TEMPERATURE TRENDS AND THE DISTRIBUTION OF GROUNDFISH IN CONTINENTAL SHELF WATERS, NOVA SCOTIA TO LONG ISLAND

JOHN B. COLTON, JR.[1]

ABSTRACT

The 1953 to 1967 downward trend in seawater temperature in continental shelf waters between Nova Scotia and Long Island did not significantly alter the distribution of four species of groundfish. There was an extension of the southern range of American plaice and a contraction of the northern range of butterfish. These shifts in distribution were not extensive. The equatorward boundary of American plaice appears to be limited by summer temperatures too high for survival and the poleward boundary of butterfish by summer temperatures too low for reproduction. There was no obvious alteration in the geographic distribution of haddock and yellowtail flounder. The distribution and movements of haddock and yellowtail flounder appear to be influenced more by restrictive spawning area and bottom type conditions than by temperature.

An alternation in sea-surface temperature has been observed at Atlantic coast stations from Nova Scotia to Cape Hatteras (Lauzier, 1965; Stearns, 1965; Welch, 1967). Coastal warming and cooling trends have been pronounced in the waters between Cape Sable and Long Island. A warming trend began in the early 1940's and reached a maximum during 1952-53. This rise in temperature was followed by a cooling period which continued with only minor checks through 1967. Since 1967 there has been an increase in sea-surface temperature, the 1969 annual mean being only slightly lower than the long-term mean. An example of these temperature trends is shown in Figure 1 in which the annual deviations from the 1940-1959 mean sea-surface temperature at Boothbay Harbor, Maine are plotted for the period 1940-1968. The base period 1940-1959 was chosen for it included approximately equal numbers of years in periods of warming and cooling.

In Figure 2 seasonal sea-surface-temperature curves at Boothbay Harbor based on monthly mean values for each year between 1940 and 1968 are compared with the 1940-1959 mean seasonal temperature curve. As would be expected, there were marked fluctuations in the seasonal temperature cycle due to variations in runoff and meteorological conditions, but for the most part, the monthly deviations reflected the annual deviations in both periods of warming and cooling.

Similar warming and cooling trends have occurred offshore, both at the surface and at depth (Taylor, Bigelow, and Graham, 1957; Lauzier, 1965, 1967; Colton, 1968a, 1968b, 1969). Though offshore temperatures varied less seasonally than those inshore, in general, the magnitude of both surface and subsurface temperature anomalies were greater offshore than along the coast. These warming and cooling trends are associated with changes in the composition of the subsurface water (Colton, 1968b, 1969). Cold years occur when slope water is displaced or modified by coastal water of Labrador origin. Warm years occur when slope water borders upon the 200-m isobath and the ratio of coastal to central Atlantic water is low.

Taylor et al. (1957) concluded that although there was evidence of northward shifts in the abundance and distribution of some marine animals as a consequence of the warming trend which commenced in the early 1940's, these

[1] National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, MA 02543.

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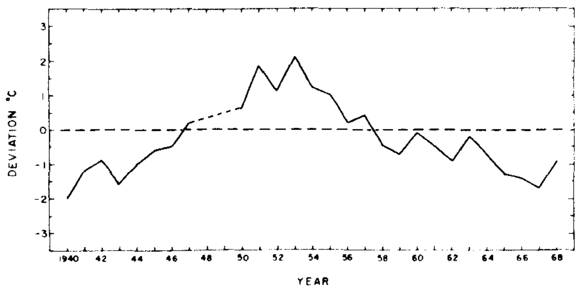

FIGURE 1.—Annual deviations from the 1940-1959 mean sea-surface temperature at Boothbay Harbor, Maine.

changes did not appear to have produced any obvious alteration of the general faunal characteristics of the Gulf of Maine. During the recent cooling period, there were a number of reports of southward extensions of range and shifts in the distribution of fish and invertebrate fauna: (1) Boyar (1964) reported the occurrence of the Greenland halibut (*Reinhardtius hippoglossoides*) off Boothbay Harbor, Maine, in February 1963. This is a southern shoal-water record for this subarctic species. (2) Substantial numbers of capelin (*Mallotus villosus*) were caught in the Bay of Fundy in the spring of 1965 (Tibbo and Humphreys, 1966) and have continued to be taken each spring through 1968 (S. N. Tibbo, personal communication). There has been no written record of the occurrence of capelin in this area since 1919 (Bigelow and Schroeder, 1953). (3) Since 1961, spiny dogfish (*Squalus acanthias*) have been collected with increasing frequency during the winter months in South Carolina coastal waters (Bearden, 1965). This species is uncommon south of Cape Lookout, N.C., and there have been no previous records of its occurrence off South Carolina. (4) Collette and MacPhee (1969) reported the collection of an arctic shanny (*Stichaeus punctatus*) in Massachusetts Bay in August 1968. This is the second record of this northern species in the Gulf of Maine and extends the known range 180 miles to the southwest. (5) Finally, the green crab (*Carcinus maenas*), which became abundant as far northeast as Nova Scotia in the mid-1950's, has declined in abundance, coincident with the decline in temperature. The green crab is now rare in Canada and eastern Maine, but still abundant in southwestern Maine and northern Massachusetts (Welch, 1968).

Such observations of northward and southward shifts in the abundance and distribution of marine animals have usually been based on sporadic observations and on commercial fishery statistics. The accumulation of records of occasional occurrences over a number of years can give the impression of a change in distribution sustained over a period of time. Many of the fluctuations in commercial fishery landings are due to changes in fishing methods, efficiency, effort, and market conditions. As Bell and Pruter (1958) have demonstrated, it is deceptively easy to infer relationships and draw false conclusions from such data. Given adequate research vessel surveys, however, it should be possible to determine the relative abundance and distribution of fish and invertebrate fauna with some precision. In this paper such otter-trawl survey data are used to determine what effect the recent cooling trend has had on the distribution of some of the important commercial species of groundfish in continental shelf waters between Nova Scotia and Long Island.

A great diversity of pelagic, hemipelagic, and demersal fish species were caught during the otter-trawl surveys. Our initial analysis was limited to the relatively abundant commercially exploited groundfish species felt to be representatively sampled by the otter trawl, e.g., those species living on or in close association with the bottom and within the depth limits covered by the surveys (approximately 30-350 m). For this study, four species were selected which represent the basic types of geographic zonation characteristic of the area. The general geographic distribution of these species is as follows:

AMERICAN PLAICE (*HIPPOGLOSSOIDES PLATESSOIDES*)

The plaice is an arctic-boreal species which is found in abundance from Greenland to Cape Cod. In the Gulf of Maine this species is most plentiful in depths ranging from 30 to 200 m.

