

Wind Regulation of Emergence Times and Early Larval Survival in Capelin (*Mallotus villosus*)¹

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Factors regulating the emergence and survival of capelin (*Mallotus villosus*) larvae from their beach gravel nest sites were investigated in the spring and summer of 1978 and 1979. In both years, the pattern of larval emergence was characterized by intermittent abrupt increases in the numbers of larvae in the nearshore waters and corresponding precipitous declines in the density of preemergent larvae in the beach gravel. Both events were strongly correlated with onshore wind-induced wave action which disturbed the beach. Larval emergence patterns were unrelated to changes in tidal amplitude or day–night variation. The generality of this wind-induced larval emergence hypothesis was tested and confirmed using published data from two separate studies conducted at three different Newfoundland sites during 1927, 1929, 1930, and 1941. The density of larvae in the beach gravel was positively correlated with the length of time separating the occurrence of onshore winds. The result was a pronounced temporal clumping of larvae hatching at different times, periodic releases of large numbers of larvae into the aquatic environment, and a progressive deterioration in the physical condition of larvae emerging as beach residence time increased. The frequency of onshore winds during the hatching period was 50% greater in 1979 relative to 1978. Egg densities were similar in 1978 and 1979 but larval densities (no./m³) in the nearshore environment were 60% greater in 1979. This increase in larval density conformed to the increase in the proportion of larvae exiting the beach in good physical condition in 1979.

Key words: capelin, *Mallotus villosus*; Newfoundland, larval emergence, larval survival, wind, population biology, beach spawning, coastal environments, year-class strength

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Au printemps et en été 1978 et 1979, les auteurs ont étudié les facteurs réglant l'émergence et la survie des larves de capelan (*Mallotus villosus*) de leurs nids de gravier des plages. Ces deux années-là, l'émergence a été caractérisée par d'abruptes augmentations intermittentes du nombre des larves dans les eaux à proximité du rivage, et par des diminutions correspondantes, tout aussi abruptes, de la densité des larves encore dans le gravier. Il y a une forte corrélation entre ces deux phénomènes et les vagues qui, sous l'influence des vents du large, dérangent la plage. Il n'y a pas de relation entre l'émergence larvaire et les changements d'amplitude de la marée, non plus que la variation nyctémérale. Nous avons vérifié et confirmé l'application générale de cette hypothèse d'une émergence larvaire déclenchée par le vent, en nous servant de données publiées à la suite de deux études effectuées à trois sites différents de Terre-Neuve en 1927, 1929, 1930 et 1941. Nous avons trouvé une corrélation positive entre la densité des larves dans le gravier des plages et l'intervalle de temps séparant l'incidence des vents du large. Comme résultat, il y a groupage temporel serré des larves éclochant à différentes périodes, des émergences périodiques de grands nombres de larves dans l'environnement aquatique et détérioration progressive de l'état physique des larves émergentes à mesure qu'augmente le temps de résidence. En 1979, les vents du large furent de 50% plus fréquents qu'en 1978. La densité des œufs était la même ces deux années-là, mais celle des larves (no./m³) près du rivage était de 60% supérieure en 1979.

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Cette augmentation de densité des larves est conforme à l'augmentation de la proportion des larves émergeant de la plage en bon état physique en 1979.

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SEVERAL fish species exhibiting marine (capelin, *Mallotus villosus*; grunion, *Leuresthes* sp.; surf smelt, *Hypomesus pretiosus*), catadromous (*Galaxias maculatus* and *Galaxias fasciatus*), and estuarine (*Fundulus heteroclitus*) life histories are known to spawn at times and in areas which cause the eggs to develop in an extra-aquatic environment. In all species except capelin, spawning dates, egg development times, and the entry of larvae into the aquatic environment are strongly linked to the tidal cycle and are highly predictable (Thompson and Thompson 1919; David 1939; Walker 1952; Thomson and Muench 1976; Moffatt and Thomson 1978; Loosanoff 1937; Pollard 1971; Hopkins 1979; Taylor et al. 1977). In contrast, while comparatively little is known of the environmental factors regulating spawning times, egg development rates, and the timing of larval emergence in capelin except in a general way, it is clear that these aspects of the early life history of capelin are less directly influenced by tides. Spawning times, development rates, and larval emergence times also appear to be more variable and hence less predictable (see Jeffers 1931; Sleggs 1933; Templeman 1948; Pitt 1958; Jangaard 1974). This lack of predictability in capelin stems partly from the fact that few systematic quantitative studies of the interaction between environmental factors and aspects of the egg and larval ecology of capelin have been made.

Details of spawning site selection and the beach spawning act in capelin are summarized in Sleggs (1933) and Templeman (1948). Highlighted briefly: (1) eggs are spawned on beaches or restricted portions of exposed beaches typified by substratum ranging in size from fine gravel to small pebbles (2–25 mm diameter), (2) spawning females normally accompanied by one or two males are carried onto the beach by an incoming wave, where they are temporarily stranded when the wave recedes, (3) eggs and sperm are shed on the beach surface, (4) fertilized eggs strongly adhere to the beach sediments, (5) wave and tidal action distributes and buries the eggs over the breadth of the intertidal zone to depths of 15 cm or more below the beach surface, (6) eggs develop and hatch in the sediments.

