

Meteorological and Hydrographic Regulation of Year-Class Strength in Capelin (*Mallotus villosus*)¹

W. C. Leggett

Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Que. H3A 1B1

K. T. Frank

Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

and J. E. Carscadden

Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, Nfld. A1C 5X1

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Year-class strength (YCS) in eastern Newfoundland stocks of capelin (*Mallotus villosus*), a beach spawning osmerid, during the interval 1966–78 was strongly influenced by onshore wind frequency during the period immediately following hatching (WIND) and water temperatures experienced during the subsequent period of larval drift (TEMPSUM). The exact form of the relationship was $\ln YCS = 16.10 - 0.19WIND + 0.19TEMPSUM$, $R^2 = 0.58$. Wind conditions subsequent to hatching are known to influence both the timing of larval emergence from the beach spawning beds and the physical condition of larvae at emergence. Our analysis suggests that the influence of wind on early larval survival is also strong. The role of water temperatures during drift may be indirect, operating via its influence on food production. This could operate by altering mortality rates due to starvation or by altering growth rates which would influence swimming performance, predator avoidance, and time to metamorphosis. The strong influence of these abiotic variables, independent of parent stock size, adds further support to the hypothesis that abiotic factors operating at critical periods in larval development may be more important than spawning stock biomass as regulators of year-class size. Our findings also suggest that these critical periods must be identified and quantified at time scales relevant to individual larvae if reliable forecasting of year-class strength is to be achieved. On the other hand, the large spatial scale of the effects suggests that the space scale of individual larvae is of lesser importance in such analyses.

L'importance des classes d'âge (YCS) des stocks de capelan (*Mallotus villosus*) de l'est de Terre-Neuve, un osméridé frayant sur les plages, a beaucoup dépendu, de 1970 à 1978, de la fréquence des vents du large lors de la période suivant immédiatement l'éclosion (WIND) ainsi que de la température de l'eau pendant la dérive ultérieure des larves (TEMPSUM). La forme exacte de cette relation était $\ln YCS = 16,10 - 0,19WIND + 0,19TEMPSUM$, $R^2 = 0,58$. On sait que les vents ultérieurs à l'éclosion influent sur l'état des larves et le moment de leur émergence des lits de frai des plages. Notre analyse indique que les vents ont aussi une forte influence sur la survie des jeunes larves. Le rôle de la température de l'eau lors de la dérive pourrait être indirect, celle-ci agissant sur la production de nourriture. Cette action pourrait prendre la forme d'une augmentation des taux de mortalité par inanition ou d'une modification du taux de croissance qui influencerait sur la capacité de nage et d'évitement des prédateurs ainsi que sur la période de pré-métamorphose. La forte influence de ces variables abiotiques, indépendantes de la taille du stock parental, vient renforcer l'hypothèse voulant que des facteurs abiotiques agissant à des moments critiques du développement larvaire peuvent être plus importants que la biomasse du stock de frai comme régulateur de la classe annuelle. Nos résultats portent aussi à croire qu'une prévision fiable de la classe annuelle ne pourra être obtenue qu'en déterminant et quantifiant ces périodes critiques aux échelles temporelles des larves elles-mêmes. L'importante échelle spatiale de ces effets donne cependant à croire que l'échelle spatiale des larves elles-mêmes est moins importante lors de telles analyses.

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Forecasting recruitment to mature or exploitable stocks has long been a central problem in fishery research. Stock-recruitment models have dominated this field since Ricker's (1954) classic treatment of the subject. These

models are based exclusively on biological interactions, integrate the entire life history into a single prerecruit class, and ignore potentially important abiotic influences on recruitment processes (Bakun et al. 1982). This may, in part, explain their relatively poor predictive power, although Walters and Ludwig (1981) have recently demonstrated that the approach also has statistical problems, the principal difficulty being unknown error in the independent variable (parent stock size).

