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Response of capelin to wind-induced thermal events in the southern Labrador Current

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ABSTRACT

The response of schooling fish (Capelin *Mallotus villosus* Müller) to coastal upwelling events in the southern Labrador Current was investigated during the summer of 1984 and 1987. Theoretical calculations showed that summer wind events, which prevail from the southwest, were capable of inducing upwelling along the western boundary of the Avalon Channel. Significant drops in the temperature of subsurface water near the coast occurred in response to longshore wind stress. Coherence of longshore winds and thermal fluctuations was significantly greater than zero at periods between 3.8 to 6.1 days at two exposed locations along the coast. Regression of temperature on longshore winds was significant when effects of cross-shore winds were removed by regression. Regression of temperature on cross-shore winds was not significant when effects of longshore winds were removed by regression. During 1984 the relative catch rate of male capelin at a trap increased when water temperature rose rapidly after upwelling events. During 1987 increases in the catch rate of males at the trap were correctly predicted from cessation of upwelling favorable winds (i.e., from the south). Shoreward movement of capelin after wind driven upwelling may synchronize spawning with periods of light wave action on beaches in eastern Newfoundland.

1. Introduction

The biological significance of coastal upwelling is well described for small organisms such as plankton, which have limited locomotory capacity in a viscous environment. The biological significance of upwelling to large, actively swimming nekton is not well understood. We investigated the response of schooling capelin to wind-induced upwelling events along the western boundary of the Avalon Channel, which carries the inshore branch of the Labrador Current southward along the coast of eastern Newfoundland. Capelin, a pelagic, smelt-like fish, arrive near this coast to spawn on beaches and subtidal gravel beds in late June and early July. Feeding during this period is limited (Templeman, 1948). Sleggs (1933) hypothesized that capelin along this coast respond to geostrophic movements of thermally distinct water masses. Subse-

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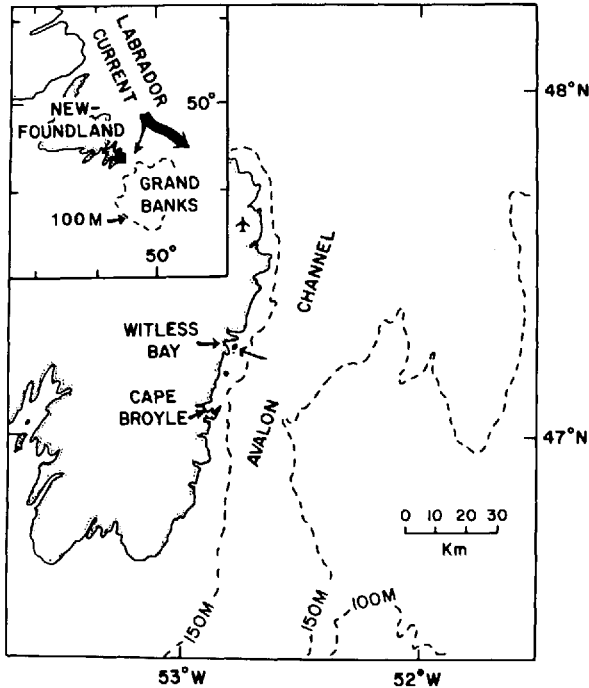


Figure 1. Location of temperature gauges at Cape Broyle, Witless Bay wharf, and Gull Island. Arrow (westward) points to Gull Island. Airplane shows location of Torbay wind gauge.

quent work (Frank and Leggett, 1981, 1982) showed that temperature fluctuations inside a small bay were correlated with cross-shore winds, which typically blow from the southwest during the summer. The biological consequences of longshore wind stress, which can cause upwelling along exposed coasts, have not been investigated in the northwest Atlantic. If wind-driven upwelling is significant, then rapid fluctuations in temperature at shallow depths can be expected after development of the seasonal thermocline, which occurs in June in the southern Labrador Current (Hollibaugh and Booth, 1981). We measured subsurface temperature fluctuations in relation to both longshore and cross-shore wind stress in the Avalon Channel, off eastern Newfoundland (Fig. 1). We also measured the relative catch rates of male and female capelin in relation to temperature fluctuations at a trap that intercepted capelin moving along the coast.

