

Not to be cited without
permission of the authors¹

Ne pas citer sans
autorisation des auteurs¹

Canadian Atlantic Fisheries
Scientific Advisory Committee

Comité scientifique consultatif des
pêches canadiennes dans l'Atlantique

CAFSAC Research Document 86/37

CSCPCA Document de recherche 86/37

Circulation and Potential Ichthyoplankton Dispersal in the
Gulf of Maine, Browns and Georges Bank Areas

by

R. Ian Perry
Marine Fish Division
Department of Fisheries and Oceans
Biological Station
St. Andrews, New Brunswick EOG 2X0

and

Peter C.F. Hurley
Marine Fish Division
Department of Fisheries and Oceans
Bedford Institute of Oceanography
Dartmouth, Nova Scotia B2Y 4A2

¹This series documents the scientific basis for fisheries management advice in Atlantic Canada. As such, it addresses the issues of the day in the time frames required and the Research Documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

¹Cette série documente les bases scientifiques des conseils de gestion des pêches sur la côte atlantique du Canada. Comme telle, elle couvre les problèmes actuels selon les échéanciers voulus et les Documents de recherche qu'elle contient ne doivent pas être considérés comme des énoncés finals sur les sujets traités mais plutôt comme des rapports d'étape sur les études en cours.

Research Documents are produced in the official language in which they are provided to the Secretariat by the author.

Les Documents de recherche sont publiés dans la langue officielle utilisée par les auteurs dans le manuscrit envoyé au secrétariat.

Abstract

The most recent understanding of the mean circulation of the Gulf of Maine, including Georges and Browns Banks, is described from literature sources to support studies of ichthyoplankton distributions and stock structure. The mean circulation consists of separate clockwise gyres about both banks, which are leaky to the southwest on Georges Bank and to the north on Browns Bank. The mean circulation of the Gulf of Maine consists of several large eddies, loosely associated with bathymetric features; it is not one large gyre. The conclusion is that consistent transport of ichthyoplankton between Georges and Browns Banks by the residual circulation generally does not occur. This is supported by both literature and field studies of cod and haddock egg and larval distributions. However, sporadic transport of ichthyoplankton between banks may occur due to strong wind-induced currents during storms.

The probability for ichthyoplankton dispersal from Browns Bank northwards and from the western Scotian Shelf towards Browns Bank is higher, as all are within prevailing current directions. However, any circulation which retains plankton on the banks would promote discreteness of spawning products.

Résumé

On a décrit d'après les sources de documentation disponibles, à l'appui d'études sur la distribution de l'ichtyoplancton et sur la structure des stocks, les connaissances les plus récentes relatives à la circulation moyenne dans le golfe du Maine, y compris dans la région des bancs Georges et Brown. La circulation moyenne, environs des deux bancs, est constituée de mouvements giratoires dextrogyres séparés. Ces mouvements présentent des pertes limitées vers le sud-ouest sur le banc Georges et vers le nord sur le banc Brown. Dans le golfe du Maine, la circulation moyenne se compose de plusieurs grands tourbillons, vaguement associés à des détails bathymétriques; on n'y observe pas un vaste mouvement giratoire unique. On en tire la conclusion qu'il n'y a généralement pas de transport régulier d'ichtyoplancton entre les bancs Georges et Brown, qui soit effectué par la circulation résiduelle. C'est ce que confirment à la fois la documentation scientifique et les études in situ de la distribution des oeufs et larves de morues et aiglefin. Toutefois, il peut y avoir un transport sporadique de l'ichtyoplancton d'un banc à l'autre, en raison de forts courants induits par les vents de tempête.

La probabilité que l'ichtyoplancton soit dispersé du banc Browns vers le nord et de l'ouest du plateau Scotian vers le banc Browns est plus élevée, étant donné que tout l'ichtyoplancton se trouve dans les directions dominantes du courant. Toutefois, une circulation quelconque retenant le plancton sur les bancs favorise une distribution discrète des produits du frai.

Introduction

Gulland (1983) describes the ideal fish stock as having a single spawning ground contained within one or more current systems, which maintains the stock within the same geographic area. Distributions of early life history stages are important components in this definition. If eggs and larvae mix over a large area, they will be susceptible to similar large-scale environmental and biological disturbances. If they are separated into smaller, discrete areas, they will also be susceptible to more local-scale disturbances. The result is isolated stocks which may respond with different recruitment success and year-class strengths.

Ocean currents are a principal mechanism determining the transport and distribution of ichthyoplankton, and therefore potentially of marine fish and invertebrate stock structure. As an aid to discussions on stock structure in the Gulf of Maine, this review examines the general oceanic circulation in NAFO Divisions 4X, 5Y and 5Ze, specifically the bathymetrically distinct areas of Browns Bank, Georges Bank and the Gulf of Maine. It summarizes from the literature the mean circulation of these areas, with the underlying question being the potential for regular transport of ichthyoplankton between Georges Bank and Browns Bank, and between the banks off southwest Nova Scotia. Previous studies have suggested larvae off the southwest Nova Scotia coast may be derived predominantly from Georges Bank (e.g. Boyar et al. 1973 for herring; Harding et al. 1983 for lobster), while other studies suggested such exchange is unlikely (e.g. Grosslein and Hennemuth 1973; Smith and Morse 1985, both for haddock). This review examines these possibilities using literature sources and original data on cod and haddock egg and larval distributions, derived from the Fisheries Ecology Program. The general and wind-driven circulations in the Gulf of Maine area are described first, followed by the distribution and behavior of gadid eggs and larvae and their relationship to the circulation.

