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The Relationship Between Oceanographic Conditions in the 1990s and Changes in Spawning Behaviour, Growth and Early Life History of Capelin (*Mallotus villosus*)

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Abstract

A review of several aspects of inshore capelin biology and behaviour in the Northwest Atlantic during the 1980s and the early-1990s is presented. Since 1991 capelin have spawned later on beaches, newly hatched capelin larvae have emerged late in the summer, mean lengths and weights of age 3 and age 4 capelin have been lower, and the proportion of mature age 2 fish has increased compared to the 1980s. Recent changes in the behaviour of capelin have also been linked to changes in the August diet of seabirds such as gannets and common Murres. Evidence of a decline in the offshore biomass and changes in diurnal movements since 1990 were observed during offshore acoustic surveys. Capelin have extended their distribution onto the Flemish Cap and Scotian Shelf in the 1990s. Cooler water temperatures in the 1990s are hypothesized as the predominant reason for changes in capelin behaviour, distribution, and biology which have been observed since 1991. These changes have affected the inshore commercial capelin fishery and the interpretation of indices of relative abundance used to assess stock status.

Key words: Biological characteristics, capelin, oceanography

Introduction

"It should not surprise us that fish stocks respond to climatic factors and to climatic change because they live their lives within the weight of the waters" – D. H. Cushing (1982)

Recent changes in the behaviour and biology of capelin (*Mallotus villosus*) in NAFO Div. 3KL during the 1990s compared to the 1980s have been observed (e.g. Frank *et al*., MS 1994; Carscadden *et al*., 1996). These changes have influenced the timing and the interpretation of recent trends in inshore abundance indices (e.g. Nakashima, MS 1992; MS 1994a, b). Fishing pressure has been low (Shelton *et al*., 1993), and therefore recent biological changes reflect, or are a response to, changes in the environment, in particular the anomalous cooler water temperatures in the Northwest Atlantic during the 1990s. Changes or thresholds in water temperature have been invoked to explain behaviours related to spawning activities (Templeman, 1948; Schneider and Methven, 1988; Carscadden *et al*., 1989) and shifting distributions of 0-group capelin (Gundersen, MS 1993). Recruitment success in capelin is at least partly a function of water temperature (Frank and Leggett 1981, 1985; Leggett *et al*. 1984). This paper brings together information from various sources to document the biological differences observed during the inshore phase of the life history cycle and to suggest that many are consistent with the hypothesis that the capelin stock in NAFO Div. 3KL is responding to cooler water temperatures. Changes in inshore fishing patterns and difficulties in reconciling relative abundance trends in the 1990s are some of the products resulting from the biological responses to a changing ocean environment.

Oceanographic conditions

The anomalous oceanographic conditions in the Northwest Atlantic in the 1990s have been characterized by a large cold intermediate layer (CIL), extensive spring ice conditions especially in 1991, and cooler spring and summer surface temperatures at Station 27 (47°32'50"N, 52°35'10"W) near St. John's (Narayanan *et al*., MS 1992; Colbourne and Narayanan, MS 1994). The extremes observed on the northeast coast of Newfoundland are indicative of general climatic and oceanographic conditions in the Labrador Sea and Labrador Shelf/Grand Banks areas (Drinkwater, MS 1994).

Biological Conditions

Arrival of schools inshore

Capelin schools appeared later in coastal waters in the 1990s as observed from annual aerial surveys of Conception Bay and Trinity Bay (Nakashima, MS 1994b). The peak appearance of capelin schools in Conception Bay and Trinity Bay in 1982–90 was from mid-June to early-July compared to 1992–94 when the peak appearance of schools was observed from mid- to late-July (Table 1). In 1991 the peak appearance of capelin schools occurred after the aerial survey time ran out on July 17 (Nakashima, MS 1992).

Information from fishing times and dates of area closures give further credence to later appearance of mature capelin in the bays along the northeast coast. The trap fishery is passive and fishing times generally reflect the arrival of marketable mature females in an area, whereas the purse seine fleet is mobile and many vessels follow the northward migration of mature capelin schools from St. Mary's Bay to White Bay. These data show that the commercial fishery for capelin along the northeast coast in the 1980s generally ranged from early to late-June with some catches in early-July usually taken in Div. 3K. However, in 1991 in Div. 3L and 3K most trap fishers fished in late-July to early-August (Nakashima and Harnum, MS 1992 a,b). In 1992 the fishery in Div. 3L was virtually nonexistent (minimal landings of 2 993 tons were recorded) with fish arriving inshore late. A similar problem of late arrival of spawning capelin also occurred in Div. 3K, however, landings there were higher (landings amounted to 16 351 tons) than in Div. 3L (Nakashima, MS 1993a; Nakashima and Carscadden, MS 1993). In 1993 mature capelin were found inshore earlier than in 1991 or 1992 but fishing times remained later than in the 1980s. In 1993, the fishery targeting large females took place in St. Mary's Bay and on the Southern Shore in late-June and early-July, respectively, in Conception Bay during 20–21 July, in Trinity Bay during 30 July–2 August, and in Bonavista Bay during 7–13 August (Nakashima, MS 1994a). Fishing was closed north of Bonavista Bay by late-July, however, spawnings observed at Cape Freels and Twillingate in mid- to late-August and at Hampden in early September (Nakashima and Winters, unpublished data) were consistent with observations made by fishers of a large school of capelin moving along the northeast coast in 1993. From the period 1991–93, one major reason given for problems with the fishery was the late and unpredictable time of arrival inshore of mature fish.

Reports indicate that avian predators also responded to the later spawning times and inshore distribution of capelin in the 1990s. Gannets on Funk Island changed their diets dramatically from mackerel, squid and saury consumed in 1977–89 to predominantly capelin with some cod and salmon in 1990–91 (Montevecchi and Myers, MS 1992). The percentage of capelin in gannet diets was inversely correlated to June–July surface temperatures. Montevecchi and Myers (MS 1992) reported that common Murres were breeding later in August on Funk Island in 1990–91. They observed that 48% of females taken by common Murres in 1991 were gravid, compared to 4% in 1990, indicating that prespawning females were still inshore in August 1991.

Spawning times

Evidence from several sources clearly demonstrates that the timing of annual beach spawning of

TABLE 1. Arrival and spawning times derived from aerial surveys (Nakashima, MS 1994b), Conception Bay beaches (Nakashima and Slaney, MS 1994), Bryants Cove and Chapel Cove peak spawning dates (Carscadden *et al.*, 1996) and spawning season for Div. 3KL from six northeast coast beaches (Nakashima and Winters, MS 1994).

