Winter storm effects on the spawning and larval drift of a pelagic fish

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Recruitment for many marine organisms depends on survival and transport of eggs and larvae from spawning grounds to nursery areas[1]. We investigated the effects of winter storms and the Gulf Stream on the spawning, development and drift of the Atlantic menhaden, *Brevoortia tyrannus*, which spawns offshore[2] and metamorphoses in estuaries[3]. Spawning was maximal during storms in water upwelled near the western edge of the Gulf Stream. Eggs and larvae drifted shoreward with abundant food in the warm surface stratum of a density-driven circulation maintained by the large sea–air heat flux. We suggest that the Atlantic menhaden and other species have evolved to reproduce in winter near warm boundary currents, including the Gulf Stream and Kuroshio, as a result of physical conditions that permit the rapid development and shoreward drift of their eggs and larvae, with consequent high recruitment and fitness.

The Atlantic menhaden spawns most intensively during winter, south of Cape Hatteras and west of the Gulf Stream[2] (Fig. 1). Within six days of fertilization, larvae feed on the microzooplankton[4] and enter estuaries and metamorphose after 30–90 days[3]. A distinct maximum in the frequency of winter storms on the US east coast exists near Cape Hatteras; cyclones and cold fronts occur every 2–14 days[5,6]. Survival from egg to recruitment at six months is highly variable for the Atlantic menhaden and was correlated to monthly estimates of Ekman transport at a station 56 km SE of Cape Hatteras for 1955 to 1970 (ref. 7), but not thereafter (W. Schaff, personal communication). We postulated that events on a scale of days rather than months, and processes other than Ekman transport, may be important to the spawning and larval development and drift of the Atlantic menhaden[8,9].

Our study was carried out during the Genesis of Atlantic Lows Experiment (GALE), a study of US east coast storms between 15 January and 15 March 1986 (ref. 10). Meteorological observations (air temperature and pressure, relative humidity, wind speed and direction, and sea-surface temperature) were made continuously at an instrumented buoy (34°10′N, 77°15′W) and from the RV *Cape Hatteras*[11]. Oceanographic observations were made from the RV *Cape Hatteras* during 12 sampling grids with stations of sea surface temperature (SST) between 14 and 21 °C. Two to seven major and up to 64 minor stations comprised a sampling grid. Major stations included a continuous vertical profile of temperature, salinity and density; a vertical profile of nitrate, plant pigments and zooplankton (≥20-μ-mesh) pumped from 10–12 discrete depths; two trawls (150-μ-mesh) from each of two depth strata (0–10, 10–30 m or bottom) for fish larvae; and one vertically integrated plankton tow (150-μ-mesh) for fish eggs. Only the latter collection was made at minor stations. All samples were from within the upper 30 m of the water column.

The dominant meteorological sequence during GALE (Fig. 2) consisted of strong NE winds (24–26 January), passage of a low-pressure system (26–27 January), and a strong cold air outbreak (CAO, 27–30 January). This sequence was followed by a 28-day period of relative calm (31 January to 27 February), punctuated by a brief period of northerly winds (13–14 February). Heat flux at the buoy was maximal (>900 W m^{-2}) during the CAO and averaged $145 \pm 14 (\bar{x} \pm$ s.e.) W m^{-2} during GALE; latent heat averaged 2.2 times sensible heat flux. Wind speed and stress were greatest during the 27–30 January CAO (13 m s^{-1}, 4.9 dyn cm^{-2}, 298°). Vector averages of winds at the buoy during GALE were, for speed, 1.4 m s^{-1} from the WNW (301°) and, for stress, 0.42 dyn cm^{-2} from the NW (317°). Spectral analysis indicated dominant periods of 7.2 days for barometric pressure and 4.1 days for heat flux and wind stress during GALE, consistent with a cycle of NE winds, cyclone passage, and NW winds (Fig. 1).

Northeast winds were coincident with or followed by increased concentrations of dissolved nitrate offshore (Fig. 2). Nitrate exceeded 2 μM near the surface (≤10 m) only offshore in '18° water', a water mass characteristic of the cool western wall of the Gulf Stream[12]. Chlorophyll concentration (μg l^{-1}) increased from 1.04 ± 0.03 ($n = 106$) before the late January storm to 1.28 ± 0.07 ($n = 91$) 1–3 days after the late January storm as a result of resuspension of settled phytoplankton, and to 1.75 ± 0.18 ($n = 35$) 11–12 days post-storm as a result of growth as nitrate was used by the phytoplankton. Similar events followed NE winds in early March. Our observations are consistent with the prediction that NE winds cause upwelling at the western edge of the Gulf Stream[13].

