

Effects of tidal streams on migrating Atlantic mackerel, *Scomber scombrus* L.

Martin Castonguay and Denis Gilbert

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During a mass prespawning migration, about 800 000 tons of Atlantic mackerel (*Scomber scombrus* L.) enter the Gulf of St Lawrence through Cabot Strait over a few weeks in the spring. Although the strait is 105 km wide, mackerel migratory activity, as revealed by fisheries acoustics techniques and trawl catches, is concentrated in the first 6 km of nearshore waters on the southern side of the strait. Current-meters moored 2 km off the southern shore showed that tidal currents alternately enter and leave the Gulf with speeds up to 75 cm s^{-1} while current-meters moored at 6 and 11 km offshore measured surface currents leaving the Gulf throughout the tidal cycle. The largest mean (1.2 kg m^{-2}) and maximum (16.3 kg m^{-2}) mackerel densities (from 11–80 m deep) were observed at slack tide. Mackerel densities increased at slack tides at the transition from a flow leaving to a flow entering the Gulf whereas they decreased at slack tides at the transition from a flow entering to a flow leaving the Gulf. Because times of slack waters were irregular, mackerel density increases did not occur on a regular semi-diurnal basis. These results suggest that mackerel use selective tidal stream transport to enter the Gulf of St Lawrence, although we were not able to document the vertical migrations through which selective tidal stream transport would be accomplished. This is the first report suggesting selective tidal stream transport in fast-swimming pelagic teleosts.

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Introduction

Atlantic mackerel (*Scomber scombrus* L.) is a fast-swimming pelagic marine fish species abundant in the north-west and the north-east Atlantic. During their mass prespawning migration, about 800 000 tons of mackerel (Grégoire and Lévesque, 1994) enter Cabot Strait (the southern entrance to the Gulf of St Lawrence) over a short period (last week of May and the first three weeks of June) on the way to their spawning grounds in the southern Gulf of St Lawrence (Fig. 1). Although Cabot Strait is 105 km wide, preliminary work suggests that mackerel migratory activity is concentrated in the nearshore area on the southern side of the strait (D'Amours and Castonguay, 1992; Castonguay and Beaulieu, 1993). Castonguay and Beaulieu (1993) also showed that Cabot Strait has strong currents, up to 75 cm s^{-1} , and indicated that mackerel schools occur mostly at flood tide and high

tide, which led us to hypothesize that mackerel use selective tidal stream transport (STST) to enter the Gulf of St Lawrence.

STST was first documented in juvenile European eel (*Anguilla anguilla*) (Creutzberg, 1959) and in adult plaice (*Pleuronectes platessa*) (Greer Walker *et al.*, 1978). The essential features of this interaction between behaviour and currents have been described by Arnold and Cook (1984): (1) fish remain near the surface when tidal currents flow in a direction appropriate for migration, (2) fish migrate vertically to the bottom when tidal currents reverse to a direction inappropriate for migration, and (3) remain there until the next slack tide, at which time (4) they migrate vertically to the surface.

The objective of this study is to determine the effects of tidal currents on migrating mackerel. More specifically, our goal is to assess whether mackerel use STST to enter the Gulf of St Lawrence. This work forms part of

