Coastal Water Mass Replacement: Its Effect on Zooplankton Dynamics and the Predator−Prey Complex Associated with Larval Capelin (*Mallotus villosus*)[1]

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We examined the hypothesis that the onshore wind-regulated initiation of larval emergence and drift in capelin (*Mallotus villosus*) was adaptive. Onshore winds were found to induce rapid water mass exchange in coastal Newfoundland resulting in the replacement of cold, high-saline, predator-laden waters with warmer, less-saline waters in which the abundance of an important fraction of the predator community was reduced 3- to 20-fold and zooplankton densities in the edible size fraction were increased 2- to 3-fold. In situ enclosure experiments indicate that the synchronous emergence of larval capelin during onshore winds, coupled with the reduced predator density at this time, results in predator satiation. Wind-induced elevations of the biomass of the edible zooplankton size fraction can produce fivefold increases in the daily growth rate of larval capelin. Capelin larvae thus initiate their drift and first feeding in a wind-induced "safe site." The abundance of eggs and larvae of 11 other marine fish species were also found to be associated with this "safe site" water mass.

Key words: capelin, *Mallotus villosus*; water mass replacement, predation, feeding, growth, larval fish, survival, wind effects, drift, dispersal, enclosures, zooplankton

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Nous avons étudié l'hypothèse selon laquelle le début de l'émergence des larves de capelan (*Mallotus villosus*) et de leur dérive occasionnées par le vent du large est adaptatif. Nous avons découvert que les vents du large provoquaient un échange rapide de la masse d'eau sur les côtes de Terre-Neuve, donnant lieu au remplacement des eaux froides de forte salinité et remplies de prédateurs par des eaux plus chaudes et moins salines. Dans celles-ci, l'abondance d'une fraction importante de la communauté de prédateurs était réduite de 3 à 20 fois, et la densité du zooplancton composant la fraction de grosseur comestible était accrue de 2 à 3 fois. Des expériences de mise en captivité in situ ont démontré que l'émergence synchrone du capelan larvaire au moment des vents du large, de paire avec une densité réduite des prédateurs à ce moment, mènent à l'assouvissement du prédateur. Les augmentations de la biomasse de la fraction de zooplancton de taille comestible provoquées par le vent peuvent quintupler le taux de croissance quotidienne du capelan larvaire, qui débute ainsi sa dérive et sa première alimentation dans un endroit rendu sûr par le vente. Nous avons en outre découvert que l'abondance des œufs et des larves de 11 autres espèces de poissons marins était également plus grande dans cet endroit sûr de la masse d'eau.

MOST marine fish species which reproduce in coastal systems rely on turbulent and horizontal water flow for the dispersal of their offspring (see review in Johannes 1978; Frank and Leggett 1981). The extent to which this transport results in the larvae being carried to areas where conditions are favorable for survival ("safe sites" Harper et al. 1961) has long been considered a major regulator of the population dynamics of marine larval fishes (Ketchen 1956; Stevenson 1962; Martin and Kohler 1965; Nelson et al. 1977). The ultimate determinants of early larval survival and hence the primary features of "safe sites" are widely held to be food conditions (see Cushing 1975; Ware 1977) and predator abundance (Hempel 1965; Cushing 1969; Ware 1975, 1980). Documenting the existence of "safe sites" and the physical processes which produce them, quantifying their role in the regulation of larval survival, and clearly establishing an adaptive relationship

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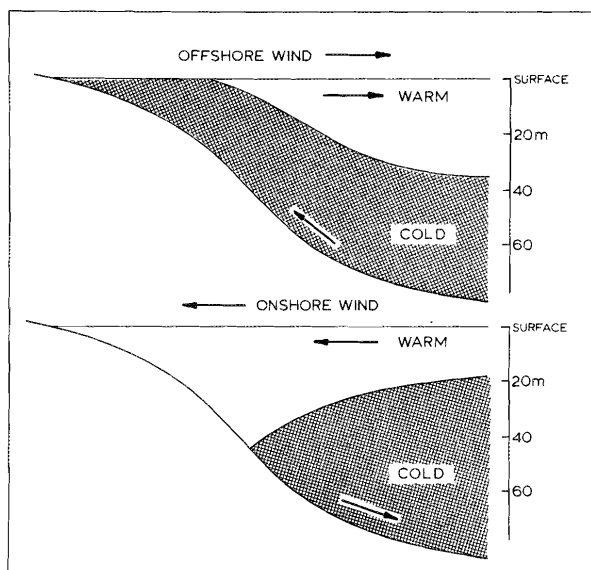Imprimé au Canada (J6737)

FIG. 1. Schematic representation of the effect of offshore and onshore winds on the summer water temperatures and water layers in the nearshore zone along Newfoundland's east coast (redrawn from Templeman 1966, fig. 27).

between reproductive behavior, transport processes, and the occurrence of "safe sites" has, however, proved very difficult in most instances.

In this paper we examine the role of physical factors in the regulation of early larval transport in capelin (*Mallotus villosus*), and the structure of the predator−prey community to which they are exposed during drift. Our working hypothesis was that factors regulating the onset and direction of larval drift would also produce favorable feeding conditions and minimize predator abundance. Inherent in the formulation of this hypothesis is the assumption that the timing of the initiation of larval drift in capelin is adaptive.

Capelin is a dominant element in the Northwest Atlantic food web (Bailey et al. 1977). In the Northwest Atlantic the major beach-spawning areas are located on the east coast of Newfoundland and Labrador. Spawning sites are typically exposed beaches located at the heads of long embayments (Templeman 1948). The adhesive eggs cling to coarse-grained intertidal sediments, wave and tidal action serving to bury the eggs approximately uniformly over the top 20 cm of the beach gravel between the low and high tide zones. Larvae hatch in the beach gravel which they exit not gradually, but as highly concentrated patches predictably linked to the occurrence of onshore winds (Frank and Leggett 1981). The timing of the dispersal event is unpredictable and its frequency low, the summer winds in eastern Newfoundland and Labrador being predominately offshore (Frank and Leggett 1981, Fig. 2). Larval capelin thus initiate their drift, and first feeding, in an environment that is transitory, predictable with respect to wind conditions, and consistent over the species range in Newfoundland (Frank and Leggett 1981). Lambert et al. (1982) have recently confirmed this fact for capelin spawning in St. Georges Bay, N.S. Equally important from the point of view of the study of capelin, the early phase of

development occurs onshore where it can be easily and economically investigated.

