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Wind-Driven Currents and Larval Fish Survival

by

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Abstract

We test the hypotheses that the survival of fish eggs and larvae is reduced by wind-driven transport off the continental shelf. A simple Lagrangian model including Ekman dynamics and vertical migrating larvae is developed to determine the cross-shelf movement of eggs and larvae in a two-layer stratified ocean. Wind stress calculated from 6 hr geostrophic winds for 1946 to 1986 are used in the study. Vertical migration is simulated by moving larvae into and out of the mixed layer diurnally and is found to significantly reduce the chances of horizontal advection by Ekman transport. No relationships are found between simulated Ekman transport of eggs and larvae and subsequent recruitment in the 10 Northwest Atlantic stocks investigated.

1 INTRODUCTION

Wind stress is one of the most important driving forces for currents on continental shelves (see Allen 1980, Winant 1980, Csanady 1982, for reviews). In that physical processes can effect recruitment of marine fish species (Shepherd et al. 1985), it follows that changes in wind patterns may partially account for the observed recruitment variability of some fish stocks. The mechanisms through which wind may effect recruitment are many. Offshore Ekman transport driven by longshelf winds could carry eggs and larvae off the shelf where survival is poor. An alternative hypothesis is that onshore Ekman transport carries larvae to their inshore nursery grounds which improves their chances of survival. Near the coast during periods of offshore Ekman transport upwelling occurs, raising nutrient levels in the euphotic zone which may increase larval survival through enhancement of the food supply (Bakun 1985). The primary response to longshelf winds is downwind longshelf currents which may increase or decrease the advection of eggs and larvae from an area depending on the strength and direction of the mean flow. This process appears to be particular important in the California current (Chelton 1981). Available evidence indicates that cross-shelf winds are generally of secondary importance in driving shelf circulations (Allen 1980) and, therefore, their effect on recruitment is expected to be minimal except for eggs or larvae in the neuston. The turbulence produced by the wind, which scales as the cube of the wind stress, causes vertical mixing, thereby introducing nutrients into the euphotic zone and in turn this may enhance larval survival through increased primary production. On the other hand, mixing may lead to mechanical stress on the eggs and larvae or disperse the food source for the larvae (Bakun and Parrish 1982; Peterman and Bradford 1987), both of which would lower larval survival. Figure 1 summarizes these various effects of wind on eggs and larvae.

In this paper we restrict ourselves to an examination of wind-driven offshelf transport of eggs and larvae and its possibility as a source of interannual recruitment variability for several species off eastern Canada. Earlier studies off the eastern seaboard of the U. S. (Nelson et al. 1976) and off California (Bailey 1981) found evidence that interannual variation in marine fish recruitment is related to variations in wind-induced Ekman transport. Our approach has been to develop a simple Lagrangian model of egg and larval drift based on Ekman transport. Data-driven simulations of egg and larval transport are carried out for years between 1946 and 1986 for which recruitment data are available. We use the results from each year's simulation model and compare it with observed recruitment in that year. On each day during the spawning season, eggs are assumed to be released at a specific location on the shelf. The cross-shelf position of the eggs and larvae are then tracked for the duration of the egg and larval stages. Their trajectories are based on Ekman

Fig. 1

transport calculated from 6-hr geostrophic wind data. The result from each year's simulation is the integral of the paths for each individual day, weighted by the proportion of eggs estimated to be spawned that day.

The model is described in Section 2 of the paper, followed by a presentation of the model results in Section 3. In section 4 we compare the model with results with the recruitment time series. In the discussion we examine patterns of interspecific variability of larval strategies with respect to Ekman transport.

2 THE MODEL

2.1 Physical Considerations

A long, straight coastline is assumed parallel to the y-axis (Fig. 1) with a distance to the shelf-slope front of B . Beyond approximately 10 km from the shore, a longshelf wind stress produces Ekman transport (M_x) to the right of the wind of a magnitude given by

$$M_x = \frac{\tau_y}{\rho f}, \quad (1)$$

where f is the Coriolis parameter, τ_y is the y component of the wind stress, and ρ is the density of sea water. The momentum imparted by the wind stress is not evenly distributed over the entire water column but is limited to a surface frictional layer. If the upper layers are turbulent, the depth of this layer, h_e , is given by

$$h_e \approx \frac{0.4}{f} \left(\frac{|\bar{\tau}|}{\rho} \right)^{\frac{1}{2}}, \quad (2)$$

Stratification can restrict the downward transfer of wind-induced momentum and reduce the Ekman layer depth. Under stratified conditions the Ekman layer is generally confined to approximately the depth of the upper mixed layer, h . The cross-shelf velocity (u) in the Ekman layer is then estimated from

$$u = \frac{M_x}{h_e}, \quad \text{if } h_e \ll h, \quad (3)$$

$$u = \frac{M_x}{h}, \quad \text{if } h_e > h. \quad (4)$$

This is referred to as a slab model because the velocities are assumed to move uniformly within the layer. The results from such models compare well with observations (Gordon 1982).

Six-hr geostrophic winds for the period 1946 to 1986 were obtained from the Canadian Atmospheric Environment Service at the grid points on the Scotian and southern Labrador shelves (Fig. 2). The data are reliable estimates of the wind over the region (Swail et al. 1984); however, they have greater directional persistence than the measured surface winds. This is the most complete data set available. Unfortunately, the data from Jan. and Nov. 1981 and Jan.-June 1983 were missing. The geostrophic estimates were adjusted by applying a constant reduction of 20% in the wind speed and 20° cyclonic rotation (Swail, V., personal communication, AES, Burlington, Ontario). The wind stress ($\bar{\tau}$) was calculated from the adjusted winds using

$$\bar{\tau} = \rho_a c_d (|\bar{w}|) |\bar{w}| \bar{w}$$

where ρ_a is the density of air, \bar{w} is the wind velocity, and c_d is an empirically determined drag coefficient. We used a drag coefficient determined empirically by Large and Pond (1981), i.e.

$$10^3 c_d = \begin{cases} 1.14, & \text{if } 4 < |\bar{w}| < 10 \text{ms}^{-1}; \\ 0.49 + 0.65|\bar{w}|, & \text{if } 10 \leq |\bar{w}| < 26 \text{ms}^{-1}. \end{cases}$$

Two versions of the model were considered. In the first version we assumed that the depth of the mixed layer varied only seasonally, and calculated cross-shelf velocities from $u = M_x/h$. In the second version, we calculated cross-shelf velocities from Eq. 3 and 4. The first version is often a good approximation to velocities calculated using the wind-dependent Ekman layer depth (equation 3) particularly during periods of strong winds, or during the summer when the mixed layer is shallow and $h_e > h$. The annual variability in the depth of the upper mixed layer was estimated from monthly mean temperature and salinity data compiled by Drinkwater and Taylor (1982) for the Scotian Shelf (Fig. 3) and was fixed for all years. A similar seasonal mixed layer depth was estimated for the Labrador Shelf from data compiled by Drinkwater and Trites (1986). The use of fixed seasonal mixed layer depths may underestimate the cross-shelf current velocities in years of light winds and overestimate them during years of strong winds.

In the 2-dimensional model we are using, volume conservation requires that the cross-shelf Ekman transport must be balanced by an equal volume of water flowing in the opposite direction below the mixed layer. We assumed that the return flow (u^*) occurs uniformly below the mixed layer, i.e.

$$u^* = \frac{-uh}{D-h}, \quad (5)$$

where D is the depth of the shelf. On the Scotian Shelf, D was taken as the mean depth of the Shelf (115 m) and on the Labrador and northern Newfoundland shelves D was taken as a constant 200 m. The model of the return flow may not be correct. The compensating flow may occur in a much shallower zone such as a bottom Ekman layer or just below the mixed layer. Also on the shelves it is likely that the flow is 3-dimensional rather than 2-dimensional and that all or part of

Fig. 2

Fig. 3

the required return flow occurs on another portion of the shelf. Lacking the data to adequately resolve the problem we chose the simplest conceptual model.