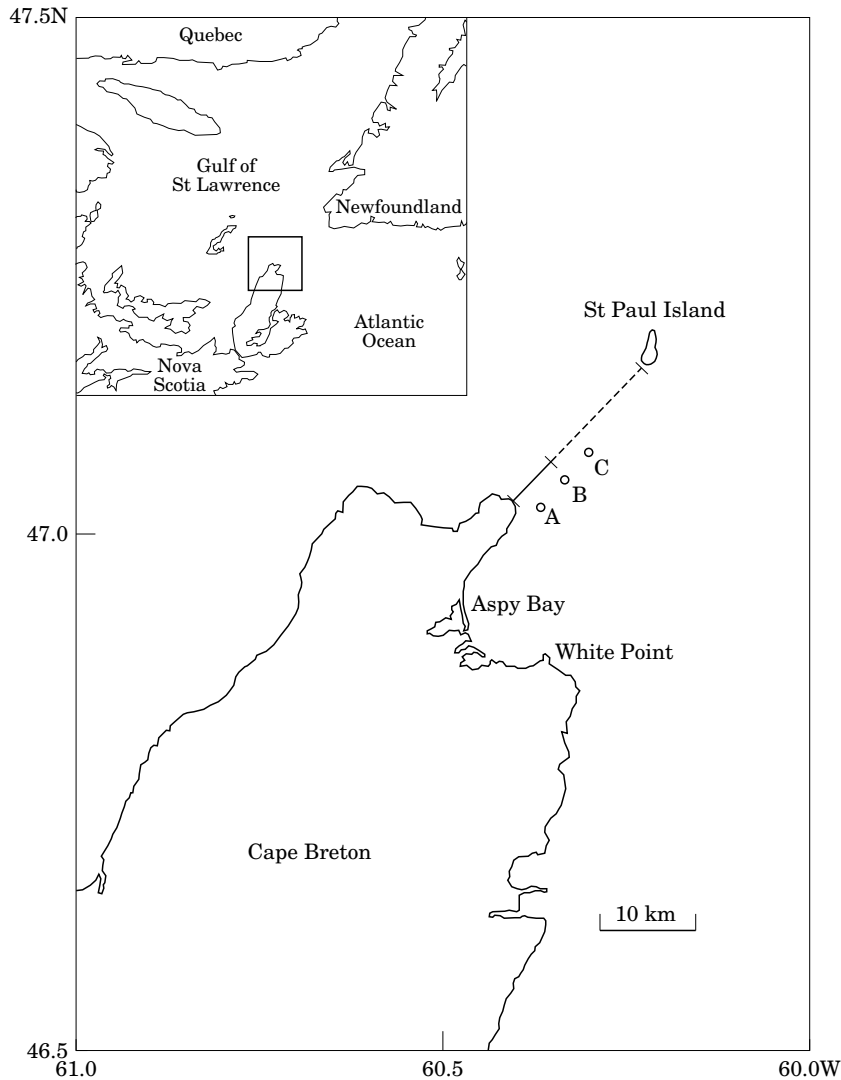


Figure 1. Study area showing southern Cabot Strait, Cape Breton, the survey transect to 5.6 km offshore (full line), the location of the three current-meter moorings, Aspy Bay, St Paul Island, and the Gulf of St Lawrence. The dotted line shows the CTD line extending to 22 km offshore. Degrees of latitude ($^{\circ}$ N) and longitude ($^{\circ}$ W) are also indicated.

a hydroacoustic abundance survey that we are currently developing for estimating mackerel stock size as the spawning stock migrates through Cabot Strait (Castonguay and Beaulieu, 1993).

Materials and methods

Survey

The study was conducted in Cabot Strait from 3–14 June, 1993. This work was part of a survey that samples a narrow migratory corridor in southern Cabot Strait

(Fig. 1) using hydroacoustics and a pelagic trawl for echogram interpretation. The survey consisted of 243 repeated passes over a single survey line from the closest safe distance (400 m) from the southern shore of Cabot Strait to several km offshore and back (Fig. 1), using a vessel equipped with a scientific echosounder. Of these 243 passes, 53 extended to 3.7 km or 2 nautical miles (nm) offshore while the rest extended to 5.6 km (3 n.mi) offshore. Ship speed was approximately 8 knots. Transects to 5.6 km offshore typically lasted 20–30 min. Three transects extended beyond 5.6 km to 11 and 22 (2 transects) km offshore (Fig. 1).

Data acquisition

Three moorings at 2, 6, and 11 km from the southern shore of Cabot Strait with two Aanderaa current-meters each were deployed on 4 June 1993 in Cabot Strait (Fig. 1). The depths of the shallow and deep current-meters and of the bottom were (A) 33, 51, and 68 m for the 2 km mooring; (B) 18, 37, and 147 m for the 6 km mooring; and (C) 14, 136, and 169 m for the 11 km mooring. The current-meters recorded current velocity, temperature, and salinity every 30 min. The mooring nearest shore was also equipped with a tide gauge that recorded the water level. All current-meters worked properly during the study period except for that which was 6 km offshore at 37 m. Temperatures and salinities in Cabot Strait were also measured along the same 22 km transect line as the acoustic transects described above (Fig. 1), with 13 CTD stations spaced every n.mi (1.85 km) from 1300 to 1600 on 13 June 1993.

The RV "F.G. Creed", a 20 m SWATH (small water-plane area twin-hull) vessel was used for the hydro-acoustic sampling. The vessel was equipped with a 120 kHz Simrad EK-500 echosounder with an output power of 1 kW. The echosounder was coupled to a hull-mounted 7° split-beam transducer and to the Hydroacoustic Data Processing System (HDPS) with a global positioning system (GPS) input. During hydro-acoustic sampling, 0.3 ms pulses were generated every 1.5 s. Digitized echoes (12 bits, 25 000 samples s^{-1}), to which a 20 log range (R) time-varied gain had been applied, were stored on optical disks for analysis. The ship speed varied from 4–8 knots. A target strength ball calibration of the echosounder using a standard copper sphere specific for 120 kHz was performed immediately prior to the survey according to procedures described in the EK-500 instruction manual.

A 20 m long trawler (RV "Calanus II") equipped with a pelagic trawl (horizontal and vertical openings: 22 × 14 m) fished, on request, fish schools responsible for observed echoes at a towing speed of 4 knots [see Beaulieu *et al.* (1993) for details of pelagic trawling]. For each trawl set, 50 randomly sampled fish of each species caught were frozen for later analysis and an additional 200 randomly-sampled fish of each species were measured (fork length). Catch composition was almost exclusively mackerel and herring (*Clupea harengus*). Mean (\pm s.d.) fork length of mackerel in trawl samples was 35.1 \pm 2.1 cm.

Data analysis

Currents ($cm\ s^{-1}$) were resolved into east (u) and north (v) velocity components. Currents flowing to the west ($-u$) and to the north ($+v$) enter the Gulf of St Lawrence, while currents flowing to the east ($+u$) and to the south ($-v$) leave the Gulf. Times of current

reversals were compared with times of measured high and low waters. Temperature and current fluctuations were also compared at the mooring nearest to the shore. Only data from the shallow current-meters are presented here. Times indicated throughout the paper are local (GMT+3 h), except in Figs. 2, 5, and 6 where GMT is used.

Echograms were edited using HDPS to remove the bottom signal and herring schools. The top 11 m of the water column also had to be deleted due to vessel noise. Herring schools were identified on the basis of trawl catches and by their echo intensity, which was much higher than mackerel. The echo intensity of herring schools was stronger than in mackerel because of a higher fish density within herring schools (Clay and Castonguay, in press) and also because mackerel have a lower target strength than herring due to their lack of a swimbladder (Foote, 1980; Collette and Nauen, 1983). Schools that contained a mixture of mackerel and herring were edited out of the echograms. Data were then echo-integrated per 10 m depth strata (except for the shallowest stratum, which was only 9 m deep). Seven depth strata were considered: 11–20 m, 20.1–30 m, 30.1–40 m, 40.1–50 m, 50.1–60 m, 60.1–70 m, and 70.1–80 m. Although the bottom depth along the 6 km transect varied from 40–160 m, the low target strength of mackerel rendered their detection impossible deeper than 80 m and may have biased downward the mackerel densities in the deeper strata considered. For this reason, echoes deeper than 80 m were excluded from the analysis.

