Physical environment and recruitment variabiliity of Atlantic herring, *Clupea harengus*, in the Gulf of Maine

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Recruitment is generally recognized as a complex ecological process determined by the interrelation of many biological and environmental variables and has always been one of the most difficult terms to estimate in fisheries science (Russell, 1931). Methods for forecasting fisheries yields with time-series analyses (Saila et al., 1980; Mendelssohn, 1980), surplus production models (Schaaf et al., 1975), and models employed to relate recruitment to egg production (Koslow et al., 1987), larval abundance (Lett and Kohler, 1976; Lough et al., 1981; Smith, 1981), or spawning stock size (Sissenwine, 1984) have had limited success. Factors dominating recruitment appear to operate on local scales (Cohen et al., 1991); changes in physical factors operating through marine food webs are a major force affecting the abundance of fish stocks (Mann, 1993).

Clupea harengus, are an important component of the fisheries of the Northwest Atlantic and show great variability in recruitment. Spawning usually begins in the eastern part of the Gulf of Maine (Fig. 1) during August (Graham, 1982; Stevenson et al., 1989) and over the Nova Scotian shelf (McKenzie, 1964), and occurs as late as November or December (Graham, 1982; Lazzari and Stevenson, 1992). Eggs are deposited on the bottom (Boyar et al., 1973; Caddy and Iles, 1973; Stevenson and Knowles, 1988) and hatch in one to two weeks depending on temperature. Larvae are transported to estuaries and embayments along the central and western Maine coast (Graham, 1982; Graham and Townsend, 1985) or remain offshore for the winter (Townsend, 1992). The planktonic larval stage lasts until spring when larvae undergo metamorphosis into the juvenile form. Recruitment to the fishery occurs primarily in the following spring (at age 2) when juveniles reach a size appropriate for canning (150–200 mm).

The recruitment success of herring may be associated with various physical environmental factors, including sea surface temperature (SST) (Sutcliffe et al., 1977; Cushing, 1982; Anthony and Fogarty, 1985; Murawski, 1993), residual surface currents (Norcross and Shaw, 1984), winds (Corten[1]; Christensen et al.[2]), or atmospheric-pressure gradients (Carruthers, 1938), or a combination of the last two. Theoretical models for predicting variations in juvenile herring production in the Gulf of Maine were developed by using sea surface temperature from the late-larval to early-juvenile period (Anthony and Fogarty, 1985), first quarter (January–March) sunshine (Ezzy, 1988), and by using either food supply and spawning distribution when year-class strength was established during the larval stage or predation for those years when year-class strength was established in the brit stage (Campbell and Graham, 1991).

In addition, several hypotheses concerning wind events or larval dispersal may help us to understand herring recruitment in the Gulf of Maine. Ridgway (1975) proposed a conceptual model of recruitment variability based on changes in the dispersal of herring larvae by ocean currents from spawning areas to nursery areas. Water column stability and its impact on the availability of food resources for larval fish at some critical life stage also has been proposed to affect recruitment (Lasker, 1975). Periodic winds that produce moderate turbulence may enhance larval survival by increasing the probability of encounter between larvae and their prey (Sundby et al., 1989; MacKenzie et al., 1994).

The purpose of this study was to associate physical environmental factors with size estimates of age-2 herring of the coastal Atlantic herring stock in order to identify the important environmental factors underlying recruitment variablity and to examine the importance of the wind and dispersal hypotheses

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[1] Corten, A. 1984. The recruitment failure of herring in the central and northern North Sea in the years 1974–78 and the mid-1970s hydrographic anomaly. ICES Mini-Symposium. Council Meeting 1984/Gen., 12 p.

[2] Christensen, V., M. Heath, T. Kiorboe, P. Munk, H. Paulsen, and K. Richardson. 1985. Investigations on the relationship of herring larvae, plankton production and hydrography at Aberdeen Bank, Buchan Area, September 1984. ICES Council Meeting 985/L, 23 p.