2.2 Biological Considerations

Eggs are assumed to be spawned a distance A offshore. Let $x(t, s)$ be the distance from the coast of an egg or larvae spawned at time s which has drifted for a time t . If an egg or larvae remains in the upper mixed layer and away from the coast then

$$x(t, s) = A + \int_0^t u(t') dt', \quad (6)$$

since

$$x(0, s) = A.$$

and where $u(t)$ be the depth-averaged velocity of the upper mixed layer due to Ekman transport. When the egg or larvae are transported near to the coast, they are assumed to remain within the near-shore zone until under the influence of an offshore Ekman transport.

Many fish and crustaceans have larvae that undergo vertical migration below the upper mixed layer. In such cases we may rewrite (6) as

$$x(t, s) = A + \int_0^t \tilde{u}(t') dt', \quad (7)$$

where $\tilde{u}(t')$ is the velocity experienced by a vertically migrating larvae. We consider larvae that is below the mixed layer during the night and within the mixed layer at night. Therefore,

$$\tilde{u}(t) = \begin{cases} 0, & \text{if } x(t, s) = 0 \text{ and } u(t) \leq 0; \\ u(t), & \text{if } x(t, s) > 0 \text{ and } t \text{ is during the night;} \\ u^*(t), & \text{if } x(t, s) > 0 \text{ and } t \text{ is during the day.} \end{cases} \quad (8)$$

Two separate modeling exercises were carried out. First, we investigated the general seasonal and interannual variability of larval drift by calculating the time histories of the cross-shelf movement of eggs and larvae assuming spawning every day from 1946 to 1986. The spawning site was taken to be 100 km offshore. The number of spawning days for which eggs and subsequent larvae were retained within 50 and 100 km offshore of the spawning site were determined for 3 cases: (i) 30 d and (ii) 60 d drift without vertical migration and (iii) 60 d drift with vertical migration. Second, we investigated the response of specific stocks taking into account their season of spawning, their development rate, and whether they undergo vertical migration. The proportion of eggs and larvae retained within 50 and 100 km offshore of the spawning site were calculated as an index of Ekman transport.

The timing and distribution of seasonal spawning for 10 stocks (Table 1) in the Northwest Atlantic for which recruitment data was available were determined from (1) seasonal ichthyoplankton surveys (Sherman et al. 1984; O'Boyle et al. 1984; Markle and Frost 1985; and Bonnyman 1981) and (2) seasonal surveys of spawning activity (Liem and Scott 1966, Colton et al. 1979, Martin and Drewry 1978, Fitzpatrick and Miller 1979, Scott 1983, Sinclair and Tremblay 1984). Estimates of the length of the larval period were based upon laboratory data on the temperature dependent development times of eggs and larvae (Culliney 1974, Laurence 1974, Martin and Drewry 1978) and upon observed differences in the peak spawning activity and the period of peak larval abundance (Table 2). These estimates are crude; the data they were based upon were sometimes inconsistent. One source of uncertainty is the natural year-to-year variability in spawning times and developmental rates of larvae due, for example, to changes in the ambient water temperature. There is insufficient information, however, to calculate a different spawning function and larval duration for each year.

The vertical distribution of the eggs and larvae relative to the upper mixed layer were available from discrete-depth tow on ichthyoplankton surveys.

3 RESULTS

3.1 General Response

Offshelf Ekman transport occurs mainly in summer on the Scotian Shelf (Fig. 4) when the wind stress in directed primarily longshore (Thompson and Hazen 1983) and the mixed layer is shallowest. Larvae within the mixed layer in July would be transported beyond 100 km of their spawning site about 30% of the time. Those larvae that underwent vertical migration, however, were never transported beyond 100 km (Fig. 4).

The seasonal response of the larvae on the Labrador shelf to Ekman transport was similar to that of the Scotian shelf but of a reduced amplitude (Fig. 4c). This reduction is primarily due to the lower frequency of longshore winds producing offshelf Ekman transport. The offshelf transport in winter is less on the Labrador shelf because the predominant winds are from the northwest which drives onshore Ekman transport. There are few years when a larvae would be expected to reach 100 km offshore from its spawning site. Larvae that vertically migrate generally move only short distances in the offshore direction from where they spawn.

Table. 1

Table. 2

Fig. 4

The interannual variability in offshore transport of larvae in January and June is displayed in Fig 4. Transport is minimum in winter and maximum in the summer. Much of the summertime variation is on decadal time scales, e.g. there was a much greater probability of being transported offshore during the 1970's than in the 1950's.

The robustness of these conclusions to the choice of the depth over which the Ekman transport is distributed was tested by comparing the results using the mixed layer depth to one with a wind-dependent Ekman layer depth (equation 2.4). Little difference was found (Fig. 4) indicating our original choice of the mixed layer depth is an adequate approximation.

3.2 Specific Responses

The proportion of the larvae spawned that was retained within 50 and 100 km offshore of the spawning site for 10 stocks are shown in Table 3. We assumed cod and haddock do not vertically migrate below the mixed layer and in only one year were more than 50% of the larvae beyond 50 km offshore of the spawning location. These are overestimates of the effect of offshore transport because many cod and haddock larvae are found in the region of the pycnocline, which should reduce their offshore transport.

Table 3

If redfish larvae were in the upper mixed layer they would suffer large mortality from Ekman transport (Table 3), however, the available evidence indicates they are found in the region of the pycnocline. For the two stocks that vertically migrate only a small portion of the larvae are advected beyond 50 km. The larvae of argentine and American plaice, which do not spawn in the summer, should not be advected offshore.

4 EFFECTS ON RECRUITMENT

4.1 Statistical Methods

We now test whether offshore Ekman transport may be responsible for a significant portion of the observed variability in recruitment of various stocks. To do this we regressed recruitment indices against our Ekman transport estimates. The residuals from this regression are checked for autocorrelation using a Durbin-Watson test. One sided significance tests were used on each regression because we were testing the *a priori* hypothesis that offshore Ekman transport reduced larval survival. If autocorrelation in the residuals was significant at the 0.10 level, the regression was repeated using regression with autocorrelated residuals. As the assumptions of an ordinary least squares regression could not always be met, the analysis was repeated using a nonparametric methods. The test we used is the ordering test, which is equivalent to Kendall's rank correlation coefficient (Sokal and Rohlf 1981).

4.2 Recruitment Data

Time series of spawning stock biomass and recruitment data for 10 stocks (Table 1) came from research surveys and sequential population analysis. Sequential population analysis includes virtual population analysis (Gulland 1965), cohort analysis (Pope 1972), and related techniques which reconstruct populations from catch at age. Sequential population analysis tends to smear estimates of recruitment year classes together because of ageing errors, i.e. the year classes before and after a strong year class will be overestimated, and the strong year class will be underestimated. This problem also occurs for research vessel data, but to a much lesser extent.

The errors in estimating recruitment from research surveys will generally be less autocorrelated than the SPA, unless there is a change in survey methods or ageing errors are large. With the exception of the surveys for capelin abundance, which were from acoustic surveys, and silver hake from 4VWX, which were from directed larval surveys, all the research survey data came from bottom trawls. Ages of fish from the research vessel surveys were determined by otoliths except for argentine and redfish whose ages were estimated from length frequencies.

For several stocks there were reliable estimates of spawning stock biomass (Table 1). For these stocks, we attempted to remove the effect stock size by using the residuals from a stock recruitment relationship as the index of recruitment in the analysis. The stock recruitment we examined was

$$R = \alpha S^\beta$$

where R is the recruitment index, S is the estimate of spawning stock and α and β are the fitted parameters. The above function was fit using a linear regression of the logarithmically transformed data.

If a reliable spawning stock biomass was not available, then a square root transformation was applied to the recruitment data before the regression analysis.

4.3 Results

In no case was there a statistically significant relationship between recruitment and our Ekman transport indices.

