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Possible Factors Responsible for the Variable Recruitment of the 1981, 1982 and 1983 Year-classes of Haddock (Melanogrammus aeglefinus L.) on Georges Bank

by

E. B. Cohen, D. G. Mountain and R. G. Lough
National Marine Fisheries Service, Northeast Fisheries Center
Woods Hole, Massachusetts, 02543, USA

SPECIAL SESSION ON RECRUITMENT

INTRODUCTION

The lack of correlation between larval abundance and subsequent year-class strength over the full range of values is widely accepted (Sissenwine, 1979). However, spawner-recruit considerations show that extremely low production or survival of eggs and larvae generally results in a poor year-class. This has the value that a bad year-class can be predicted earlier than with a pre-recruit survey. In addition, it may offer an opportunity to identify specific processes affecting the ichthyoplankton and causing a poor year-class. In 1982 the abundance of haddock larvae on Georges Bank was extremely low, and the resulting year-class of haddock was a very poor one. Therefore, the 1982 year class offers an excellent opportunity to examine effects on eggs and larvae.

Various aspects of the physical environment as well as the spawning stock biomass are considered to identify the cause of the extremely low production and/or survival of larvae in 1982. The conditions on Georges Bank in 1981-1983 and on Browns Bank in 1981 and 1983 are also reviewed to compare the processes likely to be affecting haddock abundance.

DATA SOURCES

Data on egg and larval abundance are from a series of Marine Monitoring Assessment and Prediction Program (MARMAP) (Sherman 1980) ichthyoplankton surveys in 1981, 1982 and 1983 (Table 1). Together the surveys provide good temporal and spatial coverage of the spawning period for haddock on Georges Bank. Information on the abundance and stage of the reproductive cycle for spawners is based on the National Marine Fisheries Service, Northeast Fisheries Center (NMFS, NEFC) spring bottom trawl survey 1981-1983. Water temperature and salinity data are from MARMAP (Sherman 1980) and bottom trawl survey cruises (Grosslein 1969, Azarovitz 1981). Information on warm core ring activity is derived from frontal analysis charts issued by the Atlantic Environmental Group (AEG), NMFS, NEFC, Narragansett, RI.

RESULTS

Egg Abundance

Substantial numbers of eggs were observed on the northern portion of the bank as well as in Great South Channel during March 1982, suggesting that spawning started normally (Lough, 1982). P. Berrien (personal communication, NMFS, NEFC, Sandy Hook, NJ) has estimated, based on several cruises (see Berrien et al, 1981 for methods), that the number of haddock eggs spawned in 1982 was about 25 % of the number spawned in 1981. More significantly, the estimated number hatching was only about 3 % of the number that hatched in 1981, indicating a relatively higher mortality during the egg stage in 1982 compared with other years (Table 2). If the eggs hatch in about 2-3 weeks at average spring temperatures (Marak and Colton, 1961; Laurence and Rogers, 1976), then the 98 % loss of eggs in 1982 would account for a mortality rate of 19.6 % day. In 1981, the 83 % loss of eggs be have a daily mortality rate of 10.7 %/day, half the loss rate for the 1982 season. Since early stage cod and haddock eggs are indistinguishable from each other, the number of haddock eggs is based on the ratio of cod to haddock eggs in the later stages. If there was a high mortality on haddock eggs, the number of eggs spawned would be underestimated. There is some evidence that this may have occurred as the number of cod plus haddock eggs spawned in 1982 was 88.7 X 10^{12} compared with 91.9 X 10^{12} in 1981. Unfortunately, there is no egg data for 1983 as the samples were destroyed in a fire at the Sandy Hook Laboratory.

Larval Abundance

The mean observed abundance of haddock larvae in 1982 was one to two orders of magnitude lower than in 1981 or 1983 (Table 3). In addition, from the observed larval abundance data, Morse (1984 and personal communication, NMFS, NEFC, Sandy Hook, NJ) has estimated the total number of haddock larvae hatching for each year from 1977-1983 (Table 4), which are in close agreement with the number of eggs hatching in Table 2. In his results, 1982 stands out as the year of lowest larval production and 1983 is the second lowest . The estimated initial number of larvae produced is dependent on the mortality during the larval period and is based on two assumptions: "1) that all individuals in a sample are from one source that has been producing at a **constant rate** over the time needed to reach the greatest age or length observed and 2) that mortality is constant over the entire age or length range of the sample" (Morse, 1984). The first assumption is not unreasonable as haddock have a peak spawning period on the Northeast Peak of Georges Bank in the spring. The second assumption, however, will lead to an underestimte of the number of larvae hatched if some cause of death affecting a large portion of the population acts for a short period of time.

Spawner Biomass

The abundance of haddock has declined on Georges Bank in recent years (Clark et al.,1982; Overholtz et al., 1983). The abundance of haddock on Georges Bank for the period 1981-1983 from the spring NEFC bottom trawl survey is shown in Table 5. There was a large decrease in haddock abundance from 1981 to 1982 and a smaller drop in 1983. The survey index is a reasonable indication of spawning biomass as the number of immature fish only varies from 10-20 % from year to year (Table 6). The change in biomass due to immatures is, of course, even less. Haddock biomass on eastern Georges Bank, the primary spawning ground of haddock, was about the same in 1982 and 1983, approximately 50 % less than in 1981. The fish about to spawn, in spawning condition, or recently spawned are called "spawners." The percentage of "spawners" was highest in 1982-1983, about 50 % (Table 6) of the fish sampled in the spring bottom trawl survey. The survey data indicate a normal to high spawning biomass and percentage of haddock "spawners" on Georges Bank in 1982 compared to 1981 and 1983. The age distribution of "spawners" also was similar during 1981 and 1983.

Recruits

The numbers at age 1 are considered recruits in this study. These estimates of year class size were derived from the most recent VPA of age 2 fish and back-calculated to age 1 using an M = 0.2. The 1981 and 1982 haddock year classes are equal to the poorest on record (RAD, 1984). This corresponds to 2.158 X 10^6 age 1 fish in 1981 and 0.456 X 10^6 fish in 1982 (Overholtz et al., 1982 and W. Overholtz personal communication, NMFS, NEFC, Woods Hole, MA). Results to date indicate that the 1983 year-class of about 12.214×10^6 haddock is relatively good (W. Overholtz, NEFC, Woods Hole, personal communication). In terms of relative recruitment, the three year classes are clearly different: the 1982 year class being very low and the 1983 year class considerably higher in recruits.

Hydrographic Conditions

The bottom temperature in the spawning area is indicative of the severity and duration of winter cooling that could affect the spawning and the subsequent survival of the eggs and larvae. The average bottom temperature on the eastern part of Georges Bank (see Figure 1) has been determined from data obtained on NEFC MARMAP and bottom trawl survey cruises from 1964 to 1983 (Figure 2). The data are divided into a cold period (1964-1971) and a relatively warm period (1972-1981), with 1982 and 1983 being shown individually. The range of all observations from which the averages were calculated is indicated by the dashed envelope in the figure.

On 4 March 1982 (Day 63) the average bottom temperature was 3.4°C and by 19 April (Day 109) had warmed to 4.1°C. These values are considerably colder than in other recent years, but are comparable to the temperatures from the earlier, colder period. The single entry for 1983 (19 April, Day 109, 6.1°C) was among the warmest recorded and was 2°C warmer than on the same day in 1982.

The large seasonal cycle in water temperature can overshadow variations due to changes in the water mass characteristics. Water mass changes are best indicated by salinity. The average salinity in the upper 50 m of the water column has been calculated from MARMAP data on the bank from 1978 to 1983 (Figure 3). Both seasonal and interannual variations are evident. Generally the maximum occurs in the winter and the minimum in the summer. In 1982, however, the salinity began the year at a low value - about 0.5 ‰ below the other years shown. This was due to a drop in salinity that began in the Gulf of Maine in late 1980 with the influx of low salinity water around Cape Sable (Wright, 1983). Throughout 1981 the surface layers of the Gulf showed a progressive decrease in salinity (Jewell and Mountain, 1983) which was first evident on Georges Bank in the late fall of 1981. The low salinity on Georges in early 1982 does not appear related to a large influx of water directly from the Scotian Shelf.

Warm Core Ring Entrainment

Warm core Gulf Stream rings commonly entrain water from Georges Bank around their eastern side. This loss of water from the shelf represents a potential mechanism for removing fish eggs and larvae from the bank. The only significant concentration of cod or haddock larvae found in 1982 was observed in mid-April on the southeastern side of the bank. Frontal analysis charts issued by the Atlantic Environmental Group (AEG, NMFS, NEFC, Narragansett, RI) show that for the month preceding the larval observations, Warm Core Ring 82-A was nearly stationary south of the bank near 67°W. A large amount of water from Georges Bank appeared to be entrained off the bank by the ring from March through the time of the larval observations (Figure 4). Included on the figure is the haddock larval distribution from mid-April. The contours of larval density are open at the edge of the survey area, suggesting that the distribution may have extended off of the southern side of the bank. In fact, the most seaward station had the highest number of larvae caught. The water entrained by the ring (shaded in Figure 4) appeared to be leaving the bank in the same area that the larval distribution would extend off the bank. After 19 April the ring decreased in size and by early May disappeared from the AEG charts. A CTD/MOCNESS survey of the entrainment feature around ring 82-A was made on 25-26 April, including the area of the bank where the larvae had been observed on 19 April. The survey showed that the entrainment contained water of Georges Bank hydrographic characteristics, but no haddock larvae were found in the entrainment or on the southern edge of the bank as far west as 68°W.