Nothing is known of the survival value of the reproductive mode exhibited by capelin or of the effects on survival of seasonal or year-to-year variability in important environmental factors. It has been repeatedly shown, however, that stochastic differences in environmental factors known to influence egg and larval survival can significantly influence year-class strength in fishes (see Cushing 1969, 1975; several papers in Blaxter 1974; Leggett 1977; Nelson et al. 1977; Chadwick et al. 1977). Capelin exhibit large year-to-year fluctuations in year-class strength (Winters and Carscadden 1978; Gjøsaeter 1972), and it is possible that a portion of this variability results from differential mortality in the egg and early larval stages. In view of the central position of capelin in the food web of the north Atlantic (Bailey et al. 1977) and its commercial importance (Winters and Carscadden 1978), a more quantitative knowledge of its early life history seems

long overdue.

In this paper we examine the factors regulating the emergence of capelin larvae from the beach gravel and comment on the survival consequences of seasonal and annual variability in these factors. Beach spawning among capelin represents only one of two modes of reproduction. Certain stocks of capelin (e.g. those of the Southeast Shoal of the Grand Banks) spawn offshore in deeper waters (up to 60 m, Pitt 1958). Consequently, this study relates only to the beach spawning component.

Methods

The study was conducted at Bryant's Cove, Newfoundland (Fig. 1), during the spring and summer of 1978 and 1979. The cove, and more generally the western half of Conception Bay, has a long history of significant capelin beach spawning by adults of the northern Grand Bank—Avalon stock (Campbell and Winters 1973).

The spawning beach at Bryant's Cove is located at the head of the cove and is ~ 240 m in length. A small freshwater stream crosses the beach near its midpoint. Bordering and extending 40 m on each side of this stream are beach sediments typified by particles >6 cm in diameter. The remainder of the beach is characterized by sediments ranging from less than 1 mm in diameter (fine gravel) to 4 mm in diameter (pebbles). Owing to its generally exposed character the beach is devoid of any rooted aquatic vegetation. The gently sloping (15°) beach varies in width from 7 to 12 m at low water depending upon tidal amplitude. Daily tidal amplitude ranged from 1.4 to 0.3 m during spring and neap tide, respectively (Fig. 2A).

We recorded spawning times and quantified changes in egg and larval densities in the beach gravel and larval densities in the immediate intertidal zone and at a transect parallel to and 10 m from the intertidal zone (hereafter, referred to as the nearshore sampling site).

Egg and larval densities in the beach gravel were determined by coring the beach twice weekly beginning immediately after the commencement of spawning and continuing until all eggs had hatched and all larvae had exited the beach. Cores were made at three sampling stations in 1978 and two sites in 1979 (Fig. 1). At each station one core was drawn from each of the high tide (HT), mid-tide (MT), and low tide (LT) regions of the intertidal zone. All sampling was conducted during daylight hours and at the time of low tide. To obtain each core the 5.5-cm internal diameter steel corer was forced vertically into the sediments to the maximum extent possible. The surrounding substratum was then removed and a spatula was slipped under the corer sealing its opening to retain the sample. At this time observations were made to ensure that no eggs or larvae occurred in the sediments at depths greater than the maximum penetration of the corer. A calibrated plunger was used to determine the total depth of the

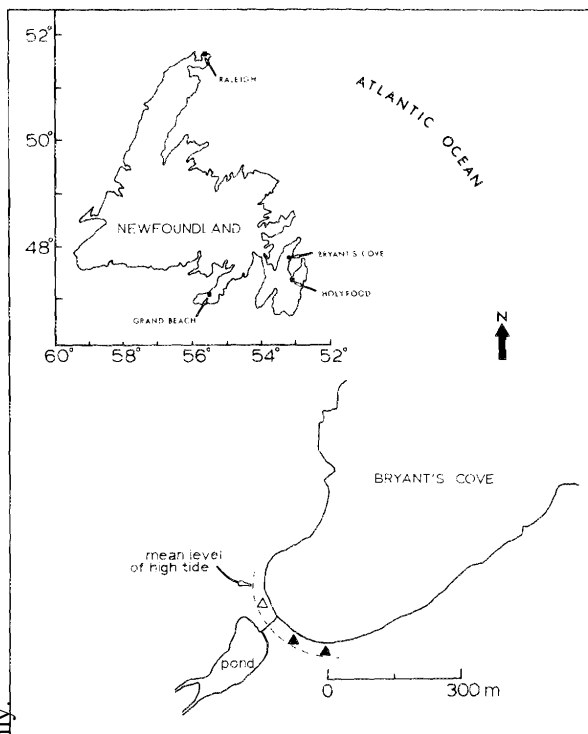


FIG. 1. Beach and nearshore sampling locations in Bryant's Cove, Nfld. Positions of beach sampling stations as follows: 1978 (Δ , Δ) and 1979 (\blacktriangle , \blacktriangle). Locations mentioned in text are indicated on inset.

core and to remove the sample from the corer. Samples were preserved in 4% buffered formalin. Numbers of preemergent larvae were determined by counting all larvae for each core. Overall densities were expressed as the geometric mean number/m³ in all cores for each of the intertidal regions (HT, MT, and LT) collected on a given sampling date.

To detect the timing and magnitude of emergence of capelin larvae we sampled the nearshore ichthyoplankton twice weekly during 1978 and 1979. All samples were collected using a 0.5-m-diameter standard plankton net fitted with a No. 10 (150 μ m) mesh net and General Oceanics flowmeter towed once parallel to the length of the beach at a depth of 1.0 m over a total depth of 3.0 m. Towing speeds averaged 1.2 ± 0.07 m/s. Samples were collected at 18:00 and preserved in 4% buffered formalin. All capelin larvae in each sample were counted and densities expressed as no./m³ of water filtered.