The accurate determination of target strength is essential in the conversion of area backscattering intensity of sound to fish density. The mean *in situ* target strength of mackerel, calculated from several thousand individual targets collected during this study, was determined to be -56.4 decibels (dB) per fish or -52.8 dB per kg of fish (Clay and Castonguay, in press). This target strength value was used to calculate mackerel density in $kg\ m^{-2}$ for the seven depth strata of each transect.

We examined changes of mackerel density under six flow conditions. These flow conditions were based on the northward velocity component ($+v$) since currents at the 2 km mooring were predominantly in the north/south direction, parallel to the local isobaths. We defined six flow conditions ($cm\ s^{-1}$) as follows: $v < -40$, $-40 \leq v < -20$, $-20 \leq v < 0$, $0 \leq v < 20$, $20 \leq v < 40$, $v \geq 40$. To match the median times of the acoustic transects, the u and v components of currents and temperatures were interpolated from the half-hourly sampled data by the current-meter located 2 km offshore at a depth of 33 m. For the three $-v$ to $+v$ current reversals and the four $+v$ to $-v$ reversals for which we had collected acoustic data, we calculated a ratio of mean mackerel densities for the 10 consecutive transects

after the onset of slack tide to densities for the 10 consecutive transects before slack tide. We also compared depths of the centre of mass of the mackerel distribution (Z_{mac}) among the same six current conditions. The Z_{mac} were calculated as:

$$Z_{\text{mac}} = \sum_{i=1}^7 p_i Z_i$$

where p_i is the proportion of mackerel density (kg m^{-2}) in the i th depth stratum, and Z_i is the mean depth (m) of the i th depth stratum. Finally, we examined the distribution of mackerel biomass (expressed as total acoustic scattering area) as a function of the distance from shore. This was done by comparing the inshore portion of the surveyed migratory corridor (0.4–1.9 km offshore, 1.5 km long) with its central (1.9–3.7 km offshore, 1.9 km long) and offshore portions (3.7–5.6 km offshore, 1.9 km long).

Statistical analysis of these data presented difficulties. The distribution of mackerel densities departed from normality and had unequal variance among current categories (even after transformation of data), preventing the use of parametric statistics. The gaps in the mackerel density series, due mostly to frequent bad weather, prevented the use of a time-series analysis. We therefore resorted to non-parametric statistics to compare mackerel densities among tidal current categories. The lack of independence between successive mackerel density estimates is probably not a problem because mackerel density data pertaining to each current category originated from several tidal cycles (P. Gagnon, pers. comm.).

Results

Temperature, salinity, and density

Current-meter data from mooring A indicated that temperatures at 33 m depth fluctuated between -1°C and 6°C during the study period, while salinities varied between 29.5–32‰ (Fig. 2). The pronounced and rapid density variations (Fig. 2) which accompanied the temperature and salinity fluctuations indicate that this high frequency variability is primarily caused by motions within the internal wave band (which includes the semi-diurnal internal tide). These internal waves cause vertical oscillations of the seasonal thermocline, which was approximately 20–40 m deep at the time of the survey (Fig. 3). Below this thermocline lies the cold intermediate layer (CIL), a relic of winter cooling typically found in the summer at a depth of about 30–100 m in the Gulf of St Lawrence (Banks, 1966; Gilbert and Pettigrew, in press).

A cross-section of temperature for the first 22 km (12 n.mi) of southern Cabot Strait indicated that surface temperatures on 13 June 1993 varied from 4.5 – 6°C

depending on the distance from shore (Fig. 3). The top of the CIL, defined here as the layer with temperatures $<0^{\circ}\text{C}$, was as shallow as 20 m in the near-shore area and 50 m further offshore, while the bottom of the CIL was at approximately 80 m. Warmer waters with temperatures of 0 – 2°C were found below the CIL, at 80–160 m. A cross-section of salinity along the same transect indicated that less saline surface waters originating from the Gulf were found in the inner portion of the transect (Fig. 4).

Currents

Stick diagrams of near-surface currents show that southern Cabot Strait is tidally energetic, with current speeds up to 75 cm s^{-1} (1.5 knots) for the nearshore mooring and up to 110 cm s^{-1} (2.1 knots) for the offshore ones (Fig. 5). The stick diagrams also show that currents regularly enter the Gulf (flow to the north) only at the 2 km mooring, where the flow is predominantly in the north–south direction (Fig. 5). The mean v components of currents from 4–15 June 1993 were 6.0, -16.5 , and -18.4 cm s^{-1} for the surface current-meters 2, 6, and 11 km offshore, respectively. This shows that the mean flow entered the Gulf only in the nearshore zone, i.e. in the first 2 km. Similarly, the mean u components for the same period were 4.5, 28.9, and 27.0 cm s^{-1} for the shallow current-meters at 2, 6, and 11 km, respectively, showing that the mean currents at the three sites flow towards the east, but that the eastward component of currents was much weaker in the nearshore zone.