	Aerial surveys		Spawning times		
Year	Conception Bay	Trinity Bay	Conception Bay	Bryants Cove and Chapel Cove	Six NE coast beaches
1982	27 Jun	29 Jun		29 Jun	
1983	23 Jun	30 Jun		19 Jun	
1984	25 Jun	26 Jun		2 Jul	
1985	2 Jul	2 Jul		27 Jun	
1986	19 Jun	28 Jun		18 Jun	
1987	18–19 Jun	19 Jun	23–30 Jun	14 Jun	
1988	24–25 Jun	22 Jun	28 Jun–4 Jul	17 Jun	
1989	16 Jun	17 Jun	26 Jun–2 Jul	16 Jun	
1990	26 Jun	29 Jun	1–8 Jul	26 Jun	24 Jun–26 Jul
1991	?	?	23 Jul–2 Aug	21 Jul	27 Jul–22 Aug
1992	13–14 Jul	8 Jul	15–21 Jul	15 Jul	4 Jul–20 Aug
1993	27 Jul	?	14–25 Jul	19 Jul	1 Jul–6 Sep
1994	12 Jul	15 Jul		7 Jul	22 Jun–23 Aug

capelin along the northeast coast of Newfoundland has been later since 1991 compared to the 1980s. The time period when newly-spawned capelin eggs were collected at 15 beaches in Conception Bay was later by three to four weeks in 1991–93 compared to 1987–89 (Table 1) (Nakashima and Slaney, MS 1994). Monitoring of capelin beaches over a wider geographic area began in 1991 (Fig. 1) and reported spawning times (Table 1) are consistent with the observations from Conception Bay beaches that spawning along the northeast coast now occurs in mid-July to early September (Nakashima and Winters, MS 1994). The latter study also indicated that the spawning season in 1991–93 extended over a broad time period.

Spawning times have shifted to later in the summer since 1991 in response to cooler water temperatures. Carscadden *et al*. (1996) reported significant negative correlations between mean monthly surface temperatures (0–20 m) recorded at Station 27 for February to June and spawning times in Conception Bay. In the same analysis, mean total lengths of mature capelin were significantly correlated to spawning times with smaller size associated with later spawning times. Carscadden *et al*. (1996) hypothesized that cold water temperatures during late-winter and early-spring delay maturation of gonads and result in late spawning.

Early life history

It is reasonable to expect that when eggs are deposited late in the year, hatching would also be correspondingly delayed. Patterns of larval emergence from beach sediments in the 1990s suggest that larvae were emerging later than in the late-1970s and 1980s. In studies at Bryants Cove in the late-1970s and early-1980s capelin larvae emerged from beach sediments in late-June to late-July in 1979 (Frank and Leggett, 1981), from Eastport and Bryants Cove in mid-July in 1982 (Frank and Leggett, 1985), and from Bryants Cove in mid- to late-July in 1983 (Taggart and Leggett, 1987). In 1990 a study was initiated to monitor the larval emergence patterns of capelin at Bellevue and at Arnolds Cove (Nakashima and Winters, MS 1995). The study was expanded in 1991 to include Chapel Cove, Eastport, Cape Freels, Twillingate, and Hampden (Fig. 1). In 1990 capelin larvae emerged from early-July to early-August at Bellevue (Fig. 2). Since 1991, larval emergence predominantly occurred between late-July and late-August on the northeast coast (Fig. 2). In a few instances in 1993 larvae were emerging as late as September (Fig. 2). Emergence times were generally later in Div. 3K than in Div. 3L. Larvae emerging later in August and in September may encounter conditions which are not conducive to survival or growth (Frank and Leggett, 1985).

Age and growth characteristics

Mean total lengths of males and females of capelin were examined for 2, 3 and 4 year-olds in Div. 3K since 1984 and Div. 3L since 1981 (Fig. 3). Total lengths of males- and females-at-age were smaller for age 3 and age 4 fish in 1991–93 compared to the 1980s, however, age 2 fish in the commercial catch did not show a comparable decline. Similarly weights-at-age of sexes combined were lower in 1991–93 compared to the 1980s for all ages except age 2 (Table 2).

Age composition of the catch indicated a higher proportion of mature age 2 fish in 1991–93 compared to most of the 1980s (Fig. 4). The high proportions of age 2 capelin in 1985 and in 1988 were related to strong year-classes produced in 1983 and 1986, respectively (Nakashima, MS 1994a). Similar to 1991–93, spring water temperatures in 1985 were cooler than normal (Nakashima and Harnum, MS 1986). It has been assumed that the presence of a high proportion of age 2 fish is a sign of a strong recruiting year-class. If this is so, then according to Fig. 4 the 1989, 1990, and 1991 year-classes should be strong. The 1989 year-class was the second most abundant year-class since 1978 (Nakashima, MS 1994a). The USSR 0-group surveys conducted in November–December 1990 indicated that the 1990 year-class in Div. 3LNO was also strong (Bakanev, MS 1991), while the 1991 year-class was considered to be average by Bakanev (MS 1992) following the November 1991 0-group survey in Div. 3LNO. However, if larval emergence data from northeast coast beaches are an indicator of year-class strength, the 1991 year-class will be weak (Fig. 2). An alternate explanation for three years of the high proportion of mature age 2 fish may be related to abundance levels. The abundance of mature age 2 capelin may not have changed during the 1990s, rather a reduction in the abundance of age 3 and age 4 fish in the spawning population could have resulted in a higher proportion of two-year-olds. If cooler temperatures lead to less available food, slower growth, and delayed maturation, then a higher proportion of mature age 2 fish is inconsistent with such an explanation. Another possible explanation may be related to the lack of separation in sizes of spawning fish in recent years. Instead of the ‘normal’ pattern of larger and older fish arriving and spawning before smaller and younger fish (Templeman, 1948; Nakashima, MS 1983), spawning runs since 1991 consist of a mixture of ages. Cooler water temperatures may have delayed maturation of older fish, more so than younger fish, resulting in a mixing of sizes and ages during spawning.

