.3	19			

*$r^2 = 0.631$ (Adjusted $r^2 = 0.562$).
†$r^2 = 0.292$ (Adjusted $r^2 = 0.233$).

did not extend to the Northwest Atlantic (Figure 7a). Temperatures declined during the 1920s at St. John's, in direct contrast to temperatures at Norway, Iceland, and Greenland, although there were increases during the 1930s. No great changes in species in Newfoundland and Labrador waters were noted in an extensive work on capelin published by Templeman (1948), although the same author does recall some changes in the Grand Bank haddock stock during the 1920s in a much later publication (Templeman, 1966).

Discussion

The present analyses indicate that both spawning and feeding distributions of North Atlantic fish are influenced by environmental factors partially regulated by climate variability, and likely, by climate change. Not all species may be impacted equally. Species whose spawning is limited to the cold waters of the Arctic or boreal regions (lower left in principal components plot, Figure 5) are expected to be most affected, and to respond relatively quickly to environmental change. Among these species are the small pelagic boreal-Subarctic species, in particular capelin. Cold-water species such as winter flounder, several species of sculpin, the eelpouts, Arctic cod, daubled

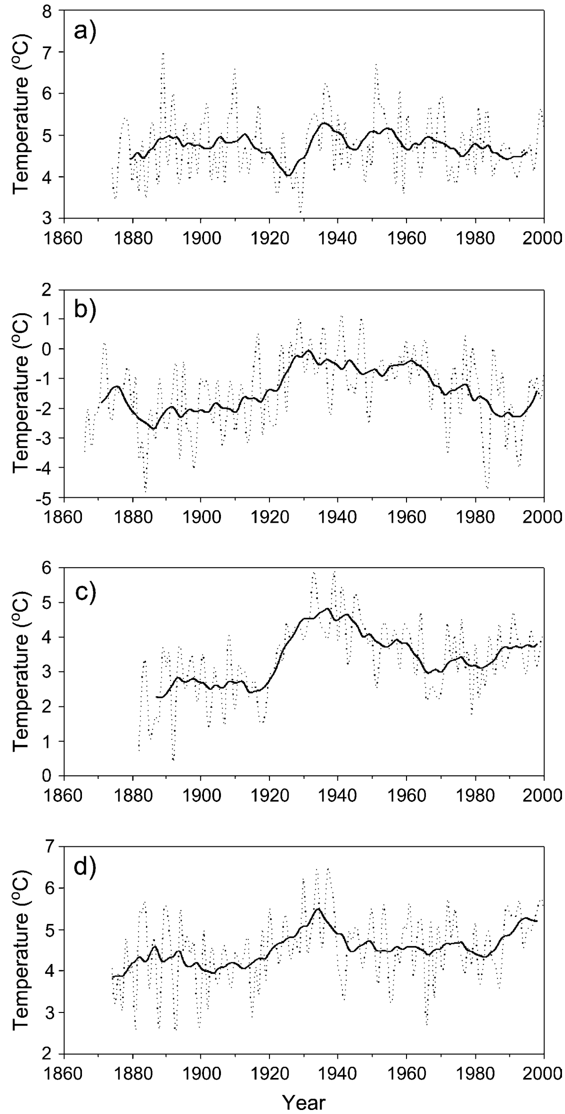

Figure 7. Surface air temperatures for (a) St. John's, Newfoundland; (b) Nuuk, Greenland; (c) Akureyi, Iceland; and (d) Bodo, Norway. Solid line is a decadal moving average. Data from NASA database at Goddard Space Center, New York.

shanny, and the alligators may be the most vulnerable. The gadoids and several flatfish and other more boreal species are mid-range in vulnerability and could benefit from warmer conditions, subject to any effects on their prey. Species that utilize the North Atlantic only for feeding (e.g. tunas and mackerel) but spawn further south, even in subtropical waters, may be influenced primarily through migration patterns that are based on temperatures and feeding opportunities. Deepwater species such as Greenland halibut, whose requirements are based on more stable hydrographic conditions in those habitats, may be least impacted (to right of plot, Figure 5), although prey changes (e.g. capelin) may modify their response. An examination of survey data from the northeast coast of the US led to similar conclusions (Murawski, 1993).