The component of current and temperature fluctuations at 33 m depth at the nearshore mooring were weakly linked (Pearson's $r=0.44$). A comparison of Figs 2 and 5 shows that warm temperatures were often associated with currents flowing into the Gulf while cold temperatures occurred when currents flowed out of the Gulf. The coupling between the v component of currents and water level was even weaker (Pearson's $r=0.28$). For example, during the spring tide period on 5 June 1993, the slack water corresponding to a change from $-v$ to $+v$ occurred at the high high tide and shortly after the low low tide (Fig. 6a). However, during the neap tide period on 12 June 1993, that same slack water occurred shortly before each of the two high tides (Fig. 6b). Tidal amplitudes during the study period varied from about 0.4 m at neap to about 1.1 m at spring tide.

Effects of tidal currents on mackerel densities

Current velocities affected mackerel densities integrated between 11 and 80 m (Table 1). Among the six current categories, the largest mean (0.85 kg m^{-2}) and maximum (11.3 and 7.5 kg m^{-2}) mackerel densities were found at the two slack water conditions (defined here as

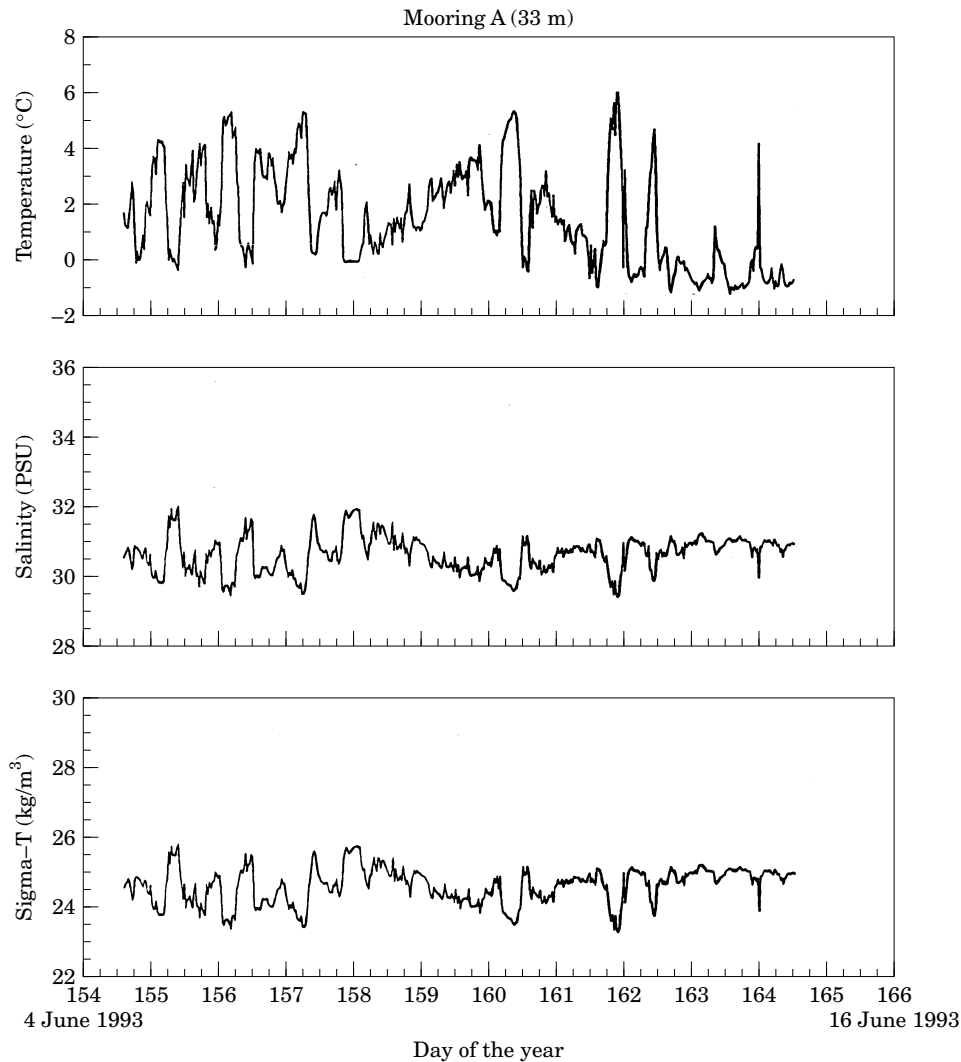


Figure 2. Temperature ($^{\circ}\text{C}$), salinity (‰ or PSU), and density (σ_t) time series measured every 30 min in Cabot Strait during the study period at the current-meter located 2 km offshore at a depth of 33 m. Time is GMT.

$-20 \leq v < 20 \text{ cm s}^{-1}$) (Kruskal-Wallis test, $p < 0.001$) (Table 1). The mean mackerel density was almost as large (0.80 kg m^{-2}) for a strong current ($\geq 40 \text{ cm s}^{-1}$) entering the Gulf as when slack waters prevailed (Table 1). The large standard deviations at slack tides indicate periods of rapid change in mackerel density. In contrast, the low standard deviation when a strong current entered the Gulf suggests that a regular “flow” of mackerel unimpeded by adverse currents entered the Gulf under this current condition. Table 1 also indicates that mackerel were still encountered on the survey line under adverse current conditions (strong flow to the south, i.e. strong negative values of v) and had mean densities as large as for one category of favourable currents ($20 \leq v < 40 \text{ cm s}^{-1}$).