2. Methods

Records of wind speed and direction were obtained from the Atmospheric Environment Service for the months May–September at Torbay Airport, which is located in an area of relatively high elevation 7 km west of the Avalon Channel (Fig. 1). Daily water

temperature was measured at three locations on the western shore of the Avalon Channel—Cape Broyle, Witless Bay wharf, and Gull Island (Fig. 1). A Ryan thermograph was attached to a fixed object within a meter of the sea bottom at each location. Thermographs were attached to a capelin trap 5 m below the sea surface (Cape Broyle), a wharf piling 5 m below the sea surface (Witless Bay), and an anchor 10 m below the sea surface (Gull Island).

Capelin from the trap at Cape Broyle were collected by a commercial fisherman in June and July. During 1984 the trap lead was perpendicular to the shore, 10 m in length, and fished from the surface to 7 m (bottom depth) between the trap and the shore. During 1987 the trap fished from the surface to 15 m at a distance of 90 m from the shore. Stretched mesh size of the trap was 19.5 mm. Design and operation of this gear is described by Jangaard (1974).

During the commercial season the trap was emptied into a boat once a day between 0400 and 1000 AM, local time. After the season the trap was emptied 2 to 3 times a week. A bucket was used to scoop capelin from the top, middle, and bottom layers of fish in the boat, to prevent bias against heavier fish sinking to the bottom. Approximately 200 capelin were taken and frozen on each collection date. Each collection was sorted to determine sex ratio and the proportion of ovid and spent females.

3. Results

Temperature changes of 2 to 7°C per day occurred at sheltered (Witless Bay) and exposed sites (Gull Island, Cape Broyle) during 1984 (Fig. 2). Temperature changes were due to rapid vertical movements of the thermocline (Fig. 3). The rise of the thermocline and the substantial thinning of the upper layer (Fig. 3) suggested that coastal upwelling was responsible for temperature fluctuations observed beneath the sea surface (Fig. 2).

A simple two-layer model with uniform depth and straight coastline was used to determine whether longshore wind stress was sufficient to bring the pycnocline to the surface in the Avalon Channel. The model, which is based on conservation of potential vorticity (Csanady, 1982, p 100), does not assume that advection of momentum is small; this is appropriate given the substantial rise of the pycnocline at Gull Island during a day (Fig. 3). The model does not include tidal forces; this was taken as a reasonable first approximation along a coast where the tidal range is less than 1.5 m, and the thickness of the upper layer (Fig. 3) is much less than the depth of the water column (Fig. 1). The condition for surfacing (Csanady, 1982, Eq 3.97) of the pycnocline is:

$$I > h_t h_b^{-1} (h_t + h_b) c_2. \quad (1)$$

In this equation I is the longshore impulse ($\text{m}^2 \text{s}^{-1}$) imparted to the water by the wind, h_t is the thickness (m) of the upper layer, h_b is the thickness (m) of the lower layer, and c_2 is the first internal mode phase speed (m s^{-1}). The offshore length scale of