In 1979 daily to twice-daily collections of emerging larvae were also made in the intertidal region using a rectangular mouth (20 \times 29 cm) No. 10 mesh plankton net attached to a sled and frame constructed of clear Plexiglas. When deployed the lower edge of the mounted net rested 4 cm above the surface of the beach sediments. All collections were made at the time of high tide. To obtain samples the net was lowered into the water from a boat located over the low tide zone (average depth \sim 2 m) and was towed by a hand line to the beach by an operator stationed there. Two 10-m tows were made at each of three stations (located directly opposite the

beach sampling stations, Fig. 1) on each sampling date. Samples were preserved in 4% buffered formalin. All larvae were counted from each sample and densities were expressed as no./m³ of water filtered.

In addition to enumerating the larvae in samples taken from the beach and in the intertidal and nearshore collections, we also classified them according to their physical condition distinguishing between robust, obviously healthy larvae and emaciated, deformed, and deteriorating larvae.

Results and Discussion

SPAWNING OBSERVATIONS

Beach spawning occurred during two distinct time intervals in both 1978 and 1979. In 1978, the first spawning occurred between June 14 and 20 and the second 15 d later from July 5 to 9. In 1979 the first spawning occurred from June 4 to 8 and the second 12 d later on June 21. Water temperatures (measured at 1-m depth in the subtidal region) during spawning ranged from 6.5 to 10°C in 1978 and 2.5 to 10.8°C in 1979. In both years spawning occurred at or near the period of maximum tidal oscillation, and always during the ebbing tide.

About 120 m of the 240-m beach was used for spawning. This area was typified by sediments ranging in size from 1 to 4 mm in diameter. The average egg deposition was similar for all four spawnings, ranging from 5.5 to 6.9×10^6 eggs/m² of beach surface at the various sampling sites. Eggs were unevenly distributed throughout the intertidal zone, there being a tendency towards greater egg densities at the high tide zone. Eggs were distributed to a maximum depth of 14 cm below the beach surface. Hatching occurred in the sediments and time to hatching was inversely related to incubation temperature. Because of the tide-dependent duration of exposure and inundation at different levels in the intertidal zone and the resulting effects on temperature in the gravel, hatching time averaged 9–11 d at the high tide zone and 22–24 d at the low tide zone.

LARVAL DENSITIES IN BEACH SEDIMENTS

Temporal changes in larval densities in the sediments were similar at the high tide, mid-tide, and low tide sampling locations in both 1978 and 1979 (Fig. 2B). Differences in larval abundance at the three locations paralleled differences in egg densities and may have been influenced to some degree by differences in development rates between areas. The abundance of larvae in the sediments in 1978 was clearly linked to the two periods of spawning, there being two distinct peaks each occurring \sim 10–14 d after spawning. This pattern was not repeated in 1979 (Fig. 2B).

Temporal changes in larval abundance in the sediments were unrelated to tidal amplitude. There was, however, a close correspondence with daily wind events as recorded at the Holyrood meteorological station (Fig. 2). In both 1978 and 1979 increases in larval abundance in the beach sediments were preceded by a predominance of offshore winds. Conversely, precipitous declines in larval density were preceded by onshore winds (Fig. 2). Offshore winds produce calm condi-