The strongest predictors of species richness are latitude and depth. In general, the warmer tropical waters sustain a higher number of species than do the colder waters farther north. If climate change results in a warming of northern waters, it is expected that more species will invade northern waters. There may be concurrent contraction of the range of a fewer number of cold-water species. More worrisome would be the climate scenario that indicates a cooling of northern oceans with a slowing of the North Atlantic heat pump (Häkkinen and Rhines, 2004). This scenario would result in a decline in species number in northern seas and an increase in range of only a few species, such as the cold-adapted eelpouts, sculpins, Arctic cod, and winter flounder. In addition, most climate models predict an increase in sea levels with a warming trend. Such changes might result in some increase in habitat for shallow-water coastal spawners such as herring and capelin. A cooling would have the opposite effect, as during the last ice age, when capelin retreated southwards (Carscadden *et al.*, 1989).

The groupings of species in the present analyses are, by and large, consistent with observed historical responses of species during 1920–1940 from Greenland to Norway for most, but not all, species. A highlight is the expectation and verification by observation that capelin will be among the most likely to respond to climate in terms of changes in distribution and spawning location. Warming will result in capelin shifts to the north as Arctic fronts relax or bend towards the pole (Tåning, 1948). Cooling would have the opposite effect, as during the last ice age, when capelin retreated southwards (Carscadden *et al.*, 1989). During the same years, the temperatures in the Northwest Atlantic did not increase, and there is little evidence of changes in the fisheries. A summary of the known excursions and shifts of capelin with respect to climate changes and variations is given by Rose (2005).

Conclusions

(i) Latitude and depth provide good predictors of species richness in the temperate to Subarctic North Atlantic. Latitude is a proxy for temperature.
(ii) North Atlantic fish feed and spawn over a wide range of temperatures from −2 to 20°C, but most species are within their limits for feeding at 0–4°C, and for spawning at 2–7°C.
(iii) Groups of species may be expected to react differently to climate change, with species that spawn in shallow, relatively low salinity waters most affected (e.g. capelin), and species that inhabit deeper, hydrographically more stable waters less so. Seasonal migrants that feed in the North Atlantic,

but spawn further south (e.g. bluefin tuna), may undergo migration shifts. Note that changes in key forage fish, such as capelin and herring, are likely to have major influences on ecosystem structure and productivity of species that feed on them.

(iv) Climate variability and change may not be uniform over the North Atlantic. History shows that differences are likely. Not all areas should be expected to warm or cool equally, and species responses must be judged accordingly.

Acknowledgements

I am indebted to the fishery researchers who have collected data on the fish of the North Atlantic for over 150 years. Nevertheless, Table 1 is still far from complete and, for many species, poorly known or contested. Additions or improvements to this fundamental knowledge are welcome. Funding was provided by the NSERC Chair in Fisheries Conservation at Memorial University and my NSERC discovery grant. I thank S. B. Fudge for help with the data compilation and two anonymous reviewers for helpful comments.

References

Able, K. W., Fahay, M. P., and Markle, D. F. 1986. Development of larval snailfishes (Pisces: Cyclopteridae: Liparidinae) from the western North Atlantic. Canadian Journal of Zoology, 64: 2294−2316.

Ahlmann, H. W. 1948. Introductory address to enquiry into the problem of climatic and ecological changes in northern waters. Rapport et Procès-Verbaux de la Conseil Permanent International pour l'Exploration de la Mer, 125: 9−16.

Allen, M. J., and Smith, G. B. 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. NOAA Technical Report, 66. 151 pp.

Ambrose, D. A. 1996. Paralepididae. *In* The Early Stages of Fish in the California Current Region, pp. 352−355. Ed. by H. G. Moser. California COFI Atlas No. 33.