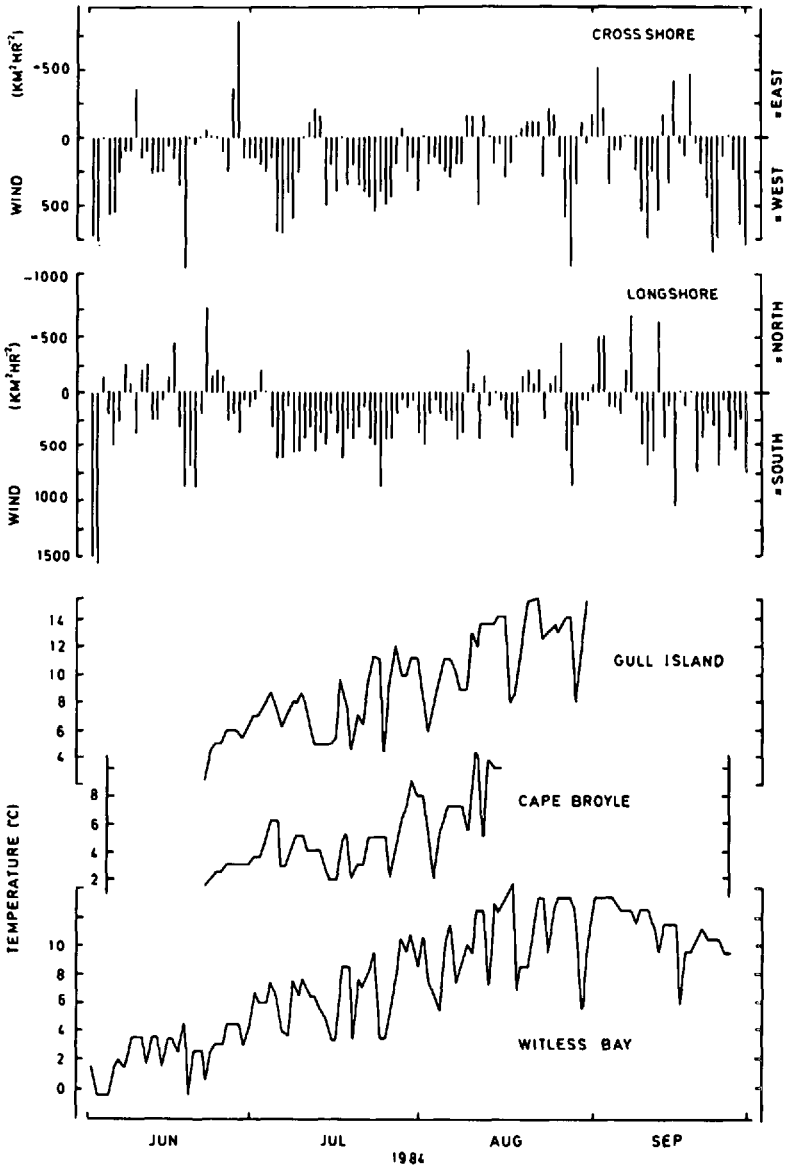


Figure 2. Specific kinetic energy of the wind WW_i ($\text{km}^2 \text{hr}^{-2}$) compared to daily water temperature at Gull Island, Cape Broyle, and Witless Bay. Cross-shore winds are positive from the west. Longshore winds are positive from the south.

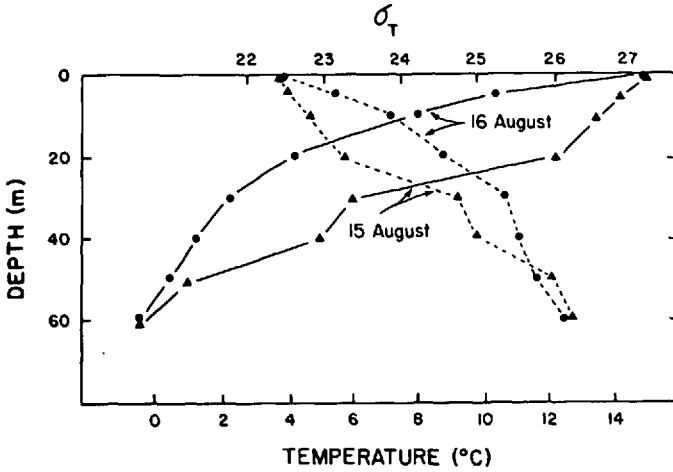


Figure 3. Temperature and density (σ_t) profile at Gull Island on the mornings of 15 and 16 August, 1984. Bottom depth is 60 m. Dashed line indicates density, solid line indicates temperature.

the upwelling response is given by the internal radius of deformation R_2 (m), which is the ratio of c_2 and the Coriolis parameter f (s^{-1}). Five parameters are needed to calculate R_2 (Csanady, 1982; Eq 3.96). Values of these parameters for the Avalon Channel (Table 1) result in a phase speed (c_2) of 0.50 m s^{-1} , and deformation radius (R_2) of 4.7 km. The critical value for surfacing of the pycnocline is:

$$I_c = 17.8 \text{ m}^2 \text{ s}^{-1}. \quad (2)$$

The impulse imparted to the water by the wind over a one day period ($T = 8.64 \times 10^4 \text{ s}$) is:

$$I = T u_*^2, \quad (3)$$

where u_* is the friction velocity calculated from a quadratic drag law (Roll, 1965):

$$u_*^2 = D_a C_{10} W_i W. \quad (4)$$

Table 1. Physical characteristics of the Avalon Channel during summer.