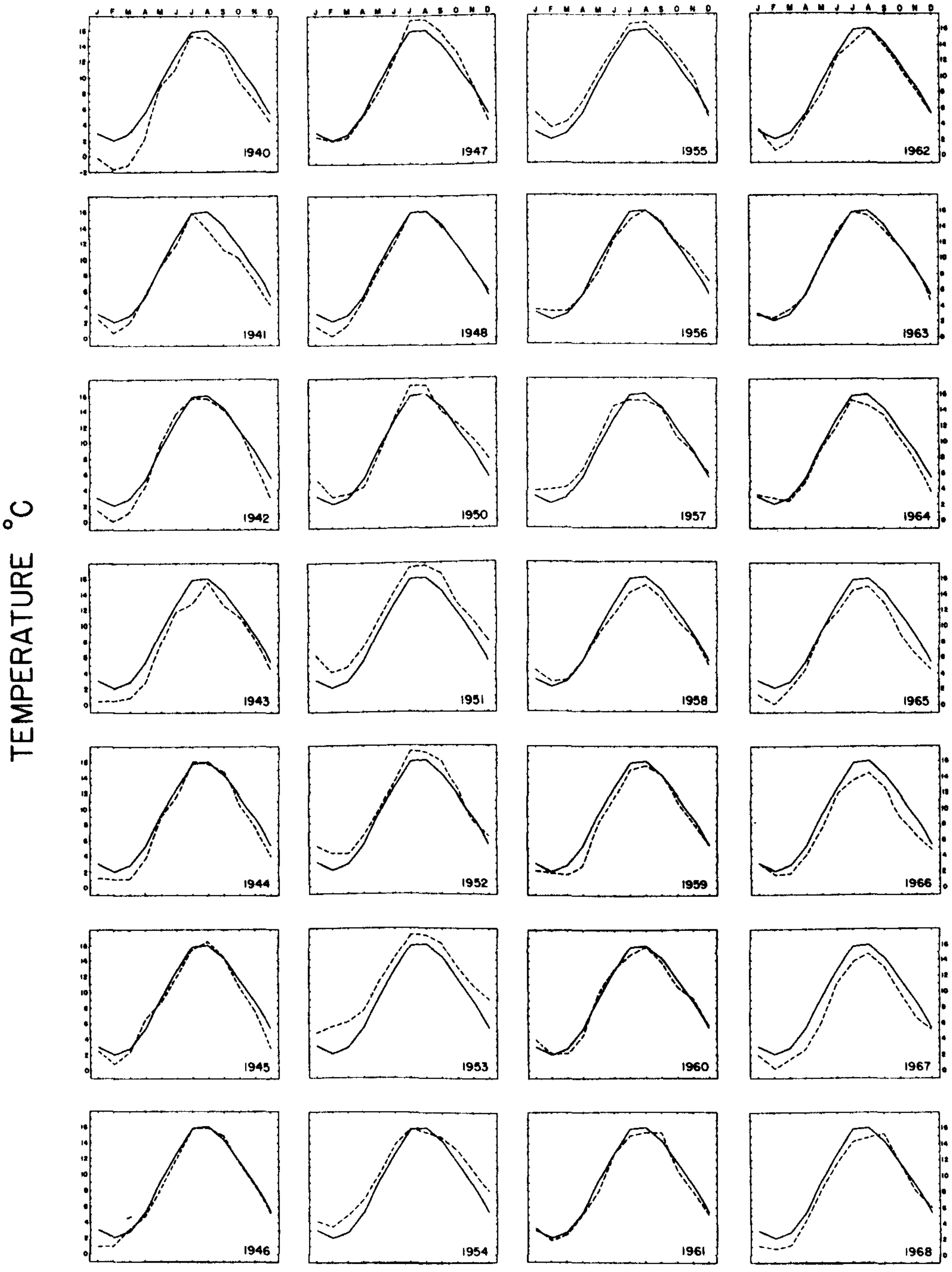

FIGURE 2.—1940-1959 mean and yearly seasonal temperature curves, Boothbay Harbor, Maine. Solid line: 1940-1959 mean, dashed line: individual year. The 1949 records are incomplete and have not been included.

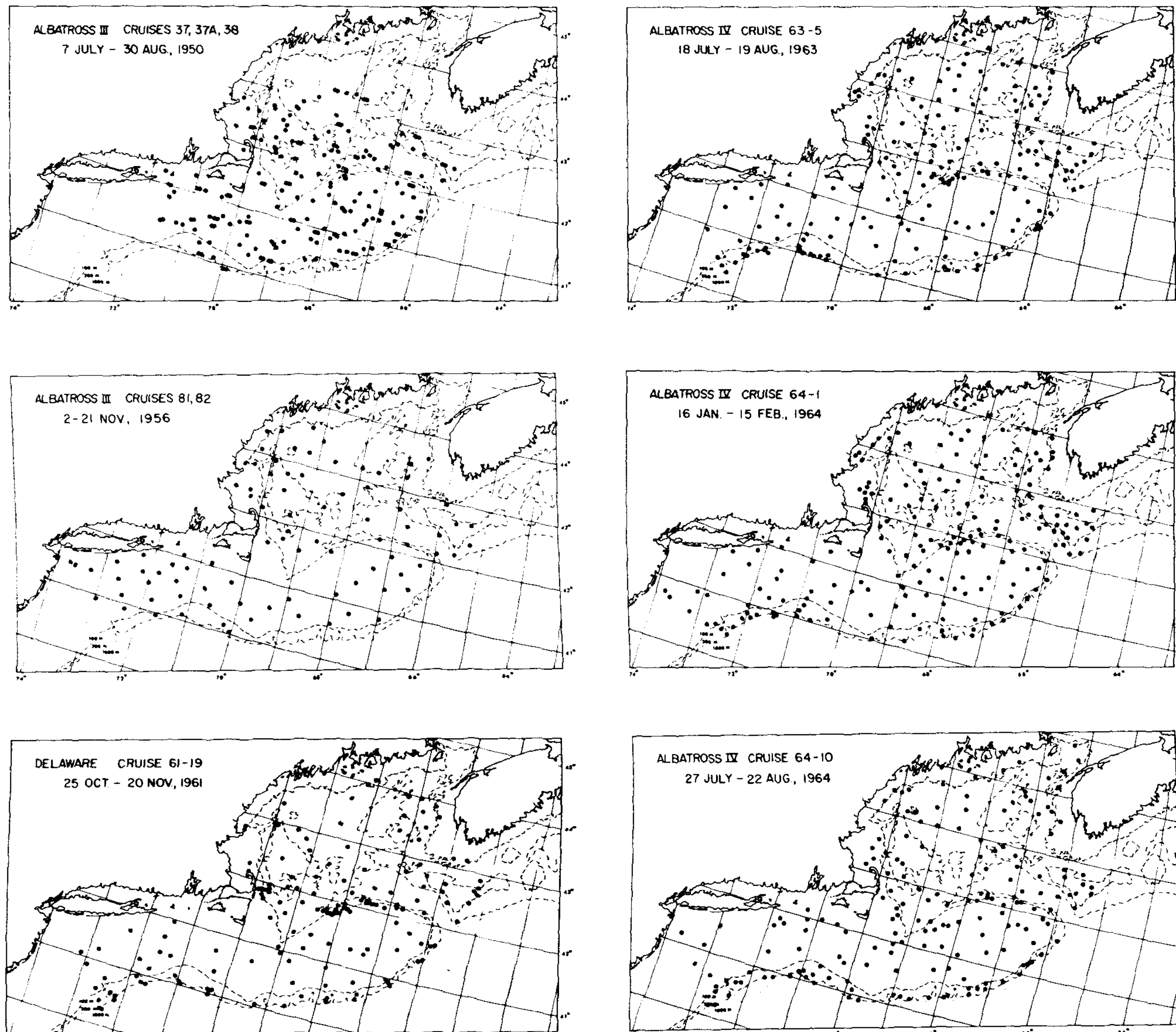

FIGURE 3.—Dates and station locations of groundfish cruises, July-August 1950 through July-August 1964.

Cape Cod (lat 40°30′N, long 70°00′W) marks the southern and western limits of its normal range, although plaice are occasionally taken west to Block Island. Tagging experiments in the Grand Banks area (Pitt, 1969) suggest that there are a number of relatively sedentary populations of plaice and that the limited migrations that do occur are associated with spawning and feeding patterns. Research ship and commercial catch statistics indicate that this is also true of the Gulf of Maine populations.

HADDOCK (*MELANOGRAMMUS AEGLEFINUS*)

The haddock is a boreal species inhabiting both sides of the North Atlantic whose distribution, for the most part, is confined to waters shoaler than 200 m. On the American coast the westerly limit of its normal occurrence is the Nantucket Shoals area (long 70°00′W) although in winter haddock are sometimes taken in the area between Nantucket Shoals and New Jersey. Young-of-the-year haddock are found in the area between Nantucket Shoals and Hudson Canyon during the summer and fall. Indications are that the majority of these young fish are concentrated at mid-depths (Colton, 1965) and caught while the trawl is being set out and retrieved. Young-of-the-year haddock are not included in the catch statistics presented in this paper. Tag returns and the distribution of commercial fishing effort indicate that in comparison with the cod, the haddock is a relatively stationary fish, and except for short-term shifts in depth distribution they do not follow any regular migratory routes (Needler, 1930; Schroeder, 1942; Schuck, 1952).

YELLOWTAIL FLOUNDER (*LIMANDA FERRUGINEA*)

The yellowtail flounder is a shallowwater species which occurs, along the Atlantic coast of North America from Labrador to New Jersey. The bulk of the catch is taken in water shoaler than 100 m. The yellowtail flounder is one of the few species which is common both to the east and west of Cape Cod at all seasons of the year. The tagging studies of Royce, Buller, and Premetz (1955) and Lux (1963) show that, in general, the populations of New England yellowtail are to be found in relatively localized groups which may make short seasonal migrations and only a limited amount of mixing takes place between groups.

BUTTERFISH (*PEPRILUS TRIACANTHUS*)

The butterfish ranges in the northwestern Atlantic from the outer coast of Nova Scotia and Cape Breton to northern Florida. There is a separate population in the Gulf of Mexico (Caldwell, 1961). This temperate-region species is only a warm season migrant to coastal waters off New England and the Maritime Provinces. In general, butterfish appear off southern New England at the end of April, but it is not until July that they are plentiful in the inner parts of the Gulf of Maine and on Georges Bank. Butterfish disappear from the coast by the end of December at the latest.

