

# Wind-Forced Hydrodynamics and Their Interaction with Larval Fish and Plankton Abundance: A Time-Series Analysis of Physical–Biological Data<sup>1</sup>

Christopher T. Taggart<sup>2</sup> and William C. Leggett

*Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, Que. H3A 1B1*

Taggart, C. T., and W. C. Leggett. 1987. Wind-forced hydrodynamics and their interaction with larval fish and plankton abundance: a time-series analysis of physical–biological data. *Can. J. Fish. Aquat. Sci.* 44: 438–451.

We evaluated methods to measure simultaneously biological and physical properties essential for estimating short-term mortality of larval fish. We used the data to test Templeman's watermass exchange hypothesis and the associated safe-site hypothesis. Synoptic estimates of larval capelin (*Mallotus villosus*) and microzooplankton particle density were obtained simultaneously with a scale resolution of 200 m (horizontal), 2–4 m (vertical) and 6–8 h (temporal) in a 1-km<sup>2</sup> coastal embayment in eastern Newfoundland. Statistically significant population estimates were derived from multiple regression models incorporating a limited number of samples. Spectral analysis of wind and current time-series and analysis of large-scale temperature oscillations were consistent with Templeman's hypothesis. Nearshore current responded to cross-shore wind forcing at periods of 2–6 d. Larval capelin abundance oscillations were coherent with wind and with current at periods of ~5 d, consistent with the watermass exchange and safe-site hypotheses. Although larvae and microzooplankton abundances showed similar spectral density and were in phase, their coherence was weak. Integrated measures of onshore wind and of the onshore–offshore wind spectrum were correlated, and either can be used as a composite measure of the considerable interannual variation evident in the frequency, magnitude, and duration of onshore winds, and hence of watermass exchange.

Afin de déterminer la mortalité à court terme des larves de poisson, les auteurs ont évalué des méthodes de quantification simultanée des propriétés biologiques et physiques. Les données ont été utilisées pour vérifier l'hypothèse de Templeman relative à l'échange de la masse d'eau et l'hypothèse connexe sur l'existence d'un endroit sécuritaire. Dans le cas des larves de capelan (*Mallotus villosus*) et de la densité particulaire du microzooplancton, ils ont obtenu simultanément des estimations synoptiques avec une résolution à l'échelle de 200 m (horizontal), de 2–4 m (vertical) et de 6–8 h (temporel) dans une baie d'une superficie de 1 km<sup>2</sup> située sur le littoral est de Terre-Neuve. Des estimations de population statistiquement significatives ont été tirées de modèles de régression multiple regroupant un nombre limité d'échantillons. Une analyse spectrale des séries chronologiques de données sur le vent et les courants et l'analyse des oscillations de la température à grande échelle s'accordaient avec l'hypothèse de Templeman. Les courants littoraux ont réagi aux vents de travers qui augmentaient d'intensité par périodes de 2 à 6 j. Les oscillations de l'abondance des larves de capelan correspondaient aux vents et aux courants par périodes de ~5 j et aux hypothèses relatives à l'échange de la masse aqueuse et à l'endroit sécuritaire. L'abondance des larves et du microzooplancton montrait une densité spectrale semblable et ceux-ci étaient en phase, mais leur cohérence était faible. Des quantifications intégrées du vent du large et du spectre du vent du large et du vent de terre étaient en corrélation; les deux mesures peuvent donc être utilisées comme mesure composée de l'importante variation interannuelle évidente dans la fréquence, la force et la durée des vents du large et donc de l'échange de la masse aqueuse.

Received October 10, 1985

Accepted October 22, 1986

(J8492)

Reçu le 10 octobre 1985

Accepté le 22 octobre 1986

Numerous attempts to measure larval fish mortality during early drift suggest that mortality can exceed 80% in 30 d or less (e.g. Blaxter 1974; Dahlberg 1979; Henderson et al. 1984; Ware and Lambert 1985; Fortier and Leggett 1985; Hewitt et al. 1985). However, there is no direct field evidence demonstrating that early larval

mortality is related to recruitment failure, although there are numerous related hypotheses (Hjort 1914; Cushing 1972, 1975; Lasker 1975; Tilseth and Ellertsen 1984; Percy 1962; Nelson et al. 1977; Bailey 1981; Frank and Leggett 1982b; Leggett et al. 1984; Sinclair et al. 1985). It is no secret that this lacuna stems mainly from the appreciable logistic problems inherent in quantitative sampling of larval fish populations and the use of inadequate space–time sampling scales (Smith 1978, 1981; Sharp 1980). Furthermore, there is little evidence regarding the relative impact of physical variables on realized mortality and on the mortality observed, which is potentially biased by the constraints of the existing techniques.

<sup>1</sup>Contribution to the program of GIROQ (Groupe interuniversitaire de recherche océanographique du Québec).

<sup>2</sup>Present address: Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2, or Department of Biology, Dalhousie University, Halifax, N.S. B3H 4J1.

These problems notwithstanding, there remains an important need to develop the sampling protocols and analytical techniques required to study and confidently estimate larval mortality directly in the field. Twenty years ago, Gulland (1965) recognized the importance of a thorough egg and larval survey designed to measure mortality directly and recommended that sampling must be frequent and concentrated in a small and well-defined area if meaningful results are to be obtained. The need to evaluate biological phenomena in light of the relevant physical variables, and to do so within appropriate time and space scales, has been repeatedly stated (Sharp 1980; Rothlisberg 1982; Norcross and Shaw 1984; Frank and Leggett 1982b; Fortier and Leggett 1984). A more general call for the use of this interdisciplinary approach has been voiced by Legendre and Demers (1984).

Fulfilling these requirements renders more difficult the already demanding task of measuring changes in abundance of larvae in space and time while at the same time continuously accounting for immigration and emigration, both of which are essential to develop precise measures of the dynamics of any population. Fortunately, during early larval drift, the horizontal movements of larvae are largely passive (Fortier and Leggett 1982). However, active vertical migration can make estimates of dispersal distances and directions, and therefore estimates of immigration, emigration, and mortality, highly dependent on the speed and direction of currents in space and with time (Rothlisberg 1982; Fortier and Leggett 1983). Several points should be seriously considered *prior* to examining mortality relationships (Smith 1981):

- (1) Different sampling strategies are required to test different hypotheses; space-extensive surveys for hypotheses concerned with transport and time-intensive surveys for those concerned with the critical period or food availability.

- (2) If hypotheses directly related to food limitation are to be evaluated, sampling must be conducted with the spatial and temporal intensity sufficient to also sample the food of the larvae with high definition.

- (3) The paucity of tests of the various hypotheses to date has been caused by failure to identify the spatial and temporal sampling intensity required to address any single hypothesis.

We conclude the following:

- (1) Research must concentrate *first* on developing methods that allow for precise short-term mortality estimates, and only then on examining how mortality may relate to various biotic/abiotic influences.

- (2) The methods employed will require sampling to be conducted at scales which approach those relevant to fish larvae, and at the scale of variation inherent to their physical environment.

- (3) Initially, it is necessary to develop and evaluate these methods in well-defined areas where the variation in the larval population size (including the effects of immigration and emigration) and variation in the physical environment can be assessed synoptically and with confidence (John 1984).

- (4) It is also necessary to begin with a temporally intensive sampling programme over a small area near the maximum concentration of larvae (Smith 1981).

Some success with this approach has been achieved by Frank and Leggett (1981a, 1981b; 1982a, 1982b; 1983a, 1983b) in their studies on the causes and magnitude of egg and pre-emergent larval mortality in beach-spawning capelin (*Mallotus villosus*) and the relationship between the sources of mortality and year-class variation in the species (Leggett et al. 1984).

We adopted a similar approach in this study.

Our overall objective was to develop precise estimates of short-term larval mortality in capelin during early drift and to evaluate the relationship between this mortality and food availability and larval abundance. In this paper we detail and evaluate sampling and analytical techniques employed to simultaneously measure biological and physical properties and sampling bias. These measurements are essential to the eventual determination of mortality estimates (in prep.).

The data developed are of the time-series form and therefore have the additional attribute of being ideally suited to a critical test of Templeman's (1966) wind-driven coastal watermass exchange hypothesis. Templeman proposed that intraseasonal variations in nearshore cod abundance in coastal Newfoundland could be explained by intermittent oscillations of warm and cold watermasses in the nearshore zones. He further hypothesized that this phenomenon was wind-driven, implying that coastal regions directionally opposite each other with respect to the prevailing winds would experience reciprocal oscillations of the two watermass types. This hypothesis was invoked by Frank and Leggett (1982b) to account for associated time-dependent variations in the abundance of emergent larval fishes and their planktonic prey and predators. This hypothesis is also fundamental to a capelin recruitment model (Leggett et al. 1984), which has been used as the basis for predictions of inshore whale abundance (Whitehead and Carscadden 1985).

## Methods and Materials

### Study Site

The study was conducted in Bryants Cove (47°40.5'N, 53°11.0'W), Conception Bay, Newfoundland. The cove is approximately 1 km long and 1 km wide at its mouth at which point depth exceeds 20 m (Fig. 1). Cove volume was estimated to be  $5.54 \times 10^6$  m<sup>3</sup>. Capelin spawn on a fine-gravel beach located at the head of the cove. Eggs incubate in the sediments, and hatched larvae are eventually dispersed into the water column during the occurrence of onshore winds (Frank and Leggett 1981a, 1981b).

### Physical Oceanographic Data

Current speed and direction, temperature, and salinity were measured in 1982 and 1983 using five Aanderaa RCM4 current meters moored at three stations (Stations 1–3, Fig. 1). In 1983 an additional current meter was moored 4 km northeast of the cove (Station 4). Data were collected at 10-min intervals from late June to early August of each year. Depth and data record lengths for each current meter are presented in Table 1. Current direction data were decomposed into U (offshore, positive northeast) and V (longshore, positive northwest) vectors resolved around 54°, corresponding to the offshore orientation of the cove axis (Fig. 1).