| Parameter | | Value | Source |
|-------------------------------|------------|--------------------------------------|---------------------|
| Density anomaly | ϵ | 0.001 | Lively, 1983, p 17 |
| Gravitational acceleration | g | 9.8 m s^{-2} | |
| Upper layer | h_1 | 30 m | Lively, 1983, p 15 |
| Lower layer | h_b | 160 m | Lively, 1983, p 15 |
| Coriolis parameter at 47N | f | $1.07 \times 10^{-4} \text{ s}^{-1}$ | |
| Air density relative to water | D_a | 0.001 | Csanady, 1982, p 11 |
| Drag coefficient | C_{10} | 0.002 | Csanady, 1982, p 11 |

In this equation W is the observed wind speed (m s^{-1}) averaged over a one day period, W_i is the wind velocity component in direction i , and the remaining parameters are listed in Table 1. For a wind of speed W blowing from an angle of A degrees relative to north, along a coast that runs 20° each of north (Fig. 1), the longshore wind component is:

$$W_y = -W \cos (A - 20). \quad (5a)$$

The cross-shore wind component is:

$$W_x = -W \sin (A - 20). \quad (5b)$$

where x is positive in the offshore direction, y is positive in the direction 90° counterclockwise of x .

The thermocline coincides with the pycnocline during the summer in the Avalon Channel (Lively, 1983) so surfacing of the thermocline is predicted to occur when the mass-specific kinetic energy of the wind along the coast (WW_y) reaches a critical value of:

$$(WW_y)_c = (R_2 T D_a C_{10})^{-1} I_c. \quad (6)$$

If $T = 1$ day then the critical value for surfacing of the thermocline is $102.5 \text{ m}^2 \text{ s}^{-2}$, or $1328 \text{ km}^2 \text{ hr}^{-2}$. Longshore winds did not attain this magnitude during any single day period in the summer of 1984 (July through August, Fig. 2). The observed maximum between day 180 (the first day of the capelin season) and day 274 (end of the temperature record at Gull Island) was $1100 \text{ km}^2 \text{ hr}^{-2}$ (Fig. 2). Repeating the calculations for a two day period, the critical value is $1328/2$, or $664 \text{ km}^2 \text{ hr}^{-2}$. Specific kinetic energies exceeded this critical value on 23–24 July and 27–28 August (Fig. 2). Note that on both occasions the critical value was exceeded during two successive days, and hence the specific kinetic energy computed from wind averaged over two days must also exceed the critical value. For three-day periods the critical value is $443 \text{ km}^2 \text{ hr}^{-2}$. The specific kinetic energy of the longshore wind exceeded this critical value on 4–6 July, 8–10 July, 12–14 July, 17–19 July, 23–25 July, and 27–29 August (Fig. 2).

These calculations show that summer winds were theoretically capable of bringing the thermocline to the surface along the western shore of the Avalon Channel, assuming a simple steady-state two-layer model (Eq 1). Examination of the temperature data (Fig. 2) showed that drops in water temperature occurred during those two or three day periods when the specific kinetic energy of the wind exceeded critical values computed from Eq. 6. To obtain a more detailed analysis of the relation of temperature to longshore winds we used spectral analysis. The coherence between longshore wind (W_y) and temperature fluctuations (Fig. 4) was significantly greater than zero at Gull Island (3.8 to 6.1 days per cycle), Cape Broyle (3.1 to 6.1 days per cycle), and Witless Bay wharf (4.7 to 5.3 days per cycle). The coherence between cross-shore winds (W_x)