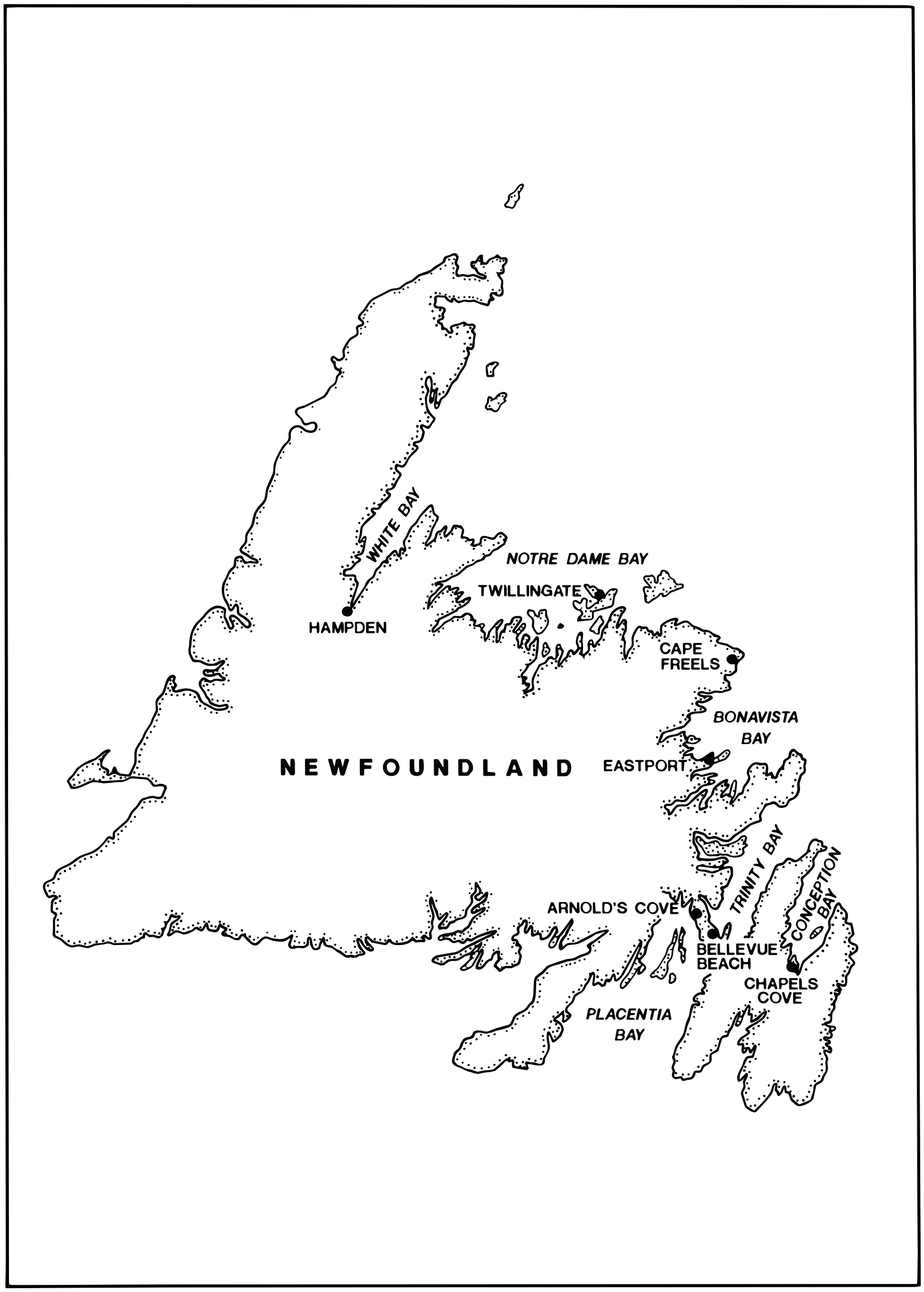

Fig. 1. Capelin spawning beaches monitored for larval emergence patterns.

Offshore differences

While this report focuses on the inshore portion of the life history, changes in capelin behaviour and abundance have also been observed in offshore surveys. Since June 1990 annual acoustic biomass estimates of capelin have been very low in the offshore survey area (Bakanev and Sergeeva, MS 1994; Miller, MS 1994). These low acoustic estimates may be related to changes in capelin distribution during cold years (Shackell *et al*. 1994). Cod stomach analyses to determine the occurrence of capelin as prey in the annual autumn groundfish surveys suggest that capelin distributions have shifted south and east since 1990 (Lilly, 1994). Canadian and Russian acoustic surveys have also reported similar changes in distribution (Bakanev and Sergeeva, MS 1994; Miller, MS 1994). The vertical distribution has changed with the typical diurnal