COLLECTION AND REDUCTION OF DATA

The data were collected during the period 1950-1968 by personnel at the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) Biological Laboratory, Woods Hole, Mass., on surveys designed to determine the distribution and relative abundance of groundfish in the Gulf of Maine and adjacent waters. The fishing gear used during these surveys was similar to that being used by the commercial haddock fleet at the time. A 1½ Iceland trawl was used prior to 1951, and a No. 36 redfish trawl has been used since that time. A description of these trawl nets is given by Knake (1956). The cod end and top belly of both type nets were lined with fine mesh netting to retain smaller fish. Three vessels were used in these surveys; the side trawlers *Albatross III* and *Delaware* and the stern trawler *Albatross IV*. On all cruises the trawl was towed for 30 min at each station at a vessel speed of approximately 3.5 knots. Various sampling patterns employing both random and grid station

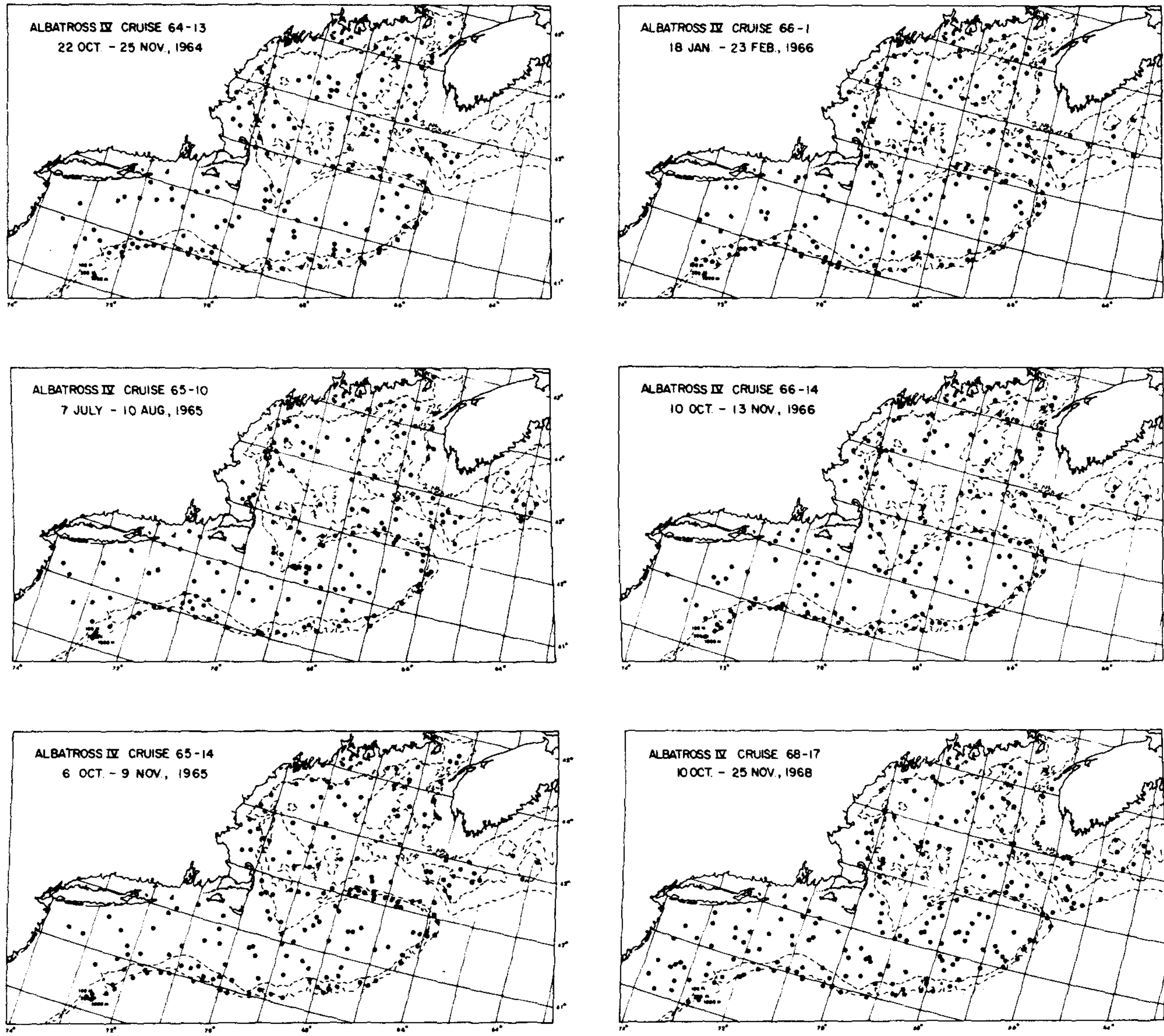

FIGURE 4.—Dates and station locations of groundfish cruises, October-November 1964 through October-November 1968.

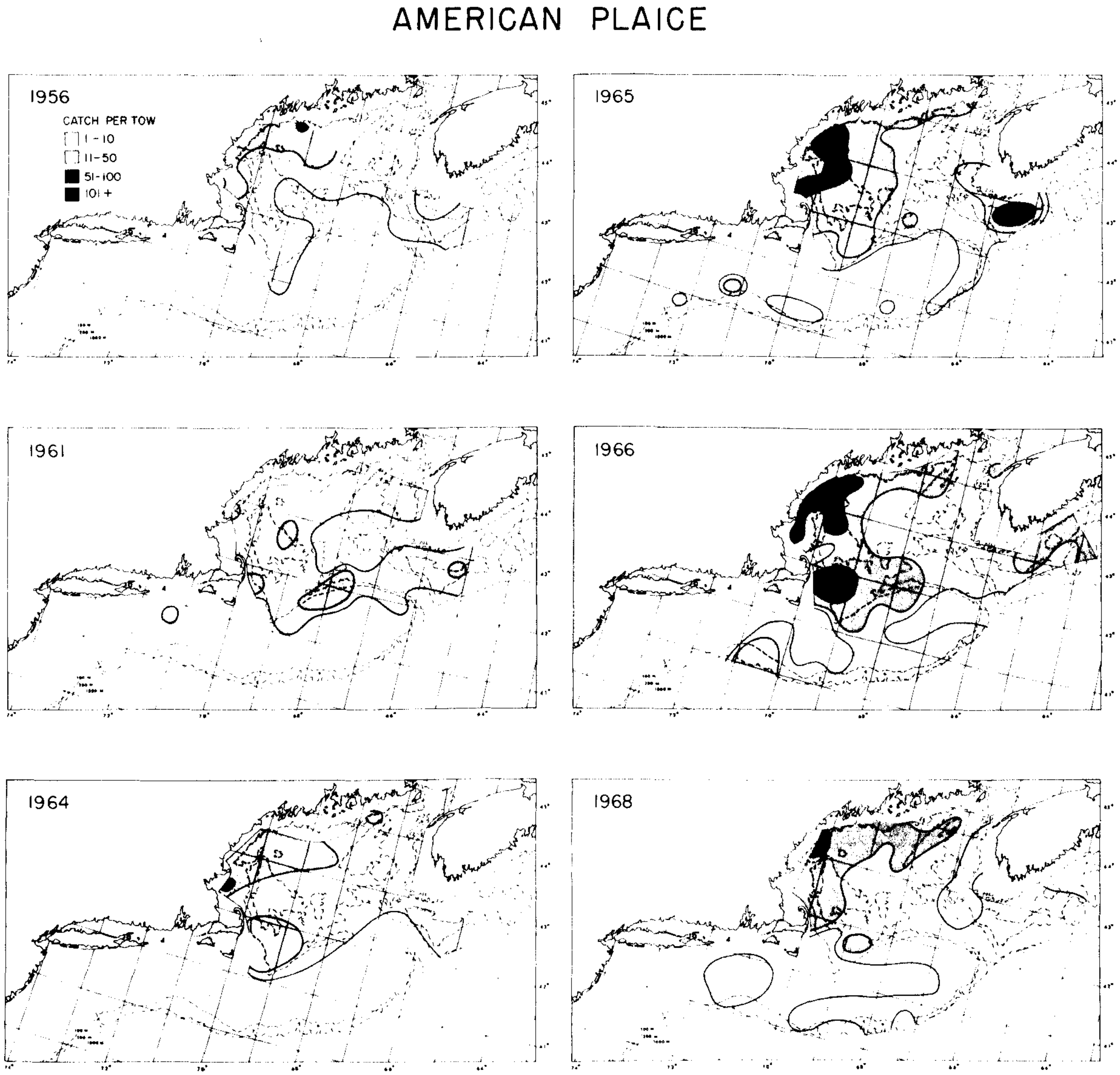

FIGURE 5.—Distribution of American plaice during October-November.

designs were used, but for most cruises a stratified random sampling technique was employed in which station location and number were prorated by area and depth zone. A complete description of the sampling design currently being employed is given by Grosslein (1969).

