

# Survival and Abundance of Young Atlantic Cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*) as Indicators of Year-class Strength<sup>1</sup>

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To identify the life history stage(s) most influential in determining yearclass strength, we constructed and analyzed survival curves of the 1983, 1984, and 1985 cohorts of cod and haddock off Southwest Nova Scotia relative to their physical and biological environment. Relative abundance of each Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) yearclass was not reflected by egg or larval abundance in any year examined. However, abundance of both pelagic and settled juveniles did appear to reflect yearclass strength. Egg and larval mortality could not be consistently linked with advection from the spawning site, and did not covary with subsequent recruitment. In both species, mortality between the larval and juvenile stage was inversely correlated with yearclass strength, but sources of the mortality could not be identified. Larval growth was inversely related to mortality of the early larval stage and independent of larval abundance. However, juvenile growth was proportional to mortality and inversely related to abundance. Despite early life coexistence and similarities in spawning time and location, the relative yearclass strengths of cod and haddock in Southwest Nova Scotia were different, suggesting that the timing of local physical and biological events may play an important role in the recruitment success of these stocks.

Pour repérer les stades du cycle biologique qui ont la plus grande influence sur l'effectif des classes annuelles, nous avons établi et analysé les courbes de survie des cohortes 1983, 1984, et 1985 de la morue franche (*Gadus morhua*) et de l'aiglefin (*Melanogrammus aeglefinus*) au sud-ouest de la Nouvelle-Écosse par rapport à leur environnement physique et biologique. L'abondance relative de chaque classe annuelle de morue et d'aiglefin ne concordait avec l'abondance des oeufs ou des larves pour aucune des années examinées. L'abondance des juvéniles aux stades pélagiques et benthiques semblait par contre en rapport avec l'effectif des classes annuelles. La mortalité des oeufs et des larves n'a pas pu être liée de façon conséquente avec l'advection par rapport aux frayères, et ne covariait pas avec le recrutement subséquent. Chez les deux espèces, la mortalité entre les stades larvaire et juvénile était en corrélation inverse avec l'effectif des classes annuelles, mais les sources de mortalité n'ont pu être repérées. La croissance larvaire était inversement liée à la mortalité des premiers stades larvaires et indépendante de l'abondance des larves. Par contre, la croissance au stade juvénile était proportionnelle à la mortalité et inversement proportionnelle à l'abondance. Malgré leur coexistence aux premiers stades de la vie et des similarités dans le moment et le lieu de la ponte, l'effectif relatif des classes annuelles de morue et d'aiglefin au sud-ouest de la Nouvelle-Écosse présentait des différences, qui semblent indiquer que l'avènement de phénomènes physiques et biologiques à l'échelle locale peut jouer un rôle important dans le succès de recrutement de ces stocks.

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**T**here are few fish stocks for which a consensus has been reached concerning the mechanisms and life history stages most influential in the determination of yearclass strength.

The complexity of the problem is typified by the wide variety of conclusions reached in recent research on the recruitment of pelagic spawners, such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). While most workers now believe that yearclass strength is determined in the first

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year of life (Gulland 1965; Cushing 1972; Dickson et al. 1974; Grosslein and Hennemuth 1973; Houde 1987; but see Daan 1987), "key" life history stages have variously been identified as that of egg production (Cook and Armstrong 1986; Rice and Evans 1986), early larval life (Hjort 1914; Corlett 1965; Dickson et al. 1974; Crecco and Savoy 1984), the entire larval stage (Cushing 1972; Jones 1973; Methot 1983; Flierl and Wroblewski 1985; Koslow et al. 1987), the postlarval stage (Lett et al. 1975; Sissenwine et al. 1984; Babcock Hollowed et al. 1987), the pelagic juvenile stage (Peterman et al. 1988; Savoy and Crecco 1988), and that of settled juveniles (Shulman and Ogden 1987; Townsend and Cammen 1988). The list of proposed "key" mechanisms includes, either individually or in combination, advective losses, starvation, predation, and developmental/growth rate, variously modified by density-dependent and/or density-independent factors (e.g. Jones 1973; Cushing 1981; Shepherd and Cushing 1981; Sissenwine et al. 1984; Peterman et al. 1988; Savoy and Crecco 1988; review by Anderson 1988). One conclusion that can be drawn from the above is that no one mechanism or life history stage is likely to be identified as the explanatory factor in all studies of recruitment.

While some excellent conceptual frameworks now exist for the analysis of recruitment dynamics (Sissenwine 1984; Houde 1987; Miller et al. 1988; Sinclair and Iles 1988), few have been tested through adequate sampling of individual cohorts (year-classes) at multiple life history stages. Gulland (1965) first suggested the preparation of cohort survival curves based on field survey data as the only definitive test of a recruitment hypothesis. Survival curves (or their equivalent, life stage tables) (Dahlberg 1979) have since been used to advantage by a number of workers, but have generally been either incomplete (Sissenwine et al. 1984; Babcock Hollowed et al. 1987) or restricted to examination of the egg and larval stages (Harding and Talbot 1973; Bannister et al. 1974; Ellertsen et al. 1986; Peterman et al. 1988). Recently, Sundby et al. (1989) developed a multiple stage survival curve for cod off the Norwegian coast, but they were limited to a single survey per year for each stage. Thus, Gulland's (1965) original insight has not yet been fully realized.

Intensive sampling of the cod and haddock populations off Southwest Nova Scotia during the Fisheries Ecology Program (FEP) facilitated the development of cod and haddock survival curves for the years 1983–85. Estimates of absolute abundance were available for the number of spawners and their egg production, as well as several of the stages of developing eggs, larvae, pelagic juveniles, and age-1 recruits. The objective of the survival curve analysis was to identify the life history stage(s) most influential in the determination of yearclass strength. In doing so, we assess the utility of abundance measures at each life history stage as indicators of yearclass strength. In addition, stage-specific mortality rates were calculated for each year and comparisons made both between years and species. Since environmental variables would be expected to influence the trajectory of the curve between stages, inter-annual and interspecific differences in curve trajectories were interpreted in light of interannual differences in environmental conditions reported in other FEP papers.

## Data Preparation and Analysis

The central product of the analysis was a set of survival curves for each of three cohorts (1983–85) of cod and haddock. The survival curves spanned a 1-yr period, from the point just prior to spawning (population fecundity) to beginning-of-year age 1

(cohort analysis). Abundance estimates for intermediate life history stages, including Stage 1 eggs, Stage 4 eggs, larvae, and pelagic juveniles, were derived from stage-specific research surveys. All survey station density estimates were converted to estimates of absolute abundance.