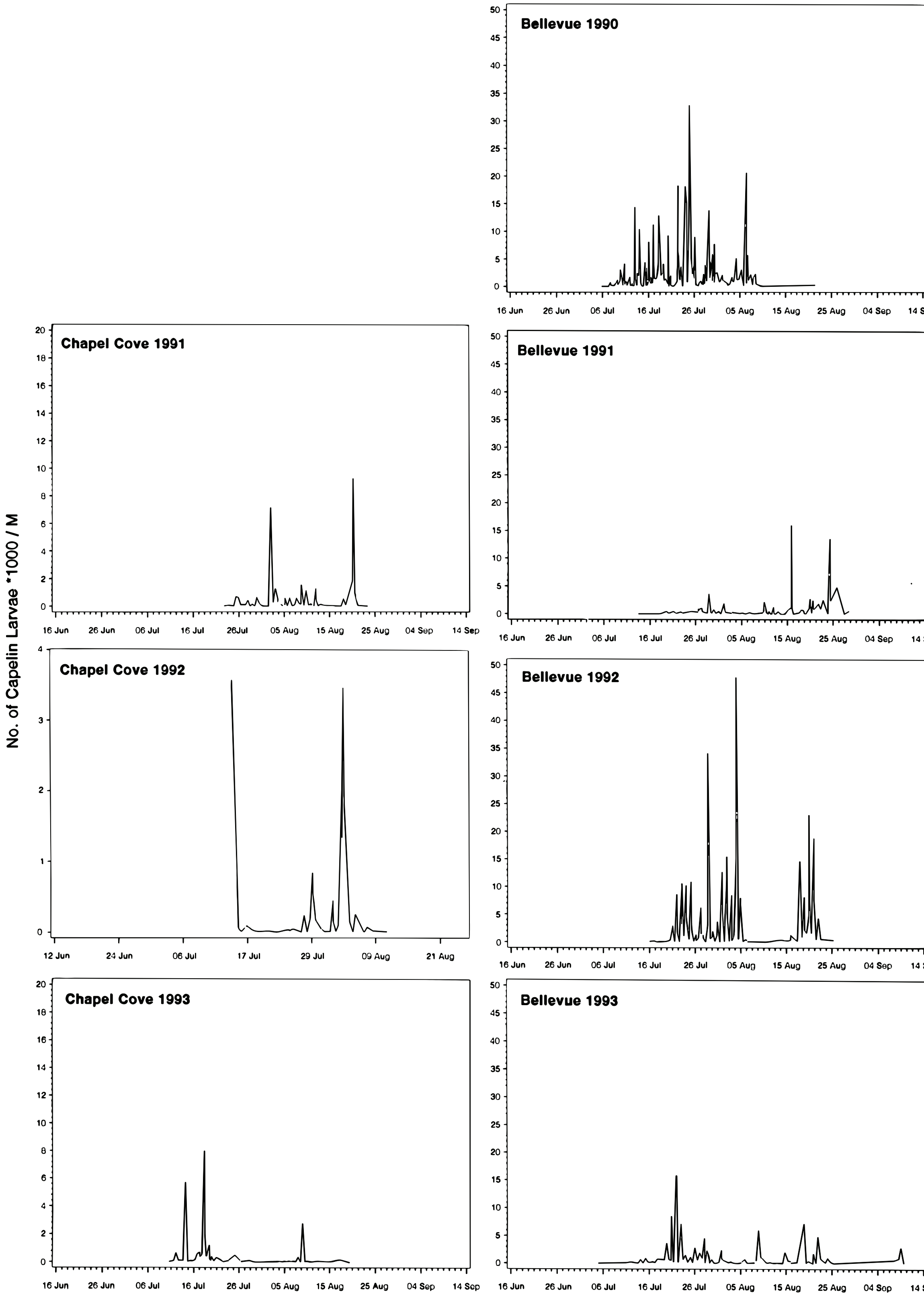

Fig. 2. Capelin larval emergence patterns from Chapel Cove, Bellevue, Eastport, Cape Freels, Twillingate and Hampden.

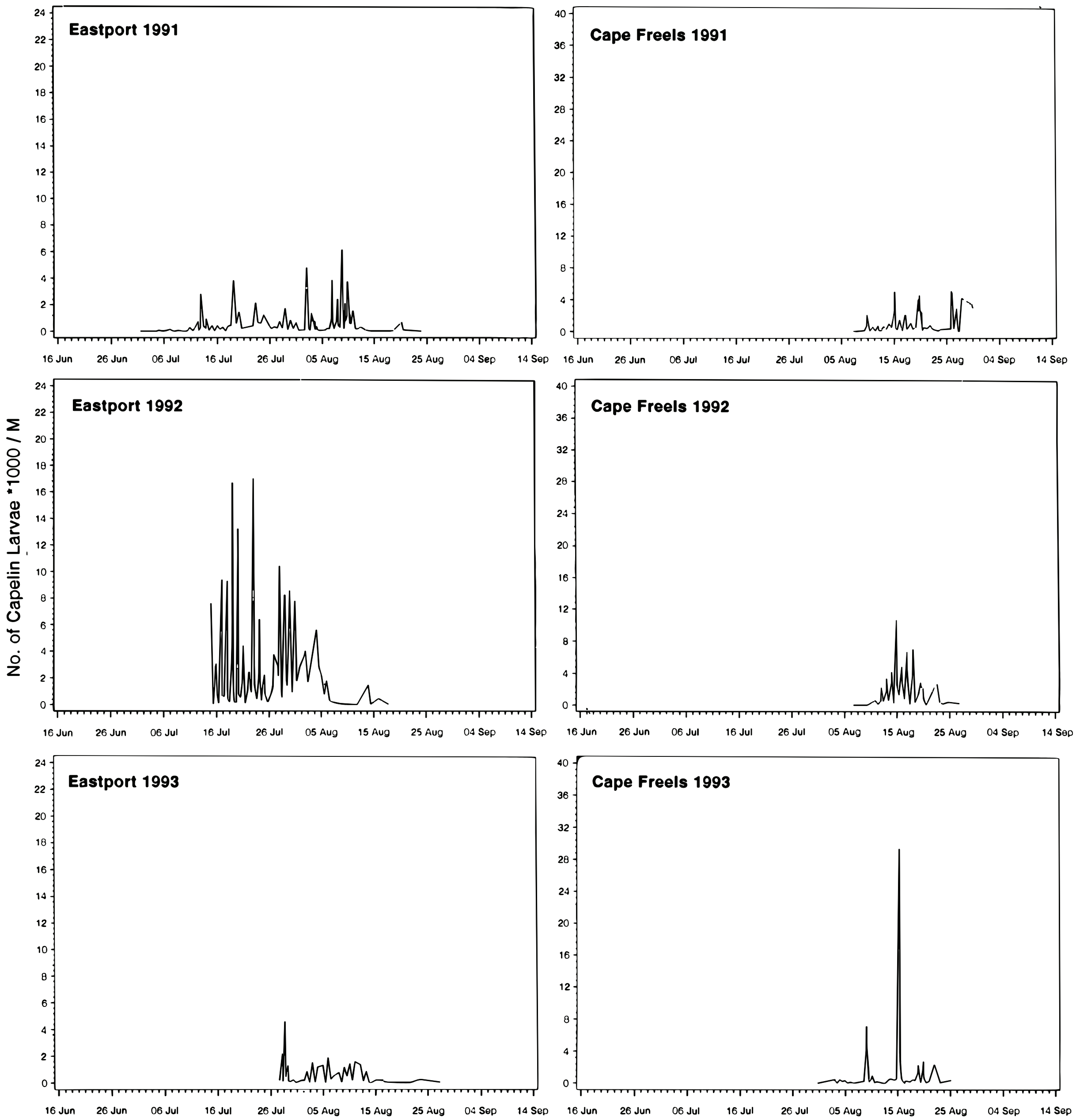

Fig. 2. (Continued). Capelin larval emergence patterns from Chapel Cove, Bellevue, Eastport, Cape Freels, Twillingate and Hampden.

vertical migration of capelin in the autumn not observed in 1992 (Shackell *et al.*, MS 1994). Spatial changes are also apparent in the 1990s with capelin being observed on the Flemish Cap and the Scotian Shelf outside their normal range of distribution (Frank *et al.*, MS 1994).