In the spring of 1983 a large entrainment feature was again observed off the southern side of Georges Bank in late March, in the vicinity of significant larval haddock concentrations as shown from surveys carried out between 6-19 April (Figure 5). By mid-April both the ring and the entrainment appeared much reduced in size, and by the end of April, only a small deformation of the shelf/slope front remained. The larval distribution did not extend to the edge of the bank and larvae did not appear to be removed from the bank by this entrainment.

Storm Events

During 6-9 April 1982 an intense storm passed through the Georges Bank region. Steady wind speeds exceeded 60 knots and gusts reached 88 knots (Ramp, 1982). A review of satellite images from the storm period indicates that the surface edge of the shelf-slope front moved offshore about 25 km from 3 April to 10 April (Figure 1) along the southern side of Georges Bank. The front off the southeastern part of the bank moved about 60 km seaward, although the situation is complicated by the entrainment feature associated with Warm Core Ring 82-A. Ramp (1982) reports that in current measurements at two sites on the southern side of the bank (shown in Figure 1) the normal southwestward flow abruptly changed to the southeast for a period of three days during the storm. A net southeastward displacement of about 40 km was indicated by measurements at 5 m depth.

Wind-driven Ekman transports have been provided (Reed Armstrong, NMFS, NEFC, Narragansett, RI) for a grid point ($42^{0}00'$N, $69^{0}00'$W) near Georges Bank for the 1981-1983 spawning seasons, March-June. The data are six-hourly values derived from the U.S. Navy Fleet Numerical Oceanography Center northern hemisphere, atmospheric model. Plots of the computed Ekman transport 90^{0} to the right of the wind direction for April and May are shown in Figure 6. However, Bumpus (1976, p. 130) cautions that in the shallow waters of Georges Bank the transport may be more directly downwind or 90^{0} to the left of the computed Ekman vectors. In 1982, the intense April 6-9 storm is readily seen with Ekman transport computed to the southeast. This agrees with the current meter data of Ramp (1982). All during April 1982 the transport vectors are southerly, off the bank. It also is interesting to note the relatively quiet May 1982 with little transport. March 1982 (not shown) also was different from 1982 and 1983 in that no significant transport was noted when the usual case is for strong winter storms throughout the month. In 1983, there were numerous storms of moderate intensity through May. However, during April 1983 note that the Ekman transport vectors are consistently in a northerly direction, which would tend to keep surface waters on the bank. In 1981, April was stormy most of the month with Ekman transport vectors consistantly to the south, but only with moderate intensity. In May 1981 there were two significant storms, 1-5 May and 21-24 May, with Ekman transport vectors to the west and northwest. The effect of the latter storm on the complete mixing of the water column to at least 80 m and the vertical distribution of the gadid larvae and their zooplankton prey was reported in Lough (1984).

The implication from these time series of results is that a significant movement of water off the Georges Bank occurred in response to the April 6-9

1982 storm with a seaward displacement of the shelf-slope front. There is no indication, however, of how much shelf water might have been permanently exchanged or mixed into the slope region.

Zooplankton

Zooplankton data provided by J. Green, NEFC, Narragansett, RI, from winter-spring MARMAP surveys are being examined for major shifts in the distribution and abundance of the dominant species (Pseudocalanus Sp., Centropages typicus, Calanus finmarchicus, and Sagitta elegans. Only the 1982 data have been processed to date so we have no real basis for comparison with the 1981 and 1983 seasons.

DISCUSSION

There are several possible causes or factors responsible for the extremely low abundance of eggs and larvae on Georges Bank in 1982 even though the available data cannot directly confirm any one of these as the actual cause. We attempt to judge the relative magnitude these factors may have had on the 1982 year class, acting individually or together, as well as their effect on the 1981 and 1983 year classes.

Biological Factors

Perhaps the simplest explanation would be that there was an extremely low spawning biomass in 1982. Both the survey index and VPA estimates of haddock biomass were low in 1982 (Figure 7) but not at historical minima. Low spawning biomass undoubtedly contributes to poor recruitment but it does not appear to be the dominant factor in 1982. For example, haddock had low spawning biomass in 1983, yet the 1983 year class is relatively strong; while the 1982 year-class from an equal or greater spawning biomass was poor (W. Overholtz, NEFC, Woods Hole, personal communication).

Variations in fecundity of the spawners also could contribute to variation in the subsequent larval abundance. Fecundity rates generally are assumed to be fairly consistent year to year. However, as Ware (1980) pointed out, "the empiricists, led by Nikolski (1969) and Bagenal (1973), have reported significant time variability in the annual size-specific fecundity rates of different species..." Ware (1980) cites fluctuations of 22-61 % in herring (Nikolski, 1969) and 39-144 % in haddock (Hodder, 1965). Pinhorn (1984) has reported on similar fluctuations in cod from Newfoundland. While similar interannual differences have been reported for Georges and Browns banks (Halliday, personal communication), we cannot make an evaluation of fecundity variation for 1981-1983. The percentage of spawning haddock was about equal in 1982 and 1983. The percentage of spawners was the lowest in 1981, perhaps contributing to the poor 1981 year-class. It does not appear that a spawning failure in 1982 is the primary reason for that year's poor recruitment success. The estimated number of eggs spawned is low, about 20-25% of the numbers during 1979-1981. However, if there was a large mortality of haddock eggs before they can be separated from those of cod, the number of eggs spawned is an underestimate. The total number of cod plus haddock eggs in 1982 is 96 %, 79 % and 143 % of the combined cod and haddock eggs in 1981, 1980 and 1979, respectively. No information is available to assess the variability in egg quality or viability from year to year.

Predation on 0-group haddock after the pelagic life stages does not seem to have contributed significantly to the poor year-class of haddock in 1982. Predation on haddock by spiny dogfish was lower in 1982 than either 1981 or 1983. Haddock was about 5 % of the diet of spiny dogfish in the autumn of 1981 and about 1 % in the autumn of 1983. No haddock were found in spiny dogfish stomachs in 1982 or during the spring of 1981 and 1983. An examination of hundreds of cod stomachs in 1981 and 1982 shows about 10 fish that can be identified as gadoids, and only about 5 of these as haddock (NEFC, unpublished data). In general, the food habits data collected at the NEFC show very little predation on the haddock by fish in the Northwest Atlantic. In fact, an examination of the stomachs of 17 species of fish including cod, silver hake, white hake and pollock shows no occurrences of either cod or haddock in the stomachs of the predators on Georges Bank (Bowman and Michaels, 1982). While predation may be important for some species in some areas (Frank and Legget, 1984; Hunter, 1982, 1984) and even on Georges Bank for silver hake (Cohen and Grosslein, 1982), it does not appear that predation by fish dramatically affects haddock populations. Hunter (1984) summarizes mortality rates of pelagic eggs (p. 535) and concludes that 98 % of cod eggs in the North Sea are probably consumed by predators before hatching. There is evidence from the Kiel Fjord that a jelly fish Aurelia aurata, consumes large amounts of herring larvae causing a significant decline in the larval herring population (Möller, 1984). Fish larvae can comprise a large part of the natural diet of other passive predators such as pelagic Cnidnarians and Ctenophores (Purcell, 1985). We do not yet have the data available to investigate what role these and more active invertebrate predators (euphausiids, hyperiid amphipods, copepods, chaetognaths) contributed to gadid egg and larval losses on Georges Bank during 1981-1983.

Physical Factors

The physical environment may contribute to egg and larval loss in several ways. The colder than normal bottom water temperature on Georges Bank (when compared to recent years) may have contributed to the loss of eggs and larvae. Low water temperature may cause poor hatching success of non-viable eggs and larvae as well as increased predation mortality on eggs and larvae as the hatching time is greater and the growth of larvae is slower. Low temperature also may reduce fecundity of the spawners. While the low water temperature may have contributed to the low larval abundance, the occurrence of comparable temperatures during the period 1964-1971 suggests that temperature alone could not cause the very low numbers observed in 1982. It may be that while the 1964-1971 period was a time of chronic low temperature allowing some physiological response while the low temperature in 1982 was an anomaly causing sever stress. There is evidence of increased hatching time and metabolic stress on larval haddock at 4°C and colder (Laurence 1978, Laurence and Rogers 1976). The former could lead to reduced hatching through increased predation on eggs and the latter was shown by Laurence and Rogers (1976) to lead to complete mortality of a larval cohort in the laboratory. The low salinity observed in 1982 on Georges Bank is not low enough to be physiologically important and probably has little direct effort on the spawning or survival of the larvae (Laurence and Rogers 1976)..

The difference in larval abundance among 1981, 1982 and 1983 may be also related in part to differences in the ring entrainment processes. The 1982 event apparently removed water from the bank proper, while in 1983, only water from the edge of the bank may have been affected. The larval distribution during 1983 was not perturbed or deformed near the entrainment feature as in 1982. Satellite imagery does suggest that the entrainment process is quite complicated and that the source of water entering an entrainment feature can vary spatially with respect to the ring.