5 DISCUSSION

Our model results suggest that Ekman transport does not strongly influence the survival of fish eggs and larvae and that larvae undergoing diurnal vertical migrations below the mixed layer have

a much restricted cross-shelf motion compared to those spending all their time in the upper mixed layer. In our model we assumed a 2-dimensional mass balance with the surface Ekman transport compensated by a return flow that is equally distributed in a lower layer extending from the bottom of the mixed layer to the ocean floor or 200m, whichever is less. As stated earlier, such a model may not be realistic. The return flow may occur in a shallow bottom Ekman Layer (Kundu 1977) or even elsewhere on the shelf, i.e. 3-dimensional effects may be important. Thus, the model may overestimate the influence of vertical migration by overestimating the strength of the lower layer return flow. It is clear, however, that vertical migration is likely to reduce the extent of the cross-shelf transport of larvae.

The physical component of our larval drift model is oversimplified, e.g. no consideration of longshelf drift, idealized vertical current structure, and a fixed seasonal variability in the depth of the mixed layer. Similarly the biological component was also simplified by fixing the spawning period and larval critical period. Therefore, care must be taken in interpreting the results. It is interesting to note, however, that our general conclusion of minimal larval drift due to Ekman transport is consistent with the findings of Power (1986) in a simulation model of Anchovy larvae off the California coast.

5.1 Among Species Comparisons

Offshelf Ekman transport is probably not an important source of the variability in recruitment because species have evolved adaptations to reduce its effect. One reason this is possible is that the season of offshelf Ekman transport is predictable (Fig. 4). Other sources of offshelf advection (e.g. Gulf Stream warm core rings) are not strongly correlated with the seasonal cycle. This is one reason which may explain the relative importance of Gulf Stream warm core rings for recruitment variability (Myers and Drinkwater 1986, in press).

There are several life history adaptations that will mitigate offshelf transport of eggs and larvae. For egg retention, Parrish et al. (1981) discuss the following strategies: ovoviviparous reproduction, anadromy, benthic eggs, spawning in seasons or locations with low probability of offshelf transport. For planktonic larvae there are fewer options; offshelf transport may be reduced if larvae are in a region of low offshelf transport, such as the pycnocline (Winant and Olson 1976; Kundu 1977), or if larvae vertically migrate.

We should thus expect vertical migration and residence in the region of the pycnocline to be common in regions and seasons with large offshelf transport. We predict that residence in the mixed layer for long periods of time should be rare in such regions.

We compiled data on the vertical distribution, spawning season (high or low transport) and predominant spawning locations (slope, shelf, inshore) to test this hypothesis (Table 4). Conclusions from different studies were not always consistent. We have identified ambiguities where they occur. These categories are not meant to be exhaustive, i.e. some species appear to migrate diurnally within mixed layer (Kendall and Naplin 1981). Furthermore, the data on vertical migration is confounded by net avoidance during the day.

There are four species whose larvae are resident in the mixed layer and vertically migrate; two of these spawn during the summer, when offshelf Ekman transport is large, and two spawn in other seasons (Table 4). This is not consistent with our above hypothesis. The adults of these four species are pelagic and wide-ranging. Pelagic species may be less susceptible to loss from the population if advected off the shelf.

The three species from the Atlantic coast spawn on the slope (redfish, argentine, and Atlantic halibut) have adaptations which reduce offshelf transport, i.e. they are ovoviviparous or the eggs are in the region of the pycnocline.

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7 Figure legends

Fig. 1. Possible effects of wind on larval fish survival.

Fig. 2. Regions used in the analysis and the location of the grid where the Ekman transport indices were calculated.

Fig. 3. Depth of mixed layer for the Scotian shelf.

Fig. 4. Results of model predictions for the proportion of larvae retained within 50 km (—) and 100 km (---) offshore. The seasonal model is the average proportion transported beyond the range from 1946 to 1986. In all cases the months refer to the month the eggs or larvae began drifting. Scotian shelf with seasonal mixed layer depth (a), Scotian shelf with variable Ekman depth (b), and Labrador shelf with seasonal mixed layer depth (b).

References

- Allen, J. S. 1980. Models of wind-driven currents on the Continental Shelf. *Ann. Rev. Fluid Mech.* 12: 389-433.
- Bailey, K. M. 1981. Larval transport and recruitment of Pacific hake Merluccius productus. *Marine Ecology Progress Series* 6: 1-9.
- Bakun, A., Comparative studies and the recruitment problem: searching for generalizations. *California Cooperative Oceanic Fisheries Investigations Reports* 26: 30-41.
- Bakun, A., and R. H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru current systems. *California Cooperative Oceanic Fisheries Investigations Reports* 23: 99-112.
- Blaxter, J. H. S., 1973. Monitoring vertical movements and light responses of herring and plaice larvae. *J. Biol. Ass. U.K.*, 53: 635-647.
- Boehlert, G. W., D. M. Gadowski, and B. C. Mundy, 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. *Fishery Bulletin*: 83: 611-621.
- Bonnyman, S. 1981. Ichthyoplankton of the Grand Banks of Newfoundland. Section VI of Grand Banks Oceanographic Studies. Mobil Oil Canada Limited.
- Chelton, D. G. 1981. Interannual variability of the California current - physical factors. *California Cooperative Oceanic Fisheries Investigations Reports*. 22: 34-49.
- Churchill, J. H., Cornillon, P. C., and G. W. Milkowski. 1986. A cyclonic eddy and shelf-slope water exchange associated with a Gulf Stream warm-core ring. *J. Geophys. Res.* 91: 9615-9623.
- Colton, J. B. 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 drift and residence time of Georges Bank surface waters with reference to the distribution, transport, and survival of larval fishes. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/NEC-24.
- 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.* 76: 911-915.
- Cox, D.R. 1975. A note on data-splitting for the evaluation of significance levels. *Biometrika* 62: 441-444.
- Csanady, G. T. 1982. *Circulation in the coastal ocean*. D. Reidel Publishing Co., Dordrecht. 279 p.
- Drinkwater, K. F., and R. A. Myers. 1987. Testing predictions of marine fish and shellfish landings from environmental variables. *Can. J. Fish. Aquat. Sci.* 44: 1568-1573.
- Drinkwater, K., and G. Taylor. 1982. Monthly means of the temperature, salinity and density along the Halifax Section. *Can. Tech. Rep. Fish. Aquat. Sci.* 1093: 67 p.
- Drinkwater, K. F., and R. W. Trites. 1986. Monthly means of temperature and salinity in the Grand Banks region. *Can. Tech. Rep. Fish. Aquat. Sci.* 1450: 111 p.
- Drinkwater, K. F., and R. W. Trites. 1987. Monthly means of temperature and salinity in the Scotian Shelf region. *Can. Tech. Rep. Fish. Aquat. Sci.* 1539: iv + 101 p.
- Ellertsen, B., P. Solemdal, S. Sundby, S. Tilseth, T. Westgard, and V. Øiestad, 1981. Feeding and Vertical Distribution of Cod Larvae in Relation to Availability of Prey Organisms. *Rapp. P.-v. Reun. Cons. int. Explor. Mer*, 178: 317-319.
- Ellertsen, B., P. Fossu, P. Solemdal, S. Sundby, and S. Tilseth, 1984. A Case Study on the Distribution of Cod Larvae and availability of Prey Organisms in Relation to Physical Processes in Lofoten. *Flødevigen rapportser.*, 1, 1984. ISSN 0333-2594 The Propagation of Cod Gadus Morhua. pp. 453-477.
- Fahay, M. P., 1974. Occurrence of silver hake, Merluccius bilinearis, eggs and larvae along the middle Atlantic continental shelf during 1966. *Fish. Bull.*, U.S. 72: 813-834.
- Fish and Wildlife Service, U.S. Department of the Interior. 1978. *Development of fishes of the mid-Atlantic bight, An atlas of egg larval and juvenile stages*. 6 volumes.
- Fisher, R. A. 1954. *Statistical methods for research workers*. 12th ed. Oliver and Boyd, Edingburgh. 356 p.