Among the 243 mackerel density estimates measured over the transects, 16 of the 20 highest ones (range: $1.67\text{--}11.30 \text{ kg m}^{-2}$) occurred at slack water whereas such current conditions occurred only in 46% of transects. The null hypothesis that mackerel densities vary regardless of current conditions is statistically rejected ($\chi^2 = 9.30$; $p < 0.005$). In contrast, the water temperature (measured at the nearshore current-meter, 33 m deep) recorded for the 20 highest mackerel density estimates (mean = 1.84°C) was not different than for the rest of the mackerel density estimates (mean = 1.68°C) (Wilcoxon two-sample test, $p > 0.74$). This indicates that large mackerel densities were found when specific tidal current conditions prevailed, regardless of water temperature. Furthermore, 11 of the 16 above-mentioned

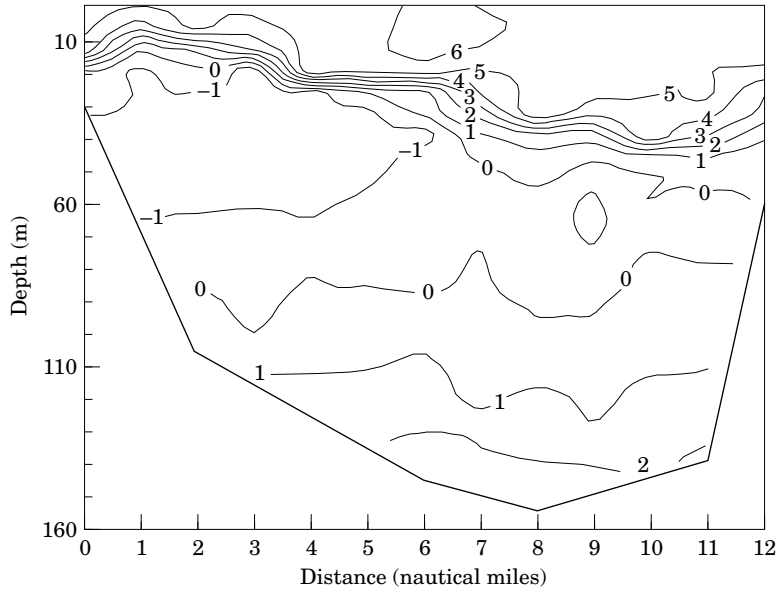


Figure 3. Temperature ($^{\circ}\text{C}$) cross-section of southern Cabot Strait on 13 June 1993. The abscissa is labelled in nautical miles from the strait's southern shore. Start time: 1300; end time: 1600 (local time). Vertical profiles were made every nautical mile (1.85 km).

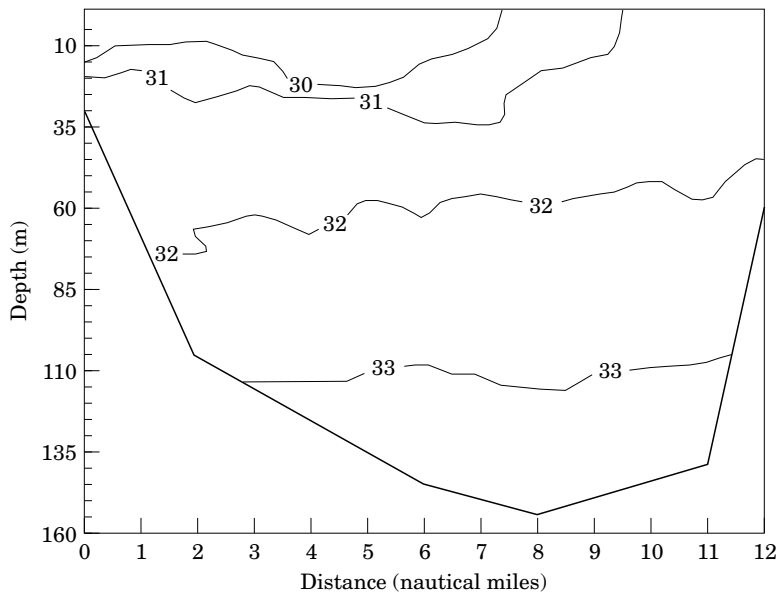


Figure 4. Salinity (‰ or PSU) cross-section of southern Cabot Strait on 13 June 1993. The abscissa is labelled in nautical miles from the strait's southern shore. Start time: 1300; end time: 1600 (local time). Vertical profiles were made every nautical mile (1.85 km).

highest mackerel densities measured at slack tide occurred when currents changed from $-v$ to $+v$ while the five others occurred during a 12.5 h period of slack currents on 11 June, during the neap tide.

We also found that mackerel densities increased when tidal currents became favourable and decreased when tidal currents became unfavourable. In two out of three

cases, mackerel densities increased at slack tides associated with the change from a flow leaving the Gulf ($-v$) to a flow entering the Gulf ($+v$), whereas they decreased in all four cases of slack tides associated with a $+v$ to $-v$ current reversal. The ratios of mackerel densities after the beginning of slack tide to densities before slack tide were 3.01, 0.84, and 2.29 when currents reversed