Effects on Inshore Indices

Aerial survey index

One of the assumptions made in the application of capelin school areas from aerial surveys as an index of relative abundance, is that the majority of mature capelin arrive inshore near spawning beaches at the same time in the survey area. The spreading out of spawning runs from early-July to late-August in the 1990s has resulted in a multimodal distribution of capelin during the spawning season. This was one of the reasons given by Winters (MS 1994) to propose another method of utilizing the aerial survey data to obtain a relative abundance index.

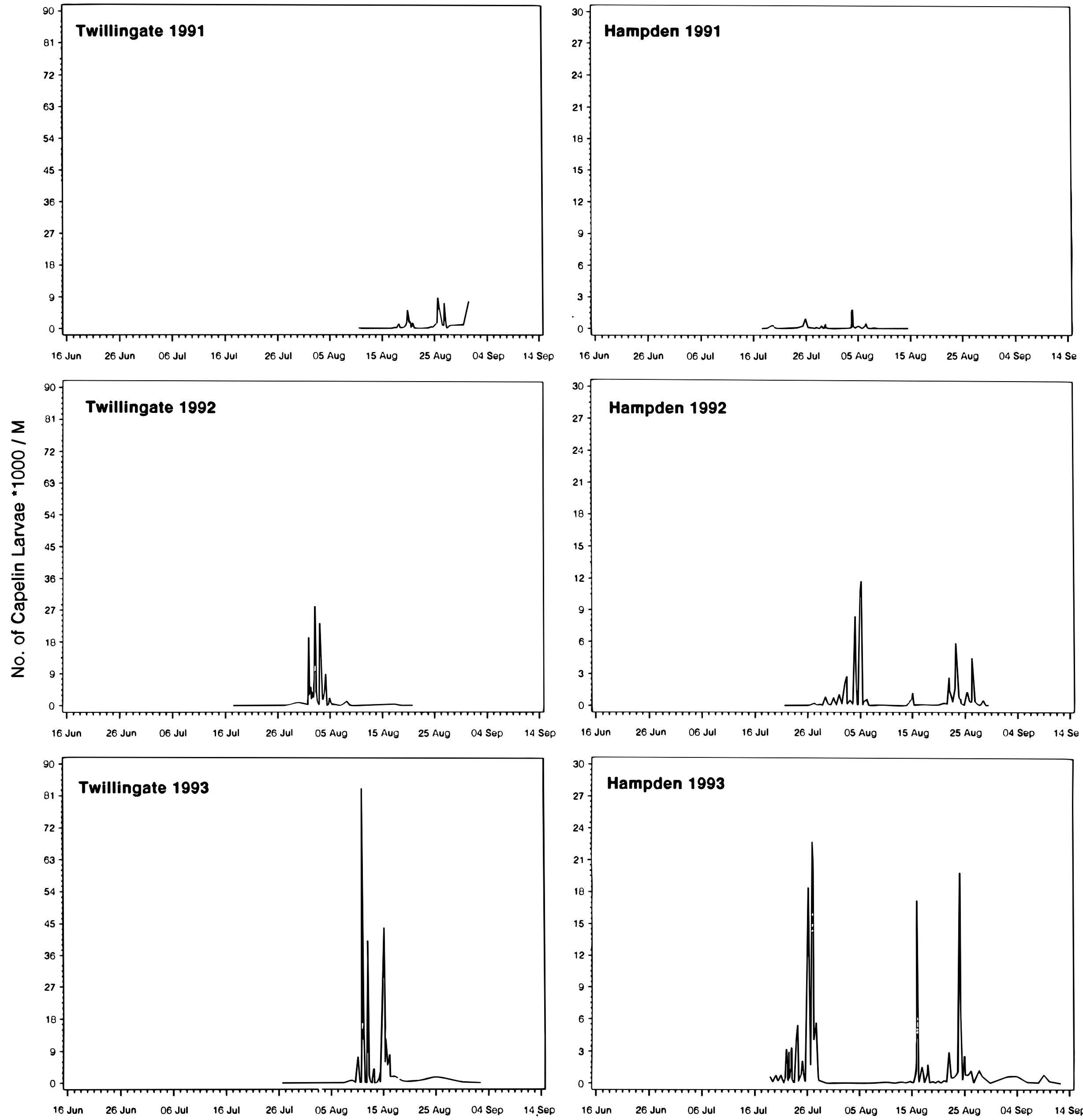

Fig. 2. (Continued). Capelin larval emergence patterns from Chapel Cove, Bellevue, Eastport, Cape Freels, Twillingate and Hampden.

Another factor influencing the survey has been the delay in arrival of capelin schools inshore. Data collected by aerial surveys in the 1980s were from a fixed period of time, generally between mid-June and early-July (Nakashima, MS 1994b). In 1985 a delay in capelin arrival, possibly due to cooler water temperatures, resulted in an abundance peak being estimated at the end of the survey period (Nakashima, MS 1986). The possibility existed that larger school areas might have been observed if the survey period could have been extended. This situation occurred again in 1991, 1992 and 1993, but was much more pronounced. In 1991 the survey ended before the peak abundance of capelin was observed inshore (Nakashima, MS 1992) and failed to reflect relative inshore abundance comparable to previous years. The 1992 survey results appeared to cover the period when egg deposition was greatest in the survey area (Nakashima, MS 1993b), however more spawnings did occur in Trinity Bay after the survey ended on July 14. The 1993 survey adequately covered the main spawning period in