Current meter data were decimated (*sensu* Koopmans 1974) to hourly values using an A6-A6-A7 filter (Godin 1972). This produced a "smoothed" signal free of high-frequency variations (periods <1 h). The data were further treated with an A24-A24-A25 filter to produce hourly "lowpassed" data to suppress semidiurnal and diurnal tide variations (Godin 1972) and to provide more representative values for comparison with the biological data (see below). Tidal analysis of the data (Forman 1978) revealed the residual circulation to be dominant

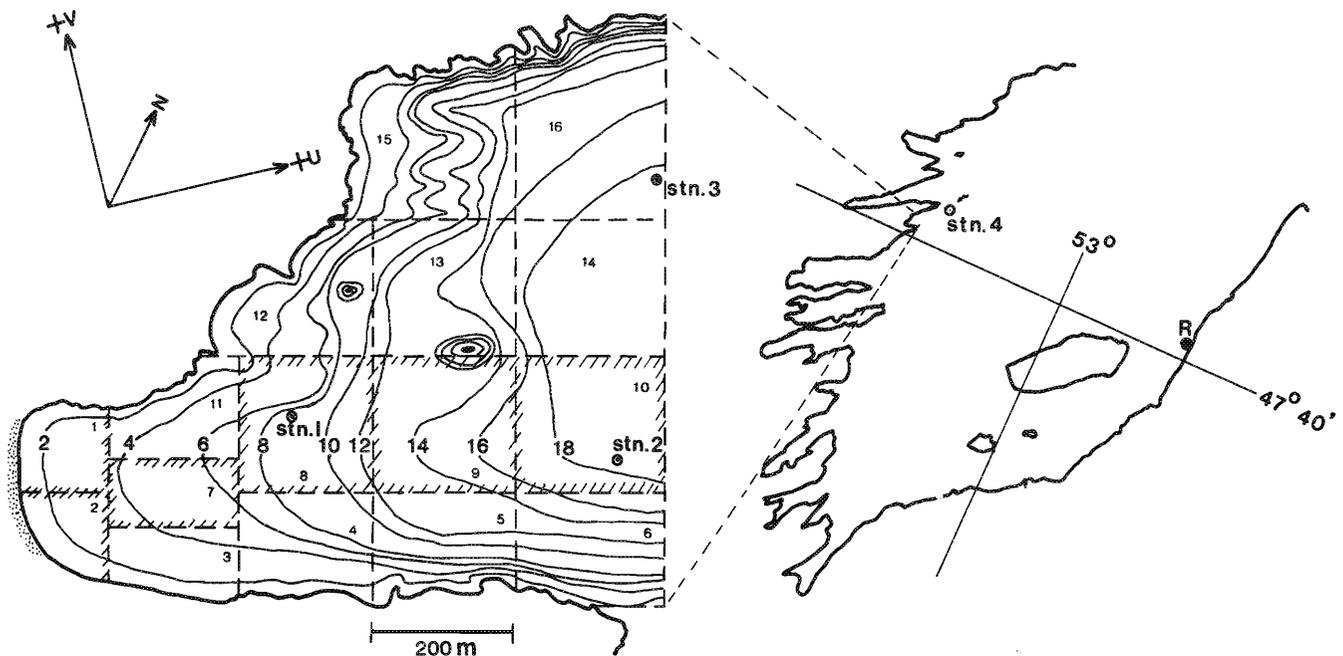


FIG. 1. Map of Conception Bay, Nfld., and bathymetric map of Bryants Cove detailing depth (m) and the dimensions and positions of the 16 grid sampling stations (1–16), the transect stations (hatched), positions of the current meter moorings (Stations 1–4), and the location of the Ryan thermograph recorder at Portugal Cove (R). The location of the capelin spawning beach is marked with stippling. Directions of U and V decomposition of wind and current are shown.

TABLE 1. Bottom and mooring depths, current speed, and length of data series for Aanderra recording current meters in Bryants Cove, Nfld.

	Year	Recording period	Depth (m)	Bottom depth (m)	Average current (cm/s)
Station 1					
Shallow	1982	10 June– 6 Aug.	4.5	9.3	6.4
	1983	13 June– 3 Aug.	4.5		6.0
Station 2					
Shallow	1982	10 June– 6 Aug.	5.9	18.3	5.5
	1983	20 June– 3 Aug.	6.4		5.3
Deep	1982	10 June– 6 Aug.	14.5		4.4
	1983	20 June– 3 Aug.	15.0		4.0
Station 3					
Shallow	1982	10 June– 6 Aug.	9.2	20.0	6.2
	1983	25 June–13 Aug.	5.8		5.4
Deep	1982	10 June– 6 Aug.	17.0		3.7
	1983	25 June–13 Aug.	15.0		3.9
Station 4					
Shallow	1983	20 June–10 Aug.	7.0	57.0	11.3

and the current at tidal frequencies to be weak. Hourly wind speed and direction data (Environment Canada, Atmospheric Environment Service, monthly meteorological summaries) were obtained for St. John's airport, located 19 km east of the centre of Conception Bay. Upwind directions in 22.5° increments were rotated 180° to downwind (oceanographic convention) and were then decomposed into U and V vectors also resolved around 54°. The hourly wind data were smoothed with a single pass of a symmetrically weighted moving aver-

age, with weightings based on the A6-A6-A7 Godin filter. Lowpassed wind signals were produced by treating the smoothed series with a symmetrically weighted moving average based on the A24-A24-A25 Godin filter. Wind stress ( $t_x$  and  $t_y$ ) was calculated for the U and V-components, respectively, using the formula of Smith and Banke (1975). Wind stress was used in most of our analyses of wind data, as it reflects the energy transferred to surface waters.

Ryan temperature records taken at the bottom (10 m) on the east side of Conception Bay (Fig. 1), directly opposite Bryants Cove, were obtained from D. Keats (Memorial University of Newfoundland, St. John's, Nfld.).

#### Biological Data and Development

In 1981–83, plankton samples were pumped at geographically defined stations within the cove using the system developed and evaluated in Taggart and Leggett (1984). An 80- $\mu$ m plankton net was employed to collect samples at the pump discharge. In 1983, samples were collected at least daily during daylight between 25 June and 9 August (with the exception of 26 June and 5, 7, and 31 July). Sampling frequency was increased to once every 6–8 h with the occurrence of onshore winds when larval emergence was pronounced. A total of 68 sampling “sessions” were conducted over a period of 46 d. During each session we systematically sampled 1–2 m<sup>3</sup> (0.6–0.8 m<sup>3</sup>/min) from each of three depth strata (0–2, 2–5, and 5–9 m, where permitted by bathymetry) either on a grid of 16 stations (a total of 31 station-strata samples) covering the entire cove or on a “transect” of 6 stations (13 station-strata samples) along the main axis of the cove and perpendicular to the spawning beach (Fig. 1). Preliminary sampling conducted in 1981 demonstrated that larval density estimates from the transect provided accurate estimates of density over the entire grid ( $r^2 = 0.98$ ,  $n = 33$ ). Grid stations were spaced on approximate 200-m centres, each grid covering  $4 \times 10^4$  m<sup>2</sup>.

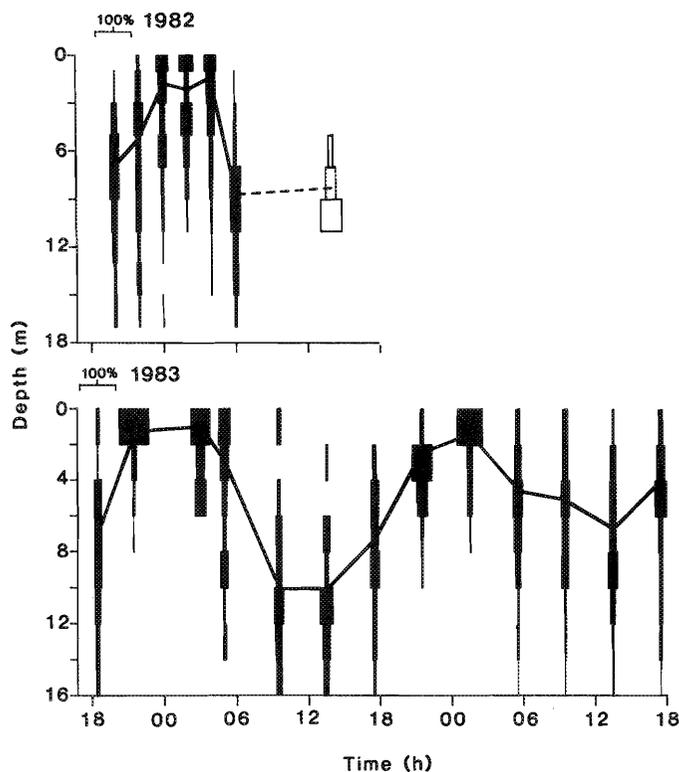


FIG. 2. Proportional diel depth distribution of capelin larvae sampled in Bryants Cove on 9–10 August 1982 and 26–28 July 1983. The solid line joins the statistical centre-of-mass of each distribution. No samples were collected below 11 m during the last sample period of 1982.

Samples were horizontally and vertically integrated by moving the sampling intake within the confines of the station while at the same time undulating the intake within the specified depth stratum. Grid boundaries were determined during daylight by noting the boat position relative to specific shore markers and at night relative to narrow-beam marker lights installed around the cove. The 16-station grid was sampled within 2 h and the 6-station transect within 1 h.

All samples were preserved immediately in 4% formalin–seawater buffered with sodium borate. Samples were subsequently completely sorted for capelin larvae and the remaining biota were then filtered through a 750- $\mu\text{m}$  sieve. The fraction <750  $\mu\text{m}$  was subsampled and its particle size composition was determined with a TA-II Coulter Counter fitted with a 2000- $\mu\text{m}$ -aperture tube. The sampling tube was calibrated with uniform spherical particles with diameters of 91, 109, 175, 278, 350, and 472  $\mu\text{m}$ . Prior to counting, each subsample was rinsed over a 40- $\mu\text{m}$  mesh, drained, and completely mixed into 1000 ml of a 75% (by volume) glycerol–distilled water (5% NaCl by weight) electrolyte. Contamination of the electrolyte by bubbles which formed on the external electrode was avoided by enclosing the electrode in a glass tube open at either end, with the upper end extending above the surface of the electrolyte. Background counts of the electrolyte were maintained below 2% of the average total particle count. Ten particle size classes were counted, but for the analysis we performed for this study we used only the particles with equal spherical diameter (esd) of 90 and 108  $\mu\text{m}$ . This was done because most elongate and slender fish larvae feed on prey that are between 20 and 50% of their mouth width (Stoecker and

Govoni 1984; Hunter 1981; Theilacker and Dorsey 1980). We determined that mouth width (MW) was strongly correlated with total length (TL) in postemergent capelin larvae ( $MW = 0.03843TL + 0.03903$ ;  $r = 0.70$ ,  $n = 62$ ). The average size of postemergent larvae is 5 mm (Taggart and Leggett 1984; Frank and Leggett 1982a). Therefore the appropriate prey size would range between 46 and 115  $\mu\text{m}$  esd (see also Frank and Leggett 1986). The smallest size class counted (75  $\mu\text{m}$  esd) was excluded, as it may have been undersampled by the 80- $\mu\text{m}$ -mesh net.

