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The Transport of Haddock Melanogrammus aeglefinus Eggs in the Northwest Atlantic

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by

Frederick H. Page

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Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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Dalhousie University Halifax, Nova Scotia November, 1990

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ABSTRACT

The displacement of the pelagic early life stages of fish is an important component of the theories, hypotheses and concepts concerning the natural regulation of fish populations. However, empirical estimates of the magnitude and frequency of the displacements are difficult to obtain. Therefore estimates are often made using indirect methods. In this thesis some of the components needed for the development of displacement indices of haddock (Melanogrammus aeglefinus L.) eggs are investigated. Haddock and cod year-class sizes, estimated from the virtual population analyses of 3 haddock and 6 cod populations, are shown to be only weakly correlated within species and uncorrelated between species, thus indicating that population specific processes are the largest contributor to recruitment variation. An examination of literature estimates of egg abundances, egg development times measured at constant incubation temperatures and time series of sea surface temperatures shows that haddock spawning times and the age of eggs at hatching vary inter-annually and between populations. Discrete-depth ichthyoplankton samples taken over Browns Bank show that the vertical distribution of haddock eggs varies ontogenetically. A one dimensional advection-diffusion model, developed to explain the observed vertical distributions, shows that the horizontal transport of haddock eggs in a surface Ekman layer is overestimated by indices cf surface velocities. A kinematic model of a constant, depth-independent Eulerian gyre illustrates the non-linear relationship between the displacement of eggs spawned inside the gyre and wind speed, when the wind is assumed to induce a horizontally uniform flow superimposed on the gyre. Finally, a two-dimensional particle tracking model for estimating the displacement of haddock eggs spawned over Browns Bank is developed. A comparison between the trajectories of drogues released over Browns Bank with those estimated with the model indicates the model is unable to reliably estimate drogue trajectories.

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In addition to the above several members of my thesis committee deserve special mention and thanks. Dr. Peter Smith endured and guided my introduction into physical oceanography and provided greatly appreciated financial and moral support along with a consistent level of scientific guidance and expectation. He provided the information on satellite tracked drogue trajectories and many insights into the art of evaluating numerical models. Dr. Ken Frank provided much needed motivation and moral support along with many hours of his time for discussions of biological issues. He also provided the opportunity and technical assistance neccessary for the collection of the information concerning the vertical distribution of the haddock eggs. Finally the thesis would never have been completed had it not been for the time, encouragement, proding and setting of standards provided by my supervisor, Dr. Keith Thompson. Keith also instructed me in the use of multi-variate statistics and in the development of partial differential equation models.

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CHAPTER 1

Perspective and Objectives

1.1 Introduction

One of the processes thought to be important in determining the location, size and number of marine fish populations, as well as the inter-annual variability in the size of the populations, is the transport, dispersal and/or migration of the pelagic early life stages (Bakun *et al.* 1982, Rothchild and Rooth 1982, Sinclair *et al.* 1986).

The possibility that transport processes may be important to fish population regulation was first suggested by Hjort (Hjort 1914). Interest in the possibility has been maintained by (1) observations that suggest anomalous displacement patterns sometimes appear to result in poor year-class sizes (eg. Walford 1938, Saville 1956, Colton 1959, Wroblewski and Cheney 1984), (2) comparisons between spawning distributions and indices of dispersion that suggest spawning often occurs at times and in areas of reduced water transport (Parrish *et al.* 1981, Iles and Sinclair 1982, Bakun 1985), (3) observed coherency in the success of year-classes of different fish populations and species over large spatial scales which may be indicative of the influence of large scale water circulation processes (Iles 1973, Koslow *et al.* 1987, Iles 1987) and (4) the correlations between indices of water displacements and year-class size that suggest circulation conditions, and by implication the displacement patterns of the early life stages, account for a significant proportion of the variance in year-class strength (Table 1.1).

In conjunction with this interest a conceptual base for role of early life stage transport in fish population dynamics has developed. This base includes the Harden-Jones' "larval drift" theory (Harden-Jones 1965, 1968), the Herring Stock hypothesis (Iles and Sinclair 1982), the larval retention hypothesis (Iles and Sinclair 1982) and the "Member/Vagrant" hypothesis (Sinclair 1988).

	SOURCE	TRANSPORT INDEX	PERIOD	SPECIES & STOCK
1938	Carruthers	Air Pres. Grad. Mean Wind Speed	4 m 4 m	E. Anglian herring North Sea haddock
1951a 1951b	Carruthers <i>et al.</i> Carruthers <i>et al.</i>	Mean Wind Speed Mean Wind Speed	4 m 1–3 m	North Sea haddock North Sea haddock, plaice & cod
1955	Chase	Non-linear ftn of alongshelf grad. in air pressure	3 m	Georges Bank haddock
1965	Corlett	Mean Wind	1 m	Norwegian Cod
1965	Saville	Mean Wind	3 w	Clyde Herring
1977	Nelson et al.	Mean Ekman Transport	3 m	Atlantic Menhaden
1981	Bailey	Mean Ekman Transport	1 m	Pacific Hake
1983	Murray et al.	Displacement due to 3% Wind Speed	14 d	Atlantic Mackerel
1984	Johnson et al.	Wind index	3 m	Blue crab
1985	Sinclair et al.	Mean Sea level	1 m	Pacific Mackerel
1986	Johnson et al.	Wind stress	3 m	Dungeness Crab
1988	Myers & Drinkwater	Displacement due to Ekman Trans. velocity	w-m	many species

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Despite the limited evidence and concepts, the role of early life stage (ELS) transport to fish population regulation remains largely unknown. This becomes particularly evident when it is recognized that (1) direct and reliable estimates of the frequency and magnitude of the displacements of pelagic early life stages are extremely difficult to obtain for technical and budgetary reasons, (2) several of the early correlations have degraded with time (Table 1.2), (3) several of the transport indices have been shown to be poor indicators of ELS transport (e.g. Saville's 1959 examination of Carruther's *et al.* 1951a wind index, Talbot 1977), (4) few descriptions of early life stage behaviour exist, and (5) almost no validated models of early life stage dispersal exist.

Efforts to evaluate the role of early life stage transport in fish population regulation can be greatly improved by process oriented or mechanistic approaches which can provide the basis for the more indirect approaches, such as models and correlations, which must be used to estimate transport patterns in the absence of observations and which may help in the interpretation of observations.

The general focus of this thesis is therefore on the processes and mechanisms governing ELS transport. The emphasis is on the transport of haddock (*Melanogrammus aeglefinus*) eggs and the transport of haddock early life stages in general. A specific objective of the thesis is to assess the adequacy of near surface indices of water transport as indices of haddock egg transport. Haddock is chosen because transport processes are believed to be important to the regulation of haddock populations (Section 1.2 below). The egg stage is chosen because of all the early life stages the egg stage is probably the least capable of controlling its dispersal. Therefore the effect of water circulation is likely to have its greatest effect on haddock population regulation (stock structure and size variation) during the egg stage.

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ORIGINAL CORRELATION			MORE RECENT UPDATE	
SOURCE	YEARS	SPECIES & STOCK	RESULT	SOURCE
Carruthers <i>et al.</i> (1951a)	1920-49	North Sea haddock	degraded	Saville (1959)
Chase (1955)	1928-51	Georges Bank haddock	degraded	Grosslein & Hennemuth (1973)
Nelson <i>et al.</i> (1977)	1955-70	Atlantic Menhaden	degraded	Lasker (1985)
Bailey (1981)	1960-75	Pacific Hake	not yet tested	
Sinclair et al. (1985)	1928-65	Pacific Mackerel	not yet tested	

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TABLE 1.2: The persistence of correlations between indices or assumed indices of water transport and year-class size or survival indices.

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1.2 The Transport and Dispersal of Haddock

Haddock (*Melanogrammus aeglefinus*) is an important commercial species throughout the North Atlantic, ranging from Cape Hatteras in the west to Porcupine Bank in the east (Fraser, 1958; Serebryakov, 1971; Scott and Scott, 1988). Spawning usually takes place over coastal and offshore banks during the winter and spring months (Schmidt 1909, Bjorke 1983, Saville 1956,1959, Fraser 1958, Serebryakov 1971, Bigelow 1927, Walford 1938, Colton and Temple 1961, Serebryakov 1971, O'Boyle *et al.* 1984, Smith and Morse 1985, Grosslein 1962). The eggs hatch within 10 to 15 days (Walford 1938, Laurence and Rogers 1976) and the juveniles metamorphose and descend to the bottom after three to six months (Colton and Temple 1961, Colton 1965, Koeller *et al.* 1986).

The eggs are believed to be released near the bottom (Hawkins *et al.* 1967). They rise toward the surface so that the highest concentrations are usually found within the top 10m (Colton and Temple 1961, Colton 1965). Sometimes the eggs are found distributed throughout the water column or concentrated near the bottom (Walford 1938, Lough 1984).

The larvae and pelagic juveniles are most abundant within the thermocline and the top 20m, respectively (Miller *et al.* 1963, Colton 1965, Lough 1984, Koeller *et al.* 1986, Frank *et al.* 1989). The juveniles are found in association with the jellyfish, *Cyanea*, (Colton and Temple 1961). Neither the larvae or pelagic juveniles vertically migrate (Miller *et al.* 1963, Koeller *et al.* 1986, Mahon and Neilson 1987, Frank *et al.* 1989).

Based on this information the haddock early life stages have been assumed to be effectively passive for 3 to 6 months (Chase 1955, Colton and Temple 1961) and their displacements have been largely estimated from the surface circulation. For example, in accordance with the the concept of "larval drift", the mean or most frequent pattern of displacement for the early life stages has been assumed to be that indicated by the residual circulation, particularly the Lagrangian residual. On Georges Bank surface drift bottles released over the haddock spawning ground during the spawning season are seldom retrieved, appearing to drift off the bank in response to cross-shelf wind events (Walford 1938, Day 1958, Bumpus and Lauzier 1965, Bumpus 1976). Colton and Temple (1961) have therefore hypothesized that the eggs and larvae are normally removed from the population by offshore transport and that the stock is maintained by immigration of early life stages from the adjacent Browns Bank spawning ground.

On Browns Bank surface drift bottles released over the northwest portion of the bank move toward the inshore and the northeastern Gulf of Maine (Day 1958, Bumpus and Lauzier 1965, Bumpus 1976, Trites 1981). The haddock early life stages have, therefore, been hypothesized to drift toward the northeastern Gulf of Maine and the mouth of the Bay of Fundy (Bigelow 1927, Colton and Temple 1961, Serebryakov 1971, Grosslein and Hennemuth 1973), areas in which the survival of larvae from pelagic spawning species such as haddock has been suggested to be low (Bigelow 1926). On Emerald and Western Banks the residual circulation has been suggested to transport the haddock ELS in a southwestward direction along the Scotian Shelf toward the Browns Bank population (Serebryakov 1971). In the northeast Atlantic the residual circulation around Iceland has been suggested to carry the ELS of the Icelandic haddock more than half way around the island (Schmidt 1909).

These scenarios have been challenged since Eulerian residual gyres have been shown to exist around several of these haddock spawning areas (eg. Georges and Browns Bank: Greenberg 1983, Smith 1983, Butman and Beardsley 1984; Southeast Shoals on the Grand Bank: Loder *et al.* 1988). A newer concept is that the ELS in these areas undergo very limited drift (O'Boyle *et al.* 1984) or are retained over the banks (Smith and Morse 1985).

Although the retention scenarios eliminate the problem of the early life stages drifting into regions where their chances for survival are considered to be exceptionally low, the implication that Eulerian gyres prevent drift is ill founded. It is well known that in a time varying flow field the Eulerian and Lagrangian residual

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circulations, the time averaged circulations, are seldom if ever realized. This is particularly true in areas, such as Georges Bank and Browns Bank, where the variance to mean ratio in the current is large (Loder *et al.* 1988).

Nevertheless the evidence from ichthyoplankton and trawl surveys, appears to support the concept of limited displacement since the distributions of eggs, larvae and juveniles seldom become distinctly separated. On Georges Bank the larval distribution overlaps and is marginally downstream of the eggs (Walford, 1938; Smith and Morse, 1985). In the Browns Bank region the distributions of eggs, larvae and juveniles remain centered over the spawning ground or displaced marginally toward the inshore (O'Boyle *et al.* 1984, Koslow *et al.* 1985). In the Emerald-Western Banks region the juvenile haddock are concentrated on Western Bank and around Sable Island (Scott 1982, 1984). On the Faroe Plateau the eggs and larvae usually remain over the plateau (Saville 1956). In the North Sea the egg and larvae distributions are very similar (Saville 1959) and on the Newfoundland Banks the distribution of demersal juveniles suggests the displacement of egg and larval stages is small (Serebryakov 1971). Even in the Iceland stock many of the pelagic juveniles remain over the spawning areas (Schmidt 1909). However, these distributions may instead be controlled by spatial variations in early life stage mortality rates.

In addition to the uncertainty surrounding the relationship between the mean circulation and the mean distribution of the ELS, the influence of circulation variation on population regulation is also unclear. Because many haddock populations spawn near the edge of the continental shelf during the winter-spring period when the local prevailing winds are in the offshore direction and the ELS were believed to be in the near surface waters, interannual variation in the wind induced circulation was thought to be a major cause of recruitment variation.

There is some direct evidence from the north-east Atlantic that circulation variation may be important to haddock year-class size. For example, in one of four years in which surveys were conducted over the Faroe Plateau, Saville (1956) observed that anomalous wind conditions were associated with the displacement of haddock

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larvae from the Faroe Plateau. Recruitment of this year-class was apparently low. The rise in abundance of haddock in the Belt Sea during the late 1920's has been attributed to a transport of larvae from the Skaggerak (Johansen 1926).

There is also some indirect evidence. Koslow (1984) has shown that variation in the size of year-classes recruiting to the haddock populations of the Northwest Atlantic are positively correlated and has suggested that this is the result of large scale atmospheric and circulation processes. Wind induced circulation is one of these processes and weak correlations exist between the cross-shelf wind and haddock year-class size in some of the Northwest Atlantic haddock stocks (Koslow *et al.*, 1987). Unfortunately the significance of these patterns and correlations are not well established because of auto-correlation in the time-series. Earlier analyses of the relationship between wind and haddock recruitment do not suffer from the auto-correlation problem and, as discussed above, some correlations were initially significant.

1.3 Thesis Objectives

It is clear from the above that sufficient evidence exists to warrant an investigation into the role of ELS transport in haddock population regulation. It is also clear that the past approaches of surveys and correlations have not be successful. Ichthyoplankton survey programs usually cover a few years at best and the results are difficult to unequivocally interpret. Correlations must be based on indices of ELS transport and these are generally difficult to validate.

This thesis focuses on an examination of the recruitment patterns, mechanisms and concepts relating to the transport process since this will provide information useful in the development of concepts of haddock egg transport and in the development of transport indices for use in evaluating haddock stock structure and the influence of transport on haddock recruitment variation.

I re-examine the hypothesis that haddock recruitment is positively correlated among stocks of the Northwest Atlantic (Chapter 2), examine the inter-annual variation in the timing of haddock spawning (Chapter 3), estimate the inter-annual variation in duration of the haddock egg stage (Chapter 3), describe the vertical distribution of haddock eggs throughout egg development (Chapter 4), describe a mathematical model that explains the vertical egg distribution (Chapter 4) and provide an estimate of the rate of wind-induced egg transport (Chapter 4), present an idealized kinematic model of egg dispersal within a permanent gyre (Chapter 5) and evaluate the capability of two existing Eulerian circulation models to simulate the Lagrangian trajectories of surface-trapped particles (Chapter 6).

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CHAPTER 2

Co-variation in the Year-class Sizes of Haddock and Cod in the Northwest Atlantic

2.1 Introduction

It is generally believed that variation in year-class (recruitment) sizes is driven by both biological and environmental forces. Since recruitment time series of yearclass size have more energy in the high-frequency band than do time series of stock size or reproductive output, the high frequency year-class variation is considered to be controlled by the environment rather than by a stock-recruit relationship (Shepherd *et al.*, 1984; Welch, 1986). The low frequency variation may be due to either or both.

One approach that has been used to help identify the driving forces is the examination of the relationships between time series of year-class size of different species and populations (Shepherd *et al.*, 1984; Table 2.1). Despite many applications of this approach (Table 2.1) the existence of large scale synchrony in recruitment and the relative importance of local to large scale factors remains controversial. One of the reasons for this, is that until recently, the null hypothesis that the recruitment series are independent is seldom tested.

Studies conducted prior to 1978 made only qualitive comparisions between recruitment series and four of the seven cited in Table 2.1 concluded that recruitment covaried in a positive manner.

Since 1978 more quantitative statistical techniques have been used. Garrod and Colebrook (1978) used principal component analysis (PCA) to define spatial patterns in the correlation matrix comparing 18 recruitment series from fish stocks distributed across the North Atlantic. They concluded significant co-variation occurred on several spatial scales and between several different species. Shepherd *et al.* (1984) re-examined Garrod and Colebrook's correlation matrix, using Bartlett's sphericity test, and could not reject the hypothesis that the matrix was consistent

TABLE 2.1: Examples of qualitative examinations of the spatial pattern in year-
class size. (R = year-class size or recruitment; NSC = no statistical
comparison; CV = co-variation; + = positive; spp. = species; PCA
= principal components analysis)

ç	SOURCE	AREA	STATISTICAL TECHNIQUE & SPECIES	RESULTS
1931	Taning*	North Atlantic	cod	suggested $+CV$
1964	Hennemuth et al.	Northwest Atlantic	NSC;haddock	suggested $+CV$
1965	Martin & Kohler	Northwest Atlantic	NSC;cod,haddock	suggested $+CV$
1965	Templeman	North Atlantic	NSC;ranks of R; cod,haddock, herring	suggested CV at variable lags between spp. & areas
1971	Tveite	Southeastern Norway	NSC;cod,pollock; catch of O-group	suggested +CV between spp. within area
1971	Dragesund	North Atlantic	NSC;ranks of R based on catch & acoustics; herring cod,saithe,haddock redfish,capelin,	no CV of a spp. between areas; no CV between spp. within areas
1972	Templcman	North Atlantic	NSC;ranks of R; cod,haddock	suggested CV between spp. & areas

* cited in Templeman (1972)

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TABLE 2.1: continued

S	OURCE	AREA	STATISTICAL TECHNIQUE & SPECIES	RESULTS
1978	Garrod & Colebrook (G&C)	North Atlantic	correlation & PCA;Log R;	concluded CV on trans-Atl. scale
1984	Koslow	Northwest Atlantic	correlations & PCA; Log R of cod & haddock	concluded large scale CV
1984	Shepherd et al.	North Atlantic	Bartlett's sphericity test applied to G& C correlation matrix	Accept Ho:stocks independent
1987	Koslow et al.	Northwest Atlantic	correlations; Log R from VPA cod,haddock	suggested within spp. +CV & weak +CV between spp.
1987	Hollowed et al.	Northeast Pacific	5 year running median; % of stocks with extreme R; chi- square; correla- tions; cluster analyses	suggested large scale +CV

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with uncorrelated variables. Smith (1978), on the other hand, concluded the matrix was suggestive of weak large scale coherence. He based this on the observation that although most of the correlations were not statistically significant more than two thirds were positive.

Hollowed et al. (1987) used a variety of statistical techniques to identify patterns in the recruitment to fifty-nine stocks of the Northeast Pacific. They concluded there was evidence for large scale coherence in the recruitment series and that recruitment success is therefore driven by environmental forcings.

Koslow (1984) used correlation and PCA to examine in more detail the patterns in recruitment to only Northwest Atlantic stocks located between Georges Bank and western Greenland. He found that recruitment to stocks of the same and ecologically similar species were positively correlated and that correlations between demersal and pelagic species were negative. He therefore concluded that "largescale physical forcing, rather than local biological interactions" were the cause of recruitment variation. Cohen *et al.* (1986), however, claimed this conclusion was spurious since Koslow did not take into consideration the non-stationarity (trend) of the recruitment series. When they removed the trend, using first differencing, the correlations were reduced and no longer significant. They therefore concluded that on the shorter time scale emphasized by the first differenced series, no large scale coherence existed and therefore the variation was generated by small scale, local processes.

Resolution of this conflict is of obvious interest to the assessment of the effect of wind driven transport on the haddock early life history and in particular its potential to influence recruitment. The low-frequency wind patterns are known to be coherent over broad spatial scales (Thompson and Hazen, 1983) but their effect on the circulation may be evident over much smaller scales. For example, an alongshelf wind stress (ca. east-west) produces an inshore (northwesterly and northerly) depth-averaged current off southwestern Nova Scotia and an offshore current along the northeastern peak of Georges Bank which is less than 100km away (Wright *et al.*, 1986).

One of the difficulties in testing the hypothesis that the recruitment series are independent is that statistical methods are not readily available to test this hypothesis when the recruitment time series are short, non-stationary and autocorrelated. However, when the non-stationarity and auto-correlation are removed there are statistical proceedures that can be used to test in a more rigorous manner the hypothesis that the recruitment series are uncorrelated.

The purpose of this chapter is therefore to briefly review the statistical problems, to describe statistical methods for testing this null hypothesis, and to use these methods to re-examine the relationship between the haddock and cod recruitment described by Koslow (1984).

2.2 Statistical Problems

2.2.1 The Choice of Variable: $\log(R)$ or $\log(R/E)$

Most quantitative analyses of recruitment patterns have log transformed the year-class sizes $(\log R)$ since 1) year-class sizes are often log-normally distributed (Hennemuth *et al.*, 1980) and log transformation therefore allows the use of standard statistical procedures, and 2) the variance in recruitment is often dominated by the extreme year-class sizes and log transforming gives more equal weighting to each observation (Shepherd *et al.*, 1984). However, $\log(R/E)$, where *E* is the annual egg production, has also been suggested as a useful variable (Sharp, 1980). It represents the cumulative mortality during the pre-recruit stage and potentially accounts for the effect of stock size variations on year-class size.

It is useful to examine more closely the biological meaning of $\log(R)$ and $\log(R/E)$. It is well known that recruitment results from a complex combination of environmental, biological, density-dependent and stock-dependent processes (Sissenwine, 1984). Some quantitative insight into how these factors influence recruitment may be gained by examining simple models of stock and recruitment.

There are three basic models. The simplest assumes that within each year the pre-recruit mortality is entirely density-independent and that the change in numbers of individuals is given by

$$\frac{dN(t)}{dt} = -M(t)N(t) \qquad 2.1$$

in which N(t) is the number of individuals at time t and M(t) is the time dependent rate of mortality. The solution to this equation is the familiar exponential decay model

$$R = E \exp\left(-\int_{0}^{t_{r}} M dt'\right)$$
 2.2

in which E is the number of eggs produced by the parent stock and t_r is the age at recruitment. The model indicates R is a linear function of E and that interannual variation in $\log(R)$ could be due to variation in egg production ($\log E$) or mortality. $\log(R/E)$, however, accounts for the stock effect and variation in this variable is usually assumed to be due to variation in the mortality term.

Equations 2.1 and 2.2 are usually considered to apply only at very low stock sizes (Harris, 1975). At higher stock sizes year-class size does not continue to be linearly related to stock (Welch, 1986). There are two basic models that attempt to take this into consideration. The Beverton and Holt (1957) model assumes the prerecruit mortality rate is the sum of density-independent (M_1) and density-dependent (M_2) rates of mortality. Since the functional form of the density-dependence was not well known Beverton and Holt assumed it was linearly related to abundance $(M_2 = \mu_2 N)$. The total mortality is therefore given by $M = M_1(t) + \mu_2(t)N(t)$. Substitution of this into eq. 2.1 gives the Bernoulli equation

$$rac{dN(t)}{dt} = -[M_1(t) + \mu_2(t)N(t)]N(t)$$
 2.3

which when integrated using an integrating factor gives the solution

$$N(t) = \frac{EB}{1 + EA}$$
 2.4

where

$$B = \exp(-\int_0^{t_r} M_1(t) dt')$$

$$A=\int_0^{t_r}B(t)\mu_2(t)dt'$$

These solutions show that when $EA \ll 1$, the solution reduces to the simple exponential decay solution 2.2. In this case the mortality is entirely densityindependent and $\log(R/E)$ indicates the pre-recruit mortality. This can occur when the stock size is low $(E \ll 1/A)$, or if there is no density-dependent mortality $(\mu_2 = 0)$.

When $EA \gg 1$, the solution reduces to R = B/A which indicates R is a complicated function of both density-independent and density-dependent mortalities. This can occur when the stock size is large $(E \gg 1/A)$. In these cases recruitment is independent of stock size and $\log(R)$ is therefore an index of a complex accumulation of density-independent and density-independent effects.

Although the Beverton and Holt (1957) specification of M is simple, Harris (1975) has shown that for all cases in which M is a function of N, the general characteristic of the Beverton and Holt relationship will usually persist: i.e. yearclass size will asymptote to a maximum as stock size (E) increases.

In summary, it is not clear from the above analysis of the Beverton and Holt stock recruit relationships whether $\log(R)$ or $\log(R/E)$ is the more informative index. In most stocks there is no correlation between R and E, indicating the majority of the data points are not in the low stock situation and thus indicate recruitment is a complex function of density independent and density- or stockdependent mortalities. In the subsequent analyses presented here, time series of both log R and log R/E have been used.

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2.2.2 Independence of Observations

The recruitment time series of many fish stocks are auto-correlated (Koslow *et al.*, 1987). This indicates the effective number of independent observations for a given statistic (n*) may be less than the total number of observations (n) in the series. Therefore using n in assessing the significance of a test statistic may result in an artificially high level of confidence. For example, the sample mean is defined by

$$\overline{X} = \frac{1}{n} \sum_{i=1}^{n} X_{i}$$

and if X_i are independent observations with variance $var(\overline{X})$

$$\operatorname{var}(\overline{X}) = \frac{\operatorname{var}(X)}{n}$$

respectively. When the observations are auto-correlated the variance of the mean is

$$\operatorname{var}(\overline{X}) = \frac{\operatorname{var}(X)}{n*}$$

where

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$$\frac{1}{n*} = \frac{1}{n} + \frac{2}{n^2} \sum_{j=1}^{n} (n-j)\rho(j)$$
 2.6

and $\rho(j)$ is the true auto-correlation of X at lag j (Bayley and Hammersley, 1946). It indicates that for n = 15, and an auto-time series ($\rho(1) = 0.5$; $\rho(j) = 0$ for j > 1), the effective number of observations is approximately one half the number of data points (n* = 8).

When testing the hypothesis that the Pearson Product-Moment correlation coefficient is equal to zero (r = 0) the standard approach is to use the Student's t test statistic (t_s) in which $t_s = r/sr$, where sr is the standard error of r and is given by

$$sr = \left(rac{1-r^2}{n-2}
ight)^{1/2}$$

When the time series are auto-correlated, Garrett and Toulany (1981) have suggested that n be replaced with n* where n* is calculated using eq. 2.6 and the $\rho(j)$'s are calculated from the cross-product series of the two time series being compared. Although this formulation assumes there are a large number of observations it has been used in recruitment analyses (Koslow *et al.*, 1987) in which n is small.

2.3 Statistical Methods

There are standard multivariate statistical techniques available to test the null hypothesis that a number of stationary, serially uncorrelated time series, with normally distributed observations, are independent. In order to use these tests on recruitment data, the original time series must be prewhitened, i.e. remove the trend and serial correlation.

2.3.1 Filtering

Several methods can be used to remove the trend. The most common use moving averages, polynomial regressions or variate-differences (Legendre and Legendre, 1983). All of these have been used with respect to fisheries catch or recruitment series (see Table 2.2 for examples). The high pass, first difference filter $(\nabla X = X_t - X_{t-1})$ is used here since i) it has been used by Cohen *et al.* (1986) in their analyses of the Koslow (1984) time series, ii) it reduces the time series by only one data point and iii) it proved adequate.

Variate-difference filters, such as the first difference filter, remove trend. Each application of the first difference reduces the degree of a polynomial by one. The method does not remove auto-correlation associated with periodicity or exponential processes (Kendall and Stuart, 1966).