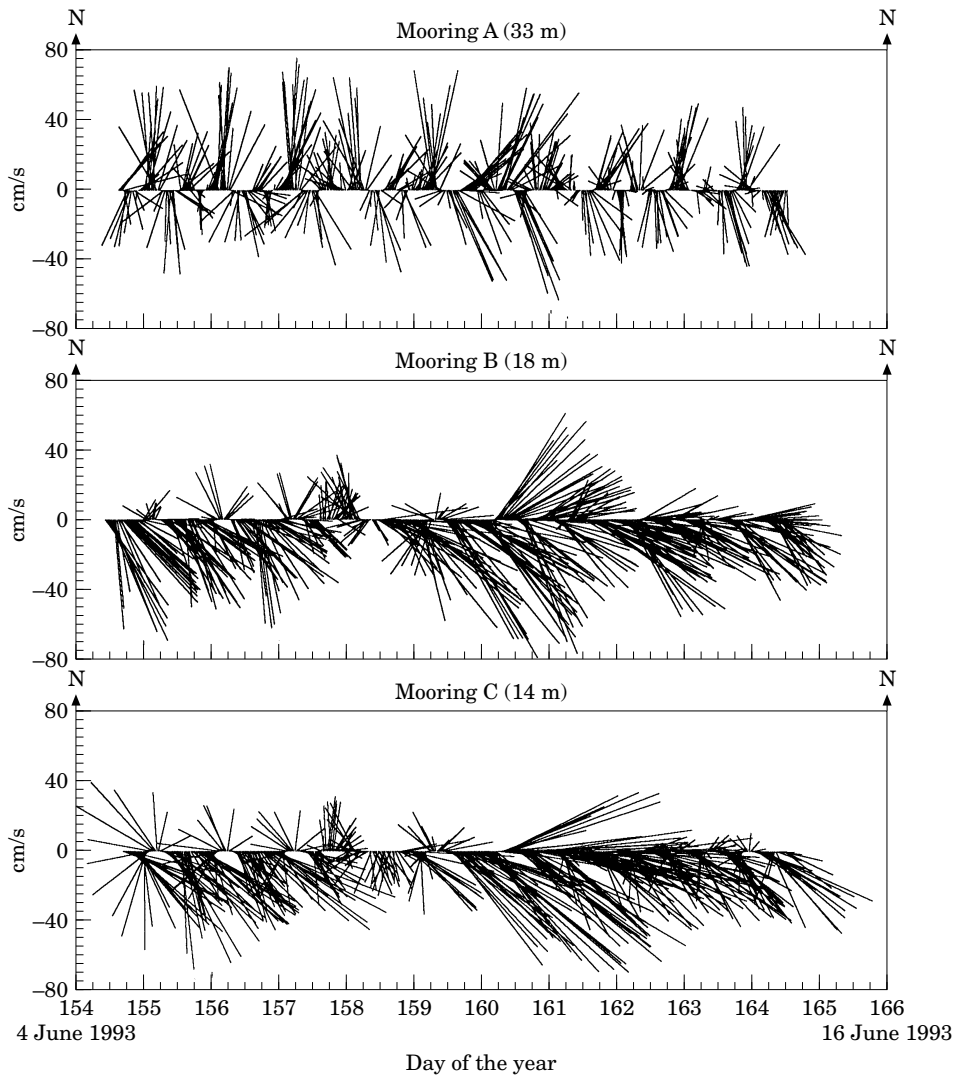


Figure 5. Stick diagrams of current velocities (cm s^{-1}) in Cabot Strait from 4 to 16 June 1993. Stick length indicates current speed while stick direction indicates the direction towards which the current flows. Currents were measured every 30 min by current-meters from mooring A (2 km offshore), mooring B (6 km offshore), and mooring C (11 km offshore). Depth of current-meters is indicated in parenthesis. Time is GMT.

from $-v$ to $+v$, whereas they were 0.35, 0.69, 0.42, and 0.49 when currents reversed from $+v$ to $-v$. Table 2 presents examples of such mackerel density fluctuations associated with current reversals: part A describes data collected during the $+v$ to $-v$ reversal, associated with the 0.35 mackerel density ratio, while part B shows data corresponding to the $-v$ to $+v$ current reversal with a density ratio of 3.01. Table 2 also indicates that mean temperatures tended to be warmer when currents entered the Gulf than when they left. This could suggest that mackerel density fluctuations associated with current reversals reflect thermal preference rather than choice of current direction. However, the statistical comparisons of the above paragraph argue against

this as they show that large mackerel densities were associated with specific tidal currents rather than a range of temperatures.

Effects of tidal currents on vertical distribution of mackerel

We have determined that mackerel densities increased at slack waters from $-v$ to $+v$ and decreased for reversals from $+v$ to $-v$. The next logical step is to determine whether mackerel migrate vertically from the deep waters beneath the CIL, consistent with STST, or if they move horizontally from the nearby Aspy Bay or from an offshore position (see Fig. 1).

