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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*)

by

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"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)

Introduction

Recent changes in the behaviour and biology of capelin (*Mallotus villosus*) in the Northwest Atlantic during the 1990's compared to the 1980's have been observed (eg. Carscadden et al. 1992; Carscadden 1994). These changes have influenced the timing and the interpretation of recent trends in inshore abundance indices (eg. Nakashima 1992, 1994a, b). Much of the 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 1990's. 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, 1992) and shifting distributions of 0-group capelin (Gundersen 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 suggests that many are consistent with the hypothesis that capelin populations are responding to cooler water temperatures. Changes in fishing patterns and difficulties in reconciling relative abundance trends in the 1990's 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 1990's are 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. 1992; Colbourne and Narayanan 1994). The anomalous cooler water conditions persisted at deeper depths into 1994, however there was a rapid warming of surface waters in late spring 1994 (Colbourne and Narayanan 1994).

Biological Conditions

Spawning Times

Evidence from several sources clearly demonstrates that beach spawning of capelin along the northeast coast has been later since 1991 compared to the 1980's. The time period when newly-spawned capelin eggs were collected at 15 beaches in

Conception Bay increased by three to four weeks in 1991-93 compared to 1987-1989 (Table 1) (Nakashima and Slaney 1994). Monitoring of capelin beaches over a wider geographic area began in 1991 (Fig. 1) and reported spawning times (Table 1) support the observations from Conception Bay beaches that spawning along the northeast coast now occurs in mid-July to early September (Nakashima and Winters 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. (1992) reported that spawning times (catches of 25000 kg by traps was used as a proxy variable) from 1983-91 were correlated to May surface (0-20 m) water temperatures, the warmer the temperature the earlier spawning occurred. A significant relationship was observed when data from 1992-94 were included (Fig. 2, $r = -0.593$, $p = 0.033$, $n = 13$). Instead of the catch data I used a spawning time series unique to Conception Bay which assumed the spawning times from Bryants Cove 1982-88, peak school abundance in Conception Bay from aerial surveys 1989-90, and spawning times from Chapel Cove 1991-94 were comparable (Table 1). Spawning time was also significantly correlated to June surface (0-20m) water temperatures (Fig. 2, $r = -0.626$, $p = 0.022$, $n = 13$). Carscadden et al. (1992) hypothesized that timing of spawning was a function of spring water temperatures and size structure of the spawning population. Including data from 1992-93 the relationship between mean total length of the spawning population and spawning times as defined in this report clearly shows that size and spawning times are related (Fig. 3, $r = -0.801$, $p = 0.002$, $n = 12$).

Arrival of Schools Inshore

Capelin schools appeared later in coastal waters in the 1990's as observed from annual aerial surveys of Conception Bay and Trinity Bay (Nakashima 1994b). The peak appearance of capelin schools in Conception Bay and Trinity Bay in 1981-90 was from mid-June to early July compared to 1992-93 when the highest school areas were observed from mid-July to early August (Table 1). In 1991 the peak appearance of capelin schools occurred sometime after the aerial survey time ran out on July 17 (Nakashima 1992b).

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. The commercial fishery for capelin along the northeast coast in the 1980's 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 1992 a,b). In 1992 the fishery in Div. 3L was nonexistent (landings = 2993 t) with fish arriving late inshore. A similar problem of late arrival of spawning capelin also occurred in Div. 3K, however landings there were higher (landings = 16351 t) than in Div. 3L (Nakashima 1993a; Nakashima and Carscadden 1993). In 1993 mature capelin were found inshore earlier than in 1991 or 1992 but fishing times remained later than in the 1980's. In 1993, fishing took place for large females in St. Mary's Bay and on the Southern Shore in late June and early July respectively, in Conception Bay July 20-21, in Trinity Bay July 30 - August 2, and in Bonavista Bay August 7-13 (Nakashima 1994). Fishing was closed north of Bonavista Bay by late July, however spawnings at Cape Freels and Twillingate in mid to late August and at Hampden in early September (Nakashima and Winters, unpublished data) are consistent with observations made by fishers of a large school of capelin slowly moving along the northeast coast in 1993. From 1991-93 one major reason given for problems with the fishery was the late and unpredictable arrival of mature fish inshore.

Avian predators responded to the later spawning times and inshore distribution of capelin in the 1990's. 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 1992). The percentage of capelin in gannet diets was inversely correlated to June-July surface temperatures. Montevecchi and Myers (1992) reported that common murrelets were breeding later in August on Funk Island in 1990-91. They observed that 48% of females taken by common murrelets in 1991 were gravid compared to 4% in 1990 indicating that pre-spawning females were still inshore in August 1991.

Early Life History

Patterns of larval emergence from beach sediments suggest that larvae were emerging later than in the 1980's. It is reasonable to expect that when eggs are deposited late, hatching would also be delayed. In studies at Bryants Cove in the late 1970's and early 1980's 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) (Fig. 4).

In 1990 a study was initiated to monitor the larval emergence patterns of capelin at Bellevue and at Arnolds Cove. This study was expanded in 1991 to include Chapel Cove, Eastport, Cape Freels, Twillingate, and Hampden (Fig. 1). Tows with a 150 μ m mesh plankton dip net were made parallel to the beach along the intertidal zone at every high tide throughout the period when larvae were emerging from beach sediments. In 1990 capelin larvae emerged from early July to early August at Bellevue (Fig. 5). Since 1991 larval emergence has predominantly occurred between late July and late August on the northeast coast (Fig. 5). In a few instances in 1993 larvae were emerging as late as September (Fig. 5). Emergence times were generally later in Div. 3K than in Div. 3L. Larvae emerging later in August and September may encounter conditions which are not conducive to survival or growth (Frank and Leggett 1985).

Growth Characteristics

Total lengths of males and females at age were smaller for age 3 and age 4 fish in 1991-93, however age 2 fish in the commercial catch did not show a comparable decline (Fig. 6). Similarly weights-at-age of sexes combined are lower in 1991-93 compared to the 1980's 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 1980's (Fig. 7). In 1985 a relatively high proportion of age 2's were also observed. The high proportion of age 2's in 1985 and in 1988 were related to strong year-classes produced in 1983 and 1986, respectively (Nakashima 1994a). Similar to 1991-93, spring water temperatures in 1985 were cooler than normal (Nakashima and Harnum 1986). Usually the presence of a high proportion of age 2 fish has been taken as a sign of a strong recruiting year-class. If so then according to Figure 7 the 1989, 1990, and 1991 year-classes should be strong. The 1989 year-class was the third most abundant year-class since 1978 (Nakashima 1994). Soviet 0-group surveys in November-December 1990 indicated that the 1990 year-class in Div. 3LNO was strong (Bakanev 1991). The 1991 year-class was considered average by Bakanev (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 then the 1991 year-class would be weak (Fig. 5). An alternate explanation for three years of the high proportion of mature age 2's may be related to abundance levels. The abundance of mature age 2's may not have changed during the 1990's, 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 1983), spawning runs since 1991 consist of a wide range of lengths and 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.

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 survey area (Miller 1994). Capelin bycatch and cod stomach analyses of capelin prey from fall groundfish surveys suggest that capelin distributions have shifted south and east since 1990 (Lilly 1994). The typical diurnal vertical migration of capelin in the fall was not observed in 1992 (Shackell et 1994). Recently, capelin were also observed on the Flemish Cap (Carscadden 1994) and the Scotian Shelf (Frank and Simon 1994) outside their normal range of distribution.

Effects on Inshore Indices

Aerial Survey Index

One of the assumptions of 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 peak abundance, ie the day with the highest total school area, represents a minimum relative abundance for a particular transect. The spreading out of spawning runs from early July to late August has caused a multimodal distribution of spawning runs. This possibility was one of the reasons given by Winters (1994) to propose another method of utilizing the aerial survey data as a relative abundance index.