Georges Bank vs. Brown Bank

Comparison of these results with observations on Browns Bank is of interest. On Brown Bank the abundance of haddock larvae was reversed for 1981 and 1983 from that on Georges Bank. The number of larvae in 1983 was about 230 times less than the mean larval abundance on the Scotian Shelf from 1979-1982, and about 150 times less than the 1982 value (Koslow et al. 1985). Koslow et al. (1985) have proposed that the number of eggs spawned was normal on Browns Bank in 1983, but that there was extremely high mortality (average egg mortality of 33% per day) during the larval yolksac stage that set the year-class size. They report that the mean water temperature (0-50 m) on Browns Bank was 3.0-6.0°C within the "normal" range for haddock embryonic development. This differs from the highest percentage of viable hatch for haddock in the temperature range of 4°-10°C found by Laurence and Rogers, (1976). In addition, Laurence (1978) reports haddock larvae to have suppressed growth and elevated oxygen consumption when reared at 4°C, a sign of physiological stress. All haddock reared at 4°C died by the fifth week (36 days) in his experiments. Those larvae hatched at 7°C appeared to be normal and were estimated to have methamorphised by the sixth to seventh week after hatch. Apparently water temperature near 4°C and colder has a long-term detrimental effect which may not be fully evident until late in larval life. The critical role of the cold water on the developing embryos and early larvae may have been underestimed by Koslow et al. (1985) in their search for factors affecting the failure of the 1983 Browns Bank year class. Another process that may have also influenced the poor recruitment of Browns Bank haddock in 1983 was the strong SE gales that occurred in April. These resulted in all the drift buoys in Browns Bank being transported to the north where they were entrained in the westward coastal current and carried to the Gulf of Maine (Smith 1983).

The data available for Georges and Browns Bank indicate that not only may the major processes effecting larval abundance be different among years, but also that within the same year the dominant processes may be different between regions quite close to each other. The conclusion is that the important processes determining year-class success are, at least in some years, local in scope. This is true not only for years that yielded poor year classes (e.g. 1981 and 1982), but may also be true for years with exceptional year classes. The 1978 spawning season yielded one of the largest haddock year classes on Georges Bank in recent decades (Clark et al., 1982). On Browns

Bank, however, 1978 was a low in year-class success among recent years (O'Boyle et al., 1983). Figure 8 shows haddock recruitment for Georges Bank and Browns Bank based on the United States and Canadian VPA's (Overholtz et al., 1983; O'Boyle et al., 1983). Good year classes co-occur in some years such as in 1963, but do not in other years, such as in 1978. Koslow (1985) has suggested that large scale physical mechanisms are responsible for setting year-class strength. He used Scotian Shelf and Georges Bank haddock as an example. A closer look at the data indicates that while there may be good correlations in general with large scale processes, individual year classes may be affected by events on a smaller spatial and/or temporal scale (Cohen et al. 1985). The situation for Georges Bank and Browns Bank may be confounded by the drastic decrease in haddock biomass and its effect on recruitment (Overholtz et al., 1984). The correspondence in year-class strength between Georges and Browns, which was fairly good in the 1960's, appears to disappear during the 1970's and into the 1980's.

The Recruitment Process

The means by which year-class size was set appear to be different in the three years we have considered.

There were several potential sources of mortality evident in the 1982 season: acute low temperature, advection of eggs and larvae off of the bank during a large storm or through WCR activity and reduced spawning biomass compared with 1981 and 1983.

The intense storm on Georges Bank in 1982 may have been responsible for advection of a large number of eggs and larvae off the bank. While storms may occur in every year, the exact timing and magnitude of a particular storm are the critical elements in egg and larvae survival. The offshore displacement of the shelf/slope-water front during the April 1982 storm (Figure 1) suggested that a large amount of surface water was removed from the southeastern portion of Georges Bank. This is the area where the haddock larvae would have been located at the time of the storm. The storm induced loss is believed to be a potentially important factor in 1982. However, when the waters on the flank of Georges Bank are well-mixed, the eggs and early larvae also are distributed throughout the water column (see Lough, 1984). So, while advection off the bank of the eggs and larvae may occur in the surface waters, part of the population probably would still remain on the bank.

The larvae that were observed on 19 April 1982 appear to have mostly disappeared by 26 April 1982 (Laurence and Burns, 1982) and certainly by mid-May 1982 when the entire bank was surveyed. The entrainment of water by Ring 82-A was occurring from the same part of the bank where the larvae were observed and appears a likely cause. In order for this to be true, the larval mortality in the feature would have to have been high as none were found in the entrained water on 26 April 1982. More importantly, the ring had been entraining water from the southeastern part of the bank since mid-March 1982. The entrainment could have been responsible for the low abundance of larvae observed on 19 April 1982, having already removed large numbers of eggs and larvae during March and April of that year. On the other hand, given an average mortality of 7 % per day from hatching through the 6 mm length class (Lough 1984), which would take 18-24 days under average April water temperature, it is still possible that the normal mortality process could account for the apparent loss of haddock larvae without resorting to advective loss from the bank. The spatial and temporal scale of these advective events may be quite small. For example, haddock may have been more seriously affected by the advective events in 1982 than cod which begin spawning on the bank earlier in February-March. Since cod larvae were older and larger than the haddock larvae, they would be better able to swim and maintain their position on the bank. They also would have been carried further westward by the water circulation and perhaps subject to different local processes. This appears to be the case in 1982 where the largest concentration of cod larvae is farther to the southwest than that for haddock (Figure 5), and unlike the haddock, is not located in the mouth of the ring entrainment feature. The spatially specific nature of the possible entrainment mortality may have had less effect on cod than haddock in 1982 leading to the relatively good year class of cod in 1982. This type of age-dependent mortality would be similar to the situation reported by Walford (1938). Walford (1938) found relatively few larvae from the early spawning period as compared to observations in 1931 despite the fact that spawning had begun normally in 1932. He attributed the low larval abundance or survivorship to a large loss of eggs and larvae by advection off the bank during the egg and early larval period. In support of his conclusion, Walford did observe large numbers of larvae in the deep water off the southern side of the bank.

In 1981 and 1983 the setting of the year-class must have occurred in the late larval or post-larval period since the larval abundances were still high through the end of April. Additional evidence that initial larval abundance was not directly related to recruitment success is that the 1983 year class of haddock is the strongest since 1978, yet the initial larval abundance was the lowest since 1977, except for 1982. Year-class size may even be set after the larval phase even when there is a large loss of larvae. For example, Walford (1938) thought that the 1932 haddock year-class was poor based on observed larval mortality. Subsequent fisheries data showed that 1932 was actually a good year-class (Clark et al., 1982). There is some evidence that in many years, year-class size may not be set until the postlarval-juvenile period in the first year of life (Cohen and Grosslein, 1982; Sissenwine et al., 1984; Cohen et al., 1984).

In summary, it appears that the various factors affecting recruitment, (e.g. predation, starvation and advective loss) can operate to varying degrees from year to year. This seems to be particularly true of advective loss as several investigators have reported evidence of its occurrence, (Walford, 1938; Colton, 1959; Colton and Temple 1961, Bigelow 1926) while others (Bumpus, 1976; Smith and Morse, 1984) found no evidence of advective loss. Colton and Anderson (1981) and Cohen et al. (1983) also found no evidence of advective loss but both papers stress that short comings in the data may have obscured significant events. As we conclude in this paper, the physical processes responsible for a significant loss of eggs and larvae may be colder than normal temperature, one storm and/or ring event. Good year classes such as in 1983 may be simply the result of few non-destructive events over their early life

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REFERENCES

Azarovitz, T.R. 1981. A brief historical review of the Woods Hole laboratory trawl survey time series. Can. Spec. Publ. Fish. Aquat. Sci., 58:62-67.

Bagenal, T.B. 1973. Fish fecundity and its relations with stock and recruitment. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 164: 186-198.

Bowman, R. and R. Eppi. 1984. The predatory impact of spiny dogfish in the Northwest Atlantic. ICS C.M. 1984/G:27.

Bowman, R. and W. Michaels. 1982. Food of seventeen species of Northwest Atlantic fish: Part I, Examination by predator length and geographic area. NMFS, NEFC, Woods Hole Lab Ref. Doc. 82-16.

Bumpus, D.F. 1976. Review of the physical oceanography of Georges Bank. ICNAF Res. Bull. 12: 119-134.

Clark, S.H., W.J. Overholtz and R.C. Hennemuth. 1982. Review and assessment of the Georges Bank and Gulf of Maine Haddock Fishery. J. Northw. Atl. Fish. Sci. 3: 1-27.

Cohen, E.B. and M.D. Grosslein. 1982. Food consumption by silver hake (Merluccius bilinearis) on Georges Bank with implicatins for recruitment. In: G.M. Cailliet andC.A. Simenstad (eds.), Gutshop '81, Fish Food Habits Studies. Wash. Sea Grant, Univ. of Washington Press, Seattle, WA, pp. 286-294.

Cohen, E.B., D.G. Mountain and W. Smith. 1982. Physical processes and year class strength of commercial fish stocks on Georges Bank. EOS, Trans. Am. Geophys. Union 63: 956. Abstract only.