## Population Egg Production

Estimates of population fecundity were calculated from published length–fecundity relationships and current estimates of population size. Length–fecundity, rather than age–fecundity relationships were used, since the former are less affected by year-to-year changes in growth rate, and in haddock at least, are considerably more precise (Waiwood and Buzeta 1989). The length–fecundity relationship for haddock (Waiwood and Buzeta 1989) did not differ significantly among the years 1983–86, so the aggregated relationship was used here:

$$\text{Log fecundity} = 0.3456 + 3.1225 (\text{Log length})$$

Since the fecundity of cod in Southwest Nova Scotia has not yet been determined, the relationship for cod in the Gulf of St. Lawrence (Buzeta and Waiwood 1982) was applied:

$$\text{Log fecundity} = -0.16749 + 3.28 (\text{Log length})$$

The application of the Gulf fecundity relationship to these data was deemed appropriate because the length–fecundity relationships for cod in other regions differ very little among themselves (Powles 1958; May 1967; Buzeta and Waiwood 1982), and the maturation schedule for cod in the Gulf of St. Lawrence is very similar to that of Southwest Nova Scotia (Holdway and Beamish 1985).

Length-structured estimates of population abundance were calculated as per Campana (1987) using the most recent stock assessments for 4X cod (Campana and Hamel 1989) and 4X haddock (O'Boyle et al. 1989). Beginning-of-year population numbers at age ( $N_0$ ) were adjusted for mortality between January 1 and the assumed spawning date with the equation:

$$N_t = N_0 \exp(- (F + M)t)$$

where  $F$  = fishing mortality ( $\text{yr}^{-1}$ ),  $M$  = natural mortality (assumed to equal  $0.2 \text{ yr}^{-1}$ ), and  $t$  = (DOY of spawning/365) yr. Spawning dates were assessed in relation to the mean weighted date of Stage 1 egg production, and set to Day 97 for haddock and Days 73, 90, and 90 for cod in 1983, 1984, and 1985, respectively. Size-at-age in the population was calculated from research vessel age–length keys for the years 1983–85, weighted appropriately by length frequency.

## Survey Calculations

Ichthyoplankton surveys were conducted at roughly monthly intervals between February and June of 1983–85 (Hurley and Campana 1989). To ensure uniform coverage of the survey grid across years, only those stations common to most surveys and representative of the cod and haddock populations were examined (Fig. 1) (Hurley and Campana 1989). Stations on Georges Bank were not included in the analysis. All station estimates of abundance were converted to numbers per square metre. The sampling emphasis on and around Browns Bank (Fig. 1) could have biased the subsequent estimates of absolute abundance. Therefore, the mean abundance estimate for all Browns Bank stations was calculated from the high-density station grid and reweighted according to the sampling density in the remainder of the survey grid. Finally, a single estimate of mean cruise

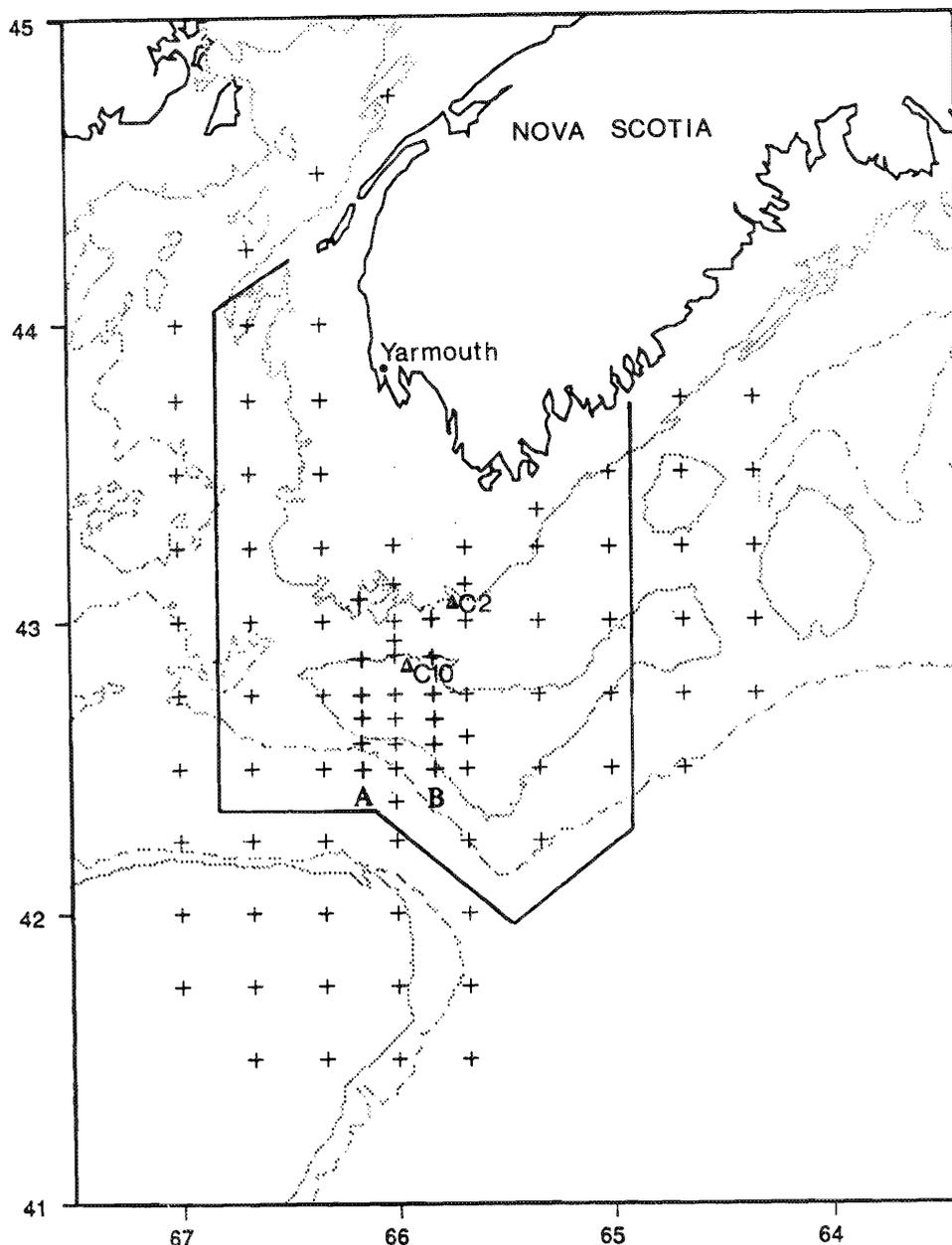


FIG. 1. Map of study area showing collection stations, current meter mooring sites (C2, C10), and wind recording site (Yarmouth). The solid line delineates those stations used in the abundance calculations. Transects A and B were not sampled in 1983.

number per square metre was calculated for each life history stage.

Pelagic juvenile surveys were conducted over the same grid as that described above (Fig. 1), using stations common to the ichthyoplankton survey and the methodology described in Koeller et al. (1986). While the 1983 survey employed oblique tows to within 5 m of the bottom, the 1984 and 1985 surveys were restricted to the upper 60 m of the water column. The vertical distribution of pelagic haddock juveniles is well suited to a depth-restricted survey (Koeller et al. 1986). However, cod juveniles may be found below 60 m (Koeller et al. 1986), implying that the survey may have underestimated their abundance in 1984 and 1985.