Another factor influencing the survey was the delay in arrival of capelin schools inshore. Data collected by aerial surveys in the 1980's were in a fixed period of time generally between mid-June and early July (Nakashima 1994). In 1985 a delay in arrival possibly due to cooler water temperatures resulted in an abundance peak being estimated at the end of the survey period (Nakashima 1986). The possibility existed that higher school areas might have been observed if the survey period could have been extended. This situation occurred again in 1991-93 but was much more pronounced. In 1991 the survey ended before the peak abundance of capelin was observed inshore (Nakashima 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 highest in the survey area (Nakashima 1993b), however more spawnings did occur in Trinity Bay after the survey ended on July 14. The 1993 survey adequately covered the main spawnings in Conception Bay but failed to cover the two more abundant spawnings in August in Trinity Bay (Nakashima 1994). Thus delays in spawning and extended 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 in those years. The unpredictable nature of capelin schools arriving late in the survey area and spawning extending over a longer time period made the task of timing the survey to cover peak inshore school abundance difficult in recent years.

Trap Catch Rate Index

One assumption for 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. The combination of monitoring areas for female quality before opening an area to fishing, the unpredictable availability of capelin at trap berths, the extended spawning season, and moratorium on cod fishing in recent years have all had negative influences on

decisions made by trap fishers to participate in the capelin fishery. The decline in fishing effort is suggested by less completed research logbooks being returned, by the trend to fishing single traps by fishers who fished two in the 1980's, and in an increase in the number of survey respondents who did not fish in 1991-93 (Nakashima and Harnum 1992a, b; Nakashima 1993a, 1994a). The effect of the extended and late spawning season on the pattern in daily catch rates was clearly depicted by Winters (1994) in Figure 8.

Discarding in the fishery has experienced an increase in small females given as the reason for discards which relates to the higher proportion of mature age 2's and slower growth of older ages. The discarding problem has been ameliorated somewhat by closing areas to fishing when size categories become too small. For example in 1994 areas were closed when female counts exceeded 50 females/kg. While actual discards have been reduced the initial problem which disrupted fishing patterns still remains.

Egg Deposition Index

The egg deposition index for Conception Bay was based on the assumption that most of the spawning was unimodal similar to the aerial survey index and estimates of newly-spawned eggs following peak egg deposition may be used as an indicator of spawner escapement. Survey teams collected samples after peak spawning had 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 1990's have resulted in the assumption of unimodal spawning not being realized. Survey times indicate that spawning has occurred later since 1991 (Table 1), however its value as an index has been questioned and was abandoned after 1993.

Summary

The evidence 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 1980's. Many of the differences such as reduced length- and weight-at-age for ages 3 and 4 fish, late arrival of mature capelin inshore, delayed and extended 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 have had a pronounced disruptive effect on fishing and the fishery. Fishing has occurred later with multiple opening and closing dates and the searching pattern of purse seiners following capelin schools as they progressed northwards along the northeast coast no longer occurs because of the unpredictable arrival of mature capelin schools inshore. The mixtures of small capelin due to higher proportions of age 2's and slower growing older fish with the larger preferred size females has resulted in area closures and inability to fulfill market requirements such as in Div. 3L in 1992 and all areas in 1994. The feeding and breeding habits of gannets and common murres were also disrupted since 1990 partly in response to the changes in capelin availability and sea surface temperatures. Changes in offshore distribution and declines in acoustic biomass, disruption of diurnal vertical migration behaviour, and appearance of capelin on the Flemish Cap and Scotian Shelf since 1990 have also been reported. 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 the 1990's.

The immediate effects on capelin populations and the fishery during 1991-93 are readily observable, however longterm implications of recent biological changes have yet to be realized. 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 three years of poor growth, delayed maturation, and late spawning? These and other questions can only be addressed when the mature progeny from spawnings since 1991 return inshore.

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Table 1. Arrival and spawning times of derived from aerial surveys (Nakashima 1994b), Conception Bay beaches (Nakashima and Slaney 1994), Bryants Cove (Carscadden et al. 1992) and Chapel Cove peak spawning dates, and spawning season for Div. 3KL from six northeast coast beaches (Nakashima and Winters 1994).

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

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

Year	Age					All
	2	3	4	5	6	
Div. 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
Div. 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

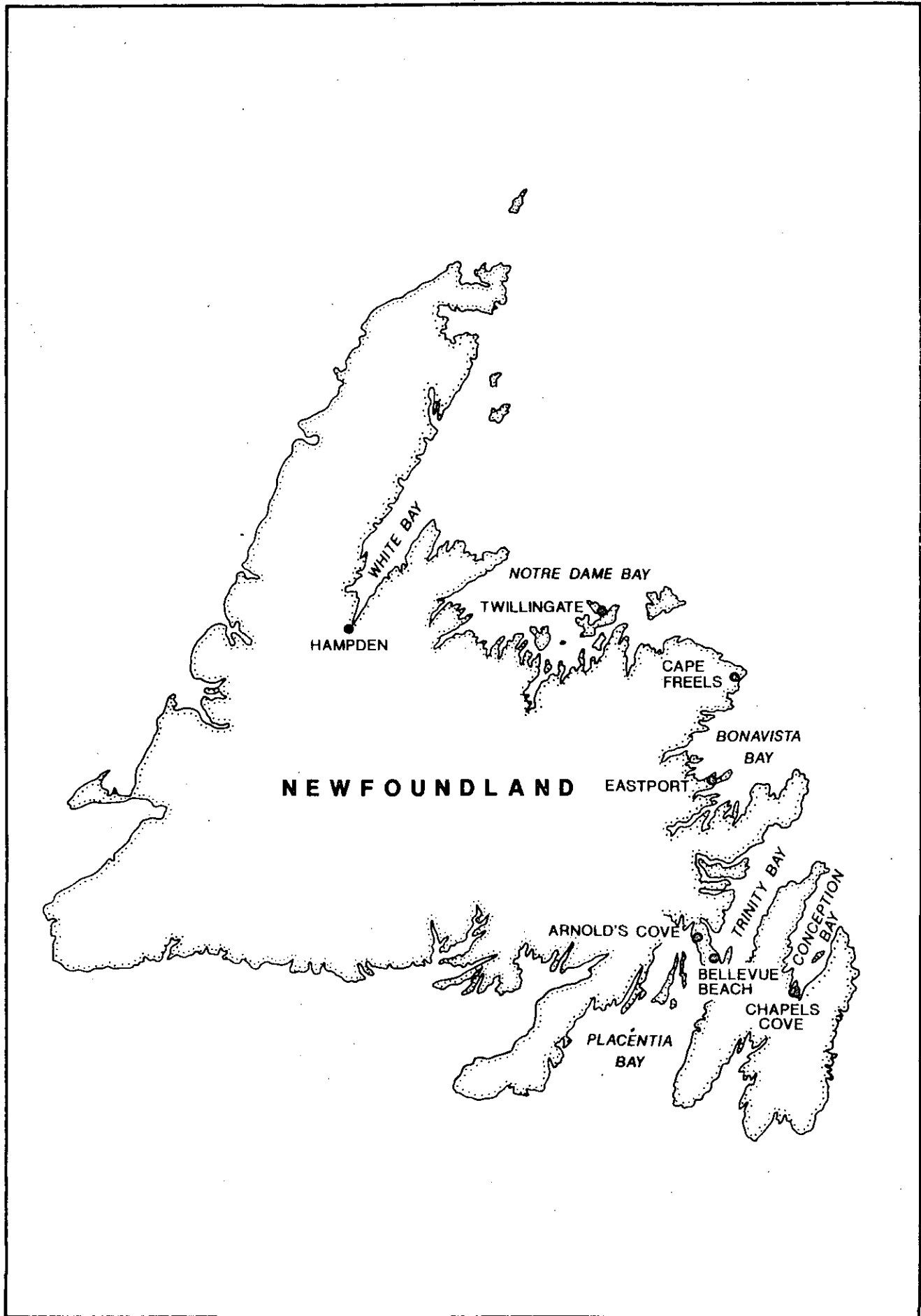


Fig. 1. Capelin spawning beaches monitored for larval emergence.