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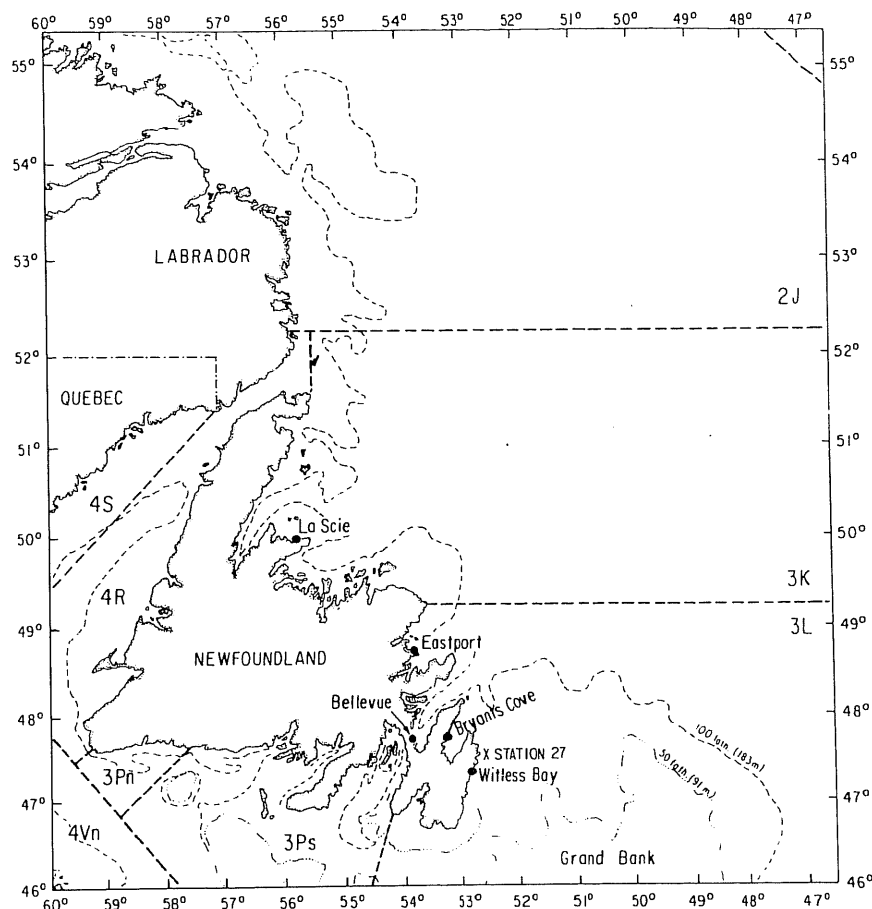


FIG. 1. Locations of NAFO areas 2J, 3K, and 3L and of sampling sites for water temperatures. Approximate northern limit of the Grand Banks is determined by the 100-fathom contour north of Bryan's Cove.

Investigators have made several attempts to account for variance in recruitment by examining the effect of abiotic factors. For example, Nelson et al. (1977) demonstrated that onshore Ekman transport of larvae explained a significant portion of the residual variance about the stock recruitment model for Atlantic menhaden (*Brevoortia tyrannus*); Bailey (1981), using a multiple regression approach, found that spawning stock biomass and the intensity of offshore Ekman transport during larval drift were the major regulators of year-class strength in Pacific hake (*Merluccius productus*); Leggett (1977) showed that water temperature during the immediate post spawning period was an important cause of residual variance in the stock-recruitment model for American shad (*Alosa sapidissima*) in the Connecticut River; and Chadwick et al. (1977) demonstrated the importance of river discharge as a regulator of year-class variations in striped bass (*Morone saxatilis*) in the Sacramento River, California. While this approach leaves unresolved the problem of unknown error in the independent variable, these studies, and others, did highlight the potential importance of abiotic regulators of year-class strength in fishes.

Concurrently, the importance of abiotic factors as regulators of a variety of other biotic processes in both freshwater and marine systems has become apparent. In coastal systems in particular, short-term (days to weeks) and long-term (months to

years) variation in the distribution, abundance, and production dynamics of a variety of organisms from plankton to whales have been related to the impact of large-scale meteorological influences on the ocean environment (seals, whales, and sea birds, Sergeant 1982; phytoplankton community structure, Lasker 1978; Côté and Platt 1983; zooplankton community structure, Frank and Leggett 1982b; phytoplankton biomass and production, Walsh et al. 1977, 1978; and fish production and biomass, Sutcliffe 1972; Haymand and Tyler 1980; Clark et al. 1975).

The capelin (*Mallotus villosus*), a key forage species in the Northwest Atlantic ecosystem (Bailey et al. 1977), exhibits large year to year variations in year-class strength. Year-class strength in the Northwest Atlantic Fishery Organization (NAFO) 2J3K stock (Fig. 1, 3) has been estimated to vary over 37-fold during the interval 1972–80 (Carscadden and Miller 1981). These large variations in capelin abundance, coupled with its importance as a prey species, have led to considerable interest and expectation that changes in capelin abundance would impact on the abundance and distribution of predators and potential competitors (Carscadden 1983a), as has been reported for other marine ecosystems (Daan 1978). While quantitative information is limited, some possible interactions have been identified in the case of squid (*Illex illecebrosus*) and arctic cod (*Boreogadus saida*, Vesin et al. 1981); Atlantic cod

(*Gadus morhua*, Akenhead et al. 1982); and Atlantic salmon (*Salmo salar*, Reddin and Carscadden 1981; Carscadden and Reddin 1982).