With respect to the structure of the environment during early larval drift, it is well known that coastal water mass replacement can occur quickly as a result of changes in wind speed and direction. This often results in pronounced changes in temperature and salinity (Sverdrup 1938; Hachey 1955; Taylor and Stewart 1959; Cooper 1960). The character of the planktonic community is also altered during periods of water mass replacement, the origin of a given water mass being frequently traceable by the occurrence of "indicator species" (see reviews in Russell 1952; Alvariño 1965).

Returning to our hypothesis, as a test of the "safe site" concept, we predicted a priori that the initiation of larval drift and first feeding in larval capelin would occur in an environment characterized by high densities of zooplankton in the edible size spectra and low densities of the major predators (i.e. that the time of drift and first feeding would be strongly matched to the existence of favorable predator−prey abundances). We predicted further, that changes in prey and predator densities would be strongly linked to wind conditions which is, also, a key factor regulating the initiation of drift (Frank and Leggett 1981).

Water Mass Replacement

GENERAL

The summer waters off Newfoundland's east coast are characterized by a shallow (~30 m thick) warm upper layer and a deeper cold layer extending from the base of the warm layer to the bottom (~180 m) (Templeman and Fleming 1963). Templeman (1966) suggested that the wind, operating on the warm surface layer, may significantly influence the thermal and biological characteristics of nearshore waters. He hypothesized that offshore winds may blow the less-dense, warm surface water offshore causing the heavier, colder bottom water to move shoreward and replace it. Onshore winds, in contrast, would cause warmer surface water to predominate along the coast (Fig. 1). Assuming water mass replacement occurs, the nearshore waters off eastern Newfoundland and Labrador should be dominated by waters whose origin is the deeper, colder, more saline layer as offshore winds predominate during June, July, and August. For example, monthly meteorological summaries for St. John's−Torbay, published by Environment Canada, show the average number of days during which offshore winds prevailed to be 24.1 (SD 2.9) and 26.8 (SD 3.0) in June and July, respectively, over the 21-yr period 1960−80 (see also Fig. 2). The occurrence of warmer, less-saline surface waters in the nearshore region would be restricted to the occasional and unpredictable occurrence of onshore winds. If water mass replacement does occur as a result of wind effects, capelin larvae would consistently be released into an environment dominated by the warmer, less-saline surface water mass and its associated biota.

TEMPERATURE

To evaluate Templeman's (1966) hypothesis concerning wind-induced water mass replacement we examined the relationship between nearshore water temperature and wind
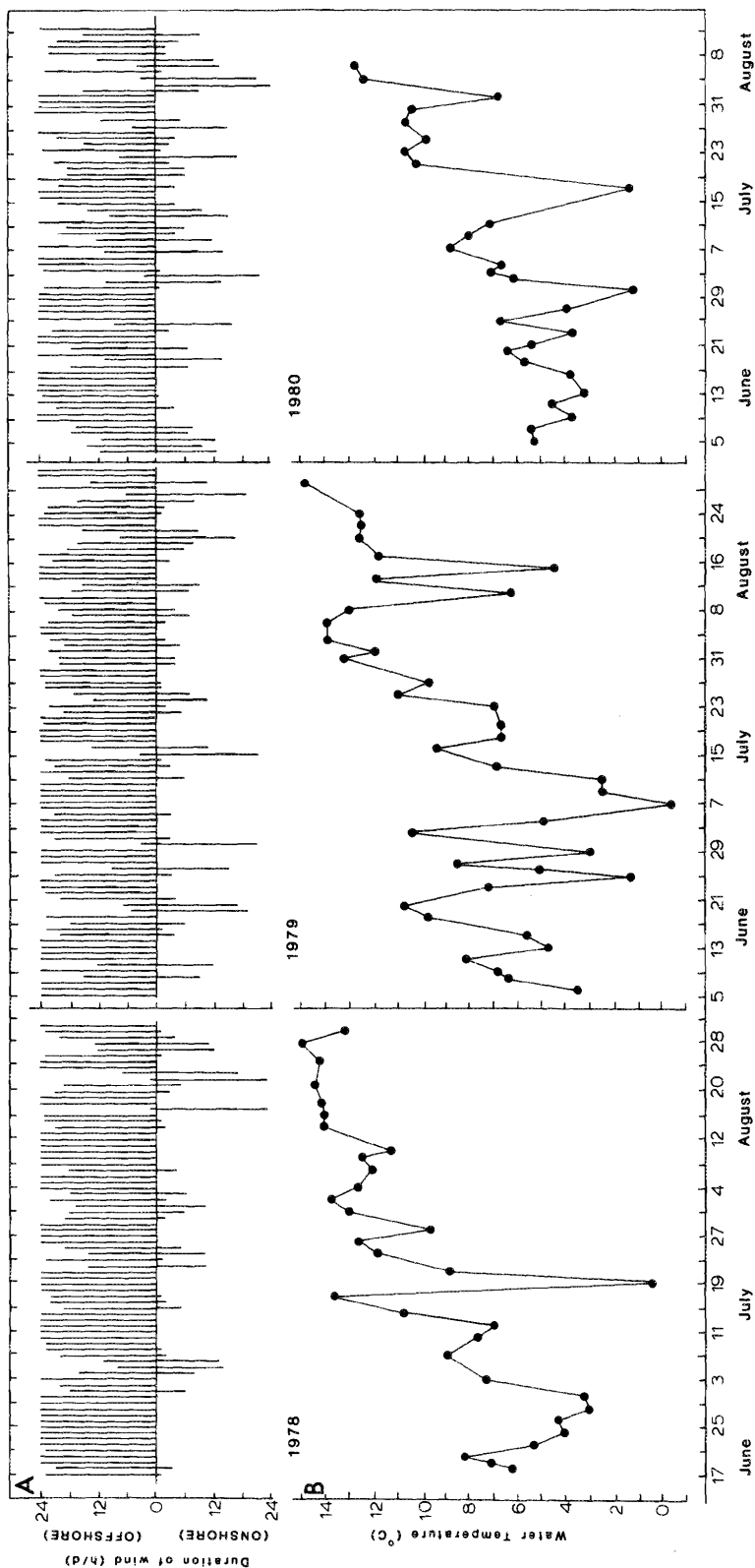
FIG. 2. (A) Daily duration of offshore (SE–NW) and onshore (N–E) wind (lines above and below the zero line, respectively) during June–August (1978, 1979, 1980). This data was obtained from the Hollyrood (Newfoundland Hydro) meteorological station located 30 km south of the study site. (B) Mean water temperatures in the 1- to 2-m-depth strata at the Bryant's Cove study site. Note the quick change in water temperature in response to changes in wind direction.