Anderson, M. E. 1994. Systematics and osteology of the Zoarcidae (Teleostei: Perciformes). Ichthyology Bulletin of the J. L. B. Smith Institute of Ichthyology, 60: 120 pp.

Andriashev, A. P. 1986a. Agonidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 3, pp. 1265−1268. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Andriashev, A. P. 1986b. Zoarcidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 3, pp. 1130−1150. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Arnoult, J. 1986. Gasterosteidae. *In* Check-list of the Freshwater Fishes of Africa, p. 280. Ed. by J. Daget, J-P. Gosse, and D. F. E. Thysvan den Audenaerde. ORSTOM, Paris.

Barsukov, V. V. 1959. The Wolfish (Anarhichadidae). Zoologicheskii Institut Akademii Nauk SSSR Novaya Seriya No. 73, Fauna SSSR, vol. 5 (5) (in Russian). English translation for Smithsonian Institution and the National Science Foundation, Washington, D.C. by the Indian National Scientific Documentation Centre, New Delhi. U.S. Department of Commerce, Springfield, VA, USA (1972). 292 pp.

Barsukov, V. V. 1996. Anarhichadidae. *In* Fishes of the North-Eastern Atlantic and Mediterranean, vol. 3, pp. 1113−1116. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Bauchot, M-L. 1987. Poisson osseux. *In* Fiches FAO d'indentification pour les besions de la pêche (rev. 1) Méditerranée et mer Noire. Zone de pêche 37, pp. 891−1421. Ed. by W. Fischer, M-L. Bauchot, and M. Schneider. Commissions des communautés Européennes et FAO, Rome.

Bigelow, H. B., and Schroeder, W. C. 1953a. Fishes of the Gulf of Maine. Fishery Bulletin of the US Fish and Wildlife Service, 53: 577 pp.

Bigelow, H. B., and Schroeder, W. C. 1953b. Sawfishes, guitarfishes, skates and rays. Fishes of the Western North Atlantic. Part 2. Sears Foundation for Marine Research, New Haven Connecticut, USA. Memoir No. 1, 264 pp.

Bowering, W. R., and Brodie, W. B. 1991. Distribution of commercial flatfishes in the Newfoundland−Labrador region of the Canadian Northwest Atlantic and changes in certain biological parameters since exploitation. Netherlands Journal of Sea Research, 27: 407−422.

Briggs, J. C. 1974. Marine Zoogeography. McGraw−Hill, New York, USA. 475 pp.

Carscadden, J. E., Frank, K. T., and Miller, D. S. 1989. Capelin (*Mallotus villosus*) spawning on the southeast shoal: influence of physical factors past and present. Canadian Journal of Fisheries and Aquatic Sciences, 46: 1743−1754.

Coad, B. W. 1995. Encyclopedia of Canadian Fishes. Canadian Museum of Nature and Canadian Sportfishing Productions Inc., Singapore. 642 pp.

Cohen, D. M. 1984. Argentinidae (including Microstomatidae). *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 1, pp. 387−388. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Cohen, P. M., Inada, I., Iwamoto, T., and Scialabba, N. 1990. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers, and other gadiform known to date. FAO Fisheries Synopsis No. 125, 10: 442 pp.

Collette, B. B., and Aadland, C. R. 1996. Revision of the frigate tunas (Scombridae, *Auxis*), with descriptions of two new subspecies from the Eastern Pacific. Fisheries Bulletin US, 94: 423.

Collette, B. B., and Nauen, C. E. 1983. Scombrids of the world. An annotated and illustrated catalogue of tuna, mackerels, bonitos and related species known to date. FAO Fisheries Synopsis No. 125, 2: 137 pp.

Compagno, L. J. V. 1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis No. 125, 4: 249 pp.

Cooper, J. A., and Chapleau, F. 1998. Monophyly and intrarelationships of the family Pleuronectidae (*Pleuronectiformes*), with a revised classification. Fisheries Bulletin US, 96: 686−726.