It has now been demonstrated for several fish populations that year-class strength is largely determined by the end of the larval period and that all age groups subsequently remain roughly proportional to the annual abundance of the fingerling cohort (see Cushing 1975; Dragesund and Nakken 1973; Chadwick et al. 1977; Leggett 1977). Meteorological factors, principally air temperature, solar radiation, and wind direction, together with water temperature, are major regulators of egg development rate and mortality in capelin (Frank and Leggett 1981a, 1981b). In turn, beach residence time in capelin is determined by the length of the interval between onshore winds, which trigger larval emergence (Frank and Leggett 1981a, 1982a). Larval condition at the onset of drift, and hence survival, is a negative function of beach residence time (Frank and Leggett 1981a). Food availability during drift is also widely held to be an important regulator of survival in pelagic fish larvae (Lasker 1975, 1981). Water temperatures are directly correlated with rates of biological production and thus with food availability (Eppley 1972; Tranter 1976).

These facts led us to speculate that the large-scale variations in year-class strength in capelin, which occur synchronously in populations in the eastern Newfoundland region, are due to the effect of large-scale meteorological and hydrographic variability acting directly and indirectly on the survival of larval capelin. This idea was strengthened by observed differences in the apparent survival of the 1978 and 1979 larval cohorts at our Bryant's Cove, Conception Bay, Newfoundland, study site and its correlation with year-class strength. Capelin egg densities were similar in 1978 and 1979 but larval emergence into the nearshore area was 60% higher in 1979. The frequency of onshore winds was 50% higher in 1979 resulting in shorter larval residence times. The 1979 year-class appears to be much stronger than the 1978 year-class and dominated the mature portion of the population in 1982 (Carscadden 1983b).

In this paper we report the results of a study conducted to evaluate the hypothesis that year to year variation in year-class strength of capelin is influenced by meteorological and hydrographic conditions. We examined the effects of (1) the frequency of occurrence of onshore winds during the period immediately following hatching and (2) the water temperatures experienced subsequent to the onset of larval drift on year-class strength in capelin. The analysis relates to the capelin stocks occupying the NAFO Divisions 2J and 3K (Fig. 1).

Methods

Our analysis is based on linear regression models incorporating the interval between onshore wind events during the period of beach residence by larval capelin, and water temperatures during larval drift, as independent variables and the natural logarithm of abundance of 2-yr-old capelin as the dependent variable. Nonlinear models were evaluated but proved to be inferior.

Model Development

Wind

A central assumption of the wind regulation hypothesis is that cyclonic atmospheric pressure systems generating onshore winds (and the related coastal water mass exchange that triggers

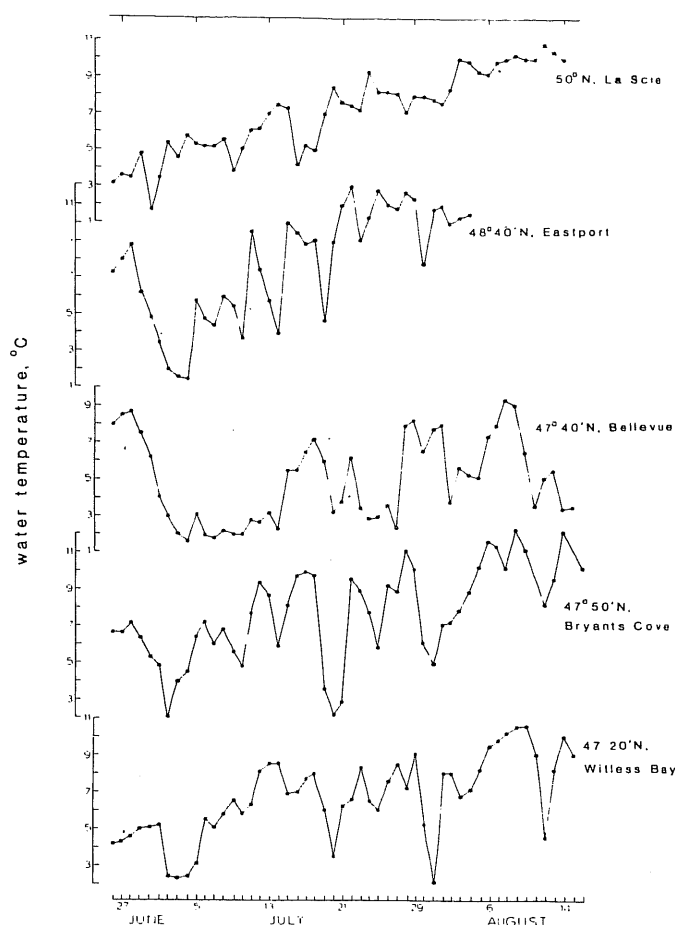


FIG. 2. Nearshore water temperatures at five capelin beach spawning sites in eastern Newfoundland, 26 June–14 August 1982.

larval emergence, Frank and Leggett 1982b, 1983) are large enough to synchronously influence water mass exchange over a large area of Newfoundland's east coast. Simultaneous recording of nearshore water temperatures at five beach spawning sites ranging over 4°40' of latitude and ~700 km of coastline (Fig. 1) during 26 June–14 August 1982 shows this to be true (Fig. 2). Major changes in nearshore water temperatures, indicative of wind-driven water mass exchange, were virtually synchronous at all sites. The transition from rising to falling water temperatures (offshore winds) or falling to rising water temperatures (onshore winds) seldom varied by more than 1 d (Fig. 2). Larval emergence data for one of these sites, Eastport, Bonavista Bay, show a significant positive relationship between larval emergence and onshore winds ($r^2 = 0.53$) (Fig. 2). The timing of emergence was also synchronous with the daily larval emergence pattern at Bryant's Cove, Conception Bay ($r^2 = 0.62$). We have previously shown that onshore winds generate similar emergence patterns at widely separated sites and over long time periods (Frank and Leggett 1981a).

