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Fishery and environmental factors affecting trends and fluctuations in the Georges Bank and Gulf of Maine Atlantic cod stocks: an overview

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The Georges Bank and Gulf of Maine Atlantic cod stocks have been commercially exploited for centuries, and continue today to support important commercial and recreational fisheries in both the United States and Canada. Prior to 1960, the two stocks were fished exclusively by the United States. During the 1960s, marked increases in exploitation occurred due to the development of Canadian and distant-water fisheries on Georges Bank. Total landings from the two stocks increased from 14 400 t in 1960 to 57 500 t in 1966, but subsequently declined to 30 000 t in 1976. Under extended fisheries jurisdiction – enacted in 1977 by both the USA and Canada – landings and stock sizes initially increased and a record-high catch (71 000 t) was attained in 1982. However, during the late 1980s and early 1990s, fishing effort and fishing mortality also increased to record-high levels, resulting in marked reductions in spawning-stock size. Research vessel indices, commercial c.p.u.e. indices, and VPA results all indicate that biomass levels in both stocks are now at record-lows. Although it is clear that fishery-induced perturbations have had a major impact on the Georges Bank and Gulf of Maine stocks, environmental and biotic influences may also have affected the stocks. These influences are not easily discernible, given the magnitude of the fishery-induced changes. Biophysical processes appear to be extremely important during the first year of life of cod and affect growth, mortality, and year-class strength. These processes are reviewed and discussed in relation to their impacts on various life history stages of cod. Current and future research studies aimed at differentiating environmental from fishery-related factors affecting recruitment and abundance of cod in the Georges Bank–Gulf of Maine region are discussed.

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Introduction

On 14 May 1602, the sailing ship "Concord" – in search of sassafras trees to obtain quantities of sassafras extract for treating syphilis in Europe – completed a 50-day trans-Atlantic voyage from Falmouth, England to "a mighty headland" in the New World. Near this promontory, the "Concord" came to anchor in 15 fathoms [27 m] where such a "great store of codfish" was taken that the area was named Cape Cod (Jensen, 1972). Sassafras trees were also found in abundance, but it was cod that was to become the source of original wealth for both the early New England colonists and for the nation that was to become the United States (Serchuk and Wigley, 1992)

The earliest USA fisheries for Atlantic cod (*Gadus morhua*) began in the 1600s in nearshore waters off the states of Maine and Massachusetts. By the early 1700s, however, vessels had started to fish much farther offshore, with the Georges Bank fishery developing between 1720 and 1750. By the end of the nineteenth century, the offshore fisheries supported a thriving domestic industry; in 1880, greater than 12 000 t of cod were landed from Georges Bank by the 163 schooners taking part in the fishery.

Continuous commercial landings statistics for cod exist from 1893 onward (Table 1). Total landings of cod from the Gulf of Maine and Georges Bank regions [ICNAF/NAFO Subareas 5 and 6: Fig. 1] exceeded 60 000 t in both 1895 and 1906, but declined to less than 20 000 t in 1915–1916 (Fig. 2). Between 1920 and 1940, cod was generally taken as a by-catch in the offshore fishery for haddock (*Melanogrammus aeglefinus*) – which had rapidly expanded in the early 1920s owing to development of a packaged trade in quick-frozen haddock fillets. During this 20-year period, annual landings of cod were relatively stable, fluctuating between 24 000 and 41 000 t and averaging 33 000 t annually. Cod catches declined in the 1940s and early 1950s, reaching a record-low of 11 000 t in 1953.

In the 1960s, Canadian and distant-water fisheries developed on Georges Bank, resulting in a rapid increase in fishing effort for cod (Table 2). Cod landings increased from 14 000 t in 1960 to 58 000 t in 1966, but afterward declined sharply to 30 000 t in 1976. In 1977,

Table 1. USA commercial landings (tonnes, live) of Atlantic cod from the Georges Bank (NAFO Division 5Z) and Gulf of Maine (NAFO Division 5Y) cod stocks (1893–1959). Prior to 1932, landings can only be assigned to Subarea 5.

Year	NAFO Subarea 5	Year	NAFO Subarea 5	NAFO Division 5Z	NAFO Division 5Y	Totals Subarea 5
1893	47 425					
1894	55 916					
1895	62 095	1930	41 341	–	–	41 341
1896	48 001	1931	33 338	–	–	33 338
1897	45 928	1932		25 122	5858	30 980
1898	44 150	1933		25 155	7025	32 180
1899	48 290	1934		15 976	11 619	27 595
1900	33 999	1935		21 162	9679	30 841
1901	45 238	1936		23 349	7442	30 791
1902	41 957	1937		32 282	7432	39 714
1903	39 024	1938		24 891	7547	32 438
1904	30 396	1939		22 048	5504	27 552
1905	36 316	1940		18 418	5836	24 254
1906	61 667	1941		25 453	6124	31 577
1907	56 516	1942		18 333	6679	25 012
1908	40 397	1943		17 341	9397	26 738
1909	39 672	1944		17 632	10 516	28 148
1910	34 796	1945		14 251	14 532	28 783
1911	26 427	1946		20 875	9248	30 123
1912	27 961	1947		16 582	6916	23 498
1913	24 101	1948		17 640	7462	25 102
1914	32 818	1949		17 681	7033	24 714
1915	18 459	1950		15 389	5062	20 451
1916	18 786	1951		14 791	3567	18 358
1917	21 330	1952		10 904	3011	13 915
1918	29 799	1953		8105	3121	11 226
1919	29 953	1954		8826	3411	12 237
1920	27 345	1955		9286	3171	12 457
1921	32 044	1956		10 535	2693	13 228
1922	30 847	1957		10 598	2562	13 160
1923	30 498	1958		11 582	4670	16 252
1924	32 639	1959		12 423	3795	16 218
1925	34 320					
1926	40 102					
1927	39 335					
1928	34 743					
1929	37 021					

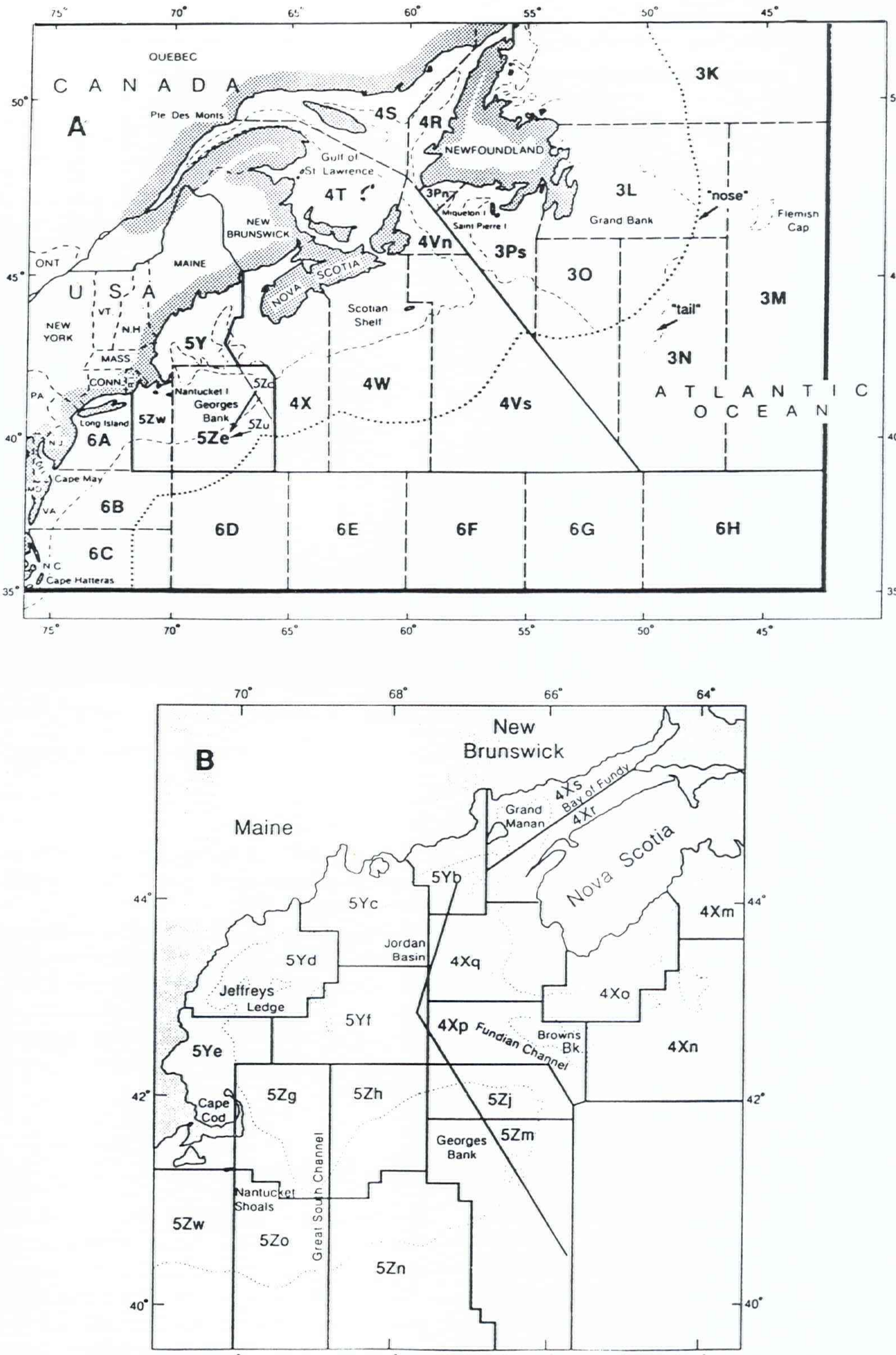


Figure 1. (A) Map depicting NAFO Subareas 3–6, and (B) statistical unit areas in the Gulf of Maine and Georges Bank (from Serchuk and Wigley, 1992).

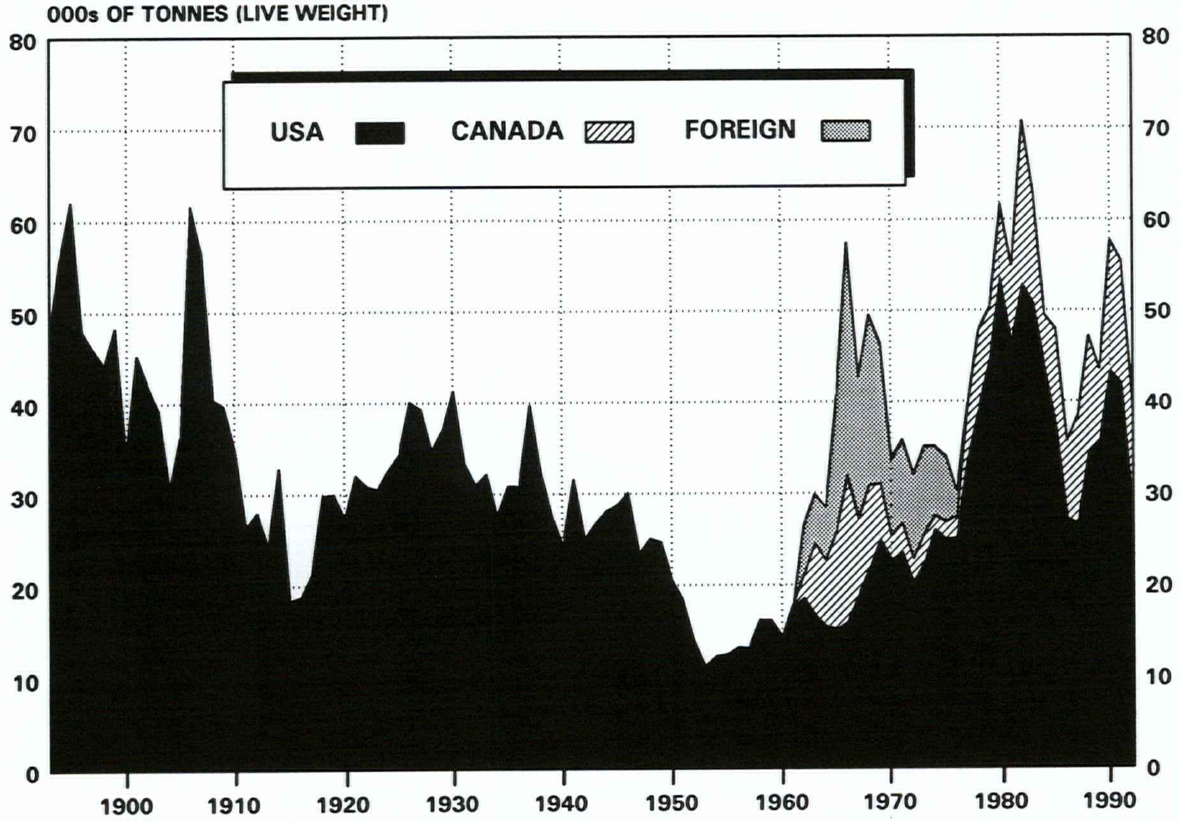


Figure 2. Total reported commercial landings of cod from the Georges Bank and Gulf of Maine stocks (1893–1992).

the USA and Canada independently enacted extended fisheries jurisdiction which prohibited distant-water fleets from fishing cod (and other species) in the USA and Canadian exclusive economic zones. By this time, the Georges Bank stocks of haddock, herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), and silver hake (*Merluccius bilinearis*) had already collapsed from overfishing ascribed largely to the distant-water fleets (Mayo *et al.*, 1992). Cod – which had always been a significant component of the groundfish complex in the Gulf of Maine and Georges Bank regions – had now become the most dominant component. Total cod landings (solely USA and Canadian) doubled between 1977 and 1982 (30 000 to 71 000 t, a record-high), declined to 36 000 t in 1986, but increased to 58 000 t in 1990. In 1992, however, landings fell to 39 000 t.

Since 1977, cod has annually accounted for more catch (by weight) than any other species in the USA Atlantic coast groundfish fishery. In recent years, cod has been so dominant that USA commercial landings of cod have typically exceeded those from haddock, redfish (*Sebastes fasciatus*), pollock (*Pollachius virens*), and six major species of flatfish combined (US Department of Commerce, 1992). In addition, between 3000 and 8000 t of cod are taken annually in recreational fisheries (Serchuk and Wigley, 1992).

Given the importance of cod off the northeast coast of the United States, in this paper we review the changes that have occurred over the past 30 years to the Georges Bank and Gulf of Maine cod stocks, and evaluate the influence of fishery and environmental factors in affecting stock size fluctuations, recruitment, growth, and maturation.

Stock definitions

In waters west of Nova Scotia and south of the Fundian Channel (i.e., NAFO Subareas 5 and 6), cod have been distinguished into three or possibly four major groups: (1) Georges Bank; (2) Gulf of Maine; and (3) one or two groups in the Southern New England–Middle Atlantic area (Wise, 1963; Serchuk and Wigley, 1992). Little interchange of cod occurs between the Gulf of Maine and Georges Bank groups, as inferred from tagging studies (Smith, 1902; Schroeder, 1930; North American

Table 2. Commercial landings (tonnes, live) of Atlantic cod from Georges Bank and South (NAFO Division 5Z and Statistical Area 6), and the Gulf of Maine (NAFO Division 5Y) (1960–1992).