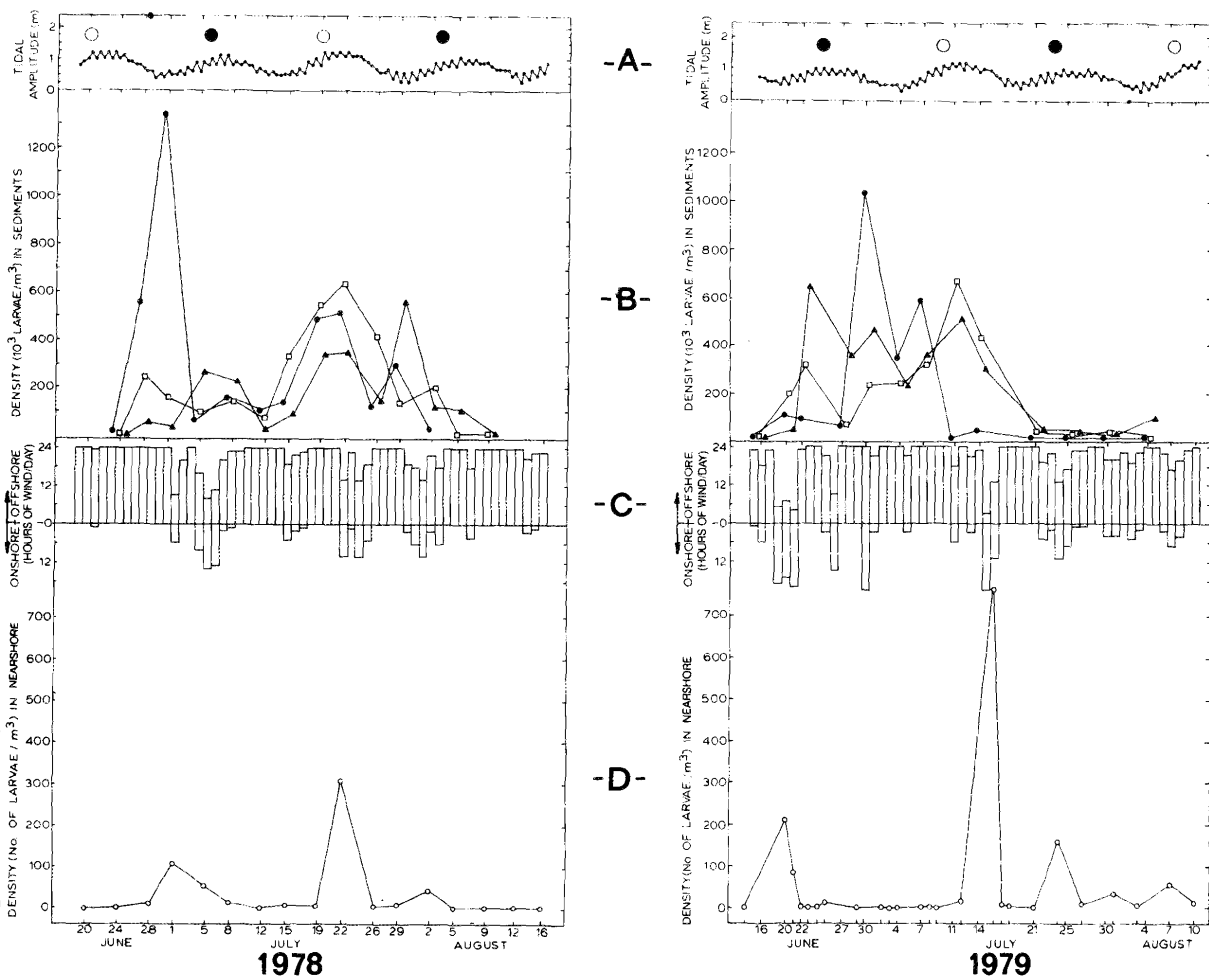


FIG. 2A. Daily tidal amplitude and the corresponding times of the new (closed circles) and full (open circles) moon. (B) Pattern of occurrence of capelin larvae in the beach sediments at each of three intertidal locations designated as high (●), mid (□), and low (▲) tide. (C) Temporal variation in wind direction and duration. Bars above and below the zero line indicate winds directed offshore (SE-NW) and onshore (N-E) at the study site, respectively. The height of each bar represents the daily wind duration in hours. (D) Occurrence of capelin larvae in the nearshore region.

tions near the beach whereas onshore winds generate wave action which disturbs the beach sediments. We therefore examined the hypothesis that wind-generated wave action was instrumental in the release of larvae from the sediments. If the hypothesis is true, the expected relationship between density of larvae in the beach sediments and time since the last onshore wind should be positive. A significant positive relationship was found ($Y = 185.4 + 2.22X$, $n = 16$, $R^2 = 0.49$, $P < 0.005$; Fig. 3A) when mean larval density (Y) from the high tide, mid-tide, and low tide locations during the principal hatching period (9–24 d after the initial spawning) was regressed against time in hours since the end of the last onshore wind event (X). Conversely, we would also expect a strong negative relationship between larval densities in the beach gravel and the number of hours of onshore wind on any given day. This negative relationship was also found ($Y = 396.2 - 6.22X$, $n = 16$, $R^2 = 0.55$, $P < 0.005$; Fig. 3B) when mean larval density (Y) in the beach gravel was

regressed against the arcsine transformed average number of hours of onshore wind per 24 hours on the day before and the day of sampling (X). Temporal variability in larval abundance resulting from different egg development times at the high tide, mid-tide, and low tide zones were thus effectively damped by the infrequent occurrence of onshore winds. The result was a pronounced temporal clumping of larvae in the sediments. The more frequent occurrence of onshore wind events in 1979, relative to 1978, may also explain the absence of a distinct relationship between spawning time and larval abundance in the sediments in that year.

LARVAL EMERGENCE

The occurrence of capelin larvae in the nearshore region was characterized by intermittent abrupt increases in density during both years of collection (Fig. 2D). Peak densities on these dates exceeded those on other sampling dates by nearly

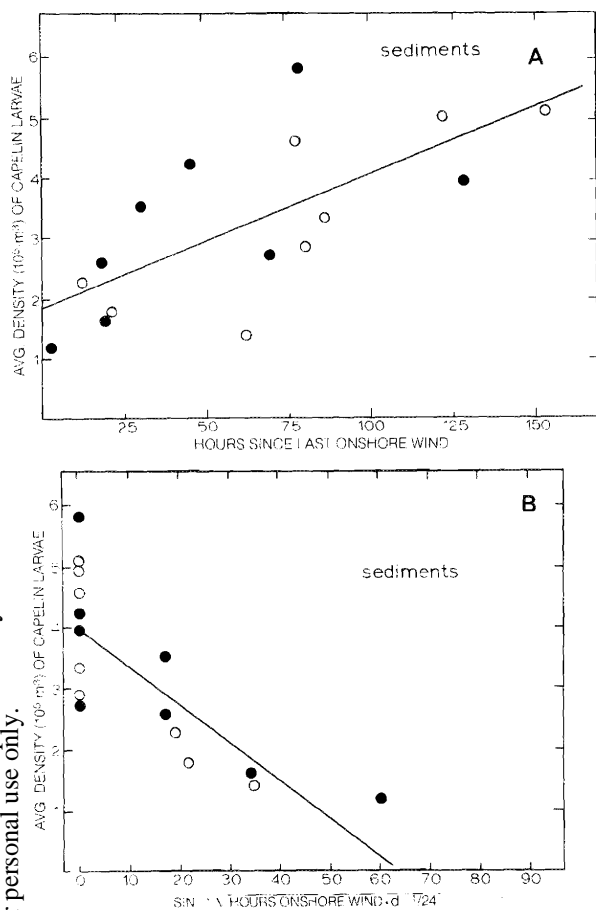


FIG. 3A. Relationship between mean larval density in the beach gravel and time in hours since the end of the last onshore wind event [1978 (○); 1979 (●)]. (B) Relationship between mean larval density in the beach gravel and variation in the duration of onshore wind conditions at the time of sampling [1978 (○); 1979 (●)].

two orders of magnitude. In 1979 there was a twofold greater frequency of occurrence of peaks in larval densities in the nearshore region relative to 1978 and the average catch of larvae per sampling date was 60% greater (38 vs. 60.5 larvae/m³ for 1978 and 1979, respectively; Fig. 2D).