Regional Oceanography

Georges Bank

The earliest general description of the circulation in the Gulf of Maine (including Browns Bank, Georges Bank and the Nantucket Shoals) was presented by Bigelow (1927) (Fig. 1). He described a large counterclockwise eddy about the Gulf of Maine, a clockwise circulation about Georges Bank (open to the south), flow into the Gulf off southern Nova Scotia and out of the Gulf to the southwest over the Nantucket Shoals. This pattern was deduced during summer (July and August) using current meters, drift bottles, temperature and salinity characteristics and plankton distributions. Descriptions of the circulation on Georges Bank by Bumpus and Lauzier (1965) and Bumpus (1973) indicated it is a relatively closed gyre in both near-surface and bottom circulation. The current atlas of Bumpus and Lauzier (1965) has been widely used, however, it is based on drift bottle experiments. Butman et al. (1982) have noted that drift bottles provide only release and recovery information and are very sensitive to slight

offshore flows, thus giving no information on the along-shore flow. These drifters provide information on the "average" current only, which may, in fact, seldom occur (Colton and Anderson 1983).

Loder and Wright (1985) and Butman et al. (1986) have recently reviewed the mean circulation on Georges Bank. They note the residual (i.e. mean or resultant) flow is clockwise about Georges Bank, oriented parallel to local isobaths. There is a seasonal variation in the strength of the mean flow, with a maximum in summer and fall, and a minimum in winter when the current speeds are also more variable. The seasonal periodicity in current speed is associated with the development of density gradients during summer due to the formation of a mixed area on the top of the bank and a stratified area surrounding it. On the southern flank of Georges Bank, the shelf-slope water front usually intersects the bottom at about the 100-m depth contour and can be interpreted as a somewhat leaky hydrodynamic barrier.

There is also spatial variability in the strength of the clockwise circulation about Georges Bank, both geographically and vertically. Due to the shape of the bank, there is an intensification of the current into a jet-like flow along the northern flank, which spreads out and slows down as it rounds the northeast peak of the bank. Vertically, the strength of the mean flow decreases with depth, but retains the same general direction.

Observations of currents at selected locations have been made using moored current meters. In winter, mean currents along the southern flank are directed to the southwest at about 5 cm s^{-1} near the surface, mid-depth and near-bottom. On the northern flank in winter, currents flow to the northeast at $13\text{--}20 \text{ cm s}^{-1}$ throughout the water column. During summer, the flow on the south side is still to the southwest at 5 cm s^{-1} near the bottom, but has increased to $10\text{--}15 \text{ cm s}^{-1}$ at mid-depth and $13\text{--}20 \text{ cm s}^{-1}$ near the surface. At these speeds, a passive particle could be expected to make a complete circuit of the bank in about 2 months (at 60 m depth). On the northern flank, near-surface flows in spring (April-May) are about $20\text{--}30 \text{ cm s}^{-1}$, increasing to $30\text{--}40 \text{ cm s}^{-1}$ in June and July. At mid-depth, mean current speeds in April-May are about 20 cm s^{-1} and up to 30 cm s^{-1} in August-September, while near-bottom speeds are about 10 cm s^{-1} . These high velocities are confined within a band $10\text{--}20 \text{ km}$ wide along the northern flank, with near-surface speeds falling to $25\text{--}30 \text{ cm s}^{-1}$ further off the bank above the 200-m isobath.

Browns Bank

The general circulation in the Browns Bank-southwestern Nova Scotia area is similar to that of Georges Bank, although more complicated due to the greater variation of bathymetry. Based on seabed drifter experiments during the early 1960's, Lauzier (1967) suggested mean flow was from east to west around Cape Sable, N.S., then northwards along the coast towards the Bay of Fundy. He also determined a definite onshore bottom flow leading to upwelling along the Yarmouth shore, but with a distinct divergence in bottom flow at the Northeast Channel between Browns and Georges Banks.

Recently, Smith (1983) examined the circulation off southwest Nova Scotia, including Browns Bank. He also noted an upwelling circulation off Cape Sable, N.S. (of order $1\text{--}2 \text{ cm s}^{-1}$ at the bottom), as well as a

westward longshore coastal current and a clockwise gyre about Browns Bank. The southwestward coastal current was consistently found nearshore at depths shallower than 110 m with speeds of 4-10 cm s⁻¹. It has seasonal variations in speed, with the strongest flow (6-10 cm s⁻¹) occurring in winter and directed to the west. Weaker summer velocities result from variations in density and stratification, in particular associated with the tidally mixed region off Yarmouth.

The gyral circulation about Browns Bank was suggested by current meter data, satellite-tracked drogues and model studies similar to those conducted for Georges Bank (Smith 1983). These results implied a closed gyre, making relatively little contribution to water mass characteristics of the Gulf of Maine. However, further experiments on Browns Bank by Peter Smith (Atlantic Oceanographic Laboratory, Bedford Institute of Oceanography, pers. comm.) have altered these conclusions. The clockwise gyre about the bank was confirmed, but it was found to be "leaky" to the north. Near-surface currents on the eastern flank were oriented towards the cap of the bank, leading to retention, while they tended to be dispersive to the north off the western flank. Maximum currents occurred along the northern edge where the bottom slope was greatest, while currents on the cap were generally weak.

Gulf of Maine

Understanding of the circulation in the Gulf of Maine has until recently, remained as described by Bigelow (1927), who showed the occurrence of a large counterclockwise eddy. Greenberg (1983) has developed a 2-D numerical model which describes the circulation in the Gulf of Maine and Bay of Fundy driven by tidal and steady wind stresses. The model is able to reproduce the general features of the clockwise circulations about both Georges and Browns Banks, but produces the counterclockwise eddy in the Gulf of Maine only when forced by strong, steady northeast winds in addition to the tide. Greenberg (1983) suggested this may be due to the strong variations of density in the Gulf that were not included in the model.