Although an effort was made to standardize sampling techniques, comparative tows made with the *Albatross III* and the *Delaware* and the *Albatross IV* and the *Delaware* showed that fishing efficiency varied to some extent between vessels and with towing methods (stern vs. side trawling). Fishing efficiency also varies with time of day and with species and age of fish (Bigelow and Schroeder, 1953; Colton, 1965; Fritz, 1965). However, for the purpose of de-

HADDOCK

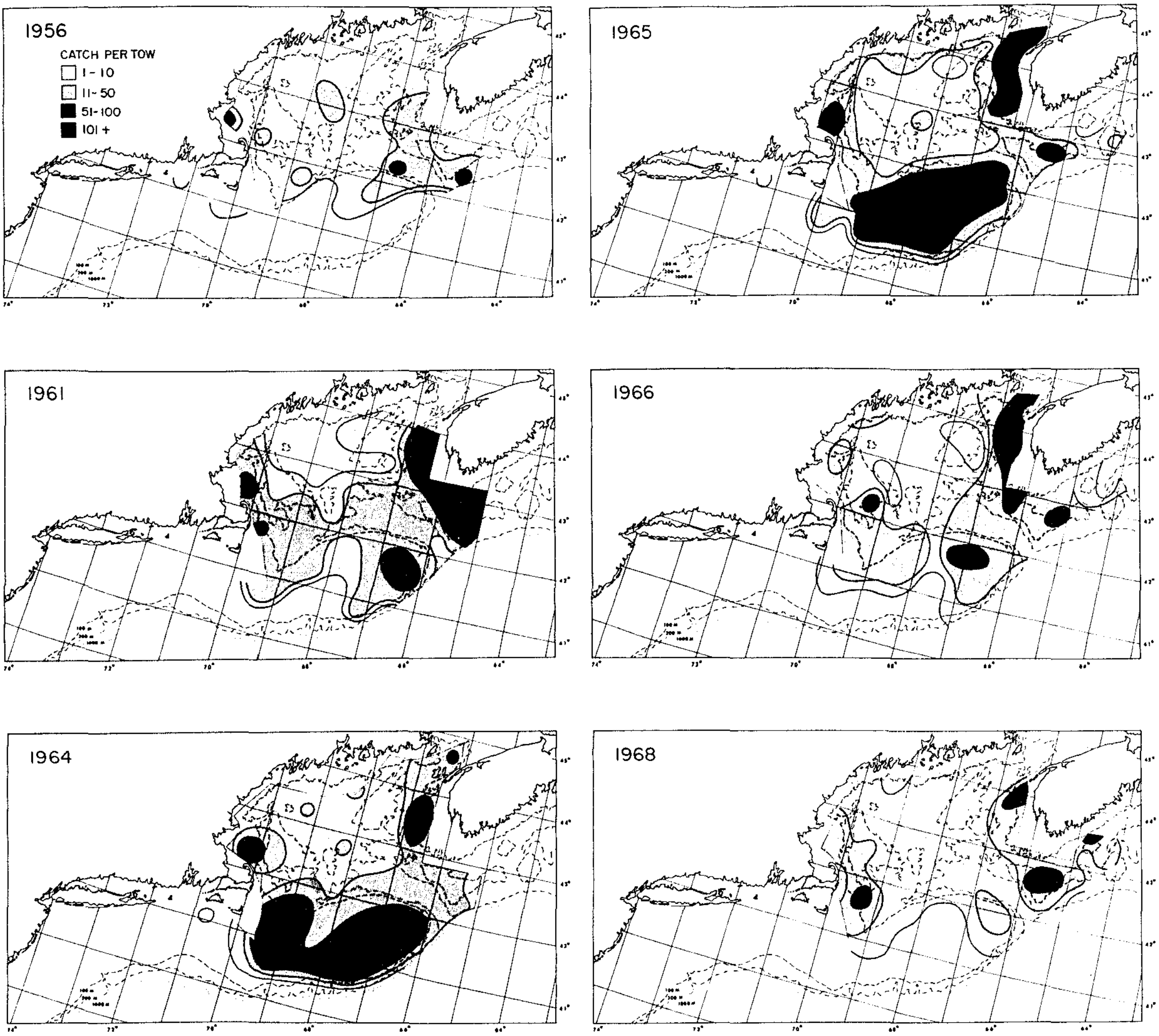

FIGURE 6.—Distribution of haddock during October-November.

lineating the general distribution patterns of the species of fish considered in this paper, the survey data would appear to be adequate.

For most species and in most areas there were marked differences in the catch at adjacent stations. In preparing the species distribution charts, the average number of fish per tow for all stations lying within 30″ latitude and longitude quadrangle areas was determined. The contour lines were drawn on a basis of these average values entered at the center of each 30″ quadrangle. Considerable smoothing and interpolation were still necessary, especially in cases where the bathymetry required adjustments in order to avoid contouring a species outside its normal depth range as indicated by individual

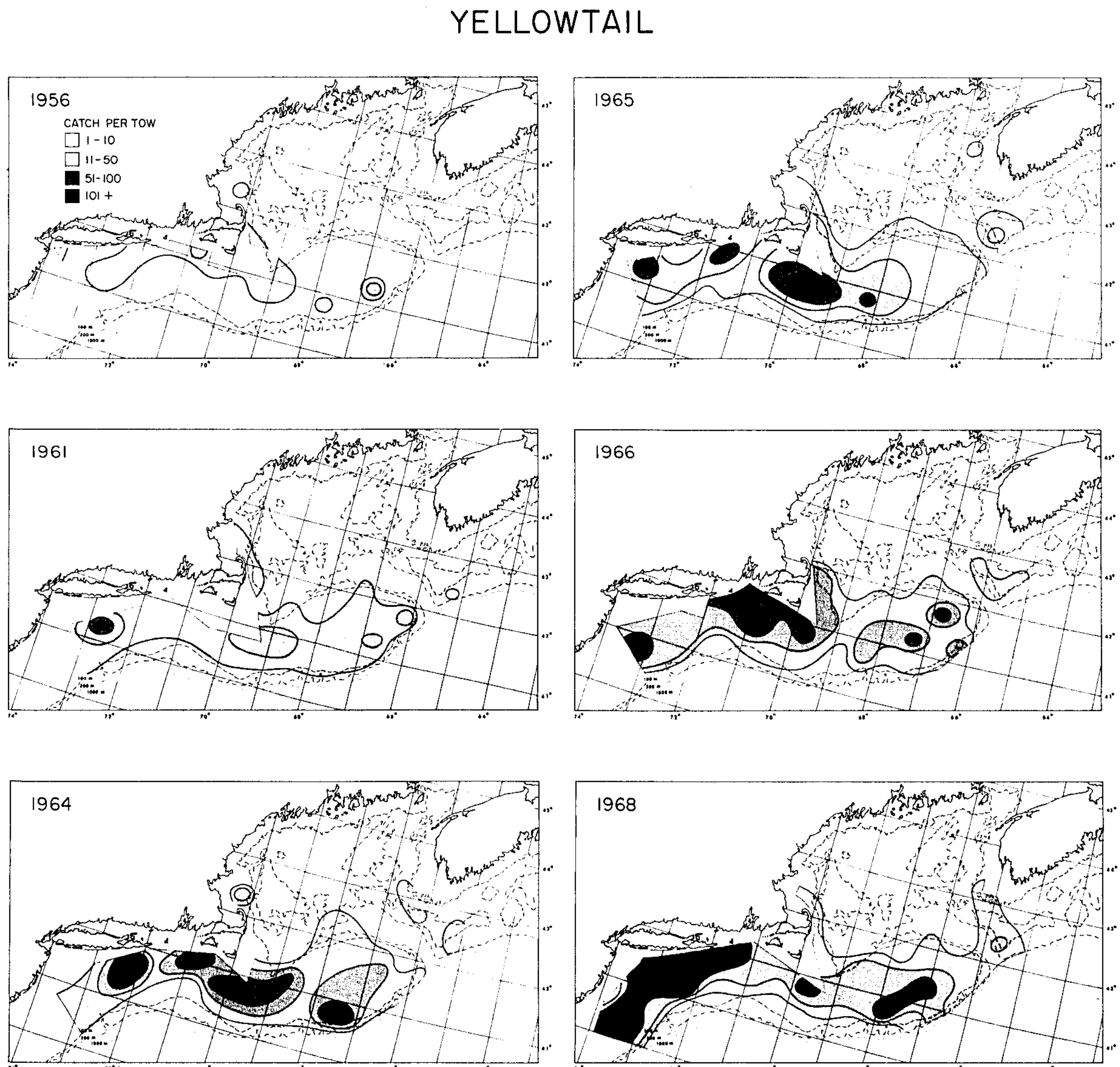

FIGURE 7.—Distribution of yellowtail flounder during October-November.

station data.

Groundfish surveys were conducted principally during the fall months in an effort to estimate the strength of new year classes of haddock, but some surveys were made at other seasons of the year. There was considerable yearly variation between cruise dates during any one season. In order to eliminate the effects of short-term shifts in distribution, only cruises spanning approximately similar time periods were used in comparing yearly distribution patterns. The dates and trawl station locations of the cruises considered in this paper are shown in Figures 3 and 4.