The pattern of intermittent abrupt occurrences of capelin larvae witnessed during the 2 years of nearshore collections was also evident in the intertidal samples. The synchronous changes in density at the three intertidal sampling stations spanning the beach was striking and suggest larval emergence was synchronous over the entire beach. The more frequent sampling routine also revealed more peaks (Fig. 4) in larval density in comparison to the number encountered in the 1979 nearshore collections of emergent larvae. The rapid decline in numbers of larvae following these peaks suggests the larvae are quickly transported seaward from the beach. The likelihood of overlapping catches (i.e. catching larvae emerging at different times in the sample) is thus reduced.

If our hypothesis that larval emergence is facilitated by onshore wind-induced wave action is valid, we would

anticipate a positive relationship between the density of larvae in the nearshore and intertidal collections and onshore wind events. A significant positive relationship ($\ln Y = 1.07 + 0.086X$, $n = 38$, $R^2 = 0.74$, $P < 0.001$; Fig. 5A) was found between larval capelin density (Y) in the nearshore samples (1978 and 1979 combined) and the arcsine transformed average number of hours of onshore wind per 24 hours (X) on the day before and the day of sampling. A similar positive relationship ($\ln Y = 4.65 + 0.054X$, $n = 35$, $R^2 = 0.38$, $P < 0.001$; Fig. 5B) was found between onshore winds (X) and larval abundance (Y) in the daily intertidal samples.

In view of the importance of tides as the trigger for larval emergence in other beach spawners, we also tested for a possible relationship between tidal amplitude and larval abundance. No such relationship was found in the 1978 nearshore data ($R^2 = 0.04$, $n = 15$, $P > 0.25$), for 1979 ($R^2 = 0.01$, $n = 23$, $P > 0.50$), or in the more frequent intertidal samples collected in 1979 ($R^2 = 0.001$, $n = 35$, $P > 0.50$).

We also tested for day-night differences in larval emergence. Because our sampling times were bimodal (day 07:00–16:00, night 21:00–24:00), we used the Kendall rank correlation (Siegel 1956) to relate the geometric mean abundance of capelin larvae in the intertidal samples to sampling time. No significant correlation occurred ($\text{Tau} = 0.17$, $n = 35$, $0.05 < P < 0.10$).

In spite of the strong correlative evidence in support of our hypothesis that onshore wind-induced wave action mediates larval emergence, the possibility remained that high larval densities in the nearshore and intertidal zones during onshore wind conditions resulted from onshore Ekman transport of larvae from offshore areas and not from the emergence of larvae from the beach.

To examine this possibility we regressed the mean density of capelin larvae in the beach sediments on day t against the mean density of larvae in the intertidal zone on day $t+1$. In this analysis the initial dates (day t) were selected to be periods of onshore wind. A strong positive relationship was found ($\ln Y = -0.27 + 1.28 \ln X$, $n = 8$, $R^2 = 0.52$, $P < 0.05$; Fig. 6). This result, combined with the previously described negative relationship between larval densities in the beach sediments and hours of onshore wind (Fig. 3B), support our thesis that the source of the larvae in the intertidal and nearshore areas during and immediately after onshore wind events is larval emergence from the beach and not Ekman transport of larvae from offshore areas.

To test the generality of our hypothesis that larval emergence is facilitated by onshore wind-induced wave action, we examined the relationship between wind events and nearshore larval densities reported by Jeffers (1931) and Templeman (1948). Jeffers' data come from three years (1927, 1929, 1930) of collections of larvae made adjacent to a spawning beach in Ha Ha Bay near Raleigh on the northern peninsula of Newfoundland (Fig. 1). We used only those collections made in areas adjacent to the spawning beach in our analysis. Templeman's data, which are characterized by more frequent samples, provide information on larval densities during 1941 at Holyrood at the head of Conception Bay and at Grand Beach, Fortune Bay, on Newfoundland's south coast (Fig. 1).