This effect of density on the circulation in the Gulf of Maine has been studied by Brooks (1985). He found a circulation pattern in spring somewhat similar to that of Bigelow (1927), except for two major differences. These are an anticlockwise gyre about Jordan Basin in the eastern Gulf near the mouth of the Bay of Fundy, and a counterclockwise recirculation of water about Georges Basin from the northern to the southern sides of the Northeast Channel. As shown by Brooks (1985), this recirculation appears to be contiguous with the southern edge of Browns Bank and the northern edge of Georges Bank, suggesting a possibility for transport of larvae from Browns to Georges Banks. However, this is in disagreement with the findings of P. Smith (pers. comm., discussed above) regarding the leak of the Browns gyre to the north not west. In the western Gulf of Maine, Brooks (1985) indicates two major flow paths: a nearshore flow along the western shore and onto the Nantucket Shoals, and an offshore flow which joins the jet-like current on the northern edge of Georges Bank. However, his findings clearly indicate flow is not continuous about the edge of the Gulf of Maine from Browns Bank to western Georges Bank. He further suggests (Brooks 1985) the

clockwise eddy that is found off Penobscot Bay over Jeffreys Bank may act to retain larval herring along the central coast of Maine, and interfere with an apparent southwestward "lobster flux" noted in tagging studies. A composite summary of the circulation based on the above discussions of Georges Bank, Browns Bank and the Gulf of Maine is presented in Fig. 2.

Wind Effects

While the residual circulation includes the general effect of winds on ocean currents, it cannot indicate the variable action of local wind on the near-surface water layers. Winds affect surface layers by causing vertical mixing and by creating a surface wind drift directed to the right (due to the coriolis force). Satellite-tracked drifters provide a means to estimate the path followed by passive particles, resulting from the combined effects of the mean circulation and local winds. Such drifters have been released on Georges and Browns Banks, with variable results. Butman et al. (1982) present results of several drifter experiments on Georges Bank. Drifters released on the northeast peak of the Bank showed a variety of trajectories, ranging from exits off the bank to the south, southwest, northwest (which then rejoined the jet current along the northern edge), and one which made a complete circuit of the bank before exiting to the northeast towards the shelf edge and then offshore. The major losses appeared to be to the south and offshore, which was presumed connected with the presence of warm-core rings.

P. Smith (pers. comm.) has also conducted drifter experiments on Browns Bank. He found similar variability, although most appeared to circulate about the bank for several days before exiting offshore, also likely in response to ring events. One buoy circled the bank for 65 days before crossing to Georges Bank in response to a strong southward wind.

Lawrence and Trites (1983) have used historical residual surface current data and offshore wind data (measured at Sable Island) to simulate the movement of oil released at various sites on Georges and Browns Banks. For oil released on the northeast peak of Georges in summer, the simulated trajectories indicate movement first to the southwest then around to the northeast, following the gyre circulation. Once on the northern edge of Georges, however, most trajectories left the bank and headed north towards the Bay of Fundy. Trajectories for oil released at this site in winter indicated movement predominantly to the south and east. The trajectories of oil released on Browns Bank in summer and winter indicated similar directions to those for Georges Bank. However, Lawrence and Trites (1983) noted two important assumptions in the construction of this model. It was realized the surface residual current already contains an effect of local winds, adding a further direct wind effect may overemphasize the influence of these winds. Secondly, they note the application of factors to convert wind speed to current speed work best for the top several centimetres of the water, which is acceptable for spilled oil but is not likely to represent the transport of particles deeper in the water column.

The above discussion indicates that winds can have an effect on the distribution and transport of fish eggs and larvae, even to the extent of

crossing from one circulation system to another. However, this effect will be most important at the surface and decreases rapidly with depth, so that drifters released at 10 m are also influenced by the mean circulation and hydrographic events such as rings. A patch of eggs or larvae would therefore be subject to this type of cross-bank transport most strongly as neuston, or perhaps during phases of vertical migration. However, this type of transport is highly erratic and variable, and it is difficult to conceive that a regular exchange of spawning products leading to formation of single stocks would be accomplished using such mechanisms.

Ichthyoplankton Studies

Several studies have examined ichthyoplankton distributions throughout the Gulf of Maine, and the potential for dispersal between Georges and Browns Banks. Walford (1938) examined the distribution of eggs and larvae of haddock on Georges Bank in 1931 and 1932, and the subsequent recruitment success. He found no evidence for any immigration of spawning products from other breeding grounds in either year. However, data from 1932 indicated the abundance of eggs and larvae was much reduced compared with 1931, which Walford (1938) suggested was a result of loss to deep water north and south of Georges Bank due to a different current regime.

Grosslein and Hennemuth (1973) considered the question of exchange of eggs and larvae of haddock between Georges and Browns Banks, particularly given evidence from commercial landings data that relative year-class strengths tend to be similar between these areas. They were unable to draw specific conclusions on this question, suggesting that similar year-class strengths could be a result of mixing during the larval phase, or common factors controlling survival over the entire area. However, they do present data suggesting that larvae on these two banks follow the general circulation (to the southwest on Georges and to the north on Browns), and thus are unlikely to mix to any great extent. Smith and Morse (1985), using data on haddock egg and larval distributions obtained from MARMAP surveys throughout the Gulf of Maine area from 1977 to 1982, were more definite in their conclusion that larvae originating on Georges Bank do not mix with those in the Gulf of Maine or from the western part of the Scotian Shelf.

Further information on dispersal of gadid eggs and larvae are gained from results of Fishery Ecology Program surveys to southwest Nova Scotia and the northeast peak of Georges Bank during spring 1983 and 1984. Results available to date are from monthly surveys covering the period February-June 1983 and February-May 1984, inclusive. In general, late stage eggs of cod and haddock (early stage eggs of these species cannot be distinguished) had similar distributions, although cod were more abundant and more widely distributed than haddock one survey earlier (i.e. about one month) in 1984, in agreement with suggestions that cod spawn earlier (O'Boyle et al. 1984; Sherman et al. 1984). Of particular note was the appearance of late stage cod and haddock eggs earlier on Georges than on Browns Bank (Fig. 3), which is consistent with the analysis of spawning times by Colton et al. (1979).