The cross-shelf circulation between the Gulf Stream and Mid-Shelf Fronts (GSF and MSF, respectively) during GALE was shoreward near the surface and offshore at depth (Fig. 1). During each sampling grid, warm water overlaid cool water and both strata were of oceanic salinity (≥35.5 g kg^{-1}). The mean pycnocline depth was 15.1 ± 1.0 ($n = 52$). Physical stability, the density difference between depth (≤30 m) and surface divided by the depth, was high on average ($1{,}108 \pm 131 \times 10^{-8}$ m^{-1}, $n = 52$), maximal for stations with 17.5–18.5 °C SST ($2{,}074 \pm 228 \times 10^{-8}$ m^{-1}, $n = 11$), and unaffected by storm passage. Surface salinity increased as temperature decreased from the GSF to the MSF (-0.012 ± 0.002 g kg^{-1} °C^{-1}, $n = 450$), indicating the occurrence of evaporative cooling. Assuming an average heat flux of 145 W m^{-2} and a 15 m thickness for the surface stratum, we calculate its mean shoreward flow to have been 2.4 cm s^{-1}. Thus, we envision a circulation in which nutrient-rich 18° water upwells at the GSF, moves shoreward near the surface with loss of heat and nutrients, sinks at the MSF, and flows offshore at depth (Fig. 1). This circulation, though episodic in intensity, persisted throughout GALE, primarily because of the interaction of cool, dry northerly winds with shelf waters warmed by the Gulf Stream, and despite the opposing average wind stress from the NW.

The distribution of the zooplankton was consistent with this circulation. Vertical aggregation of the microzooplankton available to first-feeding larvae of the Atlantic menhaden was greatest in physically stable water (that is, shoreward of upwelling at the GSF): the variance/mean ratio for the summed concentrations of rotifers, tintinnids and copepod nauplii with 40–160 μm

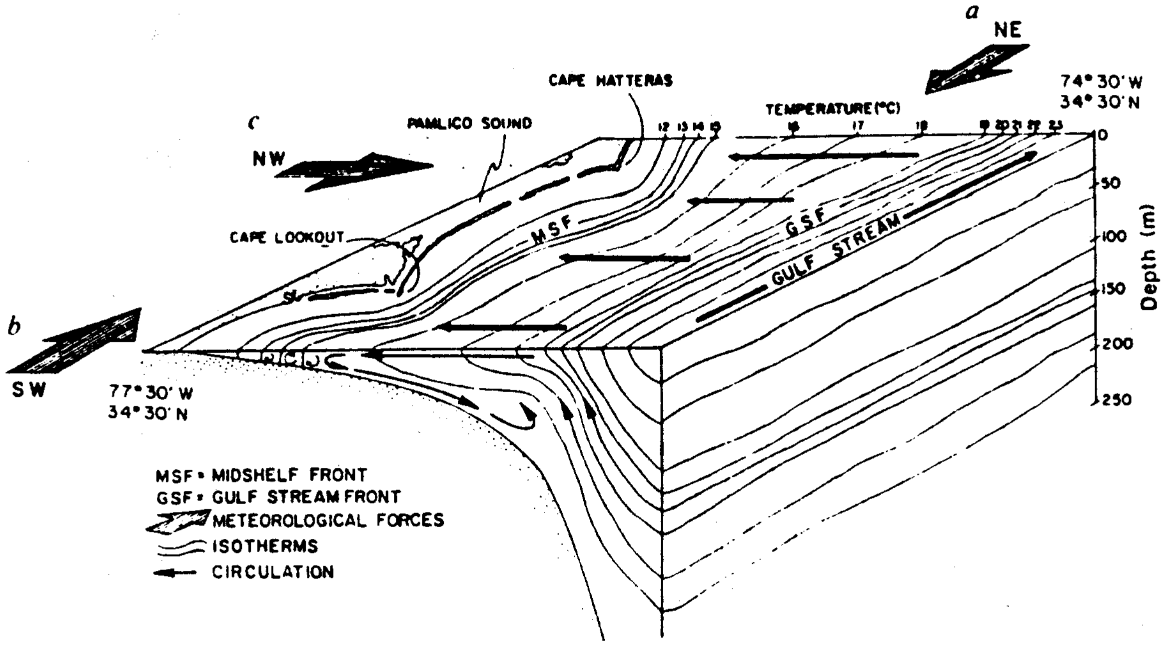

Fig. 1 Wintertime meteorological forces and cross-shelf circulation off northern North Carolina, region of greatest spawning of the Atlantic menhaden[2]. Winter weather cycle consists of *a*, cool moist NE winds; *b*, cyclone passage with warm moist SW winds; and *c*, cold air outbreak with cold dry NW winds. NE winds cause upwelling at GSF[13]. Cross-shelf circulation is maintained by sinking near MSF and oceanward bottom flow of water cooled by heat loss to atmosphere, and replacement by shoreward surface flow from GSF.