Daily wind data used in the analysis were obtained from monthly wind summaries for the St. John's, Newfoundland, meteorological station published by Environment Canada. Spawning dates and egg development rates vary between years (Frank and Leggett 1981b). This causes annual differences in the time of median hatching and hence in the timing of the critical period for larval emergence. We determined the annual timing of median hatching, and hence the critical period for

larval emergence by adding the estimated egg development time to the observed or estimated spawning data for each year. Spawning dates in the St. John's–Conception Bay area are known from direct observation for the years 1966–69 and 1972–82 (range 7 June–25 June). No latitudinal trend in spawning time within years is evident in the area under consideration (Frank and Leggett 1981b). We therefore assumed spawning dates to be synchronous over the coast. While this is not strictly true (differences of 1 or 2 d occur even within local areas), the assumption creates no systematic bias.

Spawning dates in 1970 and 1971, which were unknown, were estimated from an empirical relationship between observed spawning date (Julian days) and cumulative growing degree-days (GDD > 5°C measured from April 1 at St. John's, Newfoundland) for the years 1966–69 and 1972–81. The method used was similar to that employed by Burgner (1980) and Colby and Nepszy (1981) to predict spawning times and maturity rates in Pacific salmon and walleye (*Stizostedion vitreum vitreum*), respectively. We plotted spawning date (Y) against the equivalent growing degree-day value (X) for each year. The plot yielded a vertical cloud of points with high Y -axis variance (mean 16.5 June, 95% C.I. 12.5 June–20.6 June) and restricted X -axis variance (mean 139.5, 95% C.I. 124.3–154.7). One Julian day in the latter half of June equates to approximately 10 degree-days. Spawning date in capelin can therefore be predicted to within 3 d from a knowledge of growing degree days. We equated spawning dates in 1970 and 1971 with the Julian dates most closely approximating the mean (139.5) degree-day value for the interval 1966–82 (1970: 17 June = 144.2°C-d; 1971: 2 June = 140.1°C-d).

Egg development rates are strongly and positively related ($r^2 = 0.89$) to average incubation temperatures in the beach gravel (Frank and Leggett 1981b). Daily incubation temperatures can be predicted from the equation (Frank and Leggett 1981b)

$$Y = 0.607x_1 + 0.348x_2 + 0.392x_3 + 0.142x_4 - 0.297, \quad R^2 = 0.76$$

where Y = incubation temperature (degrees Celcius), x_1 = water temperature (degrees Celcius), x_2 = hours of bright sunlight per day, x_3 = minimum daily air temperature (degrees Celcius), and x_4 = maximum daily air temperature (degrees Celcius).

This equation predicts incubation temperatures near the high tide zone on the beach where temperatures are highest (Frank and Leggett 1981b). We chose to use the high tide estimator because (1) egg densities are greatest at the high tide zone and (2) the analysis is conservative: larvae hatching slightly later from the mid and low tide zones are automatically included in the wind analysis. Daily incubation temperatures were estimated using meteorological data from the St. John's, Newfoundland, meteorological station of Environment Canada. Data from this station for 1978 and 1979 were originally used to develop the predictive equation given above. The observed or estimated spawning date was used as the starting point for this calculation and the average incubation temperature was taken as the mean of estimated daily temperatures over the following 14 d. Average incubation temperatures varied between 8 and 15°C during the period 1966–78.

Mean time to hatching (range 12–18 d during 1966–78) was derived from the equation (Frank and Leggett 1981b)

$$\ln y = 4.29 - 0.63 \ln(x + 1), \quad r^2 = 0.89$$

where y = hatching time (days) and x = average incubation temperature (degrees Celcius).

The maximum time interval between onshore winds (defined as all winds oriented north through east) during the 10-d period immediately following the estimated annual median hatching date was used as the wind input to the model. This value ranged from 2 to 10 d (mean 4.4 d). The north through east wind orientation was established a priori based on the orientation of the coastline in the 2J3K areas and the fact that onshore winds generated by large-scale frontal systems fall predominantly within this vector field. Subsequent statistical evaluation of other vectors revealed that the north through east vector yielded the highest explained variance. The addition of wind strength and duration to the model did not add significantly to the variance explained.