It is clear that both Georges and Browns Banks are active spawning grounds for cod and haddock, and the presence of late stage eggs

continuously on these banks from March to May implies a protracted spawning period (see also Colton et al. 1979). However, there was one cruise (April 1983) during which late stage haddock eggs occurred in the Northeast Channel, although abundances were less than those on the banks (10-100 m⁻²). Late stage cod eggs were not found in the Northeast Channel. In contrast, early stage eggs of cod and haddock did occur at stations across the Northeast Channel from February to April of both years. The station spacing was too coarse to determine unequivocally if these eggs were being advected between banks, or were part of the separate gyres about each bank. As discussed above, there are no residual currents connecting these banks; therefore, if this represents actual transport between banks, the eggs most likely were in the near-surface wind drift layer. Mean wind stress during spring (March, April, May) on Browns Bank is predominantly from the northwest at 0.35 dynes cm⁻² (Saunders 1977), which is roughly 5 m s⁻¹ or 10 knots (Bowden 1983). Assuming the simplest case of pure wind drift in a homogeneous water mass, the resulting current is directed southwestward with surface speeds about 8 cm s⁻¹ (0.15 knots), as calculated by:

$$U_s = \frac{0.0127 W}{(\sin o)^{\frac{1}{2}}}$$

where W is the wind speed (m s⁻¹) and o the latitude (Bowden 1983). Given a minimum distance of 30 nautical miles between 50-fathom contours across the Northeast Channel, a concentration of eggs at the surface would take 10 days to be advected from Browns to Georges under mean conditions, i.e. almost the entire egg period (Laurence and Rogers 1974). If this were the only transport of eggs between banks, we would not expect to find any early stage cod and haddock eggs in the Northeast Channel near Georges Bank; this is not the case, however.

In addition, the buoyancy of cod and haddock eggs declines with development, such that the center of mass of the vertical distribution of early stage haddock eggs on Browns Bank in 1985 was 13 m, while that of late stage eggs was 33 m (Ken Frank, MEL-BIO, pers. comm.). Such eggs may therefore spend only a week or so in the near-surface waters before sinking into the deeper, mean circulation. However, storms may be a more efficient mechanism causing advection of eggs between banks, for example, southeast winds greater than 40 knots would be able to transport near-surface eggs from Georges to Browns in 2 days. The frequency and intensity of such storms in this area is not well known at present. Therefore, while eggs (and to a lesser extent, larvae) may be exchanged between Browns and Georges Banks under mean conditions, it is more efficiently accomplished by storms. However, the sporadic nature of such storms makes this an unlikely mechanism to unite these banks in a single recruitment area.

Additional evidence for retention of larvae on Georges Bank and lack of exchange between areas is provided by Loder et al. (1982). They estimated a horizontal dispersion coefficient for the shallow, central part of Georges Bank, based on the seasonal increase of temperature. Their results suggest that from spring to fall, about 10% of an initial patch of larvae should still remain within the 43-m isobath after 2-3 months. Loder et al. (1982)

are careful not to suggest this is due to a specific retention mechanism, but to the purely physical process of horizontal dispersion.

Fisheries Ecology Program data suggest spawning of both cod and haddock may also occur in coastal areas off Shelbourne, N.S., Roseway Bank and, for cod only, near the shelf-break between Yarmouth, N.S. and the mouth of St. Marys Bay. Late stage cod eggs consistently occurred in this latter area on these surveys, even when concentrations to the south on Browns Bank were low, however, it is unclear if this represents a separate spawning area or the results of advection. When haddock eggs occurred off St. Marys Bay, it was later in the year (e.g. May 1984; Fig. 4b), and there appeared to be a continuous distribution of eggs north from Browns Bank, implying advection from this southern spawning ground. Surface bottle drifters released on Browns Bank have been recovered along this southwestern shore of Nova Scotia from 16-90 days later; certainly the shorter times are consistent with rates for eggs spawned on Browns Bank to reach the late egg stage, provided they are not held within the gyre.

In May of 1983 and 1984, significant concentrations of late stage cod and haddock eggs occurred on the Scotian Shelf east of Browns Bank (Fig. 4). Small spawning populations of haddock are found on the banks in this area (e.g. Baccaro, Roseway, Lahave Banks; K. Waiwood, Biological Station, St. Andrews, N.B., pers. comm.), but the extent to which eggs east of Browns Bank were produced in situ, or transported from other banks, is uncertain. Assuming mean current speeds to the southwest on this part of the Scotian Shelf of 5 cm s^{-1} in spring (Smith 1983) and an approximate egg development time for cod and haddock of two weeks (at ambient temperatures and salinities; Laurence and Rogers 1974), the eggs observed to the east of Browns Bank in May 1984 (Fig. 4) could have come from anywhere within an upstream distance of about 55 km. The distance between each of Roseway, Lahave and Baccaro Banks is 45 km, and between Baccaro and Browns it is 90 km, generally within the range of origin for these eggs. However, the extent to which eggs may be retained on top of these banks by possible gyre circulations is not known, as has been described for Browns and Georges Banks.

Harding et al. (1983) have studied lobster stocks and recruitment in the Gulf of Maine area and concluded, in contrast to the above studies, that all regions bordering on the Gulf of Maine gyre are within one lobster recruitment system. They suggest that southern Nova Scotia, the Bay of Fundy and coastal Maine are all supplied with advanced larval stages from the northern edge of Georges Bank, where offshore stocks move from deep to shallow water in summer to spawn. As evidence, they note apparent inconsistencies of temperature and growth rates of larvae off southwestern Nova Scotia, and a similarity of commercial landings from ports throughout the Gulf of Maine. However, as has already been noted by Grosslein and Hennemuth (1973), such similarity may be due to mixing of larvae or factors that control recruitment operating in a common manner across the entire region. In addition, Harding et al. (1983) used current speeds and directions from Bumpus and Lauzier (1965) to estimate larval drift. More recent evidence (discussed above), using in situ measurements as well as bottle drifter returns (the basis for the Bumpus and Lauzier (1965) pattern) indicate less likelihood of larvae being transported from Georges Bank to southwest Nova Scotia and along the coast of Maine to Cape Cod. Such

exchanges may occur occasionally, as indicated by the variability in trajectories of satellite-tracked drogues and the model results of Lawrence and Trites (1983), particularly if the larvae are distributed and remain in the surface water layer. However, it is unlikely that lobster stocks depend on such a sporadic mechanism to maintain one recruitment system in the Gulf of Maine. It may be that transport between areas can occur, for example, via a connection from the outside of the northern jet current on Georges Bank, to the loop current about Georges Basin and so to Browns Bank, but obviously more detailed observations on vertical distribution of the various larval stages, and sampling of larvae actually between banks, is required.