The gain function of the first difference filter (Figure 2.1) shows that it removes more than 50% of the low frequency recruitment variance and the high frequency variance is amplified by a factor of two. The filter shifts the variance toward higher frequencies. These effects are illustrated by two examples.

FILTER	SOURCE
Low Pass	
moving average	Welch (1986)
running median (5 yr)	Hollowed et al. (1987)
low order polynomial	Mysak et al. (1982)
High Pass	
first difference	Cohen et al. (1986)
and a second state of the	Winters & Wheeler (1987)

TABLE 2.2 : Examples of low and high pass filters applied to fisheries catch and recruitment time series.

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FIGURE 2.1 Gain function of the first difference filter (after Jenkins and Watts 1968).

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2.3.2 Linear Trend Model

The first example is that of a time series with a simple linear trend. Let

$$X_t = \beta_o + \beta_1 t + \epsilon_t \qquad 2.7$$

where ϵ_t is a white noise process with zero mean and variance, $\sigma^2 N(0, \sigma^2)$. The first difference of eq. 2.7, $\nabla X = \beta_1 + \epsilon_t - \epsilon_{t-1}$, has eliminated the linear trend, but the auto-correlation function

$$ho(j) = \left\{egin{array}{cccc} 1, & j = 0 \ & & \ & \ & & \ &$$

shows serial correlation has been introduced. A polynomial regression of order one (linear regression) removes both the trend and serial correlation.

2.3.3 Sinusoidal Model

The second example is that of the simple sinusoid

$$X_t = \sin(\omega t + \phi) \tag{2.8}$$

in which ω is the angular frequency and ϕ is the phase. The first difference of this process is given by

$$abla X_t = 2\sin(\omega/2)\sin[\omega(t-1/2)+\phi+\pi/2]$$

The first difference has therefore changed the amplitude of the sinusoid from 1 to $2\sin(\omega/2)$ and has shifted the phase from by $(\pi - \omega)/2$.

To cast these changes in the context of a recruitment series assume eq. 2.8 represents a low frequency variation with a period of T = 20 years ($\omega = 2\pi/20$). First differencing reduces the amplitude of this signal by a factor of $2\sin(\omega/2) = 0.3$. In contrast, if (2.8) represents a high frequency signal with a period of 4 years ($\omega = 2\pi/4$), then the first differencing amplifes the amplitude of this signal by a factor of 1.4.

2.3.4 Serial Correlation

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In order to test the hypothesis that the observations within the unfiltered and filtered series are independent, the auto-correlation, runs test and phase length test were used. The auto-correlation function is commonly used and is described in Priestly (1981). It has the advantage that it gives some insight into the structure of the serial correlation and the disadvantage that it generally requires at least 50 to 100 observations to give statistically reliable results (Box and Jenkins, 1976; Shepherd *et al.*, 1984), although Johnson *et al.* (1986) have recently proposed a method for assessing the significance of auto-correlations when they are based on small sample sizes. The non-parametric runs and phase length tests on the other hand have the advantages that they do not require large data series , they are easy to apply, and only assume that the data are symmetrically distributed. The disadvantage of these tests is that they give less information about the form of the serial correlation.

The runs test has previously been used to assess the presence of temporal persistence in recruitment series by Rothschild and Brunneister (1984) and Rothschild (1986) and it is described by Draper and Smith (1966) and Ryan *et al.* (1981). In the present analysis the runs were calculated on the variations about the median using the MINITAB RUNS command (Ryan *et al.*, 1981). The phase length test is described by (Wallis and Moore, 1941; Kendall and Stuart, 1966) and is recommended by Legendre and Legendre (1983) as a test for periodicity rather than trend.

2.3.5 Normality

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Once the time series are pre-whitened they are checked for normality using the MINITAB NSCORE, PLOT and CORRELATION commands. These produce a correlation coefficient for the normal probability plot which is compared with a critical value. The method is based on the Shapiro-Wilk test and the Probability Plot Correlation Coefficient Test described by Filliben (1975). It is described in Ryan *et al.* (1981).

2.3.6 Pattern Detection

In order to test the hypothesis that the haddock recruitment series are independent of the cod recruitment series, the correlation between each pair of prewhitened log-transformed recruitment series is first calculated. The hypothesis that each species grouping is independent of the others is tested using the greatest eigenvalue criterion (Morrison, 1976). A comparison of this eigenvalue against a critical value which depends upon the number of cod recruitment series (p_1) , the number of haddock recruitment series (p_2) , the number of observations within each series (n) and the chosen significance level determines the significance of the interspecies interaction. In the present analyses the recruitment series are two species groupings (cod and haddock) with the cod grouping having 6 series $(p_1 = 6)$ and the haddock grouping having 3 $(p_2 = 3)$. Each of the series has 13 observations (n = 13). The sample correlation matrices of cod- cod (S_{11}) , haddock-haddock (S_{22}) and codhaddock (S_{12}) interactions are formed and the greatest eigenvalue of $S_{11}^{-1} S_{12} S_{22}^{-1} S_{12}'$ is calculated (' denotes transpose).

In order to test the hypothesis that p recruitment series of length n are independent, three tests are used and compared. These are i) Bartlett's Statistic (B) used by Shepherd *et al.* (1984), ii) the largest eigenvalue (λ_1) of the correlation matrix (S) and iii) the mean correlation of the correlation matrix (\bar{r}) - a new statistic described below.

Bartlett's Statistic is given by

$$B=-\left(n-rac{2p+11}{6}
ight)\log |S|$$

where |S| denotes the determinant of S. This statistic is useful when the correlations between the series are not necessarily all of the same sign, i.e. the synchrony between the stocks may be positive between some and negative between others. The critical value of the B statistic is obtained from the chi-squared distribution with p(p-1)/2degrees of freedom when n is large. However, for small values of n, such as those of the cod and haddock series, the chi-square distribution is not appropriate and the critical values must be empirically calculated as described below.

The largest eigenvalue test is based on λ_1/p which is the proportion of the total standarized variance (p) explained by the first principal component. As with Bartlett's statistic the correlations need not be of the same sign. This statistic is generally preferred as a general test since the eigenvector associated with λ_1 estimates the spatial pattern of the synchronous component.

The mean correlation \overline{r} is the arithmetic mean of the off-diagonal elements in the correlation matrix. This statistic is less general than the other two in that it is most effective when the actual correlations between the component series are of the same sign and magnitude. As with the other statistics the critical values for this statistic for these tests are estimated empirically.

2.3.7 Critical Values and Power of Test Statistics

In order to determine the critical values of the above test statistics Monte Carlo simulations of the null hypothesis that the time series are independent were conducted. Although these values vary with the number of recruitment series (p)and their length (n), simulations were conducted for n = 13, p = 6 and p = 3only since these values correspond with the lengths and number of the cod and haddock stocks to be analysed here. In each simulation the series were generated, using a random number generator, under the assumption that the data points are ,

independent and normally distributed with unit variance and zero mean. The test statistics were calculated after each simulation and the process repeated 1000 times. The critical value was then chosen for each statistic such that 5% of the simulated values were greater than this value. This ensures the probability of making a Type I error, that of rejecting the null hypothesis when it is in fact true, is 0.05.

The power of the tests was estimated for a single form of synchrony only: a positive and equal correlation between each series. The power for a range of correlations was estimated by repeating the Monte Carlo procedure and generating each time series so that it had the form

$$X_{ij} = a\epsilon_i + \epsilon_{ij}$$
 $i = 1, n$ $j = 1, p$

where ϵ_i and ϵ_{ij} are N(0,1), $a\epsilon_i$ is the component common to all p series and the strength of the correlation between the time series is determined by a. The value of a for a simulation is related to the true correlation (ρ) between the series by

$$\rho = \frac{a^2}{1+a^2}$$

The proportion of the simulations for which the critical values were exceeded determines the power of the statistic to detect this form of synchrony.

2.4 Data for $\log(\mathbf{R})$ and $\log(\mathbf{R}/\mathbf{E})$

The time series of haddock and cod year-class sizes analysed here are the same as those used by Koslow (1984) and Cohen *et al.* (1986). The number of recruits were therefore obtained by lagging the first age class in the numbers-at-age matrices of published virtual population analyses (Table 2.3) back to the year of birth. Following Koslow (1984) the time series are terminated with the 1975 year-class in order to remove the most recent years of the VPA numbers-at-age matrix since these are the least reliable (Pope, 1972). Unlike Koslow (1984) and Cohen *et al.* 1

(1986), time series of egg production were also estimated. This was done in order to test whether the correlations between recruitment series are due to egg production.

2.5 Egg Production

The annual production of eggs (E) for each stock was estimated as

$$E = \sum_{A=1}^{n} N(A)S(A)M(A)F(A)$$

where N(A) is the number of fish of age A, S(A) is the sex ratio, M(A) is the maturity ogive and F(A) is the fecundity relationship. N(A) was obtained from the numbers-at-age matrices and the sex ratio was assumed to be 0.5 for all ages.

Estimates of the maturity ogives exist for all of the haddock and cod stocks with the exception of cod 1 (Table 2.4). Although, the ogives may vary between stocks and through time (Beacham, 1983), these changes are not documented for all the stocks. The constant ogive

$$M(A) = \begin{cases} 0 & 1 \le A \le 2 \\ \frac{A-2}{4} & 2 \le A \le 6 \\ 1 & 6 \le A \end{cases}$$

was therefore used. A sensitivity analysis investigating the effect of A on the egg production series showed that the trend in egg production general is relatively insensitive to this parameter.

Few cod and haddock fecundity-age relationships are available (Table 2.5) and despite the fact that fecundity relationships are known to vary between stocks (Schopka and Hempel 1973; Waiwood and Buzetta 1989) the exponent of this relationship usually has a value of approximately 2. The values of the proportionality constant (Table 2.5), although different between stocks and important when estimating the absolute annual egg production, do not affect the comparisions between

TABLE 2.3: Data sources. Location is that of the major spawning ground. The years contained within the virtual population analyses (VPA) numbers-at-age matrix are shown in the column labeled VPA. Age is the age of fish in the first row of the numbers-at-age matrix. R is the span of years in which the year-classes (R) were born. E is the span of years for which an estimate of stock egg production was made. The numbers in brackets are the number of years in the time series.

STOCK	LOCATION	VPA	YOUNG- EST AGE IN VPA	R	E	SOURCE		
Haddock				, <u>, , , , , , , , , , , , , , , , , , </u>		<u>, , , , , , , , , , , , , , , , , , , </u>		
4TvW	Sable Island-							
	Emerald Bank	1960-79	1	1959-75 (17)	1960-75 (16)	1		
4X	Browns Bank	1962-80	1	1961-75 (15)	1962-75 (14)	2		
5Ze	Georges Bank	1931-78	1	1950-75 (26)	1950-75 (26)	3		
Cod								
i	West Greenland	1965-82	3	1962-75 (14)	1965-75 (11)	4		
2 J 3KL	Labrador	1962-81	4	1958-75 (18)	1962-75 (14)	5		
3N O	Grand Banks	1959-81	3	1956-75 (20)	1959-75 (17)	6		
3Ps	St. Pierre	1959-80	3	1956-75 (20)	1959-75 (17)	7		
4TVn	Gulf of St.							
	Lawrence	1950-81	3	1950-75 (26)	1950-75 (26)	8		
4VsW	Sable Island	1958-81	1	1957-75 (19)	1958-75 (18)	9		
SOURCES:	1) CAFSAC RES	DOC 80/61	1					
	2) CAFSAC RES DOC 81/24							
	3) J. Northw. At	l. Fish. Sci	., 3:1-27					

- 4) NAFO SCR DOC 82/vi/50
- 5) NAFO SCR DOC 82/ix/111
- 6) NAFO SCR DOC 82/vi/57
- 7) CAFSAC RES DOC 81/39
- 8) CAFSAC RES DOC 81/41
- 9) CAFSAC RES DOC 82/40

where CAFSAC denotes Canadian Atlantic Fisheries Scientific Advisory Council and NAFO denotes North Atlantic Fisheries Organization.

STOCK	SOURCES	YEAR(S) IN WHICH OGIVE ESTIMATED
HADDOCK	+	
4 V n	Beacham (1983b)	1959-64, 1970-79
4 V s		1959-64, 1965-69, 1970-74, 1975-79
4 W		1958-64, 1965-69, 1970-74, 1975-79
4 X	Beacham (1983b)	1959-64, 1965-69, 1970-74, 1975-79
	Clark (1959)	1949-50
	Kohler (1959)	1953
$5\mathrm{Z}$	Clark (1959)	1949-50
	Clark	
	et al. (1982)	1968-72, 1973-75
COD		
1	n a	n a
2 J 3 K L	Fleming (1960)'	1947-50
3 N O	Fleming (1960)'	1947-50
3 P s	Fleming (1960)'	1947-50
3 P n	Pinhorn (1969)	1952, 1957
4TVn	Beacham (1983a)	1954-64, 1965-69, 1970-74, 1975-79
4VsW	Beacham (1983a)	1959-64, 1965-69, 1970-74, 1975-79

TABLE 2.4: Sources of maturity ogives and fecundity relationships for cod and haddock in the Northwest Atlantic. (na – not available; ' – male and female ogives combined)

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the series of $\log(R/E)$ unless the constant varies inter-annually. The constant relationship of $F = A^2$ is therefore used.

2.6 Results

The location of the haddock and cod stocks referred to in this chapter are shown in Figure 2.2. The time series of $\log(R)$, $\log(E)$, $\nabla \log(R)$ and $\nabla \log(E)$ are shown in Figures 2.3 and 2.4. From these plots it is obvious that the $\log(E)$ time series are much smoother than the $\log(R)$ series and suggests that much of the recruitment variation is not due to annual variations in egg production. This interpretation is supported by the lack of correlation between $\log(R)$ and $\log(E)$ and is consistent with the lack of stock and recruitment relationships for these stocks (Koslow *et al.*, 1987).

2.6.1 Single Series Statistics

As expected many of the haddock and cod time series of year-class size $(\log R)$, annual egg production $(\log E)$ and pre-recruit mortality $(\log R/E)$ are autocorrelated. According to the runs test all of the $\log(E)$, 6 of the 9 log R (cod 2J3KL, 3N0, 4TvN and haddock 4VW, 4X and 5Z) and 5 of the 9 log R/E (cod 4TvN, 4VsW and haddock 4VW, 4X and 5Z) are serially correlated. The auto-correlation functions suggest all of the log R series are serially correlated (Figure 2.5). Although linear regression analyses of log(R) against time indicate significant ($\alpha = 0.05$) linear trends are present in only cod 2J3KL, cod 3N0 and haddock 5Z, polynomial regressions of the haddock log(R) series indicate the higher order quadratic and cubic terms can account for up to 85% of the variance (regression results not shown).

The first difference filter effectively removes this auto-correlation. This is illustrated by comparing auto-correlation functions of the $\log(R)$ and $\nabla \log(R)$ series (Figure 2.5) and is also indicated by the similarity of the variances for the first and

STOCK	FECUNDITY RELATIONSHIP	SOURCE
HADDOCK		
Grand Bank	$F = 7,456 A^{2.005}$	Hodder (1963)
North Sea	$F = 12,621 A^{1.88}$	Alekseyeva &
		Tormosova (1980)
COD		
Newfoundland &	$F = 21,510 A^{1.95}$	May (1967)
Labrador		

TABLE 2.5: Fecundity-age relationships for haddock. (A = age in years; F = fecundity)

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1 10 1 FIGURE 2.2 Location of the ICNAF statistical designations used to identify the haddock and cod stocks referred to in this chapter.

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Figure 2.2

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FIGURE 2.3 Time series of log(R) and $\nabla log(R)$ for cod and haddock stocks of the Northwest Atlantic.

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FIGURE 2.4 Time series of log(E) and $\nabla log(E)$ for cod and haddock stocks of the Northwest Atlantic.

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Figure 2.4

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FIGURE 2.5 Auto-correlation functions of the cod and haddock recruitment series. Solid lines are for log(R) and dashed lines are for $\nabla \log(R)$.

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second differenced series (Table 2.6). In all of the $\log(R)$, $\log(E)$ and $\log(R/E)$ series, with the exceptions of the cod 3Ps, 4TVn and haddock 5Z series of $\nabla \log(E)$, the runs test does not reject the hypothesis of independence at the 0.05 significance level. The phase length test does not reject this hypothesis for all series with the exceptions of the $\nabla \log(R)$ and $\nabla \log(R/E)$ cod 2J3KL series. All of the first differenced series are consistent with the assumption of normality.

Having established that the low frequency variation is effectively removed by the first difference filter, it is of interest to know how much of the total variance in $\log(R)$ remains and how much is removed. This is indicated for each stock by the ratio of the variance in the first differenced series to that in the original, undifferenced series. In the haddock, 20-67% of the recruitment variance is within the high frequency band and in the cod 14-58% of the variance is within this band (Table 2.6).

These results indicate that approximately 40% of the recruitment variance occurs in the high frequency band, the band which includes variation with periods shorter than about three years. Sixty percent of the variance is therefore associated with the low frequency band.

2.6.2 Test Statistics and Synchrony

The power of these statistics is plotted in Figure 2.6. All statistics are capable of detecting correlations of 0.5 or larger. The mean correlation statistic is substantially more powerful for detecting weak correlation (p < 0.5) of the form specified here than are the largest eigenvalue or Bartlett's Sphericity tests.

2.6.3 Inter- and Intra-Species Dependence

The correlation matrices for the $\log(R)$, $\log(E)$ and $\log(R/E)$ comparisons are presented in Table 2.7. The first differencing reduces the correlations such that the mean values of the haddock-haddock, cod-cod and cod-haddock are reduced from 0.76 to 0.61, 0.51 to 0.38 and 0.38 to 0.09, respectively. The correlation matrix of TABLE 2.6: Total variance of the $\log(R)$, $\nabla^1 \log(R)$ and $\nabla^2 \log(R)$ time series. The variance for the ∇^1 and ∇^2 series has been divided by 2 and 6, respectively to correct for variance amplification generated by the difference filter (Kendall and Stuart, 1966). B/A and C/A are the proportions of the total variance in the $\log(R)$ series that remains after first and second differencing.

STOCK	$\operatorname{A}_{\log(R)}$	$\mathrm{B} abla^1\log(R)$	$\mathrm{C} abla^2\log(R)$	B/A (%)	C/A (%)
Haddock					
4vW	0.25	0.05	0.03	20.0	12.0
4 X	0.18	0.12	0.11	66.7	61.1
5Ze	0.83	0.37	0.33	44.6	39.8
Cod					
1	0.19	0.11	0.11	57.9	57 . 9
2J3KL	0.06	0.01	0.004	16.7	6.7
3NO	0.07	0.01	0.01	14.3	14.3
3Ps	0.02	0.01	0.01	50.0	50.0
4 TVn	0.04	0.02	0.01	50.0	25.0
4VsW	0.01	0.004	0.003	40.0	30.0

FIGURE 2.6 Power of the test statistics used to detect within species synchrony when the synchrony has the form of equal correlations between each series. $\pi(\rho)$ is the probability of correctly detecting the synchrony.

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the $\log(R/E)$ correlations is very similar to that of the first differenced $\log(R)$ series indicating the variation in egg production does not strongly influence recruitment comparisons. The analyses of $\log(R/E)$ were therefore not continued.

As expected from the low value of the mean cod-haddock correlation (\overline{r} for $\nabla \log(R) = 0.09$) the largest eigenvalue test does not reject the hypothesis that the first differenced $\log(R)$ cod and haddock recruitment series are independent. Similarly, the suggestion that the haddock series are positively correlated and that the cod series are positively correlated is supported by the test statistics calculated using $\nabla \log(R)$ (Table 2.8). The low correlation between the cod stocks accounts for the inability of the Bartlett's Sphericity statistic to detect the cod synchrony.

2.6.4 Spatial Scale of Recruitment Dependence

Although the above tests indicate whether the recruitment series are independent of each other, they do not describe the pattern of dependence. As suggested previously, the simplest pattern may be that of a single common signal between stocks, i.e. equal correlation between stocks. This is the form assumed here for comparing the power of the statistical tests and is the form underlying the development of the mean correlation test. It is therefore of interest to test whether the recruitment series are in fact equal. The Lawley test (described in Morrison, 1976) tests this hypothesis and when it is applied to the haddock and cod correlation matrices the hypothesis can not be rejected. The correlations between the codcod and haddock-haddock recruitment series can therefore be considered as being equal, indicating the correlations do not decrease with increasing distance between the stocks and that the values of the mean correlations are representative of the real correlation between these stocks.

2.7 Summary and Discussion

The main purposes of this chapter are to 1) outline some of the statistical problems associated with comparing recruitment time series and thus inferring the

TABLE 2.7: Correlation matrices for A) $\log(R)$, B) $\nabla \log(R)$ and C) $\nabla \log(R/E)$. The mean correlations for cod-cod, haddock-haddock and cod-haddock submatrices are underlined.

A)	log	(R)
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***	COD						HADD	оск	
STOCK	1	2 J 3 K L	3 N O	3 P s	4TVn	4VsW	4VW 4	X 5Z	
1	1.00								
2 J 3 K L	0.82	1.00				0.51		0.38	
3 N O	0.58	0.78	1.00		• .				
3 P s	0.72	0.58	0.39	1.00					
4TVn	0.36	0.21	-0.20	0.46	1.00				
4VsW	0.68	0.70	0.82	0.59	0.17	1.00			
4 V W	0.54	0.73	0.63	0.51	0.26	0.55	1.00	0.76	
4 X	0.35	0.25	0.11	0.40	0.20	0.04	0.64 1	.00	
5 Z	0.55	0.56	0.40	0.38	0.20	0.28	0.82 0	.81 1.00	

B) FIRST DIFFERENCE log(R)

COD					HAI	DOC	K		
STOCK	1	2 J 3 K L	3 N O	3Ps	4TVn	4VsW	4 V W	4 X	5 Z
1	1.00								
2 J 3 K L	0.50	1.00				0.38			0.09
3 N O	0.05	0.36	1.00						
3 P s	0.34	0.47	0.45	1.00					
4TV n	0.62	0.35	0.04	0.43	1.00				
4VsW	0.44	0.24	0.41	0.53	0.54	1.00			
4 V W	-0.34	0.31	0.64	0.24	-0.01	-0.03	1.00		0.61
4 X	0.08	0.22	0.48	0.16	-0.32	-0.14	0.55	1.00	
5 Z	0.16	0.13	0.30	0.05	-0.14	-0.16	0.47	0.81	1.00

C) FIRST DIFFERENCE $\log(R/E)$

	COD					HA	DDOC	К		
STOCK	1	2 J 3 K L	3 N O	3Ps	4 T V n	4VsW	4 V W	4 X	5 Z	
1	1.00									
2 J 3 K L	0.43	1.00				0.40			0.13	
3 N O	0.04	0.35	1.00							
3 P s	0.42	0.41	0.39	1.00						
4TVn	0.79	0.46	0.20	0.38	1.00					
4VsW	0.34	0.41	0.59	0.36	0.48	1.00				
4VW	-0.45	0.41	0.68	0.39	-0.08	0.15	1.00		0.53	
4 X	-0.09	0.23	0.46	0.22	-0.26	-0.10	0.49	1.00		
5 Z	0.18	0.22	0.45	0.09	-0.08	-0.11	0.32	0.78	1.00	r

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TABLE 2.8: Values of the test statistics calculated to test the null hypothesis of within species independence of log transformed and first differenced cod and haddock recruitment series. The test statistics are described in the text along with the derivation of the significance levels. (* indicates significance at the 5% level)

TEST STATISTIC	HADDOCK	COD
В	14.1 *	18.6
$\lambda_1/{ m p}$	0.73 *	0.48 *
\overline{r}	0.61 *	0.38 *

importance of environmental factors, 2) rigorously test the null hypothesis that recruitment series are independent and 3) to re-examine the relationships between the recruitment time series of the Northwest Atlantic haddock and cod.

The main statistical problems that must be addressed when comparing recruitment time series are that the series are generally short and auto-correlated. If standard multivariate statistical procedures are to be used, the trend and autocorrelation must be either removed or accounted for in the determination of test statistic critical values.

The method adopted here is that of pre-whitening using the first difference filter. This is a commonly used and simple high pass filter which is useful for short time series since it reduces the time series by only one data point. It removes or reduces the polynomial trend component and amplifies the non-trend variance.

When this method is applied to the haddock and cod recruitment series of the Northwest Atlantic the first difference filter removes approximately 60% of the variance in the log transformed recruitment series. This may not be disadvantageous however, if the low frequency component is an artifact of the VPA analyses (Shepherd *et al.*, 1984) or if it is related to stock rather than environment effects.

Of the 40% that remains it is demonstrated that the cod recruitment series are positively correlated and the haddock recruitment series are positively correlated, but the cod series are not correlated with the haddock series. Although this supports Koslow's (1984) suggestion that large scale physical forcing rather than local biological interactions are the dominant cause of recruitment variation, this support needs to be qualified. The mean correlations between the cod recruitment series and the haddock recruitment series are 0.38 and 0.61, respectively. This indicates that only 14% (cod) and 37% (haddock) of the high frequency variance is common to all of the stocks within each species. Considering that only 40% of the variance in recruitment is within this frequency band to begin with, the large scale synchrony accounts for only a small proportion of the total variance. This estimate may represent a lower bound on the importance of the synchrony for if the synchrony is of the strength indicated by the unfiltered $\log(R)$ recruitment series the percentage due to the synchrony increases to between 26 and 58% of the total variance. The real strength of the synchrony probably lies between these two extremes at approximately 35-40%.

Whether the forcing is large scale or local, the stock and recruitment results and theory presented here indicate that detecting the variables controlling recruitment through the correlation approach will be very difficult because of the low signal to noise ratio and because the year-class size is likely to be determined by a complex series of density- and stock-dependent processes as well as density-independent processes. A better understanding of the factors controlling recruitment and the distribution of the early life stages requires more process oriented research focused on local environments.

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CHAPTER 3

Spawning Time and Egg Stage Duration in Northwest Atlantic Haddock With Emphasis on Georges and Browns Bank

3.1 Introduction

Spawning times and locations of marine fishes are generally considered to have evolved so that upon hatching the larval stage emerges into favorable environmental conditions (Scott 1979; Bye 1984). The environmental conditions at the time of emergence may differ from year to year due to variation in the timing and magnitude of the environmental conditions, variation in the timing of spawning and larval emergence or to a combination of both. Quantifying this variation, and defining the mechanisms causing it, is important to an understanding of the dynamics of the early life stages of fish and of year-class size formation (Rothschild 1986, Cushing 1975).

Analyses of recruitment variation in temperate marine fishes often assume both constant spawning time and age of eggs at hatching. Delays or advances of 10 days or less in spawning time are common and standard deviations of spawning times, estimated from detrended time series, are of order 5 days (Table 3.1). The range in the time of peak spawning may be as large as 30 days (plus or minus 3 standard deviations). Since much of the variation in year-class size is often associated with one to two extreme year classes (Shepherd *et al.* 1984), the assumption of constant spawning times and early life stage ages may, therefore, not always be appropriate. 21/20

The importance of taking spawning time into consideration has been highlighted for haddock by Chase (1955). His correlation between haddock year class strength on Georges Bank and regional winds was improved considerably when variable spawning times were used to define the temporal window over which the annual estimate of the wind index was calculated.

SPECIES and STOCK	TIME OF OBSERV. (years)	No. of Obs.	COMMENTS	SOUR	CE
A) Trends				- <u></u>	
Arcto-Norwegian Cod	1894-1968	74	smooth trend in time of peak catch trend amplitude ca 10 days	1 ; 	
	1929-1982	54	linear trend spanning a 1 week delay in time of median spawning intensity,	2	
Southern Bight Plaice	1911-1950	8	no detectable trend	1 1	
Fraser River Sockeye Salmon	1950-1966	7	no dectable trend time of peak catch	1	
Norwegian Herring	1931-1936	6	1 to 2 week delay in spawning time	μ	
B) Variation About Tre	nd		STANDARD DEVIATION (days)	RANGE	
Newfoundland Capelin	1966-198	2 15	i –	19 day	4
Southern Bight Plaice	1911-195	0 8	7	-	1
Norwegian Herring	1 931-193	66	6	-	1
Georges Bank Herring	1963-197	3 11	5.9	19 days	3
Fraser River Sockeye Salmon	1950-196	6 17	4.9	3 weeks	1
Arcto-Norwegian Cod	1894-196	8 74	4.1 2.2	20 days 35 days	1 2

TABLE 3.1: Inter-annual variation in the time of peak spawning for some north temperate and high latitude fish stocks.