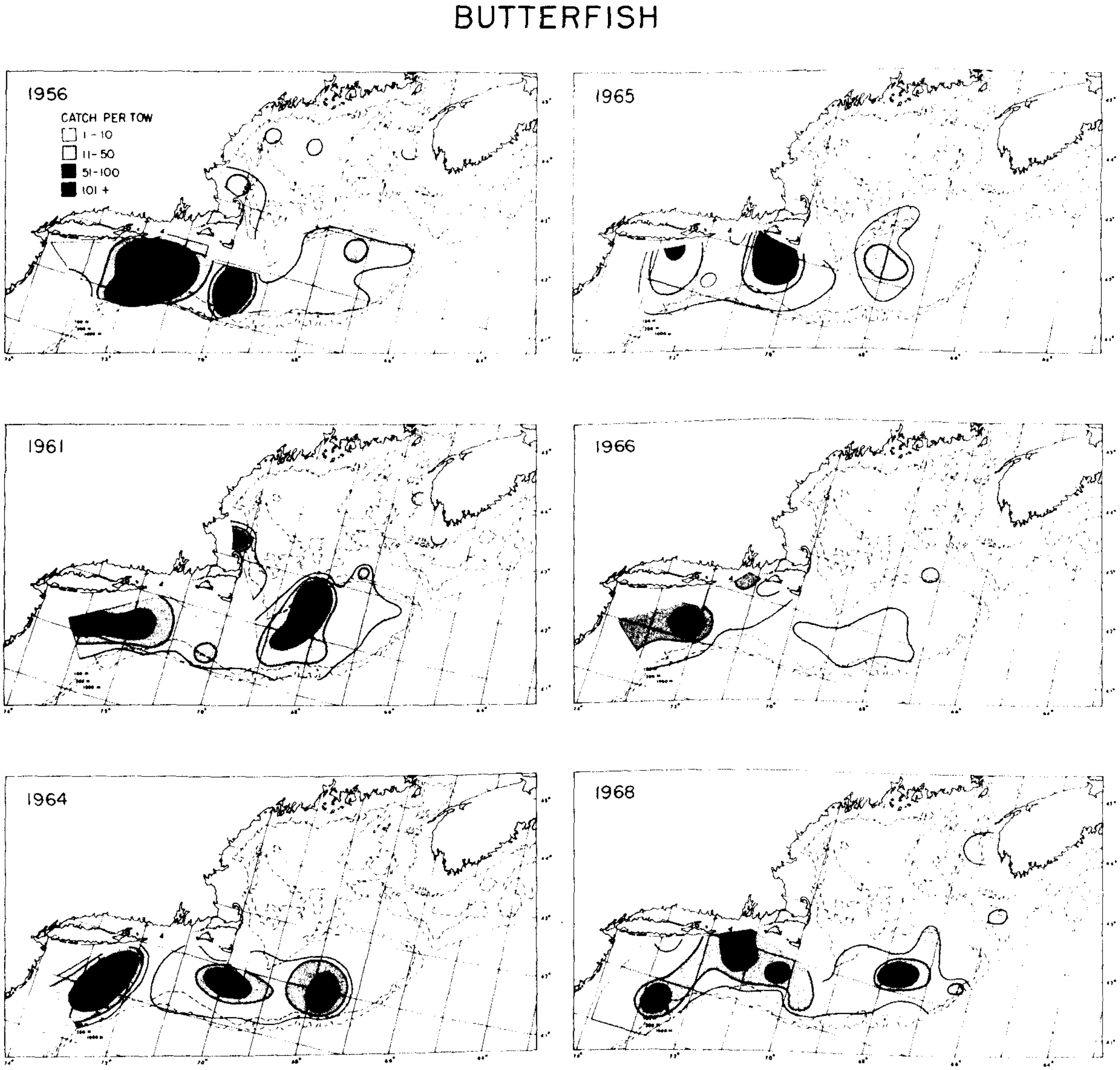

FIGURE 8.—Distribution of butterfish during October-November.

OCTOBER-NOVEMBER DISTRIBUTION

The distribution of American plaice, haddock, yellowtail flounder, and butterfish during October-November 1956, 1961, 1964, 1965, 1966, and 1968 is shown in Figures 5-8.

During 1956, 1961, and 1964, the catches of American plaice were confined to the area north of lat 41°N and east of Cape Cod. In 1965, 1966, and 1968, plaice were found over a much more extensive area. In these years plaice occurred along the southern edge of Georges Bank and off southern New England as far west as long 72°W. The abundance of plaice, as indicated by the average catch per tow, was greater during the latter 3 years.

The catches of haddock were confined to the area east of Nantucket Shoals (long 70°W). The general distribution pattern was similar during all years with the exception that in 1956 (the warmest year) the southern limit of occurrence of haddock was north of its position during the other years. For the most part, the variations in abundance and distribution of haddock between years appear to be related to changes in age composition of the catch due to the predominance of certain year classes. For example, the catches during 1964 and 1965 consisted principally of 1- and 2-year-old fish of the strong 1963 year class (Grosslein, 1969). In general, these young haddock inhabit shoaler water than do older haddock (Colton, 1955).

Although there were marked fluctuations in the abundance of yellowtail flounder between years, there was little change in the general distribution pattern. In all years yellowtail were found in relatively shoal water (<100 m) both to the east and west of Cape Cod. With the possible exception of 1956, the distribution of yellowtail extended considerably beyond the western limit of the sampling area. The bulk of the catch was made south of lat 42°N, although small concentrations occurred off the tip of Cape Cod and on Browns Bank. The greater abundance of yellowtail in later years appears to be due to a succession of strong year classes and not to a major shift in distribution (Lux, 1969).

The main concentrations of butterfish occurred on western Georges Bank and Nantucket Shoals and off southern New England and Long Island. As in the case of the yellowtail, the distribution of butterfish extended beyond the western limit of the sampling area. In 1956 and 1961 only, appreciable numbers of butterfish were caught north of lat 42°N. In these years butterfish occurred just east of Cape Cod, in the Stellwagen Bank area, and in scattered concentrations within the Gulf of Maine. Butterfish were least abundant in 1966. In this, the coldest year, few fish were taken east of Nantucket Shoals.

JULY-AUGUST DISTRIBUTION

The distribution of American plaice, haddock, yellowtail flounder, and butterfish during July-August 1950, 1963, 1964, and 1965 is shown in Figures 9 and 10.

The area of occurrence of plaice extended farther south and west with succeeding years and decreasing temperatures. The catches of haddock were confined for the most part to the area east of Nantucket Shoals, and there was little change in distribution between years. The similarity of the distribution patterns of haddock during July-August and October-November 1964 and 1965 indicates limited seasonal movement. Little change was evident in the general distribution patterns of yellowtail between years. As in the case of the haddock, the similarity of the distribution patterns during July-August and October-November 1964 and 1965 indicates little seasonal movement. There were no marked differences in the distribution of butterfish in these years, although butterfish were least abundant on Georges Bank in 1965, and 1950 was the only year in which appreciable numbers were taken in Cape Cod Bay. In contrast to October-November, the distribution of butterfish during July-August 1964 and 1965 was confined within the western limits of the sampling area.

SEASONAL DISTRIBUTION

Of the four species considered in this paper, only the American plaice and the butterfish showed any appreciable change in distribution coincident with the downward trend in temperature. During both summer and fall there was an extension of the southern and western limits of the area of occurrence of plaice and a contraction of the northern and eastern limits of the area of occurrence of butterfish. Data obtained on cruises made during January-February 1964 and 1966, together with data collected during July-August and October-November 1964 and 1965 (Figures 11 and 12), give evidence of the seasonal distribution of these two species.

Although there were no extensive seasonal changes in the distribution of plaice, the southwesterly extent of the distribution boundaries tended to be greatest during January-February and least during October-November (Figure