	Georges Bank and South				Gulf of Maine				Grand Totals			
Year	USA	Canada	Other	Total	USA	Canada	Other	Total	USA	Canada	Other	Total
1960	10 834	19	–	10 853	3448	129	–	3577	14 282	148	–	14 430
1961	14 453	223	55	14 731	3216	18	–	3234	17 669	241	55	17 965
1962	15 637	2404	5445	23 486	2989	83	–	3072	18 626	2487	5445	26 558
1963	14 139	7832	5218	27 189	2595	3	133	2731	16 734	7835	5351	29 920
1964	12 325	7108	5732	25 165	3226	25	–	3251	15 551	7133	5732	28 416
1965	11 410	10 598	16 325	38 333	3780	148	–	3928	15 190	10 746	16 325	40 696
1966	11 990	15 601	25 543	53 134	4008	384	–	4392	15 998	15 985	25 543	57 526
1967	13 157	8232	15 363	36 752	5676	297	–	5973	18 833	8529	15 363	42 725
1968	15 279	9127	18 730	43 136	6360	61	–	6421	21 639	9188	18 730	49 557
1969	16 782	5997	15 160	37 939	8157	59	268	8484	24 939	6056	15 428	46 423
1970	14 899	2583	8170	25 652	7812	26	423	8261	22 711	2609	8593	33 913
1971	16 178	2979	9022	28 179	7380	119	163	7662	23 558	3098	9185	35 841
1972	13 406	2545	9108	25 059	6776	53	88	6917	20 182	2598	9196	31 976
1973	16 202	3220	9501	28 923	6069	68	9	6146	22 271	3288	9510	35 069
1974	18 377	1374	7580	27 331	7639	120	5	7764	26 016	1494	7585	35 095
1975	16 017	1847	7144	25 008	8903	86	26	9015	24 920	1933	7170	34 023
1976	14 906	2328	2692	19 926	10 172	16	–	10 188	25 078	2344	2692	30 114
1977	21 138	6173	56	27 367	12 426	–	–	12 426	33 564	6173	56	39 793
1978	26 579	8778	–	35 357	12 426	–	–	12 426	39 005	8778	–	47 783
1979	32 645	5978	–	38 623	11 680	–	–	11 680	44 325	5978	–	50 303
1980	40 053	8063	–	48 116	13 528	–	–	13 528	53 581	8063	–	61 644
1981	33 849	8499	–	42 348	12 534	–	–	12 534	46 383	8499	–	54 882
1982	39 333	17 824	–	57 157	13 582	–	–	13 582	52 915	17 824	–	70 739
1983	36 756	12 130	–	48 886	13 981	–	–	13 981	50 737	12 130	–	62 867
1984	32 915	5763	–	38 678	10 806	–	–	10 806	43 721	5763	–	49 484
1985	26 828	10 443	–	37 271	10 693	–	–	10 693	37 521	10 443	–	47 964
1986	17 490	8411	–	25 901	9664	–	–	9664	27 154	8411	–	35 565
1987	19 035	11 845	–	30 880	7527	–	–	7527	26 562	11 845	–	38 407
1988	26 310	12 932	–	39 242	7958	–	–	7958	34 268	12 932	–	47 200
1989	25 097	8001	–	33 098	10 397	–	–	10 397	35 494	8001	–	43 495
1990	28 193	14 310	–	42 503	15 154	–	–	15 154	43 347	14 310	–	57 657
1991	24 175	13 455	–	37 630	17 781	–	–	17 781	41 956	13 455	–	55 411
1992	16 855	11 669	–	28 524	10 915	–	–	10 915	27 770	11 669	–	39 439

Council on Fishery Investigations, 1932, 1935; Wise, 1963), *Lernaeocera* infestation patterns (Sherman and Wise, 1961), spawning time data (Colton *et al.*, 1979), otolith features (Penttila, 1988), and growth rate analyses (Penttila and Gifford, 1976; Serchuk and Wood, 1979). However, significant intermixing of fish occurs between cod on Georges Bank and those in the Southern New England–Middle Atlantic region; a seasonal southwesterly movement of adult cod from the South Channel area of Georges Bank occurs in early winter (Dec–Jan) followed by a northeasterly return in late spring–early summer (May–June) (Fig. 3). In addition, there are well-defined seasonal movements of juvenile cod between the Georges Bank and Southern New England areas (Wigley and Gabriel, 1991; Wigley and Serchuk, 1992).

Management of cod in NAFO Subarea 5 was initiated in 1973 when the International Commission for the Northwest Atlantic Fisheries (ICNAF) established separate catch quotas (TACs) for the Georges Bank (Division 5Z) and Gulf of Maine (Division 5Y) cod stocks (ICNAF, 1973). Subsequently, both stocks were managed by TACs during 1974–1976 (ICNAF, 1976). With the implementation of extended fisheries jurisdiction in 1977, the USA and Canada independently assumed responsibility for the management of the fisheries resources within their respective and, at the time, overlapping 200-mile fishery zones. The Georges Bank cod stock, however, was clearly a transboundary resource.

In the management program enacted by the USA in 1977, the two cod management units established by ICNAF were adopted but the "Georges Bank" stock unit was enlarged (Division 5Z and Subarea 6) to include the cod occurring in the Southern New England–Middle Atlantic region. This recognized that extensive mixing of fish occurred between the two areas, and that strong demographic affinities existed between the cod in these regions (Serchuk and Wood, 1979). Canada also initially considered the "Georges Bank" stock as encompassing the cod in Division 5Z and Subarea 6 (Bowen, 1987; Hunt, 1988). However, in 1989, Canada re-examined the definitions of management units for groundfish species on Georges Bank [in light of the separate USA and Canadian management systems and the delimitation in 1984 of a maritime boundary between the USA and Canada in the Gulf of Maine/Georges Bank area], and concluded that the "Georges Bank" cod stock could be partitioned into two management units: (1) eastern Georges Bank cod [unit areas 5Zj and 5Zm; Fig. 1]; and (2) central and western Georges Bank cod [the remainder of Division 5Z and Subarea 6] (Hunt, 1989). Since 1989, Canada has therefore treated the cod on Georges Bank as comprised of two separate units (CAFSAC, 1989; Halliday and Pinhorn, 1990).

Although further work on the structure of the cod stocks in Subarea 5 is certainly warranted, for the purposes of this paper the stock units recognized by the USA are employed, viz. a Georges Bank stock (Division 5Z and Subarea 6) and a Gulf of Maine stock (Division 5Y). These stock categorizations also correspond well with the traditional areas used in sampling and reporting catches, thereby facilitating the use of the long time-series of existing data.

Physical environment

The Gulf of Maine–Georges Bank region is bordered on the east, north, and west by the coasts of Nova Scotia, New Brunswick, and the New England States (Fig. 4). The Gulf is open at the surface to the North Atlantic Ocean to the south. Below about 50 m depth, however, Georges Bank forms a southern boundary for the Gulf, making it semi-enclosed. The Gulf is connected to the deep North Atlantic Ocean by only two major channels – the Northeast Channel between Georges Bank and the Scotian Shelf, and the Great South Channel between Georges Bank and the Nantucket Shoals to the west. The interior of the Gulf is characterized by several deep basins (>200 m) separated by a number of shallow ridges, ledges, and banks. The largest and deepest of these basins are (1) Georges Basin near the mouth of the Northeast Channel; (2) Jordan Basin to the northeast; and (3) Wilkinson Basin in the southwestern Gulf. The Jordan and Wilkinson Basins are separated by an irregular, shallower topography which extends from the coast toward the central Gulf.

Georges Bank is a large (300 × 150 km) shallow bank that appears to be an eastward extension of the U.S. continental shelf. The Bank has a steep slope on its northern edge and a broad, flat, gently sloping southern flank. To the west, the Bank is separated from the rest of the continental shelf by the Great South Channel. The central region of the Bank is quite shallow, with scattered areas less than 20 m deep, and the bottom is characterized by large-amplitude sand waves. The rest of the Bank is sandy and flat, with regions of gravel on the northern and eastern parts of the Bank (Valentine and Lough, 1991).

To the west of Georges Bank, the continental shelf south of New England is broad and flat. The bottom is generally sandy, except for an area of silt located on the outer shelf southwest of Martha's Vineyard (Garrison and McMaster, 1966). The Nantucket Shoals region, southeast of Nantucket, has sand waves similar to those on central Georges Bank. Patches of gravel are found on the western flank of the Great South Channel.

The Gulf of Maine and Georges Bank are part of an extended coastal current system which flows southward from Labrador, through the Gulf region to the Middle

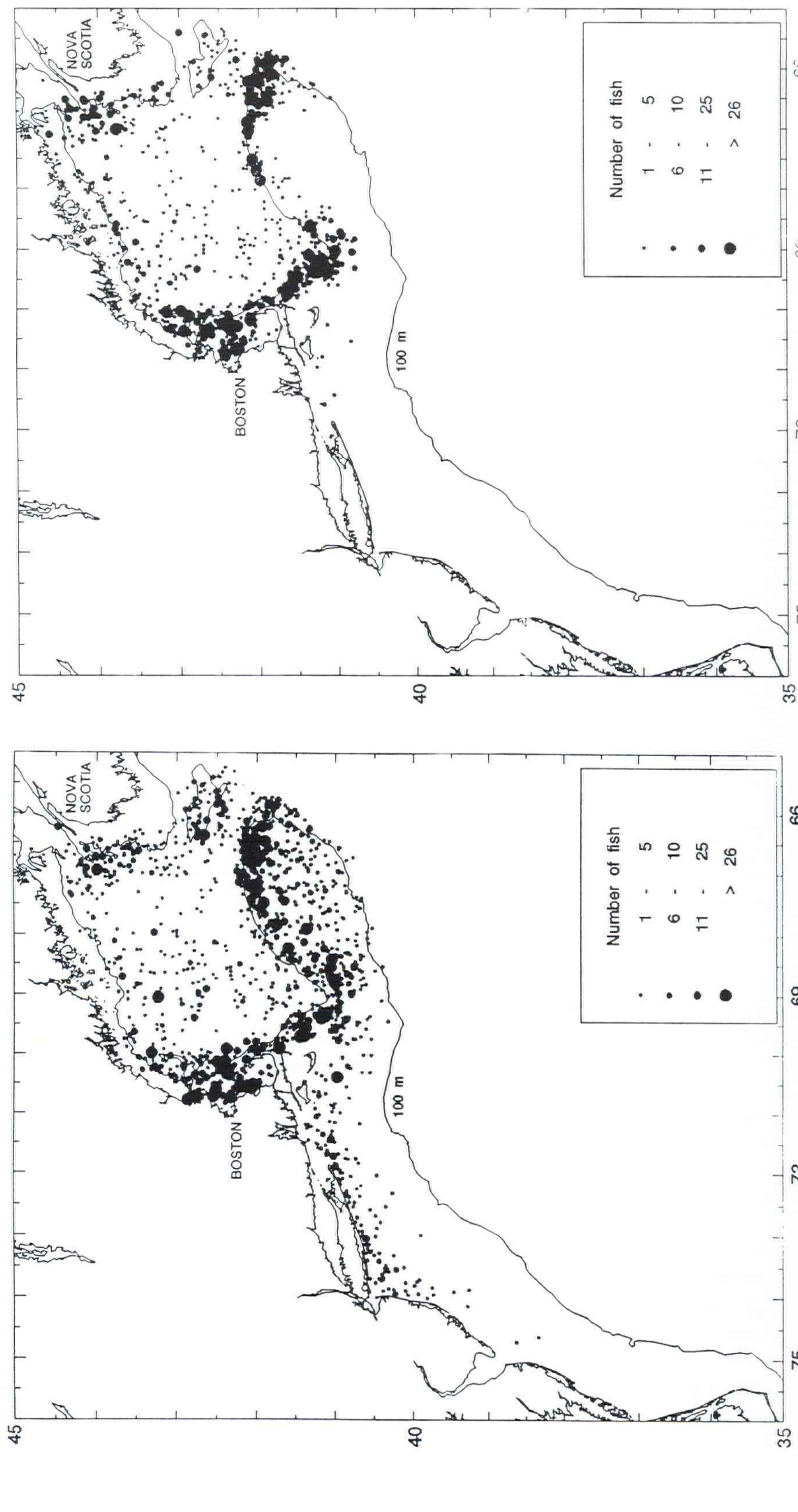


Figure 3. Geographic distribution (number/tow) of adult (≥37 cm) Atlantic cod, *Gadus morhua*, collected during NEFSC spring (left) and autumn (right) research vessel bottom-trawl surveys (1982–1992) in the Gulf of Maine, Georges Bank, and Southern New England–Middle Atlantic regions. Each dot represents a survey tow in which cod were caught.

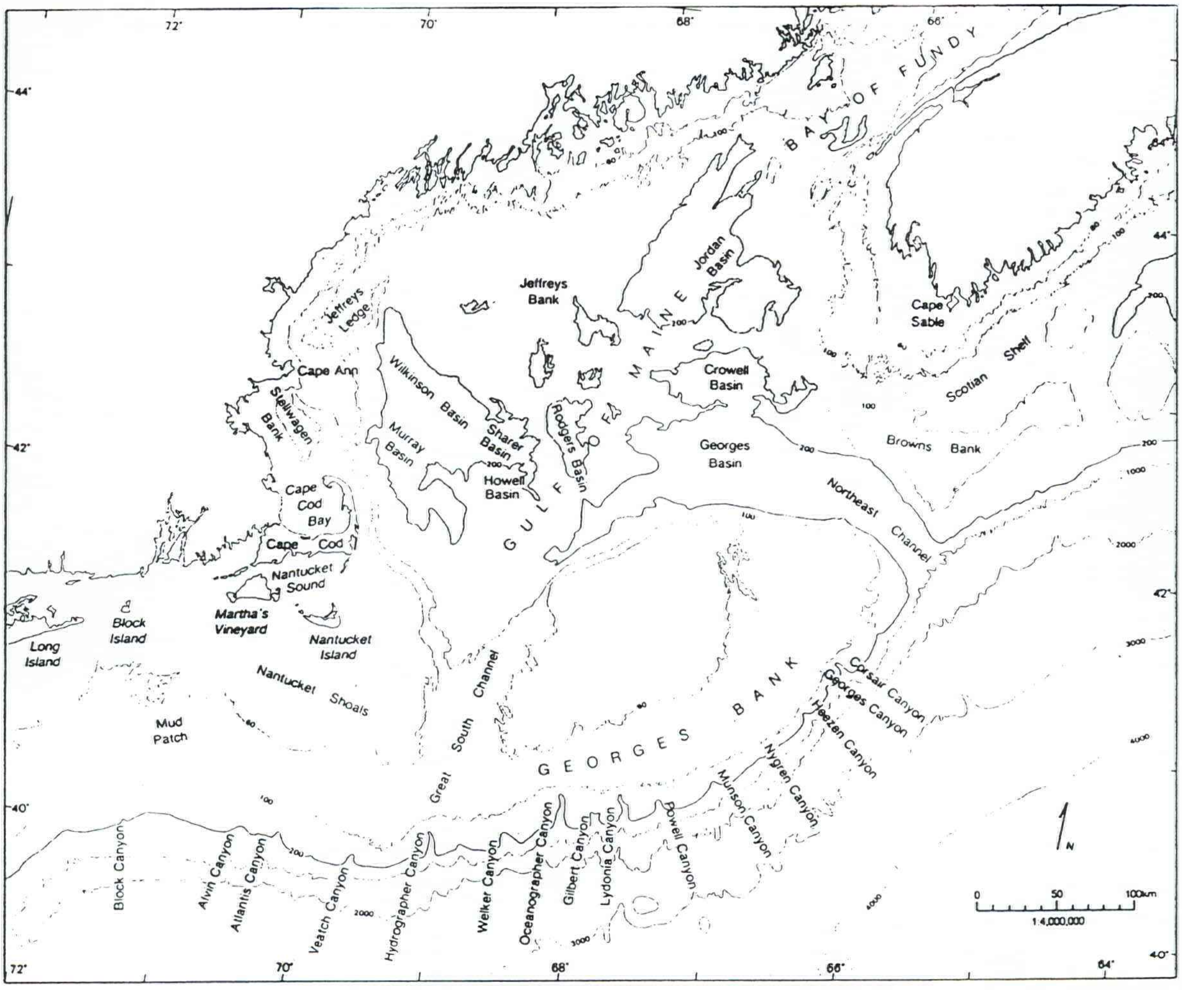


Figure 4. Topographic map showing the location of the Gulf of Maine and Georges Bank in relation to the New England shelf and the Scotian shelf. The topography inside the 60-m isobath is simplified (from Butman and Beardsley, 1987).

Atlantic Bight (Chapman and Beardsley, 1989; Fig. 5). Locally, the waters are derived from two primary water masses: (1) cold, low salinity water which flows southward from the Scotian Shelf and enters the Gulf of Maine system around Cape Sable (Smith, 1983), and (2) warm, high salinity Slope Water which enters the Gulf at depth through the Northeast Channel (Ramp *et al.*, 1985). Within the Gulf, these waters are mixed and subsequently modified by local atmospheric heating/cooling, precipitation, and coastal runoff. Because of the cyclonic circulation pattern in the region, water is carried around the Gulf to the southwest. From here, surface waters penetrate onto the northwestern side of Georges Bank (Hopkins and Garfield, 1981), entering a strong, eastward flow along the northern edge of the Bank (Fig. 6). The flow then turns south and then southwestward along the wide, southern flank of the Bank. At the Great South Channel, a portion of the flow turns north to form a recirculating gyre around the Bank, while the majority of the flow continues westward south of Nantucket Shoals and into the Middle Atlantic Bight. Along the edge of the shelf from Georges Bank to the Middle Atlantic Bight, a sharp hydrographic front exists between the shelf waters and the warmer, more saline, offshore Slope Water.