#### Species Identification

All of the cod and haddock life history stages were readily identifiable to species, with the exception of the early stage

eggs (Hurley and Campana 1989). Stage 1 cod-haddock-witch (witch flounder, *Glyptocephalus cynoglossus*) (CHW) eggs were subsequently assigned to species through use of a linear interpolation procedure. Classification difficulties prevented any further breakdown of CHW Stages 2 and 3. The species-assignment procedure was based upon the known species composition of the Stage 4 eggs (late stage) in the same and subsequent cruises, assuming a linear gradient in relative proportions between the two cruises. Position along the gradient was assigned on the basis of the duration of the egg stage and the time interval between cruises. The species segregation procedure was limited to two species at one time as witch eggs were not present before June, and cod eggs were not present in significant quantities after May. For cod, the following algorithm was used:

$$C_{t1} = CHW_{t1} \times (P_{t1} + ((D \times (t_2 - t_1)^{-1}) \times (P_{t2} - P_{t1})))$$

where  $C$  = the mean number of cod eggs,  $t_1$  and  $t_2$  are the days of the year for cruises 1 and 2,  $D$  = stage duration from Stage 1 to the beginning of Stage 4, and  $P$  = proportion of Stage 4 cod eggs relative to stage 4 cod and haddock eggs combined. Stage durations were calculated from the individual stage regression equations of Page and Frank (1989), using development temperatures observed at Station C10 (Fig. 1) at a depth of 15 m on the appropriate date (Lively 1989; Smith 1989a). For all cruises prior to June, Stage 1 haddock egg abundance was calculated as the difference between  $C_{t_1}$  and  $CHW_{t_1}$ .  $CHW$  abundances could not be decomposed in the manner described above for the last cruise of each year (June); accordingly, haddock:witch egg abundance at Stage 1 was linearly extrapolated using the proportions of Stage 4 haddock:witch eggs in the same and previous cruises. Given the later spawning time of witch flounder relative to haddock (Neilson et al. 1988), this assumption, although unavoidable, almost certainly resulted in an overestimate of Stage 1 haddock egg abundance in each of the June cruises.

### Annual Production

Virtually all of the ichthyoplankton production by cod and haddock was encompassed by the five monthly surveys. To estimate the absolute annual production (in numbers) of each life history stage, the area under the curve depicting the monthly time series of mean stage abundance was first integrated, then divided by the stage duration, and finally multiplied by the area of the survey grid.

Time series curves of abundance for each stage and year were prepared by plotting the mean cruise abundance on the median date of each cruise. Only cod and haddock larvae and late-stage haddock eggs in 1984 appear to have had any significant production after the last (June) cruise. For those stages, production was assumed to have peaked in June 1984, and declined linearly to zero by Day 198. This assumption was supported by the results of an independent ichthyoplankton survey of Browns Bank in July 1984 (see Results). With the exception of the cases listed above, production of all stages was assumed to have been initiated on Day 30 and ended by Day 170.

Egg stage durations were calculated as described previously. In theory, the duration of the larval stage extended to that of the juvenile stage. In practice however, larval catchability by the bongo gear, relative to a comparable sampling device, declined substantially at lengths exceeding 10 mm (Suthers and Frank 1989). Mean larval ages at 10 mm were approximated using observed ambient temperatures and 10% preservation shrinkage (Fowler and Smith 1983) in the age-temperature growth model of Campana and Hurley (1989). Therefore, the effective catchable duration was calculated as 42, 42, and 46 d for cod larvae, and 55, 45, and 47 d for haddock larvae, in 1983–85, respectively. Given the relatively long expected duration of the pelagic juvenile stage (Suthers et al. 1989), the annual juvenile midwater trawl survey could reasonably be expected to have sampled the entire year's production. The resulting estimate of juvenile abundance assumed that the pelagic survey occurred after peak larval production, and before the transformation to a demersal lifestyle (Koeller et al. 1986). This assumption appeared to be reasonable in 1983 and 1985, but was probably invalid in 1984 (see Results).

Estimates of absolute abundance were derived by integrating under the annual production curve for each life history stage, followed by division by the stage durations described earlier.

Absolute abundance was then calculated by multiplying the resulting mean annual station abundance (number per square metre) by the area encompassed by the population. The latter was taken to include both the survey grid and the unsampled region between the Nova Scotia coastline and the northernmost boundary of the survey grid, resulting in an overall population area of  $3.193 \times 10^{10} \text{ m}^2$ . The assumption that the unsampled region was characterized by ichthyoplankton abundances similar to those in the survey grid could not be rigorously tested, but seemed reasonable in light of independent surveys (Suthers and Frank 1989). Given the relatively small water volume in the unsampled region, moderate departures from this assumption would not alter the conclusions of this study.

Estimates of absolute abundance at an age of 1 yr were derived from the most recent stock assessments (Campana and Hamel 1989; O'Boyle et al. 1989). While sensitive to the input value of  $M$  and the most recent estimate of  $F$ , population estimates for the 1983–85 cohorts should be reasonably stable, with stability increasing for the earlier cohorts.

Survival curves were prepared by plotting the annual production estimate for each life history stage versus the mean weighted day of occurrence. Since the mean weighted date for 1983 cod larva production was influenced by the abundance of large, fall-spawned larvae early in the year (Fig. 2), the date was set to a value 42 d later than that of Stage 4 egg production.

### Mortality Calculations

We considered two alternative means of estimating instantaneous mortality rates between life history stages. Although both were based upon the standard equation,

$$M = \ln(N_1/N_0) \times (t_1 - t_0)^{-1}$$

where  $N_0$  and  $N_1$  are the absolute annual abundances of two sequential life history stages, the two estimation procedures employed different calculations for the time interval ( $t_1 - t_0$ ) between the stages. Mortality calculations where the interval was set to the difference between the mean weighted dates of the two life history stages produced qualitatively similar, but somewhat higher, values than those where  $t_1 - t_0$  was based upon the expected interval between stages (as described previously). In a series of calculations with simulated data and age-structured mortality, both approaches produced accurate estimates of mortality when stage-specific mortality rates were independent of date, and biased estimates when mortality varied with both stage and date. Since the calculations based upon mean weighted dates were slightly less accurate in the presence of date-specific mortalities, mortality rates were calculated using expected interstage intervals. However, mean weighted dates were used for the larval-juvenile interval, since the expected interval was unknown.

### Oceanographic Conditions

As a measure of the relative differences in oceanographic conditions among the years 1983–85, the low-passed data from the long-term mooring (C2; Fig. 1) on the inshore 100-m isobath off Cape Sable (Lively 1989; Smith 1989a) were taken to be representative of the entire Southwest Nova Scotia region. Smith (1989b) used a multiple regression technique in the extraction of significant annual cycles from monthly mean C2 data and other meteorological variables, such as Yarmouth wind stress, to demonstrate various correlations among the anomalies (residuals) from the annual cycle. Longshore wind stress anom-

alies were associated with deep longshore advection on the shelf which resulted in the transport of warm, salty (cold, fresh) water into the region from the Gulf of Maine (Scotian Shelf) when the wind was directed to the northwest (southeast).