Sources: 1- Cushing (1969); 2- Pedersen (1984); 3- Berenbeim and Sigaev (1978); 4- Leggett, Frank & Carscadden (1984); 5- Rothschild, (1986) .

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Haddock generally spawn during the first six months of the year (Hislop 1984, O'Boyle et al. 1984). The duration of the spawning season for each stock is typically 3 to 4 months with a peak spawning period of about one month. As with other fish species, spawning occurs progressively later in higher latitudes (Bigelow and Welch 1925, Theilacker and Dorsey 1980, Hislop 1984).

The date of spawning in some haddock stocks is highly variable. On Georges Bank, for example, the date of peak spawning can differ by 2 to 3 months (Marak and Livingstone 1970), a range much greater than for other north temperate marine fish species (Table 3.1). As with several other species (see Hela and Laevastu 1961 for a review; Colton 1968a, Marak and Livingstone 1970, Smith et al. 1979) spawning date co-varies with water temperature. On Georges Bank anomalously cold (warm) years corresponded with delayed (advanced) spawning such that a 1.5 to 2.0 °C change in the mean water temperature during March and April resulted in a one month shift in the time of spawning (Marak and Livingstone 1970). Whether spawning time varies in relation to temperature in other Northwest Atlantic haddock stocks, such as the Browns Bank stock, is not known.

Temperature also effects the age of the egg stage (Walford 1938; Laurence and Rogers 1976) and since sea surface temperatures in the Northwest Atlantic are one of the most variable in the world (Thompson *et al.* 1988) the age of egg stages may also be highly variable. The only documented egg age - temperature relationship for haddock is linear (Laurence and Rogers 1976), whereas relationships for other species are usually non-linear (see general review in Blaxter 1969 and recent examples in Table 3.2). In a recent analysis of several dozen species of marine teleosts, Pauly and Pullin (1988) showed that for a given egg size the relationship between egg stage age and incubation temperature was non-linear. Consequently, a non-linear relationship may be more appropriate for haddock as well.

The objectives of this chapter are threefold. First, compile, from the literature, estimates of haddock spawning time in the northwest Atlantic, and use these to quantify the variability in spawning time and to test the hypothesis that spawning

RELATIONSHIP	SPEC	CIES	SOURCE(S)						
Polynomial (1st O	Polynomial (1st Order): $A = a + bT$								
	Haddock	(Melanogrammus aegelfinus)	Laurence & Rogers (1976)						
	Cod	(Gadus morhua)	Laurence & Rogers (1976)						
Polynomial (2nd (Order): $A = a + bT$	$+ cT^2$							
	Garfish	(Belone belone)	Fonds, Rosenthal & Alderdice (1974)						
Exponential: $A =$	$a \exp(bT)$								
	Pacific sardine	(Sardinops sagax)	Smith (1973)						
	Cod	(Gadus morhua)	Hela & Laevastu (1961)						
			Thompson & Riley (1981)						
	Herring	(Clupea harengus)	Hela & Laevastu (1961)						
	Pacific (Sardinops sardine	Hela & melanosticta)	Laevastu (1961)						
Power: $A = aT^b$									
	Sole	(Solea solea)	Riley (1974)						
	Pacific Sardine	(Sardinops caerulea)	Lasker (1964)						
	Capelin	(Mallotus villosus)	Frank & Leggett (1981)						
	Sprat	(Sprattus sprattus)	Thompson, Milligan & Nichols (1981)						
	Hake	(Merluccius merluccius)	Coombs & Mitchell (1982)						
Other Non-linear	Forms								
	Plaice	(Pleuronectes platessa)	Ryland, Nichols & Sykes (1975)						

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TABLE 3.2: The functional form of age-temperature relationships for fish eggs.

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time variation is correlated with water temperature. Second, compile a data base of haddock egg development rates measured at constant incubation temperatures and use this to derive a robust calibration curve relating incubation temperature to egg stage age. Third, estimate the historical variation in the age of the haddock egg stage from time series of sea surface temperatures from the southwestern Nova Scotia-Gulf of Maine region.

3.2 Data Sources

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3.2.1 Spawning Time

There are at least six haddock stocks in the northwest Atlantic (Martin 1953; Templeman 1953; Grosslein 1962; Kohler 1968). The location of the major spawning grounds are shown in Figure 3.1.

The abundance of early stage eggs from three or more time periods during the expected period of spawning was used to construct annual spawning curves. Only the abundances of early stage eggs were used because the abundances of late stage eggs or larvae may not accurately reflect the true spawning curve (see Hurley and Campana 1989, Campana *et al.* 1989). Most of the available spawning time data pertains to the Georges and Browns Banks haddock stocks.

On Georges Bank, multiple ichthyoplankton surveys have been conducted during the haddock spawning season in at least sixteen years between 1931 and 1983. However, the abundances of early stage eggs were reported in only eight years and only in two years was the spawning peak clearly defined (Table 3.3). In five of the eight years sampling commenced during peak spawning. Seven of these years (1931-1968) were used by Marak and Livingstone (1970) in an analysis of spawning time variation on Georges Bank. The eighth year is reported as 1979-80 since the abundance data was an aggregate of abundances estimated from cruises in the two separate years. FIGURE 3.1 The location of the major spawning grounds of northwest Atlantic haddock stocks. (GM - Gulf of Maine; GB - Georges Bank; BB -Browns Bank; SE - Sable-Emerald; SP - St. Pierre; SGB - Southern Grand Bank) ļ

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TABLE 3.3: Spawning times of haddock populations in the Northwest Atlantic as indicated by ichthyoplankton surveys (P - time of peak egg production; c - a composite of several, T1- mean water temperature during March and April at Boothbay Harbour, T2-mean water temperature during August through March at Boothbay Harbour; - indicates peak spawning extended outside the sampled time period).

YEAR	NUMBER OF CRUISES	MONTH						SOURCE	T1 (°C)	T2 (°C)	
Georges Bank		J	F	М	A	М	J	J			
1931	(3)			-P					1	5,1	7.8
1940	(5)				Р	Р			2	0.6	5.0
1941	(4)			-P	Ρ				2	3.6	6.8
1953	(3)			-P					2	6.8	9.6
1955	(4)		-P	Ρ					2	5.5	9.4
1956	(5)		-P	Ρ	Ρ				2	4.2	8.7
1968	(6)				Ρ				2	2.6	6.6
1979-80 с				Ρ					4		
mean				Ρ							
Browns Bank		J	\mathbf{F}	М	A.	М	J	J			
1931	(3)				Р				1	5.1	7.8
1953	(3)				Ρ				5	6.8	9.6
1955	(4)				Ρ				6	5.5	9.4
1956	(5)				Ρ				7	4.2	8.7
1979-80 с						P-			4	-	
1983	(5,8)				Р				3,8	3.8	7.9
1984	(5)				Ρ				8	3.2	8.5
1985	(5)				Р				8	4.2	8.0
mean					Ρ						

Sources: 1- Walford (1938), 2- Marak and Livingstone (1970), 3- Koslow et al. (1985), 4- Smith and Morse (1985), 5- Marak and Colton (1961), 6-Marak, Colton and Foster (1962), 7- Marak, Colton, Foster and Miller (1962), 8- Campana (pers. comm.) On Browns Bank, there are also eight years in which egg abundances have been reported for three or more surveys conducted during the winter-spring period. In all years, except the 1979-80 aggregate, the spawning peak was clearly defined (Table 3.3).

The accuracy of the spawning time estimates is difficult to assess. However, the estimates of egg abundance are typically two to four weeks apart, indicating variation in the spawning time at these or shorter time scales cannot be resolved.

3.2.2 Duration of Haddock Egg Stages

The age and corresponding incubation temperatures at which haddock and cod eggs develop the morphological characteristics corresponding to the stage descriptions given in Table 3.4 were gathered from the literature. The data was extracted from the original sources because many of the sources cited in general reviews of the life history of fish (e.g. Hardy 1978, Bigelow and Welch 1925, Russell 1976, Leim and Scott 1966) are not the original sources and a listing of data derived from these sources showed frequent replication. The compiled data base of ages, incubation temperatures and sources is given in Appendices 3A-D. Information on cod eggs was included because in field samples the early stages of haddock eggs cannot be distinguished from those of the cod.

Although the data were assumed to represent the time required 'o develop to the end of each egg stage, the end of a stage does not occur instantaneously. The transition period is, however, assumed to occur on a time scale of hours, a period that is brief relative to the stage duration.

3.2.3 Temperature

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The temperature time series from Boothbay Harbour, Maine, available as monthly means measured at a depth of 5.5m, was used to evaluate the relationship between spawning time and water temperature. The Boothbay Harbour temperatures represent the longest continuous time series of water temperatures available

STAGE	STAGE designation of Meek (1924)	DESCRIPTION
Ι	1-3	from fertilization to the formation of the endoderm, ectoderm and mesoderm; at the end of this stage the blastoderm is starting to overgrow the yolk; includes the morula, blastula and early gastrula stages
Π	4-6a	from the end of stage I to closure of the blastopore at which time the embryo extends from the animal to vegetable poles (ca. 1/2 way around the yolk); during this stage the tail bud, notochord and optic vesicles appear; the beginning of this stage is marked by the formation of the embryonic shield and embryonic axis
III	7-9a	from the end of stage II to when the tail can almost touch the head; during this stage the heart begins to beat, the tail bud becomes free of the yolk, and the otoliths begin to develop
IV	10-12	from the end of stage III to hatching; tail of embryo is all the way around yolk sac to the tip of snout and perhaps past; embryo is well pigmented and begins to show characteristic pigment pattern; at the beginning of this stage the upper portion of the eye becomes pigmented.

TABLE 3.4: Description of haddock and cod egg stages.

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for this region (1906-present) and in spite of being a coastal series, it is suggestive of low-frequency trends in temperature from the offshore surface and subsurface waters of the Scotian Shelf and Gulf of Maine (Lauzier 1965, Colton 1968b) and weakly indicative of the higher frequency monthly mean offshore sea surface temperatures (Table 3.5). Unfortunately, continuous temperature time series for the offshore spawning areas that encompass the range of years of spawning times, are not available.

The Boothbay data were averaged over March and April, April and May and August through March. The March and April or April and May averages corresponded with the expected time of peak spawning on Georges and Browns Banks, respectively, and may be indicative of an environmental cue acting to trigger spawning near the end of gonad maturation. A similar index was used by Colton (1968a) and Marak and Livingstone (1970) to examine the relationship between spawning time on Georges Bank and water temperature. The August through March average was used since i) it corresponds with the period of gonadal development in haddock from the Gulf of Maine and Scotian Shelf region (Homans and Vladykov 1954, Overholtz 1987, Waiwood and Buzeta 1989) and ii) it removes some of the high frequency variation that is not coherent over large spatial scales (Akenhead *et al.* 1981).

The monthly median sea surface temperatures (SST, 1946-1980) estimated by Loucks *et al.* (1986) for the major spawning regions on the continental shelves off the eastern coast of North America were used to examine the historical variation in the age of haddock eggs.

3.3 Statistical Analyses

Several expressions are commonly used to describe the relation between incubation temperature (T) and egg stage age (see review by Blaxter, 1969) and the data have been examined in relation to the four most common forms: power, exponential, linear and 2nd order polynomial curves (Table 3.2). The power and

TABLE 3.5:	Product-moment correlation coefficients (r) relating monthly mean
	BoothBay Harbour water temperature to the monthly median sea
	surface temperatures (SST) on Georges and Browns Banks (1946-
	1980). SST's are those used by Thompson et al. (1988). (ns - not
	significant at the 0.05 level).

MONTH	GEORGES BANK	BROWNS BANK
	r	r
Jan	0.59	0.49
Feb	0.56	0.46
Mar	0.59	0.18 ns
\mathbf{Apr}	0.53	0.31 ns
May	0.47	0.64
Jun	0.38	0.44
Jul	0.57	0.40
Aug	0.62	0.60
Sept	0.58	0.59
Oct	0.52	0.50
Nov	0.30 ns	0.29 ns
Dec	0.77	0.47

exponential curves were fit after logarithmic transformation; because some of the incubation temperatures were less than or equal to 0° C temperatures were first transformed by adding the value of 2. The 2nd order polynomial was fit by using the deviation $(T - \overline{T})$ of each temperature (T) from the mean (\overline{T}). This avoids potential computational difficulties arising from a significant correlation between linear (T) and quadratic (T^2) terms (Neter *et al.* 1983). The significance of the power and exponential curve regressions was determined by testing the null hypothesis, Ho: b=0, using a t-test (b is the slope of the regression line, Zar 1974). For the polynomial regressions the hypotheses were Ho: b=c=0 (b and c are the coefficients of the regression equation, F-test; Zar 1974) and Ho: c=0 and Ho: b=0 (t-test; Zar 1974). Comparisons between pairs of regression slopes and elevations were made using t-tests (Zar 1974). All regressions were performed using the MINITAB statistical package (Ryan *et al.* 1981) which employs standard least squares procedures.

3.4 Results

3.4.1 Spawning Time

The mean time of peak spawning for the northwest Atlantic haddock stocks, superimposed on the annual cycle in the long-term (1946-1980) average monthly median sea surface temperatures (Loucks *et al.* 1986), clearly shows a delay in spawning time as one proceeds northward from Georges Bank to the Grand Banks (Figure 3.2). This delay is approximately one month between Georges and Browns Bank, and approximately two to three months between Georges Bank and the Grand Banks. Peak spawning on Georges Bank usually occurs in mid- to late March, on Browns Bank in late April or early May, on Sable-Emerald banks in late April and early May and on the Southern Grand Bank and St. Pierre Bank in June or July.

Peak spawning occurred in all regions when the mean sea surface temperature fell between 2 and 10 °C. Although the phase of the annual temperature cycle was similar for the five regions, the annual mean temperature decreased from Georges FIGURE 3.2 Estimated mean date of peak haddock spawning in relation to spawning ground location and the annual cycle in sea surface temperature (SST). The duration of each peak spawning period was assumed to be one month. Spawning dates for Georges Bank (GB) and Browns Bank (BB) are taken from Table 3.2. Egg abundance data collected in 1979 (O'Boyle et al. 1984) was used to estimate spawning date in the Sable-Emerald (SI) stock. Spawning times in the Southern Grand Bank (SGB) and St. Pierre Bank (SP) stocks were taken from Templeman et al. (1978), Templeman and Bishop (1979) and Fitzpatrick and Miller (1979) who estimated spawning time from several years of ichthyoplankton and adult catch and maturity data.



Figure 3.2



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to the Southern Grand Banks. Temperatures within the 2 to 10°C range therefore occur at progressively later dates with increasing latitude such that spawning on Georges Bank coincided with the onset of spring warming and in the other areas spawning occurred after it (Figure 3.2).

On Georges Bank the time of peak egg production varied by 3 months from early or mid-February to late April or early May (Table 3.3). This represents a deviation from the mean of about $\pm 45d$. On Browns Bank the date of peak spawning ranged from mid-April to early May, a range of less than one month (Table 3.3).

The relationship between spawning time and the average Boothbay Harbour water temperatures during March and April, April and May and August through March was evaluated in order to test the hypothesis that variation in spawning time is explained by water temperature. Spawning date on Georges Bank was significantly and negatively correlated with all three temperature indices (March-April: $r^2=0.85$, p < 0.005, Figure 3.3; April-May: $r^2=0.78$, p < 0.01; August-March: $r^2=0.78$, p < 0.01) whereas no significant correlations were found between spawning date on Browns Bank and the three temperature indices (March-April: $r^2=0.27$, p >0.20; April-May: $r^2=0.25$, p > 0.20, Figure 3.3; August-March: $r^2=0.40$, p > 0.10). The relationship for Browns Bank may, however, be biased since spawning time data were available only in relatively warm years and the Boothbay temperatures are poorly correlated with temperatures on Browns Bank. The spawning time data for Georges Bank encompassed both relatively warm and cold years (Figure 3.3 and 3.4).

3.4.2 Egg Duration as a Function of Incubation Temperature

The age of each egg stage at the corresponding incubation temperatures are shown in Figures 3.5a-d. The number of observations and the temperature range (ca. -1 to 16 °C) was greatest for stage IV eggs. At temperatures below 2 °C there were 11 determinations (4 investigations) of the age of stage IV cod eggs and only 1 determination of the age of haddock eggs. Stages I through III contain FIGURE 3.3. The relationship between the date of peak haddock spawning on Browns and Georges Bank and the average sea surface temperature (SST). Mean SST was calculated as the average of the monthly mean SST in March and April for Georges Bank spawning and April and May for Browns Bank spawning. The dashed line is the least squares regression line (Y = 4.2 - 0.4 X; r^2 =0.85, p < 0.02), relating the date of peak spawning on Georges Bank (Y) to mean temperature (X). The date of peak spawning is represented as Jan=0.5, Feb=1.5, Mar=2.5 etc.



TIME of PEAK SPAWNING (months)

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FIGURE 3.4. Time series of the annual anomalies in the average of the March and April monthly mean sea surface temperatures (SST) at Boothbay Harbour. Anomalies were calculated as deviations from the average temperature [(March+April)/2] calculated over the full length of the Boothbay time series (1906-1987). Also shown is the period (1946-1980) of the SST's derived by Thompson *et al.* (1988) and the years in which estimates of the date of peak spawning are available for the Browns (open diamonds) and Georges (open triangles) Bank haddock stocks.

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fewer observations spread over a narrower temperature range (2 to 16 °C). Only two observations exist for stage III haddock.

It could be criticized that by combining data from age determinations made on eggs of differing origin (different females, different stocks and different years) and cultured under different experimental conditions, variation in age at a given temperature would increase. The data for stage IV cod eggs indicate that this does not, however, obscure the relationship (Figure 3.6). With the exception of three values, the ages deviated only slightly from the mean $(\pm 2d)$. Pooling of the data within species therefore appears reasonable and even advantageous given that it allows estimation of a mean age-temperature relationship for a range of stocks and temperatures.

The relationship between temperature and egg age is generally non-linear and the three non-linear relationships (power, exponential and 2nd order polynomial) yielded statistically significant fits. Although 2nd order polynomials explained more of the stage I to III variance than the power curves, they explain a relatively low proportion of the variance in the stage IV eggs. Since it is common practice to use the same functional form for each stage (eg. Thompson and Riley 1981; Coombs and Mitchell 1982), the functional form explaining the greatest amount of variance in the stage IV eggs was retained. This choice also avoids the tendency for the polynomial equations to predict ages that are inconsistent with the general trend of the data, when temperatures outside the range of observation are used. The exponential relationship usually accounted for a smaller proportion of the variance than either the power or polynomial relationships. The power curve explained the greatest proportion of the variance in stage IV egg age and the second largest proportion of the variance in the other three stages (Table 3.6). Analyses of the stage IV residuals showed they were normally distributed with no obvious trends about the fitted curve.

A statistical comparison between the power curves for cod and haddock within each egg stage was considered inappropriate due to possible biases associated with ş

FIGURE 3.5. Scattergrams of age versus temperature for four stages (I, II, III, IV) of cod and haddock eggs.

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Figure 3.5

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FIGURE 3.6. Scattergram of age versus temperature for stage IV cod eggs as a function of experiment.

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TABLE 3.6: Summary of power curve $(A = a(T + 2)^{\delta})$ regression analyses using the full data set. Designations: A – age in days; P – probability level; Rej. - reject null hypothesis; Acc. – cannot reject null hypothesis; R – 100x correlation coefficient unadjusted for the degrees of freedom; n – sample size; elevation is the intercept of the regression and slope is the coefficient of the temperature variable).

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	HADDOCK	COD				
STAGE I						
$\log(a) \ b$	1.82 -1.38	1.51 -1.14				
R^2	89.8	87.6				
\boldsymbol{n}	11	6				
Ho: b=0	Rej. $(P < 0.001)$	Rej. $(P < 0.01)$				
Ho: slopes equal Ho: elevations equal	Acc. (<i>I</i> Rej. (<i>P</i>	P > 0.2) < 0.001)				
STAGE II						
$\log(a)$	2.09	1.80				
b	-1.38	-1.15				
R^2	76.3	96.5				
n	11	6				
Ho: b=0	Rej. $(P < 0.001)$	Rej. $(P < 0.001)$				
Ho: slopes equal Ho: elevations equal	Acc. (1 Rej. (<i>P</i>	P > 0.2) < 0.005)				
STAGE III						
$\log(a)$		1.63				
b	_	-0.77				
R^2	-	89.6				
n	2	7				
Ho: b=0		Rej. $(P < 0.005)$				
STAGE IV						
$\log(a)$	1.89	1.87				
b	-0.89	-0.82				
R^2	73.3	93.0				
n	60	100				
Ho: b=0	Rej. $(P < 0.001)$	Rej. $(P < 0.001)$				
Ho: slopes equal	Acc. $(P > 0.2)$					
Ho: elevations equal	Rej. $(P < 0.001)$					

differences in the range of temperatures used to incubate the eggs of each species. The power curves were therefore re-fit using the data falling within a common temperature range and the slopes were then compared (Table 3.7). The slopes of the stage IV relationships were not significantly different. The elevation of the cod relationship exceeded that of haddock by four days. This is similar to the two to three day difference found by Laurence and Rogers (1976). Dannevig (1895 cited in Laurence and Rogers 1976) found that the hatching times of cod and haddock were almost identical. The slopes of the stage I and II haddock regressions were no longer significant due to the reduced, common temperature range considered.

Although the time to hatching differed between the two species, the relationships derived from the combined cod and haddock data may be more useful because the early stages of cod and haddock eggs cannot be visually distinguished from each other. In addition, the absolute differences between the ages at hatching for cod and haddock were relatively small and the sample size would increase for stages I, II and III.

Power curve regressions of the pooled data were highly significant for all stages (Table 3.8, Figure 3.7). The fitted curves for stages II and III cross over at temperatures below 3 ° C. A similar feature was evident in the temperature dependent egg development curves reported for hake by Coombs and Mitchell (1982).

3.4.3 Historical Variation in Egg Duration

Historical variation in the age of the haddock egg stage was determined for the month of peak spawning, the month prior to peak spawning and the month after peak spawning for each year during the period 1946-1980. Ages were calculated using the combined cod/haddock power curve relationship (Table 3.8) and the monthly median sea surface temperatures for Georges Bank and Browns Bank (Figure 3.8a,b). On Browns Bank the month of peak spawning was assumed constant and equal to the long-term mean (April) and on Georges Bank peak spawning

TABLE 3.7: Summary of power curve $(A = a(T + 2)^b)$ regression analyses using only those observations within the temperature range common to both the haddock and cod data set. Designations: A – age in days; P – probability level; Rej. – reject null hypothesis; Acc. – cannot reject null hypothesis; R – 100x correlation coefficient unadjusted for the degrees of freedom; n – sample size).

	HADDOCK	COD			
STAGE I					
$\log(a)$	1.23	1.51			
Ь	-0.78	-1.14			
R^2	40.8	87.6			
n	5	6			
Ho: b = 0	Acc. $(P > 0.20)$	Rej. $(P < 0.01)$			
Common Temperature					
Range	5 -	· 11			
STAGE II					
$\log(a)$	1.65	2.06			
<i>b</i>	-0.95	-1.42			
R^2	40.6	86.0			
\boldsymbol{n}	5	5			
Ho: b = 0	Acc. $(P > 0.20)$	Rej. $(P < 0.050)$			
Common Temperature					
Range	5.2 - 8.5				
STAGE IV					
$\log(a)$	1.89	1.91			
b	-0.89	-0.86			
R^2	73.3	89.0			
\boldsymbol{n}	60	92			
Ho: b = 0	Rej. $(P < 0.001)$	Rej. $(P < 0.001)$			
Common Temperature					
Range	1 - 14				
Ho: slopes equal	Acc. (1	$^{O} > 0.5$)			
Ho: elevations equal	Rej. (P	< 0.001)			
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	$\log(a)$	Ь	$100xR^2$	n	Ho:b=0
STAGE I	1.90	-1.50	90.3	17	Rej. $(P < 0.001)$
STAGE II	2.12	-1.43	85.8	17	Rej. $(P < 0.001)$
STAGE III	1.90	-1.03	87.6	9	Rej. $(P < 0.001)$
STAGE IV	1.88	-0.85	86.6	158	Rej. $(P < 0.001)$

TABLE 3.8: Summary of regression analyses on the combined data set (cod and haddock) assuming a power curve $(D = a(T+2)^b)$ relationship between egg stage age (D in days) and temperature $(T^{\circ}C)$.

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FIGURE 3.7. Power curves relating egg stage age to incubation temperature. Curves are those estimated from the pooled cod and haddock data set. The parameters for each curve are given in Table 3.8. The dashed portion of the curves represents the extrapolated portion of the curve. •,

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AGE (days)

Figure 3.7

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was calculated from the relationship between Boothbay Harbour temperatures and spawning time (Figure 3.3).

The computed egg ages on Georges Bank varied by a factor of two, ranging from 10 to 20 days over the 34 y period (Figure 3.9a). During peak spawning the mean egg age at hatching was 15.5 d. On Browns Bank the egg age was more variable, ranging from 10 to 30 d (Figure 3.9b). The mean age during peak spawning was 18.6 d and similar to that on Georges Bank. The greater variability on Browns Bank may be due to (i) the lower temperatures typical of this region during March, April and May in comparison to Georges Bank (Figure 3.8) and the amplification of these low temperatures by the age-temperature power curve relationship and (ii) the assumption of a constant spawning time for Browns Bank but not for Georges Bank.

3.5 Discussion

It is generally believed that the time of spawning in marine teleosts has evolved so that the period when the early life stages are present coincides with an environmental regime that is suitable for their survival and development (Cushing 1975, Scott 1979, Bye 1984) and perhaps with a circulation regime that enables the spatial continuity of the larvae to be maintained (Iles and Sinclair 1982). With respect to survival and development Cushing (1967,1969,1975) has suggested that in north temperate regions the date of teleost spawning is constant and occurs prior to the spring bloom so that larvae can emerge during the bloom. Variation in the timing of the spring bloom may therefore cause recruitment variation. This mechanism has been suggested as an explanation for increase in the abundance of cod and haddock stocks in the North Sea during the 1960's (the 'gadoid outburst'; Cushing 1984).

Haddock throughout the north Atlantic spawn during the spring to summer period (Hislop 1984, Bergstad *et al.* 1987, Figure 3.2) with spawning time being progressively later in more northerly and cooler latitudes (Figure 3.2). Whether spawning in each stock occurs during the same phase of the annual production or

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FIGURE 3.8. Monthly median sea surface temperatures (SST) for February through June for the period 1948-1980 on a) Georges Bank and b) Browns Bank. (solid box: February, +: March, open diamond: April, open triangle: May, x: June)

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FIGURE 3.9. The age of haddock eggs at the time of hatching on a) Georges Bank and b) Browns Bank for the period 1948-1980. Open diamond symbols refer to one month prior to peak spawning, solid box symbols refer to the month of peak spawning and open triangle symbols refer to one month after peak spawning. The month of peak spawning on Georges Bank was estimated from Boothbay Harbour sea surface temperatures using the regression equation in Figure 3.3. Peak spawning on Browns Bank was assumed to occur in April.