The water motions in the region are dominated by strong tidal currents, particularly in the shallow central area of Georges Bank. The mean clockwise circulation around the Bank results, in large part, from rectification of the tidal currents by the bathymetry (Loder, 1980). Wind events also generate strong, transient currents which can result in the exchange of water between regions. Warm core Gulf Stream rings often impinge against the shelf break and may entrain large amounts of

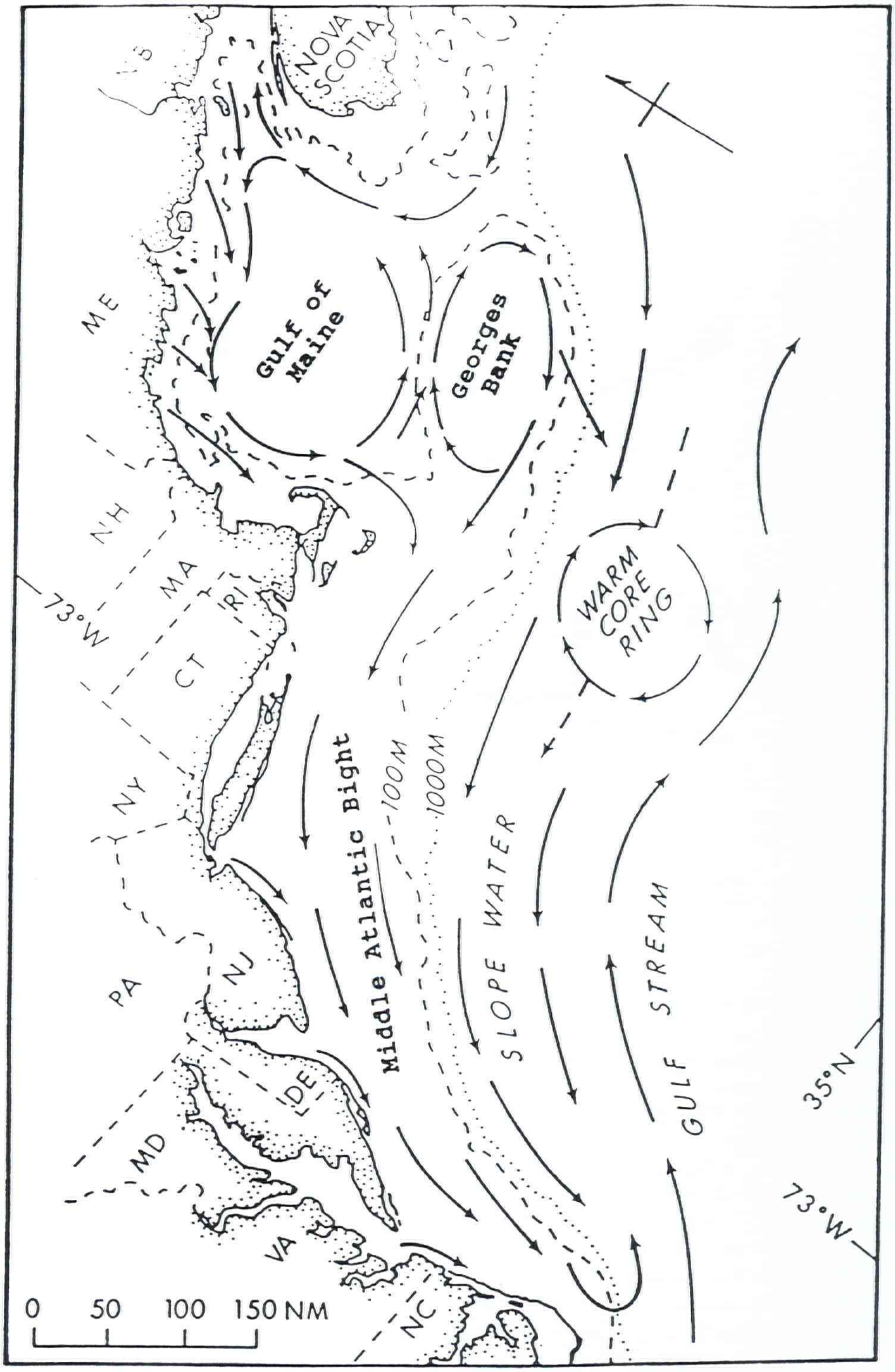


Figure 5. Generalized surface-layer water circulation patterns in the Gulf of Maine, Georges Bank, and Middle Atlantic regions (modified from Ingham *et al.*, 1982).

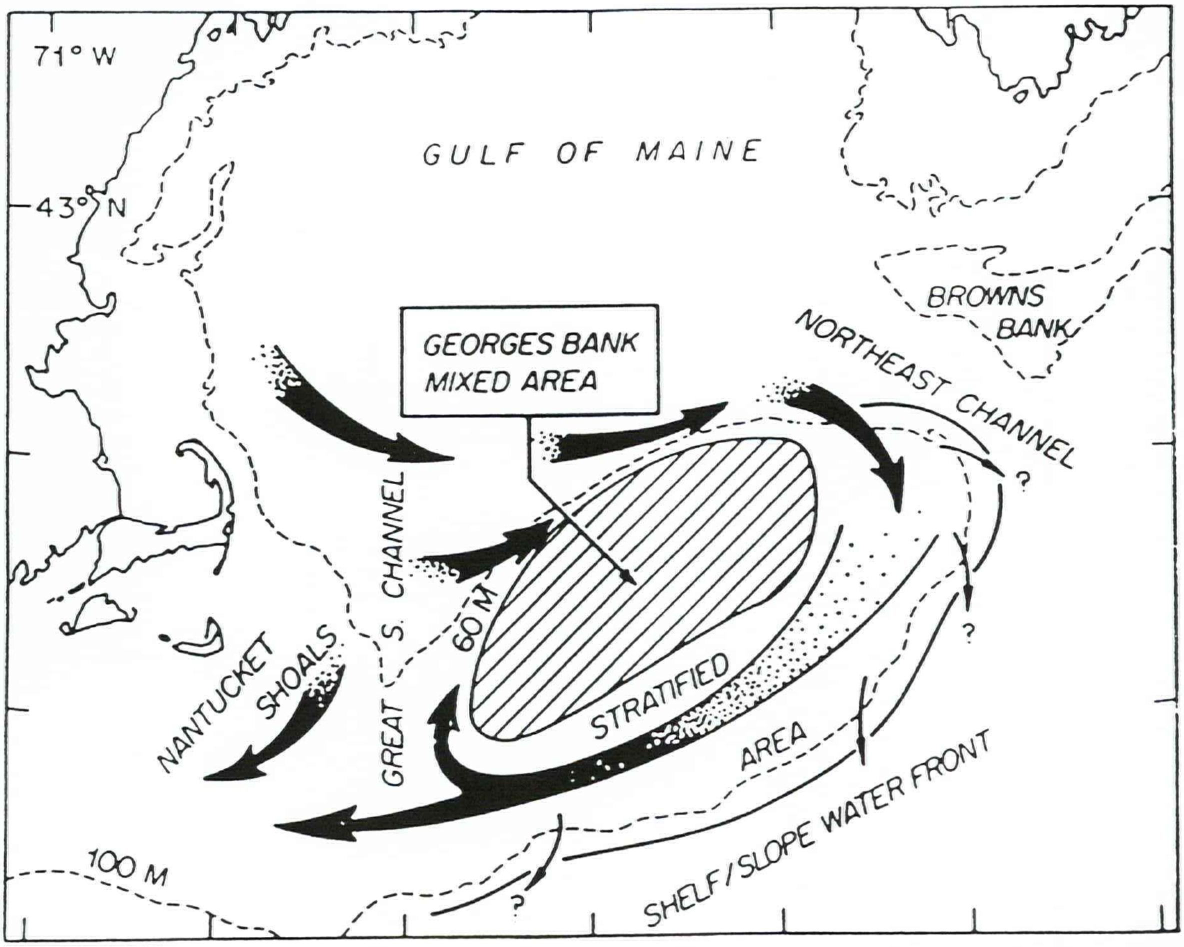


Figure 6. Schematic representation of the well-mixed and stratified water masses on Georges Bank and mean circulation flows (arrows) during spring and summer (from Lough, 1984).

water from Georges Bank and the Middle Atlantic Bight into the Slope region.

Water properties throughout the region undergo a characteristic seasonal cycle. In winter, atmospheric cooling and strong winds mix the water column from surface to a depth of about 100 m in the Gulf of Maine (Hopkins and Garfield, 1981), and to the bottom on Georges Bank and much of the Middle Atlantic Bight. During spring, surface heating and the seasonal decrease in wind forcing cause the surface waters to warm – inducing the development of vertical stratification with respect to temperature and density. In the central portion of the Bank and on Nantucket Shoals (<60 m), tidal currents are strong enough to keep the water column well mixed year round. Stratification continues to develop through the summer and into the fall, when seasonal cooling and winds again cause a return to the vertically well-mixed winter conditions. The annual minimum surface water temperature is about 4°C and occurs in March. The annual maximum surface temperature occurs during August–September at about 14–16°C on Georges Bank, and at about 18–20°C in the western Gulf of Maine and the northern Middle Atlantic Bight (Mountain and Holzwarth, 1989). Bottom temperatures in the Gulf of Maine show little seasonal pattern, but are generally higher in the eastern Gulf (6–9°C) than in the western Gulf (5–7°C), because of the influence of the Slope Water inflow through the Northeast Channel (Mountain and Jessen, 1987). On Georges Bank, maximum bottom temperatures occur in August–September at about 12–16°C.

The Gulf of Maine–Georges Bank regions experience significant inter-annual variability in water temperature (Fig. 7). Measurements from the USA (Northeast Fisheries Science Center) trawl survey program indicate a change of about 2°C in the Bank-wide spring average

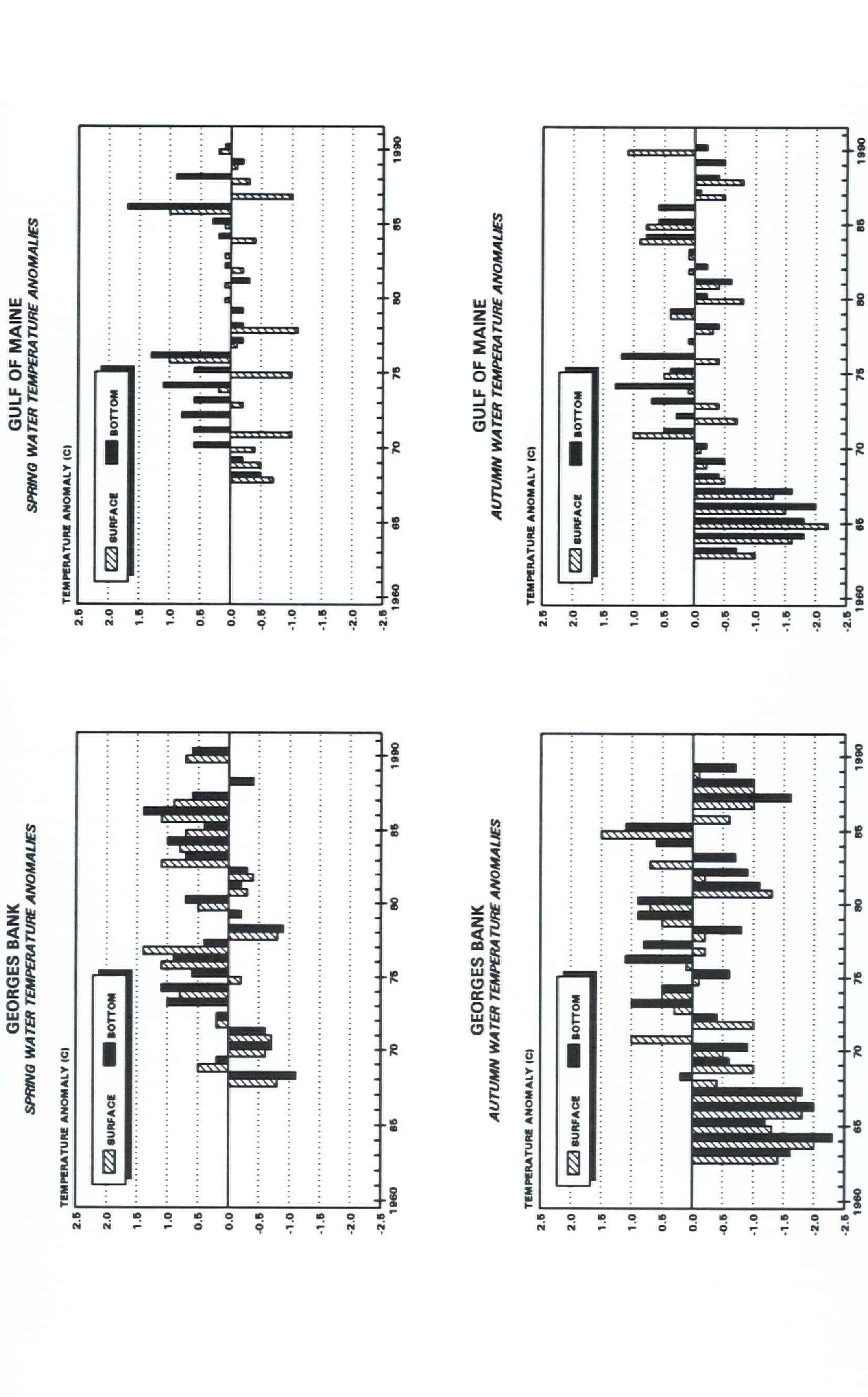


Figure 7. Average spring and autumn water temperature anomalies (surface and bottom) on Georges Bank and in the Gulf of Maine (1963–1990). Data derived from NEFSC spring and autumn research vessel bottom-trawl surveys.

water temperature between the cool 1960s and the warm mid-1970s. The years around 1980 were intermediate between the two earlier periods, while the last half of the 1980s was comparable to the mid-1970s (Holzwarth and Mountain, 1992).

Commercial fishery

Landings trends

During the past 30 years, commercial landings from both the Georges Bank and Gulf of Maine stocks have increased and attained record-high levels (Table 2). In the Georges Bank stock, landings initially peaked in 1966 at 53 000 t due to marked increases in exploitation by distant-water fishing fleets (primarily from the USSR, Spain, and Poland). Landings by these fleets, which had begun to fish cod on Georges Bank in 1961, increased dramatically from 55 t in 1961 to 25 500 t in 1966 (Fig. 8). As well, Canadian landings – which were just 200 t in 1961 – increased to 15 600 t in 1966. In contrast, USA landings of Georges Bank cod remained relatively stable, varying between 10 800 and 16 800 t during 1960–1969 and averaging 13 000 t per year. After 1968, distant-water and Canadian landings declined and, by 1976, total landings of Georges Bank cod had fallen to 20 000 t, the lowest since 1961. During 1974–1976, the Georges Bank cod fishery was regulated by ICNAF under a 35 000 t TAC, but annual catches during these years never exceeded 27 000 t.

Following the implementation in 1977 of extended fisheries jurisdiction by both Canada and the USA, Georges Bank cod landings again increased. Although USA catches peaked at 40 000 t in 1980, total catches (and Canadian landings) peaked in 1982 at 57 000 t (17 800 t, Canadian). Thereafter, catches declined, reaching a post-1976 low of 25 900 t in 1986. Total landings increased during 1987–1990 (attaining 42 500 t in 1990), but have since diminished to 28 500 t in 1992.

In the Gulf of Maine stock, virtually all landings have been by the USA fleet (Tables 1 and 2; Fig. 8). Landings peaked in 1945 at 14 500 t but then declined sharply, reaching a record-low of 2600 t in 1957. From 1960 until the early 1980s, Gulf of Maine landings steadily increased, doubling between 1964 and 1968 (3250 to 6400 t) and doubling again between 1968 and 1980 (6400 to 13 500 t). ICNAF TACs were implemented during 1973–1976 (10 000 t TAC in 1973–1975; 8000 t TAC in 1976) but only the 1976 TAC was constraining – and was overrun.