#### Advection Model

Estimates of the direction and magnitude of ichthyoplankton displacement from Browns Bank were made with the tide- and wind-driven circulation model of Page and Smith (1989). For the western cap of Browns Bank, the model calculations appeared to be qualitatively correct in terms of direction and relative displacement magnitude, although they significantly underestimated the observed displacement of near-surface drogues. On the other hand, model calculations were inadequate for predictions of displacement on the eastern portion of the Bank i.e. — in one case, the model displacement was in the opposite direction from that observed. Therefore, the results presented here will only be interpreted qualitatively and in the context of displacement from the western cap of Browns Bank.

Advection and dispersion of eggs was simulated by seeding a particle onto the cap of Browns Bank on the mean weighted date of egg production (both Stages 1 and 4) for each species and year. The particle trajectories were then calculated over an integral number of  $M_2$  cycles until the beginning of the subsequent life history stage. Surface wind stress forcing, assumed to be uniform over the region, was based on smoothed (66-h running mean) estimates from Sable Island (Smith 1989a). Single model particles were deemed to be representative of the entire displacement field for a given species and stage on the basis of the relative uniformity of particle trajectories on the bank under tidal and wind forcing (Page and Smith 1989). Inter-annual differences in net displacement were then interpreted in relation to the estimated mortality rate for that life history stage.

## Results

### Abundance and Survival

The date of peak cod spawning appeared to differ by less than 2 wk among years, as indicated by the production of Stage 1 eggs (Fig. 2). Differences in timing became more apparent in the Stage 4 and larval production curves, with the 1984 cohort lagging behind the others. Interannual differences in the abundance of each stage were first evident at Stage 1, but became progressively more pronounced with time. In particular, the abundance of the 1984 cohort decreased from a level similar to that of the 1985 cohort at Stage 1, to approximately one-tenth its size at the larval stage. In general, the annual pulse of egg and larval production was well defined by the surveys; although the 1984 larval production peaked in June, a subsequent independent survey of Browns Bank between July 16–22, 1984 (Days 197–203), collected no Stage 4 cod eggs or larvae (K. Frank, unpubl. data).

The annual production cycle of haddock eggs and larvae (Fig. 2) differed both with respect to timing and relative cohort abundance compared with that of cod. Spawning occurred 5–30 d after cod in each year. Stage 1 egg production in 1984 lagged 2–3 wk behind that of the other years, with the timing difference persisting through other stages and increasing with time. Cohort strengths at Stage 1 were roughly similar among years, although 1983 larval production was one to two orders of magnitude less than that of the other years. The relative decline in abundance of the 1983 yearclass was clearly evident

by egg Stage 4. Larval production was not circumscribed by the surveys in 1984 and 1985, nor was Stage 4 egg production in 1984; however, an independent survey of Browns Bank between July 16–22, 1984 (Days 197–203), collected few Stage 4 haddock eggs (0.01148 per  $m^2$ ) and larvae (0.02797 per  $m^2$ ) (K. Frank, unpubl. data), indicating that egg and larval production probably peaked before the last survey of each year.

Coefficients of variation for each of the survey estimates of stage abundance are presented in Table 1. The mean coefficient of variation over all stages and cruises was 285%, corresponding to a confidence interval of about 89% of the mean. The relative size of the confidence interval decreased with increased abundance. Since the variance estimates were calculated under the assumption that all stations were random and independent, and since the variance increased with the mean, the coefficients of variation in Table 1 are almost certainly overestimated.

The absolute abundance of each cohort decreased five to seven orders of magnitude in the first year of life for both species; virtually all of the decline occurred prior to the pelagic juvenile stage (Fig. 3). Considering the range in abundance that was spanned, the similarities in abundance at the age of recruitment (age 1), both between and within species, were noteworthy. However, there were large differences in abundance at intermediate life history stages. Indeed, intraspecific and interannual variability at these stages was considerably larger than at the start or end points of the survival curves.

The egg and larval production of both species was relatively early in 1983 and relatively late in 1984. In the latter, the delayed production was probably responsible for the extremely low estimate of pelagic juvenile haddock abundance, as it resulted in a mean weighted date of larval haddock production that was only 2 d earlier than the midpoint of the juvenile survey.

Interannual differences in survival curve trajectories were best described by instantaneous mortality rates (Fig. 4). On average, the instantaneous mortality rate of both the cod and haddock egg and larval stages was between 0.15–0.30  $d^{-1}$ . While postjuvenile mortality was always much lower, none of the earlier life history stages was consistently associated with particularly high or low mortalities. Substantial interannual differences in mortality rate at each stage were clearly evident, although no one cohort consistently exhibited high or low mortalities across all stages. There were also no consistent interspecific differences in mortality at a given stage.

Exponential growth rates from near the time of hatch to the pelagic juvenile stage indicated that growth varied by as much as a factor of 2.2 between years (Table 2). Independent estimates of growth rate derived from the examination of the otolith microstructure of juveniles (Suthers et al. 1989) were similar to those calculated for the 1985 cod cohort. The cod and haddock growth rates were broadly similar, but did not parallel each other across years.

### Oceanographic Conditions

The low-passed time series of C2 temperature (Fig. 5) and salinity (not shown) indicate that the deeper waters off Cape Sable were relatively warm and saline during March and April of 1985 as compared with the more normal conditions in 1983 and 1984. These conditions extended to at least the 70-m isobath on the northern flank of Browns Bank, as indicated by data from other moorings (C3, C10; Smith 1989a). The reason for the relatively warm and saline spring in 1985 may be found in the Yarmouth monthly wind stress anomalies (Fig. 6), which