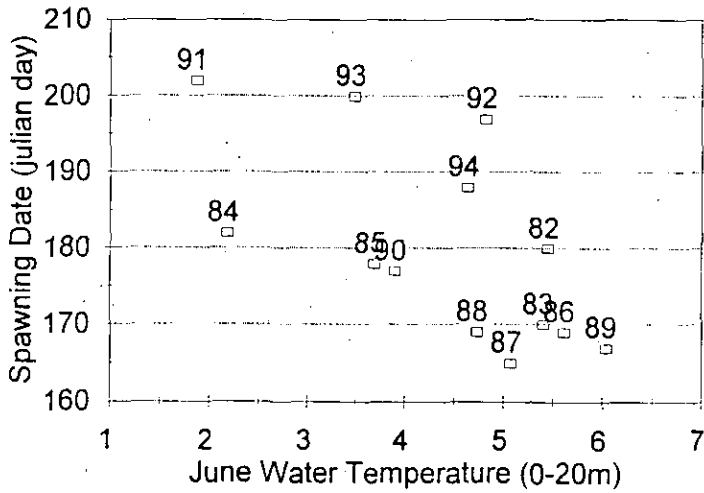
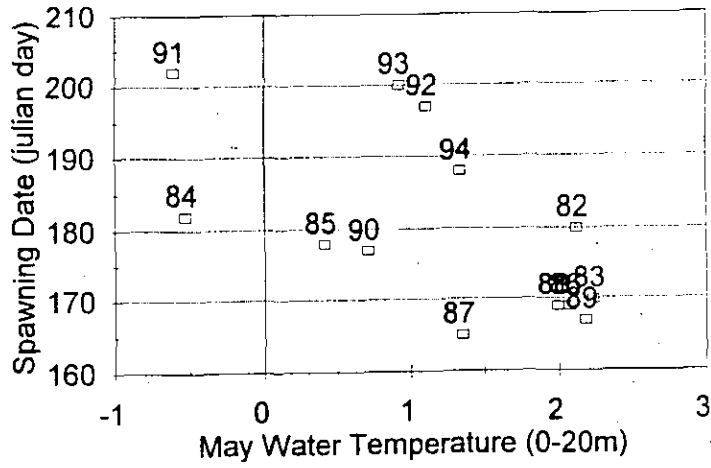


Fig. 2. The relationship between spawning time and May surface water temperatures (upper) and June surface water temperatures (lower), 1982-94.

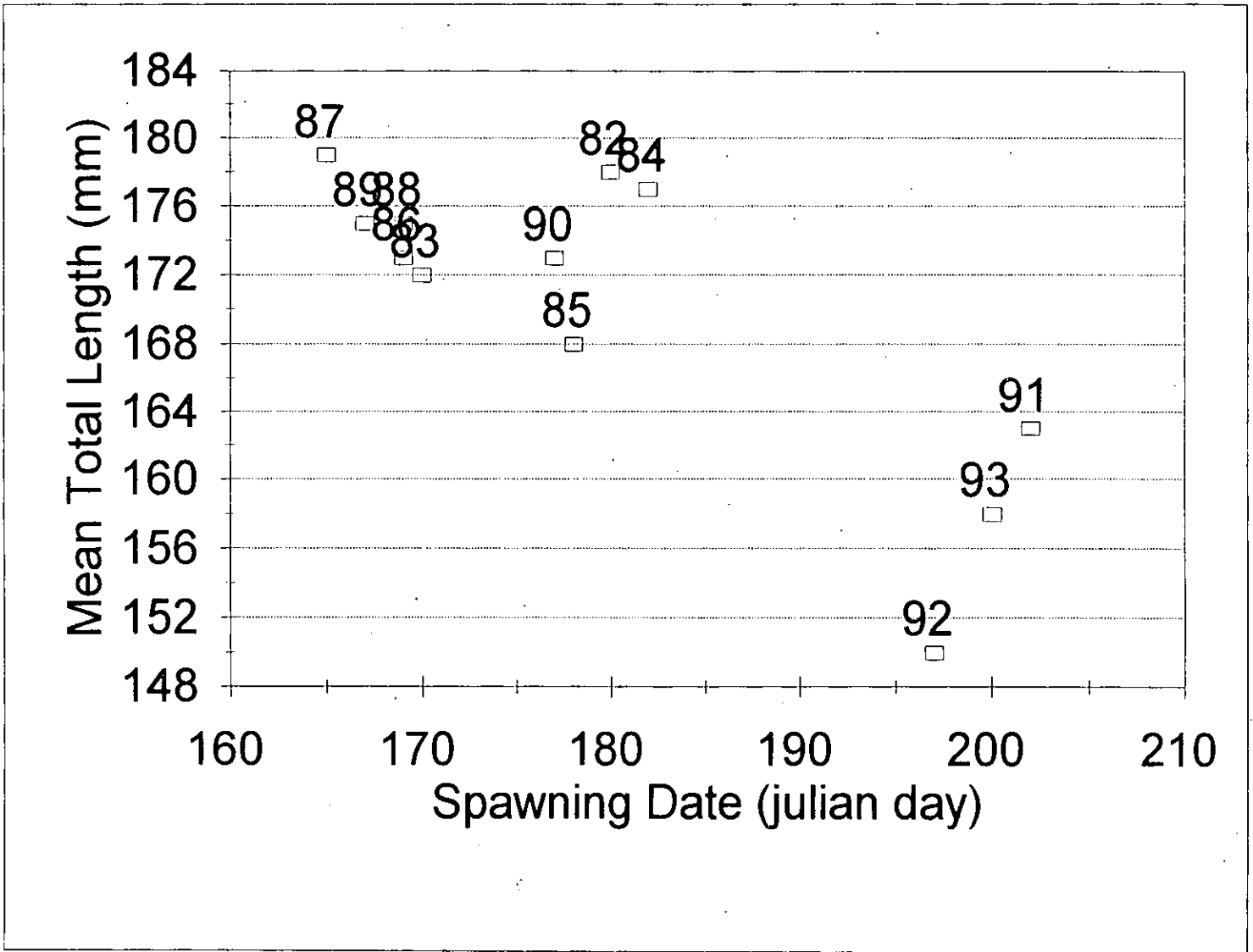


Fig. 3. Relationship between mean total length (mm) and spawning date, 1982-94.