During 1976–1985, Gulf of Maine cod landings exceeded 10 000 t in every year and averaged 12 200 t per annum. Landings declined to less than 8000 t in 1987–1988, but subsequently increased – reaching a record-high level of 17 800 t in 1991. In 1992, however, total cod landings plummeted to 11 000 t.

Although USA and Canadian management programs for cod have been in place since 1977, catches of cod from both stocks have not been effectively controlled (Anthony, 1990; Serchuk and Wigley, 1992). Catch quotas were eliminated from the USA management program in 1982 in favor of indirect controls on fishing effort, such as minimum mesh sizes, minimum fish sizes, and closed areas. Quota management has been a part of the recommended Canadian approach to regulating the Georges Bank fishery since 1978, but TACs on Canadian catches were not implemented until 1985, after the Gulf of Maine/Georges Bank maritime boundary dispute between the USA and Canada had been resolved by the International Court of Justice. Independent and/or unilateral management actions by the two countries, however, have not proved successful in constraining exploitation. Management objectives differ between the two nations and each country has pursued management strategies without regard for one another. As of now, a cooperative and coordinated joint USA/Canadian approach to the harvesting and conservation of trans-boundary fishery resources (e.g., Georges Bank cod) has yet to be established.

Stock abundance and biomass indices

Trends in commercial catch per unit effort (c.p.u.e.)

USA commercial c.p.u.e. indices for the Georges Bank and Gulf of Maine stocks are available from 1965 onwards. These indices are based on otter trawl trips and were derived based on all trips in which cod were landed, and for "directed" trips in which cod constituted 50% or more of the total trip catch by weight. During 1965–1992, otter trawl landings accounted for 86% of USA Georges Bank cod catches and for 68% of USA Gulf of Maine cod catches.

For Georges Bank cod, both total and directed c.p.u.e. indices have, since 1970, generally exhibited trends (Fig. 8). C.p.u.e. values increased during the early and mid-1970s, peaked in the late 1970s and early 1980s, and then declined precipitously between 1983 and 1987. Catch rates increased slightly in 1990, but have since fallen; in 1992, both the total and directed c.p.u.e. indices were at record-low levels. Canadian c.p.u.e. indices are not considered to be reliable indicators of stock abundance (Hunt, 1990), and are not presented here as they have not been used in any of the recent Canadian assessments of the Georges Bank cod stock (Hunt and Buzeta, 1992).

For the Gulf of Maine stock, c.p.u.e. values increased

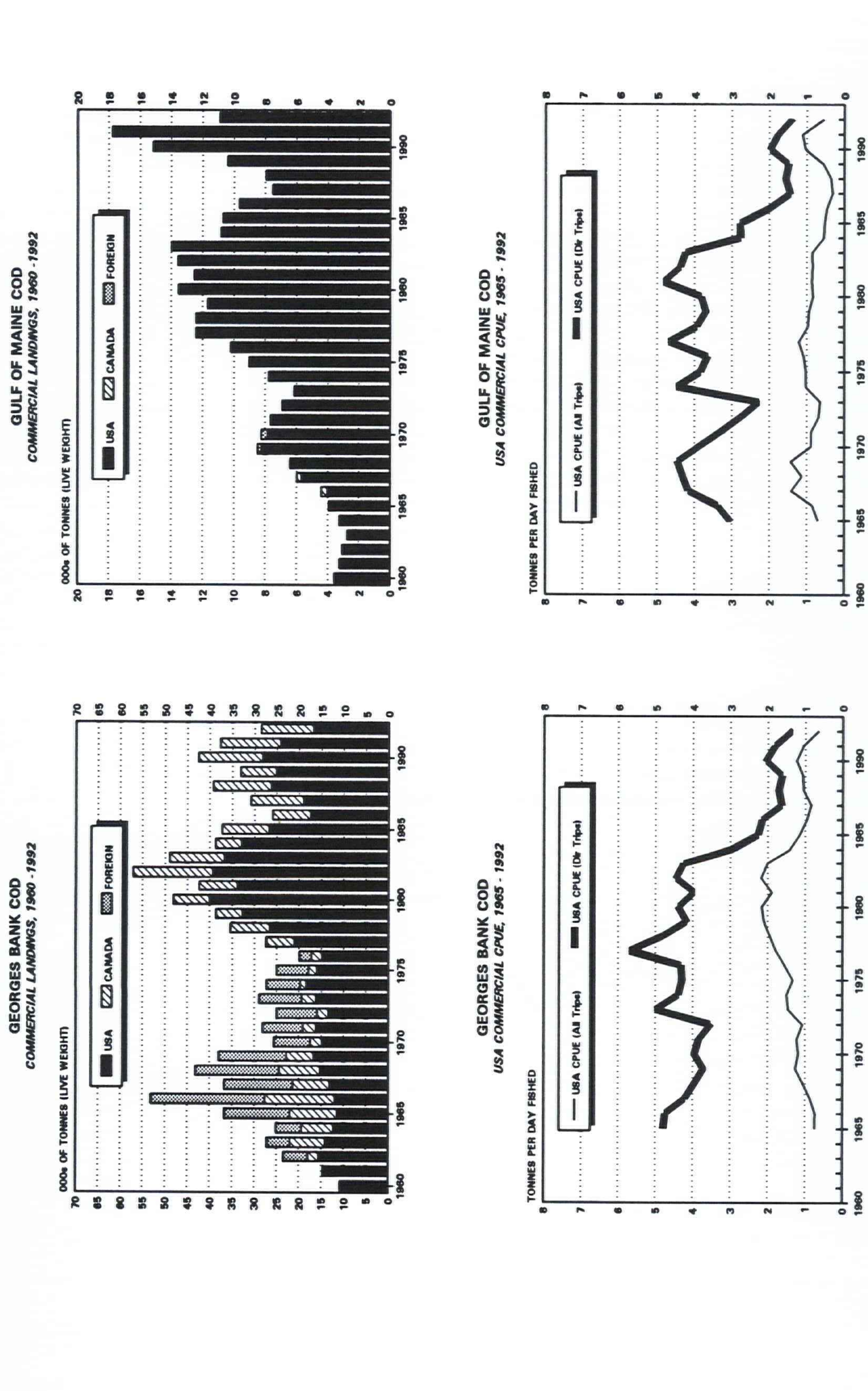


Figure 8. Total commercial landings (top) and USA commercial catch per day fished (bottom) of cod from the Georges Bank (Division 5Z and Subarea 6) and Gulf of Maine (Division 5Y) stocks.

during the late 1960s, declined during the early 1970s, sharply increased in 1974, and then stabilized at a relatively high level during 1975–1983 (Fig. 8). Subsequently, c.p.u.e. indices declined, reaching record-low levels in 1987. Between 1988 and 1991, the c.p.u.e. indices again increased, but in 1992 both the total and directed indices declined to near-record lows.

Taken at face value, the time series of c.p.u.e. values for both stocks suggest that exploitable biomass peaked during the late 1970s and early 1980s, but has since declined – in each stock – to historic low levels. On a relative basis, the present stock levels are probably even lower than indicated by the c.p.u.e. data because the c.p.u.e. indices have not been adjusted for increases in fleet efficiency in recent years.

USA otter trawl effort increased markedly after 1976 (Fig. 9). In the Georges Bank fishery, USA trawling effort for cod (nominal days fished) rose by 71% between 1977 and 1988 (11 700 to 19 800 days fished), while in the Gulf of Maine fishery trawling effort nearly doubled (7400 to 13 000 days fished). During the past few years, effort in both fisheries has been at or near historically high levels.

Trends in research vessel survey indices

Stratified-random bottom trawl surveys of the Georges Bank and Gulf of Maine regions have been conducted by the Northeast Fisheries Science Center (NEFSC) each autumn since 1963 and each spring since 1968 using the research vessels "Albatross IV" and "Delaware II" (Azarovitz, 1981). The data from these surveys have been used to derive standardized indices of relative abundance and biomass of cod (stratified mean catch per tow in number and weight, respectively) for both the Georges Bank and Gulf of Maine stocks.

For Georges Bank cod, the spring and autumn NEFSC survey indices show similar trends (Fig. 10). Survey biomass indices were relatively low and stable during 1963–1971, fluctuated at a generally higher level between 1972 and 1981, but have since declined to record-low values. Elevated survey biomass indices in 1969–1970, 1972–1973, 1978, 1981, and 1984–1985 reflect above-average recruitment of the 1966, 1971, 1975, 1980, and 1983 year classes.

For the Gulf of Maine stock, the time series of survey indices suggests that stock biomass was high in (1) the early 1960s; (2) during the late 1960s–early 1970s; and (3) and in the late 1970s–early 1980s. After 1985, however, both the spring and autumn survey biomass indices steadily declined, reaching record-low levels during 1989–1991 (Fig. 10). In 1992 [as in 1973], the spring and autumn indices were discrepant; the spring index markedly increased (due to a large contribution of fish from the strong 1987 year class) while the autumn index declined. Recruitment indices for the Gulf of Maine

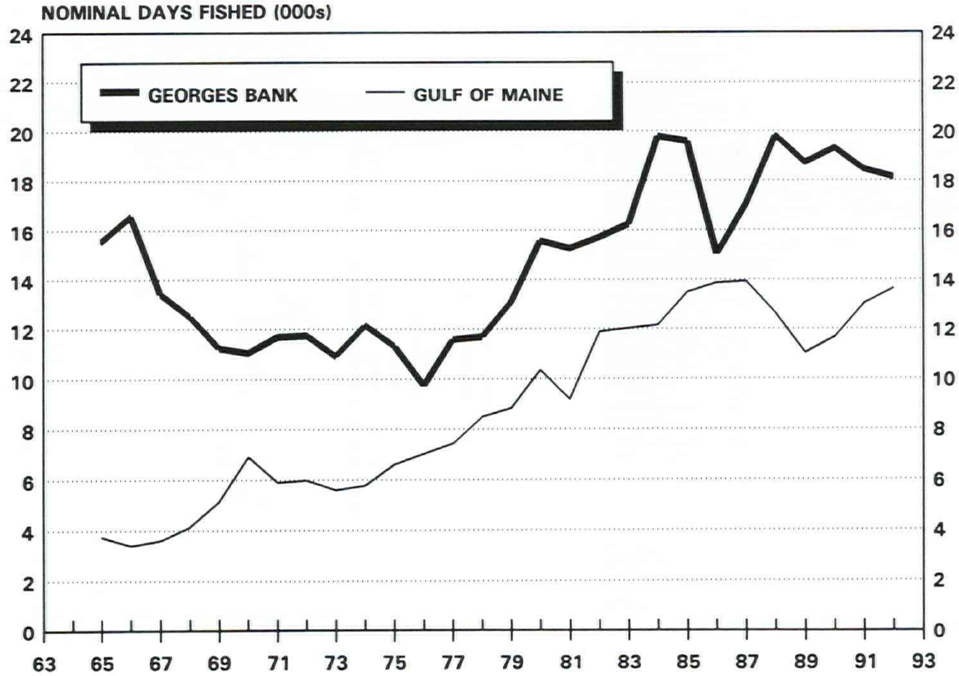


Figure 9. USA commercial otter trawl effort (nominal days fished) for trips landing cod from the Georges Bank and Gulf of Maine stocks (1965–1992).

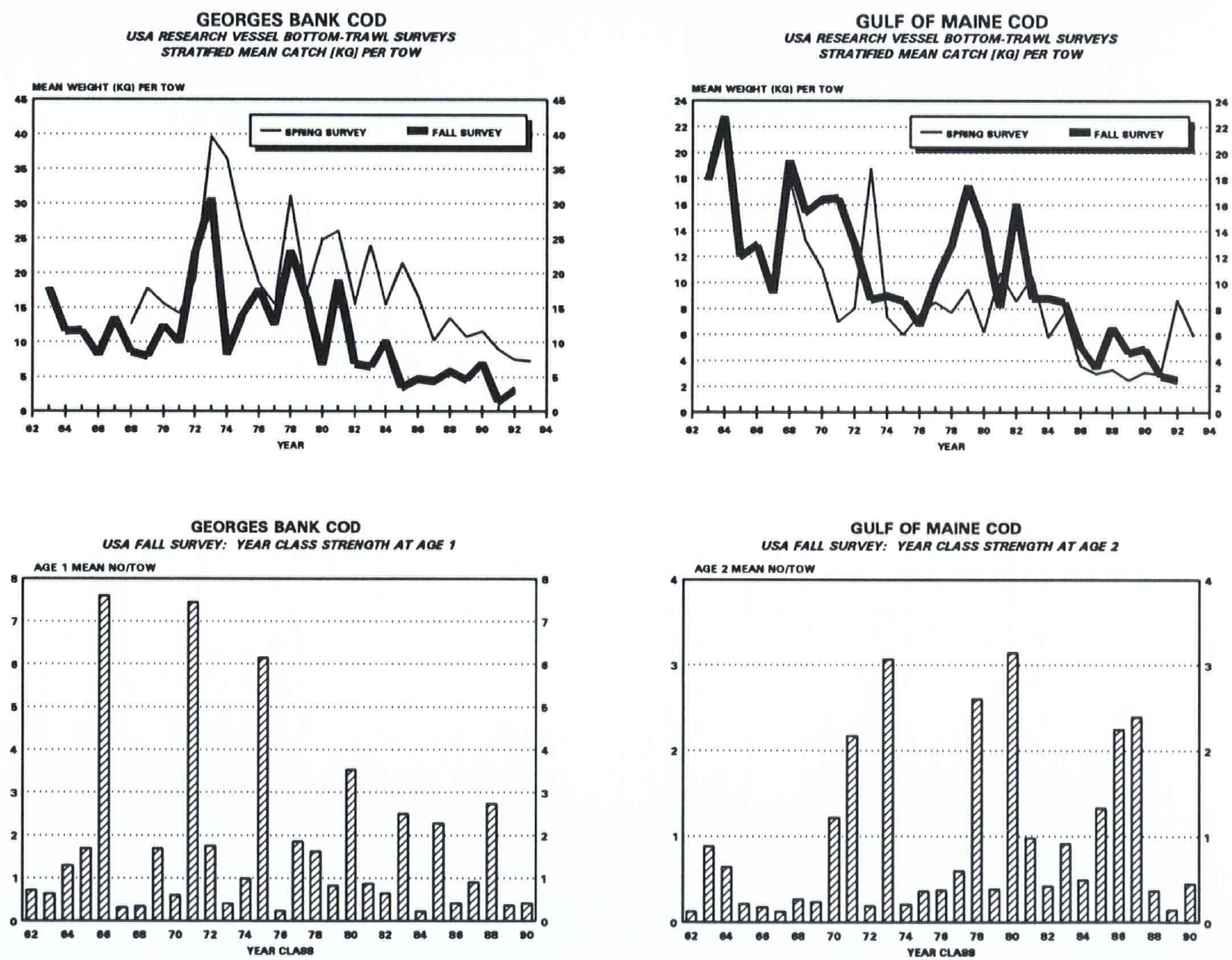


Figure 10. Standardized stratified mean catch per tow indices (top) and survey recruitment indices (bottom) for the Georges Bank and Gulf of Maine cod stocks from NEFSC spring and autumn bottom-trawl surveys (1963–1992).

stock (survey number-per-tow indices at age 2) indicate that the 1971, 1973, 1978, 1980, 1986, and 1987 year classes were all above average.

Trends in stock size, recruitment, and fishing mortality

Estimates of stock size, recruitment, and fishing mortality for the Georges Bank and Gulf of Maine cod stocks are available from virtual population analyses (VPA). For Georges Bank cod, the VPA covers the 1978–1992 period (Serchuk *et al.*, 1993); for the Gulf of Maine stock, the VPA extends from 1982–1992 (Mayo *et al.*, 1993).

During the past 10–15 years, marked reductions in the abundance of both cod stocks have occurred coincident with increases in fishing mortality rates. In the Georges Bank stock, spawning-stock biomass (SSB) declined by over 40% between 1980 and 1985 (93 000 to 55 000 t) while fishing mortality rates increased by 50% (Fig. 11). SSB increased in 1987 to 66 000 t and stabilized at about 70 000 t during 1988–1990 due to strong recruitment from the 1983 and 1985 cohorts. Fishing mortality, however, continued to rise, and increased from F = 0.63 in 1989 to a record-high F = 1.07 in 1991 (a 70% increase). SSB subsequently declined sharply in 1991 and fell to a record-low of 41 000 t in 1992. Further declines in SSB are expected in 1993 and 1994 when the 1989–1991 year classes, all below average in abundance (i.e., below 21 million fish at age 1), recruit to the spawning stock.