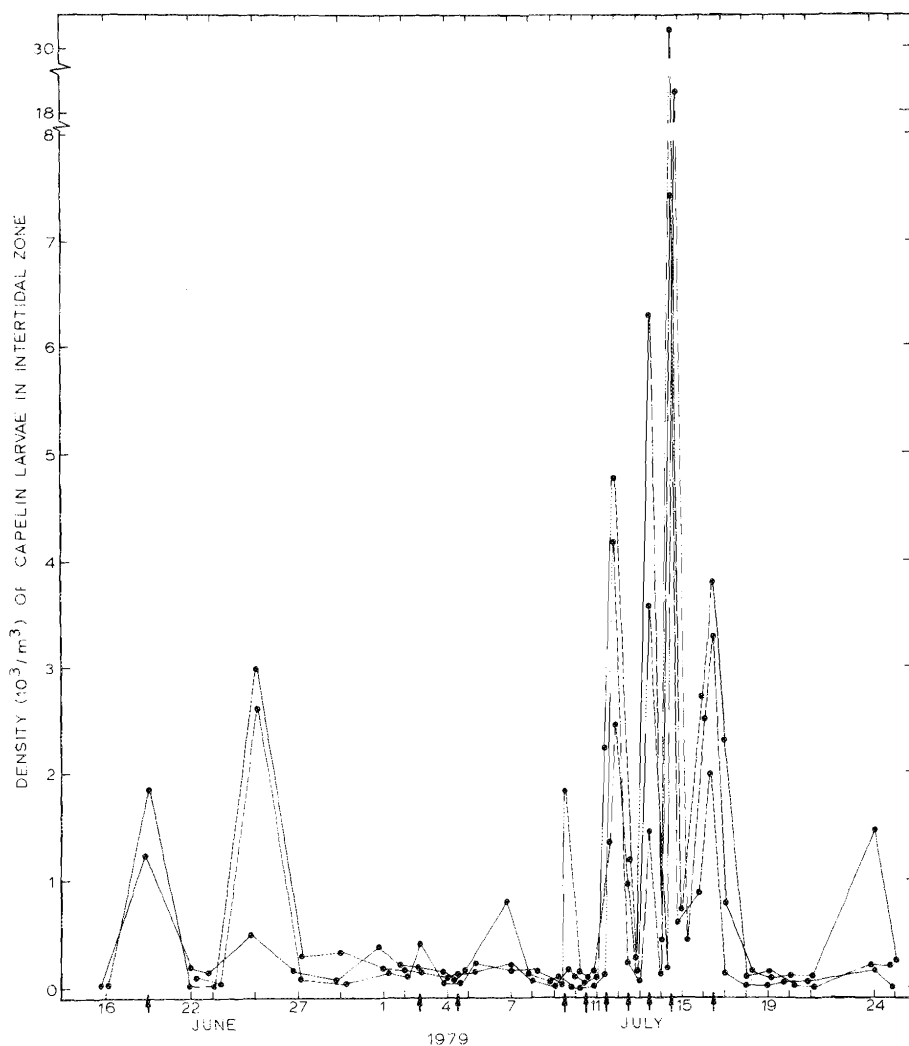


FIG. 4. Pattern of emergence of capelin larvae in the intertidal zone at three locations adjacent to the beach (see Fig. 1). Arrows intersecting the x-axis indicate times of night sampling.

All of the available data was not incorporated into the analysis. Templeman considered the first spawning at Holyrood to be minimal and was "in no way comparable to the number of eggs deposited later during the period of maximum spawning." We therefore omitted the eight collections of larvae sampled from the first spawning from our analysis. Six samples were omitted from the Grand Beach data (June 27 to July 2). These samples were taken 26 d or more after the initial deposition of eggs and thus beyond the principal hatching period of 13–19 d (Templeman 1948) and beyond the range of hatching we observed (9–24 d).

Wind data for Raleigh were based on twice daily recording of direction and velocity made at the Belle Isle meteorological station during 1927, 1929, and 1930. Any wind having an easterly component produces onshore winds in Ha Ha Bay.

Nearshore larval densities were significantly higher during onshore winds relative to offshore winds (Fig. 7). Wind data for Holyrood and Grand Beach were based on hourly recordings of direction and velocity made at the St. John's and Grand Bank meteorological stations, respectively, during 1941. Any wind having a northerly component will produce onshore wave action at Holyrood. Winds from the west and northwest will produce onshore wave action at Grand Beach. Significant positive relationships (Fig. 7) were found between onshore winds (X) and nearshore larval densities (Y) at both Holyrood ($\ln Y = 3.45 + 0.160X$, $n = 8$, $R^2 = 0.53$, $P < 0.05$) and Grand Beach ($\ln Y = -3.02 + 0.266X$, $n = 9$, $R^2 = 0.60$, $P < 0.05$). These data strongly suggest that the relationship we describe between the timing of larval capelin emergence and onshore wind events at Bryant's Cove