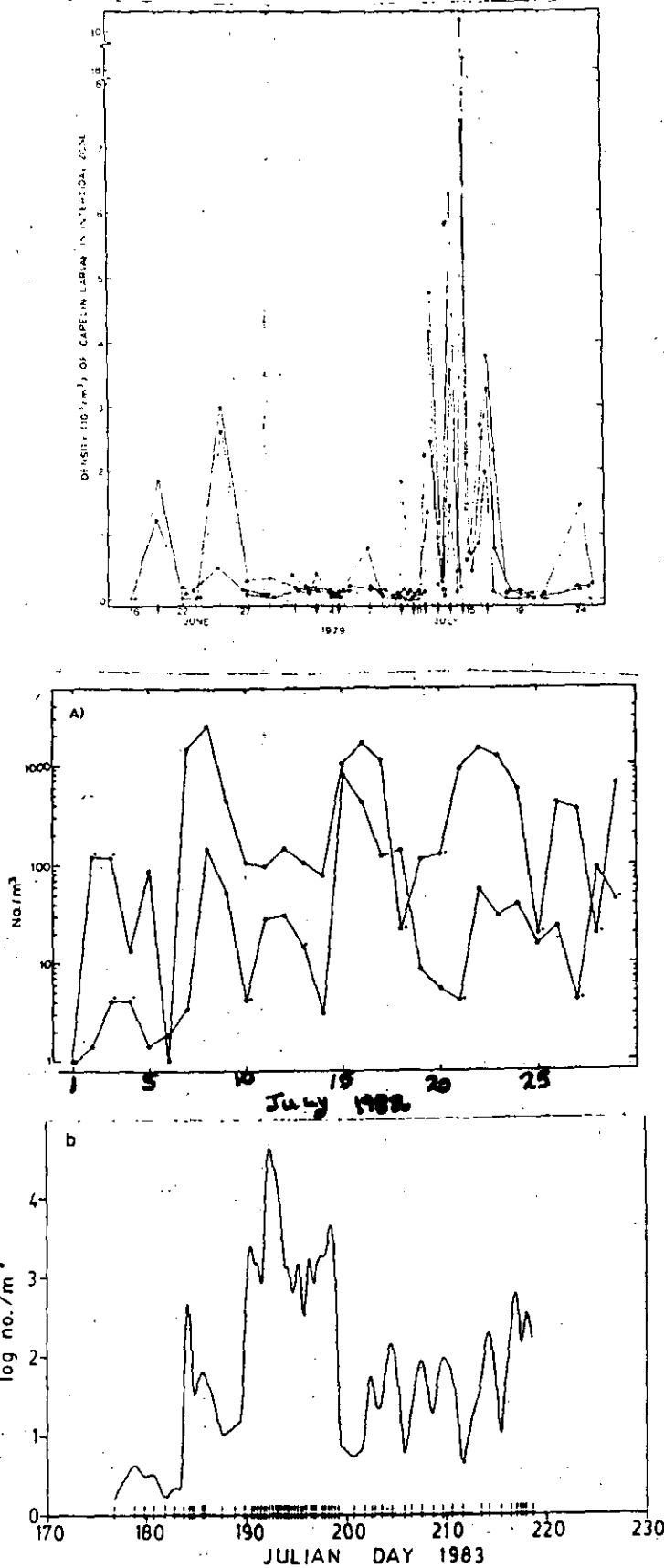
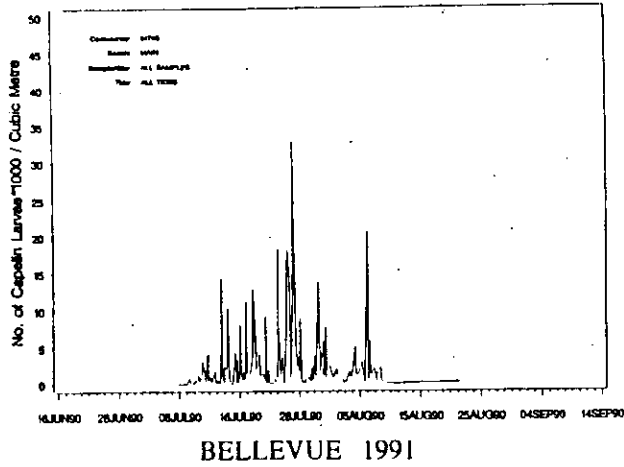
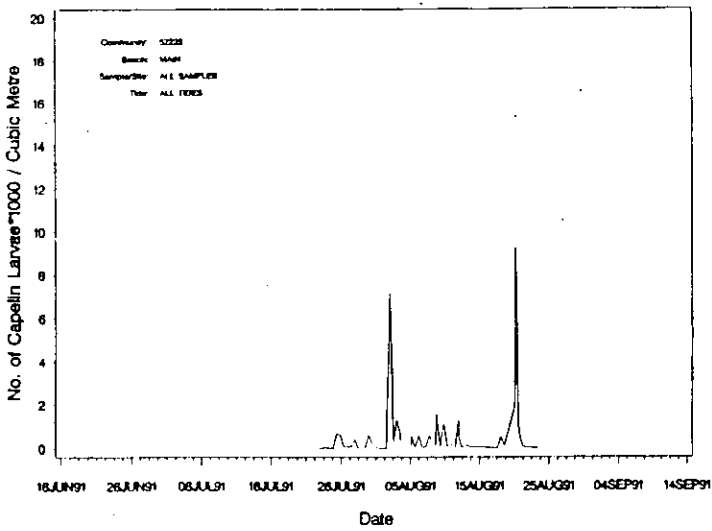
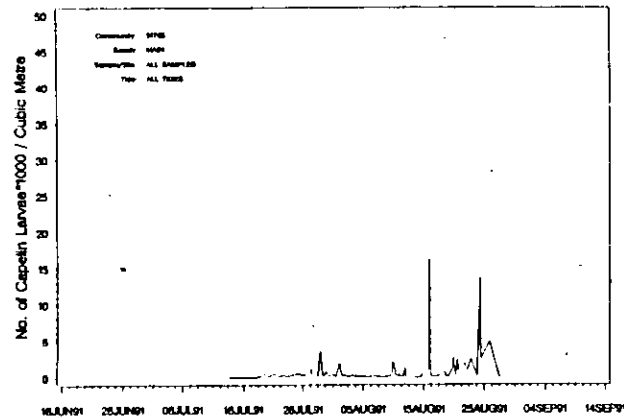


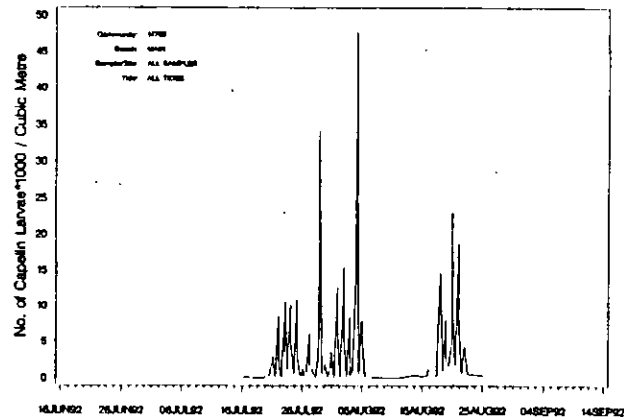
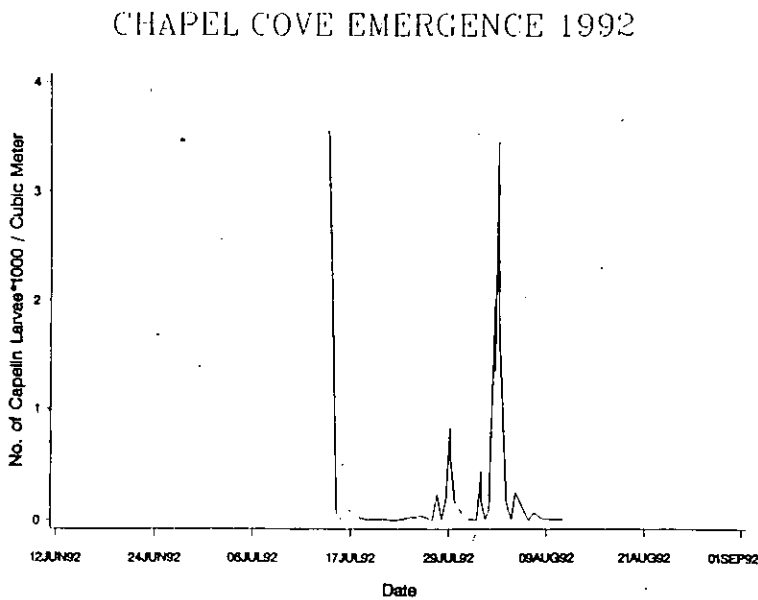
Fig. 4. Capelin larval emergence patterns from Bryants Cove in 1979 (Frank and Leggett 1981), Bryants Cove (O) and Eastport (O) in 1982 (Frank and Leggett 1985), and from Bryants Cove in 1983 (Taggart and Leggett 1987).