Water temperature during drift

Once released from the beach gravel into the pelagic environment larval capelin are quickly and passively transported into offshore waters (Fortier and Leggett 1982; C. Taggart and W. C. Leggett, unpubl. data) where they feed and grow (Jacquaz et al. 1977). During the next few months they are largely restricted to the top 20 m of the water column (Jacquaz et al. 1977; Fortier and Leggett 1982, 1983).

Water temperatures used in the model are based on data recorded at station 27 (47°32'50"N, 52°35'10"W), 2 nautical miles (3.7 km) off Cape Spear near St. John's, Newfoundland (Akenhead 1983). This is the only northwest Atlantic hydrographic station for which a reliable, uninterrupted temperature time series is available (Akenhead et al. 1982). The Labrador current is the dominant hydrographic feature of the Newfoundland–Labrador area. Hence, temperatures recorded at station 27 reflect temperature trends in the area under consideration. This assumption is supported by our earlier finding (Frank and Leggett 1981b) that mean monthly sea surface temperatures varied less than 1°C over the range latitude 47–54°N during the period 1976–80. Furthermore, Poletayev (1979) has shown that by September the distribution of capelin larvae centers on the northern portion of the Grand Banks and, as a result, is in close proximity to the position of hydrographic station 27 during this phase of the life cycle (see Fig. 1). The exact form of the temperature variable, which is labelled TEMPSUM, was the sum of these monthly means (0–20 m) for the period July–December. This we have taken as an integrated measure of the thermal conditions experienced by larvae during larval drift and feeding. Winters (1983) employed a similar TEMPSUM index, also derived from station 27 data, to demonstrate the influence of annual temperature variability on the growth rates of sand lance (*Ammodytes dubius*) in the Grand Banks region.

Capelin abundance

Annual estimates of the abundance of 2-yr-old capelin for the 2J3K stock (Fig. 3) during the years 1970–78 are based on sequential cohort analysis. Abundances of the 1966–69 year-classes as 2-yr-olds were calculated from the estimates of the abundance of age groups 3–6 in 1972. This calculation used estimates of natural mortality rate and instantaneous spawning mortality identical to those employed in the sequential cohort analysis performed by Carscadden and Miller (1981). We assumed no fishing mortality in these years, since catches in 1966–69 averaged less than 2000 t as compared with 200 000 t during the mid-1970's.

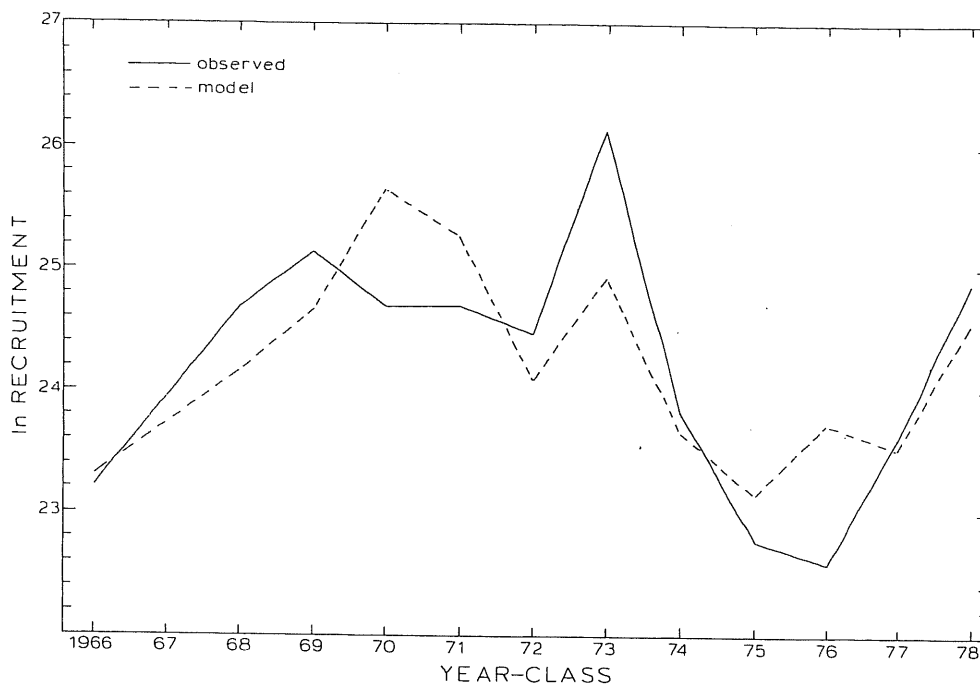


FIG. 3. Recruitment (1966–78 year-classes as 2-yr olds, from Carscadden and Miller 1981: table 7) and recruitment predicted from the model for Division 2J3K capelin stock.