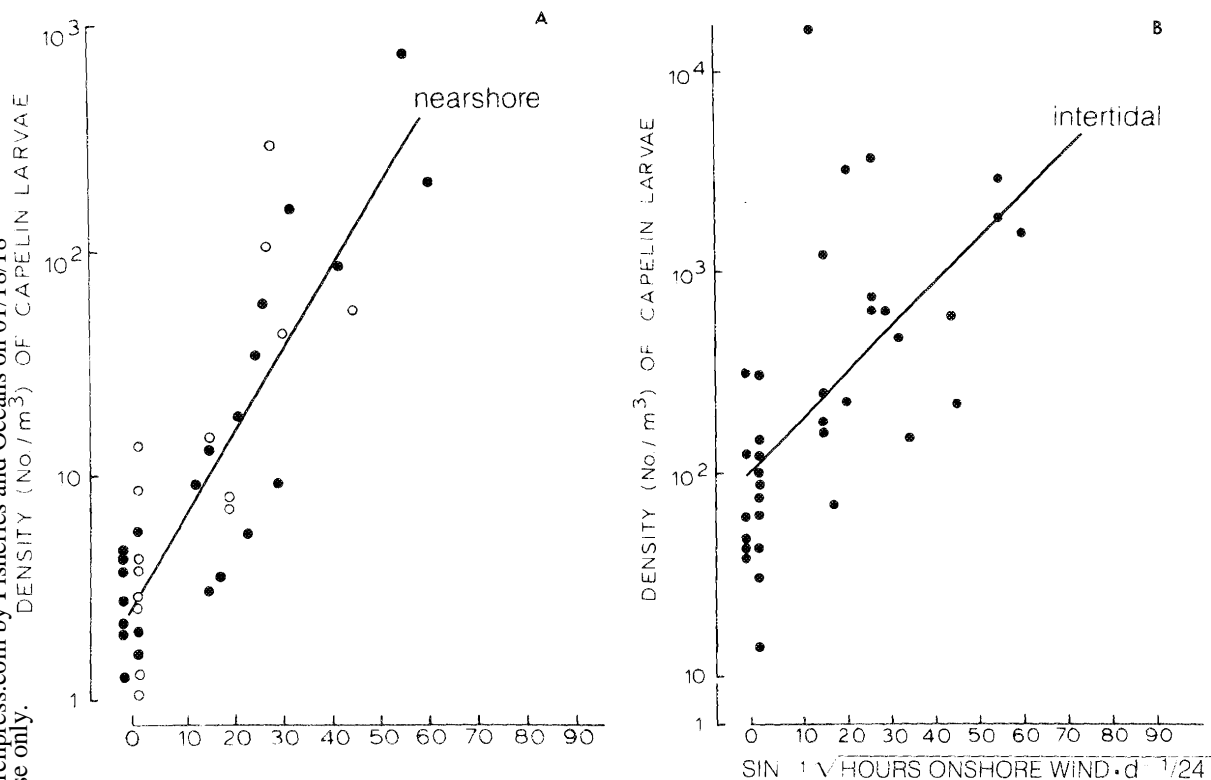


FIG. 5A. Relationship between the density of emergent capelin larvae in the nearshore waters and the duration of onshore wind for 1978 (○) and 1979 (●). (B) Relationship between the geometric mean density ($n = 3$) of emergent capelin larvae in the intertidal zone and the duration of onshore wind.

Apply to spawning beaches on all coasts of Newfoundland, and possibly to other spawning areas within the species' circumpolar distribution.

IMPLICATIONS FOR LARVAL SURVIVAL

The positive relationship between densities of capelin larvae in the beach sediments and time since the last onshore wind event depicted in Fig. 3A implies that posthatching residence times of larvae on the beach are a positive function of the duration of the interval between onshore wind events. Since virtually no food is available to the larvae while in the sediments, deterioration in physical condition would be rapid if larvae failed to exit the beach before the yolk sac reserves were exhausted. Based on this reasoning, we predicted, a priori, that the proportion of the total larvae in our samples found to be in good physical condition (Y) would be negatively correlated with the time since the end of the last onshore wind (i.e. larval residence time, X). This prediction was upheld ($Y = 66.2 - 0.11X$, $n = 21$, $R^2 = 0.20$, $P = 0.05$; Fig. 8C). While the slope of the observed relationship is not great, the rapid increase in total larvae in the sediments with time since the last onshore wind implies that the increase in the numbers of larvae in poor condition should be a strongly positive function of residence time. For the combined 1978 and 1979 data from Bryant's Cove, the equation best describ-

ing this relationship was

$$Y = 32.6 + 1.49X \quad (n = 14, R^2 = 0.34, P < 0.05)$$

where $Y = 10^3$ larvae/ m^3 in poor condition and X = time since the end of the last onshore wind event. A similar negative relationship between the proportion of larvae in good physical condition (Y) and time since the last onshore wind (X) was observed in the intertidal larval collections ($Y = 78.9 - 0.25X$, $n = 17$, $R^2 = 0.44$, $P < 0.005$; Fig. 8B). No such relationship existed in the nearshore samples ($R^2 = 0.03$, $n = 27$, $P > 0.5$; Fig. 8A).

Two interpretations of the difference in the relationship between these variables in the intertidal and nearshore samples are possible. The first is that they are the result of differences in sampling depths between the sled sampler (intertidal) and the standard plankton net (nearshore). The implication here being that the larvae in poor physical condition would be more concentrated near the bottom and hence more susceptible to capture by the sled sampler. The second interpretation is that the weaker larvae are lost due to predation and other sources immediately after release and are thus removed from the system leaving a high proportion of robust larvae at the nearshore site regardless of residence time. We believe this distinction to be insignificant since the weaker larvae, if they concentrate near the bottom, will ultimately

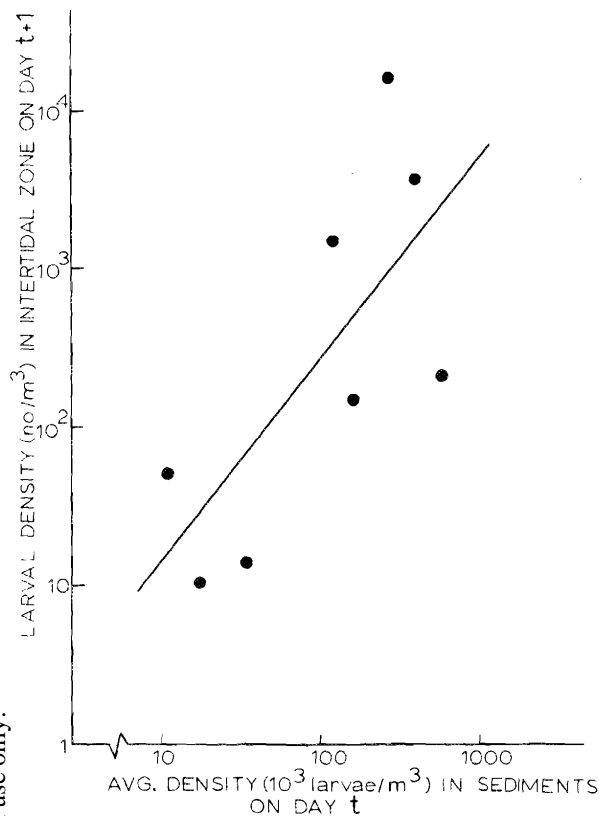


FIG. 6. Relationship between the geometric mean density of emergent capelin larvae over the intertidal zone on day $t + 1$ and the mean density of capelin larvae in the beach gravel on day t (Day t = onshore wind event).