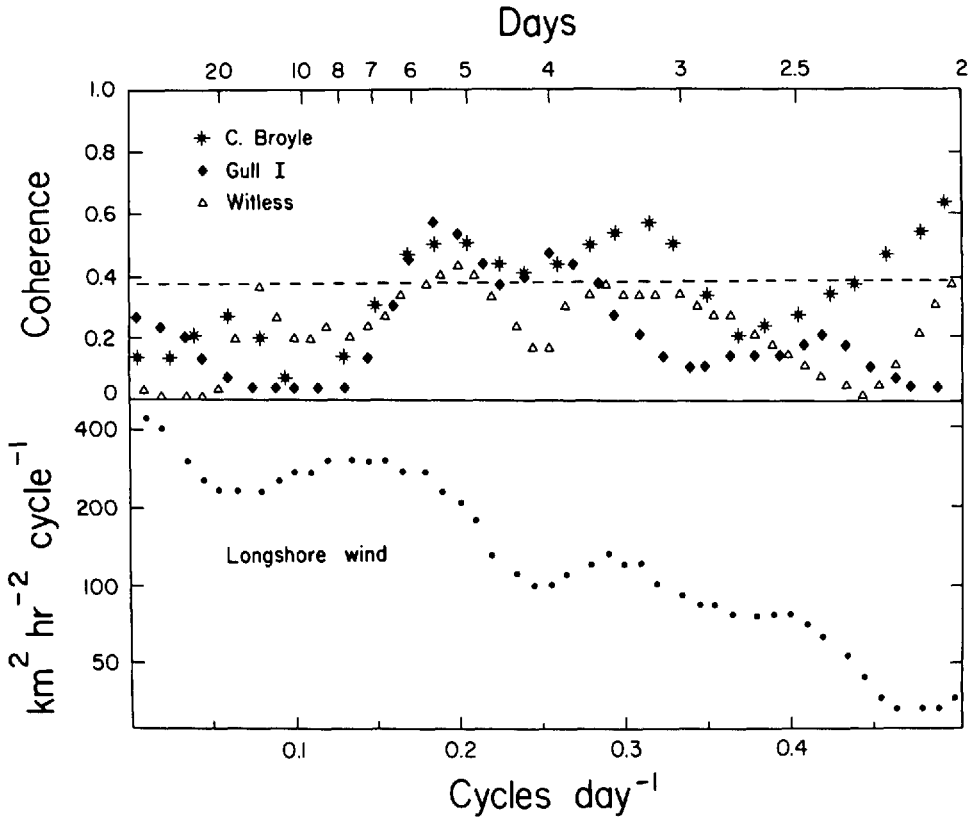


Figure 4. Coherence of longshore wind with water temperature. Values above the dashed line are significantly different from zero at the 90% confidence level, based on 20 equivalent degrees of freedom (Koopmans, 1974). Specific kinetic energy of the longshore wind W_y is shown.

and temperature fluctuations was not significant at any of the three locations. Lagged correlations in the time domain (Box and Jenkins, 1976) gave similar results.

To evaluate the contribution of cross-shore and longshore winds to nearshore thermal fluctuations we used a simple empirical model:

$$\theta = b_o J + \sum_{t=0}^n b_{xt} WW_{xt} + \sum_{t=0}^n b_{yt} WW_{yt}. \tag{7}$$

In this equation θ is average daily water temperature, b_o is the seasonal warming trend, J is Julian date, WW_{xt} is the specific kinetic energy of the wind across the shore at a lag of t days, WW_{yt} is the specific kinetic energy of the wind along the shore at a lag of t days, and b_{it} is the partial regression at lag t in direction i . The model was evaluated at lags of 0 to 5 days, which produces 11 regression coefficients. Results for the full model

Table 2. Variance in water temperature due to date, specific daily longshore wind energy, and specific daily cross-shore wind energy. Variance components are residuals after removal of all other sources. Probability levels in parentheses. Underlined values are significant at $p < 0.01$.

| Source | Lag (days) | Cape Broyle | Witless Bay | Gull Island |
|-------------|------------|---------------|----------------|----------------|
| Date | 0 | 76.1 (0.0001) | 762.6 (0.0001) | 194.1 (0.0001) |
| Longshore | 0 | 4.16 (0.13) | 0.62 (0.68) | 8.5 (0.06) |
| | 1 | 14.3 (0.007) | 0.77 (0.64) | 35.6 (0.0003) |
| | 2 | 22.8 (0.0009) | 34.5 (0.003) | 32.5 (0.0005) |
| | 3 | 2.00 (0.29) | 2.8 (0.37) | 0.21 (0.77) |
| | 4 | 0.04 (0.88) | 12.6 (0.06) | 0.30 (0.73) |
| Cross-shore | 5 | 0.33 (0.66) | 0.04 (0.92) | 0.27 (0.74) |
| | 0 | 0.58 (0.57) | 0.98 (0.60) | 0.24 (0.75) |
| | 1 | 7.21 (0.05) | 0.90 (0.62) | 1.85 (0.38) |
| | 2 | 2.08 (0.28) | 0.0003 (0.99) | 11.7 (0.03) |
| | 3 | 0.64 (0.55) | 5.6 (0.21) | 0.35 (0.70) |
| | 4 | 0.51 (0.59) | 3.3 (0.34) | 2.47 (0.31) |
| | 5 | 0.01 (0.93) | 0.07 (0.89) | 8.86 (0.06) |

