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Estimating Year-Class Strength in Capelin (Mallotus villosus) From Abiotic Variables

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INTRODUCTION

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 and fail to incorporate potentially important abiotic influences on recruitment processes. This may, in part, explain their relatively poor predictive power, although Walters and Ludwig (1981) have recently demonstrated that the approach is also fraught with statistical difficulties, the principal problem being unknown error in the independent variable (parent stock size).

Several investigators have attempted to account for the unexplained variance in stockrecruitment models by examining the relationships between residuals and a variety of abiotic factors. For example, Nelson et al. (1979) demonstrated a significant positive effect of onshore Ekmann transport of larvae on recruitment success in Atlantic menhaden; Bailey (1981) reported a negative relationship between the intensity of offshore Ekmann transport and year-class-strength in Pacific hake; 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) have demonstrated the importance of river discharge as a regulator of year class variations in striped bass (Roccus americanus) in the Sacramento River, California. While these approaches left unresolved the problem of unknown error in the independent variable, they, 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 (days to weeks) and long (months to years) term 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, Coté 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; Hayman and Taylor 1980; Clark et al. 1975).

The capelin (<u>Mallotus villosus</u>), a key element of the Northwest Atlantic ecosystem (Bailey et al. 1977) exhibits large year to year variations in year-class-strength. Year-class-strength in the NAFO* 2J3K stock (Figure 1,3) has varied over 37 fold in the interval 1972-1980 (Carscadden and Miller 1981). These large variations in capelin abundance, coupled with its importance as a prey species, have led to considerable interest and speculation concerning the effects of changes in capelin abundance on the abundance and distribution of predators and potential competitors. While little quantitative information is available, some evidence of interactions has been identified in the case of squid (<u>Illex illecebrosus</u>) and arctic cod (<u>Boreogadus saida</u>, Vesin et al. 1981); Atlantic cod (<u>Gadus morhua</u>, Akenhead et al. 1982); and Atlantic salmon (<u>Salmo salar</u>, Reddin and Carscadden 1981, Carscadden and Reddin 1982).

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It is now well accepted that in many fish populations year-class-strength is determined by the end of larval development, and that all age groups subsequently remain roughly proportional to the annual abundance of the fingerling cohort (see 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,b). Residence time of larvae in the beach gravel is also inversely proportional to frequency of occurrence of onshore winds. If residence time is long larval condition deteriorates rapidly (Frank and Leggett 1982a). These facts led us to hypothesize that the large scale variations in year-classstrength in capelin, which occur synchronously in populations in the eastern Newfoundland region, and the "ripple effects" that may occur in other species are due to the effect of large scale meteorological variability 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 also 50% higher in 1979 resulting in shorter larval residence times. Mature fish from the 1979 year class appeared in the fishery in 1982 and the year class appears to be much more abundant than others recently experienced.

In this paper we report the results of a study conducted to evaluate the hypothesis that year to year variation in year-class-strength in capelin is strongly influenced by meteorological and hydrographic conditions. The analysis relates to the capelin stocks occupying the NAFO Divisions 2J3K and Division 3L (Figure 1).

METHODS

We examined the influence of two possible regulators of year-class-strength in capelin: 1) the frequency of onshore winds during the period immediately following hatching; and 2) the water temperatures experienced subsequent to the onset of larval drift. Onshore winds were examined because of their demonstrated effect on the beach residence time of larvae and their physical condition at the onset of larval drift (Frank and Leggett 1981 a,b). Water temperatures experienced during larval drift were examined because of the known positive relationship between water temperatures and biological production which could influence the quantities of food available to the larvae during drift. Food availability is widely held to be an important regulator of survival in pelagic fish larvae (Cushing 1975).

Our analysis is based on a linear regression model incorporating the frequency of onshore winds and water temperature as independent variables and abundance of two-year-old capelin (2J3K) and 3 year old capelin (3L) as the dependent variables. Non-linear models were evaluated but proved inferior.