Results and Discussion

The Model

Several forms of linear regression models incorporating the independent variables WIND and TEMPSUM were evaluated. In all models tested, year-class strength was transformed to natural logarithms (Hennemuth et al. 1980). The specific relationship yielding the highest explained variance between the natural logarithm of year-class strength (YCR) of 2-yr-old capelin, TEMPSUM, and WIND for the 2J3K stock was $\ln YCS = 16.10 - 0.19WIND + 0.19TEMPSUM$ ($R^2 = 0.58$, Table 1; Fig. 3). Data for 1967 were excluded from these analyses because the TEMPSUM value for this year deviated greatly from all other values in our time series. For the time series used in our analysis (1966–78) TEMPSUM values ranged from 42.40 to 51.18 except for 1967, which was 58.62. We examined a longer time series (33 yr) and found that 30 of the 33 values ranged from 39.01 to 53.38. Of the remaining TEMPSUM values, one was very low (1957 = 36.30) and two were high (1961 = 56.03 and 1967 = 58.62). Inclusion of the 1967 data greatly reduced the variance accounted for by the model ($R^2 = 0.24$). The sign of the regression coefficient for WIND was always negative, while that for TEMPSUM was always positive (Table 1). These trends are consistent with the demonstrated negative effect of increased wind interval on larval condition at emergence (survival) and the assumed positive influence of increased temperature on food availability to the larvae. Univariate analyses showed that the WIND and TEMPSUM variables were approximately equivalent in their contribution to explained variation in year-class strength (WIND, $r^2 = 0.38$; TEMPSUM, $r^2 = 0.43$).

The negative relationship between WIND and year-class strength suggests that strong year-classes are derived from the frequent release of discrete batches of good-condition larvae from the beach gravel. These batches of larvae are, in essence, cohorts that exhibit strong coherence in their time of formation

TABLE 1. Results of model relating recruitment (ln) to Division 2J3K capelin as 2-yr-olds to WIND and TEMPSUM (* $p < 0.05$).

Dependent variable: recruitment as 2-yr-olds (ln)				
	df	Sum of squares	F value	r^2
Model	2	6.97	6.25	0.58*
Error	9	5.01		
Total	11	11.98		

Independent variables: WIND and TEMPSUM (Y-intercept = 16.098)

	Regression coefficient	t^a	SE	Partial r
WIND	-0.187	-1.78	0.1049	-0.51
TEMPSUM	0.194	2.09	0.0928	0.57

^aThe t values were derived to test the null hypothesis that the true value of the coefficient is equal to zero.

over large spatial scales in response to broad-scale onshore wind events. When relatively high water temperatures coincide with frequent releases, survival rate per cohort is expected to be high. This possibility is supported by the observation that the July and August mean monthly temperatures are more strongly correlated with TEMPSUM ($r^2 = 0.84$ and $r^2 = 0.73$, $n = 17$, respectively) than are the mean temperatures for other months (range of $r^2 = 0.32$ – 0.58). Substituting the July or August mean monthly temperature for TEMPSUM as an independent variable in the recruitment model did not, however, improve the fit of the model ($R^2 = 0.52$ and 0.39 for July and August, respectively).

This relationship between temperature and wind effects was further evaluated by running the model using a range of

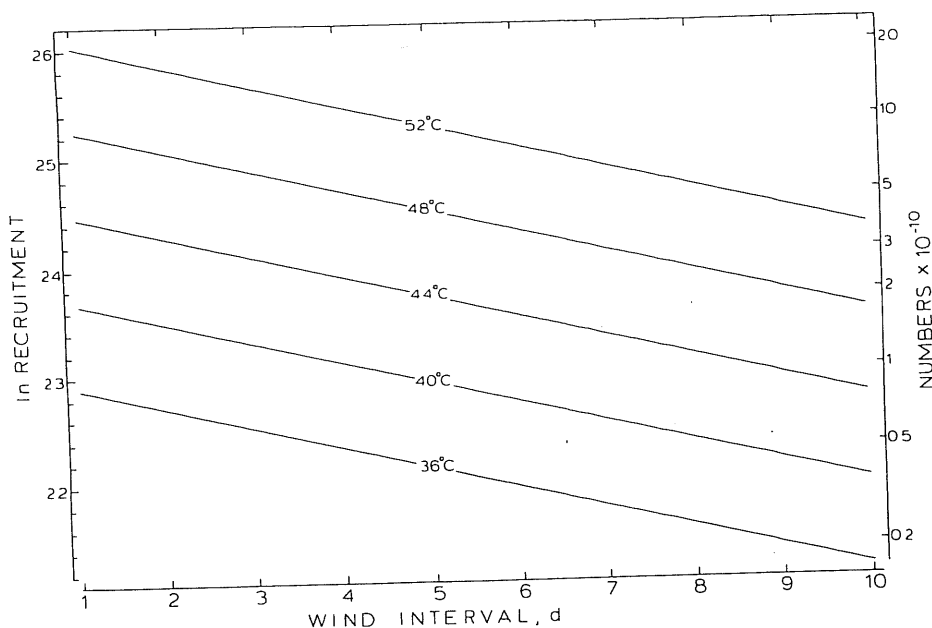


FIG. 4. Division 2J3K model run using a range of empirically derived WIND values at fixed TEMPSUM values.

empirically derived annual estimates for WIND and a range of fixed TEMPSUM values (Fig. 4). The analysis suggests that, given the range of temperatures and wind conditions experienced during the interval 1966–80, the length of the interval between onshore winds becomes progressively less critical to year-class formation as TEMPSUM increases.