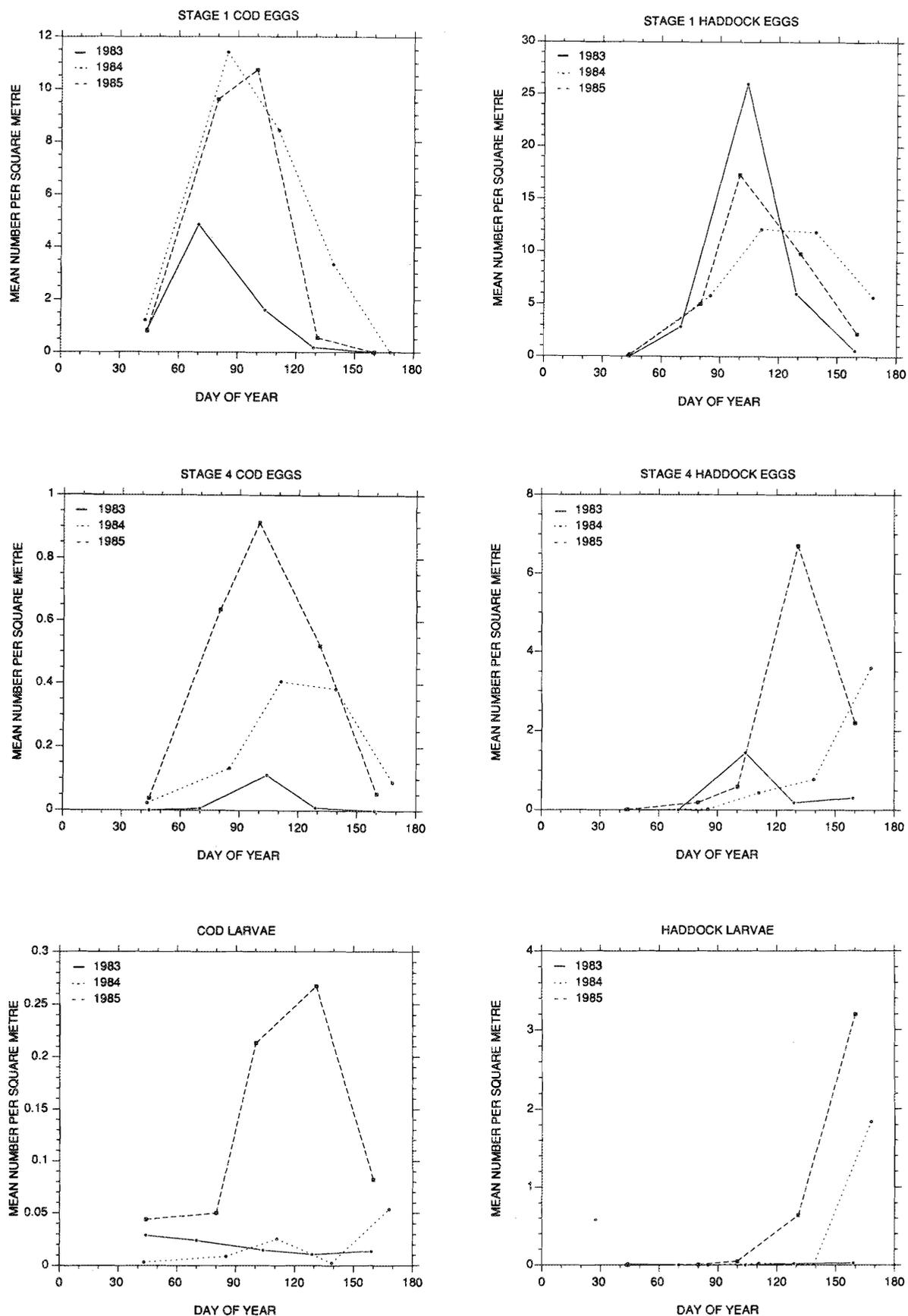


FIG. 2. Annual production cycle of cod and haddock eggs and larvae in Southwest Nova Scotia between 1983-85. An independent survey of Browns Bank in July 1984 indicated that egg and larval abundances were near zero by Day 200.

TABLE 1. Calculated coefficients of variation for each of the stage- and cruise-specific abundance estimates used in the preparation of annual production curves. Actual coefficients are probably smaller than those presented here.

Year	Month	Cruise	Coefficient of variation (%)						
			CHW Stage 1	Cod eggs Stage 4	Cod larvae	Haddock eggs Stage 4	Haddock larvae	Cod juveniles	Haddock juveniles
1983	Feb.	H091	234	—	409	—	574		
	Mar.	H093	252	574	574	—	—		
	Apr.	P288	145	206	529	276	—		
	May	H097	152	632	632	166	444		
	June	H099	147	—	624	239	437		
	June	N011						182	233
1984	Feb.	H112	327	244	453	—	—		
	Mar.	H114	263	269	656	372	—		
	Apr.	H116	132	158	227	322	306		
	May	H118	165	210	714	181	502		
	June	H120	159	326	234	150	153		
	June	N029						376	181
1985	Feb.	H130	228	182	320	558	—		
	Mar.	H132	136	165	185	160	351		
	Apr.	H133	143	175	178	172	189		
	May	H135	147	145	116	129	174		
	June	H137	133	300	176	142	178		
	June	N047/H138						106	253

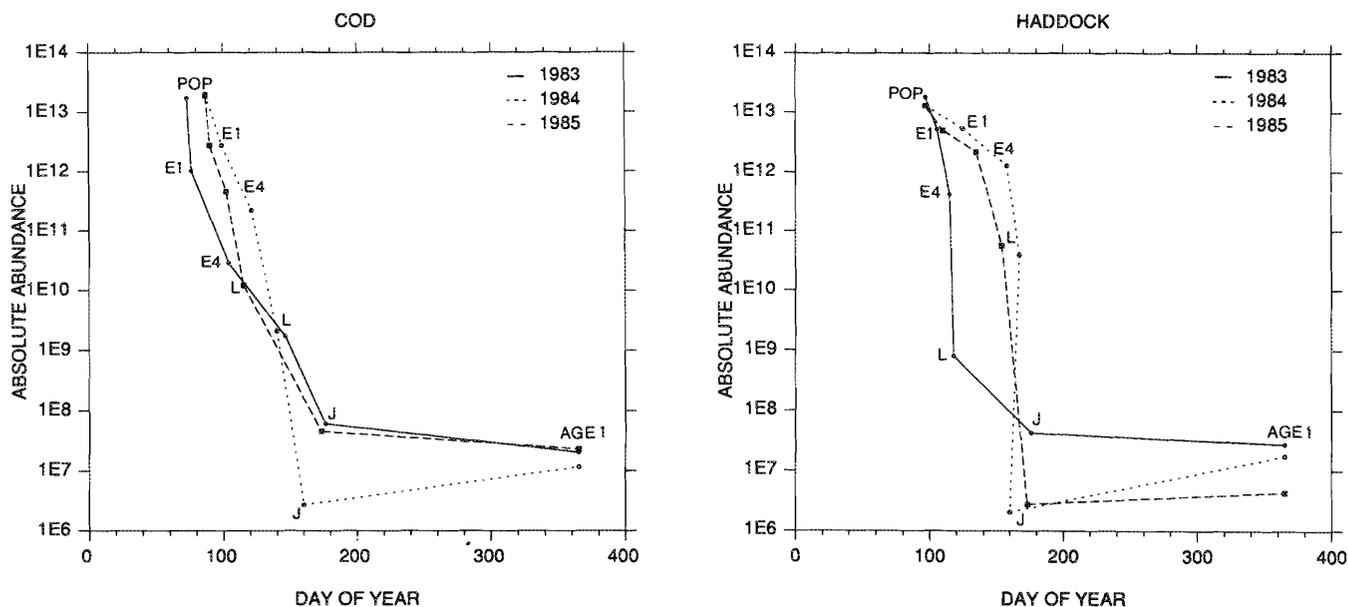


FIG. 3. Survival curves for each of three cohorts (1983–85) of cod and haddock in Southwest Nova Scotia. Estimates of absolute annual abundance (logarithmic scale) for each of the sampled life history stages have been plotted against the corresponding mean weighted date of occurrence. POP = population egg production; E1 = egg Stage 1 (early stage); E4 = egg Stage 4 (late stage); L = larvae; J = pelagic juveniles; AGE 1 = end of first year of life as derived from cohort analysis.

show large, negative longshore stress residuals in February–April of 1983–84, compared with smaller, positive residuals in 1985. The resulting longshore advection anomalies brought either cold, fresh deep water from the Scotian Shelf (negative stress) or warm, salty water from the Gulf of Maine (positive stress) (Smith 1989b). Hence the persistence of strong, longshore winds in April 1984 was associated with the prolonged period of cold temperatures throughout the water column. At depths where most eggs and larvae are found (16–50 m), April–May 1984 was cool, while the corresponding months in 1983 and 1985 were both relatively warm. Of course, temperature

effects on the eggs and larvae must also be put into the context of the timing of production; for instance, the timing of 1984 haddock larval production was sufficiently delayed so that the larvae actually experienced warmer temperatures than those of the other years.