are shown in Table 2. Only three of the terms were significant at $p < 0.01$: Julian date, WW_{y1} , and WW_{y2} . Temperature fluctuations were not related to cross-shore wind energy after the significant effects of longshore wind energy were removed by regression. The reduced model was:

$$\theta = b_o J + b_{y1} WW_{y1} + b_{y2} WW_{y2}. \quad (8)$$

In this reduced model the specific kinetic energy of longshore winds at lags of one to two days accounted for 31% (Cape Broyle), 22% (Witless Bay wharf), and 26% (Gull Island) of the daily variation in water temperature after removal of the season trend, b_o .

Figure 5 shows the relation between water temperature and the proportion of male capelin caught by the trap during 1984. The catch rate of males, relative to females, fell when water temperatures dropped at the trap, then rose when water temperatures increased. The correlation between proportion of male capelin and water temperature at the trap was statistically significant ($r = 0.59$, $p < 0.001$, $n = 17$). The catch rate of spent females did not fluctuate with water temperature (Fig. 5), which indicates that correlation is due to active response of pre-spawning capelin to thermal changes. Little is known about the behavior of capelin in relation to thermal variability (Templeman, 1948) so we used empirical models to investigate the relative catch rate of males in relation to water temperature in 1984. The first model was that change in relative catch rate of males was proportional to change in temperature:

$$dP/dt = c_1 d\theta/dt \quad \theta < \theta_{\max} \quad (9)$$

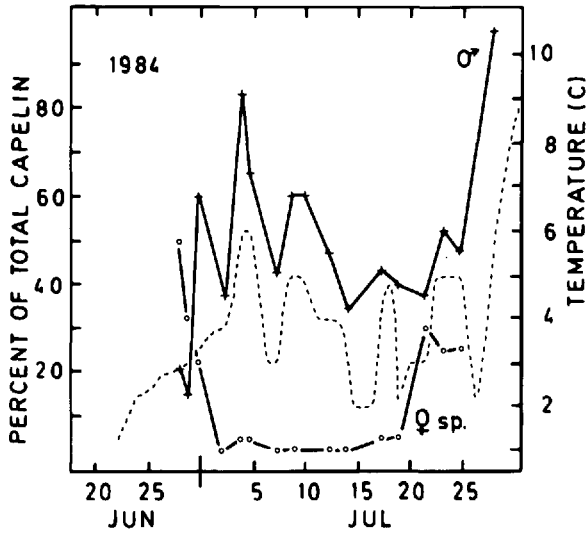


Figure 5. Proportion of male (δ) and spent (sp) female capelin caught in 1984 by a trap at Cape Broyle. Dotted line shows water temperature at the trap.

where P is proportion of males caught, t is time, c_1 is a fitted constant, θ is water temperature at the trap, and θ_{\max} is maximum observed temperature. After integration and evaluation by least squares regression, this model explained 33% of the variation in proportion of males caught. The second model was that of a threshold response to water temperatures above a critical temperature θ_k :

$$P = c_2 \quad \text{if } \theta < \theta_k \quad (10a)$$

$$P = c_3 \quad \text{if } \theta > \theta_k \quad (10b)$$

θ_k was taken as 5°C based on observations of Templeman (1948). c_2 and c_3 are fitted constants. This model explained 47% of the variation in proportion of males caught, an improvement over the differential temperature model (Eq. 9). The third model was that of an increase in male activity and hence relative catch rate with increase in temperature, analogous to a Q_{10} effect. The activity model was:

$$\log P = c_4 + c_5 \theta^{-1} \quad (11)$$

where c_4 and c_5 are fitted constants. This model explained 18% of the variation in proportion of males caught, and so offered no improvement over the critical temperature model. The fourth model was behavioral thermoregulation resulting in maximum catch rate of males at some optimum temperature. This model was rejected on the basis of the relation between P and θ , which did not show any intermediate maximum in P over the observed range in θ . We accepted the critical temperature model as a preliminary description of relative catch rate of males in relation to water temperature.