Cohen, E.B., O. G. Mountain and R.N. O'Boyle. 1986. Absence of large scale coherence in cod and haddock recruitment in the northwest Atlantic.

Colton, J.B., Jr. 1959. A field observation of mortality of marine fish larvae due to warming. Limnol. Oceanogr. 4: 219-222.

Colton, J.B., Jr. and J.L. Anderson. 1983. Residual draft and residence time of Georges Bank surface waters with reference to the distribution, transport and survival of larval fishes. NOAA Tech. Memo. NMFS-F/NEC-24, 44 p.

Colton, J.B., Jr. and R.F. Temple. 1961. The enigma of Georges Bank spawning. Limnol. Oceanogr. 6: 280-291.

Fogarty, M., M. Sissenwine and M. Grosslein. Fisheries research on Georges Bank. In: R.H. Backus, R.L. Price, and D.W. Bourne (eds.), Georges Bank. MIT Press, Cambridge, MA.

Frank, K. and W. Leggett. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (Mallotus villosus). Can. J. Fish. Aquat. Sci. 7: 991-1003.

Grosslein, M.D. 1969. Groundfish survey program of BCF Woods Hole. Comm. Fish. Rev., 31:22-35.
Hodder, V. 1965. The possible effects of temperature on the fecundity of Grand Bank haddock. ICNAF Spec. Publ. 6: 512-522.

Hunter, J. 1982. Predation and recruitment. In: B. Rothschild and C. Rooth (eds.), Fish Ecology III, Univ. of Maine, Tech. Rept. No. 82008, pp. 172-209.

Hunter, J. 1984. Inferences regarding predation on the early life stages of cod and other fishes. In: E. Dahl, D. Danielssen, E. Moksness, and P. Solendal (eds.), The Propagation of Cod, Gadus morhua L., Flødevigen rapportser., 1, 1984: 533-562.

Koslow, J.A. 1985. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 41: 1722-1729.

Koslow, J., S. Brandt, J. Dugas and F. Page. Unpublished Ms. Anatomy of an apparent year-class failure: The early life history of the 1983 Browns Bank haddock (Melanogrammus aeglefinus).

Laurence, G.C., and C.A. Rogers. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (Gadus morhua L.) and haddock (Melanogrammus aeglefinus L.). J. Cons. int. Explor. Mer, 36:220-228.

Laurence, G.C. 1978. Comparative growth, respiration and delayed feeding abilities of larval and cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) as influenced by temperature during laboratory studies. Mar. Biol., 50:1-7.

Laurence, G.C. and B.R. Burns. 1982. Ichtyoplankton in shelf water entrained by warm core rings. EOS Trans. Am. Geophys. Union 63: 998. Abstract only.

Lough, R.G. 1982. Absence of cod and haddock larvae on Georges Bank, spring 1982. Red Flag Report. Unpublished Ms. NEFC, Woods Hole, MA 02543.

Lough, R.G. 1984. Larval fish trophodynamic studies on Georges Bank: Sampling strategy and initial results. In: E. Dahl, D.S. Danielssen, E. Mokoness and P. Solendal (Eds.), The Propagation of Cod Gadus morhua L. Flodevigen rapportser., 1, 1984:395-434.

Marak, R.R. and R. Livingstone, Jr. 1970. Spawning dates of Georges Bank haddock. ICNAF Res. Bull., 7:56-58.

Mӧller, H. 1984. Reduction of a larval herring populatin by a jellyfish predator. Science 224: 621-622.

Nikolski, G.B. 1969. Theory of fish population dynamics. Oliver and Boyd, Edinburgh. 323 p.

O'Boyle, R., K. Waiwood and J. McMillan. 1983. An evaluation of the 4X haddock population characteristics during 1962-1982 with yield projected to 1984. CAFSAC Res. Doc. 83/73.

Overholtz, W.J., S.H. Clark and D.Y. White. 1983. A review of the status of the Georges Bank and Gulf of Maine haddock stocks for 1982. Woods Hole Lab. Ref. Doc. No. 83-23.

Overholtz, W., M. Sissenwine and S. Clark. 1984. Recruitment variability and its implicatins for managing and rebuilding the Georges Bank haddock to stock. ICES C.M. 1984/G:77.

Pennington, M. 1983. Efficient estimators of abundance for fish and plankton surveys. Biometrics 39: 281-286.

Pinhorn, A.T. 1984. Temporal and spatial variation in fecundity of Atlantic cod (Gadus morhua) in Newfoundland waters. J. Northw. Atl. Fish. Sci. 5: 161-170.

Purcell, J.E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull. Mar. Sci., 37:739-755.

Ramp, S. 1982. Georges Bank current meter monitoring survey scientific report. Appendix. Prepared for Mobil Research and Development Corp. Tech. Rept. #3. ENDECO Inc., Marion, MA.

Resource Assessment Division, Northeast Fisheries Center. 1983. E. Anderson (ed.), Status of the fishery resources off the northeastern United States. NOAA Tech. Memo. NMFS-F/NEC-22. NOAA, NMFS, NEFC, Woods Hole, MA.

Scott, J. 1983. Distribution of juvenile haddock. Southwest Nova Scotia Fishery Ecology Program Steering Comm. Rept. No. 3

Sherman, K. 1980. MARMAP, a fisheries ecosystem study in the northwest Atlantic, fluctuations in ichthyoplankton-zooplankton components and their potential for impact on the system. In F.P. Dumer, F.G. Vernberg, and D.Z. Mirkes (eds.), Advanced Concepts on Ocean Measurements for Marine Biology. Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina Press, Columbia, pp. 9-37.

Smith, P.C. 1983. Circulation and dispersion on Browns Bank. Pages 11-12, in Southwest Nova Scotia Fishery Ecology Program Steering Committee Report No. 3. Bedford Institute of Oceanography, Dartmouth, N.S., Canada.

Sissenwine, M.P. 1984. Why do fish populatins vary? In: R. May (ed.), Workshop on Exploration of Marine Communities. Springer-Verlag, Berlin.

Smith, W.G. and W.W. Morse. 1984. Monthly distribution patterns of larval haddock, Melanogrammus aeglefinus, off northeastern United States 1977-82, with observations on transport in the Georges Bank region. ICES C.M. 1984/G:30.

Walford, L.A. 1938. Effect of currents on distribution and survival of the eggs and larvae of haddock (Melanogrammus aeglefinus) on Georges Bank. Bull. U.S. Bur. Fish. 49: 1-73.

Ware, D.M. 1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37: 1012-1024.

Table 1. List of MARMAP[1] cruises 1980-1983 from which data was used for this paper.

Cruise	Date	Type of Cruise
1980		
Albatross IV 80-12	2-23 December	Ichthyoplankton Survey
1981		
Albatross IV 81-01	17 February-26 March	Ichthyoplankton Survey
Kelez 81-03	18 March-9 April	Ichthyoplankton Survey
Delaware II 81-02	20 April-14 May	Spring Bottom Trawl Survey
Delaware II 81-03	2-18 June	Spring Bottom Trawl & Ichthyoplankton Survey
Delaware II 81-04	7-24 July	Summer Bottom Trawl and Ichthyoplankton Survey
Albatross IV 81-07	7-21 July	Northeast Monitoring Program
Albatross IV 81-14	10 November-22 December	Ichthyoplankton Survey
1982		
Albatross IV 82-02	2-11 March	Ichthyoplankton Survey
Albatross IV 82-04	19 April-4 May	Warm Core Ring Study
Delaware II 82-02	12-23 April	Spring Bottom Trawl & Ichthyoplankton Survey
Albatross IV 82-05	10-21 May	Cod and Haddock Larval Processes
Delaware II 82-03	1-11 June	Ichthyoplankton Survey
Albatross IV 82-06	1-11 June	Scallop Survey-Ichthyoplankton Survey
Delaware II 82-06	22-28 September	Physical Oceanography-Entrainment Features
Delaware II 82-09	15-24 November	Ichthyoplankton Survey
1983		
Delaware II 83-01	17-28 January	Ichthyoplankton Survey
Albatross IV 83-01	25 February-3 March	Ichthyoplankton Survey
Albatross IV 83-02	11-22 April	Spring Bottom Trawl & Ichthyoplankton Survey
Albatross IV 83-04	6-22 June	Ichthyoplankton Survey

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[1] Marine Resources Monitoring Assessment and Prediction.

Table 2.

	Haddock Eggs-Georges Bank			Summary Table			N_s & N_h from hadd. L^1 Z from cod + haddock E^1 and L^1		30-IV-85
	Eggs Spawned			Eggs Hatching					
Year	N_s X 10^{-12}	(1 std error) (X 10^{-12})	C.V.	N_h X 1-$^{-12}$	(1 std error) (X 10^{-12})	C.V.	% survive	Z	% mort. per day
1979	33.876	(17.670)	.5216	2.339	(1.182)	.5054	6.90	.172651	15.86
1980	25.690	(12.480)	.4858	23.596	(11.741)	.4976	91.85	.009301	0.93
1981	27.471	(9.392)	.3419	4.671	(1.554)	.3327	17.00	.112992	10.68
1982	6.577	(2.584)	.3929	0.130	(0.052)	.3983	1.98	.218516	19.63

Table 3. Density (k=larvae/10m^2) and abundance estimates (no. x 10^9) for haddock larvae, based on collections in four subareas of the western North Atlantic from Cape Hatteras, North Carolina to the Gulf of Maine, 1982-83. ND = no data (not sampled).