Estimates of the total abundance of larval capelin in Bryants Cove during each sampling session were made by first summing the stratum density estimates at each grid station after multiplying by the respective stratum volume. Subsequently the abundance estimate at each grid station was corrected where applicable for bias due to diel migration below the 9-m maximum sampling depth and bias resulting from sampling only the 0- to 2-m stratum at the three outermost stations along the south side of the cove (see below). Finally the abundance estimates were summed over all stations.

Diel sampling conducted at station 10 on the transect (see Fig. 1) at 2-m depth-integrated intervals over a period of 19 h in 1982 and 48 h in 1983 revealed distinct vertical migration of postemergent capelin larvae over a depth range of 16 m (Fig. 2). The centre of distribution (the depth above which 50% of the sampled population was found) ranged over an average vertical distance of 7.2 m. Calculations of proportional depth distribution indicated that upwards of an additional 50% of the estimated larval populations sampled between 0 and 9 m could be found below 9 m during daylight hours. The migration patterns observed on these two specific occasions were consistent with the proportional depth distribution of larvae from all sampling sessions in 1981–83 at grid stations where sampling was performed to 9 m (Fig. 3). Although harmonic regression is generally used to model the observed diel pattern (Legendre and Legendre 1983), conditional time-based polynomial models were found to have greater predictive power and were therefore used to correct the systematic bias in the population estimates. Corrections were applied to the larval abundance estimates at the appropriate stations according to the time of sampling and the models illustrated in Fig. 4.

At times when only the six-station transect was sampled, multiple regression models of the relationship between larval density estimates from transect station-strata and estimates from grid station-strata were used to develop abundance estimates of the entire grid. These models were developed from data collected during 41 sessions when the 31 station-strata were sampled on the grid and were used to reconstruct abundance estimates for 27 sessions when only the 13 station-strata on the transect were sampled. All models were restricted to no more than 6 of the 13 station-strata density estimates, and model selection was made on the basis of Mallows'  $C_p$  statistic (see Hocking 1976). Each estimate retained was significant in its contribution to the regression at  $p < 0.05$ . The number of station-strata estimates in each model and the correlation coefficients for each are provided in Table 2. The average density for the "whole-cove" was calculated by dividing the sum of the station-strata absolute estimates by the sum of the station-strata volumes (cove volume). The relationship between the observed whole-cove average density and that estimated by the multivariate models (after independent diel bias correction) is provided in Fig. 5 ( $r^2 = 0.96$ ,  $n = 41$ ,  $p < 0.0001$ ).

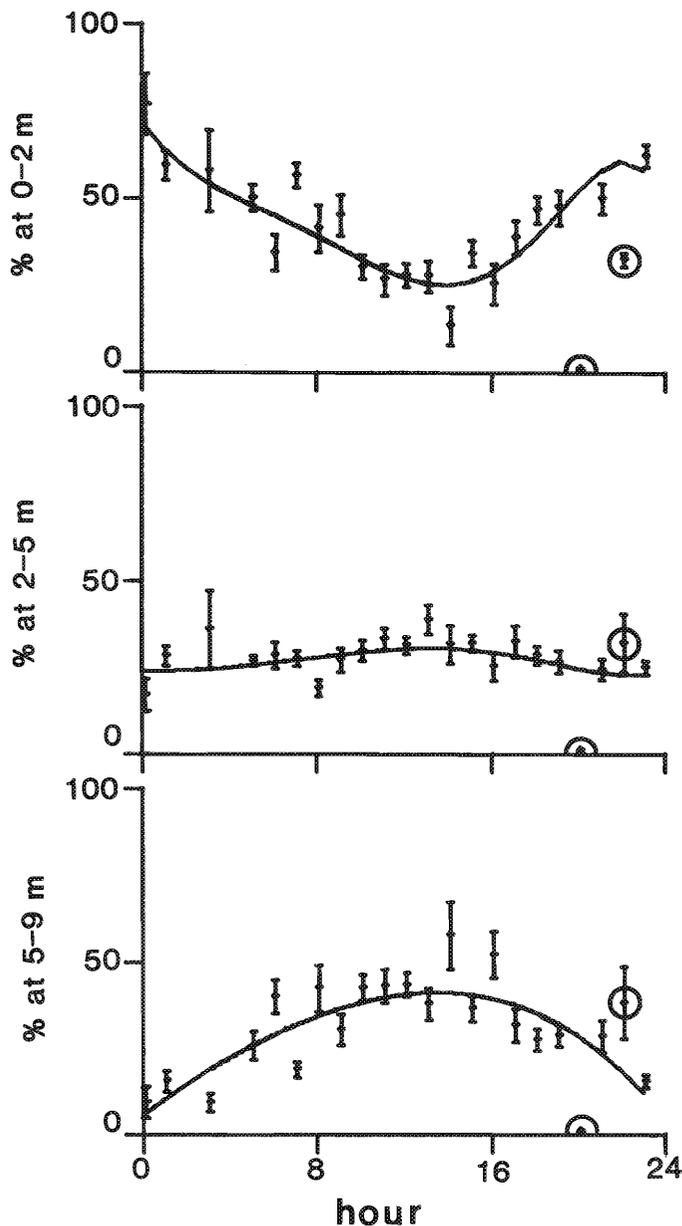


FIG. 3. Proportional diel depth distribution of capelin larvae from all sampling sessions in 1981, 1982, and 1983. Only data from stations where three depth strata (0-2, 2-5, 5-9 m) were sampled are included. The best fitting time-based polynomial joins the average percent ( $\pm 1$  SE). A total of  $N = 589$  samples make up the series. Circled averages indicate time points where  $n < 3$ .

As we were not concerned with eventually calculating mortality estimates of the plankton particle size classes, and as there was no systematic diel pattern in their vertical distribution, we simply estimated the average whole-cove density by calculating the geometric average of the density estimates from all station-strata sampled during each session.

#### Analyses

Relationships between the various physical and biological time-series were examined by spectral analyses using the ARIMA and SPECTRA procedures of SAS (1982) and the Spectral Analysis System (Cracker Version 1.011a) developed at the Bedford Institute of Oceanography. Spectral analysis is

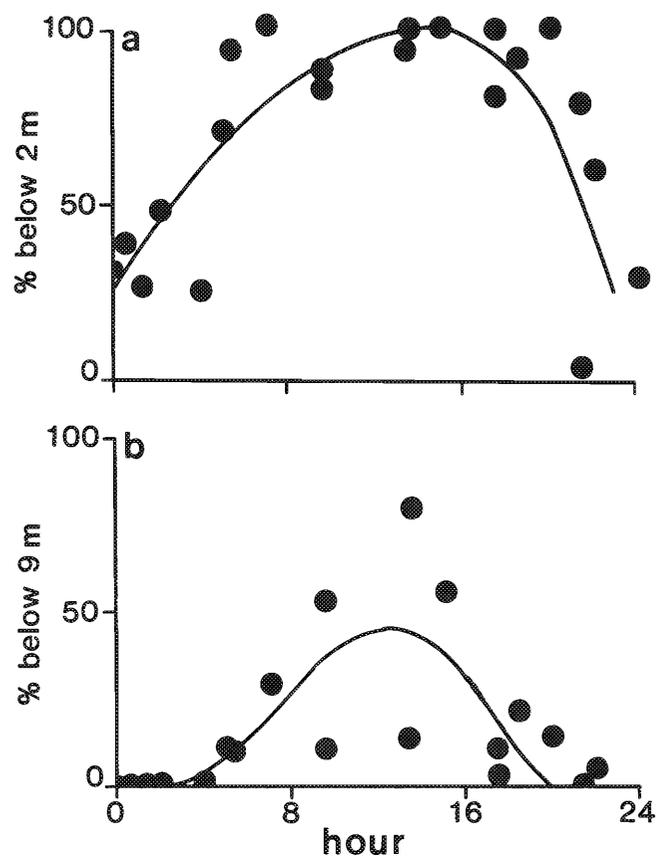


FIG. 4. Graphical description of the time-based polynomial functions fitted to the combined diel depth distributions of capelin larvae presented in Fig. 2. These models were used to correct for diel bias in the density estimates at (a) stations along the south side of the cove (see Fig. 1) where only the 0-2 m stratum was sampled and (b) deep stations where the depth exceeded 9 m.

an analysis of variance approach to a time-series which is assumed to be a single realization of a stochastic process. In the analysis, the variance in the signal (the time based measure of wind, current, larval densities, plankton particle densities, etc.) around its mean is partitioned into contributions (the spectral density estimates) at frequencies which are harmonics of the length of the time-series. The analysis thus identifies those frequencies or periods where most of the variance in the signal is concentrated. The spectral estimates were multiplied by their corresponding frequency and plotted against the common logarithm of frequency to ensure that equal areas under the curve represented equal contributions to the total variance (Denman 1975). Cross-spectral analysis provided coherence spectra (the degree of mutual dependence between two signals at given frequencies) and phase spectra (the amount of shift or lag between the first and second signal). Statistical significance was assessed by splitting the time-series into 16 blocks of equal length with 50% overlap and performing spectral analysis on each. Fewer blocks decrease the statistical significance of the estimates, while a greater number limit the estimates to be calculated at only higher frequencies (shorter periods). Cross-spectral analysis between different physical variables was performed on the smoothed data. The lowpassed oceanographic time-series were used in the cross-spectral analysis with the biological variables. As a result of the frequency of biological sampling, only frequencies  $< 1$  cpd were considered.

TABLE 2. Number of independent transect station-strata estimates ( $N$ ) and multiple correlation coefficient ( $R$ ) for each multiple regression model used to predict larval density estimates of grid station-strata not on the transect ( $n = 41$  for each model and all models had significant  $F$  statistics ( $p < 0.0001$ )).