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Figure 3.9

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biomass cycles remains uncertain. In the North Sea spawning occurs during late March to early May (Hislop 1984) and, in general, coincides closely with the spring maximum in *Calanus finmarchicus* (Cushing 1984). On Georges Bank peak egg and larval abundances may occur earlier than the spring maximum in zooplankton biomass. Spawning, particularly during the 1970's and 1980's, occurred in March or early April (Figure 3.2) and the maximum abundance of haddock larvae (1977-80) occurred in April (Sherman *et al.* 1984) in accordance with the 10 to 20 day age of the egg stage. The spring maximum in zooplankton biomass occurred in May or June (Sherman *et al.* 1984, Davis 1987). The one to two month delay between peak haddock egg and/or larval >bundance and peak zooplankton biomass therefore suggests that eggs released later in the spawning season hatch into a water column with higher zooplankton biomass. On Emerald Bank both haddock spawning and zooplankton production peak in April and May (Figure 3.2, McLaren *et al.* 1989). However, the production peak may not be indicative of the biomass peak (Davis 1987).

The spawning time of Georges Bank haddock is highly variable contrary to the general assumption of a constant spawning time among marine teleosts (Figure 3.3). Colton (1968a) and Marak and Livingstone (1970) showed that interannual variation in spawning time of the Georges Bank stock was as large as 3 months (Table 3.3) and that spawning time was qualitatively related to temperature. The relationship derived here was based on data presented by both Marak and Livingstone (1970) and Walford (1938) and although this encompasses the years from 1931 to 1968, the relationship holds true for more recent years. For example, maturity data collected during 1977 to 1983 indicates the spawning period ranged between the last two weeks of March and the third week of April, with spawning usually occurring in late March or early April (Overholtz 1987). In 1979-80 egg abundance estimates indicated peak spawning occurred in late March (Table 3.3; Smith and Morse 1985). The predicted time of spawning, based on the mean sea surface temperatures at

Boothbay Harbour during March and April of 1977 to 1983 (mean temperature ranged from 2.4 to 2 ° C), is also mid-March to early April.

On Browns Bank interannual variation in spawning time appears to be much smaller than on Georges Bank (Figure 3.3), and is within the range typically reported for other north temperate marine species (Table 3.1). The estimated mean date of peak spawning is late April (Table 3.3, Figure 3.3). This period is consistent with the April to June period estimated by Waiwood and Buzeta (1989) from maturity data collected between 1970 and 1986 and with the April or earlier date inferred from egg abundance data collected in 1979 (only two surveys; O'Boyle *et al.* 1984). The Boothbay Harbour temperatures during these years were similar to those used in the Browns Bank spawning time-temperature relationship.

Despite the limitations of the data it is interesting to speculate on why spawning time is dependent on temperature on Georges Bank but not so on Browns Bank. Adult haddock are not strong migrators and their gene ¹ distribution may not change with trends in the water temperature (Georges Bank-Gulf of Maine: Colton 1972). Most haddock are caught in areas where the water temperature falls within a temperature range that is narrow relative to what is available (Bergstad et al. 1987, Overholtz 1987, Waiwood and Buzeta 1989). It might be expected, therefore, that haddock avoid much of the temperature variation and that a spawning time-temperature dependency would not exist. On the other hand the magnitude of temperature anomalies are usually only a few degrees and, with the possible exception of stocks near the southern or northern limits of the species distribution, are often within the haddock's preferred temperature range of approximately 3 to 10 °C (Bergstad et al. 1987, Waiwood and Buzeta 1989). The Georges Bank stock is near the southern limit of the distributional range of this species in the western Atlantic and as such its reaction to environmental change may be greater relative to the Browns Bank haddock, which is closer to the middle of the distributional range. The lack of a relationship between spawning time and temperature on Browns Bank may therefore be a reflection of an inability to detect a response that is less pronounced than on Georges Bank. In addition the Boothbay Harbour temperature series is only weakly correlated with the sea surface temperatures in the Browns Bank region (Table 3.5) and the available spawning time data encompasses only a limited temperature range (Figure 3.4).

The fact that spawning time does vary in at least one haddock stock and the possibility that it may vary in others has potentially important consequences for both management and research strategies. The fishery for the Browns Bank haddock stock is regulated, in part, by the use of a spawning time closure policy (Halliday 1988). If such a policy is to be effective for this, or for other stocks, the closure period must either be quite broad, including the February through May period for the Georges Bank stock, or it must be very flexible so that closure periods can be assigned on a year to year basis with the period in each year being defined by taking water temperature into consideration. From a research perspective attempts to isolate the causal mechanisms of recruitment fluctuation should take into consideration the timing of spawning on a year to year basis. Making the assumption that spawning time is constant may lead to faulty interpretations of the data.

With respect to the dependence of haddock egg age on incubation temperature the power curve relationship derived here is consistent with that used for several other species (Blaxter 1969, Pauly and Pullin 1988, Table 3.2) and is preferrable to the linear relation used by Laurence and Rogers (1976). Due to the paucity of observations on haddock development rates at temperatures below 2 ° C and the generally few observations for stages I through III, the power curves were defined by combining the available information on haddock and cod. These relationships compare well with the times to hatch given by Thompson and Riley (1981) for cod and are probably adequate for both cod and haddock. The temperatures during the haddock spawning season seldom fall below 2 °C, although in some years such a situation may exist (Loucks *et al.* 1986, Thompson *et al.* 1988). The temperature-time to hatch relationship reconstructed from the time series of sea surface temperatures (1948-1980) revealed that the egg age ranged from 10 to 20 days on Georges Bank and 8 t. 30 days on Browns Bank. Unlike spawning time the variance i.1 the age of the egg stage, appears to be greater on Browns than on Georges Bank. This may be due to the later spawning time of the Browns Bank haddock, since the rate of increase in vernal warming is greatest during the Browns Bank spawning. In the context of a simple exponential mortality model with a constant mortality coefficient of 10%/d, this range represents an order of magnitude difference in absolute mortality during the egg stage. This suggests that egg mortalities in different stages of the annual spawning curve and in different stocks may be quite different. Consequently, mortality trajectories of cohorts spawned at different times in the spawning cycle may be quite different.

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	HA	DDOCK		COD
SOURCE	TEMP. (C)	DEVELOP. TIME (days)	TEMP. (C)	DEVELOP. TIME (days)
Meek (1924)			5.5	3.5
Walford	2.7	8		
(1938)*	3.0	7		
	4.8	5		
	4.9	4.7		
	4.9	5		
	5.2	3.6		
	6	4		
	8	2.7		
	9	3		
Bonnet			6	3
(1939)			8	2
			10	2
Marak and Colton (1961)	3.3	7		
Fridgeirsson (1978)	7.2	2.4	7.2	2.5
Iversen and Danielssen (1984)*			10	2

Appendix 3.1a: The time to the end of stage I as a function of temperature for cod and haddock eggs

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	HA	DDOCK	COD			
SOURCE	TEMP. (C)	DEVELOP. TIME (days)	TEMP. (C)	DEVELOP. TIME (days)		
MacIntosh & Prince (1887-88)**			15.5	2.4		
Meek (1924)			5.5	6.5		
Walford	4	11				
(1938)*	4.3	9.8				
	4.4	9.8				
	5	10				
	5.5	6.6				
	6	6				
	8.1	5.8				
	9	6				
	6	6				
	8.1	5.8				
	9	6				
Bonnet			6.6	5.5		
(1939)			8	4.3		
Marak and Colton (1961)	3.3	14				
Nordahl (1970)**			6-8(7.5)	5		
Schwarz (1971)	5.5	7				
Fridgeirsson (1978)	7.2	4.2	7.2	4.4		

Appendix	3.1b:	The	time	to	the	end	of	stage	Π	as	a i	function	n of	tempe	ratur	e for
	co	d and	l had	doc	k eg	gs. ((Te	n.per	atu	re o	r t	time in	brad	ckets is	the r	nean
	va	lue.)														

** - This is the original source. I have taken the data from Hardy (1978).
* - read from a graph

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	HA	DDOCK		COD	
SOURCE	ТЕМР. (С)	DEVELOP. TIME (days)	TEMP. (C)	DEVELOP. TIME (days)	
MacIntosh & Prince (1887-88)**			15	5-6(5.5)	
$egin{array}{c} { m Meek}\ (1924) \end{array}$			5.5	9,5	
Bonnet			6	9	
(1939)			8	6.5	
			10	6.2	
			12	5	
Marak and Colton (1961)	3.3	18			
Fridgeirsson (1978)	7.2	7.4	7.2	8	

Appendix 3.1c: The time to the end of stage III as a function of temperature for cod and haddock eggs.

** - This is the original source. I have taken the data from Hardy (1978).

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$\begin{array}{c c c c c c c c c c c c c c c c c c c $		HAI	DOCK	COD		
Earll -0.6 50 (1878) 0.6 34 1.1 31 2.2 24 3.3 20 5.0 16 7.2 13 Baird 6 16 (1884)** Cunningham 6-7(6.5) 16 (1885)** 6-9(7.5) 12 McIntosh & 15 6-7(6.5) Prince (1887-1888)** Rognerud 5 16 (1889)** 5 20-24(22) 7.5 15-18(16.5) Dannevig 1 42 1 42 (1895)*** 3 23 3 23 4 20.5 4 20.5 5 17.8 5 17.8 6 15.5 6 15.5 8 13 8 12.8 10.8 10 10.5 12 9.7 12 9.7 14 8.8 14 8.5	SOURCE	TEMP. (C)	TIME TO HATCH (days)	TEMP. (C)	TIME TO HATCH (days)	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Earll			-0.6	50	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	(1878)			0.6	34	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$. ,			1.1	31	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$				2.2	24	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$				3.3	20	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$				5.0	16	
Baird $(1884)^{**}$ Cunningham $6-7(6.5)$ 16 $(1885)^{**}$ $6-9(7.5)$ 12 McIntosh & 15 $6-7(6.5)$ Prince $(1887-1888)^{**}$ Rognerud 5 16 $(1889)^{**}$ 5 20-24(22) 7.5 15-18(16.5) Dannevig 1 42 1 42 $(1895)^{***}$ 3 23 3 23 4 20.5 4 20.5 5 17.8 5 17.8 6 15.5 6 15.5 8 13 8 12.8 1 10.8 10 10.5 12 9.7 12 9.7 14 8.8 14 8.5				7.2	13	
$\begin{array}{c cccccc} Cunningham & 6-7(6.5) & 16 \\ (1885)^{**} & 6-9(7.5) & 12 \\ \\ McIntosh \& & & 15 & 6-7(6.5) \\ Prince \\ (1887-1888)^{**} & & 5 & 16 \\ (1889)^{**} & & 5 & 20-24(22) \\ 7.5 & 15-18(16.5) \\ \\ Dannevig & 1 & 42 & 1 & 42 \\ (1895)^{***} & 3 & 23 & 3 & 23 \\ & 4 & 20.5 & 4 & 20.5 \\ & 5 & 17.8 & 5 & 17.8 \\ & 6 & 15.5 & 6 & 15.5 \\ & 8 & 13 & 8 & 12.8 \\ & & & 10.8 & 10 & 10.5 \\ & 12 & 9.7 & 12 & 9.7 \\ & 14 & 8.8 & 14 & 8.5 \\ \end{array}$	Baird (1884)**			6	16	
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Cunningham	6-7(6.5)	16			
McIntosh & Prince $(1887-1888)^{**}$ 15 $6-7(6.5)$ Rognerud $(1889)^{**}$ 516 $(1889)^{**}$ 520-24(22) 7.5 15-18(16.5)Dannevig $(1895)^{***}$ 142420.5420.5420.5517.85615.568138420.7129.7129.7148.8148.5	$(1885)^{**}$	6-9(7.5)	12			
Rognerud516 $(1889)^{**}$ 5 $20-24(22)$ 7.5 $15-18(16.5)$ Dannevig142 $(1895)^{***}$ 3234 20.5 420.55 17.8 5 17.8 56 15.5 6813810.81012 9.7 1214 8.8 14	McIntosh & Prince (1887-1888)**			15	6-7(6.5)	
$(1889)^{**}$ $(1889)^{**}$ $(1889)^{**}$ $(1895)^{***}$ 3 4 $(1895)^{***}$ 3 4 20.5 4 20.5 4 20.5 5 17.8 6 15.5 6 15.5 8 13 8 12.8 10 10.5 12 9.7 12 9.7 14 8.5 20.24(22) 7.5 15-18(16.5) 12.2 15-18(16.5) 17-18(16.5) 18-18(16.5) 17-18(16.5)	Rognerud			5	16	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	(1889)**			5	20-24(22)	
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$				7.5	15-18(16.5)	
$egin{array}{cccccccccccccccccccccccccccccccccccc$	Dannevig	1	42	1	42	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$(1895)^{***}$	3	23	3	23	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$. ,	4	20.5	4	20.5	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		5	17.8	5	17.8	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		6	15.5	6	15.5	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		8	13	8	12.8	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		i	10.8	10	10.5	
14 8.8 14 8.5		12	9.7	12	9.7	
		14	8.8	14	8.5	

Appendix 3.1d: The time to the end of stage IV (time to hatch) as a function of temperature for cod and haddock eggs.

** - This is the original source. I have taken the data from Hardy (1978).

*** - Taken from Jacobsen and Johansen (1908), Allen, (1917), and Laurence and Rogers (1976).

	HADDOCK		COD		
SOURCE	ТЕМР. (С)	TIME TO HATCH (days)	TEMP. (C)	TIME TO HATCH (days)	
Brice (1898)	2.8	15	-0.6	50	
	5	13	0.0	40	
			0.6	35	
			1.1	31	
			1.7	28	
			2.2	25	
			2.8	23	
			3.3	21	
			3.9	19	
			4.4	17	
			5.0	16	
			5.6	15	
			6.1	14	
			6.7	13	
			7.2	12	
			7.8	11	
			8.3	11	
Apstein (1909)****			-1	60	
			0	43	
Meek (1924)			5.5	12.0	
Fish (1928)			8.5	13	
			8.6	12	
			6.8	14	
			6.7	14	
			6.0	14	
			3.3	19	
			2.8	20	
			1.6	22	

**** - Taken from Postolaky (1968)

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	IAH	DOCK	COD		
SOURCE	TEMP. (C)	TIME TO HATCH (days)	TEMP. (C)	TIME TO HATCH (days)	
Walford	4	21			
(1938)	5	19			
	6.2	15.5			
	8,5	12.6			
Bonnet			3	23	
(1939)			6	17.2	
. ,			8	11.5	
			10	9.0	
			12	8.5	
Woodworth et al. (1946)			8.3	10	
Oppenheimer (1955)			5.0	16	
Marak and Colton (1961)	3.3	21			
Svetovidov	2.8	15			
(1962)**	5.4	13			
Westerhagen	4	21			
(1968)	6	14			
	8	11.6			
	10	10.5			
Solemdal			3.4	22	
(1970)*			5.3	15	
Schwarz (1971)	5.5	17			
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* - This source is a mimeo of an ICES CM document.
** - This is the original source. I have taken the data from Hardy (1978).

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	HA	DDOCK	(COD
SOURCE	TEMP.	TIME TO	TEMP.	TIME TO
	(C)	HATCH	(C)	HATCH
		(days)		(days)
Laurence and	2	20,20,20,19	2	24,22,21,22
Rogers				21,24
(1976)	4	13,12,11,11	4	18,18,17,13
		11,12		13,13
	6	14,14,12,11	6	12,12,12,12
		12,11		12,12
	8	10,10,9,9	8	10,10,11,10
		10,10		11,10
	10	7,8,7,8	10	9,9,9,9
		8,7		9,9
	12	7,6,6,6	12	8,8,8,9
		6,6		9,8
Fridgeirsson (1978)	7.2	10	7.2	9.5
Skreslet and			2.6	24
Danes (1978)			4.6	18
Iversen and			6	14
Danielssen			8	10
(1984)			10	9

CHAPTER 4

The Vertical Distribution of Haddock Eggs and its Influence on The Rate of Egg Horizontal Transport

4.1 Introduction

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It is generally believed that the vertical distribution of pelagic organisms plays an important role in determining the rate and direction of their horizontal displacement and their interactions with prey and predators. A considerable amount of effort has, therefore, been devoted to describing the vertical distribution of aquatic organisms, including fish larvae. However, relatively few studies have focused on fish eggs despite early suggestions that variation in egg dispersal may affect year-class size (Hjort 1914, 1926).

A variety of indices have been developed that are assumed to represent the transport of fish eggs and larvae. These include composite estimates of the residual circulation (Harden-Jones, 1968; Power and McCleave, 1983), geostrophic transport (Corlett, 1965; Parrish et al., 1981), sea level height (Sinclair et al., 1985), 3% of the wind speed (Murray it et al., 1983), Ekman transport (Nelson it et al., 1977; Parrish it et al., 1981; Bailey, 1981a,b; Bakun and Parrish, 1982), depth mean velocity of either the surface mixed layer (Reed, 1980; Spaulding et al., 1983; Reed et al., 1984) or entire water column (Ulanowicz et al., 1982), river discharge (Stevens, 1977) and pseudo-transfer functions estimated from comparisons of wind with recruitment time series (Carruthers et al., 1951a; Chase, 1955).

These indices have often formed the basis for the characterization of spawning habitats (Parrish *et al.*, 1981; Bakun and Parrish, 1982), the assessment of the importance of transport variation to year-class success (Carruthers *et al.*, 1951a,b; Chase, 1955; Nelson *et al.*, 1977; Bailey, 1981b; Murray *et al.*, 1983; Sinclair *et al.*, 1983), the simulation of egg and larval transport (Reed, 1980; Ulanowicz *et al.*, 1982) and the formulation of concepts concerning the structure, size and movements of populations (Russell, 1937; Fraser, 1958; Harden-Jones, 1968; Iles and Sinclair, 1982).

Several of these indices assume the eggs (and larvae) are near the surface where wind-driven Ekman transport can influence their displacement. This is not always correct. The vertical distribution and specific gravity of fish eggs varies between species, and throughout development (Jacobsen and Johansen 1908; Tables 4.1 and 4.2). The vertical distribution also varies with wind speed since as wind speed increases the eggs get mixed below the surface (Fish 1928).

Haddock eggs are released near the bottom during the spring when the water column is often beginning to stratify (Chapter 1). The eggs subsequently float toward the surface. Field evidence suggests that 80% or more of the eggs are found within the top 55m (Walford 1938, Colton 1965) and that ontogenetic variation in their vertical distribution pattern does not occur.

Laboratory experiments on the other hand, provide evidence that suggests ontogenetic variation in the depth distribution of haddock eggs does occur. Eggs, reared in sea water of constant density, change specific gravity with development. Early stage haddock eggs tend to adjust their specific gravity toward that of the ambient sea water (Bigelow and Welch 1925; Walford 1938). Egg specific gravity appears to decrease after fertilization to a minimum during gastrulation, and thereafter increases until hatching (Wheeler and Miller 1960; Moksness and Torstensen 1985). If such changes were to occur in the field, stage-specific variation in the vertical distribution would be expected, particularly in regions where the water column is weakly stratified and vertical mixing rates are relatively low. Such variation has not been detected because only broad depth intervals have been sampled and only coarse egg staging systems have been employed.

The possibility that ontogenetic variation in the vertical distribution of the eggs exists is supported by the fact that field surveys have usually shown that the horizontal displacements of haddock eggs or larvae are small relative to expectations based on the displacements of surface drift bottles and wind-based indices of the near

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Species	Location	Comments	Source
sprat	English Channel	vertical distribution is similar throughout development	3
pilchard	English Channel	vertical distribution is similar throughout development	3
mackerel	New England	eggs become less concentrated at the surface as they develop	1
jack mackerel	California	middle and late stage eggs are more concentrated near the surfacec than recently spawned eggs	7
cod	Nova Scotia	' eggs become relatively less concentrated at the surface as they near the time of hatching	8
	Austnesfjorden, Norway	newly fertilized eggs become more concentrated toward the surface as they develop	6
haddock	Georges Bank	all egg stages, from newly spawned to nearly hatching, have a similar vertical distribution	11
	Georges Bank & Gulf of Maine	early and late stage eggs have very similar distributions	10
cod/ haddock	Iceland	all egg stages have highest concentrations at the surface, however, the rate at which the concentrations decrease with depth decreases with egg development	12
plaice	Southern North Sea	vertical distribution is simialar throughout development, winds generally greater than 10m/s	2
		earlier developmental stages closer to the surface than older stages, winds very calm	9
halibut	Malangen, Norway	vertical distribution of all egg stages similar	4,5
	Andfjord & Soroysund, Norway	older stage eggs found deeper in the water column than younger stages	5
California sardina	California	1 to 2 day old eggs more	7
30111116	Concentrated near the surface	than newly spawned, 2-3 or 3-4 day old eggs	

TABLE 4.1: Ontogenetic variation in the vertical distribution of pelagic fish eggs.

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Sources: 1 - Sette (1943), 2 - Coombs, Harding, Nichols and Fosh (1981), 3 (1984), 4 - Haug, Kjorsvik and Solemdal (1984), 5 - Haug, Kjorsvik and Solemdal (1986), 6 - Solemdal and Sundby (1981), 7 - Ahlstrom (1959), 8 - McKenzie (1940), 9 - Pommeranz (1973 cited in 2), 10 - Colton (1:65), 11 - Walford (1938), 12 - Fridgeirsson (1984)

TABLE 4.2:	Ontogenetic variation in the density of live fish eggs (specific gravity). A brreviations
	refer to the source of the eggs used in density determinations (AF = artificially
	fertilized, PNT = plankton net tows, MSC = maintained and spawned naturally
	in captivity).

Species	Location	Comments	Source
sprat	English Channel	density increases continuously with development, PNT	3
	Flodevigen, Norway	decrease in density with development, MSC	6
	Frierfjord, Norway	maximum density during early egg development, PNT	6
pilchard	English Channel	density increases near the end of the egg stage, PNT	3
mackerel	Celtic Plateau	density decreases continuously with development, AF	1
	Plymouth, England	density increases with development, PNT	1
cod	Lofoten, Norway	density increases continuously thoughout development, AF	7
haddock	Gulf of Maine	density minimum midway through egg stage, unspecified	9
	unspecified	density minimum during gastrulation, egg source unspecified	8
plaice	Southern North Sea	no trend in density with development	2
halibut	Malangen & Soroysund, Norway	no trend in density with development, PNT	4
	Malangen, Soroysund & Andfiord Norway	density increases near the end of the egg stage, PNT	5

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Sources: 1 - Coombs (1981), 2 - Coombs, Harding, Nichols and Fosh (1981), 3 Coombs, Fosh and Keen (1985), 4 - Haug, Kjorsvik and Solemdal (1984), 5 - Haug, Kjorsvik and Solemdal (1986), 6 - Moksness and Torstensen (1985), 7 - Sundnes, Leivestad and Iversen (1965), 8 - Moskness and Selvik (1984; cited in 6), 9 Wheeler and Miller (1960) 4

surface circulation (Saville 1959; Koslow *et al.* 1985; references in Smith and Morse 1985). The displacements sometimes compare more favourably with expectations based on the mid-depth circulation (e.g. Georges Bank, Smith and Morse 1985).

This chapter therefore presents new, higher resolution, observations on the vertical distribution of haddock eggs and develops simple models of egg vertical distribution and wind induced egg transport.

4.2 Field Observations

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4.2.1 Sampling Area and Procedures

The vertical distribution of haddock eggs was derived from samples collected at thirteen stations on the eastern cap of Browns Bank during a 3-7 May 1984 cruise aboard the C.S.S. Dawson. The time and location of sampling was based on the fact that the peak spawning period for haddock occurs during April an May on Browns Bank (Chapter 3).

At each station ichthyoplankton samples were collected at seven discrete depths within the interval of 5 to 65m depth. The water depth in the sampling area varied between 90 and 100m. All samples were collected with a mini-BIONESS using $333\mu m$ mesh nets with a mouth area $0.25m^2$. BIONESS tows were made in a constant direction for 10 minutes at each depth at an average speed of 1.5m/s. Each sample therefore represented a spatial average taken over a horizontal distance of approximately 900m. Flow meters fixed to the outside and inside of the mini-BIONESS provided a continuous record of the volumes of water being filtered and the filtration efficiency. A more detailed description of the mini-BIONESS system and its mode of operation is given by Frank (1986).

Temperatures and salinities were measured continuously throughout each tow with an Applied Microsystems CTD (conductivity, temperature, depth) attached to the mini-BIONESS. Water density was calculated continuously using each discrete temperature and salinity measurement. Mean values (time average over approximately 10 minutes) for each tow and discrete sampling depth were then calculated. These mean values were used in the present analyses.

Once on deck, the plankton nets were thoroughly washed and the contents of each cod end were passed through a 4mm mesh sieve to remove the macrozooplankton, primarily gelatinous zooplankton and euphausids. The smaller size fraction (< 4mm) was preserved in a solution of 4% formalin (buffered with Borax) and sea water for subsequent sorting and enumeration.

In the laboratory all fish eggs were identified and classified into four developmental stages described in Chapter 3. Because haddock eggs cannot be distinguished from witch flounder (*Glyptocephalus cynoglossus*) until stage III or from cod (*Gadus morhua*) until stage IV, the abundances reported here for stages 1 and II include all three species and those for stage III include cod and haddock. Stage IV eggs include only haddock. Because the majority of the stage IV cod-haddock-witch eggs collected were haddock (81.1% haddock, 11.1% cod and 7.8% witch flounder), all egg stages were assumed to be dominated by haddock.

For the cod-haddock-witch complex the diameters of the preserved eggs ranged mainly between 1.4 and 1.6mm. The ratio of the preserved to fresh egg diameter is 0.98 (Hislop and Bell 1987) and the eggs were assigned a constant diameter of 1.5mm.

Water velocity measurements were made so that a scaling of the advectiondiffusion equations could be carried out to help isolate the important forcing terms. The horizontal components (north-south and east-west) of water velocity were obtained for the depth range 16.8 to 74.4 m during each mini-BIONESS tow with an Ametek Straza Doppler acoustic profiling system mounted in the hull of the C.S.S. Dawson. This system does not provide accurate estimates within the bottom 20% of the water column nor within a few meters of the transducer. It produces a temporally- and spatially-averaged estimate of the velocity along orthogonal bearings for each depth interval. Velocities were averaged over a depth interval of 6.4m and a time period of approximately 5 minutes (200 transmitted acoustic pulses). The shallowest depth interval was centered at 16.8m and the deepest at 74.4m.

4.2.2 Vertical Distribution of Haddock Eggs

The majority (> 50%) of the stage I, II and III eggs were within the top 20m of the water column and their concentration decreased with depth (Table 4.3). In contrast only 30% of the stage IV eggs were within the top 20 m (Table 4.3) and their distribution appears to be more uniformly distributed with depth with the possiblity of a sub-surface maximum. This difference is reflected by the depth of the stage IV center-of-mass which is 2-3 times deeper than that of the stage I and II eggs and 1.5 times that of the stage III eggs.

These results, with the exception of a sub-surface maximum in the stage IV eggs, are supported by linear regression analyses of the natural logarithm transformed mean and median egg concentrations versus depth (Table 4.4). The regressions were calculated once using all nine sample depths and again using only the seven most frequently sampled depths. All of the stage I, II and III regressions were statistically significant (F test, Zar 1974). Only the mean concentrations were used in the stage IV regressions since the medians were equal to zero for all depths. The slopes of these stage IV regressions were not significantly different from zero. However, the mean concentrations were greater than zero (t-test, p < 0.025).

Comparisons of the stage I, II and III regression slopes using analysis of covariance and the Newman-Keuls multiple range test (Table 4.4; Zar 1974) indicated that the slope of the stage I eggs was indistinguishable from stage II eggs, and the slope of the stage II eggs was different from the slope of the stage III eggs (Figure 4.1). The apparent maxima in the median egg concentrations at 25 and 55m are associated with the small number of samples (n=7) taken at this depth relative to that taken at the other depths (n=21 to 28).