Year	Cruise	Date	Subarea	No. of Sta.	Positive Sta.	Mean Abundance (k)[1]	Standard Error (Sx)	Abundance (no. x 10^9)
1980	ALB 80-12	Nov-Dec	GB	27	0			
1981	ALB 81-01	Feb-Mar	GB	26	6	6.026	3.105	25.194
	KELEZ 81-03	Mar-Apr	GB	26	5	12.915	6.712	53.988
	DEL 81-02	Apr-May	GB	29	8	97.066	68.383	405.822
	DEL 81-03	June	GB	29	14	41.774	19.420	174.650
	DEL 81-04	July	GB	26	0			
	ALB 81-07							
	ALB 81-14	Nov-Dec	GB	30	0	0	0	0
1982	ALB 82-02	March	GB	27	0	0	0	0
	DEL82-02	April	GB	36	3	1.635	1.100	6.837
	ALB 82-06	June	GB	30	5	0.899	0.391	3.759
	DEL 82-09	Nov	GB	30	0	0	0	0
1983	ALB 83-01	Jan-Feb	GB	28	4	2.556	1.287	10.686
	ALB 83-02	April	GB	29	12	63.997	36.837	267.563
	ALB 83-04	June	GB	30	4	1.102	0.580	4.608

[1] k = mean number of larvae/10 m^2 surface area. Refer to Pennington (1983) for discussion of rationale and procedures for use of Δ-distribution which appears to describe these data. Abundance is expansion of k to reflect subarea size.

[2] Incomplete coverage.

[3] When n_1=1, the mean is estimated by x/n, and its variance by x^2/n^2, where x is the single non-zero value; both are unbiased estimators (Pennington, 1984).

Table 4. Seasonal abundance of haddock larvae ($x10^9$) at hatching for Georges Bank 1977-1983. Data from W. Morse (NEFC, Sandy Hook Laboratory (personal communication, and Morse 1984).

Year	Initial Larval Production ($x10^{-9}$)
1977	2578.6
1978	4475.7
1979	7467.4
1980	5505.5
1981	4608.3
1982	202.2
1983	1070.0

Table 5. Abundance and haddock on Georges Bank. Stratified mean catch/tow in numbers and kg from spring bottom trawl surveys.

		Haddock	
Year	No/tow	kg/tow	avg wt (kg)/fish
1981	31.51	39.56	1.25
1982	11.08	16.53	1.49
1983	5.43	12.48	2.30

Table 6. Maturity data for female haddock on Georges Bank. Numbers and percentage inthree categories spawners, immatures and resting are shown. Spawners includes fish that are getting ready to spawn, ripe, and recently spawned. Resting fish are fish that are several months away from spawning. Data from spring bottom trawl surveys.

Year	Spawners		Immatures		Resting	
	No.	%	No.	%	No.	%
1981	47	21	26	11	157	68
1982	78	46	38	23	52	31
1983	114	47	47	20	77	32

Table [illegible]

HADDOCK

	SPAWNING SEASON		
FACTOR	1981	1982	1983
Spawning Biomass Index	8.3 kg/tow	7.6 kg/tow	5.9 kg/tow
Egg Initial Abundance Hatching Mortality	27.5×10^{12} 4.7×10^{12} 83 % (10.7% /day)	6.6×10^{12} 0.13×10^{12} 98 % (19.6 %/day)	Data destroyed
Larval Initial Abundance	4608×10^9	202×10^9	1070×10^9
Egg and Larval Distribution	In mid-April, concentration of eggs located near SE Georges Bank. By mid-May, concentration of larvae along southern flank. Both eggs and larvae between 50-m and 200-m isobaths.	In March, egg concentration on NE Georges Bank By mid-April, small larval patch located at SE edge of Georges Bank across 200-m isobath.	By late March-April large concentration of larvae extending along southern flank of Georges Bank within 50 and 200-m isobaths.
Recruits - VPA age 1 age 2	2.158×10^6 1.767×10^6	0.456×10^6 0.373×10^6	12.214×10^6 10.00×10^6
Bottom Temperature and Salinity	5-6°C March-April 33.1 ‰	3-4°C March-April 32.5 ‰	5-6°C March-April 33.1 ‰
WCR Entrainment	No ring entrainment features near Georges Bank during spring spawning period.	Ring 82-A, April entrainmen of shelf water near SE Georges Bank	Ring 83-B, late March-mid-April entrainment of shelf water near SE Georges Bank
Storm Events	1-22 April, moderate but continuous southerly transport. 1-5 May, transport 21-25 May, transport west.	6-9 April, >60 knot winds, 25-60 km seaward displacement of shelf/slope-water front. Continuous southly transport most of April. 10-12 May, transport northwest, 19-20 May, transport southeast	1-25 April, 4 storms, transport generally north. 1-4 May, transport southeast. northwest.
Zooplankton			
Predators	No significant direct evidence	No significant direct evidence	No significant direct evidence

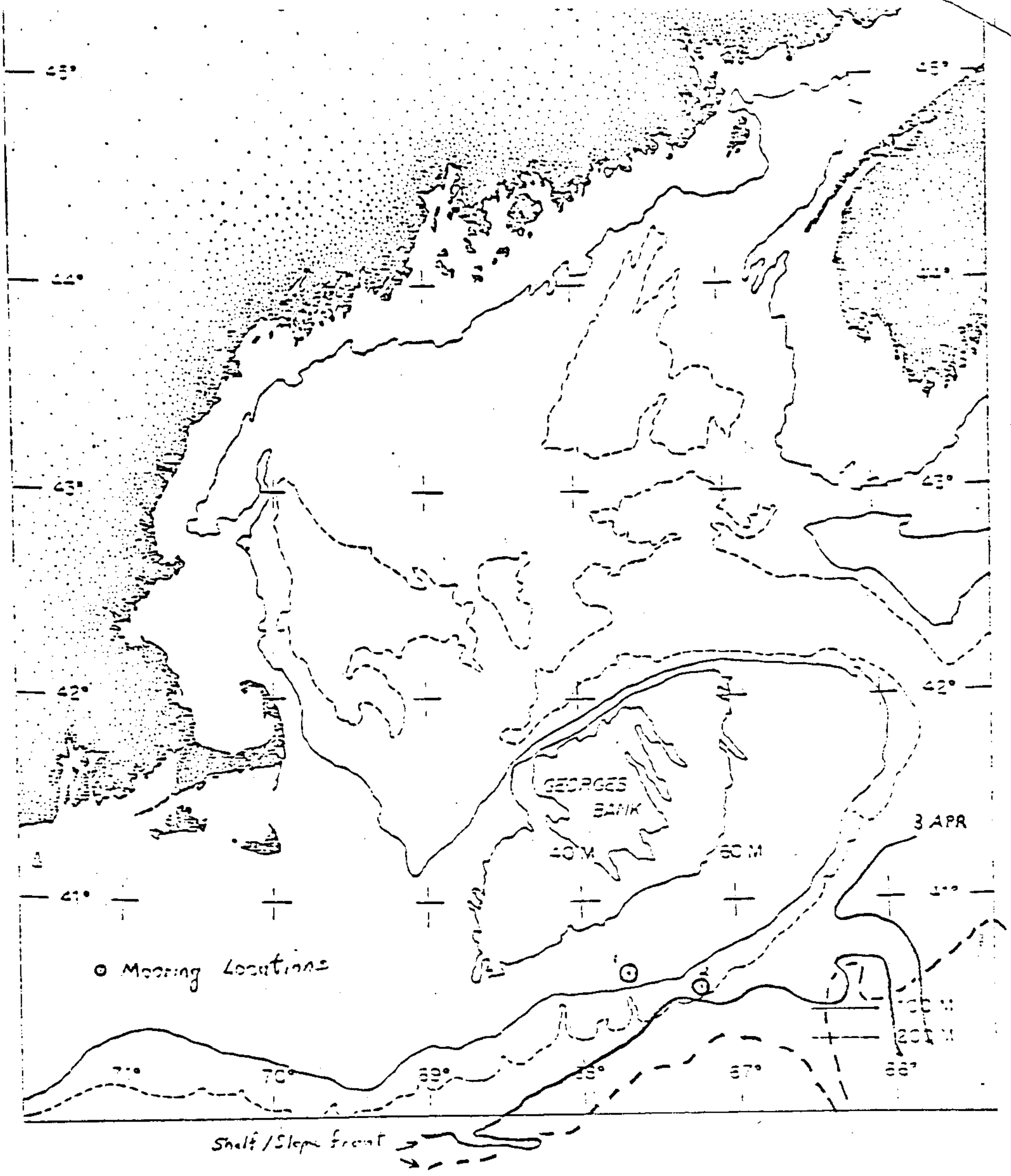

Figure 1. Georges Bank with the positions of the shelf-slope front before (3 April 1982) and after (10 April 1982) a major storm.