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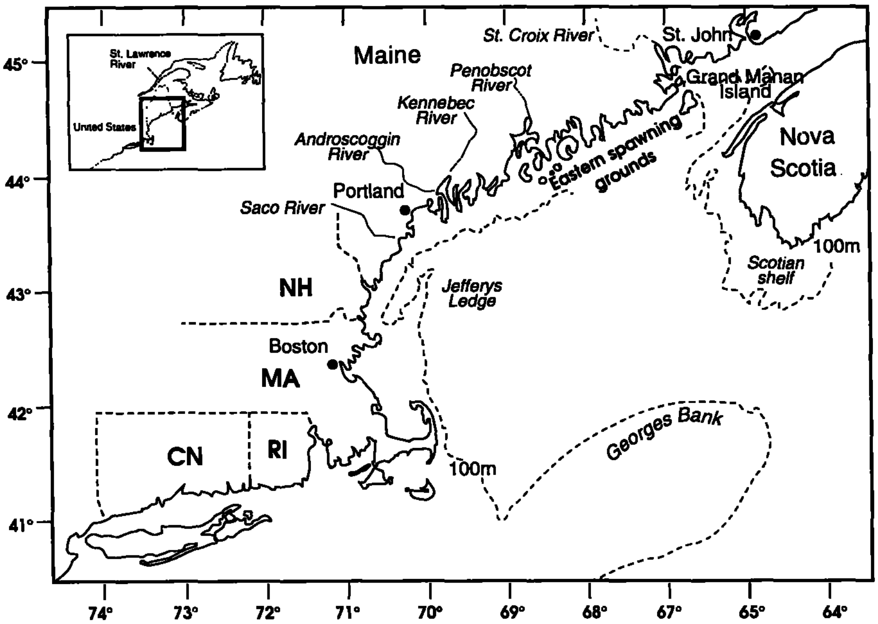

Figure 1

Map of the Gulf of Maine showing the spawning grounds of Atlantic herring, *Clupea harengus*.

as subjects for future research. Through examination of time-series data and the use of exploratory correlations, contingency tables, and *t*-tests, a search was made for those environmental factors that related positively or negatively with size estimates of age-2 herring populations.

Methods

The method of exploratory correlation (Sutcliffe et al., 1977; Hayman, 1978) was used to determine relationships between monthly means of environmental factors along the Maine coast. Records were analyzed for the larval year 1 August through 31 July for years 1965 through 1990 (Table 1). The herring recruitment index used was the virtual population analysis (VPA) estimation of two-year-olds from 1967 to 1991 in the coastal Atlantic stock (NEFC,[3] Fig. 2). For purposes of our analysis, we assumed predation to be constant and that spawning stock biomass was not a major factor affecting recruitment. Sea surface temperature (SST) records were supplied by the Maine Department of Marine Resources Laboratory, Boothbay Harbor, ME. Sunshine was measured as percent possible sunshine from observations of cloud cover conditions at the Portland, ME, airport. Long-term sunshine, atmospheric pressure, wind direction, and velocity data records were compiled for Portland as 12 monthly averages per year and archived by the National Climatic Data Center.

Wind speed and direction were measured at the Portland airport, 8 km inland, where an anemometer is situated 7 m above the ground at an elevation of 25 m. Storm frequency was also complied as days with mean winds in excess of 5 m/s. Daily average wind speed and direction were further analyzed for the period August–December when the influence of wind-driven surface currents on the dispersal of newly hatched herring larvae would be greatest. The daily resultant wind direction (a vector variable) was separated into one of four directions on the basis of compass headings of northeasterly (1–90°), southeasterly (91–180°), southwesterly (181–270°), and northwesterly (271–

Table 1

The location and origin of environmental factors tested for association with the age-2 Atlantic herring abundance estimates. ME DMR = Maine Department of Marine Resources; NCDC = National Climatic Data Center; NEFC = Northeast Fisheries Center.

Environmental factor	Location	Years	Source
Sea surface temperature	Boothbay Harbor	1965–90	ME DMR
Wind speed and direction	Portland, ME	1965–90	NCDC, Asheville, NC
Storm index (no. of days > 5 m/s)	Portland	1965–90	ME DMR
Sunshine	Portland	1965–90	NCDC, Asheville, NC
Barometric pressure	Portland	1965–90	NCDC, Asheville, NC
Herring abundance estimates	Gulf of Maine	1967–91	NEFC, 1991

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[3] NEFC (Northeast Fisheries Center). 1991. Assessment of the coastal Atlantic herring stock. Thirteenth Northeast Regional Stock Assessment Workshop. Northeast Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, 111 p.