Station	Stratum (m)	$N$	$R$
3	0-2	2	0.767
4	0-2	4	0.847
5	0-2	2	0.743
6	0-2	6	0.810
11	0-2	5	0.912
11	2-5	2	0.839
12	0-2	4	0.864
13	0-2	6	0.939
13	2-5	5	0.886
13	5-9	2	0.843
14	0-2	3	0.831
14	2-5	4	0.895
14	5-9	3	0.879
15	0-2	3	0.887
15	2-5	2	0.907
16	0-2	3	0.837
16	2-5	4	0.863
16	5-9	6	0.849

## Results

### Circulation Pattern

The circulation pattern in Bryants Cove was cyclonic in both the upper and lower strata of the water column and was consistent from year to year as shown by progressive vectors for each current meter (Fig. 6). The average current speed at each station was also consistent between years (Table 1). The average current measured further offshore at Station 4 in 1983 was predominantly north-eastward with an average speed of 11.3 cm/s (Fig. 6; Table 1). The depth-averaged speed on the inflow side of the cove (Station 3) was 4.95 and 4.65 cm/s in 1982 and 1983, respectively, and matched the depth-averaged speed on the outflow side of the cove (Station 2) in each year. The approximate flushing time of the cove calculated simply from the average circulation (4.8 cm/s) was 19 h.

### Physical Relationships: Wind and Current

Comparison of time-series (both smoothed and lowpassed) of the U-components of wind (Fig. 7b) and current (Fig. 7a) measured at Station 4 in 1983 suggests strong correlation. The power spectra of each, and of wind stress in the onshore-offshore direction ( $t_r$ ), indicate highest spectral density in the frequency bands centred at periods of 2.7 and 5.3 d (Fig. 8a, 8b). The maximum at 0.7 d in the current spectrum most probably reflects the inertial period (0.67 d) for this latitude, and the minor maximum at 1 d in the wind stress may reflect a sea breeze phenomenon. The two series (current<sub>u</sub> and  $t_r$ ) were significantly coherent at these periods, with a smooth and slightly negative phase spectrum indicating a lagged current response to the wind (Fig. 9a, 9b). The coherence and phase spectra of wind<sub>u</sub> and current<sub>u</sub> were virtually identical. We suggest that at periods of 2-6 d the local currents are primarily wind driven. Analysis of the longshore wind-stress ( $t_r$ ) revealed no significant coherence with either current component.

A comparison of temperature records for Bryants Cove (Station 4) and for Portugal Cove (24 km on the east side of

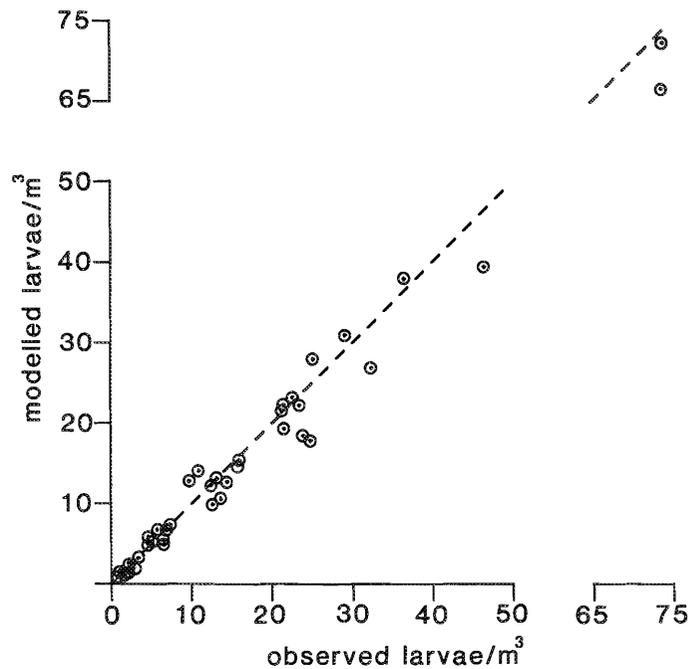


FIG. 5. Relationship between the observed and modelled whole-cove average density (total number per volume of cove). Modelled values were generated from multiple regression models (see Table 2) relating grid station estimates to transect station estimates. The slope of the relationship is not significantly different from 1.0 (broken line) and  $r^2 = 0.96$  ( $n = 41$ ,  $p < 0.0001$ ).

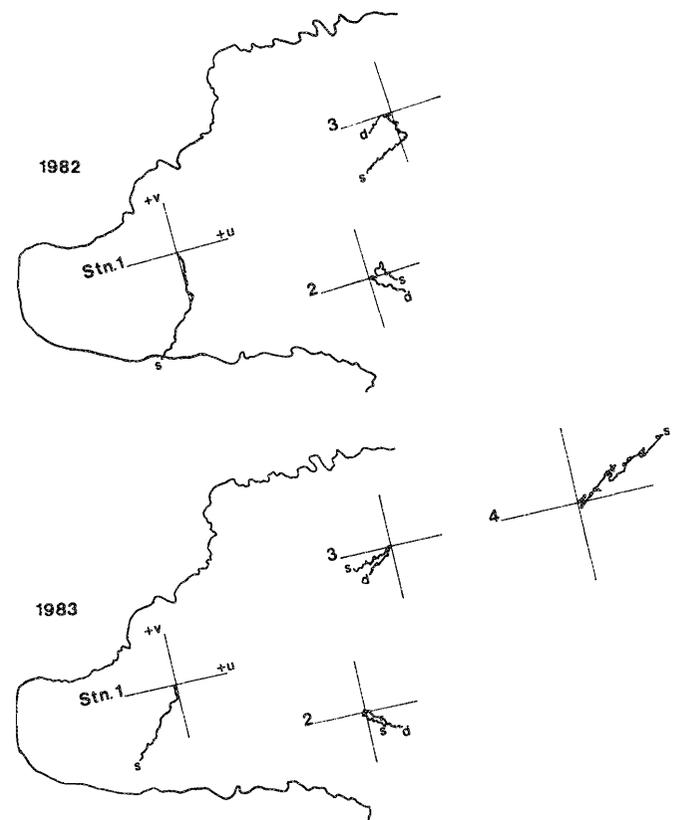


FIG. 6. Progressive vector diagrams of the smoothed current velocity for each of the deep (d) and shallow (s) instruments at each mooring station in Bryants Cove between June and August of 1982 and 1983. Positive U is oriented  $54^\circ$  east of north, and each axis from the origin represents 15 km. Note that Station 4 is not located at its true map position.

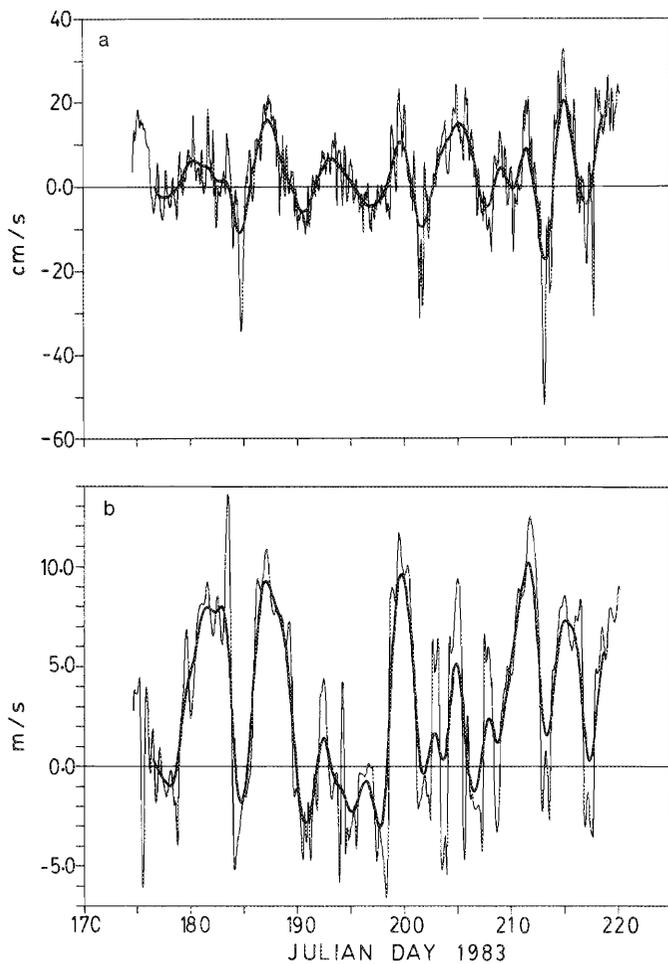


FIG. 7. Time-series (1983) of the smoothed and lowpassed (heavy line) hourly (a) current and (b) wind U-components (positive offshore; negative onshore). Wind data are from St. John's airport and current data are from Station 4 at 7 m depth.

Conception Bay, Fig. 1) strongly suggests that the wind response is not a purely localized phenomenon (Fig. 10a, 10b). The two series were significantly coherent between 2- and 6-d periods, with a  $-120^\circ$  phase shift indicating a lagged ( $\sim 4$  h) inverse relationship (Fig. 11a, 11b). The same analysis conducted on data collected in 1982 showed similar results. In addition, both series mimic (inversely in the case of the east side temperature) the major oscillations seen in the wind and current signals shown in Fig. 7. Both temperature series were significantly coherent with  $t_x$  at 5.3 d ( $-130^\circ$  phase with Bryants Cove temperature and  $0^\circ$  phase with Portugal Cove temperature). There was no significant coherence between either temperature series and  $t_x$ . The above analyses conducted with wind stress and salinity and water density showed virtually identical results, illustrating that temperature is a good indicator of watermass and that wind stress in the onshore-offshore direction is responsible for watermass exchanges in the nearshore.