BELLEVUE 1991



BELLEVUE 1992



BELLEVUE 1993

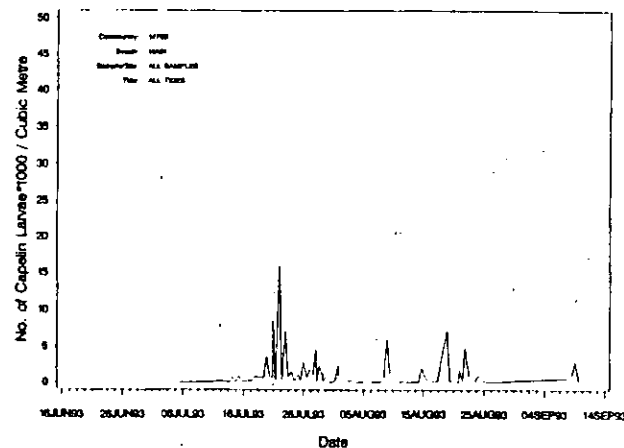
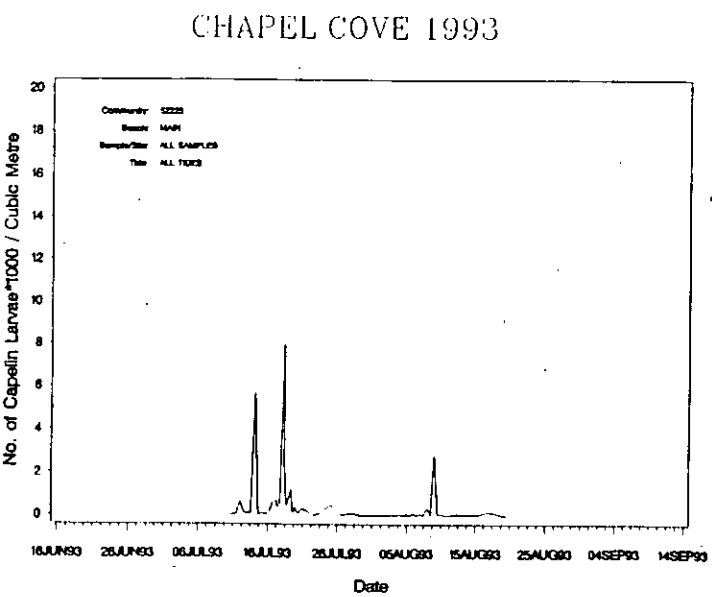
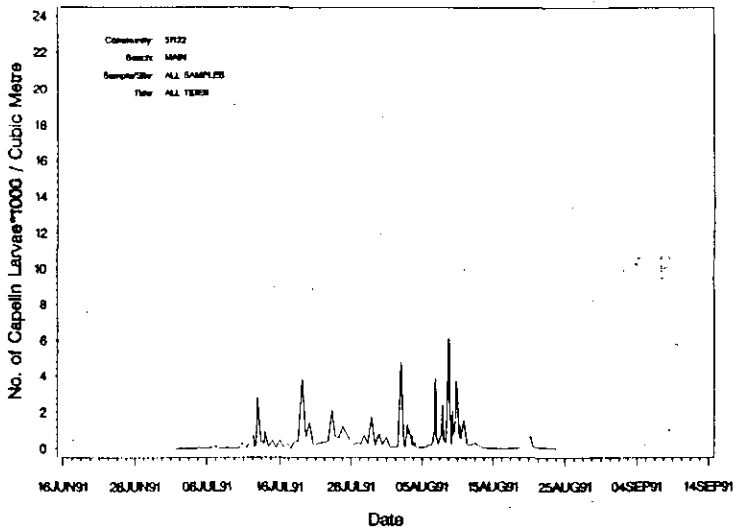
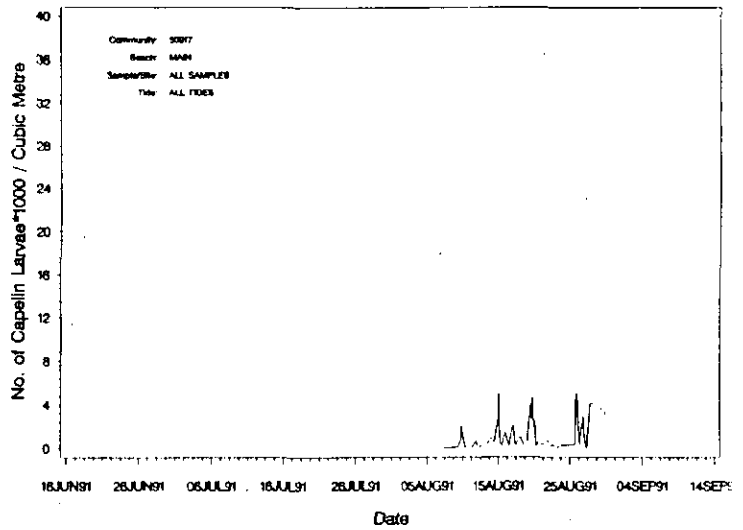


Fig. 5. Capelin larval emergence patterns from Chapel Cove, Bellevue, Eastport, Cape Freels, Twillingate, and Hampden.

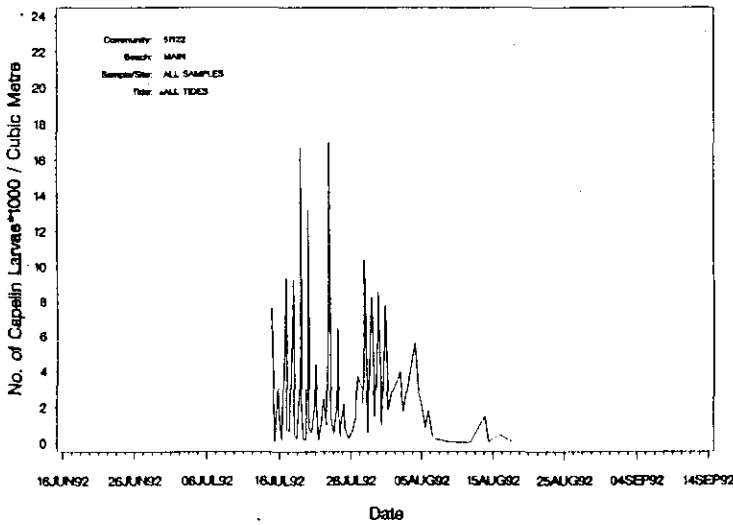
EASTPORT 1991



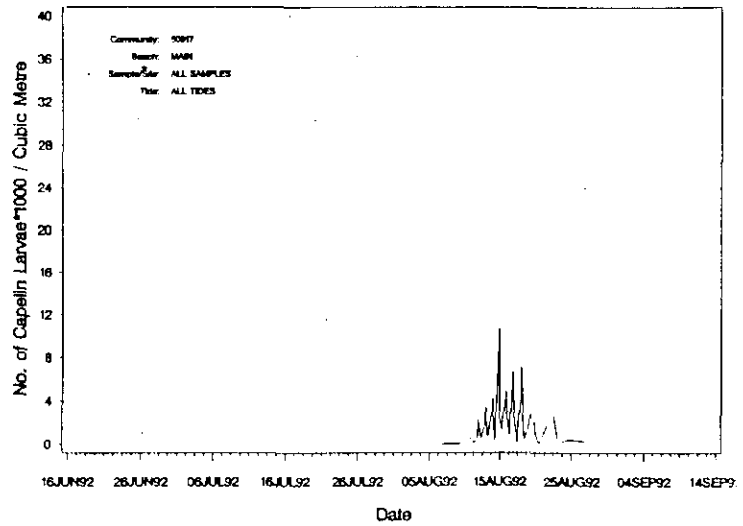
CAPE FREELS 1991



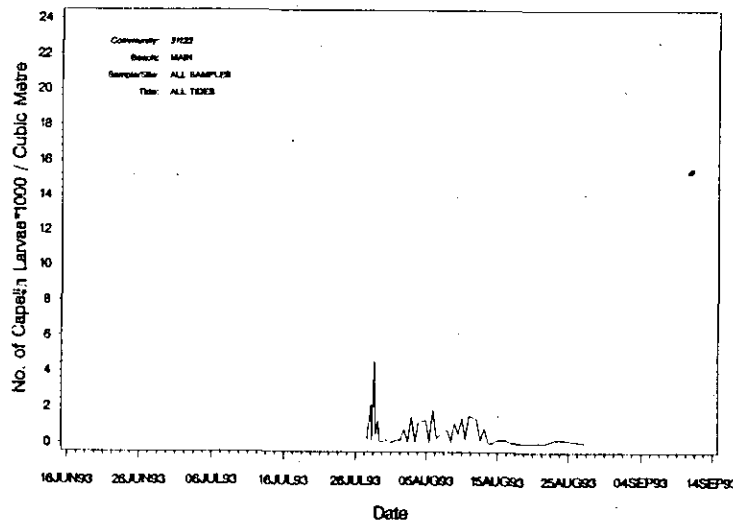
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CAPE FREELS 1992