Cushing, D. H. 1982. Climate and Fisheries. Academic Press, London. 373 pp.

Damas, D. 1909. Contribution à la biologie des Gadides. Rapport et Procès-Verbaux de la Conseil Permanent International pour l'Exploration de la Mer, 10(App 2):277 pp.

Drinkwater, K. 2002. A review of the role of climate variability in the decline of Northern cod. American Fisheries Society, Symposium 32: 113−130.

Ekman, S. 1953. Zoogeography of the Sea. Sidgwick and Jackson Limited, London. 417 pp.

Emery, K. O., and Uchupi, E. 1984. The Geology of the Atlantic Ocean. Springer-Verlag, New York. 1050 pp.

Eschmeyer, W., Herald, E., Hammann, H., and Peterson, R. T. 1983. A Field Guide to Pacific Fishes of North America. Houghton Mifflin Company, Boston, USA. 336 pp.

Fahay, M. P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. Journal of Northwest Atlantic Fishery Science, 4: 423.

Fedorov, V. V. 1986. Cottidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 3, pp. 1254−1255. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Fedorov, V. V., and Nelson, J. S. 1986. Psychrolutidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 3, pp. 1262−1263. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Fridriksson, A. 1948. Boreo-tended changes in the marine vertebrate fauna of Iceland during the last 25 years. Rapport et Procès-Verbaux de la Conseil Permanent International pour l'Exploration de la Mer, 125: 30−32.

Friis-Rodel, E., and Kanneworff, P. 2002. A review of capelin (*Mallotus villosus*) in Greenland waters. ICES Journal of Marine Science, 59: 890−896.

Godø, O. R. 2003. Fluctuation in stock properties of north-east Arctic cod related to long-term environmental changes. Fish and Fisheries, 4: 121−137.

Gunn, J., and Block, B. A. 2001. Advances in acoustic, archival and satellite telemetry. *In* Tuna: Physiology, Ecology and Evolution, pp. 167−224. Ed. by B. A. Block, and E. D. Stevens. Academic Press, London.

Häkkinen, S., and Rhines, P. B. 2004. Decline of subpolar North Atlantic circulation during the 1990s. Science, 304: 555−559.

Hansen, P. M. 1943. Capelin (*Mallotus villosus*), Greenland. Annals of Biology, 1: 121−124.

Hardisty, M. W. 1986. *Petromyzon marinus* (Linnaeus 1758). *In* The Freshwater Fishes of Europe, vol. 1, Part 1, pp. 94−116. Ed. by J. Holick. AULA-Verlag, Wiesbaden.

Hardisty, M. W., and Potter, I. C. 1971. The general biology of adult lampreys. *In* The Biology of Lampreys, pp. 127−206. Ed. by M. W. Hardisty, and I. C. Potter. Academic Press, London.

Heessen, H. J. L., and Daan, N. 1994. Cod distribution and temperature in the North Sea. ICES Marine Science Symposia, 198: 244−253.

Hodder, V. M. 1965. The possible effects of temperature on the fecundity of Grand Bank Haddock. International Convention for the Northwest Atlantic Fisheries, Special Publication, 6: 522−524.

Hulley, P. A. 1984. Myctophidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 1, pp. 429−483. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Hureau, J-C., and Litvinenko, N. I. 1986. Scorpaenidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 3, pp. 1211−1229. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Jones, P. W., Martin, F. D., and Hardy, Jr J. D. 1978. Development of Fishes of the Mid-Atlantic Bight. An Atlas of Eggs, Larval And Juvenile Stages. vol. 1, Acipenseridae Through Ictaluridae U.S. Fish and Wildlife Service. Biological Service Program FWS/OBS-78/12.

Kottelat, M. 1997. European freshwater fishes. Biologia, 52: 1−271.