STAGE	DEPTH	TOTAL NUMBER OF SAMPLES TAKEN	NUMBER OF SAMPLES WITH ECCS	NO. O PER	F EGGS 100m ³	COEF. OF VAR.	CUM. %	MEDIAN NO. OF EGGS PER 100m ³	Sk.
			Edds	ntean	(3)			100//	
I	5	22	22	246.7	(497.1)	2.0	54.4	55.0	1.16
	10	25	25	96.8	(124.3)	1.3	75.8	57.1	0.96
	20	27	27	28.7	(19.3)	0.7	82.2	25.4	0.51
	25	7	7	26.3	(19.9)	0.8	88.0	20.5	0.87
	35	28	27	15.5	(14.1)	0.9	92.5	. 11.1	0.94
	45	21	21	10.4	(12.4)	1.2	94.8	6.0	1.06
	50	7	7	16.2	(19.1)	1.2	97.2	9.6	1.04
	55	21	21	6.4	(5.3)	0.8	98.6	4.1	1.30
	65	28	28	4.7	(6.2)	1.3	100.0	2.6	1.02
TOTAL	$(eggs/m^2)$				3398.4				1445.4
CM (m)					13.1				17.8
II	5	22	20	63.8	(177.3)	2.8	50.9	10.9	0.90
	10	25	24	28.9	(39.0)	1.3	74.0	10.6	1.41
	20	27	23	13.1	(20.0)	1.5	84.5	4.5	1.29
	25	7	5	11.0	(9.4)	0.8	93.3	15.5	-1.44
	35	28	24	4.3	(5.5)	1.3	97.9	3.2	0.60
	45	21	14	0.9	(1.2)	1.3	98.6	0.5	1.00
	50	7	5	1.0	(1.0)	1.0	99.2	1.0	0.00
	55	21	14	0.5	(0.6)	1.1	99.6	0.5	0.00
	65	28	11	0.4	(0.6)	1.6	100.0	0.0	2.00
TOTAL	$(eggs/m^2)$				940.3				355.2
CM(m)	(0550/)				11.6				18.2
111	-	00	1.4		(10.0)	1.0	20.0	26	1 40
111	Э 10	22	14	0.0	(10.9)	1.4	20,2	3.0	1.40
	10	25	19	(.4	(10.1)	2.0	51.3	3.0 1.0	1.00
	20	21	19	0.0	(12.2)	2.0	77 4	1.9	1.00
	25	(0 15	11.2	(13.4)	1.2	11.4	3.9	1.03
	35	28	15	4.9	(9.0)	1.0	94,5	0.0	1.40
	45	21	10	0.1	(1.2)	1.0	94.U 07.c	0.0	1.10
	50	(01	ა 0	4.4	(3.0)	1.5	00.2	0.0	1.05
	55	21	0	0.7	(2.0)	2.0	99.3 100.0	0.0	1.00
	00	20	0	0.2	(0.5)	4.4	100.0	0.0	1.20
TOTAL CM (m)	(eggs/m ²)				$\begin{array}{c} 327.5 \\ 21.1 \end{array}$				104.0 15.6

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TABLE 4.3: A summary of the stage dependant depth distribution of haddock eggs, collected over BrownsBank in May of 1984. (s = standard deviation; Coef. Var. = s/mean; Cum % =cumulative percent of eggs within and above the sample depth; Sk = skewness).

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STAGE	DEPTH	TOTAL NUMBER OF SAMPLES TAKEN	NUMBER OF SAMPLES WITH EGGS	NO. O PTR mean	F EGGS 100m ³ (s)	COEF. OF VAR.	CUM. %	MEDIAN NO. OF EGGS PER 100m ³	Sk.
IV	5	22	4	0.2	(0.5)	2.7	9.8	0.0	1.20
	10	25	3	0.1	(0.3)	3.1	15.2	0.0	1.00
	20	27	5	0.3	(1.0)	3.2	29.8	0.0	0,90
	25	7	1	0.1	(0.2)	2.6	34.2	0.0	1.50
	35	28	7	0.8	(1.8)	2.4	84.4	.0.0	1.33
	45	21	1	0.0	(0.1)	4.6	85.3	0.0	0.00
	50	7	2	Ũ. 2	(0.5)	1.9	93.2	0.0	1.20
	55	21	3	0.1	(0.2)	2.5	96.1	0.0	1.50
	65	28	3	0.1	(0.2)	3.0	100.0	0.0	1.50
TOTAL CM (m)	$(eggs/m^2)$				15.4	31.0			0.0 undefined
Total	5	22	22	319.6	(648.8)	2.0	51.2	79.8	1.11
	10	25	25	133.3	(156.1)	1.2	72.6	72.9	1.16
	20	27	27	48.4	(37.7)	0.8	80.3	35.1	1.06
	25	7	7	48.7	(21.1)	0.4	88.1	59.1	-1.48
	35	28	28	25.5	(19.8)	0.8	93.6	20.0	0.83
	45	21	21	12.1	(12.2)	1.0	95.5	7.6	1.11
	50	7	7	19.8	(18.2)	0.9	97.6	13.4	1.05
	55	21	21	7.7	(6.3)	0.8	98.8	5.7	0.95
	65	28	28	5.4	(6.6)	1.2	100.0	3.2	1.00
TOTAL	$(eggs/m^2)$				4681.7				2250.5
CM (m)					13.4				18.7

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TABLE 4.3: continued

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EGG Stage	Inter- cept	Slope	n	r^2	Ho: slope $= 0$
····		A	ll Nine Depths		
Mean					
I	5.051	-0.054	9	0.87	Rej. $p < 0.0005$
II	4.113	-0.066	9	0.95	Rej. $p < 0.0005$
III	2.744	-0.037	9	0.80	Rej. p < 0.0025
IV	0.221	-0.001	9	0.02	Acc. $p > 0.25$
	Ho: slo	pe I = slope II	= slope III		Rej. $p < 0.025$
	Ho: slo	pe I = slope II	-		Acc. $p > 0.20$
	Ho: slo	pe I =	slope III		Acc. $p > 0.20$
	Ho:	slope II	= slope III		Rej. p < 0.01
Median					
I	4.297	-0.047	9	0.96	Rej. p < 0.0005
п	2.960	-0.046	9	0.84	Rej. p < 0.001
III	1.801	-0.032	9	0.85	Rej. $p < 0.0005$
	Ho: slo	pe I = slope II	= slope III		Acc. $p > 0.25$
		On	ly Seven Depth	IS	
Mean					

TABLE 4.4: Summary of the linear regression of Ln[C(z)+1] on depth, z. (n is the number of sample depths, r^2 is the coefficient of determination, C(z) is eggs per $100m^3$ and z is in m)

	Ho: slop	e 1 = slope 11	= slope III		Acc. $p > 0.25$
		01	aly Seven Depths	6	
Mean					
I	5.159	-0.058	7	0.91	Rej. $p < 0.001$
II	4.103	-0.066	7	0,95	Rej. p < 0.0005
III	2.594	-0.037	7	0.91	Rej. p < 0.001
IV	0.243	-0.002	7	0.04	Acc. $p > 0.25$
	Ho: slop	e I = slope II	= slope III		Rej. p < 0.05
	Ho: slop	e I = slope II			Acc. p > 0.50
	Ho: slop	e I =	slope III		Acc. $p > 0.10$
	Ho:	slope II	= slope III		Rej. p < 0.025
Median					
I	4.324	-0.049	7	0.98	Rej. p < 0.0005
II	2.728	-0.043	7	0.96	Rej. p < 0.0005
III	1.655	-0.030	7	0.92	Rej. p < 0.001
	Ho: slop Ho: slop	e I = slope II e I = slope IJ	= slope III		Rej. p < 0.005 Acc. p > 0.20
	Ho: slop	e I =	slope III		Rej. p < 0.005
	Ho:	slope II	= slope III		Rej. 0.1 > p > 0.05

FIGURE 4.1: Plots of the regression curves fit to the median egg concentrations of stages I, II and III. A) Logarithmic plot, B) Arithmetic plot. The concentration of eggs at each depth (C(z)) has units of number per 100 m^3 .

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The age of each egg stage was estimated from age-temperature relationships (Chapter 3) using the mean water temperature in the upper 35m (3.5°C). This yielded ages of 2.4, 6.9, 10.8 and 15.2 days for stages I through IV, respectively.

4.2.3 Physical Properties of the Water Column

The temperatures ranged from 3.3 to 4.1° C, with a minimum at mid-depth, salinity increased with depth from 32.0 at 5m to 33.0 at 65m, and the water density (sigma-t) increased from 25.4 at 5m to 26.1 at 65m (Figure 4.2). The variability in temperature and salinity increased below 40m. The apparent local minimum in temperature, salirity and sigma-t at 50 m is associated with the small number (n=7) of observations at this depth. Collectively these observations suggest the water column was not well mixed.

The velocity observations were dominated by the M2 tidal cycle. To determine the mean velocity, the tidal amplitude, and phase of the current as a function of depth, a curve of the form

$$v(z) = \overline{v}(z) + A(z) \sin\left[\frac{2\pi t}{T} + P(z)\right] + e(z)$$

$$4.1$$

was fitted to the north-south and east-west velocity series from each depth (Table 4.5). In this equation v(z) represents a given velocity component at depth z, $\overline{v}(z)$ the depth-dependant mean velocity, A(z) the depth-dependant amplitude, P(z) the depth-dependant phase, e(z) is the residual error and T is the M_2 tidal period (12.4 h). In all cases the regression explained a large proportion of the variance, indicating the tides were the major cause of the current variability. The tidal amplitude varied little with depth, except perhaps near the bottom. The phases increased below 50m (Table 4.5). The mean flow at all depths was generally toward the southwest with the magnitude decreasing with depth from $0.10ms^{-1}$ at 16.8m to $0.035ms^{-1}$ at 74.4 m.

The observed mean advection rate at 16.8 m was $8.6kmd^{-1}$ which, when coupled with the assumption of a passive egg and no velocity shear above this depth,

FIGURE 4.2: Depth profiles of the mean sea water temperature, salinity, and density. The straight line through the density values is the regression line $\rho_w(z) = 1.0253 - 1.17 \times 10^{-7} z$ where ρ_w has units of gm/cm^3 and z has units of cm.

Figure 4.2

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	NUMBER				
DEPTH	OF	MEAN	AMPL.	PHASE	r^2
(m)	OBSER.	(cm/s)	(cm/s)	(degrees)	
North/South (±)	Component				
16.8	222	- 5.91	39.42	- 2.28	0.79
23.2	222	- 5,04	38.78	- 3.82	0.82
29.6	222	- 4.39	37.38	- 3.28	0.84
36.0	222	- 4.39	35.97	- 3.76	0.82
42.4	222	- 4.62	36.45	- 4.79	0.85
48.8	222	- 4.86	37.58	- 5.21	0.85
55.2	222	- 5.23	39.49	- 4.04	88.0
61.6	222	- 4.86	40.48	0.51	0.87
68.0	222	- 4.17	40.75	7.05	0,86
74.4	222	- 3,26	39,45	13.59	0.85
East/West (±) Co	mponent				
16.8	222	- 8.06	49.93	226.63	0.85
23.2	222	- 8.47	48.31	226.27	6.87
29.6	222	- 7.34	47.69	225.93	0.87
36.0	222	- 5.88	47.26	225.71	0.87
42.4	222	- 4.85	48.10	226.38	0.87
48.8	222	- 4.12	49.59	227.34	0.89
55.2	222	- 3.99	49.18	229.83	0.90
61.6	222	- 3.47	47.67	233.20	0.90
68.0	222	- 2.28	44.98	237.24	0.89
74.4	222	- 1.19	42.23	240.15	0.88

Table 4.5: Summary of the regression analyses on the velocity time series. (r^2) is the coefficient of multiple determination; phase is based on an initial time of 0813 hours AST on May 3, 1984)

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indicates the haddock eggs were advected through the sampling area within about 5 days, a time similar to the duration of the sampling period (5d) and the age of the stage II eggs (6.9d). The major axes of the tidal excursion ellipses are approximately 11.8 km, one quarter the diameter of the sampling grid.

4.3 Model of Egg Vertical Distribution

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The general equation for describing the rate of change in the concentration of a non-conservative substance, such as fish eggs is (e.g. Nihoul 1975)

$$\frac{\partial C}{\partial t} + \frac{\partial (uC)}{\partial x} + \frac{\partial (vC)}{\partial y} + \frac{\partial (wC)}{\partial z} + \frac{\partial (UC)}{\partial x} + \frac{\partial (VC)}{\partial y} + \frac{\partial (WC)}{\partial z} = \frac{\partial}{\partial x} \left[K_x \frac{\partial C}{\partial x} \right] + \frac{\partial}{\partial y} \left[K_y \frac{\partial C}{\partial y} \right] + \frac{\partial}{\partial z} \left[K_z \frac{\partial C}{\partial z} \right] + \text{sources } + \text{ sinks}$$

$$4.2$$

where C = C(x, y, z, t) is the spatially- and temporally-dependent concentration, x and y denote the horizontal positions, z denotes the vertical position (depth, negative below the undisturbed sea surface), t denotes the time, u, v and w are the spatial components of the water velocity, U, V and W are the spatial components of the velocity generated by the substance (settling velocity, swimming velocity etc.), and K_x , K_y and K_z are the spatial components of the turbulent eddy diffusivity.

In the present context C is the concentration of fish eggs, and W is the terminal velocity of the egg. The source term is assumed to be zero (eggs are introduced as initial conditions) and the sink term is considered to be the loss of eggs caused by natural mortality. This is represented as -MC, where M is the rate of egg mortality.

When it is assumed the vertical water velocity is zero and that horizontal velocities and gradients in the egg concentration are sufficiently small as to make the horizontal advection and diffusion terms negligible, equation (4.2) reduces to

$$\frac{\partial C}{\partial t} + \frac{\partial (WC)}{\partial z} = \frac{\partial}{\partial z} \left(K_z \frac{\partial C}{\partial z} \right) - MC \qquad 4.3$$

This equation states that the time rate of change in egg concentration is due to the divergence of the vertical flux of the eggs and the loss of eggs due to natural mortality. The upward vertical flux is $WC - K_z \ \partial C/\partial z$.

Typical values for W, K_z and M are $10^{-3}ms^{-1}$ (Sundby,1983; Wheeler and Miller, 1960), $10^{-2}m^2s^{-1}$ (Sundby, 1983; Loder *et al.*, 1988) and $0.1d^{-1}$ (Dahlberg, 1979), respectively. A reasonable vertical scale for the depth distribution of buoyant eggs (Z) is 10m (Sundby, 1983; Fridgeirsson, 1984). These values indicate the mortality time scale $(1/M = 10d \simeq 10^6 s)$ is long relative to both the advective $(Z/W = 10^4 s = 3 \text{ hr})$ and diffusive $(Z^2/K_z = 10^4 s = 3 \text{ hr})$ time scales. The mortality term will therefore also be neglected.

Although this scaling assumes K_z is constant over time, K_z is in reality variable (e.g. Loder *et al.* (1988). However, much of the variation occurs on time scales that are long relative to advective and diffusive time scales therefore making it reasonable to assume a constant K_z in the model. Furthermore, as long as the duration of a specific egg stage is longer than the advective and diffusive time scales it is also reasonable to assume a steady-state profile which satisfies

$$\frac{\partial}{\partial z}\left(WC-K_z\frac{\partial C}{\partial z}\right)=0.$$
 4.4

When the concentration is assumed to be zero at great depth the solution to (4.4) is

$$C(z) = C_o \exp\left(-\int_z^0 W/K_z \, dz\right) \tag{4.5}$$

where C_o is the egg concentration at the surface (z = 0).

If both W and K_z are independent of depth, the concentration profile decays exponentially with an e-folding scale of K_z/W . Sundby (1983) has shown that this solution agrees well with observed depth distributions of early stage cod, mackerel and plaice eggs found within the well-mixed surface layer. This solution, however, does not include a subsurface maximum in C(z). However, the concentration profiles of the stage IV haddock eggs reported here, as well as the egg profiles of several other fish species (e.g. pilchard, Coombs *et al.* 1985; halibut, Haug *et al.* 1984, 1986) are characterized by subsurface maxima when the water column is stratified. Sundby's solution is therefore extended by deriving a solution for the case of a continuously stratified water column. This is done by parameterizing the terminal velocity of the egg as a function of the depth dependent water density.

The terminal velocity (W) can be estimated using

$$W = rac{d^2 g(
ho_w -
ho_e)}{18
u}$$
 $Re < 0.5$ 4.6

which is Stokes' equation for spherical particles, the shape of most fish eggs. In these equations ν is the molecular viscosity of sea water ($1.61 \times 10^{-3} kgm^{-1}s^{-1}$ at 5°C and 35; Dorsey, 1940), ρ_w is the density of the water, ρ_e is the density of the egg, g is the acceleration due to gravity, d is the egg diameter, and Re is the Reynolds Number ($Re = \rho_w Wd/\nu$).

Assuming that the water density (ρ_w) is a linear function of d-pth

$$\rho_w(z) = \rho_o + (d\rho_w/dz)z \qquad 4.7$$

such that ρ_o is the water density at z = 0 and $d\rho_w/dz$ is the vertical density gradient, the Stokes' terminal velocity becomes

$$W(z) = \frac{d^2 g(\rho_o - \rho_e)}{18\nu} + \frac{d^2 g(d\rho_w/dz)z}{18\nu}$$
 4.8

Substitution of equation (4.8) into equation (4.5), leads to

$$C(z) = C_o \exp\left(\frac{W_o}{K_z}z + \frac{d^2g \ d\rho_w/dz}{18\nu K_z}\frac{z^2}{2}\right)$$

$$4.9$$

where W_o is the terminal velocity of the egg at z=0,

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$$W_o = \frac{d^2 g(\rho_o - \rho_e)}{18\nu}$$

Inspection of equation (4.9) indicates there are three general cases.

Case i) $\rho_e = \rho_o$: The egg is neutrally buoyant at the sea surface $(W_o = 0)$ and positively buoyant below. The maximum egg concentration is at the surface and decreases monotonically with depth. The profile is a gaussian curve centered at the surface (Figure 4.3b):

$$C(z) = C_o \exp\left(-\frac{1}{2} \left[\frac{z}{\delta_1}\right]^2\right)$$
4.10

where δ_1 is the vertical scale (or standard deviation) of the depth distribution given by

$$\delta_1 = \left(-rac{18
u K_z}{d^2 g \ d
ho_w/dz}
ight)^{1/2}$$

Case ii) $\rho_e < \rho_o$: The egg is positively buoyant at the surface $(W_o > 0)$. Again the maximum egg concentration is at the sea surface. However, now the profile is given by

$$C(z) = C_o \exp\left(\frac{z}{\delta_2} - \frac{1}{2} \left[\frac{z}{\delta_1}\right]^2\right)$$
4.11

where δ_2 is an e-folding scale defined by

$$\delta_2 = \left| \frac{K_z}{W_o} \right|.$$

Typical profiles of this type are shown in Figure 4.3a.

Case iii) $\rho_e > \rho_o$: The egg is negatively buoyant (sinking) at the surface ($W_o < 0$). This is the most interesting case because, ir contrast to Sundby (1983), it describes a subsurface maximum. The egg concentration increases with depth to a sub-surface maximum at $z = z_n$, where z_n is the depth of neutral buoyancy (Figure 4.3b). The profile is given by

$$C(z) = C_o \exp\left(-rac{z}{\delta_2} - rac{1}{2}\left[rac{z}{\delta_1}
ight]^2
ight)$$
 4.12

FIGURE 4.3: Model output illustrating the depth distribution of eggs, assuming a range of egg densities, in a linearly stratified water column. A) $\rho_e < \rho_o$, B) $\rho_e \ge \rho_o$. The curves were generated by assuming $\rho_w(z) = 1025.3 - 1.17 \times 10^{-4} z$, $d = 1.5 \times 10^{-3} m$ and $K_z = 0.01 m^2 s^{-1}$. The values for $\rho_o - \rho_e = \Delta \rho$ in gcm^{-3} were chosen such that $\Delta \rho$ spans the range of typically observed values (see Sundby 1983).



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Note that for a homogeneous water column $d\rho_w/dz = 0$ and equation (4.9) reduces to

$$C(z) = C_o \exp\left(\frac{W_o}{K_z}z\right)$$

$$4.13$$

which is the form used by Sundby (1983).

4.4 Comparison of Theory and Observations

The steady-state theory developed above assumes the horizontal gradients in egg concentration are small and that the mortality, horizontal advection and horizontal diffusion time scales are small relative to the time scales of vertical advection and diffusion. It also assumes the duration of each egg stage is long relative to the time required for the eggs to achieve a steady-state distribution. To determine whether these conditions apply to the depth profiles of haddock eggs described here (Table 4.3) requires that the forcing time scales be estimated. In turn, this requires estimates of $u, v, W, L_x, L_y, Z, K_x, K_y, K_z$ and M from the observations.

Wheeler and Miller (1960) measured the terminal velocity of artificially fertilized haddock eggs and reported a value of $8.3 \times 10^{-4} m s^{-1}$. Bigelow and Welch (1925), Walford (1938) and Wheeler and Miller (1960) measured the specific gravity of artificially fertilized haddock eggs and found early stage eggs had a density of approximately $1023kgm^{-3}$. Assuming this value applies to the eggs sampled here gives an estimate of $\rho_o - \rho_e = 2.3kgm^{-3}$. Substituting this value into Stokes' equations, along with an egg diameter of $1.5 \times 10^{-3} m$, yields a stage I terminal velocity of $1.5 \times 10^{-3} m s^{-1}$. An intermediate estimate of W is therefore $1 \times 10^{-3} m s^{-1}$.

Loder et al. (1988) estimated a coefficient of vertical eddy diffusivity for Browns Bank of $0.02m^2s^{-1}$ which is in the range of typical values for the surface mixed layer (Kullenberg, 1976; Csanady, 1982; Sundby, 1983).

The observed profiles of stage I, II and III haddock egg concentration suggest an appropriate vertical length scale (Z) is 20m (Fig.4.4). The horizontal length scale (L) is taken as 40km, the diameter of the sampling grid, and the advection scale (u) is $0.1ms^{-1}$. K_h is assumed to be $50m^2s^{-1}$, a value appropriate to Browns Bank and the length scale of 40km (Okubo, 1971; Smith, 1989).

Using these values the vertical advection (Z/W) and diffusion (Z^2/K_h) time scales are of order 6 and 5 hours, respectively. These are small relative to the time scales of mortality $(M^{-1} = 3d)$, estimated from data in Table 4.3 by assuming a stable age distribution), horizontal advection (L/u = 5d) and horizontal diffusion $(L^2/K_h = 370d)$ and since the vertical adjustment time scale $(K_z/W^2 = 3 \text{ hours})$ is short relative to the duration of each egg stage (2-5 days) it is concluded the egg profiles are in a quasi-steady-state. Thus the model should provide an explanation for the observed egg profiles.

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The exponential decrease in concentration of the stage I, II and III eggs with increasing depth is consistent with theoretical case ii) where $\rho_e < \rho_o$. The implication that the density gradient has a minor effect on the vertical distribution of these eggs is confirmed by a multiple regression analysis of Ln(C(z)+1) on z and z^2 . The analyses (not shown) indicates the z^2 coefficient, which corresponds to the δ_1 term in equation (4.11), is not significantly different from zero. The slopes from the regressions of Ln(C(z)+1) against z (Table 4.4) can therefore be interpreted as estimates of the e-folding scale, δ_2 . For stages I, II and III this scale, as estimated from the median concentrations at each depth (Table 4.3 and 4.4), is 20.4, 23.2 and 33.3m respectively.

Using the above estimate of $W = 1 \times 10^{-3} m s^{-1}$ and the observed δ_2 value for stage I eggs (20.4m) indicates a K_z during the sampling period of $0.02m^2 s^{-1}$, a value which is consistent with previous time averaged estimates for Browns Bank (Loder *et al.*, 1988).

The ratio of the δ_2 values for different stages is indicative of the ratio of the terminal velocities assuming K_z is the same for all egg stages, an assumption consistent with the eggs of all stages occurring in the same water column at the same time. The ratio of stage I to stage III is 0.6 (Table 4.4) and indicates the stage III

terminal velocity is between 0.5×10^{-3} and $0.8 \times 10^{-3} m s^{-1}$. Given a surface water density of $1025.3 kgm^{-3}$, the density of the stage III eggs was $1023.8 kgm^{-3}$.

The estimate of K_z can also be used to predict the vertical distribution of the stage IV eggs (Figure 4.4). Although the stage IV data are limited, there is a qualitative similarity between their observed and theoretical distributions. This suggests the density of stage IV eggs is similar to, or greater than, the surface water density of $\rho_o = 1025.3 kgm^{-3}$.

4.5 Effect of Egg Vertical Distribution on Horizontal Displacement

The depth-mean horizontal rates of displacement for a patch of fish eggs are defined by

$$u = \frac{\int_{-\infty}^{0} u(z)C(z)dz}{\int_{-\infty}^{0} C(z)dz}$$

$$4.14a$$

$$v = \frac{\int_{-\infty}^{0} v(z)C(z)dz}{\int_{-\infty}^{0} C(z)dz}.$$
4.14b

In a surface Ekman layer these rates vary with the magnitudes of vertical eddy diffusivity and egg terminal velocity because the changes in these parameters change the vertical distribution of the eggs relative to the water velocities. To illustrate this, assume no stratification and that the eggs have buoyancy characteristics similar to stage I or II eggs ($\rho_e < \rho_o$). The proportion of these eggs that are above the Ekman depth (δ_e) is given by

$$\frac{\int_{-\delta_e}^{0} C(z)dz}{\int_{-\infty}^{0} C(z)dz} = 1 - e^{-\delta_e/\delta_2} = 1 - e^{-W_e(2/fK_z)^{1/2}}$$

$$4.15$$

where $\delta_e = \left(2K_z/f\right)^{1/2}$ and f is the Coriolis parameter.

For the egg profiles examined above it is assumed that K_z is constant $(0.02m^2s^{-1})$ and δ_e is approximately 20m (Figure 4.4). Ontogenetic variation in the egg terminal velocity causes the δ_e/δ_2 ratios for stage I, II and III eggs to decrease

from 1.0 to 0.83 and 0.59 and the proportions of eggs below δ_e to increase from 0.37 to 0.44 and 0.55, respectively. This indicates that as the eggs develop their rate of horizontal transport decreases because fewer eggs are within the high velocity zone of the Ekman layer.

More generally the horizontal rate of displacement can be estimated as a function of wind speed and egg terminal velocity and by assuming the vertical diffusivity for fish eggs (K_z) is the same as for momentum $(K_z = K_m)$. This latter assumption is justified by Sundby's (1983) observations that values of K_z calculated from field measurements of the vertical distribution of fish eggs (with known terminal velocity) are similar to those calculated from momentum considerations and that the functional relationship between K_z determined from fish eggs and wind speed is consistent with those derived from theoretical and empirical considerations of K_m (Table 4.6).

In a water column where the Ekman depth is less than the mixed layer depth (H), or bottom depth in the absence of stratification, the vertical diffusivity (K_z) is approximated by $K_z = \alpha u_*^2$ (Csanady, 1972, 1982). In this expression α is a proportionality constant, u_* is the surface friction velocity given by $u_* = (\rho_a / \rho_w)^{1/2} c_d^{1/2} W'$, W' is the surface wind speed in ms^{-1} , (ρ_a) is the density of air $(\rho_a = 1.3Kg/m^3$, Pond and Pickard, 1978), ρ_w is the density of sea water $(\rho_w = 1025Kg/m^3)$, and c_d is the surface drag coefficient ($c_d = 0.0014$). Values of α based on various formulations for K_z vary by a factor of about ten, ranging from 24 to 260 seconds (Table 4.6).

The horizontal displacement rate of fish eggs is plotted in Figure 4.5 as a function of wind speed. Three parameterizations are shown: that of a small α value and high egg buoyancy, that of a large α value and low egg buoyancy and that of intermediate values which are representative of the most commonly observed parameter values. In all cases the magnitude of the horizontal transport increases with wind speed although the rate of increase is sensitive to the values of terminal egg velocity (W) and the mixing proportionality coefficient (α) . At the extreme

FIGURE 4.4: Depth distribution of the observed mean concentrations of haddock eggs (solid dots). Smooth curves are the profiles generated from the model. I, II, III and IV refer to egg stages. For stages I to III the smooth curves were generated by using equation (9) and the observed values of δ_2 , K_z , and the linear density profile. The curves for stage IV were generated by assuming the same K_z and density profile as for the other stages, and by assuming two values of ρ_e chosen to represent $\rho_o - \rho_e = 0$ and $\delta_2 = 35m$. δ_e is the corresponding Ekman depth based on the same K_z .