In the Gulf of Maine stock, fishing mortality increased from F = 0.62 in 1982 to above F = 1.0 during 1985–1987 (Fig. 11). In this same time period (1982–1987), SSB declined from 25 700 t to 13 900 t. Because of above-average recruitment of the 1986 year class and the exceptionally strong 1987 year class, SSB increased sharply in 1989 and reached a record-high level of 27 500 t in 1990. However, poor recruitment of the 1988–1990 year classes, coupled with fishing mortality rates above F = 1.0 in both 1990 and 1991, resulted in SSB declining in 1992 to a record-low of 13 600 t. SSB of Gulf of Maine cod is expected to decline below 12 000 t in 1993 as the 1987 cohort (which accounted for over 60% of the catch and SSB in 1992) is further fished down.

The striking declines in biomass in both the Georges Bank and Gulf of Maine cod stocks have occurred during a period when landings, fishing effort, and fishing mortality have increased to record-high levels. For both stocks, recent fishing mortality rates have far exceeded the levels generally associated with stock replacement (F_{med} or $F_{20\%}$) or growth overfishing (F_{max}). On an annual basis, the fisheries on the two stocks currently remove between 40 and 60% of the exploitable biomass. Factors other than fishing may also have affected the stocks but these influences are not easily discernible given the magnitude of the fishery-induced perturbations.

Environmental and biotic processes affecting cod life history

Despite the long history of exploitation of cod in the Georges Bank–Gulf of Maine region, it has only been rather recently that sufficient information has been obtained to begin sorting out the environmental factors from the fishery events affecting cod abundance. This information has come largely from a time series of research vessel surveys and accompanying biological studies, which indicate that environmental effects are most significant during the first year of life. Attempts to correlate recruitment and egg/larval abundance of Georges Bank cod have failed so far (Smith *et al.*, 1981; Fogarty *et al.*, 1987), but significant correlations have been observed between recruitment and trawl survey catches of 0-group and 1-year cod on Georges Bank (Serchuk *et al.*, 1993). This supports the inference that factors controlling cod year-class success operate chiefly during the first year of life.

Approximate mortality estimates in late-larval and postlarval stages of cod (≥99.9%) are typically as high or higher than mortality in the egg and early larval stages (Sissenwine *et al.*, 1984); thus a small change in natural mortality at these late larval or juvenile stages could make the difference between a strong or weak year class. Given the high mortality rates in both the early and late 0-group stages, Sissenwine (1984) concluded that recruitment is likely to be a function of highly variable processes occurring throughout the first year of life.

While density-dependent mortality in late-larval and juvenile stages is important in regulating year-class size, a general view is emerging that the major variability in recruitment ("bumper" vs. "bust" year classes) is largely due to density-independent mortality during the egg and early larval stages. Based on a comprehensive review of egg and larval predation mortality, Bailey and Houde (1989) concluded that year-class strength is established very early (i.e., at the egg and larval stages), but that predation on later stages can have moderate to large effects on recruitment (i.e., altering year-class strength by an order of magnitude or less). Myers and Cadigan (1993a) examined juvenile mortality data from six cod stocks and found strong evidence of density-dependent mortality within cohorts, as well as a negative autocorrelation between adjoining cohorts. The Georges Bank and Gulf of Maine stocks were included in these analyses and generally fit the patterns seen in the other stocks, except that density-dependent mortality was not evident for Georges Bank cod, possibly due to the very low abundance level of this stock. Little interannual vari-

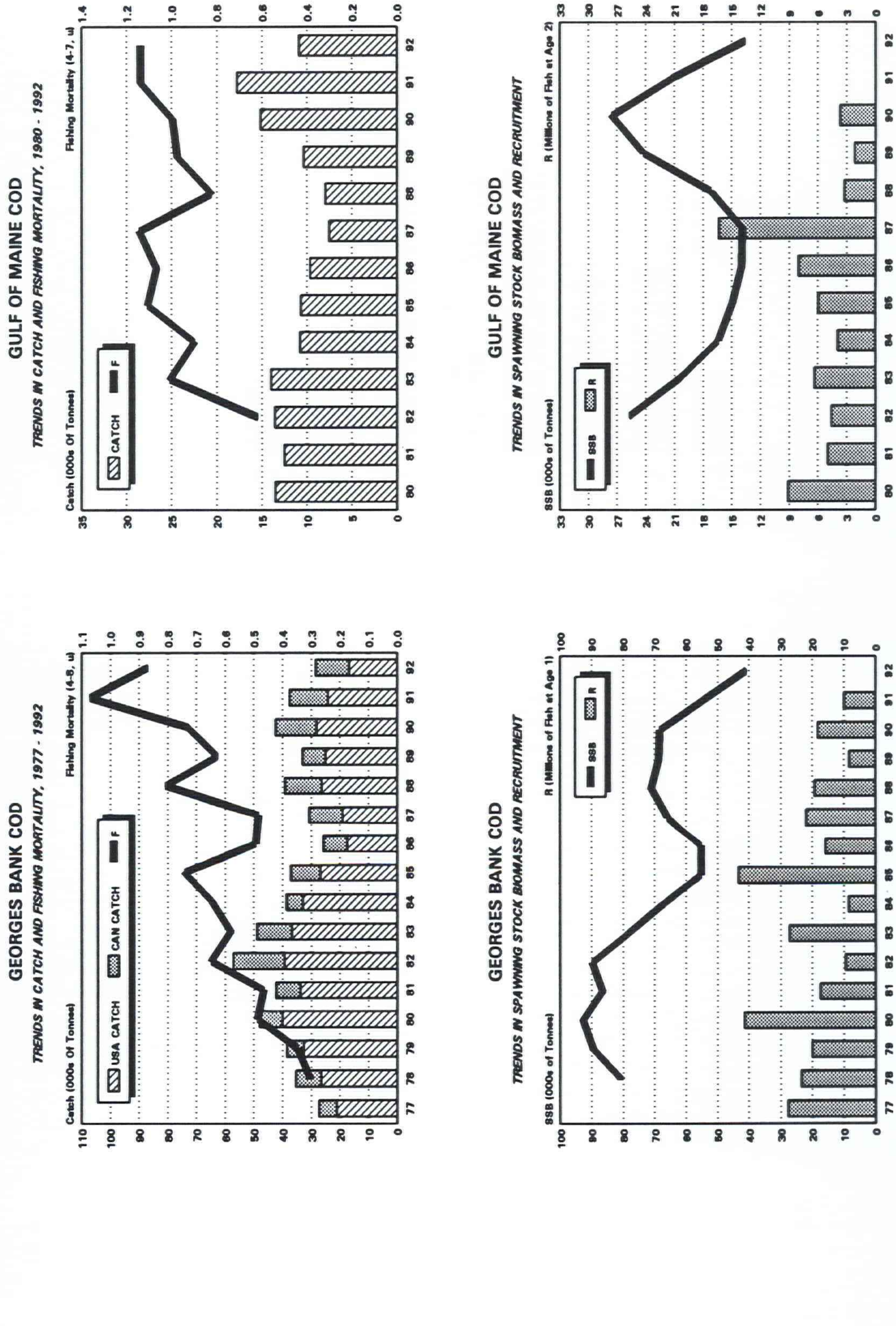


Figure 11. Trends in commercial catches and fishing mortality (top) and spawning-stock biomass and recruitment (bottom) for the Georges Bank and Gulf of Maine cod stocks derived from VPA analyses. Data derived from 1993 assessments (from Serchuk *et al.*, 1993; Mayo *et al.*, 1993).

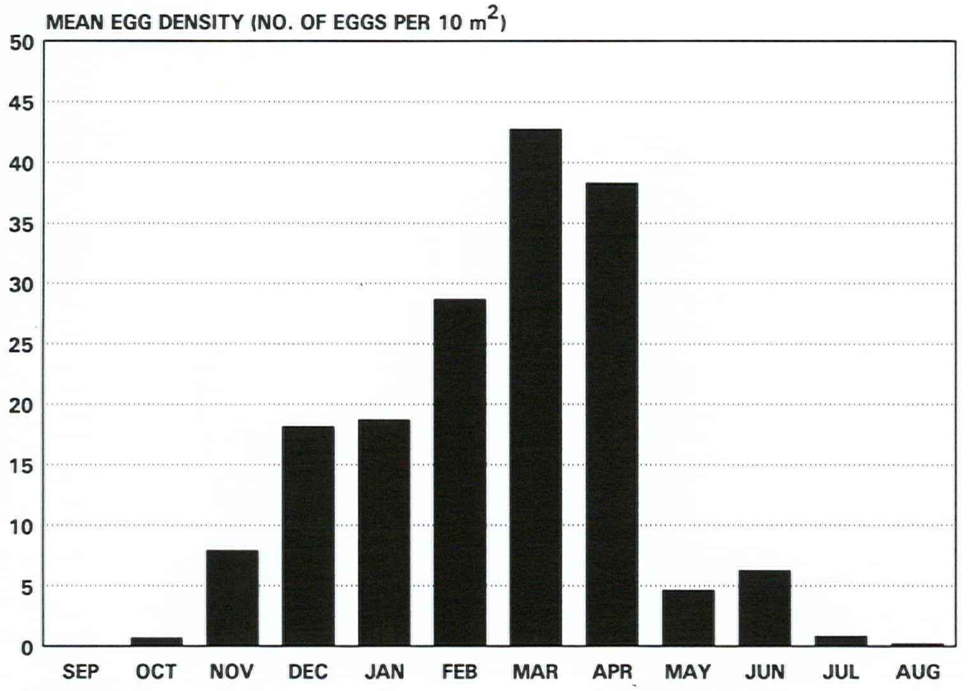


Figure 12. Average monthly egg densities of Atlantic cod off the northeastern coast of the United States (1978–1987) (from Berrien and Sibunka, 1993).

ability was found in the density-independent component of juvenile cod mortality (Myers and Cadigan, 1993b). Myers and Cadigan concluded that the major variability in year-class strength of cod (and in many other marine demersal species) was determined during the larval stage, but that this variability was subsequently attenuated by density-dependent mortality during the juvenile stage.

A number of mechanisms associated with physical factors could influence survival of eggs and early-stage larvae, including advection, food supply, temperature, and predation. Postlarval stages would be less affected by advection, but their growth and predation susceptibility would certainly be affected by food supply and temperature. For Georges Bank cod, energy balance calculations and food habits studies (Fogarty *et al.*, 1987) indicate that predation is the principal natural mortality affecting postlarval survival. Hence, the modes by which physical factors influence the survival of postlarvae are likely to be indirect – via effects on cod growth (food supply and temperature) and predation vulnerability (available juvenile habitat, and match/mismatch in the spatial/temporal distributions of juvenile cod and their predators).

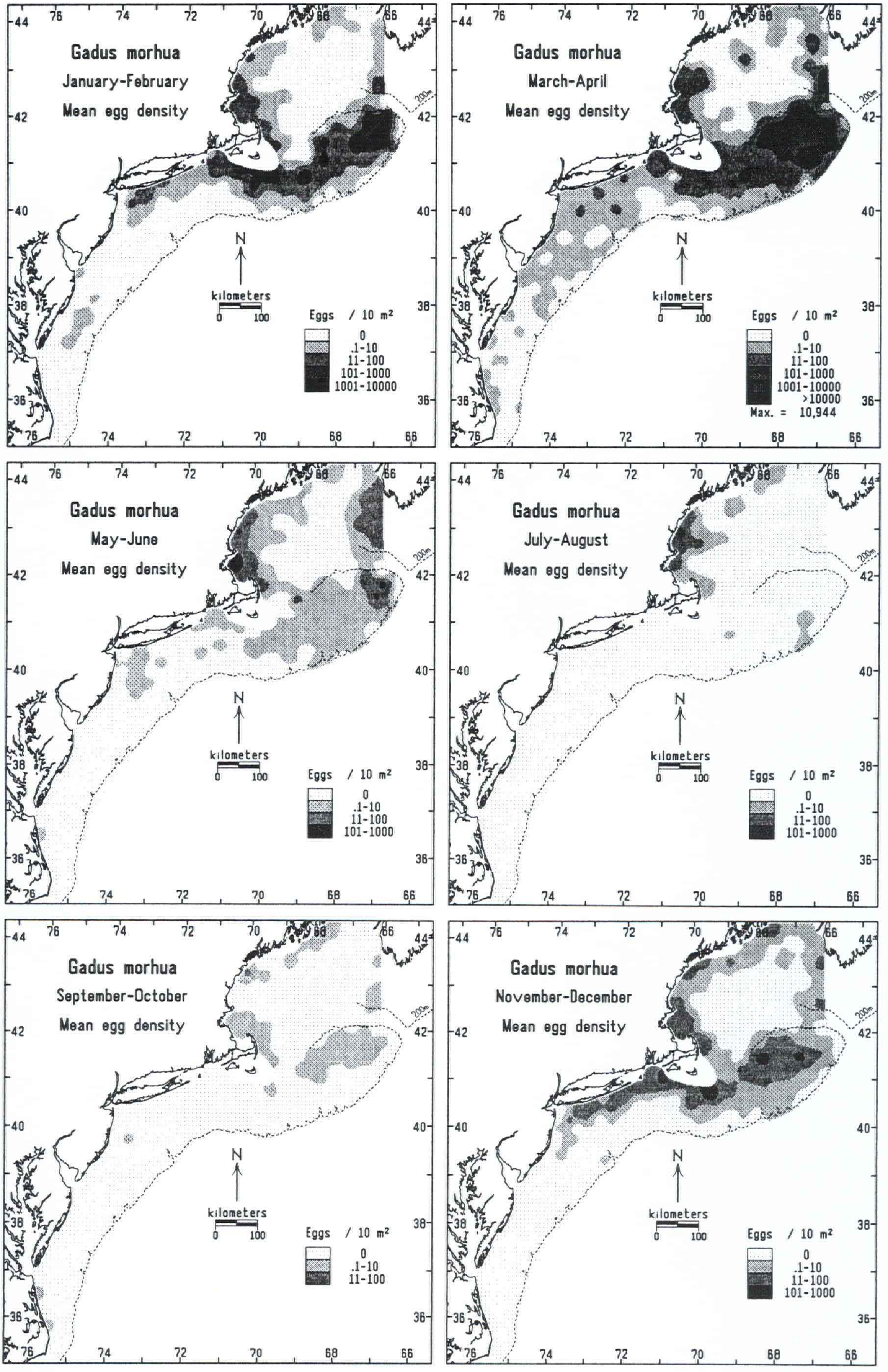
The basic features of the life history of cod in relation to both environmental and biotic processes are outlined below, as background for the review – presented in the subsequent section – on the environmental influences affecting cod. Current and future research studies aimed at differentiating environmental from fishery-related factors affecting recruitment and abundance of cod in the Georges Bank – Gulf of Maine region are discussed in the concluding section of the paper.