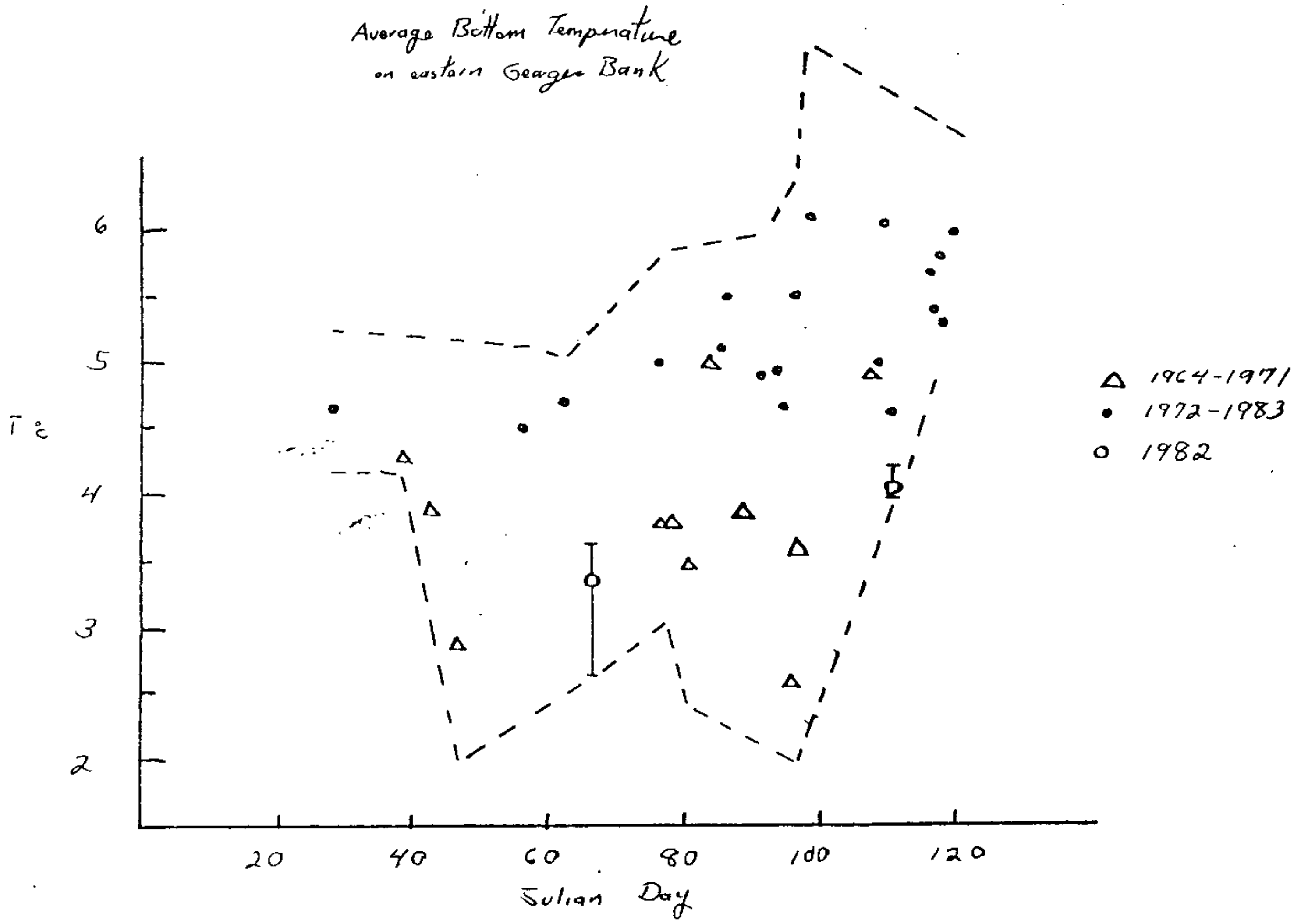

Figure 2. Average bottom temperature on eastern Georges Bank. The range of temperature is indicated by the envelope (dashed line) around the data.

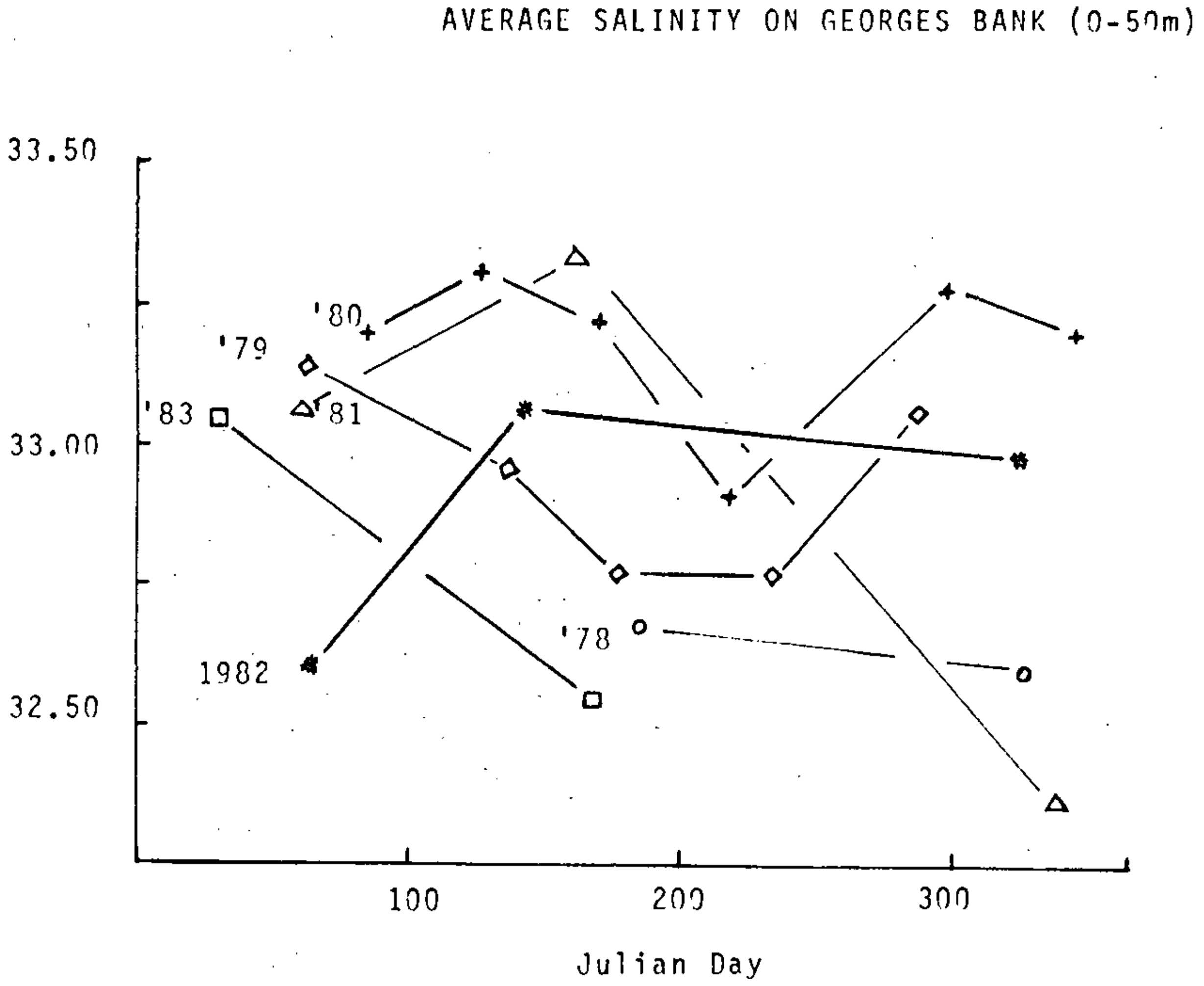

Figure 3. Average salinity (0-50) on Georges Bank for 1978-1983.