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TABLE 4.6: Summary of vertical eddy diffusivity (K_z) formulations for $\delta_c < H$. For comparision purposes formulations have been converted to a standard form using $u_* = 0.0013W'$, where W' is wind speed (m/s). The values of alpha are based on combinations of theoretical considerations and observations. Sverdrup et al. (1942), Halpern (1974), Kullenberg (1976) and Pond and Pickard (1978) used Ekman theory and empirical relationships relating the surface velocity magnitude to wind speed. Svensson (1979) derived his relationship by comparing a turbulence closure model with a constant eddy diffusivity model of the surface Ekman layer. Sundby's (1983) relationship is an empirical one derived from values of K_z estimated from profiles of fish eggs and the mean wind speed. Csanady's (1982) formulation is based on Ekman theory and the assumption the Ekman depth $(D = (2K_z/f)^{1/2}$ is equal to $0.1u_*/f$. Bowden (1983) assumes $\delta_e = \pi (2K_z/f)^{1/2} = 0.4u_*/f$.

SOURCE	FORMULATION (as reported) $(K_z; m^2/s)$	$(K_z = \propto u_*^2)$ (sec)
H > D		
Ekman (as reported in Pond & Pickard 1978)	$0.000132W^2$	78'
Sverdrup <i>et al.</i> (1942)	$0.00043W^2$	254'
Halpern (1974)	$0.00043W^{2}$	254'
Kullenberg (1976)	$0.000041W^2$	24
Svenssom (1979)	$0.026u_{\star}^{2}/f$	260
Csanady (1982)	$0.005 u_{*}^{2}/f$	50
Sundby (1983)	$0.00761 + 0.000226W^2$	134′
Bowden (1983)	$0.008u_{*}^{2}/f$	123

' calculated by assuming $u_* = 0.0013W(m/s)$

combination of a high mixing rate ($\alpha = 260s$) and a low terminal velocity (W = 0.0005m/s) the transport velocity asymptotes quickly to a value less than 3cm/s. At the opposite extreme of high terminal velocity (W = 0.003m/s) and low mixing intensity ($\alpha = 50s$), the transport rate continues to increase over the range of wind speeds. At intermediate parameter values (W = 0.001m/s, $\alpha = 100s$), transport rate increases with wind speed to a maximum slightly less than 10cm/s.

Relative to the magnitude of the surface water velocity the horizontal egg velocities drop off quickly as the eggs become mixed deeper within the Ekman layer.

In conjunction with the changes in transport rate as a function of wind speed are changes in transport direction. At low mixing rates or high terminal egg velocities, the eggs are concentrated near the surface and their horizontal displacement is close to 45 degrees to the right of the wind – the deflection angle of the surface Ekman current. This angle increases toward 90 degrees as wind speed (vertical mixing) increases and egg terminal velocity decreases.

4.6 Discussion

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It is generally recognized that the net horizontal displacement of an organism is the result of its vertical movements through the vertical profile of horizontal water velocities (Gagnon and LaCroix, 1983; John, 1984; Miller *et al.*, 1984; Power, 1984; Lewis and Thomas, 1986) and that these vertical movements may vary ontogenetically (McKenzie, 1940; Fortier and Leggett, 1982, 1983; Fridgeirsson, 1984; Frank and Carscaden, 1987), and in response to changes in the physical (Sundby, 1983; Ellertsen *et al.*, 1984) or biological environment (Fortier and Leggett, 1983). Indices, models and concepts of egg and larval transport should therefore take these factors into consideration.

The observations presented in this Chapter show that the majority of early stage haddock eggs (stages I and II) are within the top 50m of the water column, and that their concentration declines exponentially with depth. This is consistent FIGURE 4.5: Magnitude of the horizontal egg transport rate (1st moment) as a function of wind speed, egg upward terminal velocity (W in m/s) and proportionality coefficient (α) for the eddy diffusivity assuming an infinitely deep water column. A: Absolute velocity magnitude. B: Velocity magnitude scaled by the surface Ekman velocity $[2u_*^2/(fd)]$. Dotted line: $W = 0.003m/s, \alpha = 50s$, solid line: $W = 0.001m/s, \alpha =$ 100s, dashed line: $W = 0.0005, m/s, \alpha = 260s$. Levelar and

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with previous descriptions of the vertical distribution of haddock eggs (Walford 1938; Colton 1965). It is also typical of the vertical distributions of the early egg stages of cod, plaice and mackerel (Sundby 1983), pilchard (Coombs *et al.* al 1985) and in the profile of cod/haddock eggs presented by Fridgeirsson (1984). It is inconsistent with the results of Lough (1984) who presented a profile of haddock eggs that increased exponentially with depth. This would suggest that these eggs were negatively buoyant within the sampling depth range.

The result that stage III and perhaps stage IV of haddock eggs are distributed more evenly throughout the water column than the earlier stage I and II eggs, conflicts with previous field observations. Walford (1938) and Colton (1965) showed that the vertical distribution of haddock eggs was the same for all developmental stages but Walford (1938) based his conclusions on egg concentrations integrated over broad depth intervals (0-55m, 55-110m and 115-170m). The results presented here indicate that the majority of the eggs of all stages are found within the 0-55m depth interval and it is obvious that Walford's vertical sampling resolution was too coarse to detect ontogenetic changes. The discrepancy with Colton (1965) results from the egg staging systems employed. Colton used only two stages which corresponded to the present stage I and the combination of stages II, III and IV. The concentration of Colton's second stage eggs were therefore dominated by the more abundant stage II eggs (present staging system) whose vertical distribution is similar to stage I eggs.

The pattern of ontogenetic variation described conflicts with that expected on the basis of previous laboratory measurements (Wheeler and Miller 1960; Moksness and Torstensen 1985). These authors reported that egg density decreased to a minimum during gastrulation (stage II) and then increased toward hatching. Wheeler and Miller (1960) reported that the density of the late stage eggs (stage IV) was intermediate to that of the stage I and II eggs. This suggests that stage II eggs should be more concentrated near the surface than the other stages, and that stage I eggs should be the least concentrated near the surface. Only stage III and IV eggs are consistent with these expectations. Stage I eggs have a depth profile that is statistically indistinguishable from stage II eggs and more concentrated toward the surface than the stage III and IV eggs.

The vertical distribution of the stage IV haddock eggs presented suggests a subsurface maximum in concentration. This has been subsequently confirmed in follow-up studies reported by Frank *et al.* (1989) for the same season and region when the survey timing corresponded well with the availability of stage IV eggs. Peaks have also been shown to exist in the vertical egg profiles of other species such as sprat and pilchard (Coombs *et al.* 1985) and halibut (Haug *et al.* 1984 1986). All of these peaks correspond with density gradients in the water column and could be easily explained by the model presented here.

One of the motivations for the development of the present model, was for possible inclusion in simulation models of egg transport. These models sometimes patch a wind-driven surface-mixed-layer model onto an empirically-defined stationary or slowly-varying residual circulation (ex. Reed, 1980; Spaulding et al., 1983; Reed et al., 1984). The purpose of the mixed-layer model is to provide an estimate of the time-varying surface circulation. In some applications it is also used to help estimate encounter rates between pollutant and organisms (ex. Reed, 1980; Spaulding et al., 1983; Reed et al., 1984). The model presented here suggests the inclusion of the vertical dimension may be important in such applications if the organisms are fish eggs, since encounter rates or probabilities will depend upon the vertical distribution of eggs relative to the pollutant. For example, if the pollutant is a highly buoyant substance such as oil, encounter rates will be high only during light winds when the eggs are concentrated near the surface. At higher wind speeds the eggs will become mixed below the surface, but the oil will not. This will reduce encounter probabilities and cause a differential transport rate between oil and eggs, such that after a time, the distributions will become horizontally separated.

This separation concept was recognized by Fish (1928) in relation to the use or interpretation of constant depth drifters, such as surface drift bottles, as indicators of fish egg and larval transport. The drifters will separate from the patch of organisms at a rate which will be a function of wind speed, egg terminal velocity and drogue depth. The time scale of this separation should be kept in mind when inferring rates of egg and larval drift from drogue studies.

The model developed in this chapter helps quantify this separation effect and gives a simple, but useful, model of egg transport in the surface mixed layer. The vertical distribution model represents an extension of Sundby's (1983) homogeneous water column model. Sundby's model predicts an exponential decrease in egg concentration with increasing depth. However, it does not allow a subsurface maximum. Such a maximum is predicted by the theory developed here which is Sundby's model modified to include a depth-dependant water density. Although a linear gradient in water density and a constant K_z is used, other density and K_z profiles can easily be handled. The linear density gradient is used because it is consistent with the density profile of the water column in the sampling area.

The transport model is based on an Ekman layer which is an idealized representation of wind-induced near-surface circulation, evidence supporting the existence of Ekman-type velocity profiles is accumulating and circulation models often include this type of parameterization. Hunkins (1966) found an Ekman layer under the Arctic ice cap. Gonella (1971), Csanady (1972) and Stacey, Pond and LeBlond (1986) found that the depth distribution and direction of near surface current velocities measured in open coastal waters compared favourably with Ekman dynamics. McNally and White (1985) found evidence for sub-surface Ekman layers. Indirect evidence is given by Svensson (1979) who showed that a suitably parameterized depth-independant vertical eddy diffusivity gave a velocity profile very similar to that generated by a turbulence closure model, which when modified to simulate laboratory flows gave very satisfactory results. The main discrepancy between the model presented here and the contemporary concept of the velocity structure of the surface mixed layer is the omission of the very near surface logarithmic layer. This occupies the top 1m or so of the water column (Csanady, 1984; Churchill and Csanady, 1983) and can be considered to lie on top of the Ekman layer (Svensson, 1979; Csanady, 1982). Its effect is to increase the surface velocity from the 0.013 of the wind speed (W') at the top of the Ekman layer ($\alpha = 100$) to greater than 0.02W' and to decrease the surface deflection angle by about 20 degrees. In a first order model such as that presented here, this layer can be omitted since its effect on egg transport is relatively small.

The model indicates that for eggs with a relatively high positive terminal velocity (W > 5mm/s), a transport index based on the near surface water velocity is appropriate. These are often of the form, cW', where c is the 'wind factor' which varies between 0.01 and 0.05. These values include the effect of the logarithmic layer and of Stokes drift which accounts for about one half of the value (Wu, 1983). The present model does not include the Stokes transport. However, this will be a small additional velocity for low buoyancy particles such as fish eggs. Indices of this type have been used by Murray *et al.* (1983) for mackerel eggs, and by Carruthers, Lawford and Veley (1951) for cod. The terminal velocity of both of these species (mackerel, 1.8mm/s and cod, 1.0mm/s: Sundby, 1983) is such that a surface velocity index is likely to over-estimate their transport rate. A better transport estimate may be obtained by assuming the eggs have an intermediate terminal velocity (see below).

For eggs with small terminal velocities, of the order of 0.1mm/s or less, the eggs will be mixed throughout the Ekman or mixed layer. At wind speeds greater than about 10 m/s these will be transported at a constant rate. For a depth limited layer with constant depth the transport is proportional to the Ekman transport $(u_*^2/fH = aW^2)$.

For eggs with intermediate terminal velocities, of the order of 1mm/s, the transport rate is a non-linear function of wind speed. At low wind speeds the

eggs are concentrated very near the sea surface in the upper portion of the Ekman layer. As the wind speed increases the depth scale characterizing the egg profile (δ_2) increases more per unit wind speed than the Ekman depth scale (δ_e) , such that at wind speeds of approximately 7.5m/s the scales are equal, and at winds greater than this $\delta_2 > \delta_e$. This shift in the distribution of eggs relative to the Ekman velocity profile has the effect of causing the net horizontal displacement rate of eggs to asymptote to a constant as wind speed increases.

Since the terminal velocities of cod (1.0mm/s), and haddock (1.0mm/s); assumed to be similar to cod) are within this category, the suggested reduction in transport rate, relative to the surface, may help explain the enigma of Georges Bank spawning (Colton and Temple, 1961). These authors noted that cod and haddock spawning occurred on Georges Bank in areas and at times when the return of surface drift bottles was usually very low, and suggestive of off-bank transport. Icthyoplankton surveys however, have indicated the eggs and larvae remain over the bank (Smith and Morse, 1985). This discrepancy is perhaps due to the mixing of the eggs deeper into the water column during the strong wind events which presumably dominate the displacements of the surface drifters.

Several of the egg transport functions developed are non-linear functions of wind speed. When these are appropriate representations of egg transport, time averaging of a wind record before converting to displacement is inappropriate. The wind record should first be converted to transport with the appropriate transfer function to produce a record of the time dependent transport rate. This record could then be integrated to produce a total displacement or a time averaged displacement rate. The error introduced by initially time averaging the wind record will increase with the variance of the wind record. For commonly observed wind speeds (0 - 20m/s), eggs of intermediate terminal velocity (order 1mm/s), and limiting depths greater than the Ekman depth, this error is unlikely to exceed a factor of order 2.

Finally, the general perception that the egg stage is a highly dispersive stage subject to very variable and sometimes strong near surface wind driven currents

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may be misleading, at least for haddock. An ontogentic increase in the specific gravity of the eggs, coupled with vertical mixing, can reduce the wind-induced dispersive influence of Ekman transport. The observations and theory presented here indicate that even under conditions of low wind and weak stratification over 30% of haddock eggs are below the Ekman depth (δ_e). In other words, these eggs are below the depth of strong wind driven flow. This proportion increases as the eggs develop: more than 50% of the stage III and IV eggs are below δ_e . Under stronger wind conditions, the proportion below δ_e will increase because K_z also increases. Surface drift bottles and other indicators of the very near surface wind driven transport would then appear, at best, to be poor indicators of haddock egg transport.

CHAPTER 5

Transport of Pelagic Fish Eggs Within a Gyre: A Kinematic Model

5.1 Introduction

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* . 2 As stated in Chapter 1 the spawning grounds of many haddock stocks are located within gyres situated near the edge of the continental shelf (Saville, 1956, 1959, Fraser, 1958; O'Boyle *et al.*, 1984; Smith and Morse, 1985). The integrity and scale of these gyres is generally recognized as being an important physical factor affecting the abundance, survival and dispersion of the haddock early life history stages. Despite this recognition, the actual influence of these gyres on early life stage transport is poorly understood. Many correlation analyses between indices of egg and larval transport and year-class success ignore the influence of a gyre whereas other studies assume the gyre dominates the transport pattern of the early life stages (e.g. Smith and Morse 1985)

Other than ichthyoplankton surveys, few efforts have been made to quantify the residence times of eggs and larvae within the gyres. Loder *et al.* (1982) estimated the residence times of passive scalars within the Georges Bank gyre by using a radial diffusion model and Loder *et al.* (1988) suggest a variety of integral space and time scales for characterizing mixing processes on banks (gyres). Smith (1989) used drogues to estimate the effective horizontal diffusivity and residence time of scalars within the Browns Bank gyre.

In this chapter an idealized gyre is used to help identify some of the basic concepts associated with egg and larval retention within gyres. In particular the particle trajectories associated with a horizontally uniform flow superimposed on a gyre flow is examined.

5.2 Methods

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5.2.1 Flow Field

The gyre velocity (\mathbf{V}_g) is defined by the streamfunction

$$\psi = \psi_o e^{1/2 - R^2/2R_o^2}$$
 5.1

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where ψ_o is a scaling factor for the strength of the gyre, R is the radial distance from the gyre center $(R = x^2 + y^2)$ and R_o is the radial distance at which the magnitude of the gyre velocity $[|\mathbf{V}|_{gm}]$ is a maximum.

The associated flow field is

$$u = -\partial \psi / \partial y = \frac{y |\mathbf{V}|_{gm}}{R_o} e^{(1/2 - R^2/(2R_o^2))}$$
 5.2a

$$v = \partial \psi / \partial x = \frac{-x |\mathbf{V}|_{gm}}{R_c} e^{(1/2 - R^2/(2R_c^2))}$$
 5.2b

where ψ_o is equal to $|\mathbf{V}|_{gm} R_o$.

The total Eulerian flow field is defined by

$$\mathbf{V}(x, y, t) = \mathbf{V}_{g}(x, y) + \overline{\mathbf{V}}(t)$$
5.3

where $\overline{\mathbf{V}}$ is a horizontally uniform, time varying background velocity.

5.2.2 Particle Trajectories

The trajectories of particles released into this flow field are given by

$$dx/dt = u(x, y, t)$$
 5.4a

$$dy/dt = v(x, y, t) 5.4b$$

These equations were solved numerically using an iterative Lagrangian particletracking technique (e.g. Forrester 1973; Hunter 1987). At the beginning of each time step the velocity at the particle position is calculated and the new position is estimated from

$$\mathbf{p}(t + \Delta t) = \mathbf{p}(t) + \mathbf{u}[\mathbf{p}(t), t]\Delta t$$
 5.5

in which p(t) is the position vector at time t, u[p(t), t] is the velocity vector at position p(t) and time t (i.e. the position at the beginning of each time step) and Δt is the time step.

In order to reduce displacement errors generated by spatial and temporal gradients in the Eulerian velocity field the velocity at the projected position $\{\mathbf{u}[\mathbf{p}(t + \Delta t), t + \Delta t]\}$ is averaged with the velocity at the initial position and a revised estimate of the new particle position is made using this average velocity (eq. 5.6).

$$\mathbf{p}(t + \Delta t) = \mathbf{p}(t) + (\mathbf{u}[\mathbf{p}(t), t] + \mathbf{u}[\mathbf{p}(t + \Delta t), t + \Delta t])\Delta t/2$$
 5.6

This procedure is iterated until the average velocity changes by less than 0.1 cm/s.

This scheme is stable for $\Delta t < 2/|du/dx|_{max}$ (Hunter 1987). In all cases the Eulerian velocities were interpolated to particle positions using a four point bivariate interpolation scheme (Abramowitz and Stegun 1964; Press *et al.* 1986).

In order to check the accuracy of the above scheme, particle trajectories were compared with those calculated from the streamfunction of the steady background with gyre flow fields (5.3). The comparisons showed that three iterations and a time step of twelve hours produced particle trajectories that deviated little from the analytical pathlines. ;

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5.3 Results: Flow Fields and Particle Trajectories

5.3.1 Gyre with Steady Background

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The velocity field and streamlines associated with the anti-cyclonic gyre described by (5.2a,b) are shown in Figure 5.1a. When there is no background velocity the particles move clockwise in closed circles. When a horizontally uniform background velocity is superimposed on the gyre the gyre flow begins to be disrupted with the degree of disruption increasing with the magnitude of the background flow. When the background flow is less than the magnitude of the maximum gyre velocity, a region of closed streamlines called a "trapping zone" exists (Figure 5.1b). When the background flow is greater than the maximum gyre velocity no trapping zone exists (Figure 5.1c).

The effect of these flow fields on the distribution of particles is shown in Figures 5.2-5.3. Initially 200 particles were randomly distributed within a circle of radius R_o centered at the origin and 200 additional particles were evenly distributed around the perimeter of the patch. The latter particles were used to produce the envelope surrounding the patch.

In each figure, particle positions are shown for several time periods, each of which corresponds to a fraction of the circuit time (T_c) , the time for a particle to complete one circuit of the gyre at a radius of R_o . The shape of the initial particle patch becomes distorted with time as some particles leave the gyre in a tail or plume and others remain in the trapping zone. The change in shape varies with the strength of the background velocity relative to the strength of the gyre velocity and is due to the shearing and stretching properties of the flow field. Despite the change in shape, however, a numerical integration of the area within the envelope surrounding the particle patch indicates, as expected for a non-divergent flow field, that the area remains constant.

The proportion of particles within the trapping zone, and therefore the proportion of particles retained within the gyre, varies with the size of the initial particle

FIGURE 5.1: Velocity vectors (left panel) and associated streamlines (right panel) for gyre flow with steady, uniform background flow. A) no background flow $\overline{u} = \overline{v} = 0$; B) a medium strength imposed flow: $\overline{u} = 0$, $\overline{v}/|\mathbf{V}|_{gm} = 0.4$; C) background flow equal to gyre flow: $\overline{u} = 0$, $\overline{v}/|\mathbf{V}|_{gm} = 1$. The circular dashed line is the radius equal to R_o . Velocity vectors point away from the crosses.

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FIGURE 5.2: Particle position plots assuming $\overline{u}/|\mathbf{V}|_{gm} = 0$, $\overline{v}/|\mathbf{V}|_{gm} = 0.4$, $R_o = 20Km, T_c = 14.5$ days and |V|gm = 10cm/s. The gyre radius (R_o) is indicated by the dashed circle. The solid curve surrounding the particles is the particle envelope and the remaining closed solid curve is the trapping zone. A) $t/T_c = 0$, B) $t/T_c = 0.17$, C) $t/T_c = 0.34$, D) $t/T_c = 0.5$, E) $t/T_c = 0.69$, F) $t/T_c = 0.86$.













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FIGURE 5.3: Particle position plots assuming $\overline{u}/|\mathbf{V}|_{gm} = 0, \overline{v}/|\mathbf{V}|_{gm} = 0.8, R_o = 20Km, T_c = 14.5$ days and $|\mathbf{V}|_{gm} = 10cm/s$. A) $t/T_c = 0$, B) $t/T_c = 0.17$, C) $t/T_c = 0.34$, D) $t/T_c = 0.5$. The gyre radius $[R_o]$ is indicated by the dashed circle. The solid curve surrounding the particles is the particle envelope, the remaining closed solid curve is the trapping zone and the small dashed curve is the trajectory of the center-of-mass.



Figure 5.3





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patch R_p and the strength of the background flow relative to the gyre flow. For a given particle patch size the proportion within the trapping zone decreases nonlinearly as the magnitude of the background velocity increases from 0 to 1 (Figure 5.4a). For example when the particles are initially distributed within a circle with a radius equal to that of the gyre $(R_p/R_o = 1)$ all of the particles are within the trapping zone for $\overline{\mathbf{V}}/|\mathbf{V}|_{gm} < 0.2$ because the trapping zone is larger than the initial patch of particles. As the magnitude of the background velocity increases to that of the gyre, the proportion of particles within the trapping zone decreases to zero. The threshold value increases as the initial patch size decreases.

The above concepts have been developed without consideration being given to the time dependence of the particle displacements. The time dependence can, however, be important. In the absence of diffusion, particles outside the trapping zone are quickly advected from the gyre (Figures 5.2-5.3) whereas those within in the trapping zone may repeatedly leave and re-enter the gyre as the particles circuit the trapping zone.

For an initial patch the proportion of particles within a radius of R_o from the gyre center therefore quickly decreases to a mean value about which oscillations occur due to the transitting of the trapped particles in and out of the gyre (Figure 5.5). The time reguired to reach this mean value depends on the magnitude of the background velocity. When the magnitude of the background flow is less than that of the gyre, the mean proportion remaining in the gyre is reached in approximately one-half the circuit time. When the magnitude of the background velocity is greater than the gyre velocity all of the particles are removed from the gyre within the time it takes for the a particle moving at the speed of the background velocity to traverse the diameter of the gyre.

In the presence of diffusion the proportion of particles remaining within the gyre continues to decline since particles initially within the trapping zone eventually diffuse out of this zone. Whether the particle losses are dominated by diffusive or advective effects depends on the rate of advection, the rate of diffusion and the size







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of the gyre. Nevertheless, a simple criterion for estimating the effect of a background current on the displacement of particles within a gyre is that the magnitude of the background current is greater than the magnitude of the maximum gyre velocity and the duration of the background current is equal to or greater than the time to advect the particles across the gyre.

5.3.2 Gyre with Time Varying Background

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In the above simulations the background velocity was assumed to be steady. The more realistic scenario of a time-varying background flow field is illustrated in Figure 5.6. In these simulations the radius of the initial particle patch is again equal to the radius of the gyre ($R_p = R_o = 20 km$) and the background velocity is assumed to be a linear function of an observed wind speed (W') record. In particular three cases are considered: the background velocity is assumed to be 0.01W', 0.03W' and a time average of the 0.03W' record. As exported, from the predictions of the above theory, the proportion of particles remaining within the gyre is sensitive to the magnitude of the wind driven current. The loss generated by the 0.01W' background flow is less than that generated by the 0.03W' series. More importantly, however, is the fact that the time averaged 0.03W' background flow generates less than one half the loss generated by the time varying 0.03W' series. The single wind event (0.03W') of duration approximately $T_c/4$ completely flushed all particles from the gyre.

5.3.3 Gyre with Steady, Depth-Dependent Background

The above considerations have assumed the background velocity is horizontally and vertically uniform. However, as discussed in the previous Chapter, fish eggs are often found within the surface Ekman layer. The water velocities in this layer decrease in magnitude and rotate in direction with increasing depth. It is therefore FIGURE 5.5: The proportion of particles within a radius of R_o as a function of time $[t/T_c]$ and strength of the imposed velocity $[|\overline{\mathbf{V}}|/|\mathbf{V}|_{gm}]$ (number labels within figure). The solid lines represent cases in which particle trajectories determined by advection only. The initial particle patch had a radius of $R_p = R_o = 20 Km$, $|\mathbf{V}|_{gm} = 10 cm/s$, $T_c = 14.5$ days.



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Figure 5.5

FIGURE 5.6: Upper Panel: Daily mean wind speed, scaled by $|\mathbf{V}|_{gm}$, as a function of time $[t/T_c]$. The horizontal dashed lines indicate when 0.03W' = $|V|_{gm}$. The initial conditions: radius of particle patch $R_p = R_o =$ 20Km. $|V|_{gm} = 10cm/s$, $T_c = 14.5$ days, no diffusion. Lower Panel: The proportion of particles within a radius of Ro as a function of nondimensional time $[t/T_c]$ and strength of the time dependent imposed velocity [|V|] which is assumed to equal 0.03W', 0.01W' and 0.03 of the time averaged wind speed.

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worth considering the trajectories of particles when an Ekman type background flow is superimposed on the gyre.

Assume the magnitude of the Ekman current at the surface is greater than that of the gyre. Fish eggs remaining at the surface will therefore be advected out of the gyre as described above. The magnitude of the Ekman current, however, decreases with increasing depth so that below some critical depth the Ekman currents are less than the magnitude of the gyre current and subsurface trapping zones will exist. The size of these trapping zones will increase with depth so that at depths below the bottom of the Ekman layer all of the fish eggs will be trapped.

The effectiveness of this trapping (retention) mechanism will depend on the time individual fish eggs spend in the subsurface trapping zones. As discussed in Chapter 4 the vertical distribution of fish eggs depends on the balance between egg terminal velocity and vertical eddy diffusivity. Although the vertical profile of egg concentration may remain constant individual eggs are constantly being mixed throughout the water column. Therefore eggs will continually be vertically diffused in and out of the subsurface trapping zones. The highly buoyant early stage eggs will spend less time at depth than the less buoyant late stage eggs. Therefore the late stage eggs will be more effectively retained by the subsurface trapping zones than the early stage eggs.

5.4 Discussion

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A continuing topic of controversy is whether eggs and larvae spawned within gyres remain within these gyres (Colton and Temple, 1961; Colton and Anderson, 1983; O'Boyle *et al.*, 1984). Surface drift bottles often suggest they do not (Colton and Temple, 1961) whereas ichthyoplankton surveys indicate they often do (Smith and Morse, 1985).

The models examined here, although based on specific flow fields, suggest that gyres are good at retaining early life stages. Trapping zones presumably exist in any steady gyre and the area enclosed within the trapping zones should decrease as the magnitude of the background flow superimposed on the gyre increases. Although the size and shape of the trapping zones will depend on the shape and strength of the gyre, the loss of fish eggs from all symmetrical gyres will presumably be minimized if the spawning ground is located in the middle of the gyre, if the size of the spawning ground is small relative to the size of the gyre and if the gyre structure persists over the depth range occuppied by the early life stages.