Life history features

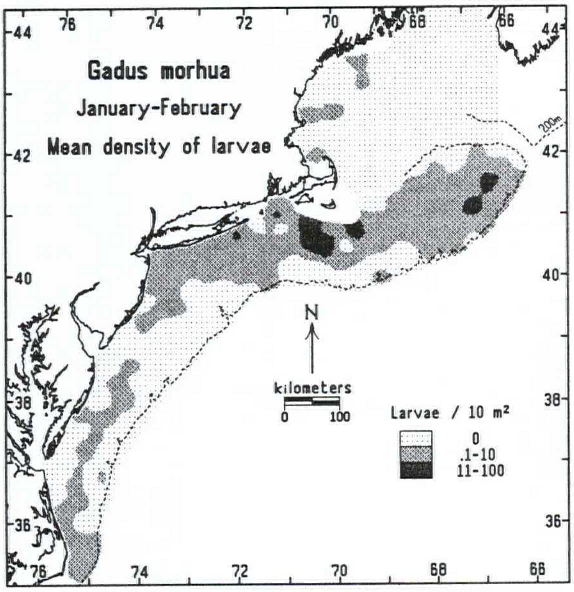
Spawning time and location

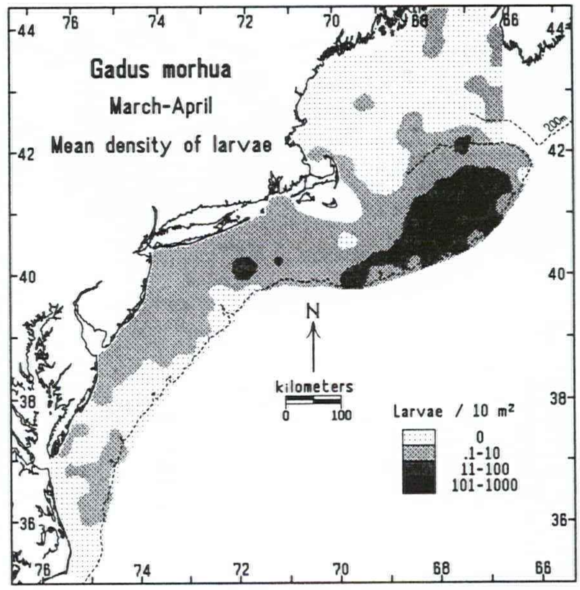
Spawning of cod in the Gulf of Maine–Georges Bank region exhibits a pronounced seasonal cycle. Monthly composite distributions of egg densities from an 11-year series (1977–1987) of ichthyoplankton surveys (i.e., the US MARMAP study) indicate that cod spawning occurs primarily between November and June, with peak spawning in March and April (Berrien and Sibunka, 1993; Fig. 12). Based on geographic distributions of cod eggs and larvae (Figs. 13 and 14), principal spawning areas occur on Georges Bank, in Southern New Eng-

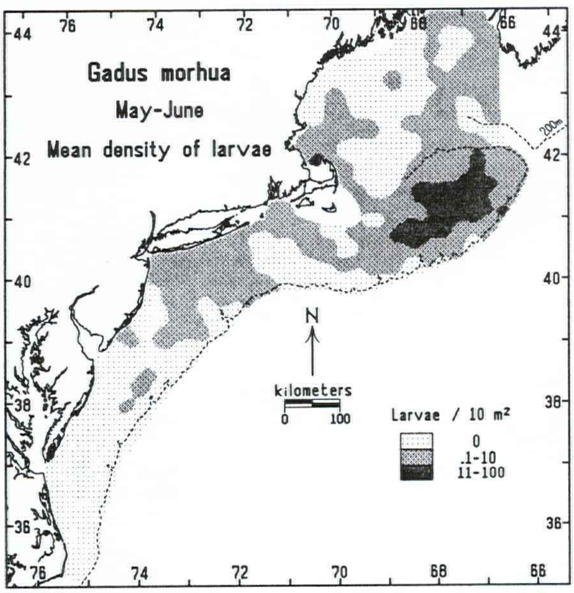
Figure 13. Composite bimonthly geographic distributions of Atlantic cod eggs off the northeastern coast of the United States from MARMAP surveys (1977–1987).

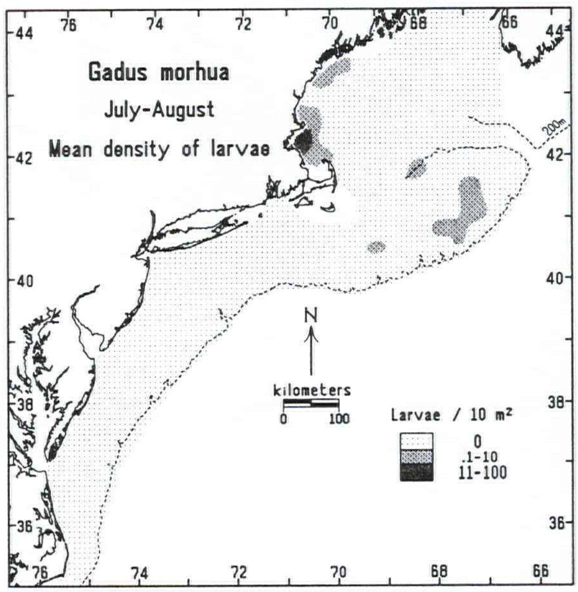


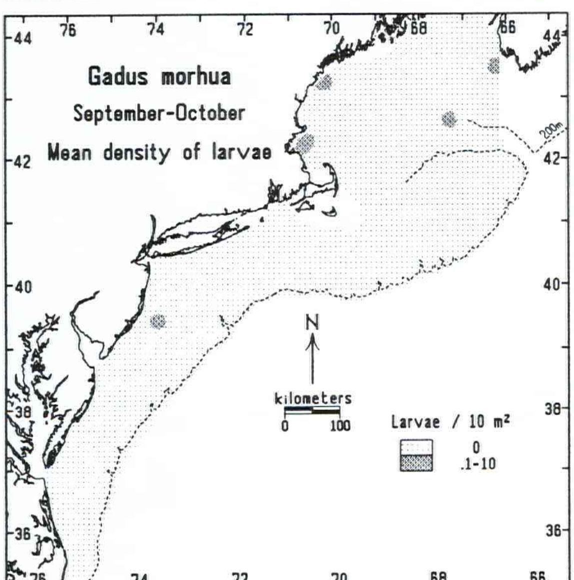
Gadus morhua
January-February
Mean egg density
Eggs / 10 m²
0
.1-10
11-100
101-1000
1001-10000
kilometers
0 100
N
200m
Gadus morhua
March-April
Mean egg density
Eggs / 10 m²
0
.1-10
11-100
101-1000
1001-10000
>10000
Max. = 10,944
kilometers
0 100
N
200m
Gadus morhua
May-June
Mean egg density
Eggs / 10 m²
0
.1-10
11-100
101-1000
kilometers
0 100
N
200m
Gadus morhua
July-August
Mean egg density
Eggs / 10 m²
0
.1-10
11-100
101-1000
kilometers
0 100
N
200m
Gadus morhua
September-October
Mean egg density
Eggs / 10 m²
0
.1-10
11-100
kilometers
0 100
N
200m
Gadus morhua
November-December
Mean egg density
Eggs / 10 m²
0
.1-10
11-100
101-1000
kilometers
0 100
N
200m

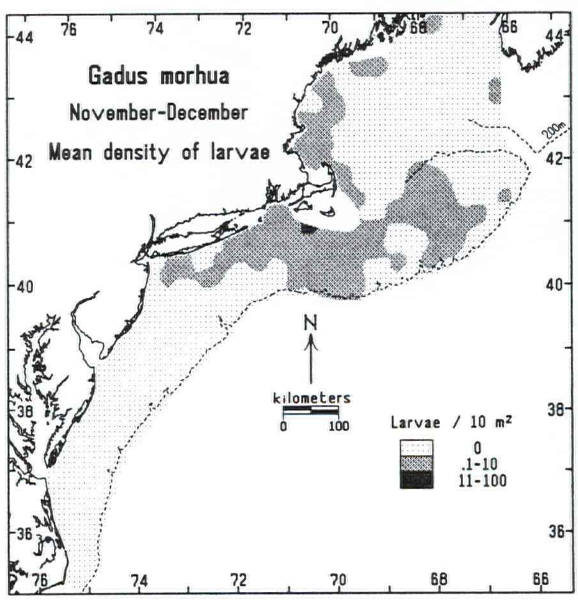

Gadus morhua
January-February
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100
200m


Gadus morhua
March-April
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100
101-1000
200m


Gadus morhua
May-June
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100
200m


Gadus morhua
July-August
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100
200m


Gadus morhua
September-October
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
200m


Gadus morhua
November-December
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100
200m

land, and along the western Gulf of Maine (Morse *et al.*, 1987; Smith and Morse, unpub. data; Berrien and Sibunka, 1993). On Georges Bank and in Southern New England, cod eggs are most abundant during November through April; generally, the highest densities of eggs occur on Georges Bank in March. In the western Gulf of Maine, eggs are abundant between November and June, with some concentrations occurring even in July (Fig. 13).

Distribution of early life stages

Eggs spawned on the northeastern portion of Georges Bank generally drift southwesterly in the clockwise gyre normally present on the Bank (Fig. 6). At typical early spring temperatures, the eggs hatch in about two to three weeks (Laurence and Rogers, 1976). Identifiable egg, larval, and pelagic juvenile patches have been followed from spawning on northeastern Georges Bank, and have been shown to be advected along the southern flank of the Bank in a sheared flow field (Smith *et al.*, 1981; Morse *et al.*, 1987; Lough and Bolz, 1989). A variable fraction of the eggs and larvae reaching the western part of the Bank near the Great South Channel are caught up in the gyre (as are the eggs and larvae spawned in the South Channel area) and are recirculated around the Bank. Some fraction, however, is advected westward to the Southern New England and Middle Atlantic regions. In unusual years, a significant fraction of larvae can be transported off Georges Bank and into Middle Atlantic waters (e.g., as occurred in 1987 with haddock larvae; see Polacheck *et al.*, 1992), although some spawning of cod also occurs in the southerly areas.

It is not known to what degree eggs and larvae are transported northeastwards from Georges Bank (i.e., to the Scotian Shelf), but advective losses do occur, especially in early spring when the Georges Bank gyre is weaker and storm events are more frequent. Eggs and larvae spawned in the Gulf of Maine tend to drift south and eastward (towards Georges Bank) owing to the counter-clockwise Gulf of Maine gyre. However, the extent of exchange of cod offspring between the Gulf of Maine and Georges Bank regions is unknown.

During early spring on Georges Bank, the waters are well mixed and eggs and larvae are broadly distributed throughout the water column (Lough and Potter, 1993). Late-stage larvae and pelagic juveniles are located progressively deeper in the water column; by the time juveniles have grown to 40 mm, most are associated with the bottom. The diel vertical movement of cod appears to be strongly related to the light–dark cycle. Larvae tend to be found deeper by day than at night, with larger fish having a greater vertical range. Recently settled juveniles remain on the bottom during the day but migrate 3–5 m into the water column at night.

Lough and Bolz (1989) found evidence for continuous recruitment of both cod and haddock larvae onto the central shoals area (<60–70 m) of Georges Bank. At depths less than 70 m, retention of larvae appears to be enhanced via interactions with cross-isobath tidal currents. Based on results from an advection model, Werner *et al.* (1993) reported that cod larvae are transported westward along the southern flank of the Bank – and are more likely to be retained on the Bank – when the larvae occur shoalward of the 70-m isobath and are near the bottom. In late spring, when stratification begins, the Georges Bank gyre intensifies and reinforces the tidally-rectified recirculation pattern (Butman *et al.*, 1987). Hence, both the time and strength of stratification influence the retention of larval cod on Georges Bank.

Prior to settling to the bottom in early summer, pelagic juveniles (20–50 mm) are broadly distributed over the entire Bank (Lough *et al.*, 1989).

Growth and mortality of 0-group cod

The growth of larval cod on Georges Bank has been described by Gompertz-type curves based on daily growth increments of otoliths (Bolz and Lough, 1988). Growth rate increases from 0.13 mm/day after hatching to about 1.0 mm/day at 100 days of age. In June, pelagic juveniles range from 20 to 50 mm in length, and most juveniles are between 50 and 80 mm in size by the end of July (Lough *et al.*, 1989). By the end of their first year of life, Georges Bank cod reach an average length of 26 cm (Penttila and Gifford, 1976).

The mortality rate of cod eggs on Georges Bank has been estimated from ichthyoplankton surveys conducted from 1979 to 1987; daily mortality estimates range from 2% to 20%, and average 10% per day over the 20-day egg incubation period (pers. comm., Peter Berrien). Average mortality of cod larvae on Georges Bank [derived from 1977–1984 ichthyoplankton surveys] is estimated at 4% per day during the approximate 100-day period between hatching (4 mm) and 20 mm size (Morse, 1989).

Using these mortality estimates, total instantaneous natural mortality for the 120 days between fertilization and 20 mm size is $M = 6.0$ [i.e., $(M_{egg} = 0.1 \times 20) + (M_{4\text{–}20\text{ mm larvae}} = 0.04 \times 100)$]. Total mortality from the

Figure 14. Composite bimonthly geographic distributions of Atlantic cod larvae off the northeastern coast of the United States from MARMAP surveys (1977–1987).

egg stage to recruitment at age 1 is estimated to be M_t = 13.8, viz.:

$$\begin{aligned} M_t &= -\ln(R/E) \\ &= -\ln[(2.2 \times 10^7)/(21.7 \times 10^{12})] \\ &= 13.8 \end{aligned}$$

where R = average number of age 1 recruits for the 1979–1984 cohorts and E = average number of eggs spawned during 1979–1984.

By subtraction (13.8 − 6.0), total instantaneous mortality for the postlarval stage is M = 7.8. These rates thus correspond to overall mortalities (expectations of death) during the egg, larval, and postlarval stages of 86%, 98%, and >99.9%, respectively. The level of postlarval mortality (>99.9%) during 1979–1984 is similar to that estimated by Sissenwine *et al.* (1984) for the 1974–1980 period.

Larval and postlarval mortality rates can also be derived by comparing direct estimates of postlarval (≥20 mm) cod abundance for the 1986 and 1987 Georges Bank cohorts [from June surveys using a 10 m^2 MOCNESS sampler] with estimates of eggs spawned and age 1 recruits for these year classes (unpubl. data, Peter Berrien and Gregory Lough). These data indicate that total egg and larval mortality rates in 1986 and 1987 were M_t = 6.8 (99.9%) and M_t = 5.6 (99.6%), respectively. Postlarval mortality (from about mid-June until age 1) was M_t = 6.2 (99.8%) in 1986 and M_t = 6.8 (99.9%) in 1987. These values are consistent with the 1974–1980 and 1977–1987 averaged estimates, and again demonstrate that postlarval mortality in cod is comparable to that experienced in the egg and larval stages.

Prey and predators of 0-group stages

In the Georges Bank–Gulf of Maine region, the prey of larval cod consists of zooplankton. Yolk sac and first-feeding larvae prey primarily on small plankton such as copepod nauplii, phytoplankton, and lamellibranch larvae. With the exception of the yolk-sac stage, cod larvae feed on the same prey species throughout their early life, selecting the most numerically dominant prey (Kane, 1984; Buckley and Lough, 1987; Auditore *et al.*, 1994).

Prey size plays an important role; as cod grow larger, they tend to select larger size prey items. On Georges Bank, cod larvae feed on copepod nauplii, copepodites, and adults of *Calanus finmarchicus, Pseudocalanus* spp., *Oithona similis,* and *Centropages typicus*. As pelagic and recently settled juveniles, cod shift to epibenthic prey and swarming species that – like cod – also undergo diel vertical migrations. These food items include mysids (*Neomysis americana*), amphipods (*Gammarus annulatus*, *Themisto gaudichaudii*, *T. compressa*), chaetognaths (*Sagitta elegans*), and euphausiids (*Meganyctiphanes norvegica*) (Auditore *et al.*, 1988; Perry and Neilson, 1988; Lough *et al.*, 1989).

Much less is known of the predation on young cod in the Georges Bank–Gulf of Maine region than of their prey and feeding. Cod larvae and pelagic juveniles are themselves likely predators of smaller cod larvae (Laurence *et al.*, 1981). However, to date, there is little direct evidence of cannibalism. Mackerel are confirmed fish predators of cod and haddock larvae, and herring very likely also prey on small cod larvae (Michaels, 1991). Dogfish, silver hake, squid, larger cod, and many other piscivores prey on juvenile cod (Edwards and Bowman, 1979).

Despite limited direct evidence, the importance of predation as a dominant source of pre-recruit mortality in many fish populations is now a widely accepted assumption (Hunter, 1981; Sissenwine, 1984; Houde, 1987, 1989; Bailey and Houde, 1989). However, there are insufficient data from the studies on Georges Bank and in the Gulf of Maine to reliably quantify egg and larval predation mortality, let alone partition these mortalities among the various predators. New research initiatives currently underway on Georges Bank are designed to address these questions (see concluding section on Future Research).

Post-juvenile growth and maturation

Georges Bank cod grow more rapidly than Gulf of Maine cod. Penttila and Gifford (1976) fitted von Bertalanffy growth curves for cod collected from research vessel surveys in the early 1970s and found that at age 2 (January 1) Georges Bank cod averaged 39.9 cm in length while Gulf of Maine cod were only 26.4 cm long. The von Bertalanffy parameters for the two stocks are as follows:

	L_{inf}	K	t_0
Georges Bank	148.1	0.120	−0.616
Gulf of Maine	146.5	0.116	0.285

Based on mean weights-at-age in commercial catches, the growth rates of Georges Bank and Gulf of Maine cod appear to be intermediate compared with those in other North Atlantic cod stocks (Fig. 15).