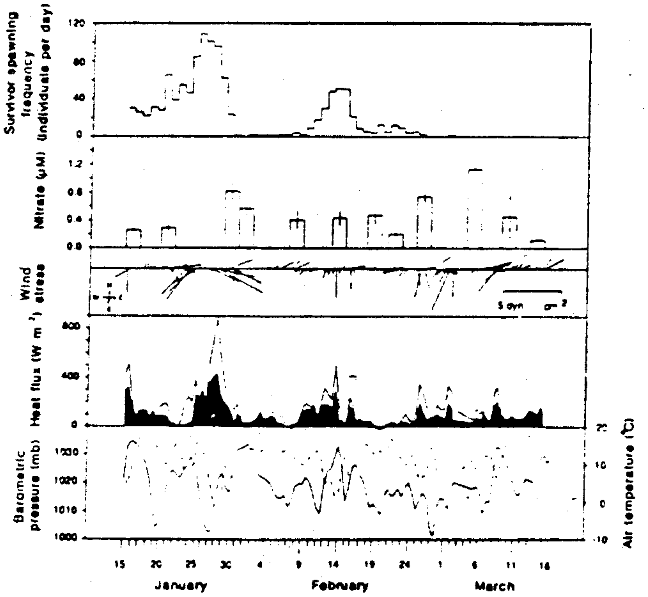

Fig. 2 Meteorological and oceanographic conditions during GALE. Barometric pressure (—), air temperature (----), heat flux (shaded, latent; line, sensible + latent), and wind stress (vectors point downwind) are 12-h averages of hourly values at 34°10'N, 77°15'W. Fluxes of latent and sensible heat and wind stress calculated using iteration method[26]. Nitrate is average (±s.e.) for upper 10 m of each sampling grid. Survivor spawning date distribution is for Atlantic menhaden larvae in GALE collections and estimated from the number of growth increments in sagittal otoliths. The first major increment in sagittae is formed at first feeding (~4 days after fertilization) and one increment is formed daily thereafter; hence, spawning date = collection date − (4 + number of increments). Distribution of eggs and small larvae and rapid changes in survivor spawning date frequency indicate rapid and large variations in spawning rather than egg and larva mortality. Spawning was greatest during periods of high wind stress in January and February; spawning has not been observed in this region in March[2]

maximal width was positively correlated with stability (Spearman's rank correlation, $r = 0.39$, $P < 0.005$, $n = 52$). The average depth of maximal abundance of this microzooplankton was 10.7 ± 1.2 m ($n = 52$) and thus within the upper stratum. Genera of rotifers (*Synchaeta* and *Trichocerca*)[14,15] and copepods (*Paracalanus*, *Clausocalanus* and *Temora*)[16] typical of estuarine and coastal waters occurred in oceanic water after storms. Copepod nauplii increased in abundance from 27 ± 1 ($n = 107$) to 40 ± 2 ($n = 90$) nauplii per litre with passage of the late January storm, with post-storm concentrations as high as 125 nauplii per litre. Similar increases occurred with passage of the early March storm and copepod nauplii were, on average, abundant (36 ± 2 nauplii per litre) between the MSF and GSF during GALE. Thus in this region, winter storms and their associated offshore upwelling and cross-shelf circulation stimulate the midshelf production and vertical aggregation of the microzooplanktonic food of larval Atlantic menhaden on the scales of days and metres. First-feeding northern anchovy, *Engraulis mordax*, in contrast, require aggregations of slow-moving dinoflagellates which are dispersed by storms and upwelling[17,18].