events. We measured water temperatures in 1978, 1979, and 1980 at six hydrographic stations located at 15-, 60-, 120-, 215-, 490-, and 730-m distances from the spawning beach in Bryant's Cove. Stations were occupied at 1- to 3-d intervals and temperature measurements were made at 1-m-depth intervals (surface to bottom) using a Hydrolab FT-3 marine hydrographic thermometer. Water depths at the respective stations proceeding seaward were 3 m, 5 m, 7 m, 10 m, 16 m, 22 m. Horizontal (between station) and vertical temperature differences were slight and nonsystematic during both onshore and offshore wind conditions during the June–August study period (1978: offshore, $\Delta H = 0.6$, $\Delta V = 1.1°C$, $n = 17$; onshore, $\Delta H = 0.3$, $\Delta V = 0.8$, $n = 15$; 1979: offshore, $\Delta H = 0.9$, $\Delta V = 2.0$, $n = 19$; onshore, $\Delta H = 0.7$, $\Delta V = 1.6$, $n = 19$; 1980: offshore, $\Delta H = 0.8$, $\Delta V = 2.5$, $n = 9$; onshore, $\Delta H = 0.6$, $\Delta V = 3.2$, $n = 19$). These findings indicate that the nearshore waters are well mixed under both wind conditions. Dramatic short-term changes in water temperature were frequent and were consistently associated with changes in wind direction (Fig. 2). Daily deviations from the monthly mean temperatures at the 1- to 2-m-depth strata were nonsystematic with respect to time, but strongly correlated to wind events ($\chi^2 = 25.8$, df $= 2$, $P < 0.001$). Eighty-five percent of the negative deviations in excess of 1°C were associated with offshore wind (SE through NW), and 81% of the positive deviations in excess of 1°C were associated with onshore winds (N through E). Exceptions to this general pattern occurred only when winds were light (<20 km/h). These observations are consistent with Templeman's water mass exchange hypothesis. Deep, cold waters appear to replace warmer surface waters in the inshore areas when winds are offshore. Onshore winds reverse this condition. The rate of change in nearshore temperatures following changes in wind direction (Fig. 2) suggest that the water mass replacement is rapid.

SALINITY

Salinity at the 1- to 2-m-depth strata was determined at weekly intervals coincident with temperature measurements in 1979. Nearshore salinities were significantly higher during offshore (mean $= 32.32‰$) relative to onshore (mean $= 31.67‰$) winds ($t = 3.5$, df $= 9$, $P < 0.01$). These findings are also consistent with the water mass replacement hypothesis.

Predator–Prey Dynamics

To examine the effect of water mass replacement on the dynamics of the potential predators of larval capelin, and on the biomass of the edible zooplankton size fraction available to larval capelin as prey, we sampled the nearshore plankton community at 1- to 3-d intervals during 1979 and 1980. All samples were collected with a 0.5-m-diameter plankton net fitted with a No. 10 (150 µm) mesh net and General Oceanics flowmeter. During the initial stages of larval drift capelin are transported as passive contaminants (Fortier and Leggett 1982) and are therefore subject to extensive vertical mixing in the nearshore area. All collections were made by towing the net horizontally in the 1- to 2-m-depth strata along six transects parallel to and at increasing distances from the beach.

Each sampling transect spanned the width of the cove and intersected the positions of the fixed hydrographic stations. Towing speeds averaged 1.2 ± 0.07 m/s. All samples were collected between 18:00 and 20:00 and were preserved in 4% buffered formalin. Five components of the macrozooplankton, known by previous work to be important predators on fish larvae, were sorted and counted. They were chaetognaths (identified as voracious predators on larval fish by Lebour 1922, 1923; Bigelow 1926; Thomson 1947; David 1955; Furnestin 1957; Stevenson 1962), jellyfish (confirmed as predators by Russell 1953; Stevenson 1962; Fraser 1969; Phillips et al. 1969; Larson 1976; Möller 1980), ctenophores (shown to be important predators by Lebour 1922, 1923; Bigelow 1926; Russell 1935a; Fraser 1962; Stevenson 1962; Fraser 1970), decapod larvae and amphipods (identified as important predators by Lebour 1925; Rosenthal 1967; Lillelund and Lasker 1971; Theilacker and Lasker 1974; von Westernhagen and Rosenthal 1976). The most common members of each group were chaetognaths — *Sagitta elegans*; jellyfish — *Sarsia tubulosa*, *S. princeps*, *Catablema vesicarium*, *Aglantha digitale*, *Leukaritiara nobilis*, *Euphysa flammea*, *Aurelia* sp., *Cyanea* sp.; ctenophores — *Pleurobrachia* sp.; decapod larvae — crab zoea of Majidae; amphipods — primarily hyperiids. Predator densities were recorded as no./m^3 of water filtered.

The balance of the plankton sample, the bulk of which was planktonic crustaceans (primarily *Calanus finmarchicus* and euphausids of a variety of developmental stages and appendicularians *Oikopleura* sp.), was fractionated into the edible (<250 µm) and inedible (>250 µm) size fractions. We washed each sample through a 250-µm sieve. Both fractions were rinsed with freshwater, resuspended, and filtered through a preweighed glass microfiber filter by aspiration. The filters were placed in a drying oven at 70°C for 24 h, removed to a desiccator, and weighed to an accuracy of 10 µg. The dry weight biomass of each size fraction was determined by difference. All dry weight determinations were expressed as µg/m^3. All prey and predator density data were log $(y + 1)$ transformed prior to analysis because the untransformed data exhibited a tendency for the variance to be positively correlated to the mean. This transformation effectively stabilized the variance. Wind data (expressed as hours of onshore wind$\cdot$d^{-1}/24) was arcsine transformed to normalize the distribution (Sokal and Rohlf 1969).