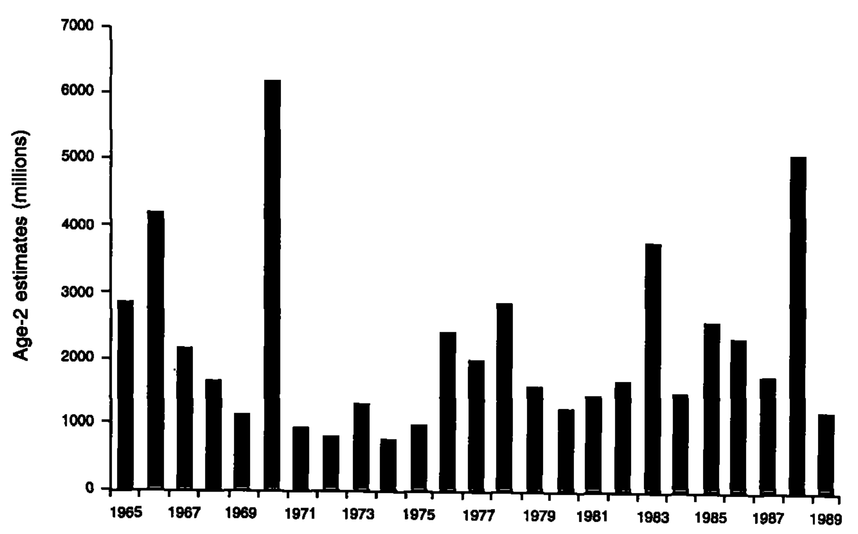

Figure 2

Age-2 Atlantic herring stock size estimates (× 10^6) for the 1965 through 1989 year classes of the coastal Atlantic herring stock.

368°) for each month from 1965 to 1989. The number of storm days, determined by daily average wind speeds greater than 5 m/s from each direction were also tabulated monthly. The number of major storms, defined as the number of periods of three or more consecutive days with mean wind speeds greater than 5 m/s were tabulated monthly. The number of major storms, defined as the number of periods of three or more consecutive days with mean winds in excess of 5 m/s were tabulated monthly and for the August–December period. The number of Lasker events, defined as the number of consecutive days when mean winds were less than 5 m/s for four or more consecutive days (Pauly, 1989) were tabulated monthly for August–September and for the August–December period.

We examined SST, percent sky cover, relative humidity, air temperature, solar radiation, and wind speed and direction at several locations in the Gulf of Maine to determine the similarity of environmental conditions within the Gulf. Wind data recorded at the Portland, ME, and Boston, MA, airports every 3 hours from August through December 1980–89 were compared for direction with contingency tables. Winds were converted from vector variables into one of four directions from compass headings of northeasterly, southeasterly, southwesterly, and northwesterly for each 3-h period. Monthly means of environmental variables including percent sky cover, relative humidity, air temperature, solar radiation, and wind velocity recorded by the National Weather Service, Logan Airport, Boston, MA, were compared by using Pearson corelation analyses and t-tests with those recorded at the Portland airport for the period 1961–90 (n=30).

Similarity of historic seawater temperature data between several sites along the Maine coast, in Massachusetts Bay, and in waters off New Brunswick (Canada) were tested by using Pearson correlation analyses. Monthly and yearly mean sea surface temperatures recorded at Boothbay Harbor (BBH) were compared with similar temperatures recorded in St. Andrews, New Bruswick, between 1921 and 1969, in Eastport between 1930 and 1971, Bar Harbor between 1947 and 1971, and in Portland between 1922 and 1971.

The 25 years of environmental data and age-2 population estimates for the Gulf of Maine were partitioned into three clusters with the KMEANS cluster analysis procedure from SYSTAT (Wilkinson, 1991). This analysis is used to divide a series of data into a selected number of clusters in order to reduce the within-group sums of squares to a minimum value. The independence of periods of low, medium, and high values of the environmental variables were tested against the observed versus the expected age-2 population estimates with 3 × 3 contingency tables.