- Fitzpatrick, C., and R. J. Miller. 1979. Review of spawning times and locations for some commercial finfish on the Newfoundland and Labrador coasts. Fish. Mar. Serv. Tech. Rep. 905: v + 14 p.
- Frank, K. T., and J. E. Carscadden. 1987. Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic. ICES C.M.1987/Mini No. 1. 30 p.
- Fritzsche, R. A.. 1978. Development of fishes of the mid-Atlantic bight. Vol. V. (Sculpin) Cottidae p. 247-254 and (Mackerel) Scombridae p. 63-167.
- Gordon, R. L. 1982. Coastal ocean response to storm winds. 87(3): 1939-1951.
- Gulland, J. A. 1965. Estimation of mortality rates. Annex to Rep. Arctic Fish. Working Group, ICES C.M.1965(3). 9 p.
- Harding, G. C., W. P. Bass, B. T. Hargrave, and S. Pearre, Jr. 1986. Diel vertical movements and feeding activity of zooplankton in St. George's Bay, N.S., using net tows and a newly developed passive trap. Can. J. Fish. Aquat. Sci. 43: 952-967.
- Hardy, J. D., 1978. Development of fishes of the mid-Atlantic bight. Vol. II. (*Gadidae*) p. 219-323 and (*Merlucciidae*) p. 327-337. Vol. III Bluefish (*Pomatomidae*) p. 339-353.
- Hardy, J. D., 1978. Family *Gadidae*: (*Gadus morhua*) Linnaeus, Atlantic cod. In Development of fishes of the Mid-Atlantic Bight, an atlas of egg, larval and juvenile stages. Vol II, p. 236-259. U.S. Dep. Inter., Fish Wildl. Serv.
- Haug, T., E. Kjærsvik, and P. Solemdal, 1984. Vertical distribution of Atlantic Halibut (*Hippoglossus hippoglossus*) eggs. Can. J. Fish. Aquat. Sci. 41: 798-804.
- Jones, P. W., F. D. Martin, and J. D. Harding, Jr. 1978. Development of fishes of the mid-Atlantic bight. Vol. I. (Herring) *Clupeidae* p. 75-150.
- Kelly, G. F. and A. M. Barker, 1961. Vertical distribution of young redfish in the Gulf of Maine. rapp. Cons. Explor. Mer., 150: 20-233.
- Kendall, A. W. and N. A. Naplin, 1981. Diel-depth distribution of summer ichthyoplankton in the middle Atlantic bight. Manuscript accepted May 1981. Fishery Bulletin: Vol. 79, No. 4. 705-726.
- Koslow, J. A. 1984. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 41: 1722-1729.
- Kundu, P. K. 1977. On the importance of friction in two typical continental waters: Off Oregon and Spanish Sahara. In, Bottom Turbulence. Proc. 8th Liege Colloq. Ocean Hydrodyn., ed. J. Nihoul. New York: Elsevier. 187-207.
- Large, W. F., and S. Pond. 1981. Open ocean momentum flux measurements in moderate to strong winds. J. Phys. Oceanogr. 11: 324-336.
- 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(3): 220-228.
- Laurence, G. C. 1978. Comparative growth, respiration and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar. Biol. 50: 1-7.
- Leim, A. H., and W. B. Scott. 1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can. Bull. 155: 1-485.
- Loder, J. W., C. K. Ross, and P. C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the Northwestern Atlantic Continental Shelf. Can. J. Fish. Aquat. Sci. (In Press).
- Markle, D. F., D. A. Methven, and L. J. Coates. 1982. Aspects of spatial and temporal cocurrence in the life history stages of the sibling hakes, *Urophycis chuss* (Walbaum 1792) and *Urophycis tenuis* (Mitchill 1815) (*Pisces: Gadidae*). Can. J. Zool. 60: 2057-2078.
- Markle, D. F., and L. A. Frost. 1985. Comparative morphology seasonality, and a key to planktonic fish eggs from the Nova Scotian shelf. Can. J. Zool. 63: 246-257.
- Martin, F. and G. E. Drevry, 1978. Development of fishes of the mid-Atlantic bight. Vol. VI. (Butterfish) *Stromateidae* p. 15-25. (Flatfishes) *Bothidae* p. 125-174 and *Pleuronectidae* p. 177-200. (Goosefish) *Lophiidae* p. 357-366. Glade, J. M., 1983.
- Miller, D., J. B. Colton, Jr., and R. R. Marak, 1963. A study of the vertical distribution of larval haddock. J. Cons. 28: 37-49.

- Myers, R. A., and K. Drinkwater. 1986. The effects of entrainment of shelf water by warm core rings on Northwest Atlantic fish recruitment. ICES C.M.1986/C:13. 18 p.
- Mysak, L. A. 1986. El Nino, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43: 464-497.
- Nelson, W. R., M. C. Ingham, and W. E. Schaaf. 1976. Larval Transport and Year-Class Strength of Atlantic Menhaden, Brevoortia Tyrannus. Fishery Bulletin: Vol. 75, No. 1, p. 23-41.
- 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.
- Parrish, R. H., and A. D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. California Department of Fish and Game Fish Bulletin 167.
- Farrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanography, Vol. 1: 175-202.
- Peterman, R. M., and M. J. Bradford. Wind speed and mortality rate of a marine fish, the northern anchovy (Engraulis mordax). Sci. Vol. 235: 354.
- Petrie, B., and C. Anderson. 1983. Circulation on the Newfoundland continental shelf. Atmos.-Ocean 21: 207-226.
- Petrie, B., and A. Isenor. 1985. The near-surface circulation and exchange in the Newfoundland Grand Banks regions. Atmos.-Ocean 23: 209-227.
- Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. ICNAF Res. Bull. 9: 65-74.
- Power, J. H. 1985. A model of the drift of northern anchovy, Engraulis mordax, larvae in the California Current. Fish. Bull. Vol. 84: 585-603.
- Sameoto, D. D., 1984. Environmental factors influencing diurnal distribution of zooplankton and ichthyoplankton. Journal of Plankton Research, Vol. 6, No. 5. p. 767-792.
- Scott, J. S. 1983. Inferred spawning areas and seasons of groundfishes on the Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 1219: iii + 14 p.
- Shepherd, J. G., J. G. Pope, and R. D. Cousens. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp P.-v. Réun. Cons. int. Explor. Merc. 185: 255-267.
- 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.
- Silverman, M.J. 1985. Distribution, abundance, and production estimates of Yellowtail Flounder, Limanda ferruginea, larvae off northeastern United States, 1982-1984. ICES C.M.1985/L:18.
- Sinclair, M. and M.J. Tremblay. 1984. Timing of spawning of Atlantic herring (Clupea harengus harengus) populations and the match-mismatch theory. Can. J. Fish. Aquat. Sci. 41: 1055-1065.
- Sissenwine, M. P. 1984. Why do fish populations vary?, p. 59-94. In R. M. May [ed.] Exploitation of marine communities. Dahlem Konferenzen. Springer-Verlag, Berlin.
- Smith, W. G., J. D. Sibunka, and A. Wells, 1978. Diel movements of larval yellowtail flounder, Limanda Ferruginea, determined from discrete depth sampling. Manuscript accepted June 1977. Fishery Bulletin: Vol. 76, No. 1.
- Smith, P. C. 1983. The mean and seasonal circulation off southwestern Nova Scotia. J. Phys. Oceanogr. 13: 1034-1054.
- Smith, P. C., and B. D. Petrie. 1982. Low-frequency circulation at the edge of the Scotian Shelf. J. Phys. Oceanogr. 12: 28-46.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, San Francisco. 859 p.
- Southward, A.J., and B. McK. Bary, 1980. Observations on the Vertical Distribution of Eggs and Larvae of Mackerel and other Teleosts in the Celtic Sea and on the Sampling Performance of different Nets in relation to Stock Evaluation. J. mar. biol. Ass. U.K., 60: 295-311.