PREDATORS

The absolute abundance of jellyfish, ctenophores, and chaetognaths showed no significant temporal pattern ($r^2 < 0.04$). Decapod and amphipod abundance showed weak correlations with time but were opposite in sign between years. Abundances of jellyfish and chaetognaths were, however, significantly negatively correlated with the daily duration of onshore winds (for the day of, and the day prior to, sampling) in both 1979 and 1980. The sign of this relationship was consistent both between years and between stations within years (Fig. 3). These findings suggest their presence is linked to the upwelling of the deeper, more saline waters. This interpretation is consistent with the known depth distribution of these organisms. The summer depth distribution of chaetognaths is reported to be in the 40- to 100-m range with very
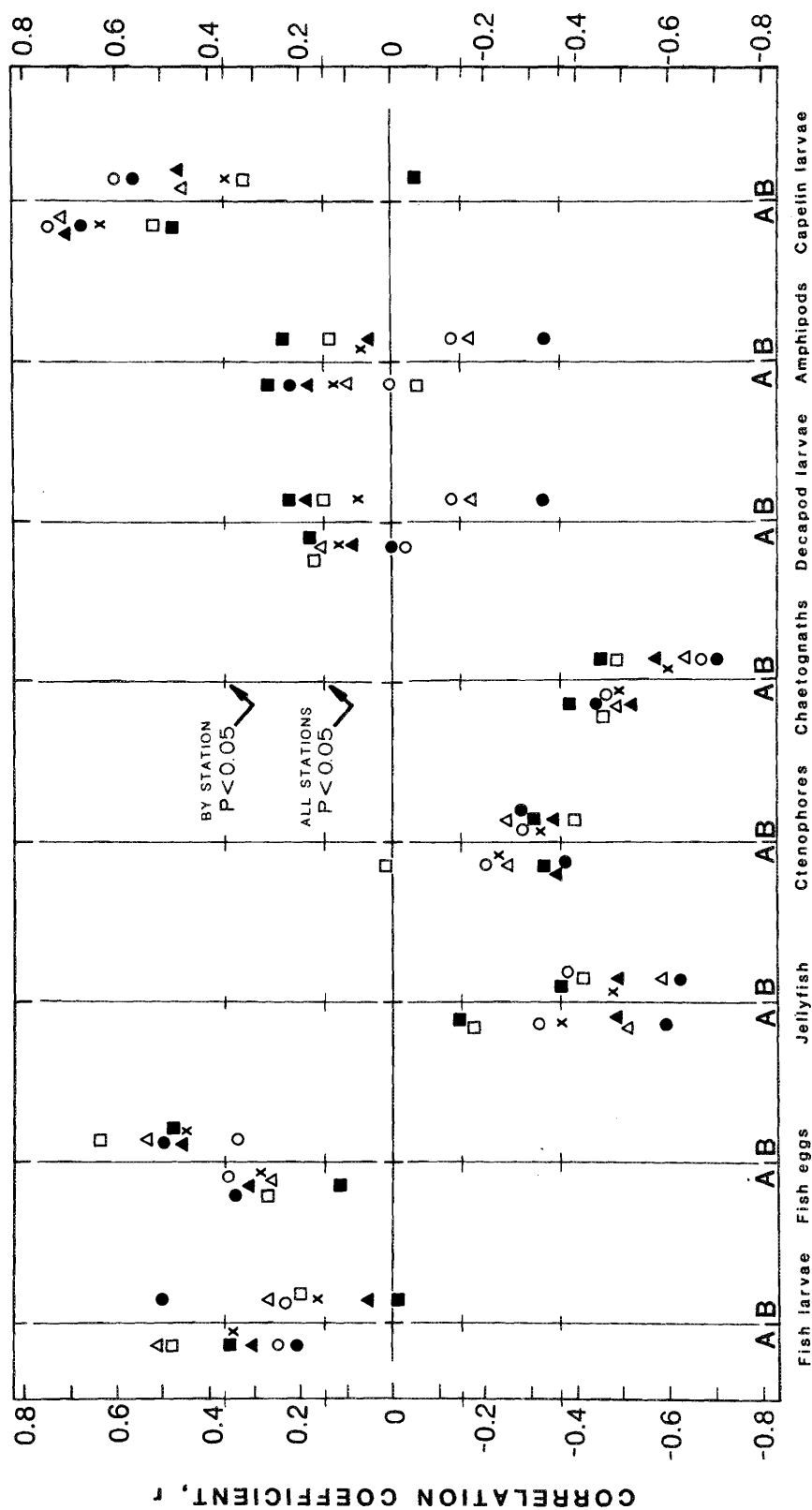
FIG. 3. Plot of the correlation coefficients resulting from the regression of macrozooplankton density (no./m³) on the daily % duration of onshore wind at each station (○, 15 m; ●, 60 m; △, 120 m; ▲, 215 m; □, 490 m; ■, 730 m; ×, all stations). (A) 1979, (B) 1980.
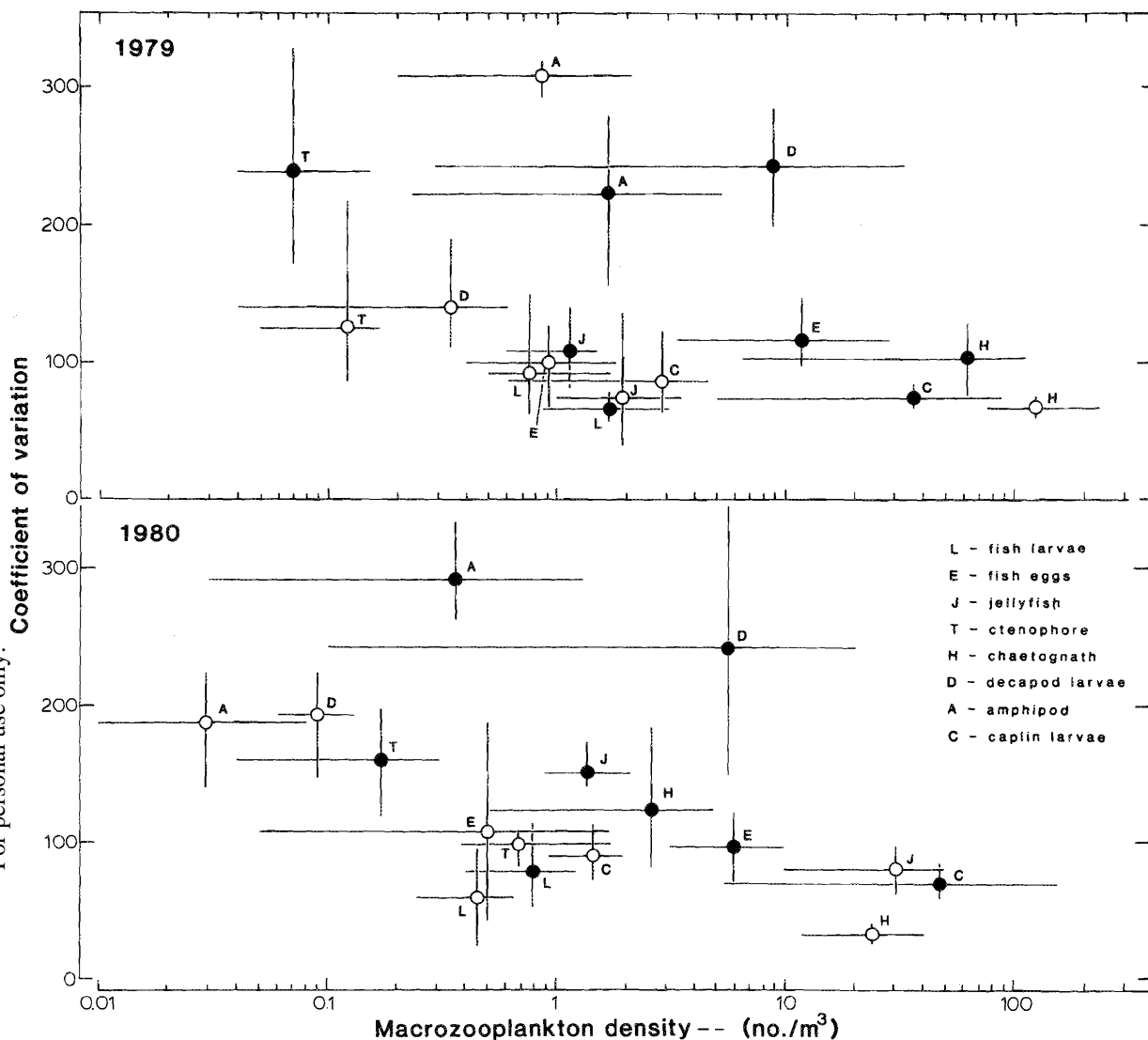
FIG. 4. Plot of the mean summer density (no./m^3) of each macrozooplankton component (Mean$_{\text{cove}}$ = Σ station means/no. of stations) against the mean coefficient of variation ($\overline{\text{CV}}$ = Σ station CVs/no. of stations) during onshore (●) and offshore (○) wind conditions for 1979 and 1980 (upper and lower panel, respectively). Horizontal and vertical lines indicate the range of station means and CVs, respectively.