MODEL DEVELOPMENT

a) Wind

A central assumption of the wind regulation hypothesis is that pressure systems generating onshore winds (and the related coastal water mass exchange that triggers larval emergence, Frank and Leggett 1982b, in press) 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 $2^{\circ}40'$ of latitude (Figure 1) during 26 June - 14 August 1982 show this to be true (Figure 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 (offshore winds) or falling to rising (onshore winds) water temperatures seldom varied by more than one day (Figure 2). Data for Eastport, Bonavista Bay, show a significant positive relationship between larval emergence and onshore winds ($r^2 = 0.53$), as has been previously documented for Bryant's Cove and other Newfoundland spawning sites (Frank and Leggett 1981a). Analysis of larval emergence data for the other sites is not yet complete.

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. It was therefore necessary to determine the <u>annual</u> timing of this critical period in order to establish the appropriate wind intervals to be considered. This was done by adding the estimated egg development time to the observed or estimated spawning date for each year. Spawning dates in the St. John's -Conception Bay area are known from direct observation for the years 1966-1969 and 1971-1982 (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 (small differences occur even within local areas) the assumption creates no systematic bias. Spawning dates in 1964-65 (3L) and 1970-71 (2J3K) were estimated from an empirical relationship between observed spawning date (Julian days) and cumulative growing degree days (°C measured from April 1 at St. John's, Newfoundland) for the years 1966-1969 and 1972-1981. The method used was similar to that employed by Burgner (1981) spawning date (Y) vs growing degree days (X). 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 June equates to approximately 6 degree days. Spawning date in capelin can therefore be predicted to within 5 days 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 1966-1982 (1964: 18 June 139.5; 1965: 27 June 143.4; 1970: 17 June 144.2; 1971: 2 June 140.1).

Egg development rates are positively related to average incubation temperatures in the beach gravel (Frank and Leggett 1981b). Daily incubation temperatures can be predicted from the equation: Y = $0.607 x_1 + 0.348 x_2 + 0.392 x_3 + 0.142 x_4 - 0.297 (r^2 = 0.76$, Frank and Leggett 1981b)

where Y = incubation temperature (°C) x_1 = water temperature (°C) x_2 = hours of bright sunlight

 x_3^2 = minimum daily air temperature (°C) x_4 = maximum daily air temperature (°C).

This equation predicts incubation temperatures near the high tide zone. Incubation temperatures vary with position on the beach being highest at the high tide zone (Frank and Leggett 1981b). We chose to use the high tide estimator because a) egg densities are greatest at the high tide zone and b) 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. Average incubation temperatures were derived from these data for each year. The observed or estimated spawning date was used as the starting point for this calculation and the average incubation temperatures over the following 14 days. Average incubation temperatures varied between 8 and 15°C during the period 1964-1978.

Mean time to hatching, (range 12 to 1/8 days during 1964-1978) was derived from the equation ln Y = 4.29 - 0.63 ln (x + 1) (r² = 0.89, Frank and Leggett 1981b)

where: y = hatching time in days

x = average incubation temperature (°C)

The maximum time interval between onshore winds (north through east) during the 10 day period immediately following the estimated annual median hatching date was the value used for the wind input to the model. This value ranged from 2-10 days (mean 4.4 days). the north-through-east wind orientation was established a priori based on the orientation of the coastline in the 2J3K and 3L areas. Subsequent evaluation of other vectors revealed that the north through east vector yielded the greatest explained variance.

b) 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; Taggart and Leggett, unpublished 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 1983, in press). To assess the effects of water temperatures during larval drift on year class formation we calculated the average monthly temperatures in the 0-20 m depth interval off eastern Newfoundland and used this value as the temperature input to the model.