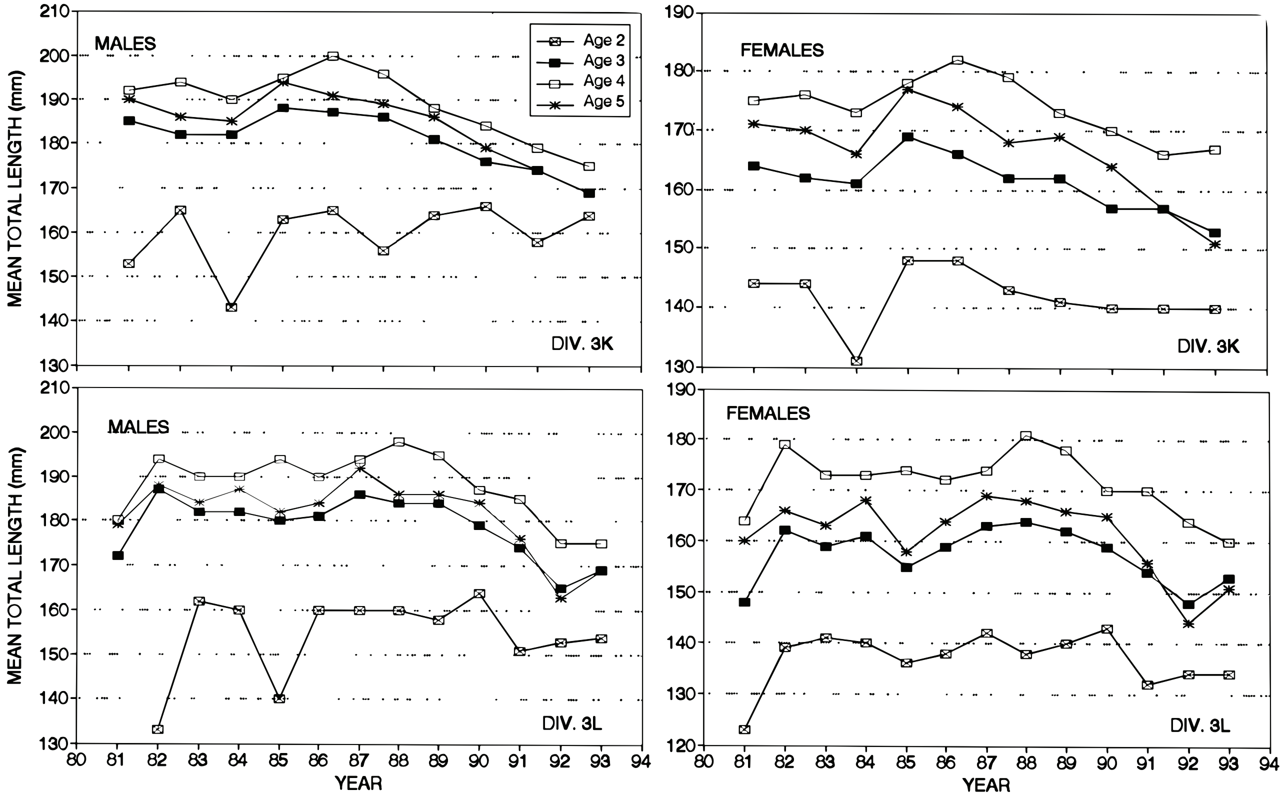

Fig. 3. Mean total lengths-at-age for Div. 3K and Div. 3L males and females, from Nakashima (MS 1994a).

TABLE 2. Mean weights (gm) for commercial capelin samples in Div. 3K and Div. 3L, sexes combined from Nakashima (MS 1994a).

	Age					
Year	2	3	4	5	6	All
Division 3K						
1984	14.7	30.5	37	34.5	32.3	35
1985	15.3	26.3	34.1	31.7	33.6	29.2
1986	11.3	27.4	34.4	32.9	35.3	30.1
1987	17	30.7	37.9	34.8	35.8	36.8
1988	17.2	31.2	42.6	36.4	38.9	34.1
1989	14.5	31.3	38.2	36.9	38.8	33.2
1990	16.4	26.1	32.6	31.3		30.2
1991	18.9	23.1	27.2	26.4	31.7	24.8
1992	15.7	25.0	27.4	26.7	37.5	24.6
1993	18.3	22.5	28.0	28.6		22.1
Division 3L						
1981	7.8	22.3	29.8	32.3	36.4	28.1
1982	12.6	32.5	37	37.2	39.9	33
1983	13.9	27.7	33.8	34	27.6	29.1
1984	13.9	27.6	34.7	30.5	33.6	31.3
1985	12	25.4	35.9	32.6	33.1	26.7
1986	18	26.2	34.2	33.7	36.8	29.1
1987	14.2	27.4	36.3	33.5	38.1	33.1
1988	14.3	29.9	39.6	36.4	38.8	30.7
1989	14.5	29.3	36.5	36.6	37.9	30.8
1990	16	25.4	32.7	32.1	37.1	29.2
1991	12.6	21.2	29.2	27.8	35.7	22.6
1992	12.9	18.7	25.2	25.0		17.1
1993	13.4	21.8	23.2	22.4	26.3	21.1

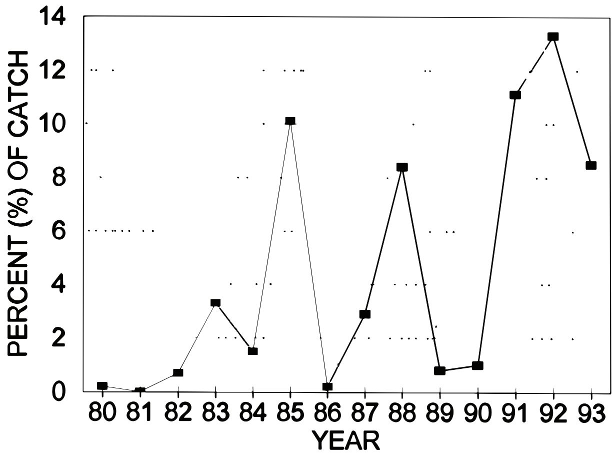

Fig. 4. The proportion of the inshore commercial catch consisting of mature age 2 capelin.

Conception Bay but failed to include two major spawnings in August in Trinity Bay (Nakashima, MS 1994b). Thus delays in spawning and protracted spawning seasons have contributed to problems in reconciling the 1991 and 1993 index values with the remainder of the series. In 1993, inadequate coverage of portions of the survey area may have negatively biased the index. Given the costs involved in maintaining survey equipment and personnel on standby, it was not possible to extend the survey period in those years. The unpredictable nature of the arrival time of capelin schools in the survey area, particularly when they arrive late, and when the spawning periods extend over a long time, has made the task of timing the survey to cover peak inshore school abundance difficult in recent years.