#### Circulation and Advection

The results of the particle-tracking circulation model (Table 3) are generally consistent with inferences made from the Yarmouth monthly wind stress anomalies (Fig. 6), which are them-

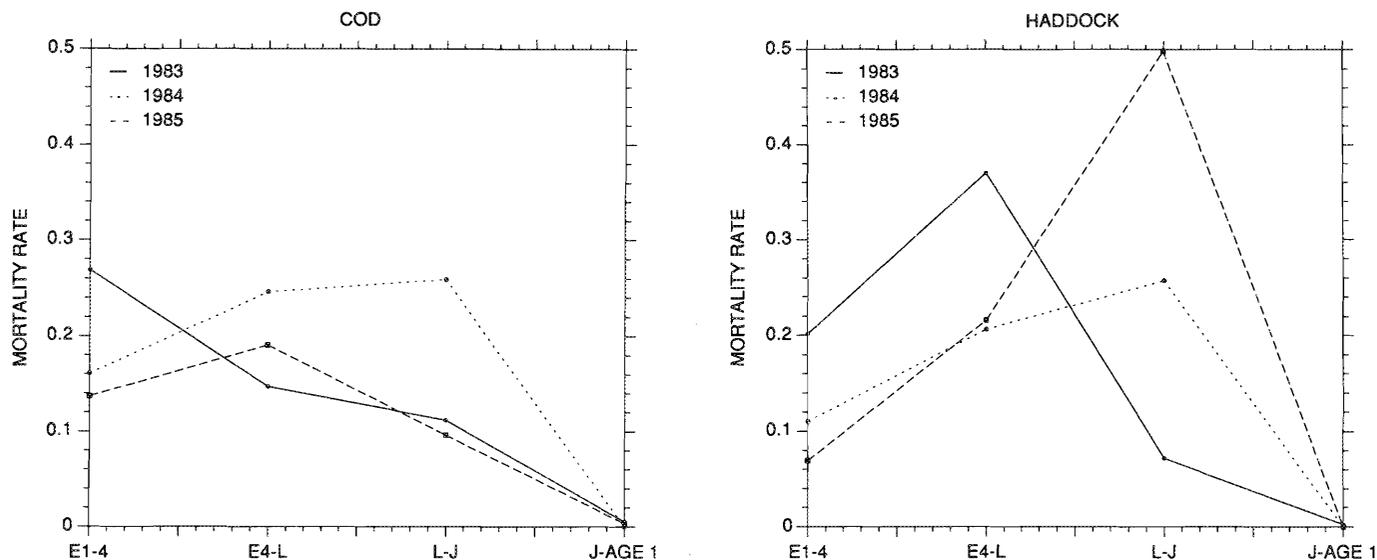


FIG. 4. Daily instantaneous mortality rates between life history stages for each of three cohorts of cod and haddock. E1 = egg Stage 1 (early stage); E4 = egg Stage 4 (late stage); L = larvae; J = pelagic juveniles; AGE 1 = end of first year of life as derived from cohort analysis. Time intervals for the mortality calculations were based on expected life-stage durations.

TABLE 2. Growth rate approximations for young cod and haddock assuming exponential growth, a mean hatch length of 4.0 mm, and a mean hatch date shortly after the mean weighted date of egg Stage 4 production. The growth of the 1984 haddock cohort was not calculated, due to the inappropriate timing of the juvenile survey. DOY = day of year; — = insufficient data.

	Cod			Haddock		
	1983	1984	1985	1983	1984	1985
Egg 4 DOY	104	121	102	115	168	135
May larvae						
DOY	—	125	135	—	—	135
Length (mm)	—	8.00	8.40	—	—	4.32
N	—	4	130	—	—	123
Juvenile						
DOY	176	160	173	176	160	173
Length (mm)	40.8	44.7	28.5	43.7	31.3	38.4
N	233	6	120	168	12	16
Instantaneous growth rate ( $d^{-1}$ )						
Egg 4 – Larvae	—	—	0.0225	—	—	—
Egg 4 – Juvenile	0.0323	0.0619	0.0282	0.0392	—	0.0595
Larvae – Juvenile	—	—	0.0328	—	—	0.0575

selves correlated with the Sable Island winds actually used in the trajectory simulations. In April 1984 for example, the strong positive along-shelf wind stress anomaly corresponds with the predicted large displacement of Stage 1 cod eggs to the northwest during DOYs 99–121. The weaker negative along-shelf anomaly in May corresponds with the predicted smaller displacement toward the east during DOYs 125–158. Although some influence of the cross-shelf stress anomalies is also evident in the model displacements, the effects are small since cross-shelf winds are not as effective in driving the circulation as are along-shelf winds (Page and Smith 1989).

The wind patterns and dispersion model results highlight important differences in the circulation during the cod and haddock spawning seasons, as well as differences between years (Table 3; Fig. 6). In all three years (1983–85), the magnitude of the wind stress anomalies and the predicted displacements decreased through the April–May period. The peak abundance

of early stage cod eggs occurred just prior to the onset of this decrease, when the anomalies and displacements were often relatively large (>40 km, except in 1985). In contrast, the peak abundance of early stage haddock eggs occurred during the seasonal transition. These differences resulted in unique patterns of predicted early life stage displacement. The early stage cod eggs were displaced large distances off the bank, toward the north or northwest, in 1983 and 1984, and largely retained on the bank in 1985. Early stage haddock egg displacement was more variable, with northwest displacement in 1983, retention on the eastern portion of the bank in 1984, and weak southwestward displacement in 1985. The displacement of late stage eggs and larvae often differed from that of the earlier stages (Table 3).