The models also suggest that the ability of a gyre to retain particles, or conversely the ability of an imposed flow to remove particles from the gyre, is characterized by the advective and circulation time scales. The advective time scale is the time to cross the gyre when moving with the background velocity. The circulation time is the typical time a particle takes to complete one circuit of the perimeter of the gyre at a radius of R_o . The ratio of circulation to advection time scales gives an index of the relative strength of the gyre. When the circulation time is greater than the advection time the background velocity dominates the particle trajectories and particles are flushed from the gyre within the advection time scale. Conversely, when the circulation time is less than the advection time the gyre circulation dominates the particle trajectories and a proportion of the particles remain trapped within the gyre. These characterizations are similar to those suggested by Loder *et al.* (1988).

The models also show the complexity of egg, and therefore, larval transport and indicate that models must ultimately be based on an accurate three-dimensional and time dependent representation of the flow field. More specifically they must include accurate representations of the vertical diffusivity (or turbulence), the time dependent flow field and they must resolve the circulation in the vertical dimension on spatial scales that are appropriate to the organisms being considered. In addition it is important that the Lagrangian, rather than the Eulerian circulation be estimated.

CHAPTER 6

Description and Evaluation of A Surface Layer Particle Drift Model For the Browns Bank Haddock Spawning Area

6.1 Introduction

In the previous chapter the horizontal transport of haddock eggs has been considered from a theoretical point of view. It was stated that although the concepts developed are generally applicable, the details will vary according to the specific characteristics of local flow fields and that transport models must ultimately be based on three-dimensional time dependent flow fields. Unfortunately, such three dimensional flow fields are uncommon, but two dimensional circulation models do and evaluation of particle trajectories based on these may provide additional insight into the problem of early life stage transport. Therefore, in this Chapter, a particle tracking model is developed for a specific haddock spawning area, that of Browns Bank off Southwest Nova Scotia (Figure 3.1).

The core of any Lagrangian particle tracking model is an accurate (Eulerian) representation of the circulation. The Southwest Nova Scotia region has been well studied from a physical oceanographic viewpoint (Bigelow 1927; Day 1958; Smith 1983, Smith 1989a,b) and numerical models of the tidal, residual (Greenberg 1983; Tee et al. 1987) and steady wind-driven circulations (Wright et al. 1986) are available. The Eulerian currents, measured at fixed locations on Browns Bank, are highly variable, with the variance in many locations exceeding the mean by a factor of ten or more (Loder et al. 1988). Furthermore, root-mean-square excursions associated with the fluctuating currents are comparable to the length scales of the mean horizontal shear, particularly near the surface. Under these circumstances, the Lagrangian circulation governing the particle trajectories may be quite different from that inferred from the Eulerian residual currents (Longuet-Higgins 1969; Zimmermann 1979; Cheng et al. 1986). Therefore the relationship between the mean circulation and the displacements of haddock eggs and larvae is uncertain. The two-dimensional model developed for the surface layer off Nova Scotia therefore includes time-varying tidal and wind-induced currents in addition to the mean currents. The purpose of this chapter is to describe the model, evaluate the importance of the time-varying tidal and wind-driven components of the circulation in determining particle trajectories and assess the model's utility by comparing predicted particle paths with the observed trajectories of satellite-tracked drogues. These comparisons are made because circulation models are usually tested in an Eulerian framework, that is, by comparing model and observed currents at fixed locations, in spite of the fact that it is the Lagrangian circulation that governs the dispersion patterns. Furthermore, in the few cases where Lagrangian validations have been attempted, the models were usually qualitatively but not quantitatively satisfactory (e.g. Trites et al. 1986).

6.2 Model Overview

Assuming linear superposition of the various components of the circulation, Eulerian horizontal velocities [u(x, y, t), v(x, y, t)] are specified at evenly spaced grid points as,

$$u = \overline{u} + A_x \cos(\omega t - P_x) + \tau_x G_{xu} + \tau_y G_{yu}$$

$$6.1a$$

$$v = \overline{v} + A_y \cos(\omega t - P_y) + \tau_z G_{xv} + \tau_y G_{yv}$$

$$6.1b$$

where $\overline{u(x,y)}$, $\overline{v(x,y)}$ are the components of the residual (mean) velocity along the x- and y-axes, $A_x(x,y)$, $A_y(x,y)$ are the M_2 tidal amplitudes, $P_x(x,y)$, $P_y(x,y)$ the tidal phases, $\omega = 2\pi/T$ and T are the M_2 tidal frequency and period (assumed to be 12.5 hours), $\tau_x(t)$, $\tau_y(t)$ are the uniform components of the surface wind stress, and G_{xu} , $G_{xv}(G_{yu}, G_{yv})$ are the spatially-varying gain factors relating τ_x, τ_y to the u and v components of the wind-driven current. $\overline{u}, \overline{v}, A_x, A_y, P_x, P_y, G_{xu}, G_{xv}, G_{yu}, G_{yv}$ have previously been computed from Greenberg's barotropic 2-D model on a Richardson lattice (Greenberg 1983; Wright *et al.* 1986). τ_x and τ_y are sea surface wind stress components estimated from hourly wind measurements at Sable Island (Smith 1989b).

In order to estimate the trajectories of particles from the Eulerian velocity field, the iterative Lagrangian particle-tracking technique described in Chapter 5 and in Figure 6.1 was adopted. Unlike Chapter 5, however, the Eulerian velocities were interpolated to particle positions using a six point bivariate interpolation scheme (Abramowitz and Stegun 1964; Press *et al.* 1986), and adjustments were made to the definition of the velocity components to account for them being defined on a Richardson lattice (Greenberg 1983). When tidal motions were included in the model a time step of 0.5 hours and an iteration accuracy of 0.1cm/s was found to give adequate results.

6.2.1 Flow Field Specification: Residual

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Two approaches have been used to define the residual velocity field. The first approach, follows that often used in oil spill trajectory modelling (e.g. Spaulding *et al.* 1983; Lawrence and Trites 1983; Trites *et al.* 1986), and employs the empirically-defined seasonal (winter and summer) velocity fields compiled by Lawrence and Trites (1983) for the Gulf of Maine (Figure 6.2). These velocities were estimated on a $1/4^{\circ}$ latitude $\times 1/4^{\circ}$ longitude grid from a wide range of information, including current meter records, drift bottle returns, satellite-tracked drifter trajectories and geostrophic calculations. The annual average velocity vectors $[(V_{sum} + V_{win})/2]$ were used as the residual velocity field since the haddock spawning season is from March through May. This approach has the advantage that all components of the residual current (barotropic and baroclinic) are included in the estimates.

The disadvantages are that errors in those estimates may render the flow horizontally divergent and interannual variation in the residual current cannot be incorporated. Also, since the grid scale (approximately $20 \times 28km$) is of the same order as the topographic length scale characterizing Browns Bank, the detailed circulation there is poorly resolved.

In order to achieve a greater spatial resolution and to ensure a dynamically consistent flow field, the residual currents predicted by the nonlinear barotropic M_2

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FIGURE 6.1 Flow Chart outlining the particle tracking scheme used for the simulations presented in this Chapter.

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Figure 6.1



FIGURE 6.2 Location map showing the perimeters of the Lawrence and Trites (1983; dashed line) and Greenberg (1983; bold solid line) subgrids superimposed on the full Greenberg (1983) grid.

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tidal model of Greenberg (1983) are also used (Figure 6.2). This depth-averaged model computes Eulerian residuals for the entire Gulf of Maine, Bay of Fundy and western Scotian Shelf regions based on sea level calibrations of the tide at various coastal and offshore stations. Only the southwest Nova Scotia portion of this model is used (Figure 6.2). The x-(36 grid points) and y-(25 grid points) axes are oriented in the cross-shore (146° T) and along-shore (56° T) directions, respectively, with equal resolutions of dx = dy = 7.25km.

The residual currents generated by the Greenberg model are similar to those generated by the three-dimensional tidal models of Isaji and Spaulding (1984) and Tee *et al.* (1987), but the agreement between modelled and observed tidal residual velocities is variable. In particular, Tee *et al.* (1987) found their 3-D tidally-induced velocities agree with those observed to within roughly 50% in the inshore region near Cape Sable, but around the edges of Browns Bank, the model underestimates the observations by a factor of approximately four at the surface. This discrepancy has been attributed to the inability of the 7- km grid to resolve the bottom topography defining the Bank and to baroclinic effects. In the inshore region between Halifax and Cape Sable, Tee *et al's* model also underestimates the observed velocities, but the magnitude of this difference is uncertain due to large spatial variation in the predicted velocities and to large error bars on the observed values (Tee *et al.* 1987).

Another disadvantage of the Greenberg model is that baroclinic components of the circulation, particularly over Browns Bank and in the Nova Scotian Current inflow, are not included. Smith (1983) attempted to account for the depth-averaged component of the Scotian Shelf inflow by adding a pressure driven current genera ed by a coastal set-up in sea level along the eastern boundary at Halifax. He found best agreement with observations using a linearized version of the Greenberg model with either a 4cm set-up at Halifax which decays exponentially offshore or a 2cm Halifax set-up which decays linearly to the shelf edge. The former boundary condition serves to concentrate the inflow currents nearer the coast, but the net alongshore transports are equivalent (Wright *et al.* 1986).

6.2.2 Flow Field Specification: Time-Varying Flow

Tidal currents are estimated using the amplitudes and phases predicted by the Greenberg (1983) model. Comparisions with observations in various regions have indicated that tidal currents are accurately estimated by the model. In the shallow waters on the northern flank of Georges Bank the model M_2 amplitudes and phases are within 5% and 4 degrees respectively of values estimated from current meter records (Marsden 1986). At a location in the deeper waters just off the northern flank the discrepancy increases to 10-35% in amplitude and 6-91 degrees in phase (Marsden 1986). This reduction in accuracy may, however, be due to mooring motion or a baroclinic tide since the predicted values are in close agreement with theoretical expectations (Marsden 1986). Off Cape Sable, both the depthaveraged component and vertical structure of the model M_2 tidal currents are in close agreement with observations (Tee *et al.* 1987).

The current variation with periods of 2 to 10 days is largely driven by the wind (Smith 1989a) and can be estimated, for the lowest frequencies at least, using the steady-state model wind-current gains of Wright *et al.* (1986). Since these gains apply to the depth-averaged current, they agree most favourably with those measured at mid-depth current meters. The observed low-frequency response near the surface (bottom) is generally larger (smaller) than at mid-depth and rotated slightly clockwise (counterclockwise). This may be inferred from the correlations between monthly anomalies of alongshore stress and current components off Cape Sable [Smith, 1989b]. At higher frequencies, the measured surface current responses to alongshore wind stress at mooring locations C3 and C4 (Figure 6.4) fall within 25% of their low-frequency limits for periods down to 3 days, after which they decline sharply. This behaviour is consistent with the Greenberg model spinup time of less than 20 hrs (Wright *et al.* 1986). Thus the steady-state model gains may be reasonably used to estimate the wind-driver, response in this region.

The forcing winds used to define the 2-D model current response were calculated from hourly winds recorded at Sable Island. The hourly observations were converted to sea surface wind stress using the formulae of Smith and Banke (1975), filtered using a Cartwright low-pass filter with 129 weights (cutoff frequency 0.036 cph, 25% power passed at 28.4 hours) and subsampled at 6-hour intervals [see Lively (1984) for further details]. Since the current gain decreases rapidly for periods below 3 days, the 6-hour winds were further smoothed with an eleven point (66 hour) running mean. This series was then linearly interpolated to half-hour intervals for input into the particle dispersion model.

6.3 Drogue Trajectories

In order to test the dispersion model, simulated particle trajectories are compared to the observed paths of satellite-tracked drogues. The drogue types, deployment times and locations and trajectories have been described by Smith (1989a). In brief during each deployment three to six holey sock drogues were released in a cluster and their positions recorded simultaneously 6-8 times a day by the ARGOS satellite system. For the present comparisions the time series of positions for each drogue were interpolated to hourly intervals. Tidal variations in position were removed by smoothing these series with a 13-hour running mean. The centroid of the cluster was then calculated at hourly intervals.

6.4 Results

6.4.1 Residual Circulation Patterns

The large-scale characteristics of the Lawrence and Trites (1983) and Greenberg (1983) Eulerian residual velocity fields are similar. The main features are clockwise gyres over Browns Bank, a westward flow between the western cap of Browns Bank and the coast of Nova Scotia and a strong eastward flow along the northeastern flank of Georges Bank. In the Lawrence and Trites (1983) residual field a single clockwise gyre surrounds the whole of Browns Bank, whereas the tidal residual field of the higher resolution Greenberg (1983) model shows two smaller clockwise gyres over the Bank (Figure 6.3a,b). To simulate Scotian Shelf inflow, the inclusion of the

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4-centimeter coastal set-up with an offshore exponential decay scale of 39km on the eastern boundary of the Greenberg model enhances the magnitude of the westward flow into the Gulf of Maine, reduces the magnitude of the flow along the northern flank of Browns Bank, increases the cross-isobath component of this flow, increases the magnitude of the flow along the southern flank of the Bank and aligns this flow more closely with the isobaths (Figure 6.3c). However, the flow on Georges Bank is not significantly affected. Henceforth the model flow field driven by nonlinear tidal interactions and the 4cm coastal setup at Halifax will be referred to as the Greenberg residual circulation.

6.4.2 Comparison of Model and Observed Eulerian Residual Circulations

The Greenberg residual circulation is essentially the same as the one that Smith (1983) compared favourably to the observed depth-averaged annual-mean currents in the area. However, a comparison between model and observed near-surface Eulerian velocities at several mooring locations indicates that both models are underestimating the seasonal mean flow (Figure 6.4). For this comparison the measured currents were averaged over the late-spring haddock spawning season (March, April and May) using all available monthly mean data [Smith 1983, 1989a,b]. At two locations (C4 and C7, Figure 6.4) the Lawrence and Trites (1983) and Greenberg velocities are similar and both underestimate the observed means by factors of 3 or 4. At moorings C3 and C8 (Figure 6.4) the Lawrence and Trites (1983) velocities exceed the Greenberg velocities by a factor of approximately 3 to 5. The Lawrence and Trites (1983) velocities, in turn, underestimate the observed velocities by a factor of 2 to 5.

On Browns Bank both models also under-estimate observed mean Lagrangian velocities. The Greenberg residuals predict the time to circuit the western gyre of Browns Bank is approximately 40 days. This is four times greater than the 8-12 days indicated by the trajectories of satellite tracked drifters drogued between 5

FIGURE 6.3 Model velocity fields showing the Eulerian residual velocity vectors. a) Lawrence and Trites (1983; $[V_{sum} + V_{win}]/2$), b) Greenberg (1983) pure tidal residual, c) Greenberg (1983) tidal residual + 4cm setup (exponential decay offshore) in coastal sea level on the eastern boundary of the full Greenberg grid at Halifax. (+ specifies the origin of the vector)



Figure 6.3

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FIGURE 6-4 A comparision of observed and model Eulerian mean current velocities.
Observed currents are averaged over the haddock spawning months on Browns Bank (Mar, Apr, May). (+ specifies the origin of each vector; LTR - Lawrence and Trites residual; GR - Greenberg Residual; M - observed mid-depth velocity; S - observed near surface velocity; C1,C3,C4,C7,C8 are current meter locations)





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and 15m depth (Smith 1989a). The enhanced velocities of the Lawrence and Trites model would not account fully for this discrepancy.

6.4.3 Lagrangian Residual Circulation Pattern

As a check on the stability and accuracy of the numerical particle tracking scheme, the particle-tracking model was tested against the analytical solution of Cheng et al. (1986) for the particular case of a Sverdrup wave propagating in the positive x-direction. The Sverdrup wave particle trajectories, calculated using a time step of 0.5 hours and an iteration accuracy of $0.001 ms^{-1}$, produced Lagrangian residual model displacements which differed from the analytical displacements by less than 3% after one and two tidal periods. The iteration accuracy was generally achieved with three or fewer iterations. Unless otherwise specified, a 0.5 hour time step and a $0.001 ms^{-1}$ iteration accuracy is used for all model runs presented here.

To estimate the Lagrangian residual velocity field, the model particle trajectories from each grid point were calculated over one tidal cycle (12.5 hrs) and the displacement vectors to the end points were divided by the elapsed time. Not surprisingly, the Lagrangian velocities estimated from the Greenberg (1983) residuals alone (Figure 6.5) are similar to the Eulerian velocities themselves (Figure 6.3). When the tidal currents are included in the Eulerian field, the lowest order difference between the Lagrangian and Eulerian velocity is the Stokes drift (u_{SD}, v_{SD}) , plus a slight variation of the magnitude and direction of the Lagrangian current with the time of particle release (Figure 6.6a) due to higher order terms in the Eulerian-Lagrangian transformation residual current. In the nearshore region north of Browns Bank, the velocities may be deflected to the right or left of that estimated from the Eulerian residual only. On the southwestern flank of the Bank, bordering Northeast Channel, the off-bank component of the velocity is increased by the time-varying tidal flow, while on the northern flank nearest Cape Sable, the flow is opposite to that resulting from mean Eulerian flow. The velocities along the eastern flanks of the Bank are relatively unchanged by the introduction of tidal currents. On the northern flank of Georges Bank, the Lagrangian velocity is in the same direction as the Eulerian velocity, but the average (over the tidal phase of release) magnitude is roughly two thirds the Eulerian residual velocity, consistent with the theoretical expectations of Loder (1980). These differences are magnified in the comparison of 15-day particle trajectories (Figure 6.6b).

6.4.4 Effect of Wind on the Circulation

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The depth-averaged velocity fields generated by a 0.1 Pa wind stress (corresponding to a wind speed of about 7 to $8ms^{-1}$) in the positive along-shore and cross-shore directions are the same as those presented by Wright *et al.* (1986; their Figures 4 and 5). The currents produced by the cross-shore stress are generally very weak and show little spatial variation. The along-shelf stress, on the other hand, produces relatively strong currents (order $0.05ms^{-1}$) throughout the southwest Nova Scotia region. When these are added to the residual currents, the along-shelf wind-driven circulation is found to dominate the residual, whereas the cross-shelf wind has little effect in most of the region (Figure 6.7). This is also reflected by the 4-day particle trajectories (Figure 6.8a,b). In response to a steady along-shelf wind of 0.1 Pa, the particles move along an east-west axis at a rate of approximately $0.04ms^{-1}$, but cross-shelf winds produce very little net displacement of the particles.

These velocity fields and particle displacements are calculated using depthmean currents which are most representative of the current pattern at mid-depth, i.e. away from the surface and bottom frictional layers. This level is appropriate for haddock larvae and perhaps the late-stage eggs. The earlier stage eggs, however, are concentrated within the surface Ekman layer. In the two-dimensional form of the equations, the Ekman transport $(\tau/\rho f)$ is averaged over the depth (h) of the water column so that its contribution to the depth-averaged current is quite small, except in shallow (order 10m) areas. A more realistic estimate of the effect of

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FIGURE 6.5 Model velocity field showing the Lagrangian velocity vectors calculated after one tidal cycle using the Greenberg (1983) pure tidal residuals (dotted vectors) and tidal residuals + 4-cm coastal set-up at Halifax (solid vectors; see text). (+ specifies the origin of the vector; 0 specifies the particle was released at $t_o = 0$)





FIGURE 6.6 a) Model Lagrangian velocity field calculated after one tidal cycle using the Greenberg (1983) tidal residuals + 4-cm coastal set-up (dashed, 'R' at top) and the tidal residuals + 4-cm coastal set-up + tidal currents (solid). The complete field of solid vectors represents Lagrangian velocities for particles released at to=0. At selected grid points, numbers shown at the tips of the four solid vectors correspond to different times (tidal phases) of particle release (0: $t_o = 0$, 1: $t_o = T/4$, 2: $t_o = T/2$, 3: $t_o = 3T/4$, $T = 2\pi/\omega =$ tidal period). b) 14.5-day (28 tidal cycles) particle trajectories. The solid and dashed lines refer to trajectories calculated using the Eulerian currents as specified in Figure 6-6a. (+ specifies the origin of each vector or trajectory; diamonds specify the end position of a trajectory; large dot marks the end of every 4th tidal cycle)



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FIGURE 6.7 Model Eulerian velocity field including pure tidal, 4-cm coastal setup on eastern boundary at Halifax and depth-averaged response to 0.1 Pa wind stress. a) $-\tau_y$, alongshelf, b) $+\tau_y$, c) $+\tau_x$, cross-shelf, d) $-\tau_x$. (+ specifies the origin of each vector)

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Figure 6.7

FIGURE 6.8 4.2-day (8 tidal cycles) particle trajectories calculated using Greenberg pure tidal residuals + 4-cm coastal set-up at Halifax + tidal currents $(t_o = 0)$ + depth-averaged responses to constant 0.1 Pa alongshelf (a) and cross-shelf (b) wind stresses. The solid (dashed) lines refer to trajectories calculated with (without) a wind-driven component. (+ specifies the origin of each trajectory; diamonds specify the end position of a trajectory; large dot marks the end of every 4th tidal cycle)





Figure 6.8

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Ekman transport on the displacement of haddock eggs in the surface layer can be gained by subtracting the depth-mean Ekman transport from the total of winddriven current plus residual, then adding back the velocity obtained by distributing the Ekman transport over the depth of the surface Ekman layer, assumed to be 30m (based on scaling estimates for a 0.1 Pa wind stress and observed mixed layer depths in spring). The enhanced surface velocity fields are shown in Figure 6.9ad. The current field associated with the along-shelf wind is much the same as with depth-averaged Ekman transport, although the velocities are now somewhat greater. On the other hand, the surface circulation associated with the cross-shelf stress is greatly increased and consists primarily of a uniform Ekman-dominated current approximately $0.05ms^{-1}$. By comparison to Figure 6.7, it is clear that the surface-enhanced components of a circulation driven by 0.1 Pa stresses dominate the pure residual flow, although for cross-shelf wind, a weak gyre still exists over the western cap of Browns Bank (Figure 6.9c,d). In all of these cases, the southwestward along-shelf wind (opposite to that in Figure 6.10a) causes the gyre on the western cap of Browns Bank to open, such that particles can escape from the Bank in a northerly direction. An offshore wind allows some particles to escape toward the west (Figure 6.10b).

The question now arises as to whether steady or time-dependent stresses are more effective in controlling particle trajectories in the surface layer. The mean alongshore stresses at Yarmouth and Sable Island are small (about.01 and .02 Pa respectively) and correspond to currents of only $.003m s^{-1}$ (Smith 1989b). Variable stresses, on the other hand, have amplitudes of about 0.1 Pa for periods less than one month (.08 and .13 Pa for periods of 10-30 d and 2-10 d respectively; Smith 1989a), and therefore drive significant currents on the biological time scales of interest. In order to investigate further the influence of the wind-driven currents, the particle trajectories were calculated using a periodic wind stress with an amplitude of 0.1 and 0.4 Pa and a period of eight days. The eight-day trajectories of single particles released at several locations were estimated using 1) residual + tidal currents and FIGURE 6.9 Model Eulerian velocity including pure tidal residual, 4cm coastal setup at Halifax, and surface-enhanced responses to 0.1 Pa wind stresses (see text) a) $-\tau_y$, alongshelf, b) $+\tau_y$, c) $+\tau_x$, crosshelf, d) $-\tau_x$. (+ specifies the origin of each vector)

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Figure 6.9

FIGURE 6-10 4.2-day (8 tidal cycles) particle trajectories calculated using Greenberg pure tidal residuals + 4-cm coastal set-up at Halifax + tidal currents (tc=0) + surface-enhanced responses to constant 0.1 Pa alongshelf (a) and cross-shelf (b) wind stresses. The solid (dashed) lines refer to trajectories calculated with a surface-enhanced (depth-averaged) wind-driven components. (+ specifies the origin of each trajectory; diamonds specify the end position of a trajectory; large dot marks the end of every 4th tidal cycle)

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2) wind + residual +tidal currents. Figure 6.11a,b shows that the 0.1 Pa oscillatory wind has little effect on the net particle displacements. This result also applies to the stronger wind stress forcing (0.4 Pa; results not shown).

6.4.5 Drogue Trajectories

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In order to evaluate the model's ability to reproduce the trajectories of passively drifting particles in the surface layer, hypothetical particles were introduced into the model flow fields at the co-ordinates corresponding to the centroid of a cluster of satellite-tracked drifters drogued at 10m. We chose four drogued drifter trials for comparison: April and November 1983, May 1984 and May 1985.

During April of 1983, drifters were released over the western cap of Browns Bank, in the eastern half of the cap gyre, and quickly drifted off the Bank in a northerly direction. Smith (1989a) suggested this was due to the westward wind component prevailing throughout the deployment period. The simulated trajectory, using the Greenberg residual flow plus surface-enhanced wind drift (Figure 6.12a) qualitatively reproduces the observed trajectories, but underestimates the net displacement by roughly a factor of four. This comparison also shows the danger in using the residual circulation as the sole estimate of the circulation. The particle trajectory estimated from the residual circulation alone is toward the east in compliance with the western cap gyre and toward the northwest when the tidal currents are included. Inclusion of the wind accelerates the displacement in this latter direction.

A similar conclusion is reached by comparing observed and simulated particle tracks in November, 1983 (Figure 6.12 b). Drogues were released on the northwest peak of the Bank at the start of two consecutive periods and recovered after drifting for approximately two days. During the first period, the prevailing wind was from the east (easterly) and the drogues were displaced to the northwest. The model tracks also show this but underestimate the displacement by nearly a factor of 5. At the start of the second period, the prevailing wind was westerly and the drogues FIGURE 6-11 8.3-day (16 tidal cycles) particle trajectories calculated using Greenberg pure tidal residuals + 4-cm coastal set-up at Halifax + tidal currents (to=0) + surface-enhanced responses to 0.1 Pa periodic $[0.1sin(2\pi t/P)]$, P = 16 tidal cycles] alongshelf (a) and cross-shelf (b) wind stresses. The solid (dashed) trajectories were calculated with (without) the wind-driven components of the circulation. (+ specifies the origin of each trajectory; diamonds specify the end position of a trajectory; large dot marks the end of every 4th tidal cycle) Figure 6.11

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FIGURE 6-12 A comparision between observed and simulated drogue trajectories. a) northwest quadrant Browns Bank: April 1983; southeast quadrant Browns Bank:May, 1984, b) northwest quadrant Browns Bank: November 1983; southeast quadrant Browns Bank: May 1985. (GR -Greenberg residual $+M_2$ tide only; GRW - Greenberg residual $+M_2$ tide + surface enhanced wind driven current; LTR - Lawrence and Trites residual + 0.03 of the vind speed; O - Observed drogue trajectory; + specifies the origin of each trajectory; triangles specify the end position of a trajectory; large dot marks the end of every 4th tidal cycle)



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were displaced to the southwest. The model track (with wind) shows this tendency also, but some of the effect is lost because of the smoothing of the wind field for the model calculation. Clearly, though, the model displacements are smaller than observed for this trial as well.

The third and fourth drifter trials were conducted in almost identical positions on the eastern flank of Browns Bank: one cluster released in May 1984 and the other in May 1985. In 1984 the drogues drifted rapidly toward the west, skirted the perimeter of the western cap gyre and exited the Bank from its northern flank (Figure 6.12a). In 1985 the drogues drifted slowly in the opposite direction, toward the east (Figure 6.12b). The model cannot reproduce these trajectories. The pure residual and residual plus tidal circulations produce slow trajectories toward the east. When the wind is included, the 1984 model trajectory is toward the east, in the opposite direction to the observed displacements. In 1985 the wind was weak and produced no significant current.