Water temperatures used in the model are based on data recorded at Station 27 (47°32'50"N; 52°35'10"W) located in Division 3L, 2 nautical miles off Cape Spear near St. John's, Newfoundland. 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-Lab rador area which includes Divisions 2J3K, 3L. Hence, temperatures recorded at Station 27 reflect temperature trends in the areas under consideration. This assumption is supported by our earlier finding (Frank and Leggett 1981b) that mean sea surface temperatures varied less than 1°C over the range latitude 47° to 54°N during the period 1976-1980. The exact form of the temperature variable, which is labelled TEMPSUM, was the sum of these monthly means for the period July-December. This we have taken as an integrated measure of the thermal conditions experienced by larvae during the initial period of 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 (<u>Ammodytes dubius</u>) in the Grand Banks region.

c) Capelin Abundance

Annual estimates of capelin abundance for the 2J3K (Carscadden and Miller 1981, Table 7) and 3L (Carscadden et al. 1981, Table 10) stocks during the years 1966 to 1978 and 1964 to 1978 respectively are based on sequential cohort analysis. Abundances of the 1966-1969 year classes as 2 year-olds for the Division 2J3K stock were calculated from the estimates of the abundance of age groups 3-6 in 1972. This calculation used estimates of natural mortality rates and instantaneous spawning mortality rates identical to those employed in the sequential cohort analysis performed by Carscadden and Miller (1981). We assumed no fishing mortality since catches in 1966-1969 averaged less than 2000 tons as compared to > 200,000 tons during the mid 1970's. Analyses for the 3L stock were based on the abundance of 3 year-olds. Direct year-class-strength estimates were available only for 1972-1977 because of a lack of independent estimates of abundance in other years, but estimates of year-class-strengths in the 2J3K and 3L stocks (Carscadden and Miller 1979, Carscadden et al. 1981). These estimates are considered less reliable than those for the 2J3K stock for these reasons.

RESULTS AND DISCUSSION

a) The Models

Several forms of linear regression models incorporating the independent variables WIND and TEMPSUM were evaluated for the 2J3K and 3L stocks. In all models tested year-class-strength was transformed to natural logarithms (Ricker 1975; Hennemuth et al. 1980). The general model yielding the highest explained variance for year-class-strength for both stocks took the general form in YCS = a + (b TEMPSUM - c) WIND. The specific relationship between year-class-strength of 2 year-old capelin, TEMPSUM, and WIND for the 2J3K stock was in YCS = $25.13 + (0.06 \text{ TEMPSUM} - 3.0) \text{ WIND} (r^2 = 0.73, Table 1, Figure 3)$. For the 3L stock the relationship was in YCS = $23.91 + (0.01 \text{ TEMPSUM} - 0.85) \text{ WIND} (r^2 = 0.55, Table 2, Figure 4)$. Data for 1967 were excluded from these analyses because the TEMPSUM value for this year deviated greatly from all other values suggesting an error in the data set. Inclusion of the 1967 data greatly reduced the variance accounted for by the model $(r^2 = 0.33)$.

Univariate analyses showed that the sign of the correlation coefficient for the relationship between year-class-strength and WIND was consistently negative, while that for year-class-strength and TEMPSUM was consistently positive. 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 temperatures on food availability to the larvae. The wind variable was the major contributor to explained variation in year-class-strength in both the 2J3K and 3L stocks ($r^2 =$ 0.61 and 0.51 respectively).

The biological significance of the crossproduct term TEMPSUM x WIND in the models is not obvious. One possible explanation is that temperature and wind conditions at the <u>onset</u> of larval drift are the major regulators of larval survival and, hence, year-class-strength. This hypothesis 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 $r^2 = 0.32 - 0.58$). The main period of larval emergence in our study sites in 3L and 3K is July and, based on known spawning times in Labrador (Templeman 1948), the main period of larval emergence in 2J would be July or August.

This hypothesis was further evaluated by running the 2J3K and 3L models using annual estimates for WIND and a range of fixed TEMPSUM values (Figures 5, 6). The analysis suggests that, given the range of temperatures and wind conditions experienced during the interval 1966-1980, the length of the interval between onshore winds becomes progressively more critical to year class formation in the 2J3K stock as TEMPSUM declines below approximately 49° C (at which temperature recruitment is independent of wind). At TEMPSUM values > 49° C temperature appears to override the effect of wind. The probability of specific combinations of TEMPSUM and WIND conditions co-occurring, and their effect on recruitment, based on TEMPSUM-WIND records for the 14 year interval 1966-1980, are also given in Figure 6. These "recruitment windows" define the probability that the year-class-strengths of 2 year-old fish in the 2J3K stock will fall within specified bounds of abundance.