few occurring near the surface (Huntsman and Reid 1921; Bigelow 1926; Russell 1933; Alvariño 1965). The center of distribution of jellyfish is reported to be in the 50- to 150-m-depth range, strongly overlapping that of chaetognaths (Mayer 1910; Kramp 1913b; Kramp and Damas 1925; Bigelow 1926). Both jellyfish and chaetognaths have previously been reported to exhibit pronounced changes in abundance related to the influx of different water masses into the areas sampled (Meek 1928; Russell 1935a, 1935b; Maaden 1942a; Thiel 1962; Alvariño 1965; Russell 1970). Given the relatively large number of correlations presented the possibility of chance significant correlations must be considered. We believe this serendipitous effect to be minimal because of the very low probability levels associated with most cor-

relations (jellyfish 8 of 14, $P < 0.01$; 6 of 14, $P < 0.001$. Chaetognaths 11 of 14, $P < 0.01$; 10 of 14, $P < 0.001$).

The abundances of amphipods and decapod larvae were largely independent of wind condition (Fig. 3). Both species are known to exhibit diel vertical migration and are often found in dense swarms at the surface under low light intensities (Bigelow 1926). Their association with specific water masses is thus transitory and time dependent. This would explain the absence of consistent correlations of their density with either onshore or offshore wind conditions.

Ctenophore abundance was weakly negatively correlated with onshore winds. The reported catholic behavior of ctenophores with respect to temperature and depth (Kramp 1913a; Rose 1913; Bigelow 1926; Fraser 1970) is consistent with the

TABLE 1. Hypothetical differences in the physical and biological characteristics of the surface and subsurface water masses entering into Bryant's Cove during mid-July.

| | Wind direction | | |
Water mass properties	Onshore[a]	Offshore	Magnitude of difference
Physical			
T° water	High	Low	$\geqslant 3°C$
Salinity	$32‰<$	$>32‰$	$0.65‰$
Biological — Predator density			
Chaetognaths	Low	High	$10-20 \times$
Jellyfish	Low	High	$3-5 \times$
Decapod larvae	Same	Same	—
Ctenophores	Low	High	$1.1-1.5 \times$
Amphipods	Same	Same	—
Zooplankton biomass by size[b]			
Zoo. >250 μm (inedible)	Same	Same	—
Zoo. <250 μm (edible)	High	Low	$2-3 \times$
Density of capelin larvae	High	Low	$100 \times$
Effect on larval capelin			
Death due to predation	Low	High	
Expected daily growth rate	High	Low	$1.2-5.5 \times$

[a]Assuming average daily duration of onshore winds = 18 h.
[b]Growing degree-day value (GDD) was set at 600°C·d for these calculations.

TABLE 2. Results of stepwise regression to predict the biomass ($\log_{10}$ μg·m^{-3}, dry wt) of edible (<250 μm) and inedible (>250 μm) zooplankton from cumulative growing degree days and the daily % duration of onshore wind (arcsine transformed) (**$P < 0.01$; ***$P < 0.001$; ns, $P > 0.05$).

Zooplankton size fraction	n	Variable	Estimated coefficient[a]	Multiple R^2	Increase in R^2	$|t|$[b]
Edible (<250 μm)	51	GDD	0.001353	0.4529	0.4529	7.1***
		WIND	0.004511	0.5359	0.0830	2.9**
		$y_{intercept}$	3.04289	—	—	33.1***
Inedible (>250 μm)	51	GDD	0.002246	0.6178	0.6178	8.7***
		WIND	−0.001471	0.6217	0.0040	0.7 ns
		$y_{intercept}$	3.05056	—	—	24.9***

[a]The estimated coefficients and their t values are those for the final step of the regression analysis.
[b]t values were derived to test the null hypothesis that the true value of the coefficient is equal to zero.

weak nature of this correlation.

These findings are fully consistent with the water mass replacement hypothesis. The temporal coefficient of variation of ctenophores, chaetognaths, and jellyfish densities was always greatest during onshore winds (Fig. 4). This observation is also in agreement with our suggestion that inshore waters off eastern Newfoundland are dominated by the upwelling of deeper cold waters induced by the prevailing offshore winds. The duration and magnitude of the replacement of these waters, and their associated biota, by warmer surface waters is expected to be a variable function of the duration and intensity of onshore winds. Hence the higher variability of the deep-water-associated predators under onshore wind conditions.

We conclude that the density of an important fraction of the potential predator community is directly controlled by prevailing wind conditions which generate water mass replacement. Assuming an 18-h average duration of onshore winds we estimate a 3- to 5-fold decrease in the abundance of

jellyfish and a 10- to 20-fold decrease in the abundance of chaetognaths relative to periods of offshore wind (Table 1).

PREY

The absolute biomass of both zooplankton size-classes in both 1979 and 1980 was positively correlated with cumulative growing degree days (GDD) beginning on April 1 (as reported in monthly meteorological summaries, St. John's—Torbay, published by Environment Canada) (Table 2). To separate this seasonal effect from the potential effect of wind on the biomass of edible and inedible zooplankton, we performed stepwise multiple regression analyses incorporating as independent variables both cumulative growing degree days (seasonal effect) and the duration of onshore wind (expressed as $\sin^{-1}$ (h onshore wind·d^{-1}/24)$^{0.5}$ for the day of, and the day prior to, sampling). The seasonal effect was then held constant and the wind effect analyzed for the direction and intensity of its impact on the two zooplankton size-classes. We

were particularly interested in the effect on the <250-μm size-class as Bjørke (1976) had shown that the diet of first feeding capelin larvae consists mainly of copepod eggs and nauplii which, in our study area, ranged in size from 132 to 155 μm for eggs and up to 300 μm for early naupliar stages.