The eggs and larvae of the Atlantic menhaden benefit from this circulation by drifting shoreward during winter in warm water with abundant food. Atlantic menhaden eggs float[19] and Atlantic menhaden larvae were 1.5 times more abundant (individuals per square metre) near the surface (0-10 m) than deeper down (10-30 m or bottom). Rapid development due to warm temperature and abundant food in the surface stratum shortens the exposure of eggs and larvae to predators and thus enhances their survival. Otolith analysis (Fig. 2) and the offshore occurrence of eggs (21-22 January 1986) and small (≤5-mm standard length) larvae (30-31 January 1986) indicate that spawning occurred near the GSF and was maximal during the late-January storm. The production, growth and shoreward transport of this cohort to the MSF are apparent when larval fish size is expressed in relation to SST and collection date (Fig. 3). This cohort moved shoreward between the GSF and MSF at ~2.0 cm s^{-1}, in close agreement with the shoreward transport speed estimated from the heat flux, thermocline depth, and cross-shelf temperature gradient. The largest menhaden larvae,

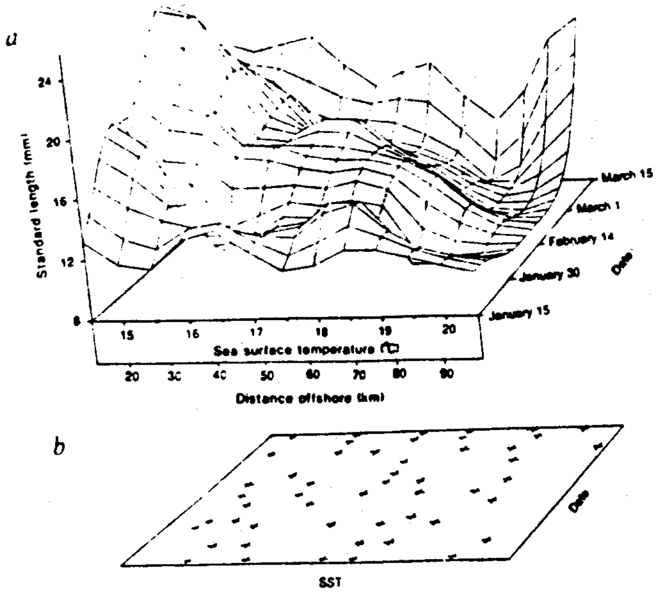

Fig. 3 Mean standard length of larval Atlantic menhaden, corrected for shrinkage, in relation to collection date (1986) and SST (mean standard length at grid nodes (*a*) interpolated[27] from measured values at 51 stations (*b*)). Approximate distance offshore (DO), estimated from regression of GALE data, $DO = 9.37\ SST - 108$ ($n = 241$, $r = 0.81$), shown for comparison. Maximal spawning, inferred from occurrence of eggs and analysis of otoliths (Fig. 2, top), preceded collection of smallest larvae (18 °C SST, 3 February, 9.5 ± 0.3 mm average length ($n = 57$), 4.7 mm minimum length). Resultant cohort, manifest as 'ridge' of temporally increasing standard length and decreasing SST, developed and drifted shoreward in surface stratum, cooled by persistent heat loss to atmosphere, at $\sim 2\ \mathrm{cm\ s^{-1}}$, consistent with rate ($2.4\ \mathrm{cm\ s^{-1}}$) estimated from measured heat flux, pycnocline depth, and cross-shelf temperature gradient. Thus, large larvae collected at 15 °C SST in early March appear to have resulted from the late January spawn in 18 to 20 °C SST offshore waters. Menhaden larvae of 12–17 mm standard length were found offshore at 19.9 and 20.4 °C SST in mid-March; such larvae are presumed to die if not transported to the MSF.

apparently of this cohort, were collected on 2 May at 15 °C SST, 6 km offshore. Thus, this circulation brings menhaden larvae to within ~20 km of shore on average and much closer at times. Subsequent movement of menhaden larvae to and through the inlets is believed to result from their vertical movement combined with the nearshore and estuarine circulations[20,21].

Our results indicate that the Atlantic menhaden has evolved to reproduce under physical conditions optimal for the survival and shoreward transport of its eggs and larvae. These include storms, during which upwelling and spawning occur, and persistent heat loss and stratification, during which rapid development and shoreward transport occur. Spot (*Leiostomus xanthurus*), croaker (*Micropogonias undulatus*), flounder (*Paralichthys* spp.), striped mullet (*Mugil cephalus*) and pinfish (*Lagodon rhomboides*) also spawn south of Cape Hatteras and west of the GSF in winter and have estuarine nursery areas[3,9,22,23]. The Japanese sardine (*Sardinops melanosticta*), which supports the world's second largest fishery[24], spawns in winter at the western edge of the Kuroshio and its larvae occur in dense aggregations nearshore, supporting the shirasu ('white children') fishery[25]. We suggest that each of these species has evolved to spawn during winter shoreward of a warm boundary current as a result of physical conditions, especially storm-induced upwelling and buoyancy-driven transport, which make possible the rapid development and drift of their eggs and larvae and hence enhanced recruitment and fitness. Variation in these physical conditions may explain significant interannual variation in recruitment of these fish.

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