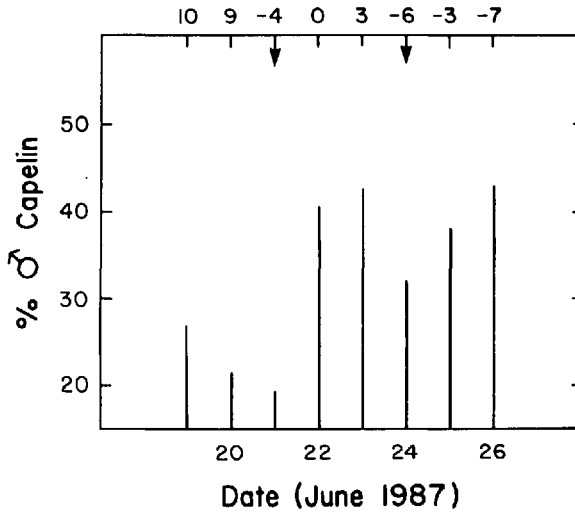


Figure 6. Proportion of male capelin caught in 1987 by a trap at Cape Broyle. Numbers at top are daily longshore wind velocities (km hr⁻¹) obtained by averaging hourly data. Positive numbers indicate upwelling favorable wind (from south). Arrows show predicted dates of increase in catch rate of males.

The least squares regression estimates for this equation were:

$$P = 0.38 \quad \theta < 5^\circ \quad (12a)$$

$$P = 0.62 \quad \theta > 5^\circ \quad (12b)$$

The 1984 results at Cape Broyle suggested that relaxation of wind-induced upwelling increased the catch rate of male capelin by a trap set at the coast. To test this prediction we measured catch rates of males relative to females at the same location in 1987. Our prediction was that cessation of winds with a strong northward component would result in an increase in relative catch rate of males. During the 1987 commercial capelin season (19–26 June) cessation of northward blowing winds occurred twice, once on the 21st, and again on the 24th. As predicted, the catch rate of male capelin increased after both events (Fig. 6).

4. Discussion

Calculations based on a simple two-layer model (Csanady, 1982) showed that prevailing winds from the southwest were theoretically capable of imparting enough momentum to surface waters to raise the pycnocline to the surface along the western shore of the Avalon Channel during the summer. This theoretical result is consistent with previous surveys of the temperature and density fields in the Avalon Channel. A cross-channel profile by Lively (1983, p 14) showed that upward deflection of both the thermocline and the pycnocline occurred near the coast during June, 1980. Hollibaugh

and Booth (1981, p 56) reported that cold water is evident near the coast in satellite imagery of the sea surface in the Avalon Channel. Our time-series data from three locations on the west coast of the channel showed that significant reductions in water temperature occur 5 to 10 m below the sea surface during winds favorable for upwelling.

Coherence between longshore wind and water temperature reached values of 0.5 at the two more exposed locations, Gull Island and Cape Broyle. Coherence between longshore wind and water temperature was generally lower at the more sheltered location, Witless Bay wharf. These results indicate that forcing by longshore winds is not the only source of variation in subsurface temperatures at the coast. Capes and headlands are known regions of strong tidal currents, tidally rectified flow, and pronounced upwelling. Thus, temperature fluctuations may be due in part to tidal period upwelling/mixing processes (e.g., fortnightly). Local forcing may also be important, especially in sheltered areas such as Witless Bay, where southwest, west, and northwest winds are steered seaward by low hills and cliffs on either side of the Bay. Response to cross-shore winds can be important in bays that are narrower than the first internal Rossby radius (cf Gill, 1982). This may explain why cross-shore winds were found to be related to thermal fluctuations inside the small cove studied by Frank and Leggett (1981, 1982).