Georges Bank cod mature earlier than Gulf of Maine cod, and fish in both stocks appear to mature earlier – and at a smaller size – than in most other North Atlantic stocks (Table 3). During the early 1970s, Georges Bank cod reached 50% maturity at about 2.8 years old as compared to 3.5 years for cod in the Gulf of Maine (Livingstone and Dery, 1976). Recently, however, the A_{50} values have declined in both stocks and are now 1.8 and 2.2 years, respectively (O'Brien *et al.*, 1993; Table 3). These A_{50} values are probably the lowest in any North Atlantic cod stock, including the North Sea stock, where cod display even faster somatic growth than on Georges Bank (Table 3, Fig. 15).

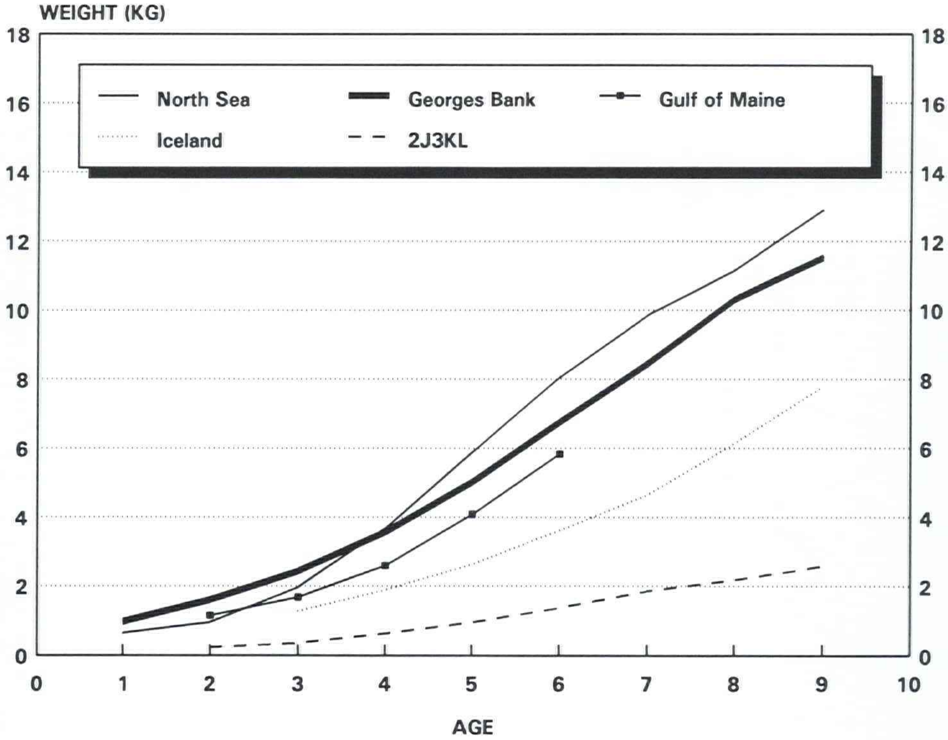


Figure 15. Mean catch weight-at-age values for five North Atlantic cod stocks. Values depicted are those used in the most recent stock assessments.

Of the few studies conducted on cod maturation in the Georges Bank–Gulf of Maine area, only the most recently completed study (O'Brien, 1990) is temporally and spatially comprehensive. This study, based on data from NEFSC spring research surveys collected during 1970–1990, indicates that both length and age at maturation have declined in both stocks over the past two decades. On Georges Bank, the estimated median age (A_{50}) and median length (L_{50}) at maturity for female cod declined from 2.7 year and 53.4 cm for the 1970 year

Table 3. Median age at maturity (A_{50}) and median length at maturity (L_{50}) of Atlantic cod in various North Atlantic stocks. Data are provided for females (F) and males (M), or sexes combined (C).

Area	Time period	A_{50} (years) F	A_{50} (years) C	A_{50} (years) M	L_{50} (cm) F	L_{50} (cm) C	L_{50} (cm) M	Source of data
Georges Bank	1972	2.9	–	2.6	51.5	–	44.0	Livingstone and Dery (1976)
	1985–1990	1.7	–	1.9	38.8	–	41.0	O'Brien *et al.* (1993)
Gulf of Maine	1878	4.0	–	3.0	–	–	–	Earll (1880)
	1972	3.5	–	3.5	–	–	–	Livingstone and Dery (1976)
	1985–1990	2.1	–	2.3	32.1	–	36.0	O'Brien *et al.* (1993)
Nova Scotia to Cape Hatteras	1977	–	–	–	49.6	–	53.7	Morse (1979)
Scotian Shelf	1963	5.0	–	3.9	52.0	–	51.0	Beacham (1983)
	1978	2.0	–	2.0	35.0	–	38.0	Beacham (1983)
NAFO Area 2J3KL	–	–	6.0	–	–	49.7	–	Xu *et al.* (1991)
Iceland	–	–	3.4	–	–	–	–	ICES (1993a)
North Sea	–	–	3.7	–	–	–	–	ICES (1993b)

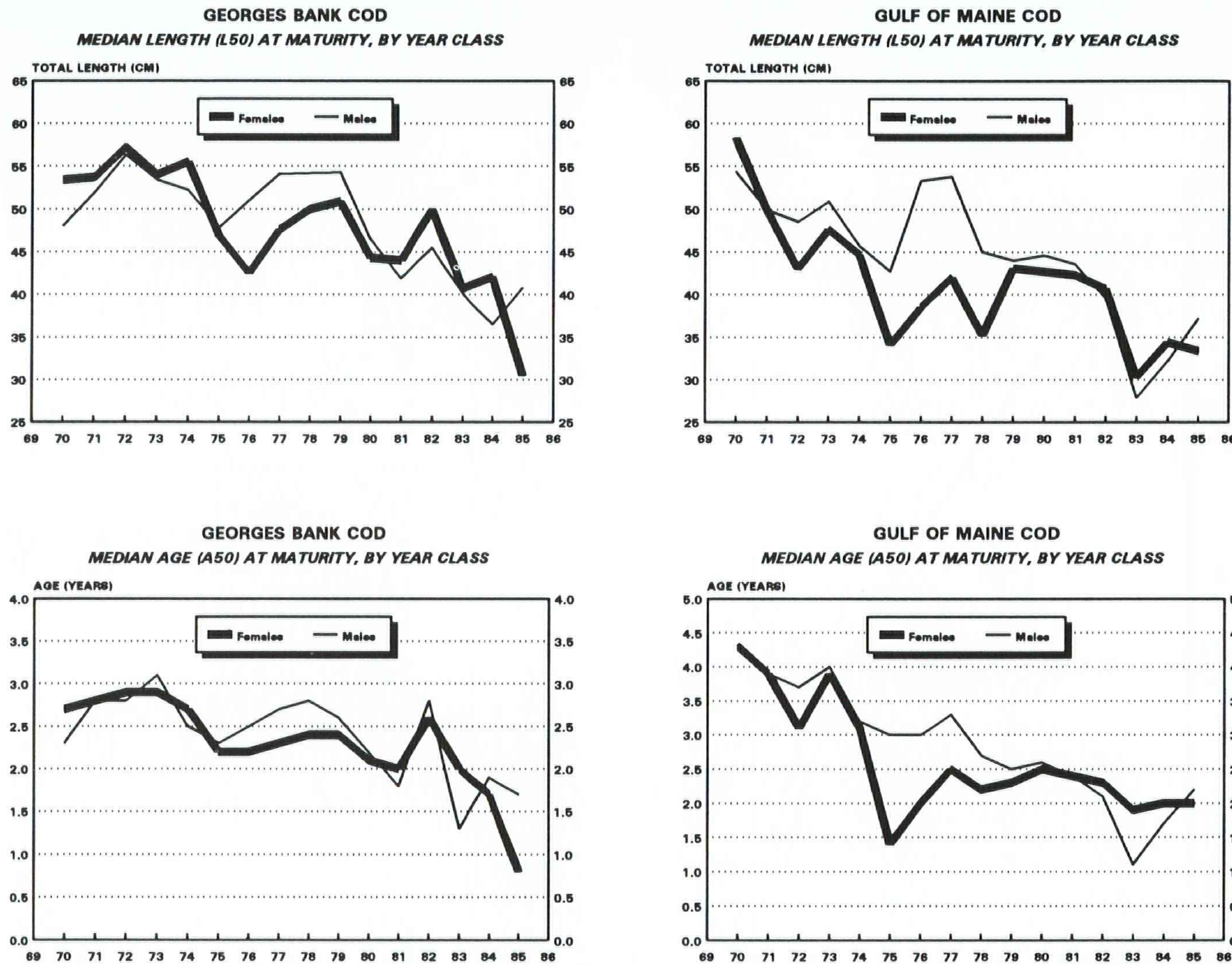


Figure 16. Trends in median length at maturity, by year class (top) and median age at maturity, by year class (bottom) for the Georges Bank and Gulf of Maine cod stocks. Data derived from NEFSC bottom trawl surveys.

class to 0.8 years and 30.5 cm, respectively, for the 1985 year class (Fig. 16). Similar trends have occurred in Gulf of Maine cod for the same year classes; A_{50} and L_{50} values for females declined from 4.3 years and 58.3 cm (1970 year class) to 2.0 years and 33.4 cm (1985 year class). In both stocks, A_{50} and L_{50} for males have declined in tandem with those for females (Fig. 16).

The accelerated maturation rates in both stocks have occurred over a time period during which marked reductions in stock abundance have occurred. Changes in maturation show a significant correlation with changes in abundance of the two stocks, but not with annual changes in water temperatures (O'Brien, 1990).

Food and feeding of juvenile and adult cod

Extensive studies of food habits of fishes on Georges Bank and in the Gulf of Maine have been conducted in conjunction with the NEFSC research vessel surveys in these areas (Grosslein *et al.*, 1980). These studies show that the diet of juvenile and adult cod in both areas is basically similar to that found in other North Atlantic cod stocks; fish represent the major prey item (in terms of percentage weight of stomach contents), followed by crustaceans and mollusks (Edwards and Bowman, 1979; Fig. 17). On Georges Bank, fish comprised 62% of the diet of cod during 1969–1972, with about 15% each for crustacea and mollusks (Langton and Bowman, 1980). During the same time period, the diet of Gulf of Maine cod was comprised of 70% fish, 26% crustaceans, and 1% mollusks. The major fish prey of cod in both areas was clupeids (chiefly *Clupea harengus*), but flounders and other gadids were also consumed on Georges Bank, while redfish, mackerel, and other gadids were taken as prey in the Gulf of Maine (Langton and Bowman, 1980).

The principal crustaceans consumed by cod in both areas are decapod crabs and shrimp. Of the mollusks eaten, squid constitute the major prey of Gulf of Maine cod, while the discarded remains of sea scallops (from scallop vessels shucking at sea) are often an important molluscan component of the diet of Georges Bank cod (Langton and Bowman, 1980; Bowman and Michaels, 1984). Juvenile cod (6–10 cm) consume some fish but depend most heavily on amphipods and small decapod shrimp. Larger crustacea and more fish are eaten by cod as they grow. By the time cod attain a length of 50–60 cm, their overall diet is about half fish and half invertebrates; thereafter, the proportion of fish in the diet continues to increase (Bowman and Michaels, 1984).

During the mid-1960s and early 1970s, large declines in fish biomass occurred on Georges Bank due to intensive fisheries exploitation (Mayo *et al.*, 1992). Comparisons of cod diets before and after this period indicated a change in diet composition; the percent frequency occurrence of fish (all species) in cod stomachs dropped from 37% in 1963–1966 to 29% in 1973–1976 (Grosslein

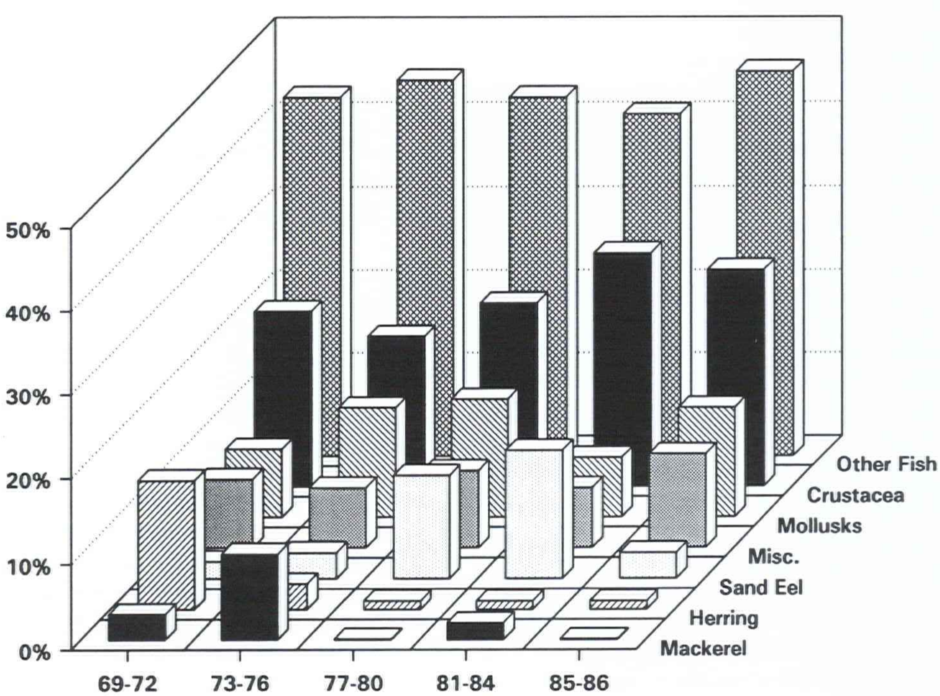


Figure 17. Diet composition (% by weight of prey) of Atlantic cod off the northeast coast of the United States (1969–1986).

et al., 1980). The reduced incidence of fish in the diet of cod was due to decreased consumption of gadids, since the incidence of clupeids remained unchanged (Grosslein *et al.*, 1980). Although the stomach sampling protocols were quite different between the 1963–1966 and 1973–1976 periods (and hence the data not strictly comparable), the reduced incidence of gadids in the post-1972 diet appears to be a real reflection of the diminished abundance and availability of the Georges Bank gadid stocks. On the other hand, sea herring abundance was considerably greater on Georges Bank during 1963–1966 than in 1973–1976, yet the frequency of occurrence of clupeidae in cod stomachs was virtually the same in both time periods (Grosslein *et al.*, 1980). In more recent years (1977–1986), cod diets in both the Gulf of Maine and on Georges Bank have shown a lower fraction of fish balanced by an increased proportion of invertebrate prey (Fig. 17). This apparent shift could be a reflection of reduced availability of preferred fish prey and partial compensation (substitution) of invertebrate prey for fish (ICES, 1992).

Estimates of daily ration for cod in the Georges Bank–Gulf of Maine region range from about 1–2% body weight per day (Edwards and Bowman, 1979; Grosslein *et al.*, 1980; Cohen and Grosslein, 1981; Durbin *et al.*, 1983). These estimates are somewhat higher than the daily ration estimates of 0.8–1.0% body weight per day for similar-sized cod (50–60 cm) in the North Sea (Daan, 1973) – despite the fact that mean weight of gut contents is more than twice as great in North Sea cod (Ursin *et al.*, 1985) and both stocks have similar growth rates (Ursin, 1984). However, the mean stomach content weights of cod on the Scotian Shelf and off Newfoundland are also much larger than those observed on Georges Bank, but growth rates of cod in these areas are much slower (Ursin, 1984; Ursin *et al.*, 1985). Recent analyses of cod food habits data by the ICES Multispecies Assessment Working Group indicate that for most North Atlantic cod stocks stomach content weight is inversely correlated with temperature; the lower mean stomach content weights of cod off the northeastern United States are thought to result from higher ambient water temperatures (ICES, 1992). The fraction of fish in the diet of Georges Bank/Gulf of Maine cod is also generally lower than observed in other North Atlantic cod stocks (ICES, 1992). More investigations on the effects of prey size and prey type (as well as temperature) on digestion rates are considered to be essential in resolving these apparent paradoxes, as well as to obtain more accurate estimates of consumption rates by cod and other species (Ursin *et al.*, 1985).