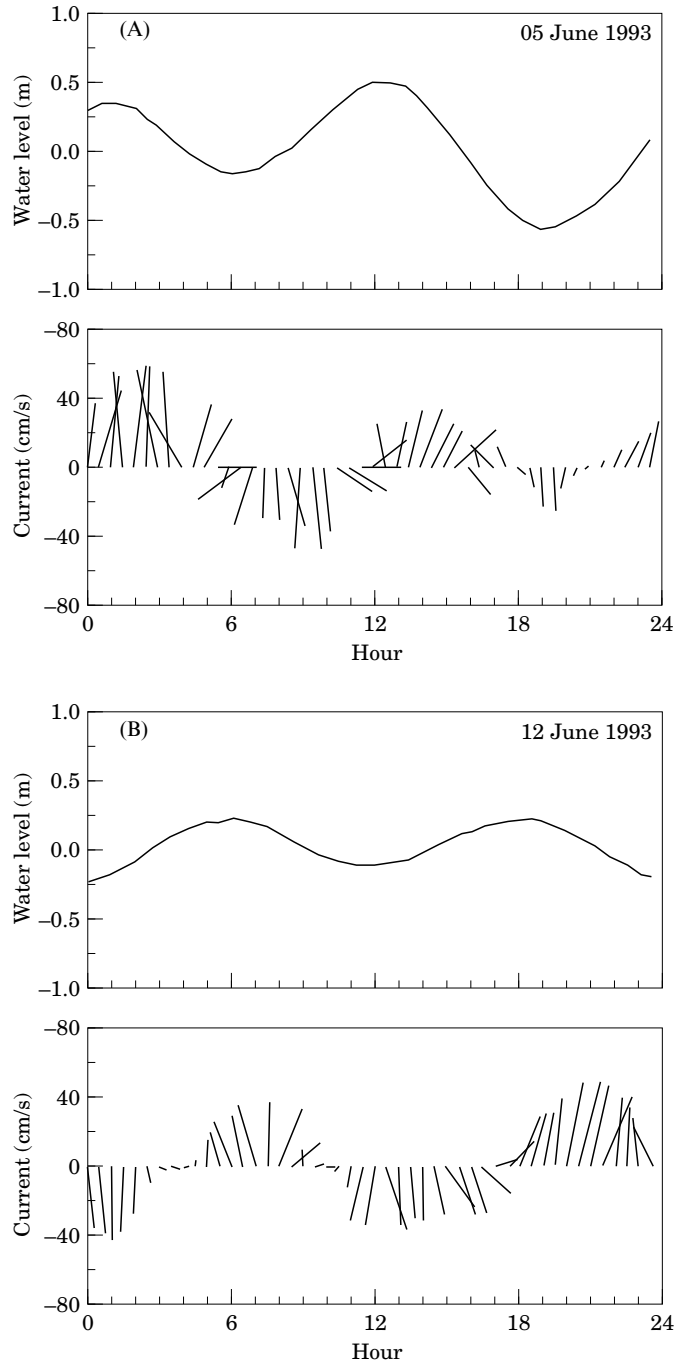


Figure 6. Current velocities in relation to tidal heights in Cabot Strait for 5 June 1993, during the spring tide period (A) and for 12 June 1993 during the neap tide period (B). Stick length indicates current speed while stick direction indicates the direction towards which the current flows. Currents were measured every 30 min by a current-meter from mooring A, 2 km offshore, and 33 m deep, and water level was measured by a tide gauge at the same mooring. Time is GMT.

In order to take into account a possible aliasing day/night effect on the vertical distribution of mackerel in Cabot Strait, we first compared day-time and night-time vertical distributions. No

significant day/night effect was found because day-time (Z_{mac} 28.5 m) and night-time (Z_{mac} 27.7 m) did not differ statistically (Wilcoxon two-sample test, $p > 0.2$).

Table 1. Mean mackerel densities (kg m^{-2}) from 11–80 m dep under different conditions of v current (cm s^{-1}). Z_{mac} =depth of centre of mass of the mackerel distribution (m).

v (cm s^{-1})	Mean density \pm s.d. (range)	Z_{mac}	n
< -40	0.48 ± 0.39 (0.12–1.19)	31.8	9
-40 to -20	0.49 ± 0.66 (0.01–3.24)	25.5	46
-20 to 0	0.85 ± 1.54 (0.03–7.49)	27.1	40
0 to 20	0.82 ± 1.52 (0.01–11.30)	26.9	71
20 to 40	0.48 ± 0.46 (0.01–1.62)	28.2	34
40 to 60	0.80 ± 0.43 (0.10–1.91)	33.3	43

We carried out a survey of nearby Aspy Bay (Fig. 1) (maximum depth: 60 m) on 4 June 1993 consisting of five survey lines that started 5 h prior to a favourable slack water and ended at slack water (1730) in order to determine if mackerel made a horizontal movement to the migratory corridor from Aspy Bay. No mackerel schools were detected in the bay, although a school approximately 1.5 km long and 15 m thick was detected immediately afterwards on the regular transects. These observations suggest that horizontal movement of mackerel does not explain sudden mackerel density increases according to current on the transect line.

Currents seem to have little effect on the vertical distribution of mackerel. The largest mean mackerel density was always found at 20–30 m depth regardless of the current condition (Fig. 7). In fact, 60% of the mackerel were located at a depth of 20–40 m, regardless of light and current conditions. Mean Z_{mac} , averaged per current condition, varied between 25.5 m for $-40 \leq v < -20 \text{ cm s}^{-1}$ and 33.3 m for $v \geq 40 \text{ cm s}^{-1}$ (Table 1). Few mackerel were detected below 50 m.

The only evidence we gathered regarding an effect of tidal currents on vertical distributions is that mackerel were found at significantly greater depths at slack water when adverse v current conditions preceded the slack water than when favourable v current conditions preceded the slack water (Wilcoxon two-sample test; $p < 0.02$); this observation is consistent with STST. We compared Z_{mac} between two subsets of the $-20 \leq v < 0$ current category (the only category for which our data base permitted such a comparison): currents that were preceded by stronger ($-40 \leq v < -20$) currents flowing to the south (adverse) versus those preceded by weak ($0 \leq v < -20$) currents flowing to the north (favourable). Mean Z_{mac} of transects preceded by favourable and adverse current conditions were 25.8 ($n=8$) and 32.6 m ($n=32$), respectively.