Simple physical models are useful as a starting point for investigating complex circulation patterns in poorly known coastal areas. In the Avalon Channel, a simple two-layer model (Csanady, 1982, Eq. 3.97) was used to determine whether longshore wind stress was sufficient to raise the thermocline to the sea surface during summer conditions. The model predicted major drops in temperature at exposed coastal locations, and provided insight into the time required to raise the thermocline substantially (typically two days of 20 to 25 knot winds from the southwest). The model was not used to predict circulatory features such as rate of spin-up or upward water velocities. More realistic models would be needed to take into account tidal currents, capes and headlands, longshore propagation of coastally trapped waves (Yao, 1987), bottom topography, or seasonal changes in density anomaly (ϵ) and depth of thermocline (h_t).

Model calculations did not take into account seasonal changes in the density anomaly (ϵ) or thickness of the upper layer (h_t). Maximum seasonal values were used, so our calculations provide conservative estimates of whether wind induced upwelling was sufficient to raise the thermocline to the surface during the summer. Model calculations did not take into account the differences between wind velocities measured on land and over the water. Winds measured inland typically underestimate winds measured at sea (Hsu, 1981) so our calculations will give conservative estimates of whether longshore wind stress was adequate to raise the thermocline to the surface.

Model calculations did not take into account the momentum of the upper and lower layers due to net southward flow, which is on the order of 20 to 30 cm s⁻¹ in the Avalon

Channel (Petrie and Anderson, 1983). The literature provides little theoretical guidance on this, although Hay and Kinsella (1986) have examined the case of a surface current moving without friction over a motionless bottom layer with the coast to the right in the Northern Hemisphere. These authors found that winds prevailing on the Grand Banks were capable of reducing the thickness of a southward moving surface layer near a coastal (wall-like) boundary. We found that cold water appears at the coast after sustained winds with a strong northward component. Cold water disappeared as soon as the wind relaxed (Fig. 2).

Wind-induced thermal events near the coast successfully predicted increase in catch rates of male capelin, relative to female capelin. Capelin are largely confined to the warmer surface layer during the summer (Atkinson and Carscadden, 1979). Avoidance of a rising thermocline at the coast would tend to concentrate capelin in the vertical dimension. Outcropping of the thermocline, followed by offshore propagation of a cold water front, would then tend to concentrate capelin in a horizontal direction. We speculate that capelin, especially males, move shoreward behind a collapsing front after it has been spun up by sustained winds from the southwest. This would tend to synchronize shoreward movements of capelin, and ensure spawning during periods of minimum wave heights at beaches along the eastern coast of Newfoundland.

Wind-induced changes in water circulation and temperature near the coast can have a number of biologically important consequences. Potentially important effects include changes in the distribution and productivity of passively drifting phytoplankton (Walsh *et al.*, 1978), changes in exposure of fish larvae to predators (Frank and Leggett, 1982), daily doublings or halving of physiological rates of sessile plants and animals, changes in microbial activity (Pomeroy and Deibel, 1986), and changes in the concentration of depth-keeping nekton (Olson and Backus, 1985; Simard *et al.*, 1986).

The substantial energy input of intermittent winds favorable to upwelling may increase primary production in a current regime where nutrients are depleted above the thermocline during the summer (Hollibaugh and Booth, 1981). We note that cold water appeared within 10 m of the sea surface on 25 out of 62 days in July and August of 1984 (Fig. 2). We also note that intervening warm episodes persisted from 1 to 6 days, which would allow 3 to 18 doublings between upwelling events, assuming a doubling rate of 3 day^{-1} (Eppley, 1977). A well-verified physical model of upwelling in the Avalon Channel will be required to estimate the rate of upward advection of "new" nitrate into the warm upper layer in the summer.

The energy input of winds favorable for upwelling may also explain the abundance of upper trophic level organisms along this coast, including a capelin fishery (Templeman, 1948, 1966; Jangaard, 1974), an important inshore cod fishery (Templeman, 1965, 1966), and some of the largest seabird colonies in the northwest Atlantic (Brown *et al.*, 1975). Thermal events may be important in producing spatially predictable concentrations of capelin, which are fed on by cod (Templeman, 1965, 1966; Akenhead

et al., 1982), seabirds (Brown and Nettleship, 1984; Piatt and Methven, 1986; Piatt, 1987), and whales (Whitehead and Carscadden, 1985) in the Avalon Channel. Upwelling could potentially increase the concentration and spatial predictability of capelin, thus reducing the costs of foraging by large, highly mobile predators such as whales and seabirds. The effect of upwelling on capelin concentration and predator activity has yet to be measured directly.

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