The general form of the 3L recruitment diagram (Figure 6) is similar to that for 2J3K. The two differ principally in the magnitude of the temperature effect and the fact that at no time does temperature override wind. Survival appears, in general, to be lower, and to decline more rapidly at lower TEMPSUM values. There is no obvious biological reason for these differences. The inferior quality of the 3L data and the fact that the slopes of the WIND and TEMPSUM relationships in the 3L model do not differ significantly from zero (Table 2) cannot be ignored.

b) The Biological Basis for Year Class Variation

These analyses indicate that abiotic variables, principally the frequency of onshore winds during the immediate post-hatching period and, secondarily, 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, for which year class data are most reliable, 73% 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 3-8 days (mean 5.5) at the high and mid-tide beach locations depending on temperature condition (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, in press). 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. 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 further 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 $\hat{\xi}$ urrent dominates the hydrographic characteristics off eastern Newfoundland resulting in quite similar temperature conditions over large areas. We found TEMPSUM to be strongly correlated to cumulative growing degree days at St. John's, Newfoundland measured from April 1 to August 31 (y = 11.32 + 0.40 x, r = 0.86, n = 17). Frank and Leggett (1982b Table 2, Figure 7) documented a significant (p < 0.01) positive relationship between the biomass of zooplankton and growing degree days. During the interval 1964-1981 cumulative growing degree days (April 1 - August 31) at St. John's varied from 660 to 1060. Applying these results to Frank and Leggett's (1982b) analysis indicates that this variation could result in an approximate 250% change (8.5 - 29.5 $mg \cdot m^{-3}$) in the biomass of < 250 μm zooplankton, 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 (mm/day) and the biomass ($\mu g \cdot m^{-3}$) of zooplankton < 250 μm (y = 0.0337 ln x - 0.2524, 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 μ 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 direct or indirect. The occurrence of favourable food conditions has long been considered an important direct regulator of larval survival in fishes (Cushing 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).

c) Recent Changes in Capelin Abundance - Over Exploitation or Recruitment Failure?

Sequential cohort analyses for stocks in NAFO Division 2J3K and 3L reveal a pronounced increase in total capelin biomass between 1974 and 1976 followed by a more dramatic decline between 1976 and 1979 (Figure 7; 8). The one year lag in the peak biomass for 3L is an artifact of methodology. Biomass data for 2J3K include two year-old and older fish, those for 3L only 3 year-old and older fish. The impact of the strong 1973 year thus appears one year earlier in the 2J3K stock estimate.

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 tons of capelin were taken annually for bait, fertilizer and food for dog teams (Templeman 1948). During the 1970's interest in capelin as a commercial species increased. Catches

came predominantly from the offshore areas in the early and mid 1970's and inshore in the late 1970's and early 1980's (Figure 9). The dramatic decline in total capelin biomass in the Divisions 2J3K and 3L stocks resulted from poor year classes (Figures 3 and 4) some of which were produced during the periods of 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 in both areas was small in relation to estimated total biomass throughout the period (Figures 7, 8). The results of our analysis argue against overfishing as a major factor in recent fluctuations in capelin biomass. Rather, recruitment failure resulting in a series of progressively weaker year classes between 1973 and 1976 appear to be the major cause of the decline in total capelin biomass between 1976 and 1979. The most probable cause of this recruitment failure was unfavourable meteorological and water temperature conditions during and subsequent to larval emergence from the beach gravel.

d) Recruitment Forecasts

The success of the models developed in explaining past variation in year-class-strength of capelin, especially in the 2J,3K area, suggest that they may be useful as forecasting tools. Input data required (spawning date, air and surface water temperatures, hours of sunlight and wind conditions) are easily and inexpensively obtainable.