- Swail, V. R., L. D. Mortsch, and D. A. Carr. 1984. Intercomparison of marine wind data sets. Canadian Climate Centre Report No. 84-15. Atmospheric Environment Service, Downsview, Ontario.
- Templeman, W. 1972. Year-class success in some North Atlantic stocks of cod and haddock. ICNAF Spec. Publ. 8: 223-239.
- Thompson, K. R., and M. G. Hazen. 1983. Interseasonal changes of wind stress and Ekman upwelling: North Atlantic, 1950-80. Can. Tech. Rep. Fish. Aquat. Sci. No. 1214: 175 p.
- Thompson, K. R., and F. H. Page. In Press. Detecting synchrony of recruitment using short autocorrelated time series. Can. J. Fish. Aquat. Sci.
- Winant, C. D. 1980. Coastal circulation and wind-induced currents. Ann. Rev. Fluid Mech. 12: 271-301.
- Winant, C. S. and J. R. Olson. 1976. The vertical structure of coastal currents. Deep-Sea Res. 23: 925-936.
- Wood, R. J., 1971. Some observations on the vertical distribution of herring larvae. Rapport et procès-verbaux des réunions. Conseil international pour l'exploration de la mer, 160, 60-64.
- Wright, D. G., D. A. Greenberg, J. W. Loder, and P. C. Smith, 1986. The steady-state barotropic response of the Gulf of Maine and adjacent regions to surface wind stress. J. Phys. Oceanogr. 16: 947-966.

Table 1. Recruitment data used in the analysis. The location of the stock is given by the North Atlantic Fisheries Organization (NAFO) designation. The method used to obtain the recruitment data is from Sequential Population Analysis (SPA) or from research vessel (RV) surveys. For the RV surveys, the ages that were used for the analysis are given in parenthesis. The data sources are: NAFO Scientific Research Council Documents or Canadian Atlantic Scientific Advisory Committee (CAFSAC) Research Documents.

NAFO	Years	Method	Source
<i>Cod (Gadus morhua)</i>			
2J3KL	58-81	SPA	Baird and Bishop, CAFSAC Res. Doc. 87/42
4VsW	57-85	SPA	Sinclair and Smith, CAFSAC Res. Doc. 87/72
4X	47-83	SPA	Campana and Sinclair, CAFSAC 87/30
<i>Haddock (Melanogrammus aeglefinus)</i>			
4VW	47-84	SPA	Zwanenburg and Fanning, CAFSAC Res. Doc. 87/103
4X	61-84	SPA	O'Boyle and Wallace, CAFSAC Res. Doc. 87/101
<i>Redfish (Sebastes sp.)</i>			
4VWX	69-85	RV(1+2)	Zwanenburg and Hurley, CAFSAC Res. Doc. 87/35
<i>American Plaice (Hippoglossoides platessoides)</i>			
4V	66-84	RV(3+4)	Neilsen and Perley, CAFSAC 86/48
<i>Silver Hake (Merluccius bilinearis)</i>			
4VWX	69-83	SPA	Fanning et al., NAFO SCR Doc. 87/56
<i>Herring (Clupea harengus)</i>			
4WX	64-84	SPA	Stephenson et al., CAFSAC 87/75
<i>Argentine (Argentina silus)</i>			
4VWX	68-83	RV(2)	Dale and Halliday, CAFSAC Res. Doc. 87/19

Table 2. The proportion of eggs that were assumed to be spawned in each month. Cod from NAFO divisions 4VsW and 4X begin to spawn November and December of the year previous to their nominal year class.

NAFO	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cod														
2J3KL	0	0	0	0	.50	.50	0	0	0	0	0	0	0	0
4VsW	.30	.30	.25	.15	0	0	0	0	0	0	0	0	0	0
4X	0	.15	.15	.05	.40	.20	.05	0	0	0	0	0	0	0
Haddock														
4VW	0	0	0	0	.10	.40	.40	.10	0	0	0	0	0	0
4X	0	0	0	.10	.35	.50	.05	0	0	0	0	0	0	0
Redfish														
4VWX	0	0	0	0	0	0	.05	.30	.30	.30	.05	0	0	0
American Plaice														
4VWX	0	0	0	0	.25	.25	.25	.25	0	0	0	0	0	0
Silver Hake														
4VWX	0	0	0	0	0	0	.05	.15	.30	.30	.15	.05	0	0
Herring														
4WX	0	0	0	0	0	0	0	0	0	.80	.20	0	0	0
Argentine														
4WX	0	0	0	0	.33	.34	.33	0	0	0	0	0	0	0

Table 3. The proportion of larvae from 1946-1986 advected a distance B from the shore if larvae are spawned a distance A from the shelf. The assumed critical period, T_{crit} , and whether the larvae are assumed to undergo vertical migration (V.M.) is also given. The spawning period is given in Table 2. See text for details.

NAFO	Assumptions				Proportion Advected			
	A	B	T_{crit}	V.M.	$P < 50$	$50 \leq P < 80$	$80 \leq P < 95$	$95 \leq P$
Cod								
2J3KL	160	210	60		0	0	3	97
4VsW	160	260	45		0	0	0	100
4VsW	160	210	45		3	28	8	63
4X	160	260	45		0	0	0	100
4X	160	210	45		3	5	18	74
Haddock								
4VW	160	260	45		0	0	8	92
4VW	160	210	45		0	20	50	30
4X	160	260	45		0	0	0	100
4X	160	210	45		0	7	5	88
Redfish								
4VWX	160	210	50		72	10	5	13
American Plaice								
4VWX	160	260	50		0	13	2	85
Silver Hake								
4VWX	160	210	30	yes	0	0	0	100
Herring								
4WX	160	260	90	yes	5	5	0	90
Argentine								
4VWX	160	260	50		0	0	0	100

TABLE 4. Spawning location, egg strategies, and larval strategies, for species on the East and West Coasts of North America. Egg strategies have been classified as resident in the region of the pycnocline (PY.), resident in the mixed layer (M.L.), Benthic (B.), or ovoviviparous (OVI.). The same classification applies to the larval stage; however, only three of the categories are relevant.