EASTPORT 1993



CAPE FREELS 1993

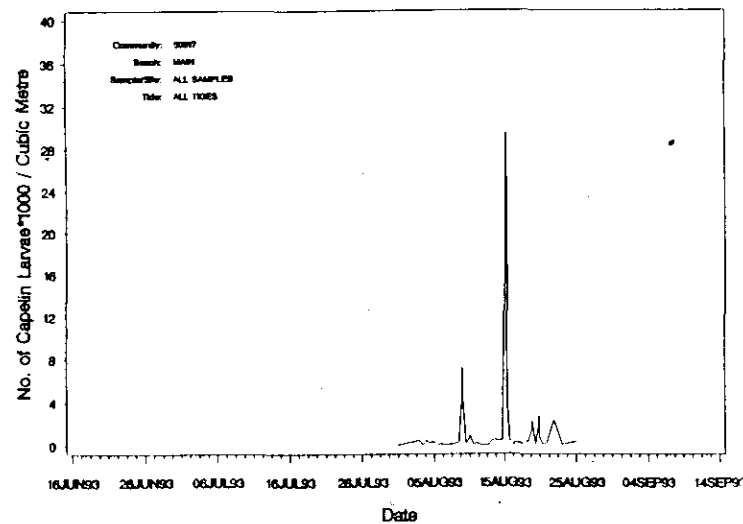
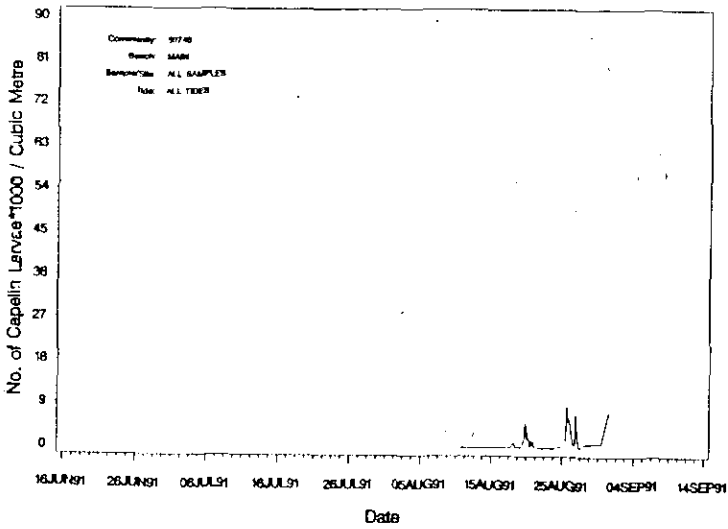
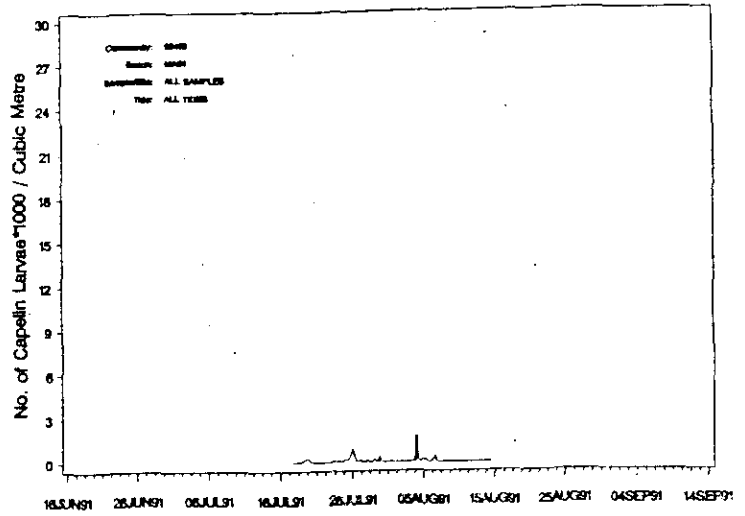


Fig. 5. Continued ...

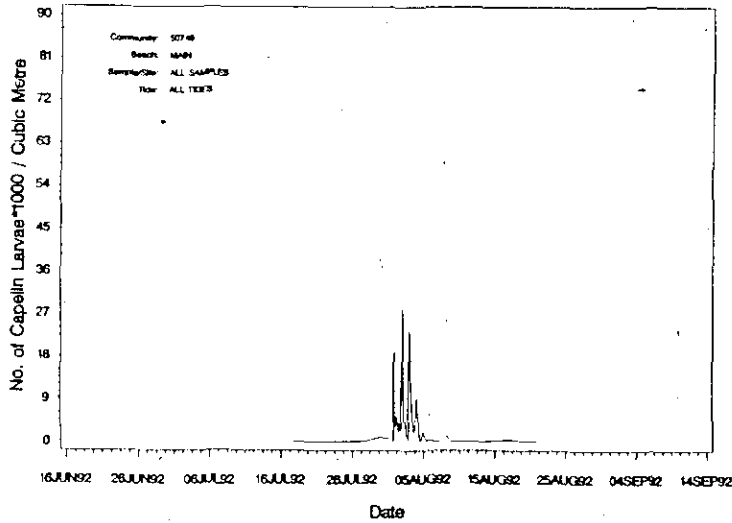
TWILLINGATE 1991



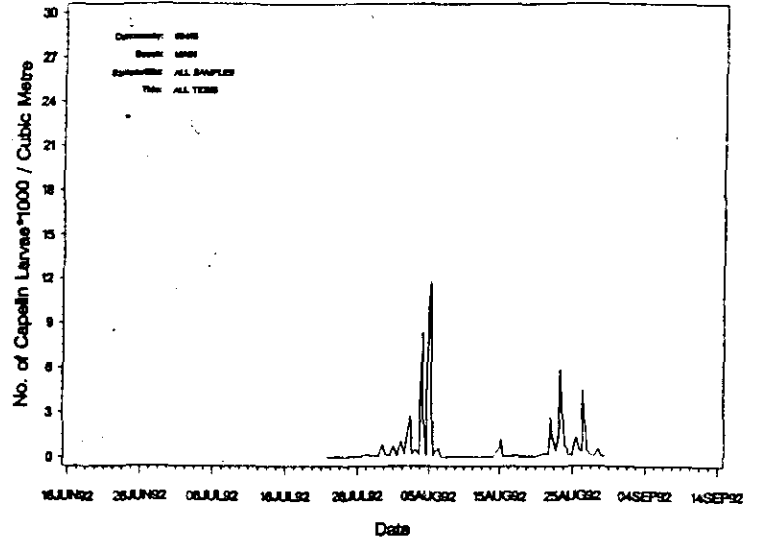
HAMPDEN 1991



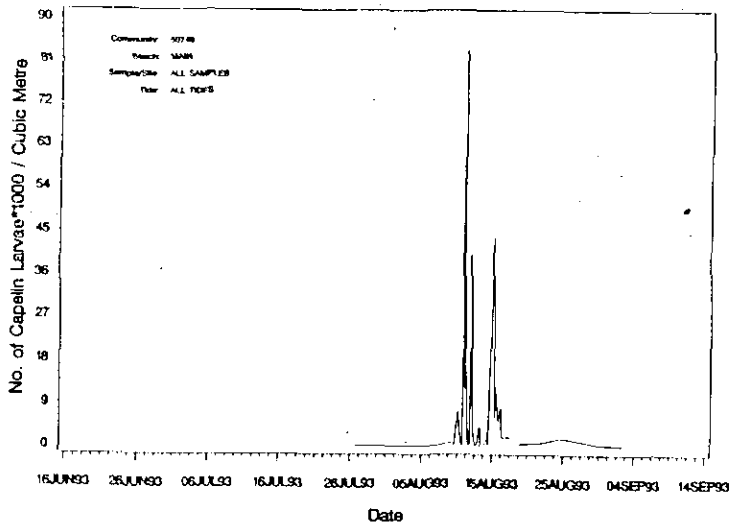
TWILLINGATE 1992



HAMPDEN 1992



TWILLINGATE 1993



HAMPDEN 1993

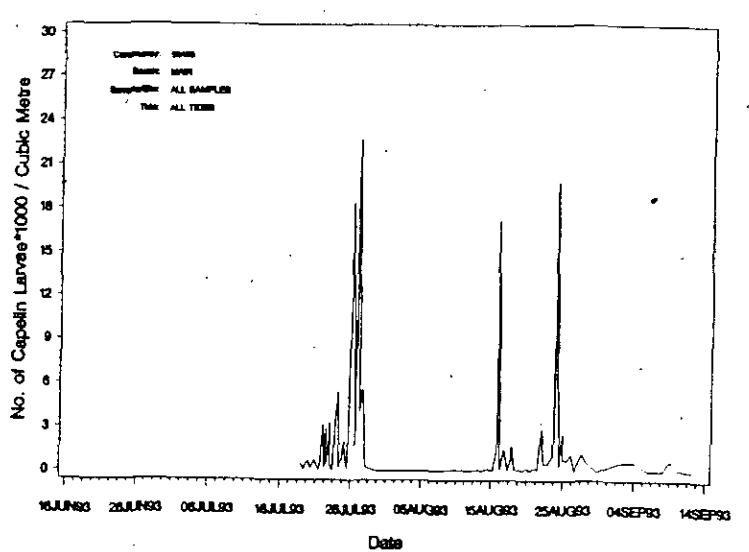


Fig. 5. Continued ...