As a selection criterion to identify important variables, we used a significant ($P<0.05$) result for the 3 × 3 contingency tables. The existing low, medium, and high cells were then combined to form 2 × 2 contingency tables from these results. All environmental factors of interest and the age-2 abundance estimates were tested again in four ways. To test the hypothesis that high estimates were associated with low values of an environmental factor, low and medium age-2 estimates and medium and high values of the factor were combined. To test the hypothesis that high estimates were associated with high values of an environmental factor, low and medium age-2 estimates and low and medium values of the environmental factor were combined. To test the hypothesis that low estimates were associated with high values of an environmental factor, medium and high age-2 estimates and low and medium values of the factor were combined. To test the hypothesis that low estimates were associated with low values of an environmental factor, medium and high age-2 estimates and medium and high values of the environmental factor were combined. The 2 × 2 tables were tested for independence by using Fisher's exact test because one cell often had zero observations (Zar, 1984).

A *t*-test for unequal variances (Zar, 1984) was used to determine whether the mean environmental factors differed between years of good and poor recruitment. The hypothesis that the mean environmental factor was higher (or lower, depending on the relationship with the age-2 estimates) during higher than expected recruitment years (1966, 1970, 1983, 1988, n=4) than during lower than expected recruitment years (1971, 1972, 1974, 1978, n=4) was tested.

Results

Our examination of SST, percent sky cover, relative humidity, air temperature, solar radiation, and wind speed and direction revealed widespread coherence at several locations in the Gulf of Maine. The null hypotheses of independence were rejected in all months for the wind directions recorded every 3 hours between Portland and Boston, August through December 1980–89 (P<0.001, n>2,200). Wind direction at both locations showed a definite seasonal trend from May into September when more southerly winds predominated. Monthly mean wind speeds for the period 1961–90 between Portland and Boston were always significantly greater at Boston in all months (*t*-test, P<0.001, n=30), except in January and October. In addition, significant Pearson correlations (P<0.001, n=30) were found for all monthly means of solar radiation (r^2=0.80), total sky cover (r^2=0.79), air temperature (r^2=0.95), relative humidity (r^2=0.68), and precipitation (r^2=0.91) between Portland and Boston for the same period.

The null hypothesis of independence was rejected for the age-2 Atlantic herring abundance estimates and ten environmental factors with 3 × 3 contingency tables. These environmental factors were November storms, March sunshine, and October sea surface temperature, October and first quarter (January–March) barometric pressure, December and August–September Lasker events, the number of days of southwesterly winds in September, the total number of days of southeasterly winds between August and December, and the number of storm days with southeasterly winds in November.

Five environmental factors were associated with either high or low age-2 abundance in the 2 × 2 contingency table analyses (Table 2). Low abundance was associated with reduced sunshine in March and with fewer days of southeasterly winds from August to December. Associations with high age-2 abundance occurred with more November storms, with more days of southwesterly winds in September, and with more days of southeastern storms in November.

Table 2

Probabilities of 2 × 2 contingency table (Fisher's exact chi-square test) results for the environmental factors associated with the age-2 Atlantic herring estimates. ns = not significant.

	2×2 contingency tables			
	Low age-2 estimate		High age-2 estimate	
Environmental factor	High factor	Low factor	High factor	Low factor
November storms	ns	ns	0.020	ns
March sunshine	ns	0.012	ns	ns
September SW wind	ns	ns	0.002	ns
Aug–Dec SE wind	ns	0.005	ns	ns
November SE storms	ns	ns	0.026	ns

Comparison of environmental factors (mean values) between the four best and four worst recruitment years revealed only March sunshine and three southern wind direction factors were significantly different. The amount of monthly March sunshine and the number of days of southwesterly winds in September, the number of days of southeasterly winds from August to December, and the number of storm days with southeasterly winds in November were all significantly higher during good recruitment years than during lower recruitment years (Table 3). The four strongest year classes (1966, 1970, 1983, 1988) were associated with greater than 50% of the possible March sunshine and were associated in eleven out of twelve cases with above average September southwestern, August–December southeastern winds and November southeastern storms (Fig. 3). In eight cases, conditions were greater than 50% above normal for the entire period. The only exception during the four years of above average recruitment occurred in 1970 when August–December southeastern winds were extremely low.