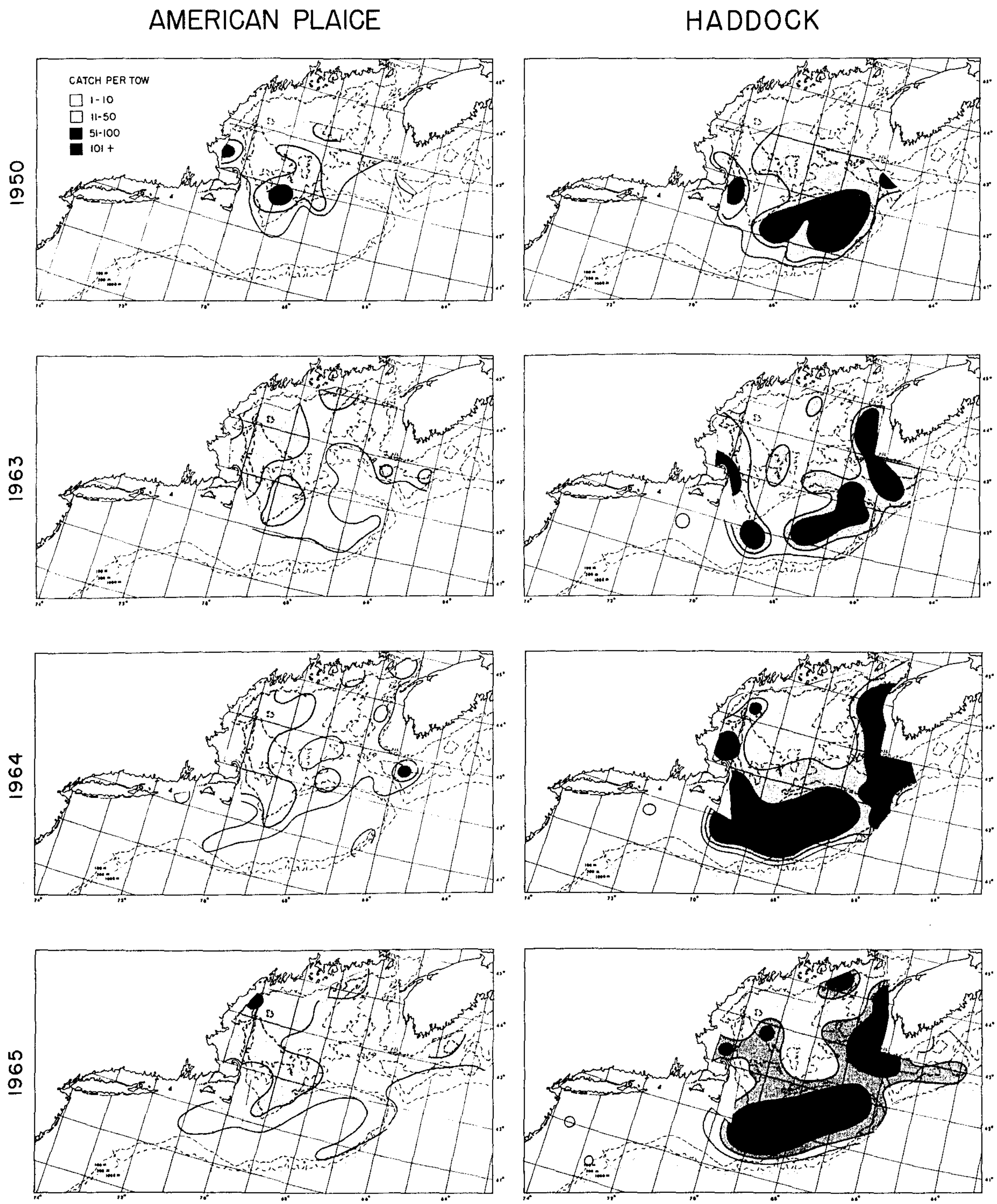

FIGURE 9.—Distribution of American plaice and haddock during July-August.

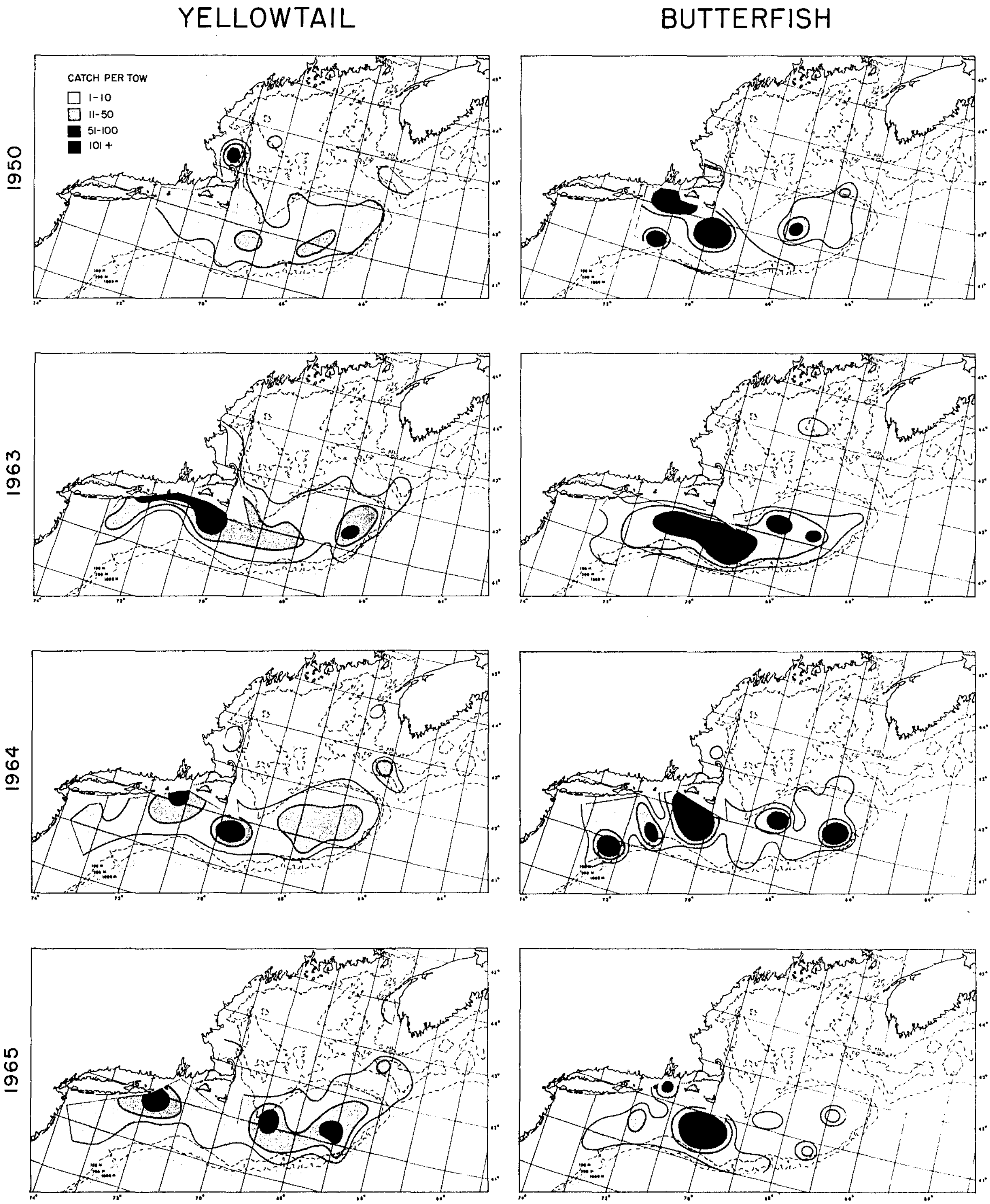

FIGURE 10.—Distribution of yellowtail flounder and butterfish during July-August.

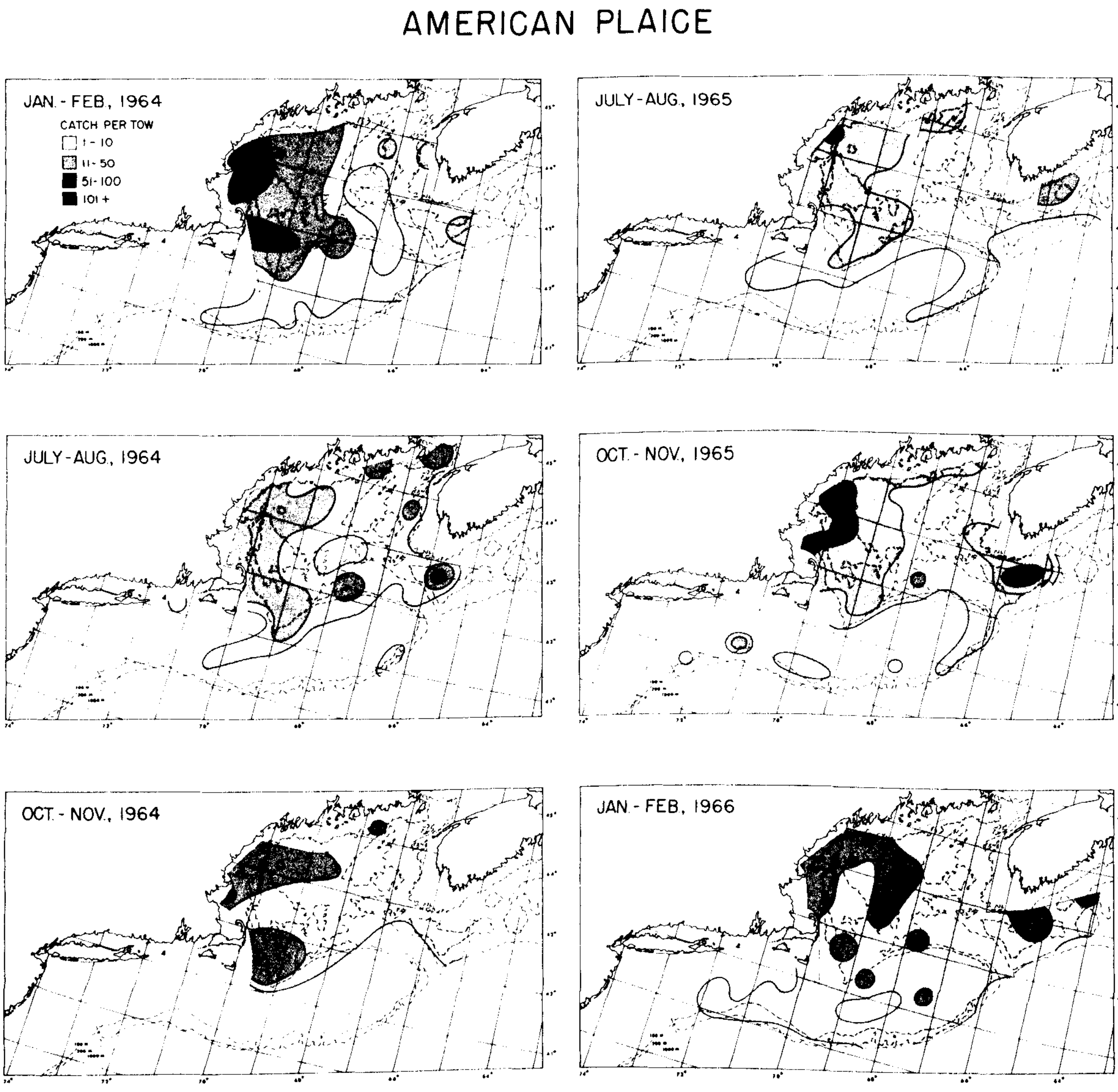

FIGURE 11.—Seasonal distribution of American plaice.