Acknowledgments

We wish to thank J. Loder for very useful discussions on the oceanography of the region, and for directing us to several of the literature sources. We also thank P. Smith and K. Frank for allowing us to use as yet unpublished data collected during the Fisheries Ecology Program.

Literature Cited

- Bigelow, H. B. 1927. Physical oceanography of the Gulf of Maine. Fish. Bull., U.S. 40: 511-1027.
- Bowden, K. F. 1983. Physical oceanography of coastal waters. Ellis Horwood, England.
- Boyar, H. C., R. R. Marak, F. E. Perkins, and R. A. Clifford. 1973. Seasonal distribution and growth of larval herring (Clupea harengus L.) in the Georges Bank-Gulf of Maine area from 1962 to 1970. J. Cons. int. Explor. Mer 35: 36-51.
- Brooks, D. A. 1985. Vernal circulation in the Gulf of Maine. J. Geophys. Res. 90(C3): 4687-4705.
- Bumpus, D. F. 1973. A description of the circulation of the continental shelf of the east coast of the United States. Progr. Oceanogr. 6: 111-157.
- Bumpus, D. F., and L. M. Lauzier. 1965. Surface circulation on the continental shelf of eastern North America between Newfoundland and Florida. Am. Geograph. Soc. Serial Atlas of the Marine Environment, Folio 7, 92 p.
- Butman, B., J. W. Loder, and R. C. Beardsley. In press. The seasonal mean circulation on Georges Bank: observation and theory. In Backus, R.H. (ed.) Georges Bank. MIT Press.
- Butman, B., R. C. Beardsley, B. Magnell, J. A. Vermersch, R. J. Schlitz, R. Limeburner, and M. A. Noble. 1982. The mean circulation on Georges Bank. J. Phys. Oceanogr. 12: 569-591.

- Colton, J. B., Jr., and J. L. Anderson. 1983. Residual drift 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., W. G. Smith, A. W. Kendall, Jr., P. L. Berrien, and M. P. Fahay. 1979. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. Fish. Bull., U.S. 76: 911-915.
- Greenberg, D. A. 1983. Modeling the mean barotropic circulation in the Bay of Fundy and Gulf of Maine. J. Phys. Oceanogr. 13: 886-904.
- Grosslein, M. D., and R. C. Hennemuth. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-v. Réun. Cons. int. Explor. Mer 164: 77-88.
- Gulland, J. A. 1983. Fish Stock Assessment. Wiley-Interscience, N.Y.
- Harding, G. C., K. F. Drinkwater, and W. P. Vass. 1983. Factors influencing the size of American lobster (Homarus americanus) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence and Gulf of Maine: a new synthesis. Can. J. Fish. Aquat. Sci. 40: 168-184.
- Laurence, G. C., and C. A. Rogers. 1974. 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.
- Lauzier, L. M. 1967. Bottom residual drift on the continental shelf area of the Canadian Atlantic coast. J. Fish. Res. Board Can. 24: 1845-1859.
- Lawrence, D. J., and R. W. Trites. 1983. Surface oil spill trajectory modelling for Georges and Browns Banks. Can. Tech. Rep. Hydrogr. Ocean Sci. 29: 30 p.
- Loder, J. W., and D. G. Wright. 1985. Tidal rectification and frontal circulation on the sides of Georges Bank. J. Mar. Res. 43: 581-604.
- Loder, J. W., D. G. Wright, C. Garrett, and B.-A. Juszko. 1982. Horizontal exchange on central Georges Bank. Can. J. Fish. Aquat. Sci. 39: 1130-1137.
- O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological and physiographic features. Rapp. P.-v. Réun. Cons. int. Explor. Mer 183: 27-40.
- Saunders, P. M. 1977. Wind stress on the ocean over the eastern continental shelf of North America. J. Phys. Oceanogr. 7: 555-566.

- Sherman, K., W. Smith, W. Morse, M. Berman, J. Green, and L. Ejsymont. 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production and pulses in zooplankton off the northeastern United States. *Mar. Ecol. Prog. Ser.* 18: 1-19.
- Smith, P. C. 1983. The mean and seasonal circulation off southwest Nova Scotia. *J. Phys. Oceanogr.* 13: 1034-1054.
- Smith, W. G., and W. W. Morse. 1985. Retention of larval haddock Melanogrammus aeglefinus in the Georges Bank region, a gyre-influenced spawning area. *Mar. Ecol. Prog. Ser.* 24: 1-13.
- Walford, L. A. 1938. Effects 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.