We have estimated year-class-strength for the 1979 through 1982 cohorts in the 2J3K and 3L stocks (Figures 3,4). Input data for these years were obtained fom the sources previously described. The predicted values for the 1979–1981 year classes in subdivision 2J,3K suggest that the 1979 and 1981 cohorts will be strong and approximately equal to the dominant 1973 year-class which contributed to the peak in capelin biomass in the 1975–1977 era. The 1980 year-class is predicted to be below average but still above the weakest year classes experienced in recent years (1975–1977) (Figure 3). Given that the mature stock is composed primarily of 3 and 4 year olds, this suggests that the total biomass of capelin in the 2J,3K area should approximate the 1975–1976 level of 3-4 x 10⁶ tons during the interval 1982–1985.

The predicted pattern of year class variation in subdivision 3L during the years 1979-1981 is similar although the year to year variation is less pronounced. All three year-classes are predicted to yield above average recruitment with 1979 and 1981 being slightly superior (Figure 4). Year-class-strength in 1979-1981 in the 3L stock should approximate that of 1969-1970 and result in a total biomass of approximately $0.3 - 0.4 \times 10^6$ tons during 1982-1985.

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Winters, G.H. 1983. Analysis of the biological demographic parameters of northern sand lance (<u>Ammodytes dubius</u>) from the Newfoundland Grand Bank. Can. J. Fish. Aquat. Sci. 40: 409-419. Table 1. Results of model relating recruitment (ln) of Division 2J,3K capelin as 2 year-olds to wind interval and tempsum.

Dependent Variable: Recruitment as 2 year-olds (1n)

	DF	Sum of squares	Mean square	F value	r ²
Model	2	8.75	4.37	12.17	0.73** ^a
Error	9	3.23	0.36		
Total	11	11.98			
	1.1		and the second		

Independent Variables:

	Estimate	t ^b	Standard Error
Intercept	25.13	55.88***	0.45
Wind	-3.00	-3.75**	0.80
Tempsum x Wind	0.06	3.43**	0.02
	• • • • • • • • •		

a ** p < 0.01 *** p < 0.001

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

Table 2. Results of model relating recruitment (ln) of Division 3L capelin as 3 year-olds to wind interval and tempsum.

Dependent Variable: Recruitment as 3 year-olds (1n)

	DF	Sum of squares	Mean square	F value	r ²
Model	2	4.77	2.38	6.70	0.55* ^a
Error	11	3.92	0.36		
Total	13	8.69			

Independent Variable:

	Estimate	t b	Standard Error
Intercept	23.91	56.94***	0.42
Wind	-0.85	-1.42 n.s.	0.60
Tempsum x Wind	0.01	0.98 n.s.	0.01

a * p < 0.05 ** p < 0.01 *** p < 0.001

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

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Fig. 1. Map showing general locations of capelin stocks (2J3K stock and 3L stock) and location of sampling sites for water temperatures (see Fig. 2).







Fig. 3. Observed recruitment (1966-77 yearclasses as two-year-olds), recruitment predicted from the model and 95% confidence limits (1966-81 yearclasses as two-year-olds) for Div. 2J3K capelin stock.





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Fig. 5. The Div. 2J3K model run using a range of WIND values at fixed TEMPSUM values. The probabilities (25%, 50%, 75%, 100%) of specific combinations of TEMPSUM and WIND conditions co-occurring, based on historical TEMPSUM-WIND records, are shown as "recruitment windows".

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Fig. 6. The Div. 3L model run using a range of WIND values at fixed TEMPSUM values. The probabilities (25%, 50%, 75%, 100%) of specific combinations of TEMPSUM and WIND conditions co-occurring, based on historical TEMPSUM-WIND records, are shown as "recruitment windows".



Fig. 7. Estimated total biomass (age 2+, 1972-80) from Carscadden and Miller (1981) and annual catches (1972-81) for the Div. 2J3K capelin stock.