Krefft, G. 1956. Ein Beitrag zur Kenntnis des Grolandrochens, *Raja spinicauda*, Jensen 1914. Archiv fur Fischereiwissenschaft, 7: 139−145 (in German).

Leim, A. H., and Scott, W. B. 1966. Fishes of the Atlantic coast of Canada. Bulletin of the Fisheries Research Board of Canada, 155: 485 pp.

Lockwood, S. J. 1988. The Mackerel: its Biology, Assessment and the Management of a Fishery. Fishing News Books, Farnham, Surrey, UK. 181 pp.

Loeng, H., Nakken, O., and Raknes, A. 1983. The distribution of capelin in the Barents Sea in relation to water temperature in the period 1974−1982. Fisken og Havet, 1983: 1−17 (in Norwegian).

Lysgaard, L. 1948. Recent climatic fluctuations. Rapport et Procès-Verbaux de la Conseil Permanent International pour l'Exploration de la Mer, 125: 17−20.

Makushok, V. M. 1986. Pholidae and Lumpenidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 3, pp. 1124−1127. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Markle, D. F. 1986. Alepocephalidae. *In* Smith's Sea Fishes, pp. 218−223. Ed. by M. M. Smith, and P. C. Heenstra. Springer-Verlag, Berlin.

Markle, D. F., and Quéro, J-C. 1984. Alepocephalidae (including Bathylaconidae, Bathyprionidae). *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 1, pp. 228−253. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Markle, D. F., and Sazanov, Y. I. 1990. Alepocephalididae. *In* Check-list of the Fishes in the Eastern Tropical Atlantic, pp. 218−223. Ed. by J-C. Quéro, J-C. Hureau, C. Karrer, A. Post, and L. Saldanha. UNESCO, Paris.

McEachran, J. D., and Dunn, K. A. 1998. Phylogenetic analysis of skates, a morphologically conservative clade of elasmobranchs (Chrondricthyes, Rajidae). Copeia, 24: 271−290.

McGinn, N. A. (Ed). 2002. Fisheries in a Changing Climate. American Fisheries Society Symposium 32, Bethesda, Maryland. 295 pp.

Miller, D. 1966. The blue whiting, *Micromesistius poutassou*, in the western Atlantic, with notes on its biology. Copeia, 2: 301−305.

Moyle, P. B., and Cech, J. J. 2004. Fishes: an Introduction to Ichthyology. Pearson Prentice Hall, Upper Saddle River, NJ. 726 pp.

Murawski, S. A. 1993. Climate change and marine fish distributions: forecasting from historical analogy. Transactions of the American Fisheries Society, 122: 647−658.

Murdy, E. O., Birdsong, R. S., and Musick, J. A. 1997. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington, DC. 528 pp.

Muus, B. J., and Nielsen, J. G. 1999. Sea Fish. Scandinavian Fishing Year Book. Hedehusen, Denmark, 340 pp.

Muus, B. J., Salomonsen, F., and Vibe, C. 1990. Gronlands fauna (Fisk, Fugle, Pattedyr). Nordisk Forlag A/S, kobenhavn. 426 pp. (in Danish).

Nakashima, B. S., and Wheeler, J. P. 2002. Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters − the interaction between beach and demersal spawning. ICES Journal of Marine Science, 59: 909−916.

Nielsen, J. G. 1986. Pleuronectidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 3, pp. 1299−1307. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Norman, M., and Greenwood, P. H. 1963. A History of Fishes, 2nd edn. Ernest Benn, London. 398 pp.

Page, L. M., and Burr, B. M. 1991. A field guide to freshwater fishes of North America North of Mexico. The Peterson Field Guide Series. Houghton Mifflin Company, Boston, Massachusetts. 432 pp.

Petuch, E. J. 2004. Cenozoic Seas: The View for Eastern North America. CRC Press, Boca Raton, Louisiana, USA. 308 pp.