Trap catch rate index

One assumption in the application of the trap catch-rate index is that fishing occurs during the time mature capelin are inshore, prior to spawning. This assumption has not always been satisfied during the 1991–93 period. Many factors have had a negative influence on decisions made by trap fishers to fish capelin since 1991. Monitoring areas have been organized to assess the condition of females before opening an area to fishing. In previous years each fisher was responsible for checking and deciding to sell the catch. Under a monitoring program a few fishers periodically check their catches and only when specific criteria are met is the area opened to fishing. Consequently, many fishers do not set fishing gear until there are strong indications of marketable females. Fishers are unable to predict as well as they did in the 1980s when capelin would arrive inshore before setting their traps. Protracted spawning seasons have also contributed to the uncertainty. Some fishers have left the fishery or are participating in programs which preclude their involvement in the capelin fishery. The decline in fishing effort is indicated by the return of fewer research logbooks, by the trend to fish single traps by fishers who fished two in the 1980s, and by the increase in the number of survey respondents who did not fish in 1991–93 (Nakashima and Harnum, MS 1992a, b; Nakashima, MS 1993a; MS 1994a). The effect of the extended and late spawning season on the pattern in daily catch rates was clearly depicted by Winters (MS 1994) as shown in Fig. 5.

There has been a recent increase in the discarding of capelin due to small females in the capelin fishery. This relates to the higher proportion of mature age 2 capelin in the catches, and the slower growth of older aged capelin. Some attempts have been made to ameliorate the discarding problem by closing areas to fishing when size categories become too small. For example in 1994, areas were closed when female counts in the catches exceeded 50 females/kg. While actual discards have been reduced, the initial problem which disrupted fishing patterns still remains.

Commercial fishing for capelin is being conducted differently in the 1990s because of the changing biology of capelin and changing management measures. Consequently, trap catch-rate data have been more difficult to obtain and to interpret.

Egg deposition index

An egg deposition index has been developed for Conception Bay (Nakashima and Slaney, MS 1994). The index was based on the assumption that most of the spawning was a unimodal occurrence, similar to the aerial survey index. Estimates of newly-spawned eggs following peak egg deposition may be used as an indicator of spawner escapement. The survey method consists of teams collecting samples after peak spawning has been identified from aerial survey observations, and initial checks of some of the beaches for fresh eggs. However, the delays in spawning and multiple spawning runs over an extended period of time in the 1990s have violated the assumption of unimodal spawning. Survey times indicate that spawning has occurred later since 1991 (Table 1). The value of this index has diminished as a result of timing uncertainties and was discontinued after 1993.

Summary

The evidence from a variety of sources clearly demonstrates that changes have occurred in the behaviour and biology of capelin inshore on the northeast coast of Newfoundland since 1991 compared to the 1980s. Many of the differences such as reduced length- and weight-at-age for ages 3 and 4

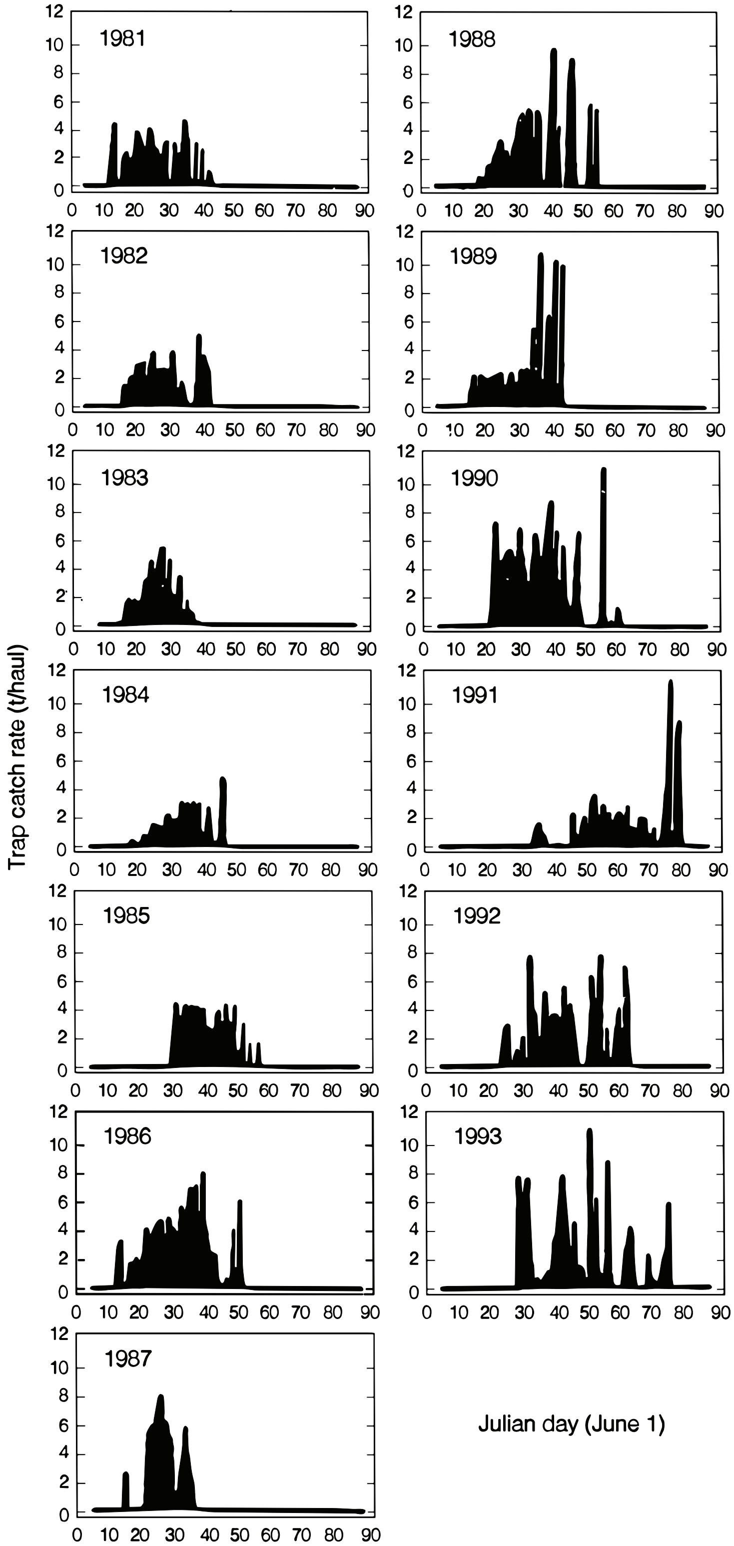

Fig. 5. Daily trap catch rates (t/haul) of capelin traps in NAFO Div. 3KL for 1981–93, from Winters (MS 1994).

fish, late arrival of mature capelin inshore, delayed and protracted spawning times and later emergence of larval capelin, are probably the result of the anomalous cooler water temperatures experienced by capelin populations since 1991. The changes in capelin behaviour related to later spawning times and smaller sizes have had a pronounced disruptive effect on fishing and the inshore fishery. Fishing has occurred later with multiple opening and closing dates. The searching pattern of purse seiners, which follow capelin schools as they progressed northwards along the northeast coast, no longer occurs because of the unpredictable times of arrival of mature capelin schools inshore. The presence of small capelin in the catches, due to higher proportions of age 2 and slower growing older fish has resulted in area closures and inability to fulfil market requirements for larger females. The pattern was initially apparent in Div. 3L in 1992, and in all areas by 1994. The feeding and breeding habits of predatory birds such as gannets and common Murres have also changed since 1990, partly in response to the changes in capelin availability and correlated to colder sea surface temperatures.