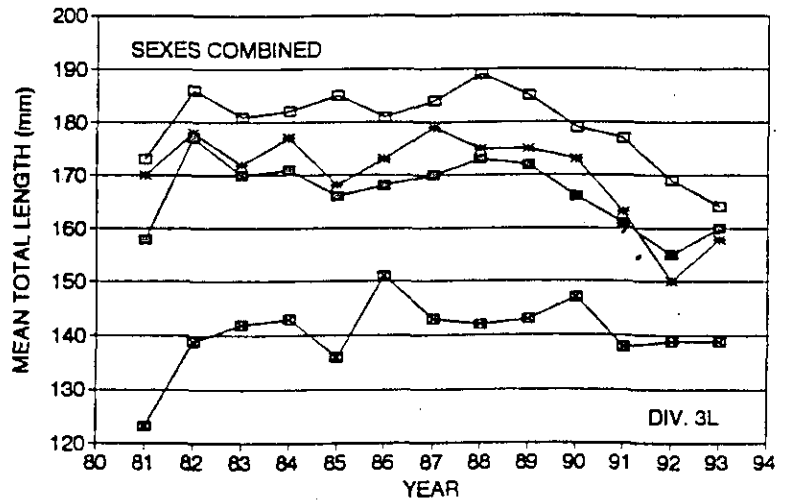
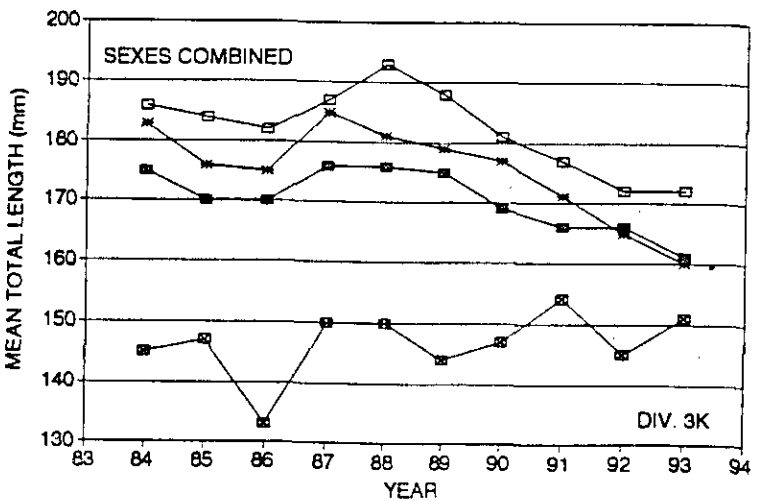
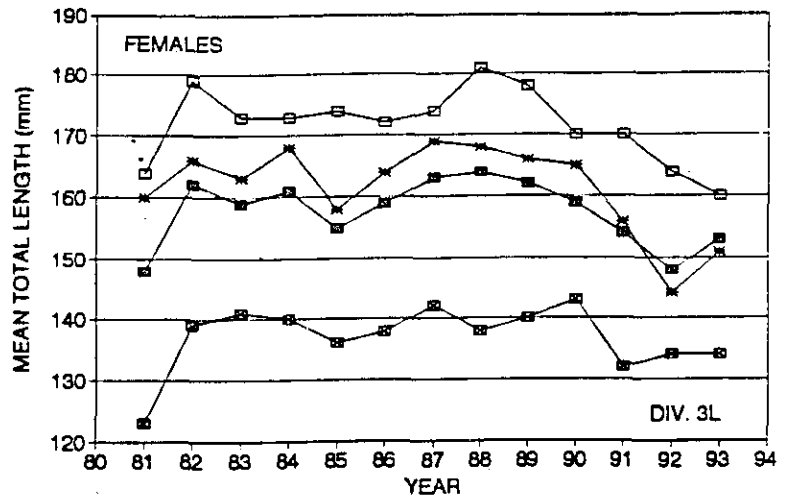
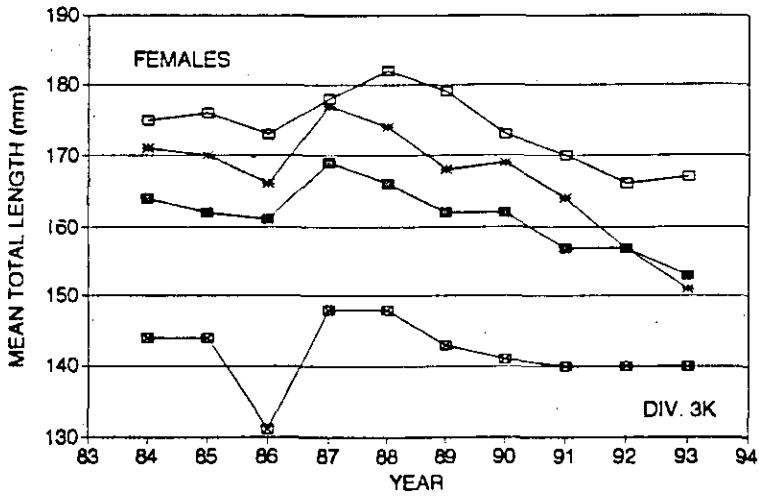
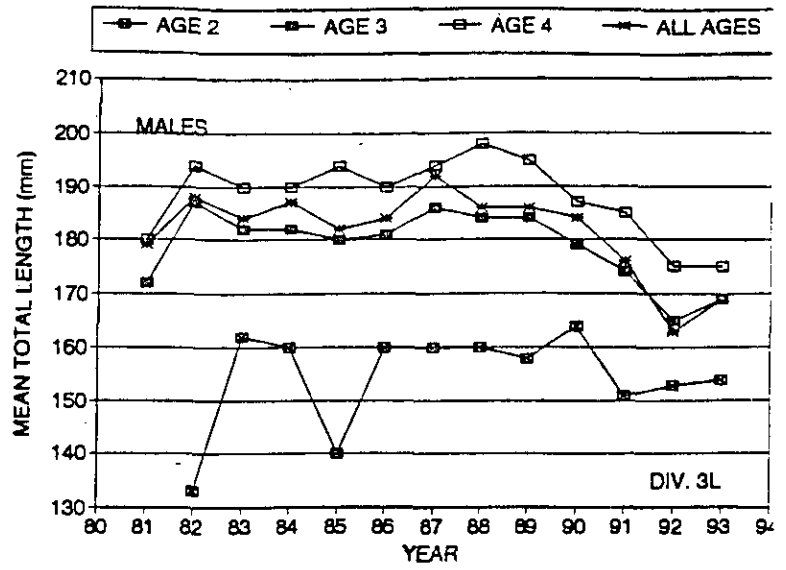
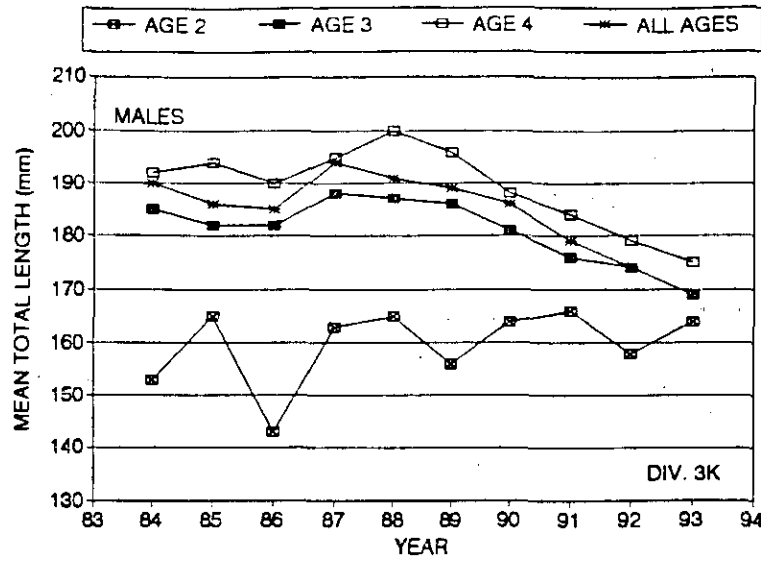


Fig. 6. Mean total lengths-at-age for Div. 3K and Div. 3L males, females, and sexes combined from Nakashima (1994).