#### Biological Relationships: Larvae and Microzooplankton

Spectral analysis requires that a fixed sampling frequency is strictly maintained and that the resultant series is stationary (i.e. stable variance across the series). Neither requirement is typical of most biological data. As spectral analysis is reason-

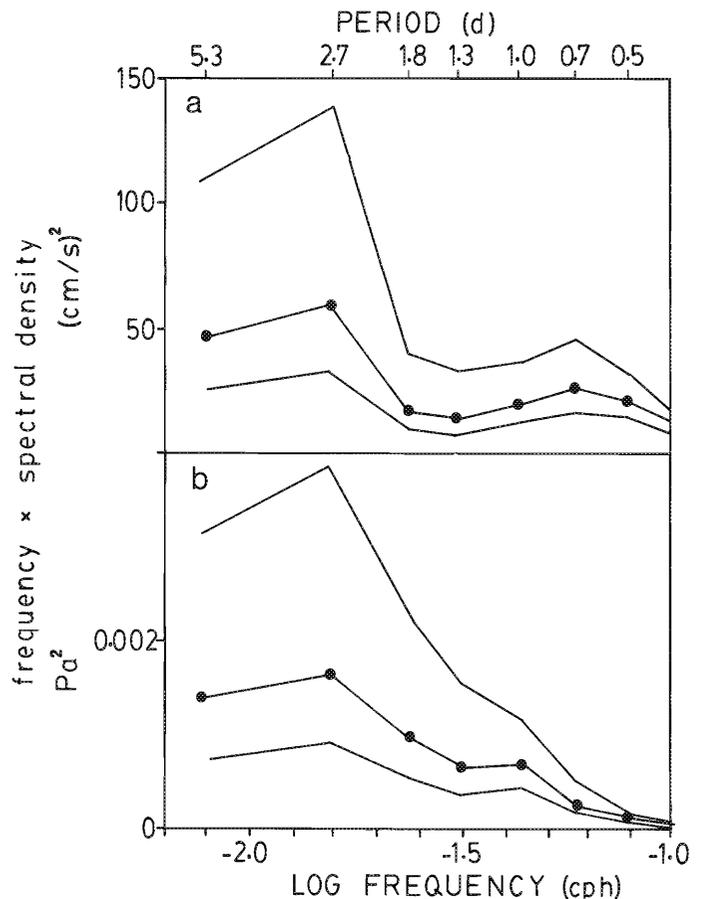


FIG. 8. Spectral density estimates of the (a) U-current and (b) wind stress ( $t_x$ ). Spectral density estimates are bounded by 95% confidence intervals.

ably robust against deviations from Gaussian assumptions (Koopmans 1974), the latter requirement is not a serious constraint, particularly if repeated spectral estimates are consistent (Denman 1975; Platt and Denman 1975). As the biological data were not evenly spaced in time, the observed larval and microzooplankton data series ( $n = 68$  for each) were linearly interpolated, log transformed to improve stationarity, and smoothed using the lowpass filter to provide 1006 hourly estimates (Fig. 12a, 12b) which matched the physical data series. Interpolation per se is an acceptable procedure (Steven and Glombitza 1972; Legendre and Legendre 1983), however, the spectral estimates may be seriously biased when the number of "observations" in the interpolated series exceeds that of the original series. For this reason, analysis of the interpolated series proceeded as follows to assess the validity of the estimated variance spectrum and of using the interpolated series for cross-spectral analysis with the physical data:

(1) The interpolated series were analyzed in a manner similar to that of Steven and Glombitza (1972) by sampling each at 12-h intervals to provide a total of 84 evenly spaced observations from the 64 original observations. Spectral analysis was performed as above but without blocking because of the short length of the series. The resultant spectra shown in Fig. 13a and 13b (for which there are no confidence interval estimates) reveal two distinct maxima in the larval series in the frequency bands centred at periods of 5.8 and 16–30 d. The microzooplankton series showed elevated spectral density between 3 and 8 d.

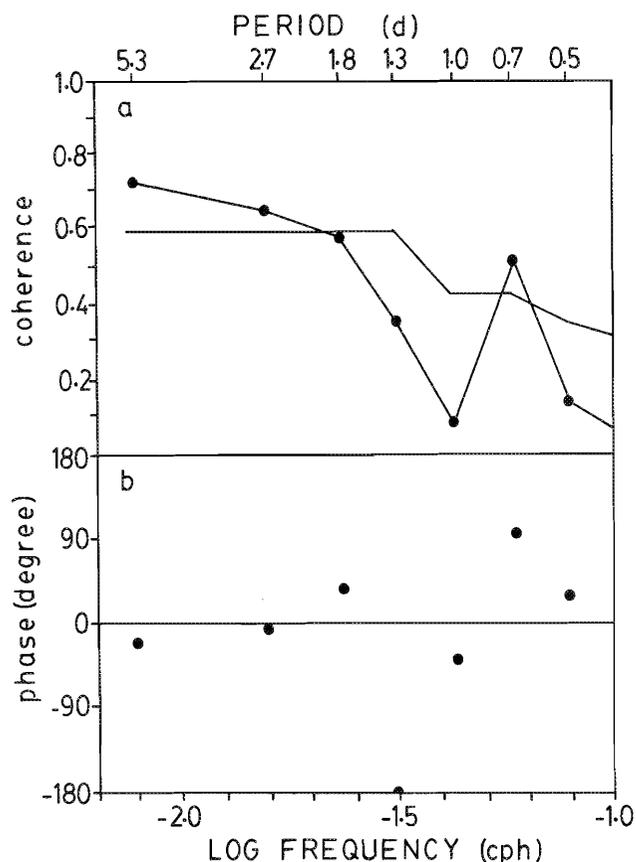


FIG. 9. (a) Coherence and (b) phase spectra of wind stress ( $t_x$ ) and U-current. Significance for coherence ( $p < 0.05$ ) is marked by the solid line.

(2) Spectral analysis was next performed on the two interpolated series with blocking as in the physical data. The resultant spectra (Fig. 14a, 14b) indicated significant spectral density at 2.7 and 5.3 d in both series. Blocking precluded longer period estimates. The apparent concordance at periods  $< 6$  d between spectra produced in the two analyses indicates that the interpolated series can be used for cross-spectral analysis with the physical data series, provided periods  $< 1$  d (the shortest biological sampling period) are excluded. This conclusion is further supported by the fact that the original biological data series were based on a non-uniform sampling interval which should greatly reduce the possibility of serious aliasing (Denman 1975) and the fact that during periods of onshore winds and pronounced larval emergence (and increased variation over time), the biological sampling frequency was increased from  $1/d$  to between 3 and  $4/d$ . Consequently the interpolated data series for both larvae and microzooplankton were used in subsequent analyses.

Although the larval and microzooplankton series had similar spectral density distributions and were in phase, there was no significant coherence at periods  $> 1$  d. This result is important, as it indicates that while the two signals varied together at similar frequencies (in phase), their respective amplitudes did not vary together, i.e. increases or decreases in larval density were not proportional to increases or decreases in plankton particle density. The higher amplitude fluctuations in the larval series relative to the plankton particle series are evident in Fig. 12. The 16-d maximum evident in the first larval spectrum was conspicuously absent from the microzooplankton spectrum (Fig. 13).

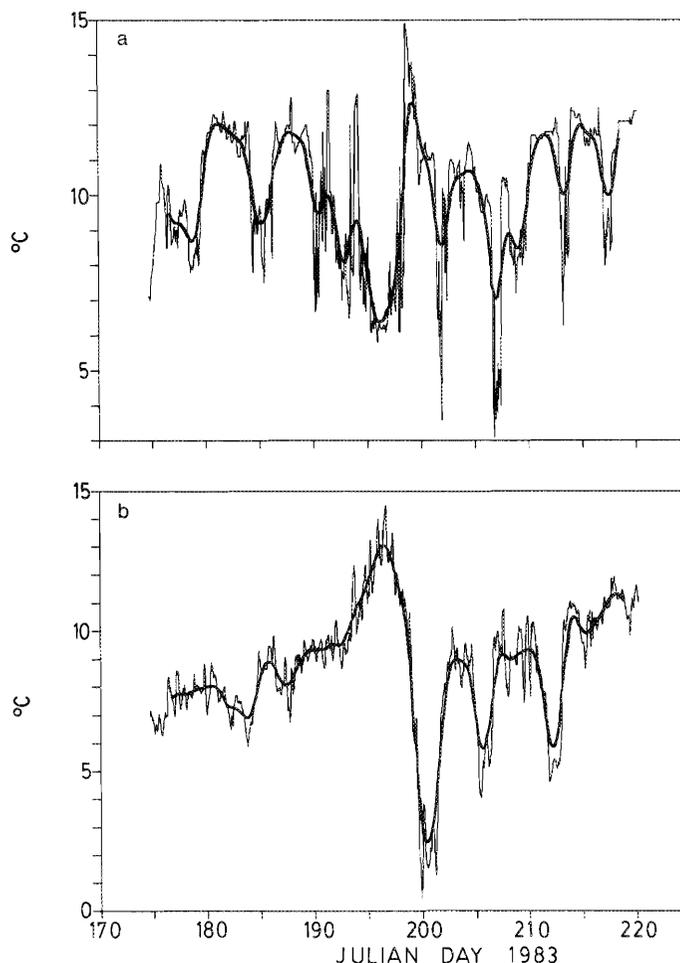


FIG. 10. Time series of temperatures recorded in 1983 at (a) Portugal Cove on the east side of Conception Bay and (b) Bryants Cove on the west side of the bay, 25 km distant from Portugal Cove. (Portugal Cove records provided by D. Keats, Memorial University of Newfoundland).

#### Physical-Biological Relationships

The major pattern emerging from the independent spectral analyses of both the physical and biological time-series is one of recurrent spectral maxima at periods of between 3 and 6 d. Cross-spectral analysis resolved significant coherence between the larval capelin series and  $t_x$  at 5.3 d (Fig. 15a). Furthermore, the phase spectrum (Fig. 15b) showed a  $130^\circ$  shift demonstrating a lagged inverse relationship (increased onshore wind stress leading an increased larval density). The larval series was also significantly coherent with the U-components of wind and current at the same period and showed similar phase relationships. There was no significant coherence between the larval series and any of the other physical variables.