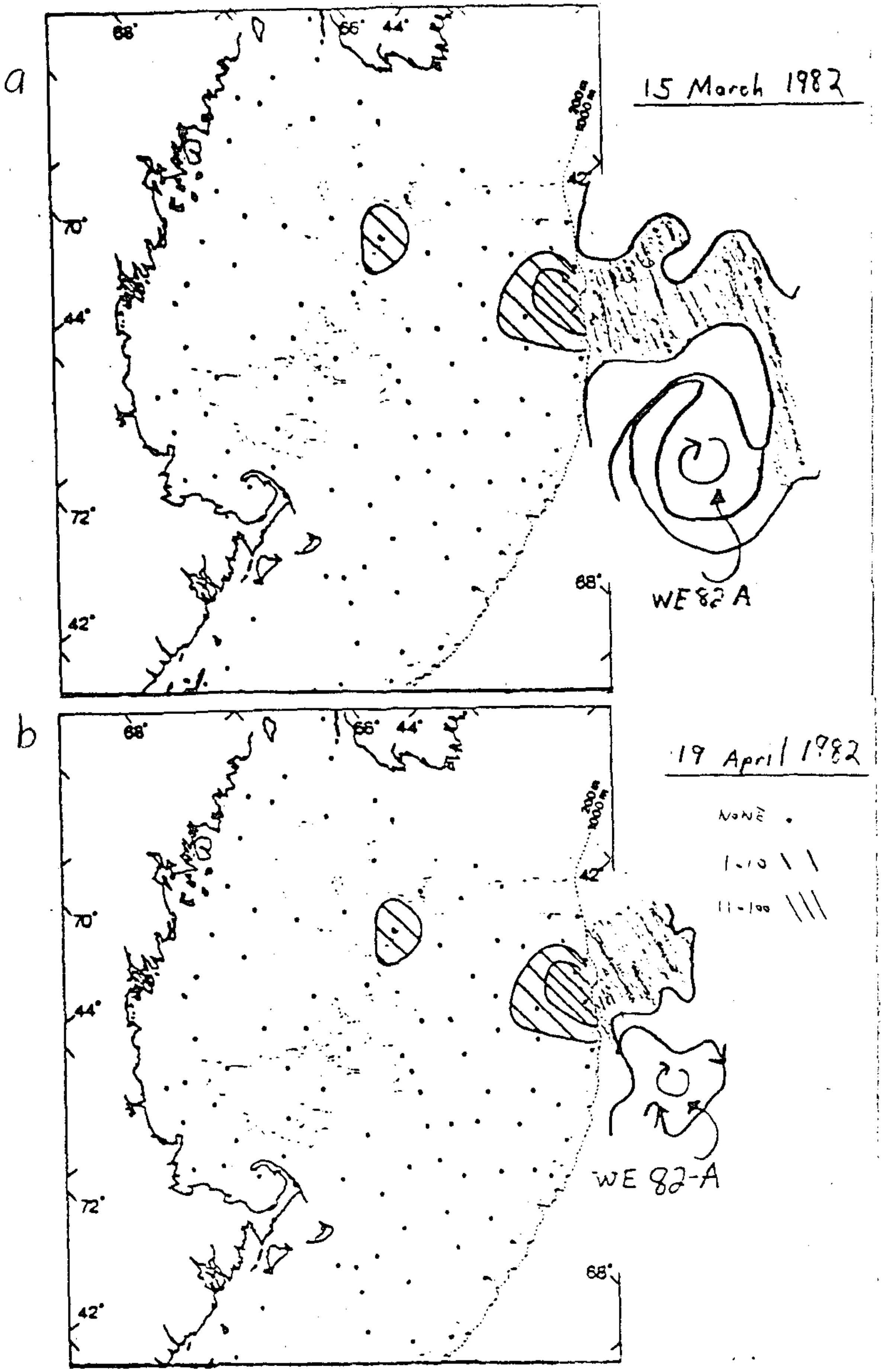

Figure 4. Warm Core Ring WE 82-A with associated entrainment feature of shelf water (shaded area) and contours of haddock larval densities on Georges Bank. Dates are 15 March 1982 and 19 April 1982 for A & B respectively.

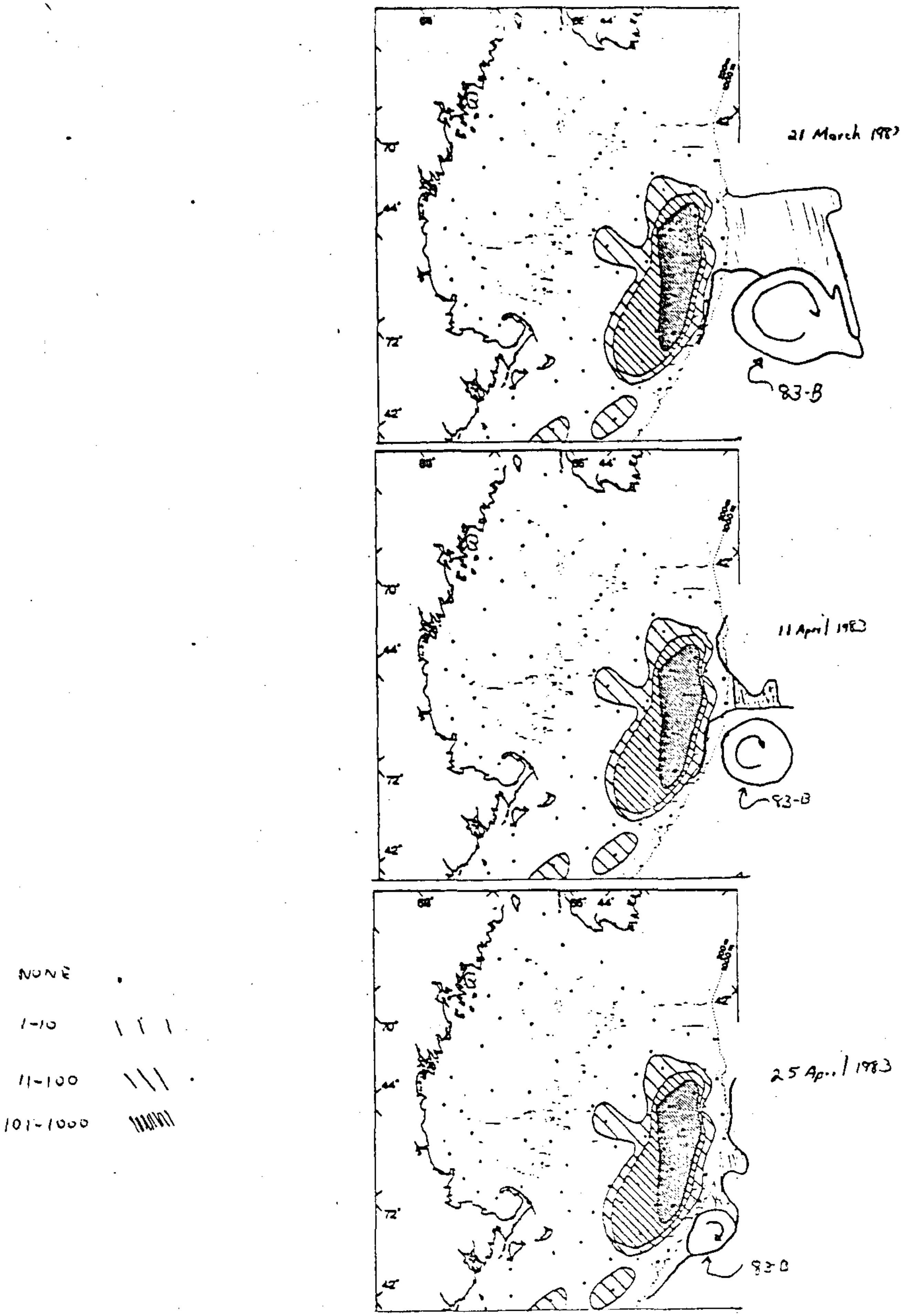

Figure 5. Warm Core Ring 83-B with associated entrainment of shelf water (shaded area) and closed contours of larval density.

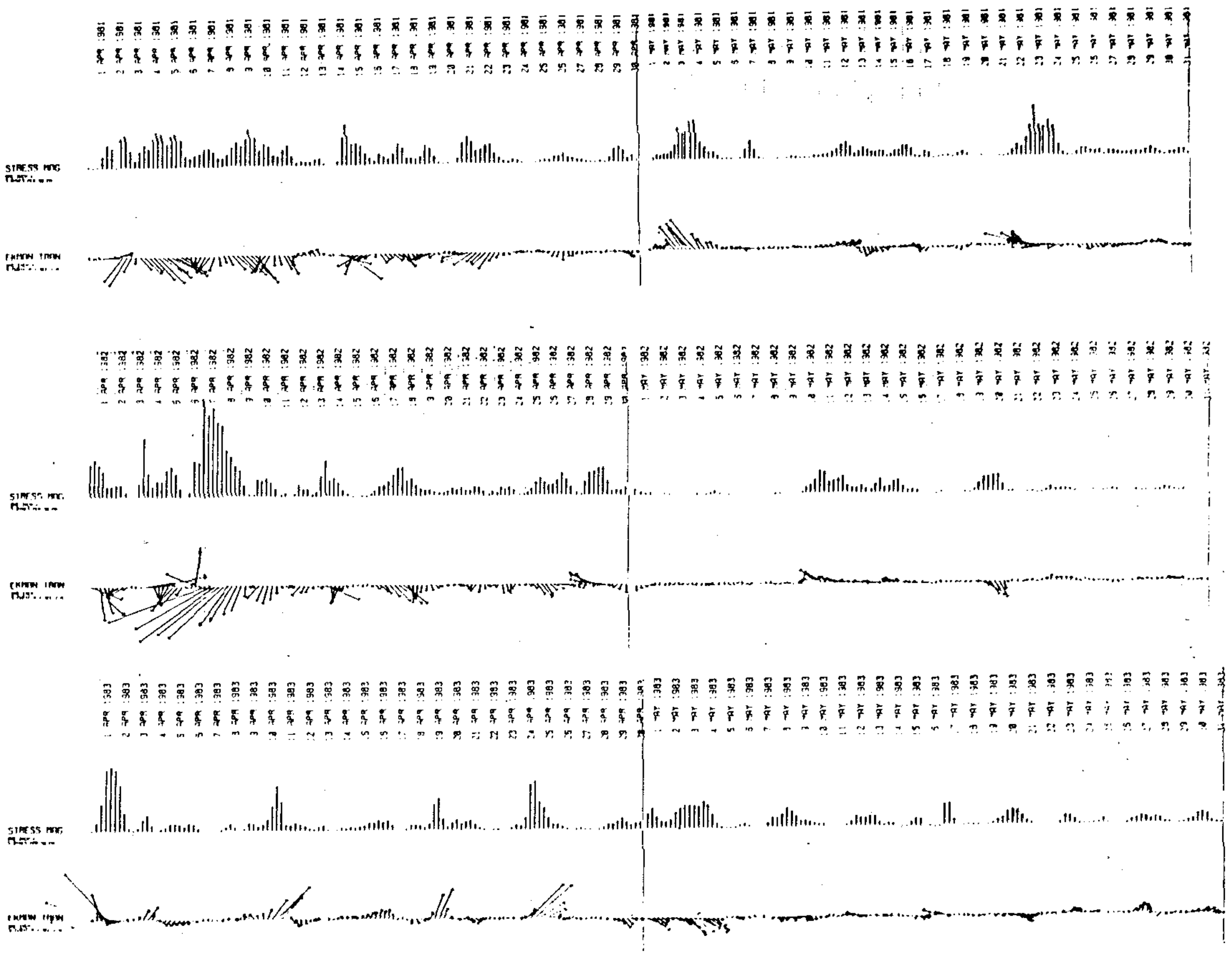

Figure 6. Wind stress magnitude and Edman transport vectors for April-May 1981, 1982, and 1983.