Scientific Name	Common Name	Spawning	Egg Strategy	Larval Strategy	References
MID ATLANTIC BIGHT TO SCOTIAN SHELF (FALL/WINTER/SPRING)					
<i>Argentina silus</i>	Atlantic argentine	slope	PY.	?	Southward & Bary 1980
<i>Auxis</i> sp.	Frigate mackerel	shelf	?	M.L.	Kendall & Naplin 1981, Fritzsche 1978
<i>Ammodytes</i> sp.	Sand lance	shelf	B.	V.M.	Sherman et al. 1984, Fritzsche 1978
<i>Brevortia tyrannus</i>	Atlantic menhaden	shelf	M.L.	M.L.?	Hardy 1978, Nelson et al. 1977
<i>Clupea harengus</i>	Atlantic herring	shelf	B.	V.M.	Jones et al. 1978, Wood 1971
<i>Gadus morhua</i>	Atlantic cod	shelf	M.L.	PY. ML?	Hardy 1978, Lough 1984
<i>Melanogrammus aeglefinus</i>	Haddock	shelf	M.L.	PY. ML?	Hardy 1978, Miller et al. 1963, Lough 1984
<i>Myoxocephalus octodecemspinosus</i>	Longhorn sculpin	inshore	?	V.M.	Coitton et al. 1979, Fritzsche 1978
MID ATLANTIC BIGHT TO SCOTIAN SHELF (SUMMER [UPWELLING])					
<i>Citharichthys arctifrons</i>	Gulf Stream flounder	shelf	M.L.	V.M.	Kendall & Naplin 1981, Markle & Frost 1984,
<i>Glyptocephalus cynoglossus</i>	Witch flounder	shelf	pelagic	V.M.	Sameoto & Lewis 1979, Martin & Drewry 1978
<i>Paralichthys oblongus</i>	Fourspot flounder	shelf	M.L.	V.M.	Kendall & Naplin 1981, Martin & Drewry 1978
<i>Hippoglossus hippoglossus</i>	Atlantic halibut	slope	PY.	?	Haug et al. 1984
<i>Limanda ferruginea</i>	Yellowtail flounder	shelf	M.L.	V.M.	Martin & Drewry 1978, Smith et al. 1977,
<i>Merluccius bilinearis</i>	Silver hake	shelf	M.L.	PY., V.M.	Kendall & Naplin 1981, Sameoto & Lewis 1979
<i>Scomber scombrus</i>	Atlantic mackerel	shelf	M.L.	M.L.	Murray et al. 1983, Liem & Scott 1966
<i>Scophthalmus aquosus</i>	Windowpane flounder	shelf	pelagic	V.M.	Markle & Frost 1984, Sameoto 1984
<i>Sebastes</i> spp.	Redfish	slope	OVO.	PY.	Sameoto & Lewis 1979, Kelly & Barker 1961
<i>Tautoglabrus adspersus</i>	Cunner	inshore	M.L.	V.M.	Fritzsche 1978, Harding et al. 1986
<i>Urophycis chuss</i>	Red hake	?	?	PY.M.	Markle et al. 1982
<i>Urophycis tenuis</i>	White hake	shelf	pelagic	PY.M.	Hardy 1978, Markle et al. 1982
<i>Etropus microstomus</i>	Smallmouth flounder	inshore	M.L.	V.M.	Kendall & Naplin 1981, Martin & Drewry 1978
<i>Glyptocephalus cynoglossus</i>	Witch flounder	inshore	pelagic	V.M.	Sameoto & Lewis 1979, Martin & Drewry 1978
<i>Peprilus triacanthus</i>	Butterfish	shelf	M.L.	V.M.	Kendall & Naplin 1981, Martin & Drewry 1978
<i>Pomatomus saltatrix</i>	Bluefish	shelf	M.L.	M.L.	Kendall & Naplin 1981, Hardy 1978

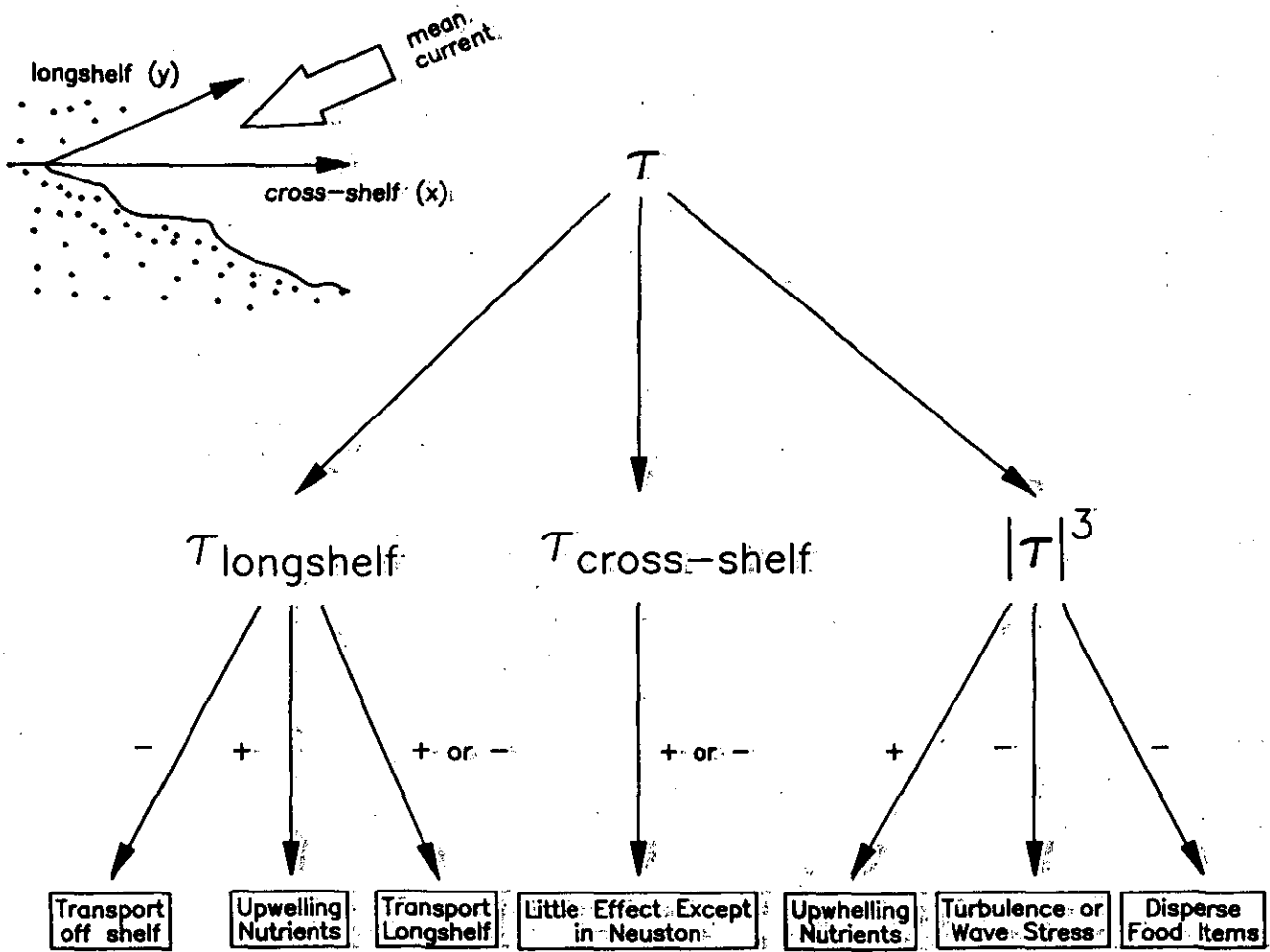


Fig. 1. Possible effects of wind on larval fish survival.