The four worst year classes (1971, 1972, 1974, 1978) were associated with less than half of the possible March sunshine and with average or below average September southwesterly, August–December southeasterly winds and November southeasterly storms in 9 of 12 cases. In eight of these cases, conditions were at least 25% below normal for the entire period. However, two below average year classes (1979 and 1984) were produced despite the fact that all three of the significant wind factors were above

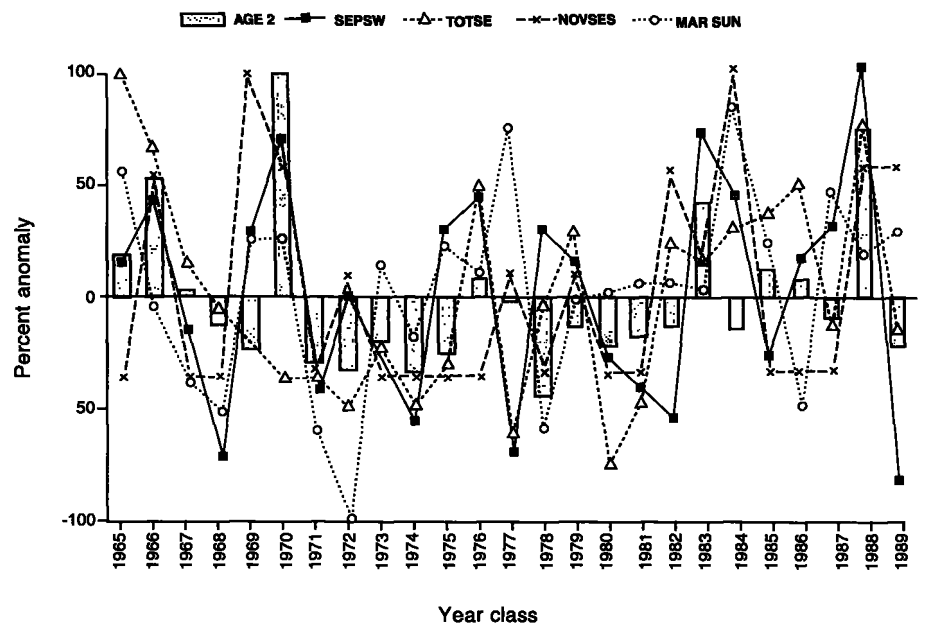

Figure 3

Percent anomalies of the number of days of September southwesterly wind (SEPSW), number of days of southeasterly wind from August through December (TOTSE), and number of storm days in November with southeasterly winds (NOVSES) and March sunshine (MAR SUN) compared with anomalies of the 1965–89 age-2 Atlantic herring abundance estimates.

Table 3

Mean and standard deviation (in parentheses) and *t*-test results assuming unequal variances for the environmental factors associated with the high and low age-2 Atlantic herring estimates. ns = not significant.

Environmental factor	Low age-2 estimate (n=4)	High age-2 estimate (n=4)	*t*-test probability
November storms	7.20 (1.64)	7.00 (5.23)	ns
March sunshine	40.75 (6.94)	57.00 (3.16)	0.012
September SW wind	11.40 (2.79)	17.00 (1.63	0.008
Aug–Dec SE wind	14.40 (2.30)	19.75 (3.30)	0.039
November SE storms	0.20 (0.451)	1.75 (0.50)	0.003

normal in those years. Average year classes were much more common during the 25-yr period and, in 14 of these 17 years, August–December southeasterly winds were also below average. September southwesterly winds and November southeasterly storms, on the other hand, were below average during about half of these years.

Discussion

In our study, we observed associations of sunshine, wind direction, and velocity with the number of age-2 herring estimated to recruit to the coastal Atlantic stock. Strong year classes were produced in years with more days of southerly fall (September) winds and storms (November), and weak year classes were produced in years with less sunshine in March and fewer days of southeasterly fall (August–December) winds. However, because southwest wind velocities are lower than velocities from other directions in the Gulf of Maine in fall, it is not possible to differentiate between the effects of wind direction and strength in this study. We believe that our results, without specifically addressing how wind events influence herring larval survival, show that recruitment success and, therefore, larval survival are related to wind events. In general, wind-driven transport and turbulence are two processes hypothesized to affect the survival of marine fish larvae (Lasker, 1975; Norcross and Shaw, 1984), but strong evidence linking larval survival to wind conditions remains inconclusive. Wind-related transport is believed to influence the recruitment of many species of marine invertebrates (Roughgarden et al., 1988; Farrell et al., 1991) and fishes (Bailey, 1981; Heath, 1989).