11). In addition, it was only during January-February that plaice were caught in the shoal-water areas of Georges Bank. This seasonal shift in distribution appears to be associated with temperature change. The seasonal maximum and minimum bottom-water temperatures at the depths most frequented by plaice (30-200 m) occur during October-November and February-March respectively (Colton, 1968a; Colton and Stoddard, In press). Bottom-water temperatures over the shoal-water areas of Georges Bank are appreciably higher than those along its periphery during the summer and fall while in the winter and spring the reverse situation exists.

There were no appreciable changes in the dis-

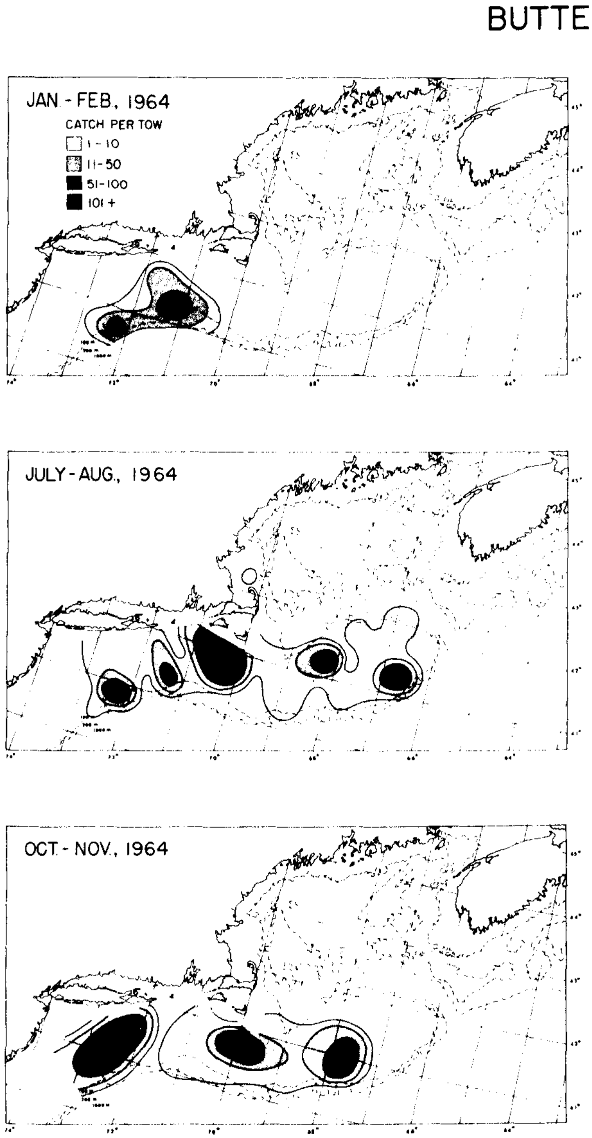

FIGURE 12.—Seasonal distribution of butterfish.

tribution of butterfish between July-August and October-November (Figure 12). However, the fact that the distribution during October-November extended beyond the western limits of the sampling area indicates that butterfish begin their offshore migration from New England coastal waters at this time. By January-February the offshore migration was completed and butterfish were only found in deep water in the southwest corner of the sampling area.

DISCUSSION

A seasonal cold-water temperature barrier in the region of Cape Cod and Nantucket Shoals separates the coastal waters of the Gulf of Maine and the Middle Atlantic Bight from the end of

June to the end of September (Bigelow, 1927; Parr, 1933). This barrier is marked by the presence of a surface pool of cold upwelled water. At other seasons of the year there is open continuity between coastal temperature conditions north and south of Cape Cod. This temperature barrier coincides with the poleward and equatorward boundaries of many species of marine fauna, both pelagic and benthic (Bigelow and Sears, 1939; Parker, 1948; Fritz, 1965; Schopf, 1965).

The seasonal ranges of surface- and bottom-water temperatures in most areas within the Gulf of Maine are less extreme than those characteristic of the Middle Atlantic Bight. The seasonal range of temperature in the shoal-water area of Georges Bank, however, is as great as that at similar depths in the area between Nantucket Shoals and New Jersey (Colton and Stoddard, 1972 and In press). Parr (1933) has described the ecological relationships between homothermal and heterothermal regions separated by a seasonal temperature barrier and has discussed the effect that these contrasting temperature regimes have on the period, extent, and character of the migratory activities of shallow-water fish populations. There is a marked seasonal alternation in the composition of the fish fauna of the Middle Atlantic Bight. In summer this area contains a very rich population of southern migratory fishes which follow the northward dispersal of isotherms as far north as Cape Cod. Winter temperature conditions compel this population to vacate the area, and it is replaced to a considerable extent by northern species, such as herring and cod, which at this season have free access to penetrate as far south as the neighborhood of Cape Hatteras. Although there is no thermal barrier during the winter, the qualitative composition of the fish fauna is not uniform from north to south around Cape Cod. As Parr (1933) has pointed out, this seasonal diffusion of northern populations into areas where no significant temperature differences exist is distinguishable in both its character and effects from the northerly and southerly migrations of complete populations such as occur under thermal compulsion within the Middle Atlantic Bight. In contrast to the Middle Atlantic Bight which contains very few permanent residents, the bulk of the fish fauna in the Gulf of Maine are endemic to the area and there is little seasonal alternation in species composition.

Hutchins (1947) recognized four basic types of temperature zonation which depend on maximum and minimum temperatures critical for survival and repopulation. With the exception of estuarine species such as the green crab which may be subject to winter kill, the distribution of benthic organisms in the area off New England appears to be controlled by summer rather than winter temperatures (Hutchins, 1947; Schopf, 1967). The equatorward boundary of potentially southward-migratory forms is limited by summer temperatures too high for survival and the poleward boundary of northward-migratory forms by summer temperatures too low for reproduction (type 3 of Hutchins, 1947). This is in agreement with the assumption of Hutchins (1947) that at localities having a temperature barrier at only one season (summer at Cape Cod), all distributions terminating there are associated with that barrier.

It is difficult to categorize fish species by strict temperature zonation characteristics. Fish do not have built-in integrators and so must react to prevailing rather than to average conditions. Unlike many benthic invertebrates, fish are able to make short-term excursions and are not dependent solely on passive migrations. It should also be stressed that the distribution within the broad limits set by temperature extremes for survival and reproduction is controlled to some extent by other factors such as food supply (Blackburn, 1969) and substrate conditions (Bigelow and Schroeder, 1953). Of the species considered in this paper, only the American plaice and the butterfish exhibited the expected response to cooling, e.g., extension of the southern range of northern endemic forms and diminution of the northern range of southern migrants.

The butterfish is the only species considered which shows a sensitivity to small changes in temperature and which migrates under the thermal compulsion. Ripe butterfish are taken throughout their entire range (Caldwell, 1961). In the Gulf of Maine spawning occurs from June through August (Bigelow and Schroeder, 1953). In general, the first arrivals at any point along the coast are in spawning condition, and it would appear that the summer poleward boundary is governed by the minimum temperature suitable for reproduction. Although one can only generalize as to temperature dependence, the timing of arrival of butterfish at various points along the coast of New England and the Maritime Provinces suggests that the minimum spawning temperature is approximately 15°C. The time at which butterfish leave the coastal waters and their distribution in deep water along the continental slope during the winter months indicate a minimum temperature for survival of about 10°C. These temperature approximations are based on average values given by Colton and Stoddard (1972 and In press).

Bigelow and Schroeder (1953) state that the American plaice spawns throughout the Gulf of Maine, but principally in water shoaler than 100 m. More recent observations (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962) confirm that the plaice has no well-defined spawning area, although plaice eggs were most abundant in the western Gulf of Maine and over the southeastern part of Georges Bank. Plaice spawn from March through May (Bigelow and Schroeder, 1953). Long-term temperature data in the areas of maximum spawning (Colton and Stoddard, In press) suggest an optimum spawning temperature of 3°-6°C. During the spawning period such bottom-water temperature conditions prevail over most of the area within the 100-m isobath from Cape Cod to New Jersey. Thus, the equatorward boundary of plaice appears to be limited by summer and fall temperatures too high for survival rather than temperatures during the spawning season that are too high for reproduction. As noted previously, plaice were not caught in the Georges Shoal area during the summer and fall. The long-term temperature distribution in this area indicates a maximum temperature for survival of about 12°C. Bigelow and Schroeder (1953) give a range of 10°-13°C as the upper limit of regular occurrence of American plaice.