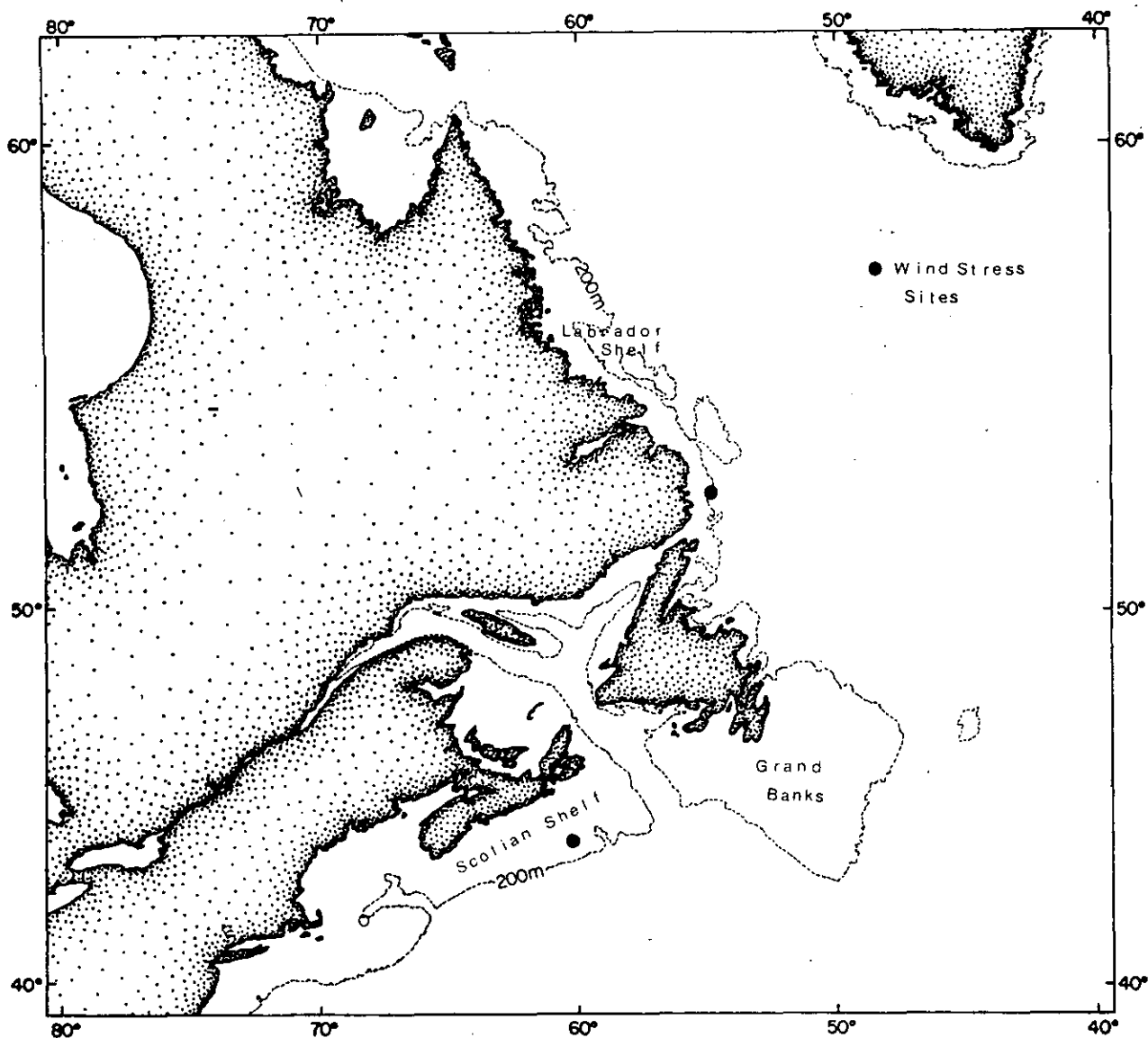


Fig. 2. Study region showing the location of the wind stress sites where Ekman transport indices were calculated.

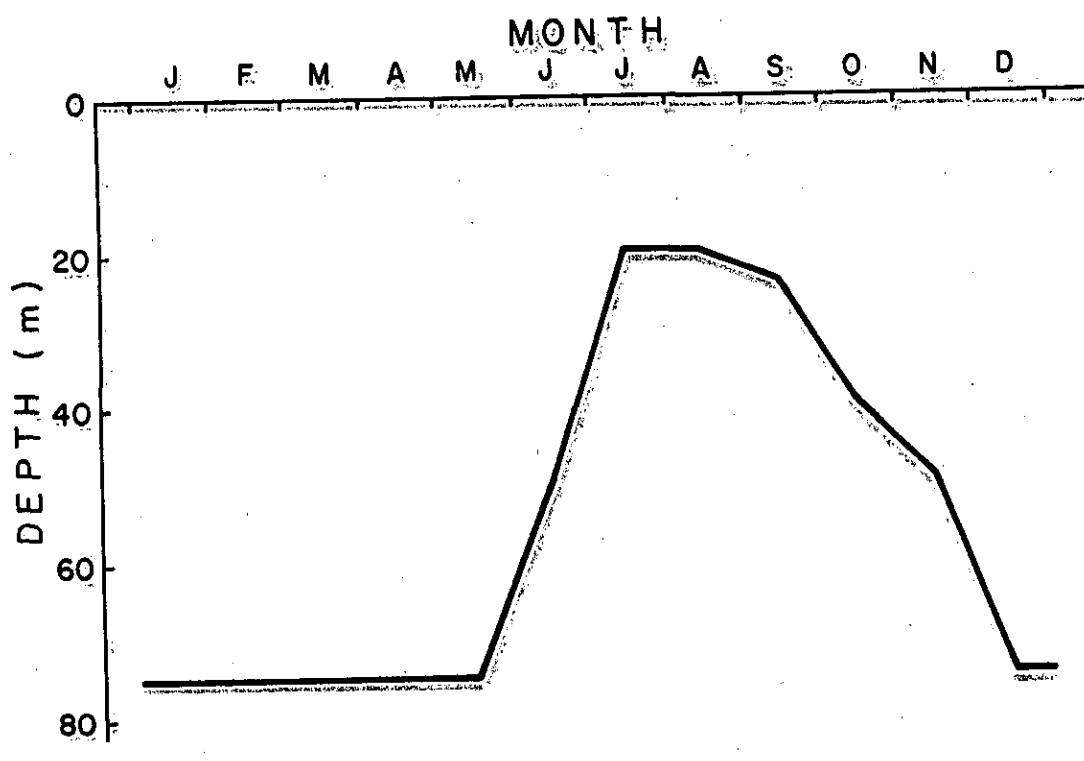


Fig. 3. Mixed layer depth.

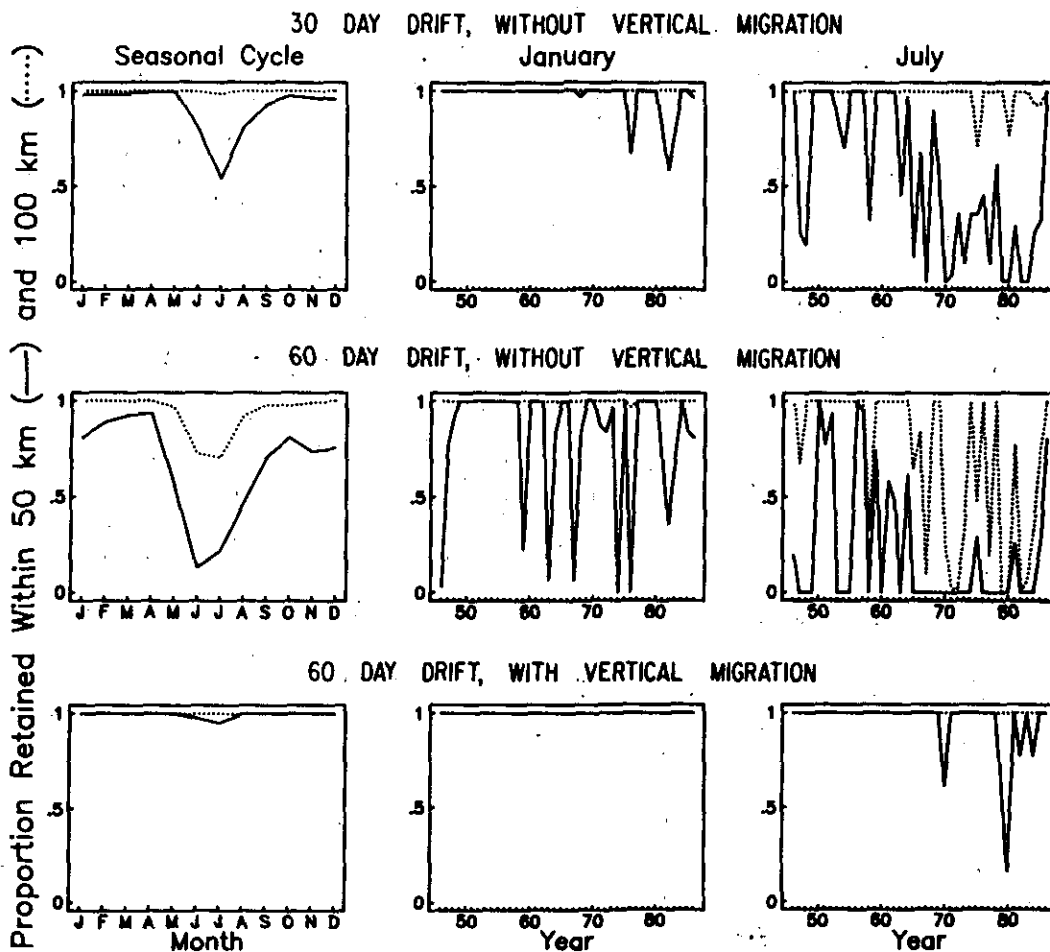


Fig. 4a. Model predictions for the proportion of larvae retained within 50 km (—) and 100 km (...) offshore. The seasonal model is the average proportion transported beyond the range from 1946 to 1986. In all cases the months refer to the month the eggs or larvae began drifting. The results are for the Scotian Shelf using the seasonal mixed layer depth.