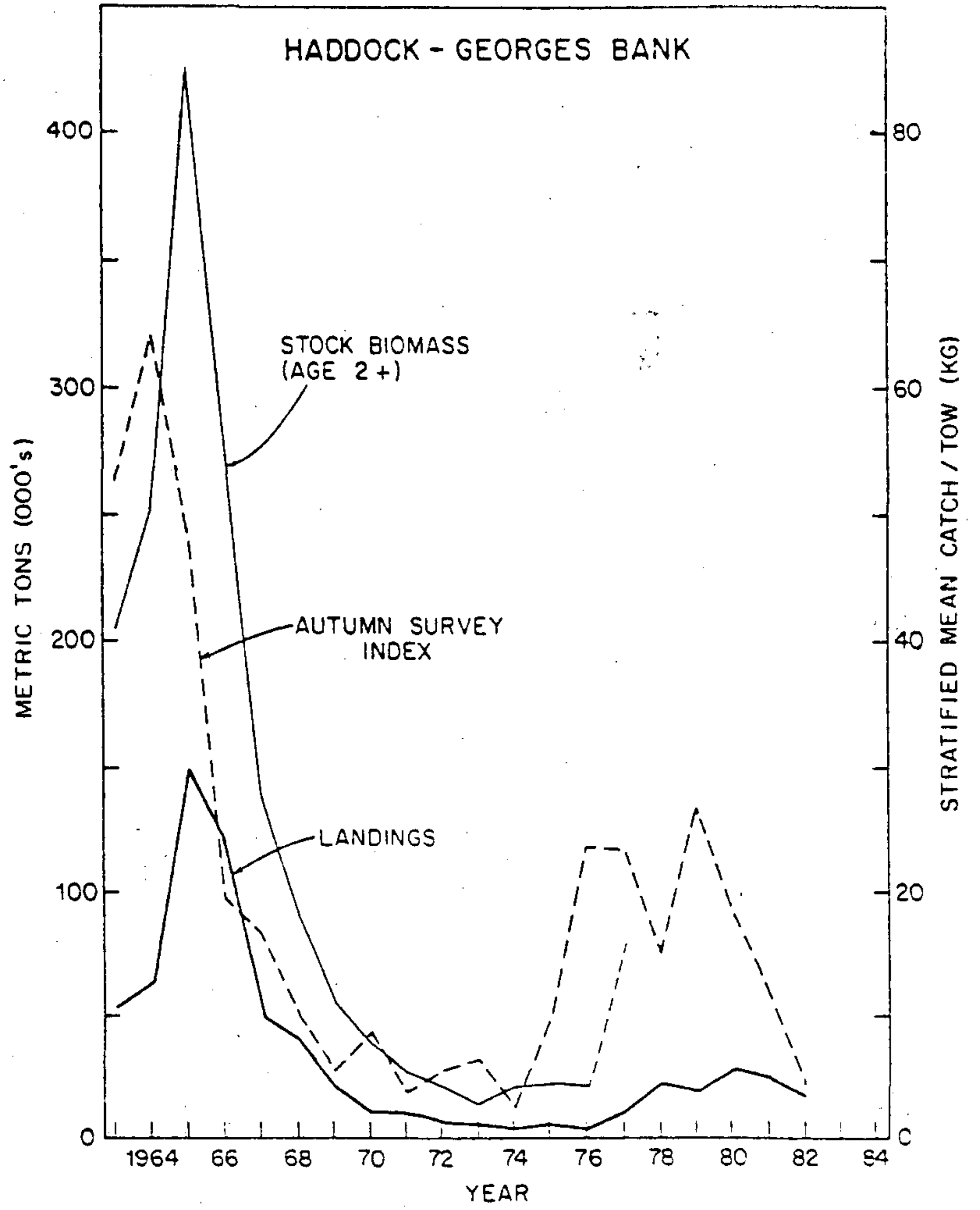

Figure 7. Nominal catches, stock biomass and NMFS survey index of abundance for Georges Bank haddock. From Status of the Stocks Rept. 1983.

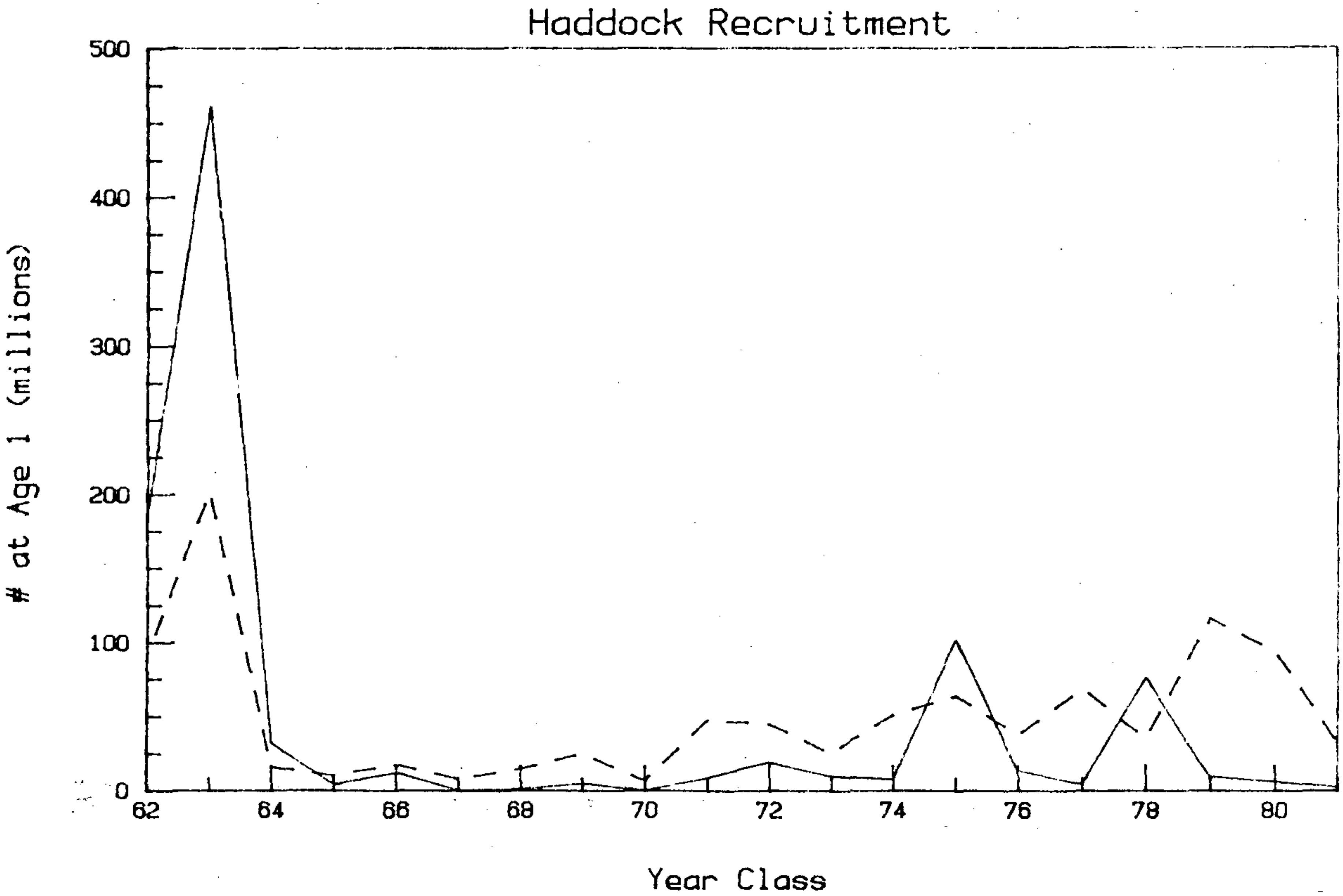

Figure 8. Haddock recruitment on Georges Bank (——) and Browns Bank (- - -) for year classes 1962-1982.