A significant fraction of the daily variation in the absolute biomass of the edible (<250 μm) size-class was explained by the wind variable (Table 2), the biomass of this fraction being positively related to the duration of onshore winds. The biomass of the >250-μm fraction was not significantly correlated with the duration of onshore winds (Table 2). Assuming an 18-h-average duration of onshore wind we estimate an approximate $2-3\times$ increase in the absolute biomass of the <250-μm-size fraction relative to its abundance during offshore winds (Table 1).

The positive relationship between onshore winds and the absolute biomass of the <250-μm-size fraction is consistent with the water mass replacement hypothesis as the reported depth distribution of copepod eggs and nauplii is within the upper 30-m strata, there being little tendency for the young of most planktonic crustacea to exhibit vertical migration until the later developmental stages. The absence of a significant relationship between the abundance of the >250-μm-size-class and wind events is also consistent with the hypothesis as these older, larger elements of the plankton are known to make extensive diel vertical migrations thereby associating themselves alternatively with both the deep and surface water masses (With 1915; Nicholls 1933; McLaren 1963).

Water Mass Replacement and "Safe Sites" for Capelin

We have shown that onshore winds in the eastern Newfoundland area have at least four predictable effects: they facilitate the release of capelin larvae from the beach gravel and their entry into the pelagic environment (Frank and Leggett 1981); they induce water mass changes in the nearshore water causing it to be dominated by warmer, less-saline surface waters; they cause a 3- to 20-fold reduction in the abundance of an important fraction of the potential larval capelin predator complex; and they induce a 2- to 3-fold increase in the absolute biomass of the potential food resource for larval capelin. These last two effects are directly linked to water mass replacement. The direction and approximate magnitude of these related effects are summarized in Table 1. These findings are consistent with our initial hypothesis. The timing of the entry of larval capelin into the pelagic environment to coincide with periods of onshore winds is thus interpreted to be adaptive. This conclusion is strengthened by the results of recent experiments (Frank and Leggett unpublished data) showing that the increase in water temperature associated with onshore winds is a significant stimulus to larval emergence. This increased emergence rate is independent of the role of physical disturbances of the sediments in larval release. We conclude that the emergence of larval capelin during periods of onshore winds minimizes their potential mortality due to predation and maximizes their probability of encountering abundant food resources in the appropriate size spectra at the onset of exogenous feeding.

The reciprocal patterns of predator/larval capelin densities, mediated by wind events, are illustrated in Fig. 5 which por-

trays a simulation of the absolute abundance of these predators, relative to larval capelin, at various distances from the spawning beach under different durations of onshore winds. These simulations are based on the analysis of the relationships between wind condition and predator density summarized in Fig. 3. We have previously shown (Frank and Leggett 1981) that the high concentration of capelin larvae in the nearshore areas during onshore wind events results from the synchronous emergence of larvae from the gravel during onshore winds and not from concentration of larvae in the nearshore area due to Ekman transport from offshore areas. The high concentrations of larvae in the nearshore area, depicted in these simulations, reflect the situation up to 1 d after the onset of onshore winds. The subsequent time course of larval distributions indicates that larvae move offshore in patches, associated with surface waters, under the influence of offshore winds (C. Taggart personal communication). The reduction in predator densities, resulting from water mass replacement, is significant over the entire nearshore area, ranging from 3- to 30-fold depending on location and wind condition.