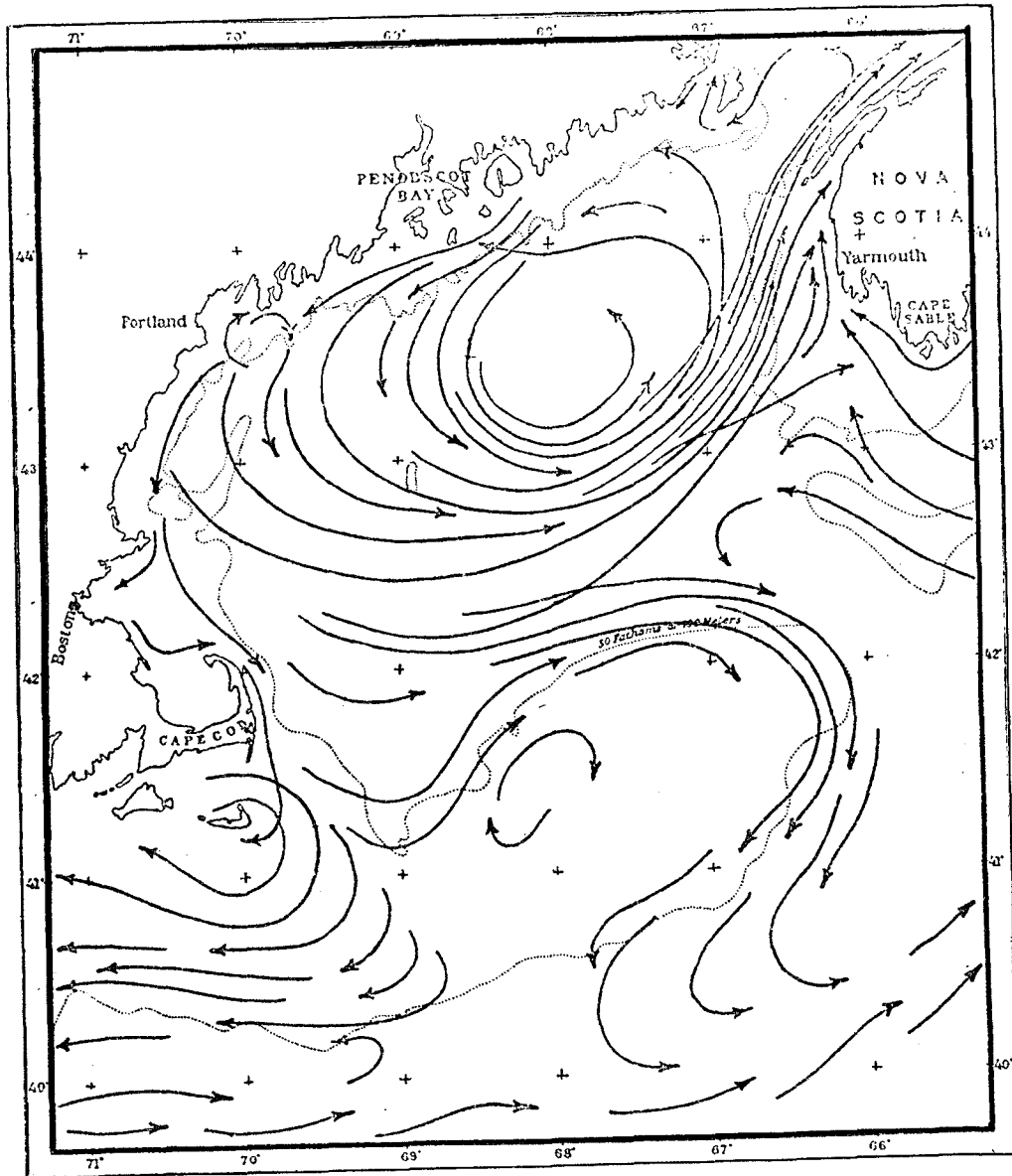


Fig. 1. General summer circulation of the Gulf of Maine area as proposed by Bigelow (1927).