For Atlantic herring in the Gulf of Maine, the eastern Maine–Grand Manan Island spawning ground presents a unique case in how southwesterly winds enhance larval transport and survival. Bigelow (1927) found that winds from the southwest tend to "build up" surface waters in the Bay of Fundy causing an "overflow" in the shape of a westerly drift that increases the flow of the coastal current along the eastern Maine coast, i.e. against the prevailing winds. Herring larvae depend on these currents for dispersal to more productive nursery areas (Graham, 1982; Graham and Townsend, 1985; Townsend et al., 1986, 1987) because the area of extensive tidal activity in the Bay of Fundy and off eastern Maine (Garrett et al., 1978) leads to pronounced vertical mixing and less stratification of the water column off eastern coastal Maine (Yentsch and Garfield, 1981). As a result, primary production is much lower in the northeastern Gulf of Maine because the mixed layer extends deeper than the critical depth for plankton production (Townsend et al., 1987). Zooplankton prey organisms that support larval growth and survival are extremely rare on this spawning ground in the fall, only reaching adequate densities about 100 km "downstream" from the spawning ground (Townsend et al., 1986, 1987); therefore, increased dispersal of recently hatched larvae that originate on the eastern Maine–Grand Manan Island spawning ground is a mechanism that could enhance the recruitment of juveniles to the coastal herring stock.

This study generally supports the Campbell and Graham (1991) theory that release of larvae from the eastern Maine–Grand Manan spawning ground is mediated by wind events that generate horizontal flows and can carry larvae out of retention areas into the counterclockwise residual flow that moves from northeast to southwest along the Maine coast. Bigelow and Schroeder (1953) thought that this circulation is set in motion by wind and freshwater inflow and that it influences the availability of two-year-old herring because the fish follow the drifting planktonic animals on which they feed. Furthermore, Chenoweth et al. (1989) observed that larvae hatched in this spawning area at the same time had different horizontal displacements away from the spawning area; some larvae remained in the area for up to a month after spawning, whereas others were transported up to 100 km southwestward down the coast during the same time period. Townsend (1992) attributes this variable release of larval herring from the eastern Maine retention area to the intrusion of slope water into Jordan Basin (a deep offshore basin located in the northeastern Gulf of Maine), the timing of hatching (to coincide with lunar periodicity and the intensity of tidal mixing), and the location of egg beds in relation to the front between the area of tidal mixing and more stratified water offshore, where the geostrophic flow that would pull larvae out of the retention area is greatest (Brooks and Townsend, 1989). In addition, Brooks (1990) found a relation between wind stress and currents that suggested the action of a density-modulated coastal upwelling mechanism in which the deep inward currents over Lindenkohl sill respond directly to northeastward alongshore wind stress at times of weak stratification, such as occurs in fall.

Once entrained within the coastal current, the larvae are dispersed to an overwintering area that has not been conclusively determined as yet. Greater advection of larvae from the eastern Maine–Grand Manan Island spawning area to the southwest as hypothesized by Graham (1982) would distribute larvae among more coastal overwintering areas. This distribution would improve recruitment success by lessening density-dependent mortality within the estuarine and nearshore waters shallower than 100 m that act as a nursery area and would establish a carrying capacity for larvae on the Maine coast for a given year. Research has shown that larvae from this spawning ground reach at least as far south as the Sheepscot River in mid-coastal Maine (Graham, 1982; Graham and Townsend, 1985; Stevenson et al., 1989). However, recent research shows that larval herring overwintering "offshore" may have a higher survival rate than those wintering in nearshore waters (Townsend et al., 1989; Townsend, 1992) and that dispersal associated with southerly winds could enhance offshore transport. In either case, dispersal of larvae away from the eastern Maine–Grand Manan Island spawning area is critical for good larval survival (Graham, 1982; Campbell and Graham, 1991; Townsend, 1992). Wind-induced effects on transport have been shown to affect the distribution and recruitment of other marine fishes (Stevenson, 1962; Checkley et al., 1988; Fechhelm and Griffiths, 1990; Koutsikopoulos et al., 1991; Castillo et al., 1993).