Pflaumann, U., Sarnthein, M., Chapman, M., d'Abreu, L., Funnell, B., Huels, M., Kiefer, T., Maslin, M., Schulz, H., Swallow, J., van Kreveld, S., Vautravers, M., Vogelsang, E., and Weinelt, M. 2003.

Glacial North Atlantic: sea-surface conditions reconstructed by GLAMAP 2000. Paleoceanography, 18(3): 10-1–10-28.

Pietsch, T. W. 1993. Systematics and distribution of cottid fishes of the genus *Triglops reinhardt* (Teleostei: Scorpaeniformes). Zoological Journal of the Linnean Society, 109: 335–393.

Post, A. 1984. Alepisauridae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 1, pp. 494–495. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Post, A. 1990. Paralipididae. *In* Check-list of the Fishes of the Eastern Tropical Atlantic, pp. 373–384. Ed. by J-C. Quéro, J-C. Hureau, C. Karrer, A. Post, and L. Saldanha. UNESCO, Paris.

Prowse, D. W. 1895. A History of Newfoundland. MacMillan and Co., London, England. 742 pp. (republished by Boulder Publications, Newfoundland and Labrador, 2002).

Reddin, D. G., and Friedland, K. D. 1993. Marine environmental factors influencing the movement and survival of Atlantic salmon. *In* Salmon in the Sea and New Enhancement Strategies, pp. 79–103. Ed. by D. H. Mills. Fishing News Books, London.

Robichaud, D., and Rose, G. A. 2004. Stock structure and range in Atlantic cod (*Gadus morhua*): inference from 100 years of tagging. Fish and Fisheries, 5: 1–33.

Robins, C. R., Bailey, R. M., Bond, C. E., Brooker, J. R., Lachner, E. A., Lea, R. N., and Scott, W. B. 1991. Common and scientific names of fishes from the United States and Canada. American Fisheries Society Special Publication, 20: 37 pp.

Robins, C. R., and Ray, G. C. 1986. A Field Guide to Atlantic Coast Fishes of North America. The Peterson Field Guide Series Houghton Mifflin Company, Boston, USA. 354 pp.

Rose, G. A. 2005. Capelin (*Mallotus villosus*) distribution and climate: a sea "canary" for ecosystem change. ICES Journal of Marine Science, 62 (7): 1524–1530.

Rose, G. A., and Kulka, D. W. 1999. Hyperaggregation of fish and fisheries: how catch per unit effort increased as the northern cod (*Gadus morhua*) declined. Canadian Journal of Fisheries and Aquatic Sciences, 56: 118–127.

Rose, G. A., and Leggett, W. C. 1988. Atmosphere–ocean coupling and Atlantic cod migrations: effects of wind-forced variations in sea temperatures and currents on nearshore distributions and catch rates of *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Sciences, 45: 1234–1243.

Rose, G. A., de Young, B., Kulka, D. W., Goddard, S. V., and Fletcher, G. L. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences, 57: 644–664.

Sæmundsson, B. 1932. Probable influence of changes in temperature on the marine fauna of Iceland. Rapport et Procès-Verbaux de la Conseil Permanent International pour l'Exploration de la Mer, 38: 1–6.

Sambilay, Jr V. C. 1990. Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. Fishbyte, 8: 16–20.

Scarratt, D. J. 1996. Atlantic Mariculture: Flounders. Communications Branch, Department of Fisheries and Oceans Canada, Scotia-Fundy Region, Halifax, Canada. 6 pp.

Scott, W. B., and Crossman, E. J. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada, 184: 966 pp.

Scott, W. B., and Scott, M. G. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences, 219: 731 pp.

Sinclair, A. F., and Murawski, S. A. 1997. Why have groundfish stocks declined? *In* Northwest Atlantic Groundfish: Perspectives on a Fishery Collapse, pp. 71–94. Ed. by J. Boreman, B. S. Nakashima, J. A. Wilson, and R. L. Kendall. American Fisheries Society, Bethesda, Maryland.