The drogue trajectories were also simulated using the Lawrence and Trites residual flow field plus 3% of the smoothed wind speed (66 hour running mean), an approach used by Lawrence and Trites (1983) and commonly used in oil spill models. Although the simulated displacements generally exceeded those produced using the Greenberg model, the displacements still underestimated the observed trajectories. The directions of the Lawrence and Trites based trajectories are not as close to the observed directions as are the Greenberg-based simulations. This is probably due to the fact that the 3% of the wind speed estimation of the wind response does not account for topographic steering of the wind driven flow. This effect is particularly evident in the April 1983 simulations in which the wind drives the drogues off the bank toward the no⁻¹ west in the Greenberg simulations and toward the southwest in the Lawrence . .d Trites simulations.

Existing empirical descriptions of the mean Lagrangian (Bumpus and Lauzier 1973; Harding and Trites 1988) and pseudo-Lagrangian (Lawrence and Trites 1983) circulations are of low spatial resolution and are not readily adapted to include time-varying circulations. Since the Eulerian circulation in the southwest Nova Scotia area is dominated by M_2 tidal and wind-driven components (Smith 1983, 1989a), this chapter has focused on the high-resolution (ca. 7km grid squares), depth-averaged tidal and wind-driven models of Greenberg (1983) and Wright *et al.* (1986). In spite of known discrepancies between the model residual circulation and observations, the analysis has been pursued in order to 1) test the hypothesis that the dominant components of the Eulerian circulation control the Lagrangian displacement fields, 2) investigate the sensitivity of Lagrangian drift, and 3) provide a framework for future studies.

The spatial variation in tidal amplitudes and phases gives rise to Lagrangian mean velocities which differ from the Eulerian means. The magnitude of this difference varies spatially, with greatest differences found on the northern flank of the western cap of Browns Bank. In this region, where Smith (1989a) observed most of his satellite drifters to exit the Bank, the Lagrangian velocities are generally deflected northward toward Cape Sable and, during particular phases of the tide, are opposite in direction to the Eulerian currents. Physically, particles released at various stages of the tide are injected into different water columns whose average displacements over the tidal cycle are not the same. The differences in displacement are most acute on the northern flank because of the sharp changes in the tidal currents and strong mean shears. In most other areas the Lagrangian velocities are similar in magnitude and direction to the Eulerian velocities.

For persistent moderate wind stresses (0.1 Pa), the wind-driven currents may dominate the residual flow field and therefore have a strong influence on the model particle trajectories. This is particularly true of alongshelf winds which produce strong pressure gradients as well as a surface Ekman layer to drive the current, whereas cross-shelf winds produce only a significant surface Ekman flow. Using rough estimates of the average wind-driven response in the surface layer, Smith (1989a) showed that the winds alone in April and Nc⁻⁻:mber, 1983, were sufficient to "kick" the satellite drogues off the Bank to the north, though the observed displacements were underestimated. He felt that a more accurate description of the tidal and residual circulations would produce quantitative agreement.

However, the model computations have shown that the net displacements caused by oscillatory winds of realistic amplitude are small, and hence the accurate specification of the residual circulation appears to be crucial for simulating the displacement fields over the biological time scales of interest. When forced with real winds and tides, the model does not accurately reproduce the trajectories of satellite-tracked drifters, particularly over the eastern half of Browns Bank. Over the western cap the simulated trajectories are qualitatively, but not quantitatively, similar to observed the trajectories. As Smith (1989a) suggested, the "leakiness" of the western cap gyre is partly due to wind-driven currents, but the model indicates that the mean longshore pressure gradient (associated with the 4*cm* residual setup at Halifax) and the tidal currents are also important components driving this off-bank Lagrangian flow. However, the model underestimates the observed displacements, probably as a result of underestimation of the magnitude of the seasonal residual circulation by a factor of 2 to 5 (Figure 6.4). Part of this discrepancy is due to the fact the Greenberg (1983) model does not adequately resolve the bottom topography and therefore underestimates the tidally-rectified current (Tee et al. 1987), but a significant portion of the difference between model and observation might also be due to the presence of strong unmodelled baroclinic currents. The seasonal supplies of fresh coastal water in the Nova Scotian Current and warm, salty slope water in Northeast Channel give rise to strong horizontal and vertical density gradients that support baroclinic currents on the order of $0.10m \ s^{-1}$ (Smith 1983; 1989a).

On the eastern half of Browns Bank the model does not simulate the drogue trajectories either qualitatively or quantitatively. Furthermore, comparison of the drogue tracks from May 1984 and 1985 indicates a distinct component of interannual variability. Rather than seasonal density variations, these differences may be associated with the presence of Gulf Stream rings in the slope water to the south. Rings were observed in satellite infrared images south of Browns Bank in both 1984

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and 1985, during the period of the drogue releases. In 1984, a surface streamer of modified ring water extended shoreward along the eastern edge of Northeast Channel, but in 1985 there was no evidence for the active intrusion of slope water. The 1984 event may have caused the large difference in the drogue trajectories for that year versus 1985 (Figure 6.12).

Although model and drogue trajectories were not compared in the nearshore region to the north of Browns Bank, the reasonable agreement between model and observed residual currents in this area (Figure 6.4) suggests that the model particle trajectories may have some reality. However, long-term current meter records suggest that the nearshore circulation off Cape Sable varies considerably on time scales of a month and longer. In particular, the annual cycles of the alongshore currents have amplitudes in the range of 0.04 to $0.06m \ s^{-1}$ (i.e. comparable to the annual mean), while interannual variations that are not accounted for by the wind also measure $0.04m \ s^{-1}$ (Smith 1989b). Thus even if the annual cycle and wind-driven components of the circulation are modelled, a significant unknown component remains. It too is probably related to baroclinic forcing (Smith 1983).

Obviously, the model cannot now be applied confidently without some means of testing the outcome, or at least validating the model circulation and spawning distribution in the time period of interest. Although the Greenberg based model appears to give trajectories that are qualitatively more representative of the observed trajectories than are the Lawrence and Trites based trajectories, particularly with respect to direction over the western cap of Browns Bank, substantial improvements in the capabilities of this and similar models requires some means of monitoring and incorporating baroclinic components of the circulation. Time series of satellite infrared imagery will be of some use, however, since these are not always good indicators of the circulation (Smith 1989b) some sort of in situ measurements at strategic locations may be required. Another important step would be to improve the spatial resolution of the model in order to reflect the observed tidally-induced circulation more accurately, particularly on the northern flank of the Bank.

CHAPTER 7

Summary and Discussion

7.1 Overview

As stated in the introduction to this thesis it has been recognized for nearly a century that the transport and dispersal of the early life stages of fish may be an important component of fish population regulation and in particular to haddock population regulation. It was also stated that surprisingly little is known about the actual transport mechanisms. No direct estimates of individual egg or larval displacement exist and very few direct estimates of cohort displacement exist. Consequently, assumptions have been made in order to estimate early life stage (ELS) displacements and their role in population regulation. Unfortunately many of the assumptions appear to be incorrect and consequently the evidence indicating that transport processes are important is, in fact, weak.

Investigations conducted more than 10 or 20 years ago were limited by technology and by a lack of appreciation of the complexity of water circulation and the behavioural capabilities of early life stages (see reviews by Russell 1937, Marty 1965, Harden-Jones 1968, Cushing 1975, 1981, 1982). The majority of this empirical information was of low spatial and temporal resolution and was concerned mainly with the horizontal distribution of the ELS and the surface circulation. Little was known of the behavioural capacity of marine ELS so their swimming abilities were considered to be very limited and their displacements to be dominated by the surface residual circulation. Time varying currents, particularly tidal currents, were believed not to contribute to this residual or to the trajectories of organisms. It is from consideration of this relatively sparse, early information that the first of two main concepts concerning the natural regulation of marine fish populations emerged: the 'triangle or circuit of migration' theory proposed by Harden-Jones (1965, 1968) and perpetuated by Cushing (1975, 1981, 1986). In the past two decades, however, a wider variety of species, stocks and habitats (particularly coastal and estuarine) have been studied (see John 1984, Miller et al. 1984, Norcross and Shaw 1984, Power 1984 and Sinclair 1988 for reviews). Advances in sampling and computer technology have enabled the patterns and processes characterizing the displacement of early life stages to be examined throughout a broader range of temporal and spatial scales. This has lead to the recognition that important physical and biological processes occur on the small time (hours to days) and space scales (centimeters to meters) characteristic of the physiological needs and sizes of early life stages (Bakun et al. 1982). It is now well documented that larvae have substantial swimming abilities (Bishai 1960, Rvland 1965) and that pelagic fish eggs and larvae have species and perhaps stock specific vertical distribution and vertical migration patterns which may vary with developmental stage (for example see Jacobsen and Johansen 1908, Russell 1926, Ahlstrom 1959, Fortier and Leggett 1982, 1983; Henri et al. 1985, Frank and Carscaden 1987).

It is also well documented that these behavioural capabilities and patterns affect the rates and directions of horizontal displacement (Bull 1951, Graham 1972, Fortier and Leggett 1983, Rothlisberg *et al.* 1983, Iles 1985). Observations on the rates and directions of ELS transport and dispersal, although few, indicate that for the eggs and very young larvae of some species the rates and directions are consisten qualitatively with expectations based on passive scalars (Fortier and Leggett 1982, Smith and Morse 1985, Munk *et al.* 1986, Heath and MacLachlan 1987), whereas the rates observed or estimated for post-larvae often differ from these expectations (see for example Hewitt 1981, Fortier and Leggett 1983, Houde and Lovdal 1985). This ontogenetic divergence between observed and expected patterns of displacement usually corresponds with the onset of exogenous feeding and the development of sensory and locomotory capabilities (Hunter and Coyne 1982). The implication of these observations is that the transition from a physically to a behaviourally controlled distribution pattern can occur very early in the life history. This is the basis of the newest hypotheses on fish population regulation, that of the Herring Stock Hypothesis(Iles and Sinclair 1982), the Member/Vagrant Hypothesis (Sinclair 1988) and the Larval Retention Concept (Iles and Sinclair 1988).

The main objective of this thesis was to continue the development of the understanding of the mechanistic components of early life stage transport and to provide information that is necessary for successful use of this knowledge in correlation and comparision approaches aimed at identifying and quantifying the effects of transport on population dynamics.

The first objective was to examine the temporal and spatial scales characterizing the variation in haddock year-class size. This took the form of a re-examination of the hypothesis that year-class size in the cod and haddock stocks of the Northwest Atlantic varied in a synchronous manner - all stocks having good and bad year-classes in the same years. Previous analyses had suggested that the year-class sizes of cod and haddock stocks were positively correlated over spatial scales of 100's of kilometers (Koslow 1984). However, the statistical significance of these correlations had not been established and the relationships were thought by some to be spurious (Coher *et al.* 1986). The controversy was based upon the fact that recruitment series are auto-correlated.

The analysis of year-class sizes in Chapter 2 avoided this problem by removing the auto-correlation using a simple first difference filter. Several statistical tests were then used to test the hypothesis that the remaining high frequency variation was positively correlated between stocks. The conclusion that the year-class sizes of different species (haddock and cod) are uncorrelated and that stocks of the same species (haddock vs haddock and cod vs cod) are only weakly correlated is consistent with the concept that the stocks are in fact separate and that although broad scale processes may be important, it is the localized processes that are mainly responsible for recruitment variation, at least the high frequency portion, and that efforts to identify the processes should begin with localized process oriented studies.

The second objective of the thesis was to define the time of haddock spawning and the duration of the egg stage. This information is essential for the successful utilization of transport indices in habitat characterization and correlation studies. Analyses of published egg abundance data showed the time of peak spawning is progressively delayed from Georges Bank to the Newfoundland banks and that despite large inter-annual variations in water temperature throughout the Northwest Atlantic a relationship between the time of haddock spawning and temperature is apparent only in the Georges Bank stock, the southern most haddock stock. The variations in water temperature however do influence the duration of the egg stage such that it is on average fifteen days with a range as large as 8 to 30 days (Chapter 3).

The third objective was to describe and model the vertical distribution of haddock eggs. In Chapter 4 it was shown that contrary to previous beliefs, haddock eggs are not consistently concentrated near the surface, especially during the latter stages of development and during strong winds when a large proportion of eggs are mixed below the Ekman depth. This results in the eggs being displaced at approximately one half the rate of surface-trapped particles. Surface circulation patterns derived from surface drift bottles may therefore not be reliable indicators of the trajectories of fish eggs, particularly since the drift bottles are trapped at the surface indefinitiely and the eggs and larvae are in the surface layer for only a few days to weeks. Concepts of egg and larval drift that are based on surface drift bottles must therefore be viewed with considerable caution.

The fourth objective was to examine, in an idealized framework, the effect of a steady and spatially uniform current on the trajectories of particles released within a permanent gyre. This idealized situation was chosen because many haddock stocks spawn within permanent Eulerian gyres. In Chapter 5 it is shown that the advective loss is a non-linear function of the size (diameter) of the gyre, the magnitude of the gyre velocity, the magnitude of the perturbing current and the duration and vertical distribution of the particles. The ratio of the magnitudes of the maximum gyre velocity to that of a perturbing velocity is shown to define the extent of particle trapping within the gyre. When the perturbing velocity is less than the maximun 1

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gyre velocity a trapping zone exists and a proportion of the particles intially within the gyre are retained within the trapping zone. When the perturbing velocity is greater than the maximum gyre velocity particles will be flushed from the gyre within a time scale that is linearly proportional to the gyre diameter divided by the magnitude of the perturbing velocity.

The fifth objective (Chapter 6) was to evaluate the potential for existing Eulerian circulation models to simulate the displacement of haddock eggs and larvae from the Browns Bank spawning ground. By comparing predicted trajectories with the those of satellite tracked drifters, it was shown that the models are not capable of accurately simulating particle trajectories, and by implication the trajectories of haddock eggs. The main short-coming in the circulation models appears to be that they underestimate the magnitude of the residual circulation. This is because they do not resolve the topography well enough to accurately estimate the tidally rectified current and because they do not include the baroclinic flow which is a major component of the flow in the Browns Bank region.

7.2 Haddock Spawning Location and Time in Relation to Circulation

In contrast with the belief that many fish with pelagic early life stages spawn in areas and at times characterized by reduced water transport (Parrish *et al.* 1981, Iles and Sinclair 1982), haddock spawn in areas that are generally perceived to be characterized by advective losses to regions not suitable for the survival of the early life stages (Colton and Temple 1961, Grosslein and Hennemuth 1973). More specifically haddock in the Northwest Atlantic spawn at a time when the seasonal mean wind-stress is offshore and the surface currents over much of the Georges Bank spawning ground and those over the eastern half of the Browns Bank spawning ground appear to be offshore in accordance with the wind direction. Although the mean Lagrangian drift over the western portion of Browns Bank, the main spawning area for the Browns Bank haddock is inshore in opposition to the mean wind, the wind may influence the magnitude of this drift (Day 1958, Smith 1989). Haddock spawning on Georges Bank occurs in the January through May period; peak spawning is usually in February or March (Chapter 3) and the majority of eggs are consistently released over the Northeast peak of the bank (Smith and Morse 1985). Current meter and drogue measurements confirm the year-round existence of a par 'ially closed mean subsurface gyre around the bank (Butman and Beardsley 1987). They also indicate the strength of the gyre is weaker during the winter than in the summer and that surface off-shore (southerly) flow is greatest during the winter and least during the summer (Flagg *et al.* 1982). As earlier believed, the haddock are spawning when (1) the surface drift is offshore, (2) the gyre strength is minimal and (3) the resic nce time of surface drifters within the 60m isobath is only about 50 days (Loder *et al.* 1988). Although this appears to favour the concept of an offshore loss of haddock eggs and larvae, ichthyoplankton surveys indicate many of the larvae remain over the bank (Smith and Morse 1985).

The eggs and larvae however, may be able to remain on the bank because they are not drifting in the surface layer for a long enough time to traverse the width or length of the bank. The spawning location on the northeast peak of the bank is where (1) the residual gyre currents are strongest and therefore hardest to disrupt, (2) the distance from the spawning ground to the weakest link in the gyre, that of the divergence near the South Channel, is maximized, and (3) the distance from the spawning ground to the southern edge of the bank is maximized such that the influence of major current anomalies such as those induced by Gulf Stream Rings or cross-shelf winds is reduced. Although the spawning time is when the gyre strength is weakest this means the time needed for the eggs and larvae to transit the width or length of the bank is maximized. Furthermore the highest concentrations of eggs and larvae, with the exception of the youngest egg stages, occur at mid-depths where the offshore oriented current is not as prominent as near the surface. It therefore appears, as suggested by Loder *et al.* (1988), that the large size of Georges Bank coupled with the time and location of spawning and the actual rates of water and early life stage displacement may be sufficient to prevent major losses from the bank.

Off southwest Nova Scotia spawning occurs during March through June; peak spawning occurs in late April or early May (Chapter 3). The majority of eggs are released over the western half of Browns Bank as defined by the 100m isobath (Koslow *et al.* 1985, H[.]:rley and Campana 1989, Frank *et al.* 1989). The earlier concept of Bumpus and Lauzier (1965) and Bumpus (1973) that the surface drift over the western portion of Browns Bank is toward the inshore has generally been confirmed by recent Lagrangian drift studies (Smith 1989). However, the rate of this inshore transport may be slower than the 5km/d estimated by Bumpus and Lauzier since the mean time for near surface (10m) drogues to leave the bank is approximately 10 days (Loder *et al.* 1988). Neverthel ¬s, loss from the bank within a time comparable to the duration of the egg stage (10 to 30 days, Chapter 3) seems assured. As on Georges Bank, however, ichthyoplankton surveys indicate many eggs and larvae remain over the bank (Hurley and Campana 1989).

However, the residence time of eggs and larvae may be longer. The physical residence time estimates are based on near surface drifters and on drifters released over the western cap of the bank whereas the spawning area includes the whole of Browns Bank (Hurley and Campana 1989). Residence time estimates for the whole bank are 12 d based on drifter data (Loder *et al.* 1988) and between 40 and 180 days when estimated from Eulerian considerations (Loder *et al.* 1988). This discrepancy may be due to the fact the drifter estimate, although more direct, is based largely on releases over the western cap of the bank. The Eulerian estimate, although less direct, may therefore be a more reasonable estimate. If so, the residence time is long enough for eggs and larvae to remain over the bank until metamorphosis in the late summer.

Unlike haddock spawning on Georges Bank, the spawning time on Browns Bank seems to be more closely related to the seasonal maximum in the integrity of the Browns Bank gyre. On the northern flank of the gyre the near surface (15m)
cross-isobath flow is always in the on-bank direction but the strength of this flow is maximum during January and February and minimum during June and July (Smith 1989b). The along-isobath flow is always in the clockwise direction with no statistically significant seasonal cycle. On the southern edge of Browns Bank the cross-isobath flow is off-bank during September through February and on-bank during March through August (Smith 1989b). This tends to suggest the haddock are spawning during the season of minimal off-bank flow.

Other indications that the Browns Bank spawning ground is an area of locally reduced transport are that (1) the spawning area, the western half of Browns Bank, is the region where the wind driven current is steered by the local topography such that little cross-shelf and off-shelf flow is generated, (2) the effect of the strong inshore Nova Scotian current is minimal, (3) the presence of the western cap gyre appears to slow down what would otherwise be a more direct flow into the Gulf of Maine and (4) although surface drift bottles released over the eastern portion of Browns Bank are seldom recovered (Bumpus 1973) the fact that late egg stages and larvae are most abundant at depths of 30m or greater (Chapter 4, Frank *et al.* 1989) indicates surface drift may not indicate the displacement of the eggs and larvae which may remain on the bank.

In conclusion the physical evidence, in contrast to previous interpretations, now suggests that rather than spawning in areas characterized by high transportinduced losses the haddock, like many other species, are spawning in areas with minimal losses. Furthermore, the effect of behaviour on dispersal of even the egg stage should be considered.

7.3 Haddock Year-Class Size Variation and Wind Driven Transport

It has long been hypothesized that current variation, particularly the winddriven current, has a major influence on haddock recruitment variation (Chapter 1). The hypothesis has been supported mainly by correlative evidence such as (1) the observation that naddock recruitment patterns are coherent over spatial scales comparable to those characterizing coherence in the wind field, (2) the observation that temporal variation in haddock recruitment is characterized by a low frequency trend that is similar in form to that in the north-south (approximately cross-shelf) winds (Koslow *et al.* 1987), and (3) the finding of significant correlations between wind and year-class size (Chase 1955, Koslow *et al.* 1987).

This support is, however, weak on both statistical and physical grounds. The low frequency correspondences are difficult to establish statistically because of the low degrees of freedom inherent in the short data sets characteristic of recruitment series. The correlation reported by Chase (1955) has not persisted (Grosslein and Hennemuth 1973). The correlations found by Koslow *et al.* (1987) are sensitive to the choice of statistical technique, and the more recent and statistically more rigorous correlations between Ekman transport and haddock recruitment produced by Myers and Drinkwater (1988) are not statistically significant.

The analyses of haddock spawning times in Chapter 3 indicates that due to progressively latter spawning times in the Georges Bank, Browns Bank, Sable Island and Grand Banks haddock stocks the early life stages of each of these stocks are in the pelagic phase for different periods. Any influence of transport on the coherent portion of the recruitment variance must therefore be persistent throughout the entire period of the pelagic phase (February through July) or the effect on yearclass size is manifested during the demersal stage. Any driving force or combination of forces responsible for the low and high frequency coherence in recruitment must either have a phase lag consistent with the latitudinal lag in spawning time or it must be a low frequency force that persists for the entire duration of the haddock ELS pelagic phase. Although the low frequency component of the wind field satisfies these cliteria (Thompson and Hazen 1983), the high frequency components, such as those represented in Chase's (1955) wind index, have much smaller scales of coherency.

In the Georges Bank and Browns Bank regions, the wind drives both a surface Ekman current and a pressure-driven current. The later is generated primarily by the along-shelf wind stress (Wright et al. 1986, Chapter 6). On the relatively shallow offshore banks where the haddock early life stages are found the Ekman currents are weaker than the pressure driven currents. The Ekman currents are restricted to the surface layer and therefore have little effect on the displacements of the late stage eggs and larvae which are most abundant below this layer (Chapter 4, Frank et al. 1989). Even the effect on the displacement of the early stage haddock eggs, which are largely within the Ekman layer, is modified because of the effect of vertical mixing on the egg vertical distribution (Chapter 4). Furthermore haddock pawning locations are located within permanent residual gyres and these gyres act to reduce the impact of Ekman transport (Chapter 5). Since this reduction effect will vary between stocks because of differences in the size and strength of the gyres, it is unlikely that Ekman transport induced egg and larval displacements contribute to the recruitment variation that is synchronous.

Upon initial examination, the barotropic pressure driven current seems more likely to affect the transport of haddock early life stages. This current exists throughout the water column and therefore affects all of the pelagic early life stages. The current is topographically steered so the currents are unique locally in direction and magnitude. On Georges Bank for example, the pressure driven current is largely in the east-west direction and on Browns Bank in the southeast-northwest direction. If the wind is blowing toward the west, the current on Georges Bank is westward and may transport eggs and larvae out of the Georges Bank gyre by carrying them along the shelf into the Mid-Atlantic Bight. If the wind is toward the east, the current is toward the east and the eggs and larvae are transported toward the northeast corner of Georges Bank where they may be prevented from leaving the bank by the strong tidal residual.

On Browns Bank the westward wind produces a northwestward flowing current which assists in transporting eggs and larvae toward the inshore regions off southwestern Nova Scotia. The eastward wind produces a southeastward current which may help to maintain the eggs and larvae over the bank. Therefore the large scale , , , , , , wind pattern produces locally unique current patterns that have potentially similar effects on the survival of the early life stages in accordance with the coherence between the year-class sizes of haddock on Georges and Browns Banks (Chapter 2)

A closer examination of this mechanism indicates that the along-shelf wind stress during the 1950-1980 period has a marginal trend toward stronger easterward winds (Thompson and Hazen 1983). By the above reasoning, this should produce enhanced retention (less drift). This may aid the production of larger year-class sizes by reducing transport losses or hinder year-class size production if densitydependence becomes important. The observed recruitment pattern is a pronounced parabolic trend toward reduced year-class sizes. Therefore the trend in wind does not closely match that in year-class size. Furthermore, an examination (not shown) of the relationship between the along-shelf wind and the detrended (first differenced) recruitment series of the 4VW, 4X and 5Z haddock stocks shows no significant relationships.

It therefore appears that haddock recruitment may not be sensitive to winddriven currents since the transport of the early life stages may be insensitive to these currents (above section). Therefore if egg and larval transport variation is important to haddock year-class size variation factors other than wind must be driving this variation. This conclusion is consistent with the findings that much of the low frequency variation in the circulation on Georges and Browns Banks is due to changes in the density field rather than the wind field (Butman and Beardsley 1983, Smith 1989).

7.4 Haddock Recruitment Variation: Management Implications

The analysis of recruitment patterns presented in Chapter 2 showed, as did Koslow (1984), that the variation in annual production of young cod and particularly haddock in the Northwest Atlantic is dominated by a low frequency trend. By its nature the trend changes slowly (decorrelation time scale approximately 5 years) so that recruitment forecasts based on an average of the most recent years may be much more appropriate than a long-term geometric mean year-class size.

The fact the recruitment series are dominated by low-frequency trends also makes it difficult to establish statistically robust and useful relationships between year-class size and environmental variables. Since over 50% of the variance is associated with the low frequency trend in several stocks (4X and 5Z haddock, 1,3Ps and 4TvN cod) this means there are fewer independent data points than indicated by the length of the recruitment series and because the series are relatively short (10 to 30 years) statistical confidence in recruitment-environment relations is difficult to establish and confidence limits on forecasts made from these relationships are large.

Although the high frequency variation in the recruitment series does not have the auto-correlation problem and therefore offers the best opportunity for the establishment of recruitment-environment relationships and recruitment forecasting, the variation in most stocks represents a relatively small portion of the total variation in recruitment. Nevertheless relationships between this component of recruitment variation and environmental variables may allow managers to forecast whether recruitment will be above or below the average taken over the most recent years.

7.5 Future Research

From the above discussion it is obvious that a complete understanding of the processes controlling the transport of haddock early life stages, particularly in the Browns Bank region, is not yet achieved. However, the information presented in this thesis does help clarify some of the research directions that should be pursued. With respect to statistical analyses the thesis indicates that efforts must be made to determine whether or not the low frequency trends in recruitment series are artifacts of the assessment procedures or true indications of year-class success. With respect to the transport of ELS the thesis supports the approach of local process-oriented research and in particular that the focus with respect to haddock early life stage transport be shifted from a surface oriented, largely wind induced, drift concept to one of subsurface transport dominated by baroclinic and behavioural processes.

This shift in focus suggests that several approaches be taken to further develop understanding of the transport of the early life stages of haddock and other species. More field and monitoring programs aimed at describing the vertical and horizontal distributions of the early life stages on the appropriate spatial and temporal scales are required to establish and document how these change through time and space and in relation to different hydrographic conditions. Three dimensional, idealized and realistic, baroclinic circulation models must be developed along with models of early life stage vertical distributions so the sensitivity of early life stage transport (vertical and horizontal) to the hydrography and baroclinic flow field can be assessed. Encouragingly, new circulation modelling techniques such as threedimensional finite element models and data assimilation models are beginning to be developed and once available these will substantially improve the prospects for identifying the components of the circulation that influence early life transport the most. In addition, comparative and experimental approaches such as those advocated by Parrish et al. (1981), Mayr (1982), Bakun (1985, 1989) will be necessary for identifying some of the basic needs and behavioural capabilities of ELS.

These developments will certainly contribute to the understanding of the processes controlling population richness and abundance and whether populations reduced by excessive fishing pressure can be expected to be reseeded by the infusion of ELS from adjacent populations. The developments should also contribute to the understanding of year-class size variation and perhaps to year-class size forecasting. This can occur on at least two accounts. A better understanding of the processes controlling stock structure should give insight into the processes important to year-class success and the availablitity of operational models will greatly aid in the planning and execution of field programs aimed at identifying the processes

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controlling early life stage survival. If these efforts are successful then the appropriate variables can be monitored and be used to improve forecasts of recruitment.

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