Cross-spectral analysis of the microzooplankton and physical data series determined marginal coherence with  $t_x$  (and U-wind) at 5.3 d and had a similar phase relationship as seen with the larval series. Microzooplankton variations were coherent with temperature at Bryants Cove at periods of 3–6 d with a near-zero phase (Fig. 16). Almost identical coherence spectra were derived from cross-spectral analysis of the microzooplankton with salinity, density, and with temperature measured at Portugal Cove. This result is not unexpected given the previously described coherence between these variables and

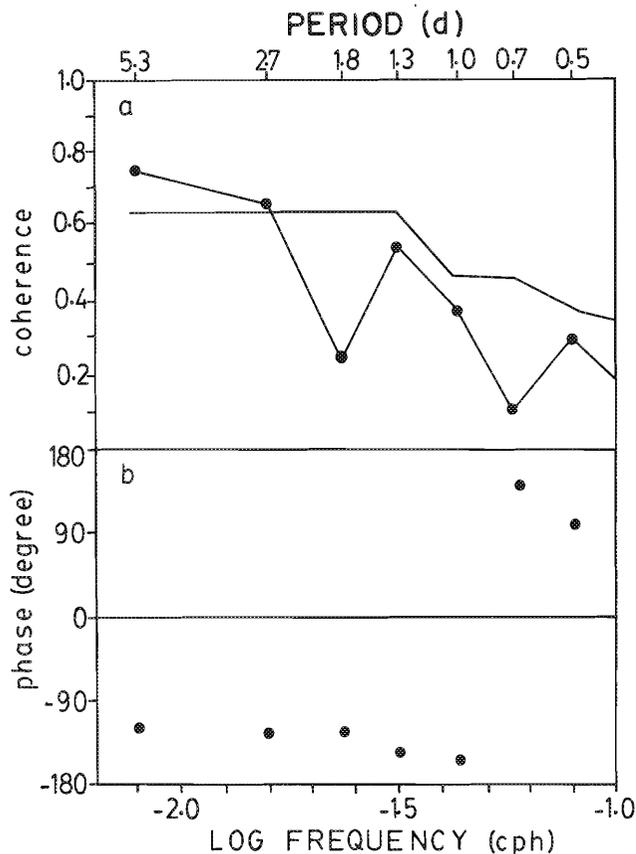


FIG. 11. (a) Coherence and (b) phase spectra for the temperature time-series illustrated in Fig. 10. Significance for coherence is marked by the solid line ( $p < 0.05$ ).

temperature measured at Bryants Cove. Microzooplankton were not significantly coherent with any other physical variables.

## Discussion

### Development of the Biological Data

Legendre and Demers (1984) have suggested that probing the significant scales of variation in dynamic biological oceanography and limnology will require the merging of horizontal and vertical studies in an integrated approach and the design and application of new sampling techniques and schemes. The methodology and results reported here indicate that a time-series of larval population estimates within a small and well-defined region can be obtained with good spatial and temporal resolution. In addition we have shown that statistically significant estimates of population size can be derived from multiple regression models incorporating a limited number of spatial density estimates (i.e. grid estimates from single transect observations), thereby greatly reducing the sampling effort. In the particular case we considered, the level of statistical significance of the models developed is likely a function of the point source of larvae at the head of the cove and the cove circulation. The seasonally cyclonic current pattern in the cove is such that the current sets landward on the northern half of the sampling grid and seaward on the southern half, each with equivalent average flow. The sampling transect was thus located just south of, and parallel to, the region where the current bends from inflowing to outflowing. This appears to

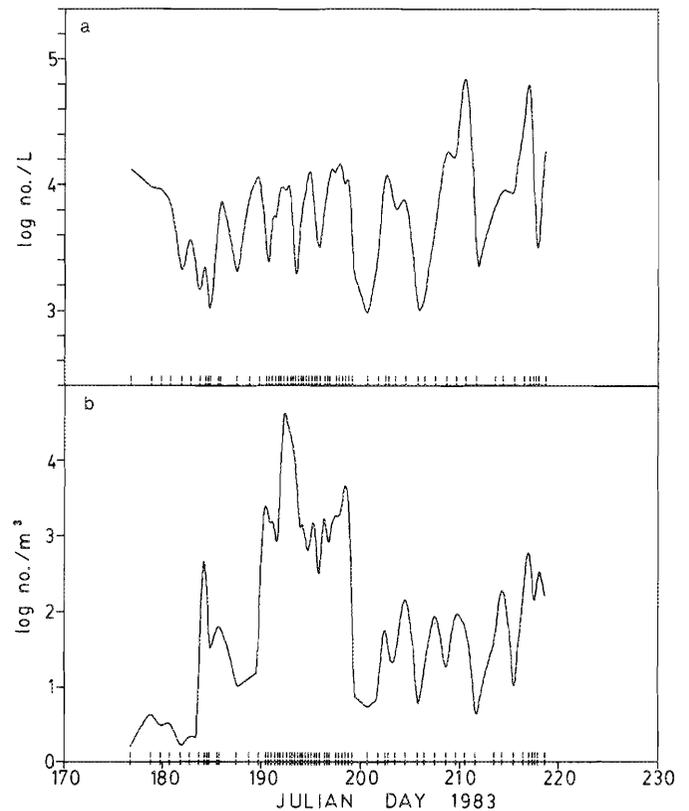


FIG. 12. 1983 time series of log-transformed (a) 90–108  $\mu\text{m}$  esd microzooplankton particles (whole-cove average density) and (b) capelin larvae (whole-cove average density) generated from a filtered hourly linear interpolation of the 68-observed estimates. Times when the observed estimates were made are marked on the date axis.

have caused the majority of larvae to be transported from their source on the beach to beyond the cove boundaries along the transect. This interpretation is supported by the fact that the best multiple regression models for estimating larval density in the cove relied on transect estimates. Furthermore, a series of dye diffusion–advection studies (not presented) showed the centre of mass of dye concentration to be advected seaward along the transect. These findings suggest that many of the logistic difficulties inherent in plankton surveys could be surmounted, without a significant loss of information, by the prior development of statistical models relating total area densities to densities on reduced sampling grids. This will require that sufficient effort be expended initially to define the distribution pattern in detail and to concurrently define the physical processes responsible for determining the pattern so that the appropriate stations can be chosen. We caution that this approach may prove useful only in lakes, embayments, and offshore banks which have predictable and dominant circulation features.

The systematic sampling approach we employed precludes statistical error estimation which would be possible had a randomized sampling design been employed. However, given the need to integrate samples both vertically and horizontally on a short time scale in order to deal with horizontal and vertical differences in current velocity and with diel vertical movements, randomized designs are likely to quickly become logistically impossible and to be less precise. We believe the approach adopted represents a viable compromise between error estimation and the need for synoptic high resolution on

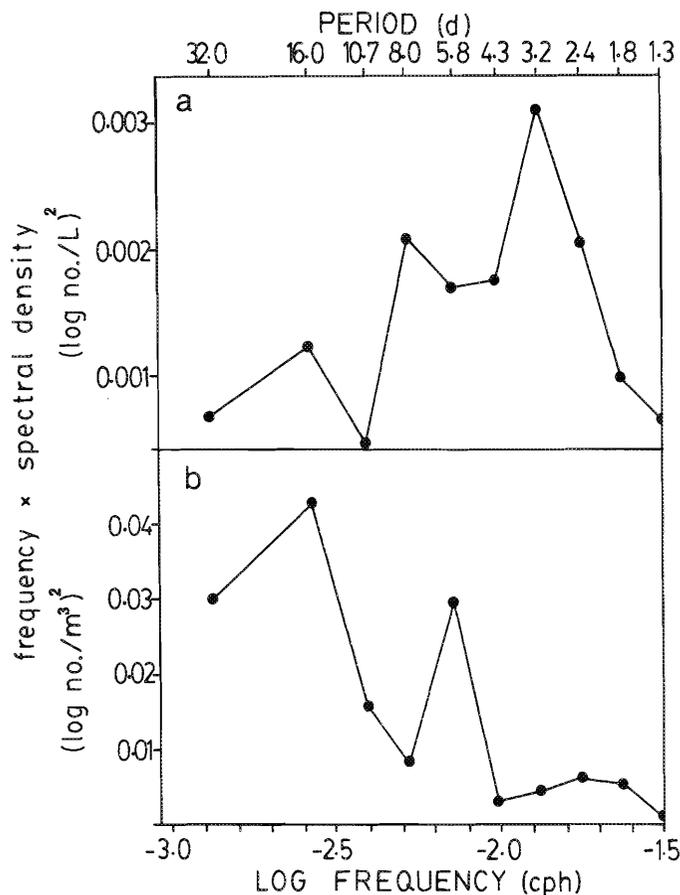


FIG. 13. Spectral density of (a) microzooplankton density and (b) capelin larvae density derived from sampling the interpolated series (Fig. 12) at 12-h intervals for a total of 84 "observations."

the horizontal and vertical scale in order to achieve precise estimates of abundance. The viability of the approach is strengthened by the fact that the population estimates of larvae derived using this method, and those from simple geometric average densities, were highly correlated ( $r^2 = 0.89$ ,  $n = 41$ ,  $p < 0.0001$ ) and had both slope and intercept values not significantly different from 1.0 and 0.0, respectively.

A further advantage of the pump sampling method and the systematic sampling design employed is that they allowed for synoptic estimates of both larval and plankton particle concentrations at precisely the same time and place with a horizontal scale resolution of 200 m, a vertical scale resolution of 2–4 m, and a temporal resolution of 6–8 h. This type of resolution is necessary if the various larval/food survival hypotheses (see the introduction) are to be rigorously tested. The physical-biological relationships identified by spectral analysis at higher frequencies (periods of 3–6 d) are unlikely to be resolved with a low-frequency broad-scale sampling programme.