Predator Swamping

The low predator densities during onshore winds, coupled with the pulsed, high-density entry of capelin larvae into the pelagic environment, suggests that the impact of predation may be further reduced by predator swamping. To evaluate this hypothesis we conducted a series of experiments designed to assess the effect of larval density on mortality rate due to predation. We used in situ enclosures having the following specifications: 1 m diam $\times$ 5 m deep, cylindrical, volume 4 m^3, construction nitex 150 μm, steel hoops at 1-m intervals, bottom panel tapered to cod end. Enclosures were suspended from wooden boxframe floats anchored in water $7-8$ m in depth and were stocked with yolk sac larvae obtained from the beach sediments. Larval densities, which ranged from 20 to 1070/m^3, spanned the average range of larval densities observed in situ. Each enclosure was stocked with 20 ctenophores giving an initial density of 5/m^3. This initial density was $2-5$ times the average density of ctenophores in the nearshore area. This high density was used to ensure that evidence of predator swamping, if obtained, was unequivocal. In addition, ctenophores are known to swarm in response to high prey concentrations (Fraser 1970), hence actual concentrations in local areas may exceed our integrated density estimates which were based on plankton tows. All ctenophores (*Pleurobrachia* sp.) were collected either by dipnetting from a boat or by SCUBA-equipped divers using slurp guns. All experiments were of 3-d duration. Each treatment was paired. Six trials were conducted in 1979 and 12 in 1980. Paired control enclosures stocked with 500 larvae but lacking predators were run in both years. At the end of each trial the enclosures were lifted, the contents retrieved from the cod end, and the number of larvae remaining assessed. Mortality unrelated to predation was assessed from the controls. Mortality due to predation in the experimental enclosures was determined as total mortality-control mortality. There was no apparent relationship between larval mortality and water temperature ($r = -0.271$, $P > 0.05$). Ctenophores were used because their densities were found to be least affected by
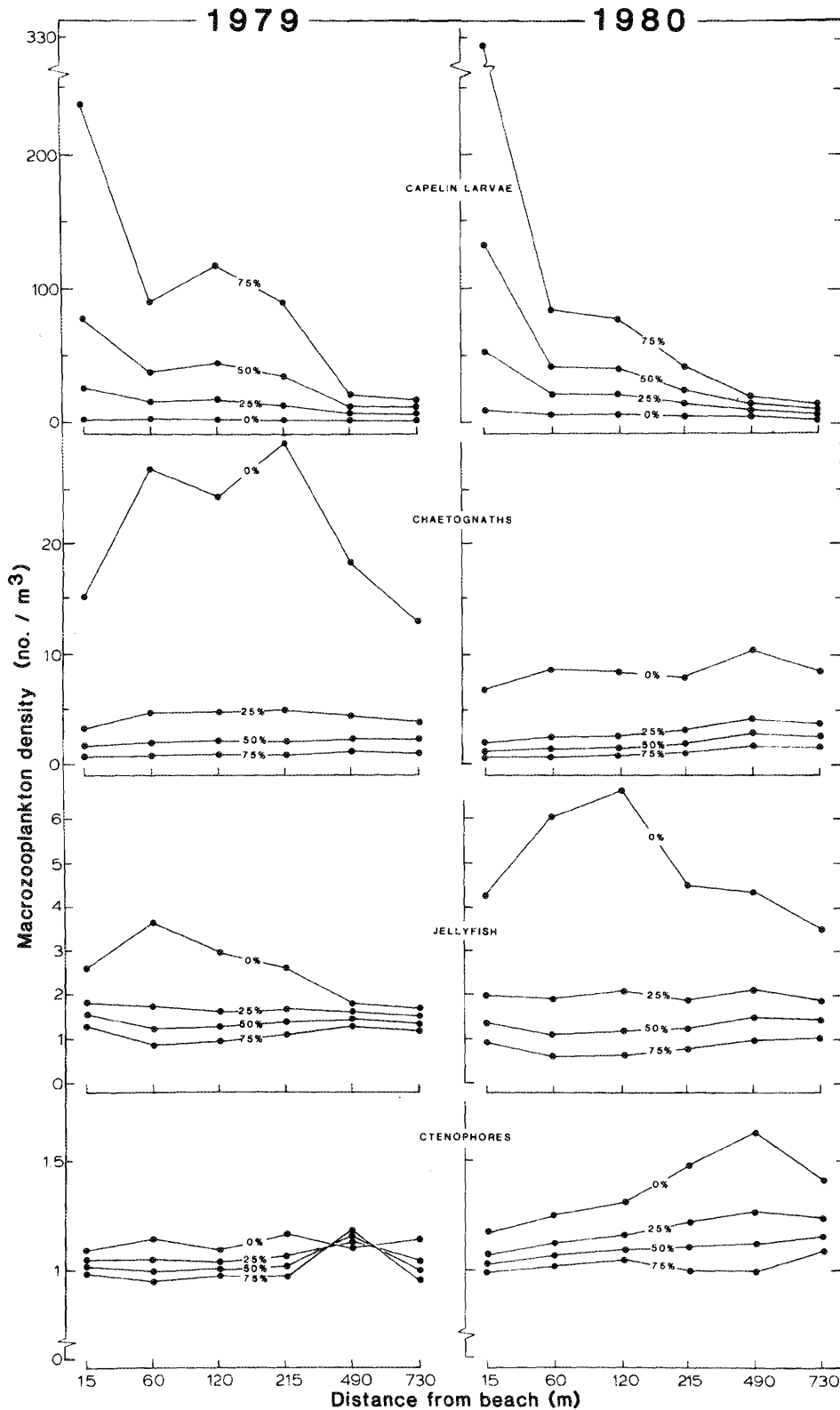
FIG. 5. Simulation of densities of larval capelin, chaetognaths, jellyfish, and ctenophores under variable durations of onshore wind for 1979 and 1980. Predictions were derived from the regression models used to construct Fig. 3.
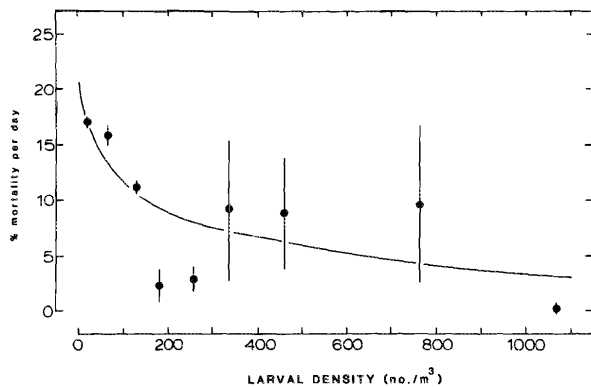
FIG. 6. Relationship between % mortality per day of capelin larvae (mean, $n = 2$) resulting from predation by ctenophores under increasing densities of capelin larvae. In situ enclosure experiments were used to develop this data set. Vertical bars show the range.
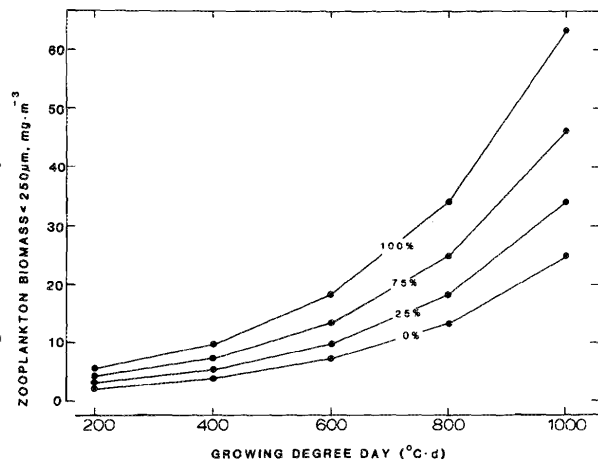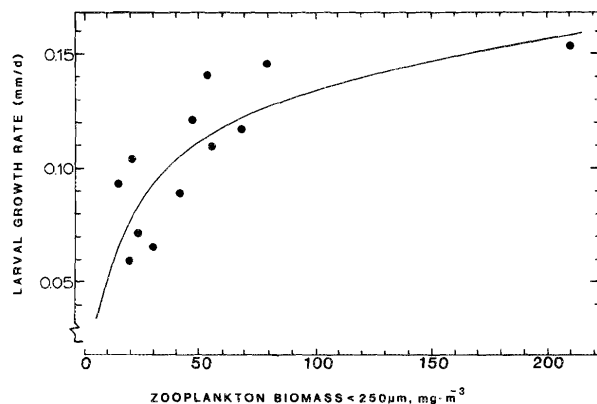

FIG. 8. Relationship between daily larval growth rate and biomass of edible (<250 μm) zooplankton determined from experiments conducted with in situ enclosures.