In contrast to the American plaice, the spawning of haddock is restricted to limited areas within the Gulf of Maine. The most productive spawning grounds are in depths ranging from 40 to 100 m on the northeastern part of Georges Bank and on Browns Bank (Walford, 1938; Bigelow and Schroeder, 1953; Colton and Temple, 1961). Limited and less consistent spawning occurs in the South Channel, Stellwagen Bank, and Jeffreys Ledge areas. Haddock spawn from February through May with the height of spawning occurring on Georges Bank during March and April and on Browns Bank during April and May. Long-term temperature data in the areas of maximum spawning suggest an optimum spawning temperature of 4°-6°C, although spawning does take place at temperatures below and above this range (2°-7°C). There is no evidence that haddock spawn west of Cape Cod, although favorable temperature conditions exist over most of this area during the spawning season.

It is not apparent why haddock select restricted spawning areas, but this limitation may govern in part the extent of their seasonal diffusion into waters west of Cape Cod. Bigelow and Schroeder (1953) give 11°C as the upper temperature limit of the normal range of occurrence of haddock, but the fact that haddock are caught in the Georges Shoal area during the warmest part of the year indicates that haddock can survive temperatures at least as high as 15°C for limited periods. Bottom-water temperatures well below this upper limit occur over much of the area between Cape Cod and Long Island during the summer and fall.

Although seasonal shifts in depth distribution and the timing of spawning of haddock appear to be regulated in part by temperature (Bigelow and Schroeder, 1953; Colton, 1968a), the fact that there was no appreciable change in the geographic distribution of haddock coincident with the downward trend in temperature suggests that factors other than temperature are also critical in the geographic zonation of this species. Bigelow and Schroeder (1953) note that haddock are selective as to substrate type. Haddock avoid areas of rock, kelp, and exceptionally soft mud and are chiefly caught over broken ground, gravel, pebbles, clay, and smooth hard sand. However, there are no conspicuous differences in the sediments of the Continental shelf east and west of Nantucket Shoals (Uchupi, 1963). Sediments on Georges Bank consist of coarse sand and scattered patches of gravel. In the area between Nantucket Shoals and Hudson Canyon, there is a nearshore zone of silty sand and sandy silt and scattered patches of gravel. Between the 30- and 60-m isobaths is a zone of coarse sand and scattered patches of gravel. From the 60-m isobath to the edge of the shelf, the sediments are similar to those in the basins of the Gulf of Maine and consist of silty sand, sandy silt, and silt.

On a basis of a stomach content analysis of haddock collected on Georges Bank during 1953-54, Wigley (1956) concluded that haddock are exceedingly omnivorous. Their diet consisted principally of sedentary or slow-moving invertebrate animals. The primary food organisms in decreasing order of abundance were crustaceans, mollusks, echinoderms, annelids, and fish. There was considerable variation in dietary components from one location to another. Having no supplementary data on the distribution of benthic fauna, it could not be determined if this variation in diet was related to faunal composition. More recent studies of the distribution of benthic fauna on the continental shelf between Nova Scotia and Long Island (Wigley, 1961; Wigley and McIntyre, 1964; R. L. Wigley—personal communication) show that haddock prefer crustaceans to other food organisms and that the quality and quantity of the benthic fauna to the west of Nantucket Shoals are more than adequate to support a large population of haddock. It is possible that competition for food by the very rich summer and fall populations of such species as the spiny dogfish, silver hake (*Merluccius bilinearis*), and red hake (*Urophycis chuss*) is a factor in restricting the haddock from the Middle Atlantic Bight.

As mentioned previously, the yellowtail flounder is common both to the east and west of Cape Cod at all seasons of the year. Bigelow and Schroeder (1953) observed that the restricted depth range and the nonmigratory habit of this species indicate that yellowtail can tolerate a wide range of temperature. This eurythermic tolerance is further evidenced by the long spawning season and extensive spawning area of this species. The yellowtail breeds over its entire range and from March through August. The spawning period appears to be no later east of Cape Cod than to the west. In addition, Bigelow and Schroeder (1953) noted that individual females evidently spawn over a considerable period of time for only a small part of the eggs ripen simultaneously. The above authors estimated that the yellowtail was subject to a range of temperature from season to season in one part of its area of occurrence or another from about 1° to 12°C. However, the distribution of yellowtail off southern New England and Long Island during the warmest part of the year indicates that they can tolerate temperatures at least as high as 16°C for limited periods.

Yellowtail flounder are only found over sand and sand-mud bottoms and never over rocks, stony ground, and very soft bottom (Bigelow and Schroeder, 1953). This preference for sand sediments is especially evident if one compares the distribution of yellowtail shown in Figures 7 and 10 with the distribution of sediment type shown by Uchupi (1963, Figure 94.1). This predilection for sand sediments is also shown in the data of Fritz (1965, Plates B and 14). It would appear then that except at the extreme northerly and southerly limits of its range, the geographic distribution of yellowtail is more strongly inffuenced by bottom type than by temperature.

It is possible that changes in distribution occurred which were not evident from the survey data due to limitations of sampling and analysis. For example, a number of groundfish species inhabit areas shoaler than that covered by the surveys (<30 m). Among such species is the summer flounder (*Paralichthys dentatus*), which is representative of species restricted for the most part to the area southwest of Cape Cod at all seasons of the year. Pelagic species such as menhaden (*Brevoortia tyrannus*), a warm season migrant having wide fluctuations of occurrence in the Gulf of Maine, and herring (*Clupea harengus harengus*), a boreal species which ranges as far south as Cape Hatteras in the winter, were not representatively sampled by the otter trawl. Studies undertaken on the distribution of tunas (Blackburn, 1965, 1969) indicate that, in general, pelagic species are much more sensitive to temperature than groundfish species.

There is some evidence to the effect that sensitivity to temperature varies with age of fish. Rollefsen (1949) noted that immature cod can tolerate lower temperatures than mature cod. It is only during the spawning season that appreciable numbers of the older year classes of haddock are caught on Georges Bank (Colton, 1955). In summer these older fish move off into deeper and cooler water, and the Georges Bank population is made up principally of the younger year classes of haddock (1- to 3-year-olds). It would appear that young haddock can withstand higher temperatures than older haddock. The fact that we grouped all age fish in this study may have concealed shifts in distribution associated with specific age-groups.

Any attempt to relate geographic distribution to the direct result of physical processes involves gross oversimplification. It is apparent, however, that there was no major change in the distribution of groundfish coincident with the cooling trend, i.e., the establishment of resident populations south of Cape Cod of species that were formerly winter migrants or a northern diminution of the range of southern migrants. It would appear that the magnitude and rate of temperature change were not sufficient to significantly alter the groundfish composition in the area between Nova Scotia and Long Island. A similar conclusion was reached by Taylor et al. (1957) in their study of changes in the distribution and abundance of marine animals in the same area during a period of warming.

SUMMARY

An alternation in seawater temperature has been observed in coastal and offshore waters in the area between Nova Scotia and Cape Hatteras. There have been a number of reports of southward extensions of range and shifts in distribution of fish and invertebrate fauna during the cooling trend which commenced during 1952-53.

Research vessel survey data is presented to determine what effect the cooling trend has had on the distribution of some important commercial groundfish species in continental shelf waters between Nova Scotia and Long Island. Four species representative of the basic types of geographic zonation characteristic of the area are considered in this paper: American plaice, haddock, yellowtail flounder, and butterfish.

The American plaice and the butterfish showed a change in distribution coincident with the downward trend in temperature, but these shifts were not extensive. During both summer and fall there was an extension of the southern and western limits of the area of occurrence of American plaice and a contraction of the northern and eastern limits of the area of occurrence of butterfish. The equatorward boundary of plaice appears to be limited by summer temperatures too high for survival and the poleward boundary of butterfish by summer temperatures too low for reproduction.

There was no change in the general distribution of haddock and yellowtail flounder. In all years and seasons the catches of haddock were confined for the most part to the area east of Cape Cod. Restricted spawning areas and competition for food may govern, in part, the seasonal diffusion of haddock into waters west of Cape Cod.

Yellowtail flounder occurred both to the east and west of Cape Cod at all seasons. Their distribution was limited to depths shoaler than 100 m and to areas of sand bottom. The restricted depth range, long spawning season, extensive spawning area, and nonmigratory habit of the yellowtail flounder indicate that this species can tolerate a wide range of temperature. It appears that except at the extreme northerly and southerly limits of its range, the geographic distribution of yellowtail flounder is more influenced by bottom type than by temperature.

Although it is possible that changes in distribution did occur which were not evident from the survey data, it appears that the magnitude and rate of temperature change during the cooling period were not sufficient to significantly

alter the distribution of groundfish in the area between Nova Scotia and Long Island.

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