The vertical resolution achieved by our design also permitted resolution of diel vertical migrations of yolk-sac larvae at a scale even smaller than that reported by Fortier and Leggett (1983), who noted the ecological significance of this behaviour in terms of feeding success and rate and direction of advective transport. Such resolution of diel migratory patterns allows it to be satisfactorily modelled in a purely empirical manner. These models can then be used to correct for biases in population estimates introduced by larval behaviour and sampling problems related to logistics and bathymetry. It is because of

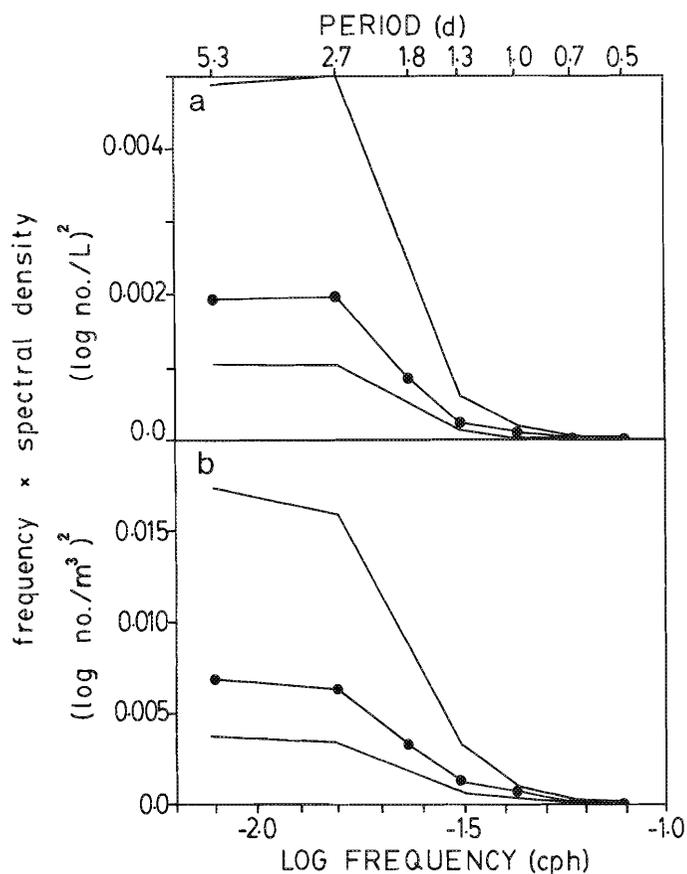


FIG. 14. Spectral density estimates of (a) microzooplankton density and (b) capelin larvae density time-series illustrated in Fig. 12. Spectral densities are bounded by 95% confidence intervals.

these biases that large-scale programmes have wisely employed bottom-to-surface integrated sampling. However, such methods eliminate all possibility of relating larval and food density distributions to each other and to the physical regime at relevant scales. The consistent and systematic diel vertical migrations exhibited by immediate postemergent capelin larvae contradict the earlier assumptions made by Fortier and Leggett (1982) and Frank and Leggett (1982b) that the yolk-sac larvae can be considered passive contaminants on the vertical scale and are therefore subject to extensive vertical mixing. The failure of this assumption to be met (also recognized by Fortier and Leggett 1983) can lead to significantly biased estimates of population size through slight differences in the time and depth of sampling, particularly if sampling occurs when larvae are migrating at their greatest rate. Our model (Fig. 4) for correcting migration bias has room for improvement. However, analysis of all the data was consistent with the model and suggests that although bias was not totally accounted for, it was much reduced.

It is equally possible to bias the change in population size through changes in sampling frequency. We infer from our calculation that cove flushing could occur within 24 h that the probability of sequentially sampling the same population is severely reduced if sampling frequency is less than once per day. Both of the above potential biases highlight the influence of inappropriate temporal and spatial scales when working in a dynamic environment. Frequent sampling of larvae following wind-driven emergence in 1983 revealed declines in larval density of more than an order of magnitude in periods as short

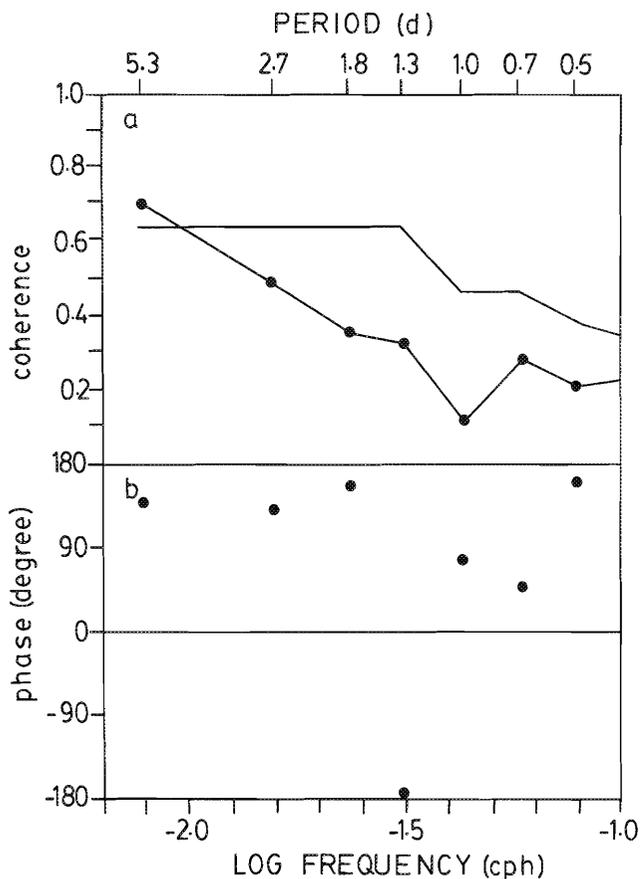


FIG. 15. (a) Coherence and (b) phase spectra of cross-shore wind stress ( $t_x$ ) and capelin larvae density. Significance for coherence is marked by the solid line ( $p < 0.05$ ).

as 6–8 h. These data indicate that the proportion of larval loss attributable to advection, as opposed to mortality, is considerable. Having developed the diel correction models, it is a relatively straightforward but nontrivial task to incorporate the migratory behaviour of the larvae, their population distribution at a given time, and the simultaneously determined current velocity data to calculate measures of advective loss (emigration) and realized mortality. The results of this work are forthcoming.

#### Watermass Exchange Hypothesis

Templeman (1966) proposed a coastal watermass exchange phenomenon to explain intraseasonal variation in the nearshore abundance of cod on the eastern coast of Newfoundland. The hypothesis called for the intermittent presence, in the nearshore, of warm surface water and cold subthermocline water. He further hypothesized the watermass exchanges to be wind-driven. Frank and Leggett (1982b) adopted Templeman's hypothesis to explain temporal variation in nearshore temperature changes and related changes in larval fish and zooplankton abundance. It was further demonstrated that the short-term nearshore temperature fluctuations were generally synchronous along the eastern coast of Newfoundland (Leggett et al. 1984), implying a large-scale phenomenon. Spectral analyses of the time-series of wind and current in the nearshore areas of Conception Bay in 1983 are fully consistent with the watermass exchange hypothesis and leave little doubt that the near-

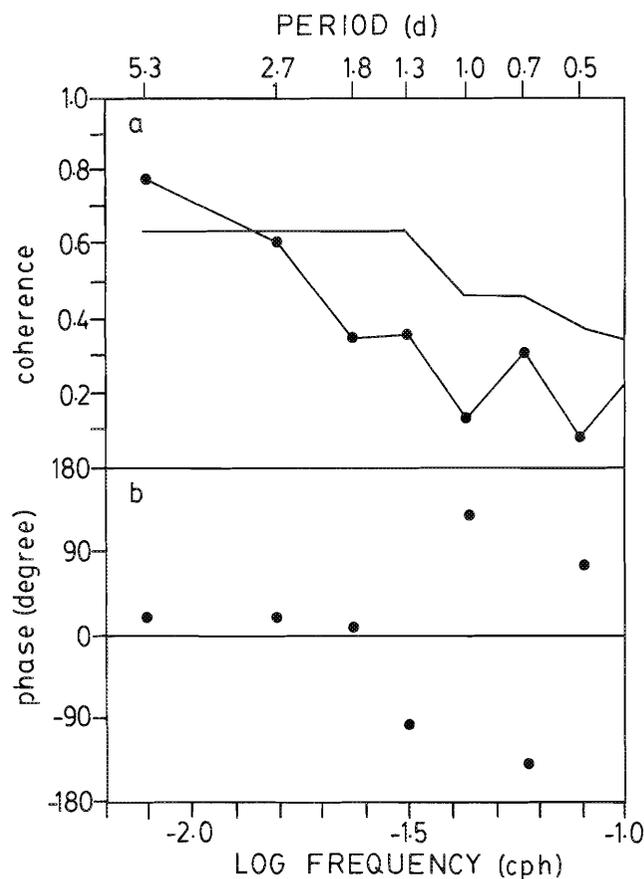


FIG. 16. (a) Coherence and (b) phase spectra of temperature and microzooplankton. Significance for coherence is marked by the solid line ( $p < 0.05$ ).

shore currents, and related temperature, salinity, and density, respond to wind forcing at periods ranging from 3 to 6 d.

Our finding that the longshore wind component ( $V$ ) showed no coherence with current and temperature oscillations is at odds with the more general observation that longshore winds drive offshore surface water excursions and coastal upwelling. We attribute our findings in part to the angle ( $54^\circ$ ) around which we resolved the data. The main axis (longshore) for Conception Bay is  $\sim 25^\circ$  and therefore closely corresponds to the cross-shore axis of Bryants Cove. Thus the hydrodynamics in the cove may be responding more directly to the large-scale effects of wind on Conception Bay. This interpretation is supported by the dominant large-scale longshore wind effects on Trinity Bay documented by Yao (1986).

The physical-biological cross-spectral analyses showed larval abundance oscillations to be coherent with wind and current at periods of  $\sim 5$  d. The abundance oscillations of microzooplankton concentration, although marginally coherent with cross-shore wind forcing, showed greater coherence with temperature. These observations demonstrate a greater biological significance of the watermass exchange hypothesis than suggested by Templeman (1966) and support the speculation of Leggett et al. (1984) that water temperature influences early larval survival through a more direct influence on food production. However, our analyses also demonstrate that although larvae and their potential prey oscillate in synchrony with wind, currents, and temperature, they are not proportionally related to each other. This finding implies that various levels of