Therefore, we propose that more southwesterly wind conditions in September increased dispersal of eastern Maine–Grand Manan Island larvae in 1966, 1970, 1983, and 1988, setting up an initial situation of high larval survival, which, when combined with more southerly wind conditions through December and more sunshine in March, resulted in the success of these year classes. A continuation of a more summer-like (southwesterly) wind pattern through September may result in better larval herring survival in the Gulf of Maine during these years. Average frequencies of southwest winds off Nova Scotia can vary between 10% and 39% for the months of July–September, 1955–1980 (Hudon, 1994), and summer (June–August) wind stress over the eastern continental shelf is generally toward the northeast and about 0.25 dyn/cm; whereas in fall (September–November), wind stress shifts toward the southeast and can be twice as strong (Saunders, 1977).

Effects of turbulent mixing on food encounter rates must be considered because southwesterly winds are lower in velocity in the Gulf of Maine during the early (August–December) larval phase. The effects of turbulence on the availability of zooplankton prey for larvae are related to those biological processes (primary production) that are disturbed by physical processes, i.e. turbulence generated by wind mixing (Rothschild and Osborn, 1988; Sundby et al., 1989; MacKenzie and Leggett, 1991). Recently, the overall probability of larval feeding has been described as a dome-shaped function of turbulent velocity with maximum feeding, depending on turbulence level and behavioral characteristics of predator and prey (MacKenzie et al., 1994). Calmer wind conditions through September when most first-feeding larvae are present, could enhance larval survival and result in the success of these year classes. Strong recruitment to walleye pollock, *Theragramma chalcogramma*, stocks in the Gulf of Alaska (Megrey et al., 1994) and Bering Sea (Bailey et al., 1986) has been linked to initially calm wind conditions and is associated with calm periods preceded and succeeded by periods of stronger mixing (Bailey and Macklin, 1994). For Atlantic herring in the Gulf of Maine, these conditions would result from periods of calm southwesterly winds in conjunction with stronger southeasterly winds. However, strong mixing can disrupt layers of prey (Lasker, 1975; Wroblewski and Richman, 1987; Owen 1989) and has also been linked to reduced growth of Atlantic herring larvae (Heath, 1989).

Three other environmental variables, the amount of March sunlight, August–December southeasterly winds, and November southeasterly storms, were related to herring year-class size. Dispersal associated with the latter two southeasterly wind factors could result in a positive effect on recruitment by transporting larvae spawned in the western Gulf of Maine and on Jeffreys Ledge toward inshore larval overwintering and juvenile nursery areas along the Maine coast (Lazzari and Stevenson, 1992). Because herring larvae feed on zooplankton, spring phytoplankton production and, ultimately, sunshine should be positively related to larval survival. The timing of plankton blooms in the Gulf of Maine was highly influenced by the amount of sunshine available early in the year (Townsend and Spinrad, 1986). Therefore reduced sunshine in March would have a detrimental effect on the spring bloom, resulting in fewer food resources for herring larvae and reducing recruitment as seen in Ezzy's (1988) model using first quarter sunshine.

Recruitment of animals with planktonic stages is a complex process; we would not expect any single factor affecting the early larval stage to dominate the entire survival process (Wooster and Bailey, 1989; Campbell and Graham, 1991). In our study, although more days of southerly winds were generally associated with higher than expected age-2 recruitment, this was not always the case. For example, in two of the six years (1976 and 1984, Fig. 3) when southwestern winds averaged > 25% higher than normal, strong year classes were not produced. Other factors may have reduced year class size (e.g. predation on larvae or age-1 juveniles) during these periods of lower abundance, or some other conditions may not have been suitable for prey production or feeding. We would have been surprised if the relation of any environmental factor and recruitment had always been consistent, because a high larval survival rate appears to be a necessary, but not sufficient, condition for strong recruitment. Year-class strength can instead be determined by conditions that prevail during the juvenile life stage in some years (Campbell and Graham, 1991; Bailey and Spring, 1992). The environment does not act alone in affecting recruitment success; biotic effects, competitive interaction between species, and the removal of adults caused by fishing mortality, should be considered (Drinkwater, 1987). The results of our analyses to date are interesting and worth expanding, with more research and analyses, to other Atlantic herring stocks to determine the effects of the environment, particularly the wind-driven transport of larvae, on their recruitment variability

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