Snelgrove, P. V. R., and Haedrich, R. L. 1985. Structure of the deep demersal fish fauna off Newfoundland. Marine Ecology Progress Series, 27: 99–107.

Stehmann, M. 1990. Rajidae. *In* Check-list of the Fishes of the Eastern Tropical Atlantic, pp. 29–50. Ed. by J-C. Quéro, J-C. Hureau, C. Karrer, A. Post, and L. Saldanha. Junta Nacional de Investigaçao Cientifica e Technógia, Lisbon, Portugal.

Stein, D. L. 1986a. Cyclopteridae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 3, pp. 1269–1274. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Stein, D. L. 1986b. Liparidae. *In* Smith's Sea Fishes, pp. 492–494. Ed. by M. M. Smith, and P. C. Heenstra. Springer-Verlag, Berlin.

Stein, D. L., and Able, K. W. 1986. Liparidae. *In* Fishes of the North-Eastern Atlantic and Mediterranean, vol. 3, pp. 1278–1279. Ed. by P. J. P. Whitehead, M-L. Bauchot, J. Nielsen, and E. Tortonese. UNESCO, Paris.

St-Pierre, J. F., and de Lafontaine, Y. 1995. Fecundity and reproduction characteristics of beaked redfish (*Sebastes fasciatus* and *Sebastes mentella*). *In* The Gulf of St. Lawrence. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2059, 32 pp.

Svetovidov, A. N. 1948. Gadiformes. *In* Fauna of U.S.S.R.: Fishes, Gadiformes vol IX, No. 4 Ed. by E. N. Pavlovskii, and A. A. Shtakel'berg. Zoological Institute of the Academy of Sciences of the U.S.S.R. (in Russian). English translation (1962) by W. J. Walters and V. W. Walters, Israel Program for Scientific Translations. 304 pp.

Svetovidov, A. N. 1952. Clupeidae. *In* Ed. by E. N. Pavlovskii, and A. A. Shtakel'berg. Zoological Institute of the Academy of Sciences of the U.S.S.R. (in Russian). English translation (1963) by Z. Krauthamer and E. Roifer, Israel Program for Scientific Translations. 428 pp.

Svetovidov, A. N. 1984. Salmonidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 1, pp. 373–385. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Svetovidov, A. N. 1986. Gadidae. *In* Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 2, pp. 680–710. Ed. by P. J. P. Whitehead, M-L. Bauchot, J-C. Hureau, J. Nielsen, and E. Tortonese. UNESCO, Paris.

Tåning, Å. V. 1948. On changes in the marine fauna of the North-Western Atlantic area, with special reference to Greenland. Rapport et Procès-Verbaux de la Conseil Permanent International pour l'Exploration de la Mer, 54: 27–29.

Templeman, W. 1948. The life history of the capelin (*Mallotus villosus*) in Newfoundland waters. Bulletin of the Fisheries Research Board of Canada, 17: 151 pp.

Templeman, W. 1966. Marine resources of Newfoundland, 1966. Bulletin of the Fisheries Research Board of Canada, 154: 170 pp.

Van Guelpen, L. 1986. Hookear sculpins (genus *Artediellus*) of the North American Atlantic: taxonomy, morphological variability, distribution and aspects of the life history. Canadian Journal of Zoology, 64: 677–690.

Vilhjálmsson, H. 1994. The Icelandic capelin stock. Journal of the Marine Research Institute, Reykjavik, 13: 1–281.

Whitehead, P. J. P. 1985. Clupeoid fishes of the world (suborder Clupeioidei). An annotated and illustrated catalogue of the herring, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 1: Chirocentridae, Clupidae and Pristigasteridae. FAO Fisheries Synopsis No. 125, 7: 303 pp.

Wisher, R. L. 1990. Scomberesocidae. *In* Check-list of the Fishes of the Eastern Tropical Atlantic, pp. 598–603. Ed. by J-C. Quéro, J-C. Hureau, C. Karrer, A. Post, and L. Saldanha. UNESCO, Paris.