FIG. 7. Simulation of model (Table 2) which predicts the edible (<250 μm) zooplankton biomass as a function of cumulative growing degree days and the % daily duration of onshore wind (indicated by values intersecting each line).
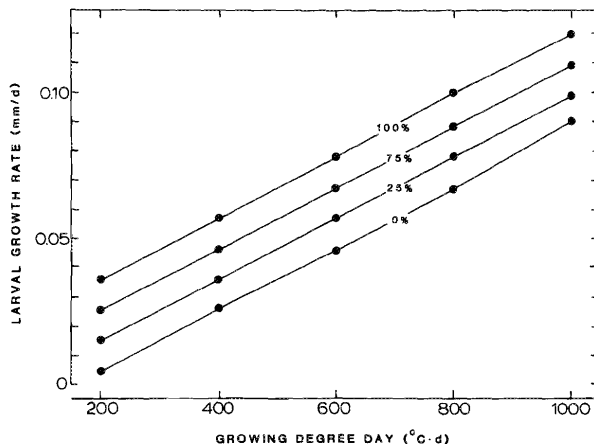

FIG. 9. Daily growth rate of larval capelin predicted from wind-induced changes in edible zooplankton biomass (see Fig. 9 and equation 2). Note elevation in larval growth rate under increasing duration of onshore wind (% values) at each growing degree day.

water mass replacement (Fig. 3, 5). Average densities of chaetognaths and jellyfish during onshore winds are below the ctenophore densities tested (Fig. 7). Strong evidence of predator satiation was obtained (Fig. 6). The equation to predict larval mortality (y, %/d) is:

(1) $y = 26.51 - 3.3409 \ln$ (no. of capelin larvae/m³),

$$R^2 = 0.51, P < 0.01, n = 9.$$

This effect, coupled with the reduction in predator densities in the water mass occupied by capelin (Fig. 5), should significantly reduce mortality due to predation during early larval drift in capelin.

Growth Responses

The effect of water mass replacement on the biomass of the

edible zooplankton size fraction is depicted in Fig. 7 which portrays a simulation of the average biomass of this fraction at various growing degree days (calculated from April 1) and wind combinations. This simulation is based on the multiple regression model detailed in Table 2. The significant influence of wind condition at any stage in the growing degree day cycle is apparent.

To assess the potential effect of this elevation in edible zooplankton biomass on larval growth rates we again performed a series of enclosure experiments in which the biomass of edible zooplankton was manipulated. All enclosures were identical in design to those previously described. Twelve trials were performed in 1980. Four enclosures were constructed of <5 μm mesh. These were filled with 10 μm filtered seawater to produce below ambient edible zooplankton biomasses. The remaining eight enclosures were constructed of 150 μm nitex. All eight were allowed to fill with water which passed through the mesh. The zooplankton

biomass of six of these enclosures was enhanced by adding zooplankton collected with a $\frac{1}{2}$-m, 150-μm standard plankton net towed at a velocity of <0.5 m·s^{-1}. Two enclosures received the contents of paired 18-m^3 samples, two the contents of paired 54-m^3 samples, and two the contents of paired 120-m^3 samples. All samples were passed through a 355-μm filter before addition. Zooplankton >355 μm was discarded. Six hundred and fifty yolk sac larvae were collected from the beach sediments for stocking in each enclosure. Six hundred were stocked and the remaining 50 were measured to the nearest 0.1-mm TL to determine the mean length at stocking in each enclosure. No significant difference in the mean length of stocked fish in the 12 enclosures was observed ($P > 0.05$). Duration of the trials was 7 d. The average water temperature was 6.5°C during these experiments. At the end of the trial the enclosures were lifted, the contents collected from the cod end, and the final size of the remaining larvae and the dry weight biomass of the <250-μm, 250- to 355-μm, and >355-μm size fractions were determined. Daily larval growth rate was correlated with the final biomass of the three zooplankton size fractions. Daily growth rates were strongly positively correlated with the biomass of the <250-μm size fraction ($r = 0.79$, $n = 12$, $P < 0.01$). No correlation was observed between larval growth rates and the biomass of the 250- to 355-μm ($r = -0.11$, $P > 0.05$) and >355-μm ($r = -0.46$, $P > 0.05$) size fractions, supporting our earlier assumptions regarding the importance of the <250-μm size fraction as food for larval capelin. The relationship between daily growth rates (y, mm/d) and the biomass of the <250-μm size fraction (x, μg/m^3) is illustrated in Fig. 8. The equation to predict larval growth rate is:

$$y = 0.0337 \, \ell nX - 0.2524, \quad R^2 = 0.62, P < 0.01.$$

The potential effects of changes in food level resulting from water mass replacement were assessed by substitution of predictions of the average biomass of the edible zooplankton size fraction at varying times (growing degree days), and under varying wind conditions, into the model describing the relationship between food levels and daily growth rate (Fig. 8). The results, depicted in Fig. 9, indicate daily growth rates could be increased by up to eightfold under conditions of continuous onshore wind. A more realistic increase, given the nature of the wind patterns in eastern Newfoundland, is 3.2- to 5.5-fold. The effect of this increase in daily growth rate on larval survival is presently unquantified but is under investigation. Several authors have hypothesized that accelerated growth rates yield better survival because the larvae more rapidly pass through the size range at which they are most vulnerable to the suite of predators to which they are exposed (Ware 1975; Jones 1973).

At a more general level, it is worthy of note that the abundance of eggs and larvae of 11 marine fish species (*Tautogolabrus adspersus, Glyptocephalus cynoglossus, Gadus morhua, Hippoglossoides platessoides, Liparus atlanticus, Pseudopleuronectes americanus, Sebastes marinus, Clupea h. harengus, Myoxocephalus aenaeus, Ulvaria subbifurcata,* and *Stichatus punctatus*) represented in our plankton collections also showed a strong association with surface water masses (Fig. 3). Association with this water mass presumably conveys to them advantages similar to those experienced by capelin.

In our review of the literature on larval fish ecology we have been struck by the paucity of studies documenting reproductive and behavioral patterns which may minimize predator impact and maximize food availablility. Exceptions are the works by Bams (1969), Ware (1977), and Fortier and Leggett (1982). Such strategies, commonly exhibited among other organisms (Lloyd and Dybas 1966; Janzen 1969, 1971; Smith 1970; Giesel 1976), are probably more common among fishes than is currently evident. The lack of such examples among fishes stems, in part, from the survey approach to larval fish studies which are often of limited scope and typified by large-scale (spatial and temporal) sampling programs. Given these facts greater caution should be exercised when attempting to infer mechanisms from the results of such studies in the absence of a thorough understanding of the system dynamics; the inference that an inverse relationship between predator and larval fish abundances results from predation (Alvariño 1981; Möller 1980), or that a sudden change in larval densities in response to abrupt temperature or salinity changes, indicative of water mass exchange, is due to the temperature or salinity effect (Dickson et al. 1974; Postuma and Zijlstra 1974) being cases in point. Or, as Richard Barber, Duke University, has expressed it "physical and biological processes are in sequence, so understanding the ecosystem requires understanding the sequence. A [marine] biologist ... with no understanding of the meteorology or currents is just whistling in the dark" (Hartline 1980). We concur that the measurement scale must be reduced (in space and time), and that an ecosystem approach must be adopted if future studies are to be successful in defining the important physical and biological processes regulating the dynamics of larval fish populations.

Acknowledgments

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