A measure of the relative importance of cod as a piscivore on Georges Bank is provided within the framework of energy budget calculations for Georges Bank. Fish consumption by cod represented only 3% of the total estimated production of fish (including pre-recruit stages) and just 4% of the pre-recruit fish production component for the periods 1964–1966 and 1973–1975 (Sissenwine *et al.*, 1984). By comparison, the consumption of fish by silver hake represented 55% and 67% of the total estimated fish production and 69% and 93% of the pre-recruit fish production. While there is considerable uncertainty about the accuracy of the absolute values of the energy budget calculations, they provide a reasonable basis for concluding that cod is not the controlling fish predator in the Georges Bank and Gulf of Maine regions. Given that the biomass of both cod stocks has recently sharply declined while other piscivorous species (notably spiny dogfish) have markedly increased (US Department of Commerce, 1992), it is believed that cod plays only a minor role in regulating the current production and composition of the finfish biomass in the Georges Bank/Gulf of Maine ecosystems.

Environmental factors affecting cod

Seasonal and interannual changes in the environmental conditions on Georges Bank and in the Gulf of Maine exert influences on the cod stocks – in terms of both their distribution and abundance. Environmental factors affecting the abundance of cod most likely occur at the early life history stages. While a number of physical and biological properties and processes can potentially influence growth and survival of cod larvae and juveniles, different properties or physical processes may be important during each of the different life stages. Many hypotheses have been proposed linking environmental conditions and cod recruitment success, but so far few relationships have been established based on actual observations and none have yet led to an in-depth understanding of the actual mechanisms involved.

Temperature

The environmental influence most easy to document is the effect of temperature changes on stock distributions. During NEFSC spring trawl surveys, when bottom water temperatures are 4–6°C, adult cod are widely dispersed across Georges Bank (Fig. 3). In autumn, when bottom water temperatures are above 10°C, the distribution of cod shifts with the highest concentrations of adults found in the cooler, deeper waters off the northern side of the Bank and in the northern part of the Great South Channel (Fig. 3). A similar seasonal pattern is also evident for juvenile fish (Wigley and Serchuk, 1992). Interannual changes in temperature also affect cod distribution patterns. Mountain and Murawski (1992) compared the average bottom water temperature on Georges Bank during spring NEFSC surveys with the average temperature at which cod were caught in the surveys. The two temperature series were related ($p < 0.05$) with a regression slope of 0.58, such that for each degree increase in Georges Bank temperature the average catch temperature increased by 0.58°C. These findings suggest that cod compensated for about 40% of the interannual changes in temperature by changing their spatial distribution. However, this interannual temperature compensation could not simply be explained by movements of fish between depths (e.g., shallow to deep) or across latitudes (e.g., north–south shifts).

Optimum spawning and hatching temperatures for cod are between 5 and 7°C, which typically occur on Georges Bank in March and April (Heyerdahl and Livingstone, 1982). However, water temperatures and peak spawning vary from year to year (Smith, 1985). In warm to moderate winters, peak spawning can occur as early as December, but during unusually cold winters the spawning peak may be delayed until the end of April (Smith *et al.*, 1981). Although temperature clearly affects the timing of peak spawning, there is so far no indication that overall egg production is affected by temperature. During the period 1978–1987, Berrien and Sibunka (1993) reported a downward trend in cod egg abundance over the entire northeast shelf region (Middle Atlantic to the Gulf of Maine). Temperature data (Holzwarth and Mountain, 1992) indicate that the second half of this decade was about 1°C warmer than the first half; water temperatures in the 1983–1987 period were comparable to the warm mid-1970s, particularly on Georges Bank (Fig. 7). However, the decline in cod egg production is most likely due to the sharp decline in spawning-stock biomass that occurred between 1980 and 1986 (Fig. 11).

In several stocks of Atlantic cod, higher water temperatures have been associated with higher growth rates (Taylor, 1957). In the autumn (during the latter part of the growing season for cod off the US coast), bottom temperatures on Georges Bank (Holzwarth and Mountain, 1992) are warmer (8.6–13.4°C) than in the Gulf of Maine (5.8–9.2°C). The accelerated growth and maturation rates of Georges Bank cod compared to Gulf of Maine cod may thus be partly due to higher average temperatures on Georges Bank. Georges Bank also appears to have higher fish production than the Gulf of Maine; this production is represented largely by juvenile fish which would be potential prey for cod (Cohen and Grosslein, 1987). However, as noted earlier, no correlation exists between maturation rates and bottom water temperatures. The significant correlations found in both stocks between maturation and abundance (O'Brien, 1990) suggest that the acceleration of maturation is a compensatory response associated with reduced stock size levels in recent years.

Based on ichthyoplankton data collected during the 1977–1984 MARMAP surveys, Morse (1989) reported that both larval growth of cod and length-dependent larval mortality were positively correlated with water temperatures in the Georges Bank–Gulf of Maine region, and postulated that the increased metabolic requirements of predators were primarily responsible for the higher larval mortality. Larval metabolic requirements also increase with temperature. Buckley *et al.* (1992) recorded larval cod mortalities ranging from 2 to 10% per day in predator-free tanks at a constant temperature of 7°C, and at prey densities of 10–500 plankters/l which provided normal larval cod growth rates of 8–10% per day. Thus, even under near-optimal conditions, some cod larvae will not survive. Since both larval metabolic requirements and larval growth (at food densities above a critical level) increase with temperature, temperature must also play a role – independently of predation – in regulating larval mortality .

Studies of the copepod populations sampled with 0.333 mm mesh during the 1977–1984 MARMAP surveys showed: (1) no correlation between water column temperature and total copepod abundance on Georges Bank and in the western Gulf of Maine; (2) no correlation between temperature and *C. finmarchicus* on Georges Bank; and (3) a negative correlation between temperature and *C. finmarchicus* in the Gulf of Maine (Meise-Munns *et al.*, 1990). These results seemingly indicate that during spring, food of the larger cod larvae is less plentiful (or, at least, no different) at higher water temperatures. It is recognized that most of the diet of smaller cod larvae comprises smaller-bodied copepod species not fully sampled by the 0.333 mm mesh. However, no evidence exists to suggest that food supplies at higher water temperatures are insufficient to sustain higher growth rates. As such, part of the increase in mortality with temperature is likely attributable to intrinsic temperature effects.

Koslow *et al.* (1987) considered the influence of a number of climatic variables on recruitment in various cod stocks in the Northwest Atlantic, and found that both local and large-scale winds were significant correlates for a number of stocks but sea-surface temperatures generally were not. Although the Georges Bank cod stock was not included in this study, subsequent analysis of Georges Bank recruitment (Serchuk *et al.*, 1993) and spring and fall temperature anomaly estimates (Holzwarth and Mountain, 1992) revealed no correlation between recruitment and the local interannual temperature patterns.

Advection

The characteristic circulation pattern on Georges Bank transports gadid ichthyoplankton from spawning areas on the northeastern part of the Bank to the southwest. The rate of water movement is such that, by the time watermasses reach the Great South Channel, many larvae have moved shoalwards and are thus retained on the Bank. Variability in the circulation pattern, however, can result in a greater or lesser advective losses of larvae from the Bank.

Polacheck *et al.* (1992) documented an unusual westward drift of haddock larvae from Georges Bank into the Middle Atlantic region in the spring of 1987. The larvae appeared to have survived through the summer and autumn because of unusually cool bottom water temperatures on the outer half of the shelf. Georges Bank cod larvae were not similarly advected into the mid-Atlantic area in 1987, but this may occur in some years. In general, however, advective losses of larvae would be less significant to recruitment success for cod than haddock, because cod has a more protracted spawning season.

Gulf Stream warm-core eddies near the southern edge of Georges Bank may play an important role in some years in both entraining larvae and in moving water on and off the shelf (Lough, 1982; Joyce and Wiebe, 1983). The southeast flank of Georges Bank is particularly vulnerable to advective losses during periods of strong northerly windstress (Walford, 1938; Cohen *et al.*, 1986). Myers and Drinkwater (1989) investigated the relationship between warm-core ring frequency and recruitment in a number of Northwest Atlantic fish stocks. Although there was a tendency for decreased recruitment with increased ring frequency, no relationship was found between warm-core rings and cod recruitment on Georges Bank.

Difficulties in identifying the influence of environmental processes on larval survival were illustrated by Cohen *et al.* (1986). Comparisons were made of the development of the 1981, 1982, and 1983 cod and haddock year classes on Georges Bank in relation to various physical processes which could affect larval survival. In 1982, after what appeared to be normal spawning, low larval abundance suggested unusually high egg and larval mortality. This mortality was most likely due to: (1) a large storm event in early April, which satellite imagery indicated drove a large amount of water off the southeastern flank of the Bank; (2) a Gulf Stream ring which entrained a large volume of water from the southeastern part of the Bank during March and April; or (3) a combination of these events.

Stratification

The development of water column stratification during spring on the southern flank of Georges Bank leads to increased phytoplankton and zooplankton in the vicinity of the pycnocline. This concentrating mechanism for the larval food organisms is believed to be important for the growth and survival of gadid larvae. Buckley and Lough (1987) investigated the effect of water column stratification on Georges Bank on the short-term growth and condition of haddock and cod larvae, and found that haddock larvae from a site where the water was well mixed were in poor condition, while larvae from a nearby site where the water was stratified were in good condition. Cod larval condition did not show as strong a relationship with stratification as did haddock. Cod collected at the same sites as haddock were in better condition and were faster growing. Cod larvae appear to be better adapted to winter conditions – when prey densities are generally lower. Haddock larvae require higher prey densities than cod and seem more adapted to spring conditions when prey are concentrated by stratification (Lough, 1984). The findings suggest that interannual changes in stratification conditions on Georges Bank could have a marked influence on the survival of haddock larvae and thereby affect recruitment, but probably a lesser effect on cod.

Turbulent mixing

Turbulent mixing generated by strong tidal currents and surface windstress on Georges Bank may affect the encounter rate between larvae and prey organisms (Rothschild and Osborn, 1988). Studies from other regions have indicated a relationship between water-column turbulence and larval feeding (Sundby and Fossum, 1990). Although information is not yet available on water turbulence and the feeding of cod larvae in the Georges Bank–Gulf of Maine region, Meise-Munns *et al.* (1990) found a significant positive correlation between total copepod abundance and windstress during February–April on both Georges Bank and in the western Gulf of Maine. Windstress could conceivably affect larval growth and mortality via effects on prey density and temperature, but specific linkages have not yet been established.

Fish food production

Although maturation rates of both Georges Bank and Gulf of Maine cod have been influenced by stock size, the faster growth and maturation rates of Georges Bank cod relative to Gulf of Maine cod may be due to environmental differences. As noted previously, water temperatures and apparent fish prey production on Georges Bank are higher than in the Gulf of Maine. However, secondary production (zooplankton and macrobenthos) appears to be about the same in both areas (Cohen and Grosslein, 1987) and the proportion of fish in the diet of Gulf of Maine cod is as high – or higher – than for Georges Bank cod (Langton and Bowman, 1980; Bowman and Michaels, 1984). Once again the pieces of the puzzle do not fit neatly into place.

Another problematic aspect is that somatic and gonadal development appear to be de-coupled in Georges Bank cod but not for cod in the Gulf of Maine. Mean lengths-at-age for Georges Bank cod do not show any trend over time, despite declines in age/size at maturity, whereas in the Gulf of Maine there is evidence for increased growth of cod along with faster maturation (O'Brien, 1990).

If Georges Bank cod were already at or near their physiological limit for growth, it is plausible that any excess energy might be diverted towards gonadal growth, resulting in acceleration of maturation. Although changes in maturation are usually associated with changes in growth, this is not always the case (Roff, 1982). If the Gulf of Maine is a less productive environment for cod (relative to Georges Bank), then an increase in available prey might enable the stock to shunt excess energy into both somatic and gonadal growth, thereby accelerating both growth and maturation rates. However, there are no data that indicate that secondary production in the Gulf of Maine has increased in recent years.

Predator/prey biomass changes

Large-scale fluctuations in abundance of mackerel, herring, and sand lance have occurred in the Georges Bank–Gulf of Maine region during the past several decades (Sherman, 1986). These species are not only prey for cod but also significant predators of cod eggs and larvae (Grosslein *et al.*, 1980; Michaels, 1991). The relative occurrence of mackerel/herring/sand lance in the diet of cod (Fig. 17) broadly reflects changes in the abundance levels of these prey. Empirical evidence exists that mackerel and herring exert predatory control on sand lance abundance (Fogarty *et al.*, 1991). Given these interactions, the predator–prey linkages among just these four species may be extraordinarily complex.

Presently, there are insufficient data to adequately quantify predation mortality on cod eggs, larvae, or juveniles. To obtain quantitatively reliable measures of critical rates, intensive studies of the first year of life – including a life table along with concurrent studies of physical/biological processes – are urgently needed.

Future research

Although many attempts have been made to correlate environmental variables with variations in stock abundance of cod, nearly all of these lack long-term predictive power and usually break down when re-examined with new data (Myers *et al.*, 1993a). Large-scale synchrony in recruitment patterns of cod stocks from Labrador to Nova Scotia were reported by Koslow (1984) and linked to large-scale meteorological pressure fields and offshore winds (Koslow *et al.*, 1987). Thompson and Page (1989), using more appropriate analytical methods, also detected a synchrony in recruitment patterns for these same cod stocks but showed that the correlation with large-scale weather patterns was not significant. More recently Myers *et al.* (1993a) reported a strong relationship between salinity and recruitment for cod stocks in the Newfoundland region, but the causal oceanographic and food chain mechanisms linking these variables were not identified. In another study of northern cod stocks (Grand Bank of Newfoundland, Labrador, and West and East Greenland Shelves), Myers *et al.* (1993b) examined cod spawning times in relation to seasonal cycles of plankton abundance, ocean temperature, water column stability, and oceanic transport; no consistent relationships between these features and cod spawning times were detected, and only a very general match existed between timing of larval production and planktonic food.

Cohen *et al.* (1991) updated and re-examined the time series of recruitment estimates for cod (and haddock) stocks throughout the entire Northwest Atlantic (including the Gulf of Maine and Georges Bank stocks) and found that these stocks fell into two groups: a northern group in the Labrador/Newfoundland region, and a southern group extending from the Gulf of St Lawrence to Georges Bank. Recruitment synchrony was stronger within the groups than between them, suggesting that local-scale physical factors exert more control over recruitment than large-scale climatic effects.

Attempts to link recruitment to physical environmental factors on Georges Bank have so far been unsuccessful (Fogarty *et al.*, 1987). Since cod recruitment appears to be a compound function of largely density-independent factors operating in the egg and larval stages and density-dependent factors operating during the juvenile period, correlation analysis alone will certainly be inadequate to sort out the controlling mechanisms. Achieving predictive capability will require a better quantitative understanding of the dynamics of key processes controlling growth and mortality throughout the first year of life. These processes are the focus of two new research initiatives on Georges Bank being conducted under the auspices of: (1) the US GLOBEC Program; and (2) the NOAA Coastal Ocean Program.

The goal of the US GLOBEC NW Atlantic/Georges Bank Study is to predict the potential effects of climate change on Georges Bank gadid stocks (US GLOBEC, 1992). The Program will involve intensive investigations of those processes believed to be most susceptible to alteration by climate change and which are likely to be important to the population dynamics of gadid larvae and their primary prey organisms, *Calanus* and *Pseudo-*

calanus. Three physical processes will be studied in detail: (1) stratification of the water column; (2) retention and loss of water from the Bank; and (3) frontal exchange processes. Concurrent biological studies will be conducted on feeding, growth (and physiological condition), abundance, distribution, and mortality of cod and haddock eggs/larvae (as well as principal zooplankton species). Identification of major invertebrate predators and estimation of predation rates on pelagic stages of 0-group gadids will also be attempted.

Studies of fish predation on larval and juvenile gadids will be conducted under the NOAA Coastal Ocean Program (COP) research initiative on predator/prey interactions in the Georges Bank ecosystem. The chief goal of the COP Georges Bank study is to understand the interactive effects of exploitation and interspecific interactions on the fish community dynamics of Georges Bank. This program involves: (1) retrospective studies of changes in fish biomass, species composition, and predator–prey interactions; (2) process-oriented studies in the field and laboratory on predation on 0-group stages, digestion rates, etc.; and (3) multispecies modelling to test and evaluate hypotheses about controlling mechanisms, and to examine long-term effects of different fishery management strategies on the productivity of the Georges Bank ecosystem.

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