### Discussion

The relative abundance of each of the cod and haddock year-classes was not reflected by spawning stock biomass. Popula-

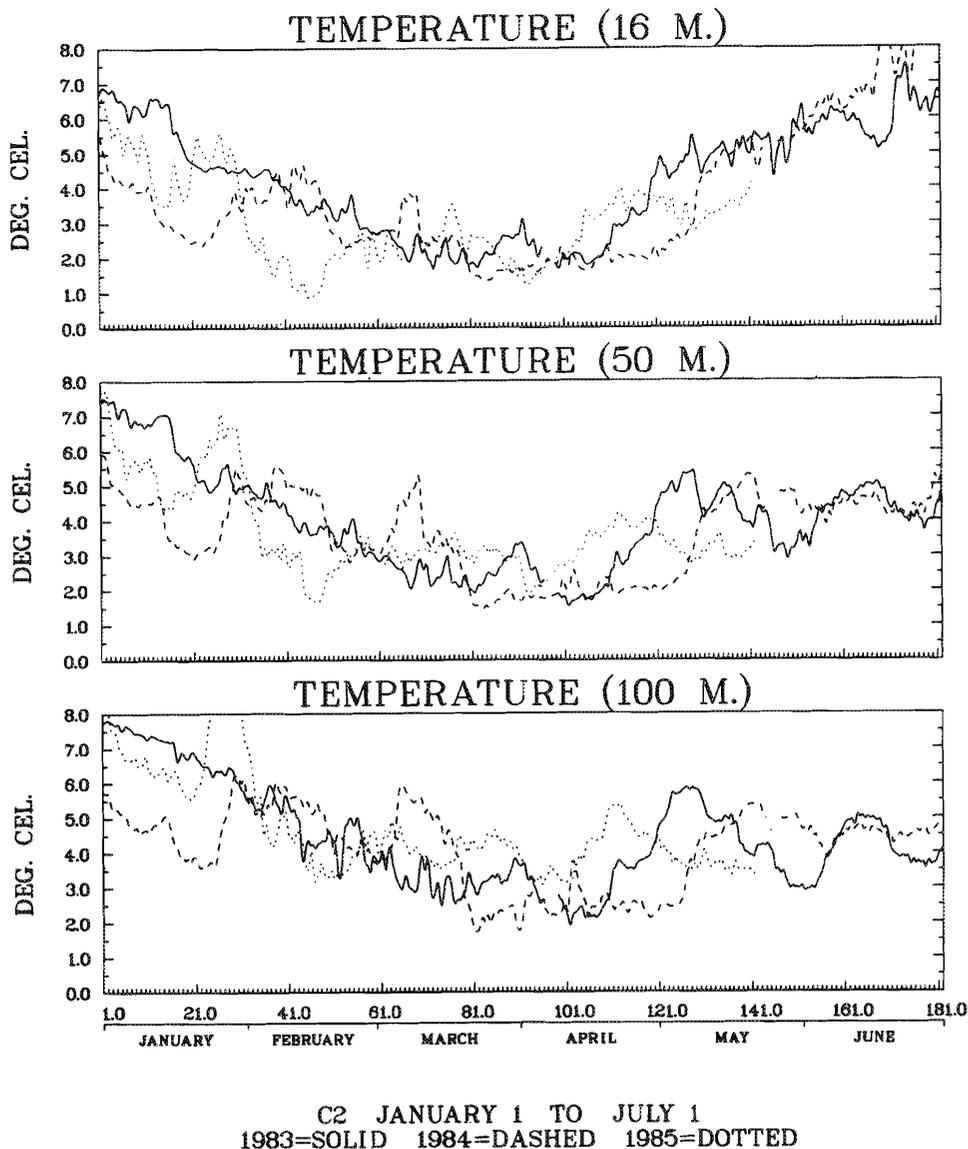


FIG. 5. Low frequency temperature time series at mooring C2. Hourly temperatures were low-pass filtered (half-power point at 31 h) and subsampled at 6-h intervals.

tion egg production varied by less than 30% among years for the two species, while yearclass strength at age-1 differed by up to a factor of six. This result was not surprising, since most workers have been unable to detect a stock-recruitment relationship in either cod or haddock (Gulland 1965; Grosslein and Hennemuth 1973; Jones 1973; Koslow 1984). Of greater interest is the fact that neither egg nor larval abundance could be used to even rank the recruitment levels of cod or haddock, although significant correlations have been reported in other species (Cushing 1972; Brander and Houghton 1982; Leggett et al. 1984; Crecco et al. 1986). While much longer time series were used in the above studies, a rank correlation might have been expected in our data given similar relationships. Indeed, on the basis of extremely low larval abundance, Koslow et al. (1985) predicted recruitment failure for the 1983 yearclass of haddock in Southwest Nova Scotia; that yearclass has since been demonstrated to be only slightly below the long-term mean (O'Boyle et al. 1989). Sampling error cannot account for our results, since the interannual variability in abundance of a given stage was often more than an order of magnitude larger than

our sampling error. Substantial changes in ranked abundance even occurred within the egg stage, between Stages 1 and 4. In the absence of appropriate qualifiers (e.g. condition factor; Frank and McRuer 1989), it is difficult to foresee measures of egg or larval abundance being used to predict the yearclass strength of cod or haddock in this region.

While the 1984 juvenile haddock survey was probably an inaccurate reflection of abundance because of the delayed production of the cohort, the abundance of the remaining pelagic juvenile cohorts did appear to reflect subsequent yearclass strength, as has been reported for other populations (Lett et al. 1975; Cook 1984; Randa 1984; Peterman et al. 1988; Sundby et al. 1989). In addition, bottom trawl surveys conducted approximately 1 mo after each of the pelagic juvenile surveys provided similar indices of recruitment success (Campana and Hamel 1989; O'Boyle et al. 1989). Of course, given the cumulative effect of large interannual variations in stage-specific mortality through the early life history, stage-specific recruitment indices would be expected to converge on the final estimate as older stages were sampled. While Koeller et al. (1986)

TABLE 3. Qualitative estimates of the direction and magnitude of advection during the egg and early larval period for cod and haddock between 1983–85. Displacement estimates were based upon the tide- and wind-driven dispersion model of Page and Smith (1989). Start and end points for the calculations are the mean weighted dates of egg production for stages 1 and 4.

			DOY		Displacement	
			Start	End	Direction	Magnitude (km)
1983	Cod	Egg 1	80	104	NW	45
		Egg 4	104	130	NW	38
	Haddock	Egg 1	104	115	NW	38
		Egg 4	115	125	E	14
1984	Cod	Egg 1	99	121	NW	116
		Egg 4	121	140	E	14
	Haddock	Egg 1	125	158	E	43
		Egg 4	158	167	SE	7
1985	Cod	Egg 1	99	102	N	7
		Egg 4	102	120	SE	69
	Haddock	Egg 1	110	135	SW	25
		Egg 4	135	154	SE	11