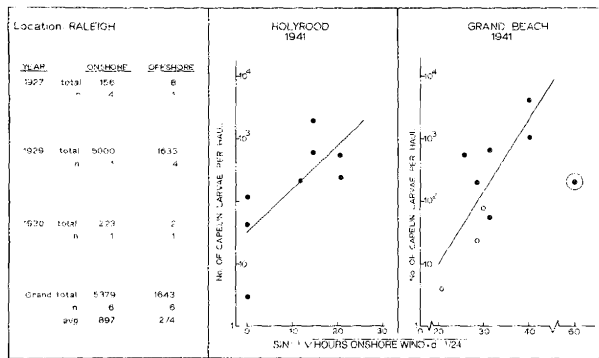


FIG. 7. A general test of the wind-induced larval emergence hypothesis. Raleigh data from Jeffers 1931; Holyrood and Grand Beach data from Templeman 1948. Collections of capelin larvae made at Grand Beach were characterized by larvae from two distinct egg cohorts designated as \bullet and \circ , the circled point was omitted from the analysis.

be easy prey for the high numbers of juvenile winter flounder (*Pseudopleuronectes americanus*), juvenile tomcod (*Microgadus tomcod*), and other predators in the nearshore

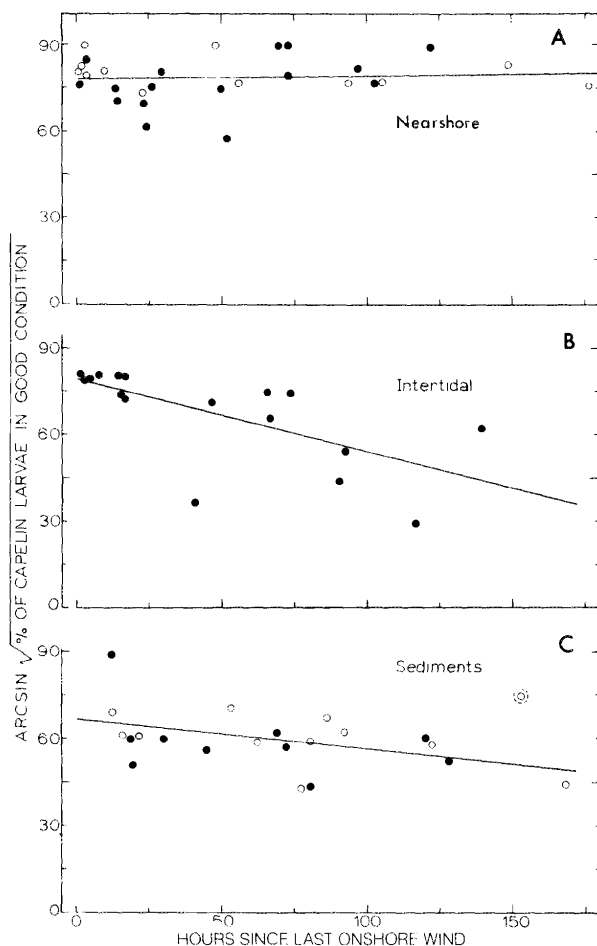


FIG. 8. Effect of larval beach residence time (hours since end of last onshore wind) on the proportion of larvae in good physical condition collected from (A) the nearshore region, 1978 (\circ) and 1979 (\bullet); (B) the intertidal zone, 1979 only; and (C) the beach gravel 1978 (\circ) and 1979 (\bullet).

benthic environment. The inability of fish larvae to recover from starvation is also well documented (Blaxter and Hempel 1963; Lasker et al. 1970). For these reasons we believe the interval between onshore wind events to be a significant regulator of early larval survival in capelin. In this connection we consider it to be more than chance that the density of larvae/ m^3 in nearshore collections at Bryant's Cove was 60% greater in 1979 when the frequency of onshore wind events was 50% greater than in 1978 over a comparable time period, and when egg deposition in the 2 years was similar. This reduction in larval density is fully consistent with the decrease in the proportion of larvae in good condition in the intertidal zone over the range of times between onshore wind events recorded in 1979 (Fig. 8B). It is also possible that year-to-year differences in the major wind patterns could, through their influence on larval survival, contribute to the large annual variation in year-class strength in capelin. Templeman's (1948) survey of beach spawning sites in

Newfoundland indicates that the great majority of the capelin beaches have an easterly exposure. Anomalous shifts in wind patterns could thus influence survival over large geographic areas. The geographic extent of this influence would be further magnified if, as the data of Carscadden and Misra (1980) suggest, the spawning population of insular Newfoundland constitutes a single stock. It is clear, however, that wind effects are only one of a number of factors influencing year-class strength since, in recent years, two year-classes (the 1969 and 1973 year-classes) have been strong from all areas in the Northwest Atlantic including the predominantly deepwater spawning population on Newfoundland's west coast (1973 year-class only because of lack of data) and the offshore spawning population on the Southeast Shoal (Carscadden and Miller 1979, 1980) which would be less, if at all, influenced by wind events.

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