The Biological Basis of Year-Class Variation

These analyses indicate that abiotic variables, specifically the frequency of onshore winds during the immediate posthatching period and water temperatures experienced during larval drift, are the most important ultimate regulators of year-class strength in capelin in eastern Newfoundland. In the 2J3K stock 58% of the year to year variation in year-class strength was accounted for by these two factors.

The most probable proximate cause of wind-related variation in year-class strength is deterioration in physical condition of larvae prior to emergence from the beach gravel. Yolk sac absorption is rapid, ranging from 3 to 8 d (mean 5.5) at the high- and mid-tide beach locations depending on temperature conditions (Frank and Leggett 1982a). Larval emergence is keyed to the occurrence of onshore winds, presumably because of survival advantages conveyed by increased food abundance and reduced predator densities created by the water mass exchange induced by such conditions (Frank and Leggett 1982b, 1983). When the interval between onshore winds exceeds that required for complete yolk sac absorption larval condition deteriorates rapidly (Frank and Leggett 1982a). If prolonged offshore wind conditions are coupled with high beach gravel temperatures, direct mortality prior to emergence may be high. This effect was apparently responsible for the four lowest levels of recruitment observed during the time series (1966, 1975–77) when the wind interval ranged from 5.5 to 10 d. Even under less severe conditions larval survival can be negatively influenced by wind interval. Frank and Leggett (1981a) found that the proportion of larvae in poor condition declines rapidly in samples taken progressively farther from the release site. This suggests that larvae weakened by prolonged beach residence are quickly lost

from the population. Swimming ability is directly coupled to larval condition (Frank and Leggett 1982a). Depressed swimming ability can reduce both predator avoidance (Bams 1967; Lillelund and Lasker 1971; Theilacker and Lasker 1974; Hunter 1972) and feeding success (Laurence 1972; Rosenthal and Hempel 1970; Ware 1975). This may explain, in part, the higher loss rates of weakened larvae subsequent to emergence.

The evidence available also supports our working hypothesis that the proximate basis for the influence of TEMPSUM on year-class strength is the effect of water temperature on plankton production. As noted previously the Labrador Current dominates the hydrographic characteristics off eastern Newfoundland resulting in quite similar temperature conditions over large areas. We found TEMPSUM to be strongly correlated with cumulative growing degree-days at St. John's, Newfoundland, measured from April 1 to August 31 ($y = 11.32 + 0.40x$, $r = 0.86$, $n = 17$). We have previously documented a significant ($p < 0.01$) positive relationship between the biomass of zooplankton and growing degree-days (Frank and Leggett 1982b: table 2, fig. 7). During the interval 1964–81 cumulative growing degree-days (April 1–August 31) at St. John's varied from 660 to 1060. Applying these results to our earlier analysis (Frank and Leggett 1982b) indicates that this variation could result in an approximate 250% change (8.5 – $29.5 \text{ mg} \cdot \text{m}^{-3}$) in the biomass of zooplankton $< 250 \mu\text{m}$, the principal prey of first feeding larvae, over the period in question. Enclosure experiments employing first feeding larvae indicate a strong positive relationship between larval growth rate (millimetres per day) and the biomass (milligrams per cubic metre) of zooplankton $< 250 \mu\text{m}$ ($y = 0.0337 \ln x - 0.0658$, $r^2 = 0.62$, $p < 0.01$; Frank and Leggett 1982b). The variation in edible zooplankton caused by annual differences in water temperatures could thus cause a variation of up to 100% in growth rate of first feeding larvae. The biomass of zooplankton $> 250 \mu\text{m}$ could vary up to 700% based on relationships between this size fraction and degree-days given in Frank and Leggett (1982b: table 2). This size fraction is presumably an important food component for later stage larvae and could similarly influence growth rates. The effect of such food variation on larval survival could be