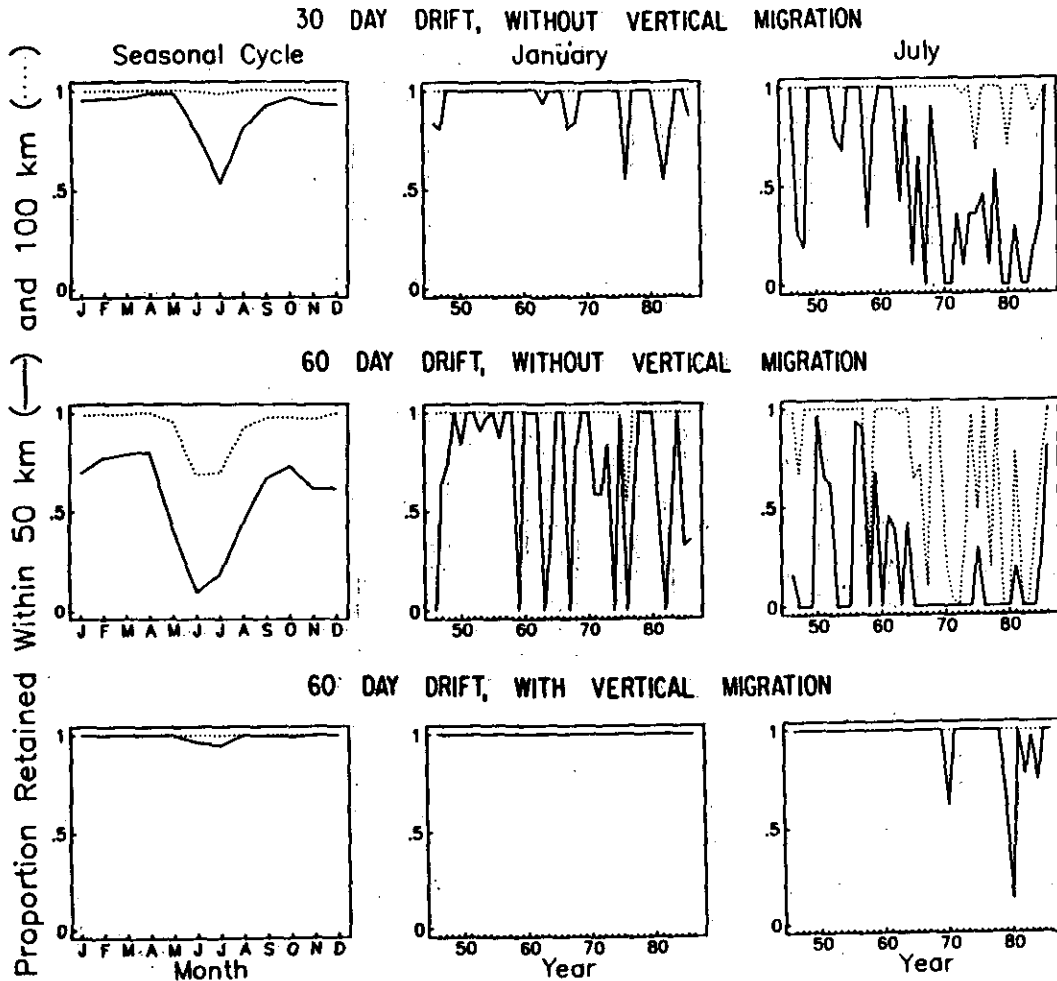


Fig. 4b. Model predictions for the proportion of larvae retained within 50 km (—) and 100 km (....) offshore. The seasonal model is the average proportion transported beyond the range from 1946 to 1986. In all cases the months refer to the month the eggs or larvae began drifting. The results are for the Scotian Shelf using a wind-dependent Ekman depth.

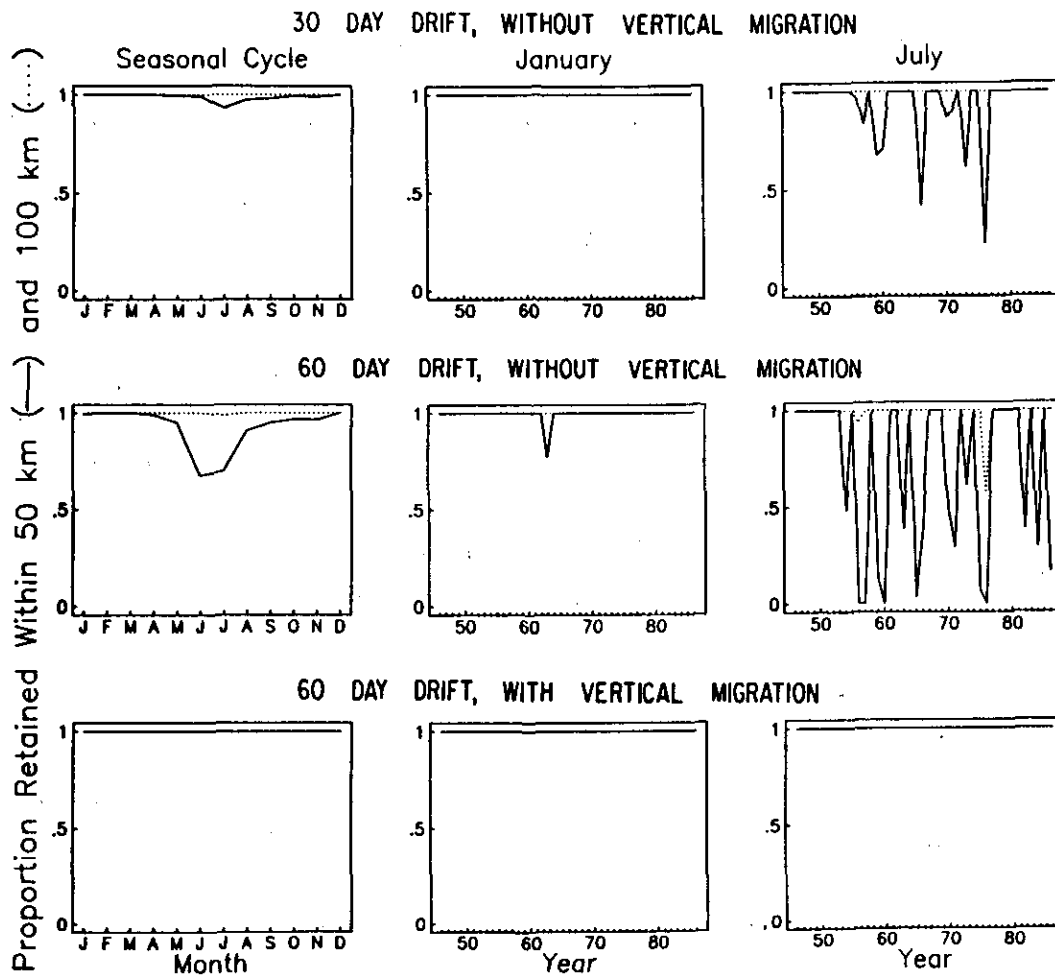


Fig. 4c. Model predictions for the proportion of larvae retained within 50 km (—) and 100 km (...) offshore. The seasonal model is the average proportion transported beyond the range from 1946 to 1986. In all cases the months refer to the month the eggs or larvae began drifting. The results are for the Labrador Shelf using the seasonal mixed layer depth.