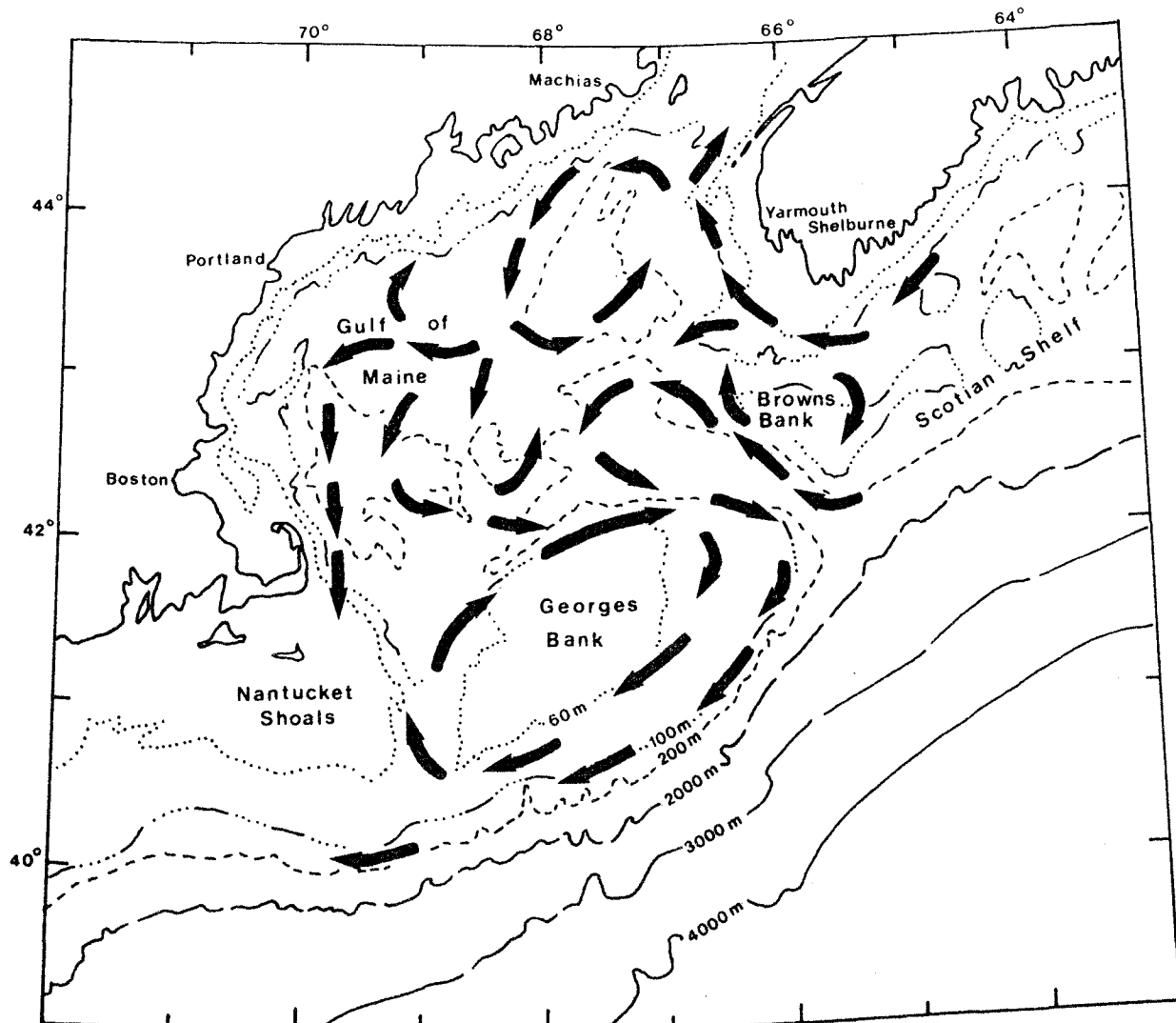


Fig. 2. Schematic representation of the spring circulation in the upper layers of the Gulf of Maine, Georges and Browns Banks, and southwest Nova Scotia; no current speeds are implied. Compiled from Brooks (1985), Smith (1983), and Butman et al. (1982).

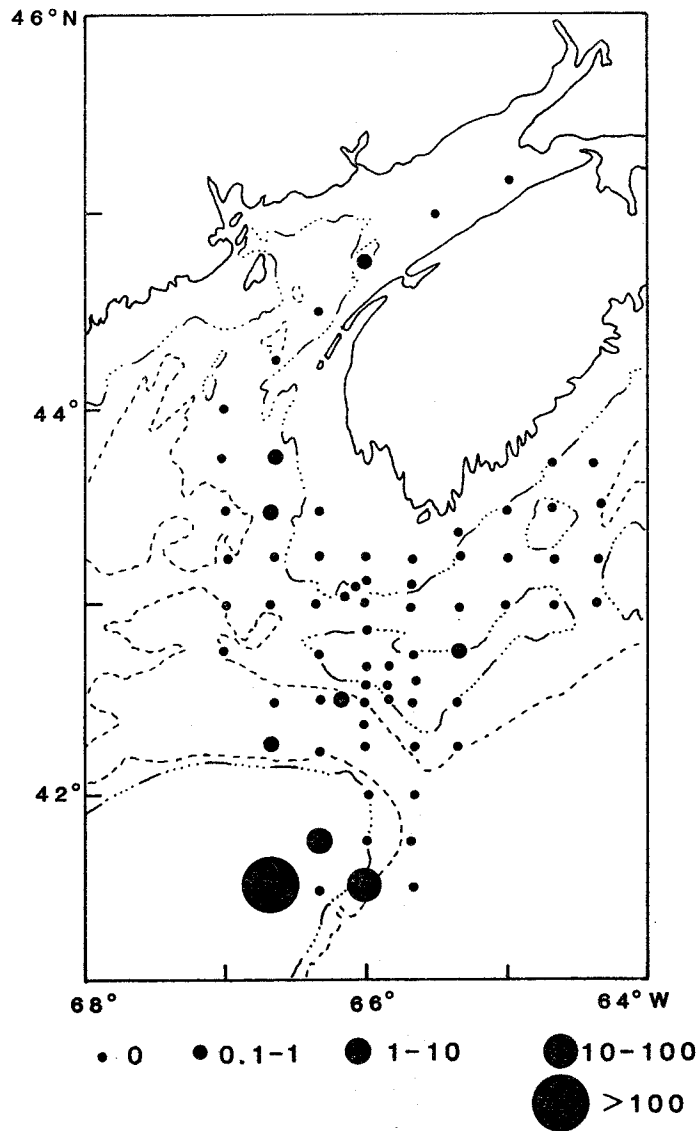


Fig. 3a. February 1984 cod egg distribution and abundance from Fisheries Ecology Program ichthyoplankton survey. Data as number m^{-2} , collected by oblique bongo tows.

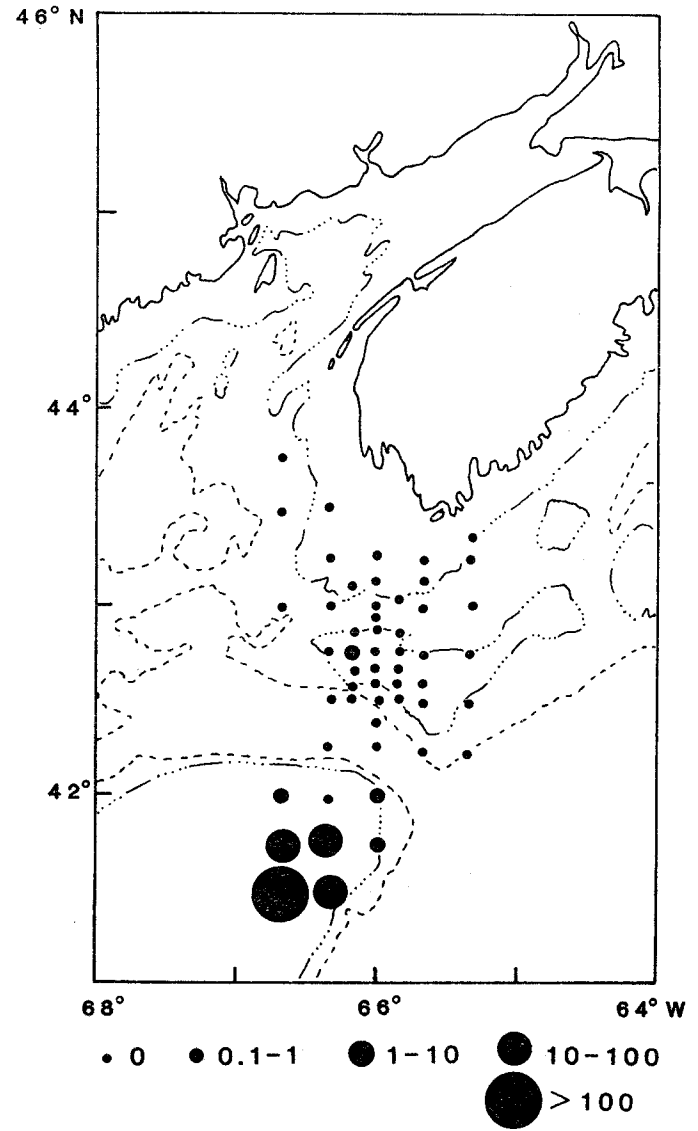


Fig. 3b. March 1984 haddock egg distribution and abundance from Fisheries Ecology Program ichthyoplankton survey. Data as number m^{-2} , collected by oblique bongo tows.