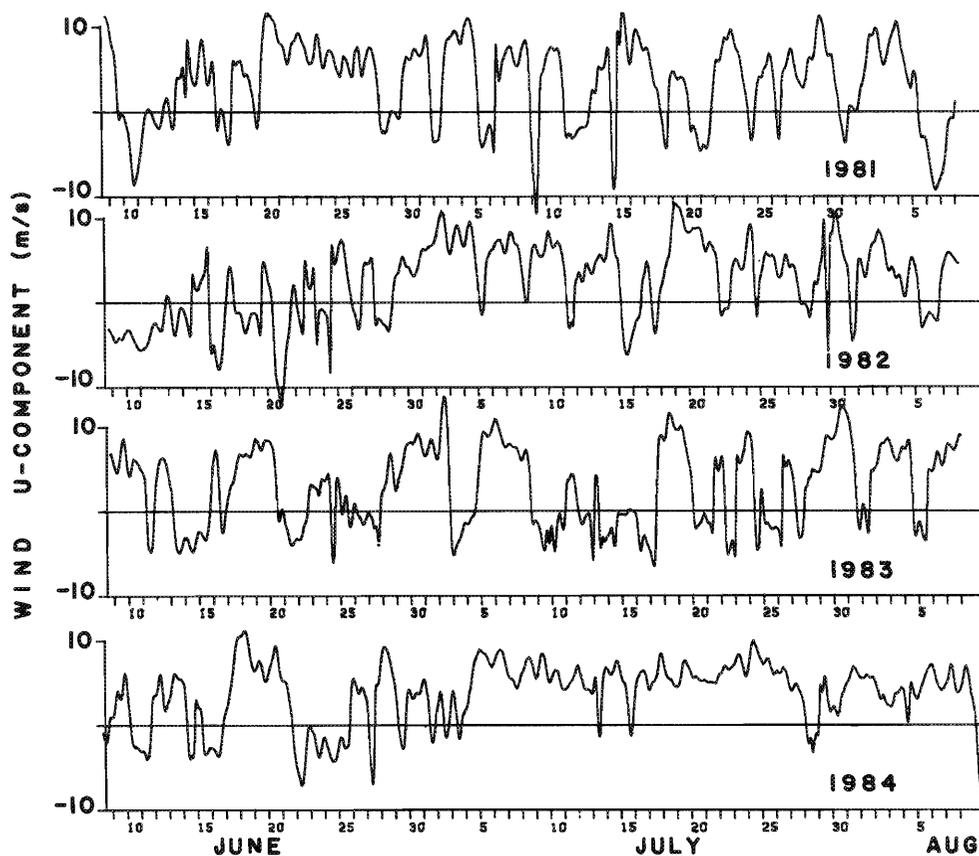


FIG. 17. Time-series of smoothed wind U-component at St. John's airport for June and July of 1981–84.

elevated food concentrations can be coincident with high concentrations of larvae.

The spectral maxima in larval density at 16–30 d in the first spectral analysis (Fig. 13b) appears to be related to capelin spawning and hatching periodicity. In 1983, capelin spawned on the beach at Bryants Cove between 15 and 21 June (heaviest on 18, 20, and 21) and again on 20, 21, and 24 July, a spawning interval of 30 d. The time to median hatching varies between 9 and 13 d in the high-tide zone and between 18 and 24 d in the low-tide zone (Frank and Leggett 1981a, 1981b). This range of incubation periods will result in a median hatching period of 16 d. The absence of spectral maxima at these periods in the microzooplankton abundance supports our interpretation.

The conclusions drawn from the spectral analysis of the biological data and the cross-spectral analysis of that data with the physical data are necessarily deficient due to our necessary interpolation of the biological data. We do, however, believe them to be essentially correct for the several reasons given under Biological Relationships: Larvae and Microzooplankton.

#### Implications of Watermass Exchange Variability

The influence of cross-shore wind forcing, and the water-mass exchange which results, on the nearshore biological community structure is significant. The importance of the frequency of onshore wind events to capelin larvae derives from the fact that the majority of larvae resident in beach sediments have depleted their yolk sac within a 4- to 7-d posthatch window, beyond which their physical condition is severely affected (Frank and Leggett 1982a). This relatively short period for successful larval emergence led Frank and Leggett

(1982b) to analyze the St. John's wind field over a period of 20 yr. They calculated the average number of days of prevailing offshore winds to be 24.1 ( $SD = 2.9$ ) and 26.8 ( $SD = 3.0$ ) for June and July, respectively. Assuming that onshore winds endure for an average of  $\sim 24$  h, the average frequency of onshore winds would be once every 6.3 d for both months combined. The concordance between average onshore wind frequency and viable posthatch beach residence time for larvae led to the argument that early summer beach spawning was adaptive (Frank and Leggett 1983a, 1983b). However, we found that by considering  $\pm 1$   $SD$  in the calculation of the 20-yr average, a much greater range of onshore wind frequencies emerged (every 3.4–25.8 d), demonstrating that there is considerable interannual variation in onshore wind frequency and hence in the "matching" of the emergence "window" (4.2–6.7 d). Time-series of the U-component (onshore–offshore) of the wind field for June and July of 1981–84 detail the extreme variability in periodicity, strength, and duration of onshore–offshore wind oscillations among years (Fig. 17). It is readily apparent on inspection that in 1981 and 1983, onshore winds were stronger, more frequent, and of greater duration than in 1982 and 1984. This was particularly true in the latter part of each record when the majority of capelin hatching and emergence took place. Integration of the onshore wind component (scaled to a constant 10 m/s onshore wind) for the period of 25 June to 7 August measured 0.148, 0.104, 0.120, and 0.059 for 1981–84, respectively. Spectral analyses of these same signals revealed spectral maxima between 5.5 and 6.0 d in all but the 1984 spectrum (Fig. 18). This is consistent with the earlier analyses of onshore wind intervals. However, the proportion of variation in the wind signal found at these periods was itself extremely variable among years. There were dominant and

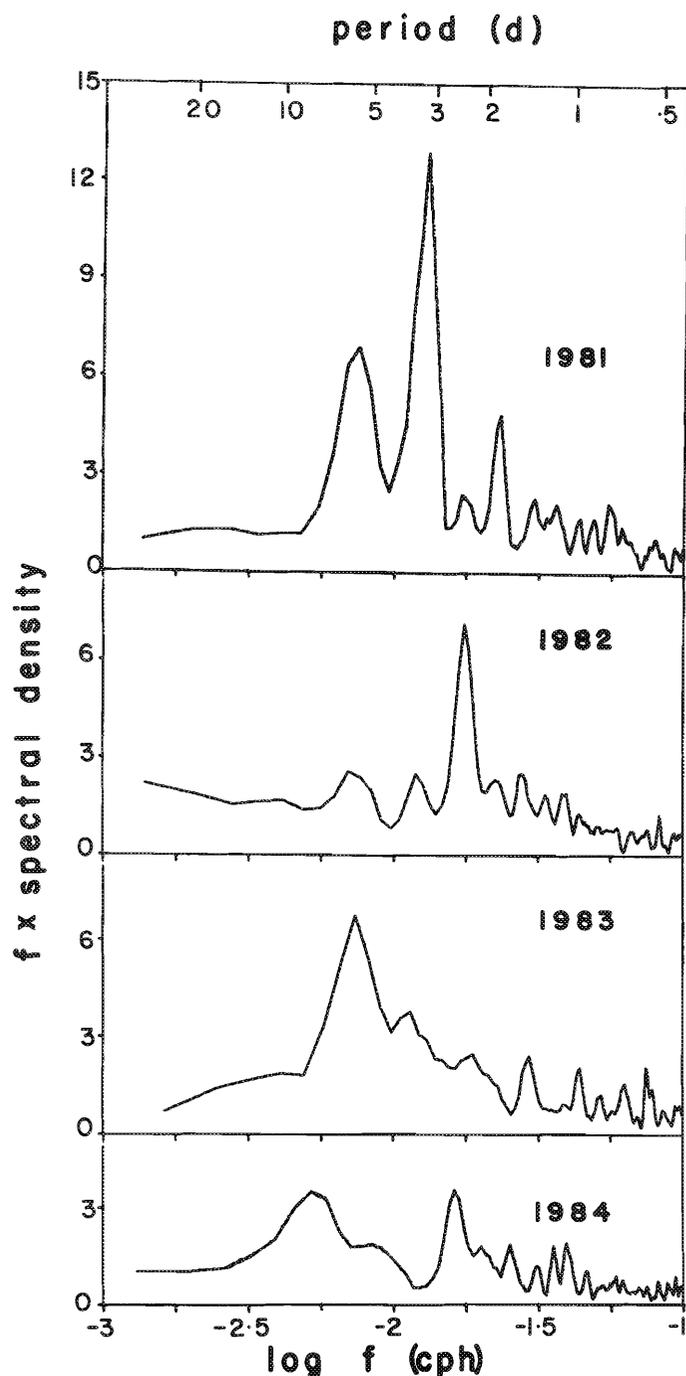


FIG. 18. Spectral densities of time-series of wind U-components illustrated in Fig. 17.

sharp maxima in the 1981 spectrum at periods of 1.8, 3.2, and 5.6 d. In comparison, the 1982 spectrum was less sharp and weak, while the 1983 spectrum was very broad and relatively strong. The 1984 spectrum was particularly broad and weak, reflecting the virtual absence of onshore winds during the latter two thirds of the signal when the majority of larvae were ready to emerge. Integration measures of the spectra between periods of 1 and 7.4 d (scaled to a broad-band unit spectrum) were 0.230, 0.133, 0.179, and 0.089 for 1981–84, respectively. The scaled integrals of the onshore U-component and of the spectra were significantly correlated ( $r^2 = 0.95$ ,  $n = 4$ ,  $p < 0.05$ ), suggesting that either method can be used as a composite measure of onshore wind frequency, magnitude,

and duration. The generally declining frequency and intensity of onshore winds and watermass exchange during the critical larval emergence period over the years 1981–84 lead us to hypothesize that the strength of capelin year classes hatched in these years (assuming equal spawning biomass) should also generally decline from 1981 to 1984. We plan to test this hypothesis using either the U-component or spectral integrals of annual summer wind data and year class strength data for capelin (with an appropriate discounting for spawning biomass) in an effort to test and perhaps improve the Leggett et al. (1984) recruitment model for possible application to stock management.

### Acknowledgments

This work was supported by grants to W.C.L. from the Natural Sciences and Engineering Research Council of Canada (NSERC) and from the Department of Fisheries and Oceans (DFO). C.T.T. was supported by an NSERC postgraduate scholarship, a McConnell Memorial Fellowship (McGill), and a bursary from Group inter-universitaire de recherche océanographiques du Québec. We are grateful to J. Carscadden and DFO, St. John's, Nfld., for considerable logistic support and to D. Keats, Memorial University of Newfoundland, for providing his temperature records. N. Chalouhi, K. Tallon, M. Dolan, J-C. Dequise, G. Maillet, J-Y. Anctil, C. Gravel, and G. Kerhuel provided expertise in the field and laboratory. We also thank K. Drinkwater and L. Fortier for introducing us to the intricacies of spectral analysis and K. T. Frank, G. Ingram, and Y. de Lafontaine for their advice and criticisms. W. Parsons and the crew of the *Lady Christine* and residents of Bryants Cove gave us valuable assistance on numerous occasions.

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