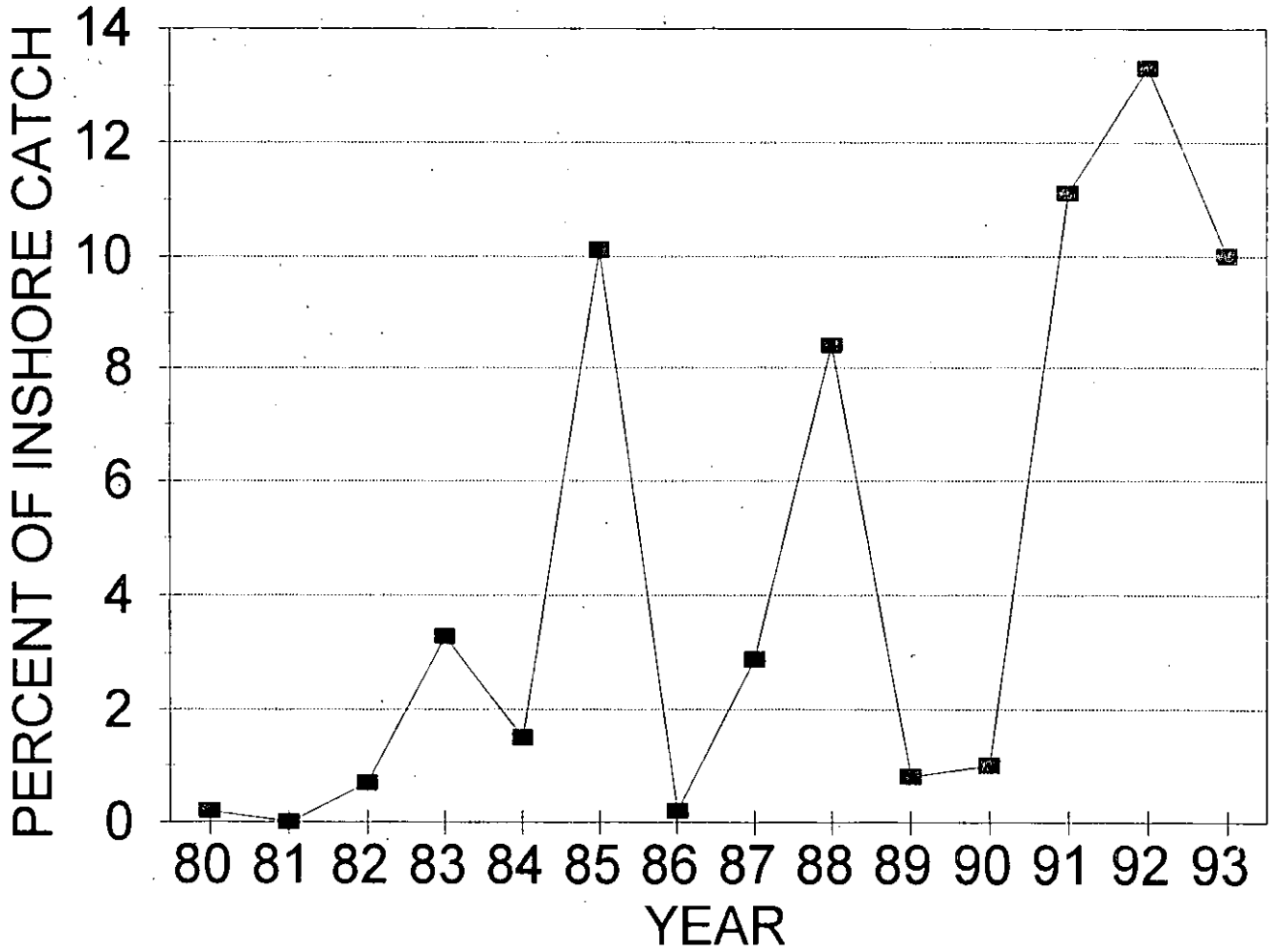


Fig. 7. The proportion of the inshore commercial catch consisting of mature age 2 capelin.

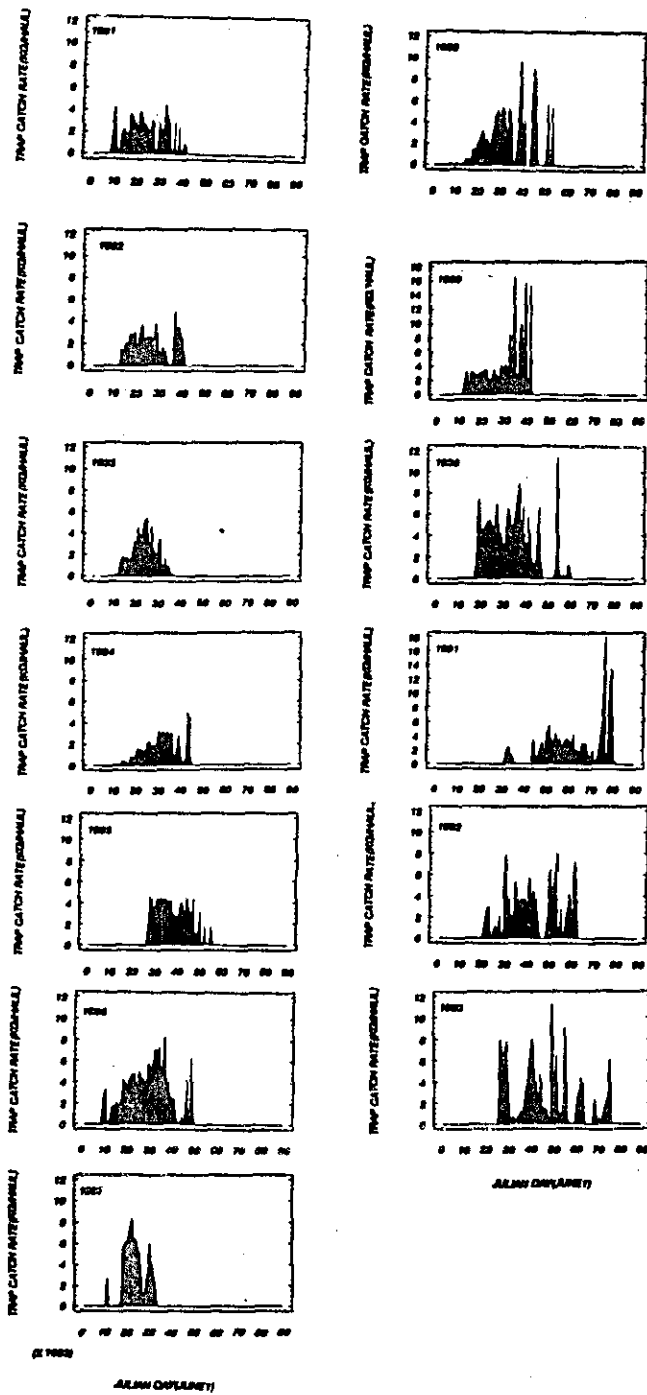


Fig. 8. Daily trap catch rates (kg/haul) in NAFO Div. 3KL for 1981-93 from Winters (1994).