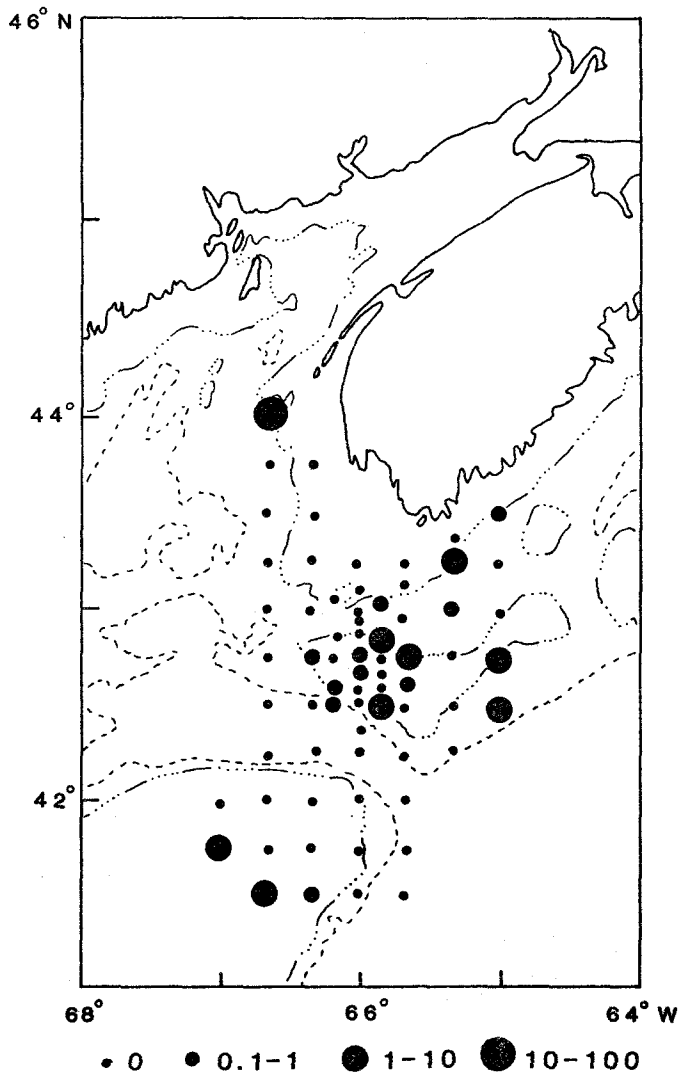


Fig. 4a. May 1984 cod egg abundance and distribution from FEP ichthyoplankton survey. Data as number m^{-2} , collected by oblique bongo tows.

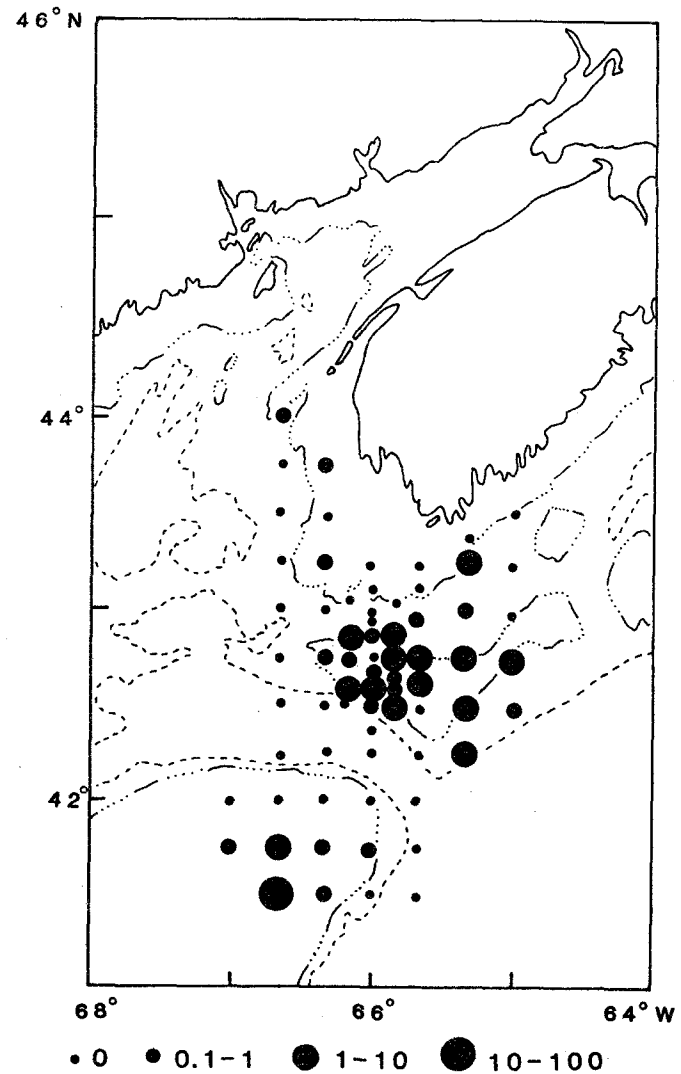


Fig. 4b. May 1984 haddock egg abundance and distribution from FEP ichthyoplankton survey. Data as number m^{-2} , collected by oblique bongo tows.