Changes have also been recorded offshore. The offshore distribution showed marked changes with the appearance of capelin on the Flemish Cap and Scotian Shelf since 1990 correlated to cooler temperatures. A decline in biomass has been reported from the annual offshore acoustic surveys by Canada and Russia. The surveys have also shown disruptions in capelin diurnal behaviour affecting vertical distribution patterns. These observations taken together demonstrate that significant shifts in behaviour, distribution, growth and early survival have occurred in capelin stocks in the Northwest Atlantic since 1990.

The immediate effects on capelin populations and the fishery during 1991–94 are readily observable, however, long-term implications of recent biological changes have yet to be realized. Several questions arise, e.g. has delayed spawning resulted in lower survival of capelin larvae, thereby producing weak year-classes? How quickly will capelin stocks adjust to warmer or 'normal' conditions after at least four years of poor growth, delayed maturation, and late spawning? These and other questions may be addressed when the mature progeny from spawnings since 1991 return inshore.

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Discussions

Question: Perhaps capelin could be a biological indicator of climate change. Norwegian work in the Barents Sea indicates that capelin feed on calanus and calanus abundance is closely linked to water temperature. Is there comparable information for the Northwest Atlantic?

Response: There exist few studies in the Northwest Atlantic but during main feeding in fall, euphausiids and copepods are the major prey items. However, no data collected on zooplankton here are comparable to Barents Sea. There are likely similar relationships but there is no direct information on trends in planktonic changes.

Comment: 1. Gannets generally feed on mackerel and saury and the change to capelin in 1990–91 is because their preferred prey are unavailable. Also recent reports show that seabirds are in trouble because there is no capelin available as food.

Comment: 2. It is true that gannets prefer saury, mackerel and squid in the 1970s and 1980s and there is indication for a recent shift to capelin because of availability. There are close links to sea surface temperatures. The fauna prey are associated with warm water but in 1990–91, sea surface temperatures have been cooler. There is inverse correlation between the percentage of capelin in diet and June–July sea surface temperature. Evidence of birds in trouble probably refer to kittiwakes. There is preliminary evidence that these populations have had reduced clutch sizes and low chick survival in recent years. However, these birds are very dependent on capelin and are surface feeders. Gannets are deep-diving feeders. The main reasons for the dietary evidence from birds was to give additional support to the presence of capelin inshore in August, later spawning.

Question: All the information presented also suggest that stock sizes of capelin are low. Should these stocks still be fished?

Response: Refer to Ken Frank's table that landings have not exceeded 4% of the biomass, a negligible fishing mortality. There is much evidence especially from Frank and Leggett that capelin recruitment is related to environmental factors. As to whether stocks are low, one of the problems with current assessments since the dramatic decline in offshore acoustic biomass and the higher relative abundance displayed by inshore indices is our inability to reconcile the differences. Stocks are probably lower than observed in the late-1980s but how low – slightly, average or low? It is also reflected in the subcommittee assessment reports that we have been unable to provide a biomass estimate in recent years. The fishery is market-driven and heavily monitored so that when fish quality is low, fishing ceases. For example in 1994 fish were small and many areas remained closed to fishing.

Question: Are there data for times when larvae emerge in the late-1980s. When did monitoring of spawning begin?

Response: The only information for 3KL is from the Bryants Cove work in the late-1970s and early-1980s. Our work began in 1990.

Spawning has been monitored in Conception Bay since 1987. There is some good information from aerial surveys which span 1981–94. Dedicated monitoring under the Northern Cod Science Program (NCSP) only began in 1991 during the time that change has occurred.

Question: There were indicators that capelin were spawning in deeper water away from the beaches – do you have any evidence of this?

Response: No direct measurements but those monitoring the beaches in our study plus anecdotal information from a variety of sources have indicated that sub-tidal spawning was going on in 1994. The amount of such spawning cannot be estimated. Moreover, there is no way to determine whether this was more or less or similar to previous years because it has never been estimated.

Question: When you compare spawning time to May temperatures, perhaps you should look at winter temperatures – size and maturity may be determined in January–February?

Response: In the initial work by Carscadden *et al.*, several monthly temperatures and a winter series were examined and the May temperatures had the best correlation. Further temperature and size of fish were both found to be related to spawning time. The next step would be to look at a multiple correlation but this has not been done on this data set to date.

Comment: 1. Given that spawning occurs away from beaches, I have trouble with using the egg deposition on beaches and larval emergence data as predicators of stock size.

Comment: 2. The egg deposition data were never used to indicate future recruitment. There is no evidence for capelin of a stock-recruitment relationship. The egg deposition was used as indicating if egg deposition had shown declines or not. As for larval emergence data, true we do not know whether larvae from off beach spawning will have similar, better or poorer survival. As to whether it reflects good or poor year-classes that remains to be seen. It is too early to tell for our 1990–94 series because the first of year-classes are now starting to show up inshore. However, much of the work by Frank and Leggett show that recruitment is fixed in the early life history, probably no later than 8 months following spawning. Some preliminary findings from fall larval surveys by Anderson and Dalley seem to confirm relative year-class size for a few years in the 1990s which are similar to expectations from the emergence data.

Question: Is there a reason behind the multimodal distribution in catches?

Response: It would appear that capelin have spread out their spawning times, i.e. instead of 4–6 weeks, now 6–8 weeks or longer. In the 1980s, most of the spawning took place at one time perhaps taking 10–12 days along the northeast coast as evidenced by the fishing activities shown earlier. But in the 1990s, especially evident in 1993 and 1994 that spawning runs are separated by as much as 14 days. This was one of the reasons why we have been having problems matching the recent aerial surveys with the earlier part of the series.