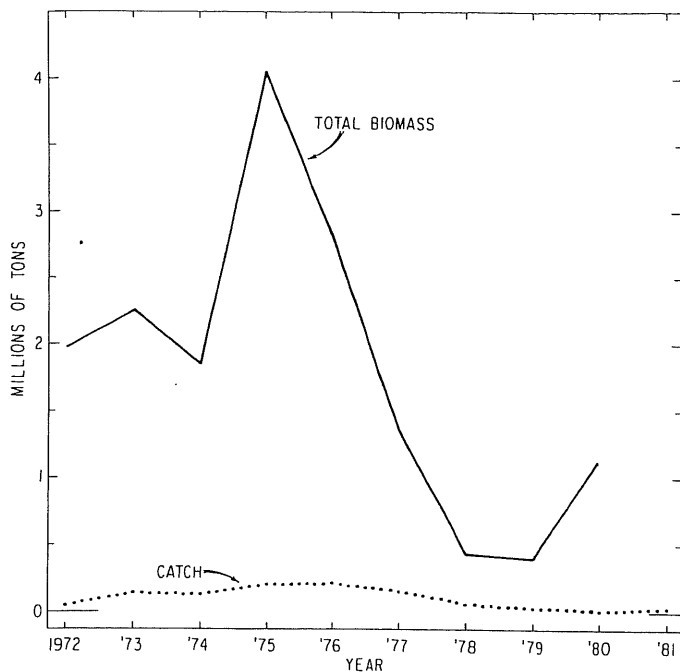


FIG. 5. Estimated total capelin biomass (age 2+, 1972–80, from Carscadden and Miller 1981) and annual catches (1972–81) for the Division 2J3K capelin stock.

direct or indirect. The occurrence of favorable food conditions has long been considered an important direct regulator of larval survival in fishes (Cushing 1975; Lasker 1975). In addition, larval growth rates have frequently been implicated in predator avoidance (Ware 1975; Marak 1960; Sysoeva and Degtereva 1965; Sherman and Honey 1971) and foraging ability (Rosenthal and Hempel 1970; Blaxter and Staines 1971; Hunter 1972). More recently, Policansky (1982) has shown that the onset of metamorphosis in flounders (*Platyichthys stellatus*) is more strongly linked to size than age. If this is a general result, rapid growth under favorable feeding conditions may also operate to shorten the larval period, thereby increasing survival during the larval phase.

Recent Changes in Capelin Abundance — Over Exploitation or Recruitment Failure?

Sequential cohort analyses for the capelin stock occurring within NAFO Divisions 2J and 3K reveal a pronounced increase in total capelin biomass between 1974 and 1976 followed by a more dramatic decline between 1976 and 1979 (Fig. 5). It is only in the last decade that man has become a significant predator of capelin although capelin have been taken on and near the spawning beaches for generations. Prior to the 1950's, 20 000–25 000 t of capelin were taken annually in Newfoundland and Labrador for bait, fertilizer, and food for dog teams (Templeman 1968; Barnes 1974). During the early 1970's commercial exploitation of capelin by an international offshore fleet increased to approximately 200 000 t. The dramatic decline in total capelin biomass in 2J3K coincident with this increase in catch resulted from poor year-classes (Fig. 3), some of which were produced during the periods of relatively high capelin catches. This relationship implicated fishing as a major factor in the decline of the capelin stocks during the last half of the 1970's. However, total catch was small in relation to estimated total biomass throughout the period (Fig. 5). The results of our analysis argue against overfishing as the major factor in recent

fluctuations in capelin biomass. Rather, recruitment failure resulting in a series of progressively weaker year-classes between 1974 and 1977 appears to have been a major contributor to the decline in total capelin biomass between 1977 and 1979. We believe the most probable cause of this recruitment failure was the occurrence of unfavorable meteorological and hydrographic conditions during and subsequent to larval emergence from the beach gravel.

The correlation ($Y_{int} = 0.003$, slope = 0.99, $r = 0.76$) between predicted and observed year-class strength for 2J3K capelin over the period 1966–78, in the absence of considerations of parent stock size, emphasizes the importance of factors relevant to the survival of individual fish at various key stages in their development to year-class formation. Such factors may, in fact, greatly outweigh the importance of parent stock size as the prime determinant of recruitment success. We believe a more systematic approach to the identification of these key stages in the early life history of other species could yield similar positive results. Of central importance is a quantitative knowledge of the variable(s) regulating survival during these "critical periods." With such knowledge reliable forecasts of future abundance should be possible given careful monitoring of relevant variables at appropriate time and space scales. The long-term inadequacy of several previously derived environmentally determined recruitment models (Gulland 1953, 1965; Bell and Pruder 1958) may result from their failure to conform to this scalar requirement. As a result they are unable to accommodate interannual or longer term shifts in the timing of important phenological events such as spawning times, development rates, and the timing of the initiation of drift which can significantly alter the timing of key responses to changing environmental conditions.

The approach we have described is not, however, without problems. The apparent precision in estimates of the timing of critical periods is subject to the compounding of errors due to the sequential dependency of empirical models used in their derivation. Such errors are no less important than those identified by Walters and Ludwig (1981) in the case of traditional recruitment models. Moreover, the errors in estimates of year-class size remain. For this reason the number of such sequential steps used to "time" the key developmental periods should be kept to a minimum and every effort should be made to minimize the unexplained variance in the intermediate level models employed. The major advantages of our approach are that the relevant parameters are easily measurable and that the model is open ended in the sense that greater complexity can be incorporated, if necessary, as additional key variables are identified without resorting to an entirely new model. This derives from the fact that the model is based on realistic biological mechanisms rather than a simple empirical fit to the data (Roff 1983).

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