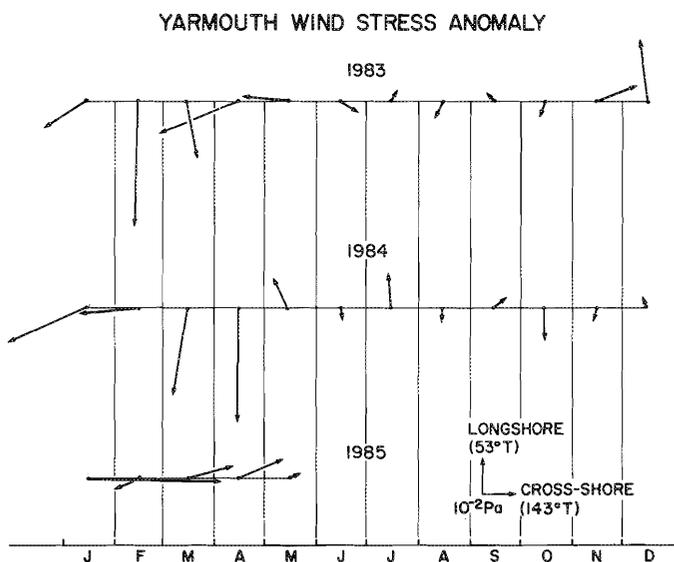


FIG. 6. Monthly mean wind stress anomalies at Yarmouth. Anomalies were computed as deviations from the average annual cycle over the period 1979–85 (Smith 1989b). Positive longshore direction ( $53^{\circ}\text{T}$ ) is upward.

have outlined the difficulties in using juvenile surveys to obtain unbiased abundance estimates, our results suggest that species-specific refinements in juvenile survey design may have the potential to provide even closer approximations of relative yearclass strength.

Mortality rates up to and including the larval stage were not rank-correlated with yearclass strength, although substantial interannual variations were observed. Similar results have been reported elsewhere (Peterman and Bradford 1987), although a consensus is not yet evident (Gulland 1965; Methot 1983; Savoy and Crecco 1988). In contrast, the mortality rate between the

larval and juvenile stage appeared to be inversely related to subsequent yearclass strength. As noted by a number of authors, the mortality rate during the postlarval/juvenile stage would be expected to be an influential modifier of recruitment success, if only because of its duration relative to the other stages (Sissenwine et al. 1984; Houde 1987; Peterman et al. 1988). This was certainly the case in these populations, given mean egg development times of about 16 d (Page and Frank 1989), mean larval ages of about 20 d (Campana and Hurley 1989), and juvenile ages of at least 80 d (Suthers et al. 1989). While the change in cohort abundance during the larval–juvenile stage was not necessarily greater than that of any other stage, our results suggest that the mortality rate during that period resulted in cohort strengths that changed very little over the remainder of the first year of life. Such a conclusion is also in keeping with the observations of relative abundance at the pelagic juvenile and settled juvenile stages.

Advection out of the survey area could not be consistently associated with high mortality rates, although it was the process which might be expected to contribute the most to the mortality of eggs and early larvae. On an annual basis, 1983 advection was predominantly off-bank to the northwest, 1984 featured the largest advective event for a given stage (cod E1–E4), and 1985 was characterized by generally small displacements, indicating retention on the bank, especially for haddock. However, large advection events that occurred at the peak of egg and early larval production could not be consistently identified as significant sources of mortality. While advection off the bank need not necessarily result in mortality (Campana et al. 1989), nearshore waters have been identified as less favourable environments for both late-stage haddock eggs and haddock larvae (Frank and McRuer 1989; Frank et al. 1989). The apparent absence of a relationship between advection and cohort mortality in this study may either reflect inadequacies in the circulation model used to assess advection (Page and Smith 1989), buffering of the local influences of advection by the relatively wide-spread distribution of eggs (Hurley and Campana 1989), or masking by other effects. In any event, it appears that interannual differences in off-bank advection had little effect upon subsequent yearclass strength.

While measures of predator and prey abundance were available to this analysis, their collection was made on a scale that was too coarse to be biologically meaningful (Ellertsen et al. 1984; Fortier and Leggett 1984; Taggart and Frank 1989). On an annual basis, 1985 has been characterized as a year of high primary and secondary production (Koslow et al. 1989). However, this high level of production was not reflected in reduced larval mortality or enhanced yearclass strength of the 1985 haddock cohort, which was among the weakest on record (O’Boyle et al. 1989). Since prey and predator abundance would be expected to influence egg and larval survival, we conclude that annual production estimates are a poor measure of availability, and that characterizations of yearly production as “good” or “bad” (Koslow et al. 1989) are unlikely to aid in the prediction of cod and haddock recruitment.

As a covariate of the major mortality processes, growth rate is widely considered to be an important modifier of early life survival (Houde 1987; Peterman et al. 1988). Both the cod and the haddock larval growth rates (Campana and Hurley 1989), based on observed temperatures after the time of peak late-stage egg production, were inversely related to the observed mortality rates, but appeared to be independent of larval abundance. While tentative, these results are consistent with the conceptual

framework linking growth and mortality through its influence on stage duration (Houde 1987; Miller et al. 1988). However, larval growth rate through to the pelagic juvenile stage appeared to influence mortality differently. Postlarval growth in each year and species was proportional to the larval–juvenile mortality rate, and inversely proportional to juvenile abundance. Despite apparent consistency with density-dependent processes, our observations were too few to test previous reports of density-dependent growth and mortality in the juvenile stage (Shepherd and Cushing 1981; Zijlstra et al. 1982). However, our size-at-date data did not serve as useful proxies for yearclass strength.

Broad similarities in the yearclass strengths of sympatric cod and haddock stocks (Martin and Kohler 1965; Templeman 1972; Koslow 1984) suggest that large-scale environmental effects influence recruitment (Koslow 1984; Babcock Hollowed et al. 1987). However, despite the fact that the stocks that we studied experienced the same large-scale effects, the recruitment success of cod and haddock differed in 1984, and was totally divergent in 1985. These recruitment dichotomies can probably be attributed to more local events, such as those due to heterogeneous spatial or temporal effects. For example, consider the interannual comparison of temperatures at mooring C2 (Fig. 5), which represents the temperature field of the local region. On a gross scale, the spring of 1984 could be classified as cooler than that of 1983, primarily because of the prolonged period of cold temperatures in March–April, 1984. Yet, because of the delay in the time of haddock larval production, the ranking of the yearly temperatures to which the larvae were exposed would be reversed. These phasing effects may well be responsible for reported univariate relationships between the environment and yearclass strength in some populations (Martin and Kohler 1965; Dickson et al. 1974; Hansen and Buch 1986) but not in others. Similar arguments can be made with respect to annual assessments of advection and zooplankton production (Koslow et al. 1989), both of which were too coarse as measures to provide consistent explanations for the divergence in cod and haddock survival patterns.

Questions left unanswered by this analysis can be used to suggest avenues for further research. In particular, we recommend further research on the growth, sources of mortality, and susceptibility to oceanographic influences of the juvenile stage. Improvements to the particle dispersion model could be used to compare the observed and expected distribution of ichthyoplankton throughout the spawning season, and thus test more completely the hypothesis that advection is (or is not) an important source of egg and larval mortality. And finally, more work is required to assess the influence of larval condition on subsequent survival. In an applied context, fisheries managers may view these research recommendations as a means of enhancing our ability to predict the strength of upcoming yearclasses.

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