Effects of currents on the width of the mackerel migratory corridor

Mackerel appear to migrate nearshore in Cabot Strait because it is only there that the currents flow in a

direction appropriate for migration on a regular basis. An unusual current pattern on 10 June 1993 at mooring B provides further evidence that currents affect the width of the migratory corridor. While near-surface currents 6 km offshore generally flowed out of the Gulf, there was an 8 h period (0100–0900) on 10 June 1993 during which currents at this location flowed strongly into the Gulf, as did currents at the nearshore mooring at that time (day 160, Fig. 5). The mean percentages of mackerel biomass found in the 0.4–1.9, 1.9–3.7, and 3.7–5.6 km portions of the surveyed migratory corridor for the 18 transects made during that 8 h period were 21.4, 53.8, and 24.8%, respectively. In contrast, mackerel migrated significantly more inshore for the rest of the transects extending to 5.6 km ($n=159$), as the corresponding mean percentages were 56.1, 27.9, and 15.9%, respectively. Statistical comparisons using the Wilcoxon two-sample test indicated that the percentage of biomass in the 0.4–1.9 km portion was significantly lower during the 10 June event than for the rest of the time ($p < 0.03$). In contrast, this percentage was higher in the 1.9–3.7 km portion ($p < 0.05$) while it was not different in the 3.7–5.6 km portion ($p > 0.05$). In other words, the mackerel migrated further offshore when the corridor of water entering the Gulf was wider, as was the case during the unusual current event of 10 June 1993. This current event coincided with a period of weak winds from the south-west, and was preceded the day before by strong winds from the south-west.

The three transects that extended further offshore than 5.6 km only partially confirmed previous observations on the narrowness of the migratory corridor reported in Castonguay and Beaulieu (1993). The first and second transects, which surveyed out to 22 km off the southern shore, recorded 79% and 46% of the mackerel biomass in the first 6 km offshore, respectively. The third transect, extending to 11 km offshore, measured 77% of the biomass in the first 6 km. The small biomass proportion nearshore for the second transect was caused by a large mackerel school detected 21 km offshore, 1 km south-west of St Paul Island (see Fig. 1).

Discussion

We have determined that mackerel densities increase with slack waters associated with reversals from unfavourable to favourable current conditions and decrease with reversals from favourable to unfavourable conditions. Our survey of nearby shallow Aspy Bay (shortly before locating a large school on a transect) did not locate any mackerel schools. It seems that if a 1.5 km long \times 15 m thick school were in the bay in the hours preceding its detection on the transect, we should have detected it there. Mackerel could also make a horizontal movement to the study area from offshore surface waters at the appropriate slack tide. However, it seems

Table 2. Mackerel density variations for two types of current reversals. Z_{mac} = depth of centre of mass of the mackerel distribution. V (north/south) component of current and temperature were measured at the 2 km mooring, 33 m deep. Observations at and after slack tide are in bold character. Consecutive transects within each of the two subsets of data were 20–30 minutes apart.

Transect	Mackerel density (kg m ⁻²)	Z_{mac} (m)	v (cm s ⁻¹)	Temperature (°C)	Start and end time
A: +v to -v					
58	0.90	30.30	47.63	3.12	4 June 21:26
59	1.66	31.78	53.78	3.40	
60	0.79	27.60	56.44	3.33	
61	1.67	28.98	59.08	2.86	
62	1.91	29.07	59.97	3.70	
63	0.93	28.67	58.88	4.02	
64	1.34	33.89	57.16	3.98	
65	0.78	30.10	47.34	3.95	
66	0.51	30.39	37.13	3.91	
67	0.51	27.45	33.56	3.80	
68	0.53	32.86	17.38	3.02	5 June 06:39
69	0.28	26.36	-4.06	1.69	
70	0.19	29.77	-13.85	0.90	
71	0.39	23.50	-21.42	-0.15	
72	0.18	30.11	-33.13	0.14	
73	0.33	24.67	-29.70	-0.06	
74	1.11	22.00	-31.23	-0.23	
75	0.35	26.26	-34.77	-0.14	
76	0.26	31.76	-47.51	-0.27	
77	0.19	28.94	-48.38	-0.41	
B: -v to +v					
111	0.61	23.97	-29.13	0.20	6 June 05:35
112	0.60	23.34	-29.14	0.03	
113	0.30	25.19	-29.55	-0.20	
114	0.74	29.71	-29.61	-0.36	
115	1.16	28.47	-27.27	-0.01	
116	0.44	28.57	-27.08	0.27	
117	1.38	29.86	-29.47	0.35	
118	1.11	24.29	-33.58	0.36	
120	3.24	29.35	-26.75	0.03	
121	2.91	34.66	-21.70	-0.08	
122	2.60	34.47	-17.29	-0.05	6 June 12:52
124	5.96	35.37	-15.77	1.66	
125	2.12	34.05	-13.48	3.30	
126	7.49	40.54	-9.87	3.58	
127	2.48	39.74	-6.47	3.70	
128	1.31	31.59	-3.73	3.65	
129	1.29	33.98	4.84	3.61	
130	11.30	38.48	14.89	3.57	
132	1.21	32.42	15.19	3.67	
134	1.93	31.29	16.23	2.75	

unlikely that they would be found in surface waters offshore during adverse currents, considering that currents there almost always flow in a direction inappropriate for migration. In addition to the lack of evidence for a horizontal movement of mackerel at the appropriate slack tide, there was also no detectable effect of currents on vertical distribution, except for the comparison at slack tide that showed that mackerel were found in shallower water when favourable currents preceded than when adverse currents preceded slack tide.

Although statistically significant, this depth comparison is based on a small sample size and the Z_{mac} differed by only 7 m.

The mackerel schools detected in Cabot Strait when appropriate currents prevailed may have performed a horizontal movement from either inshore or offshore positions, or a vertical migration from near-bottom waters. Faced with a lack of solid evidence for either a horizontal or a vertical movement, we nevertheless suggest that mackerel are migrating through Cabot

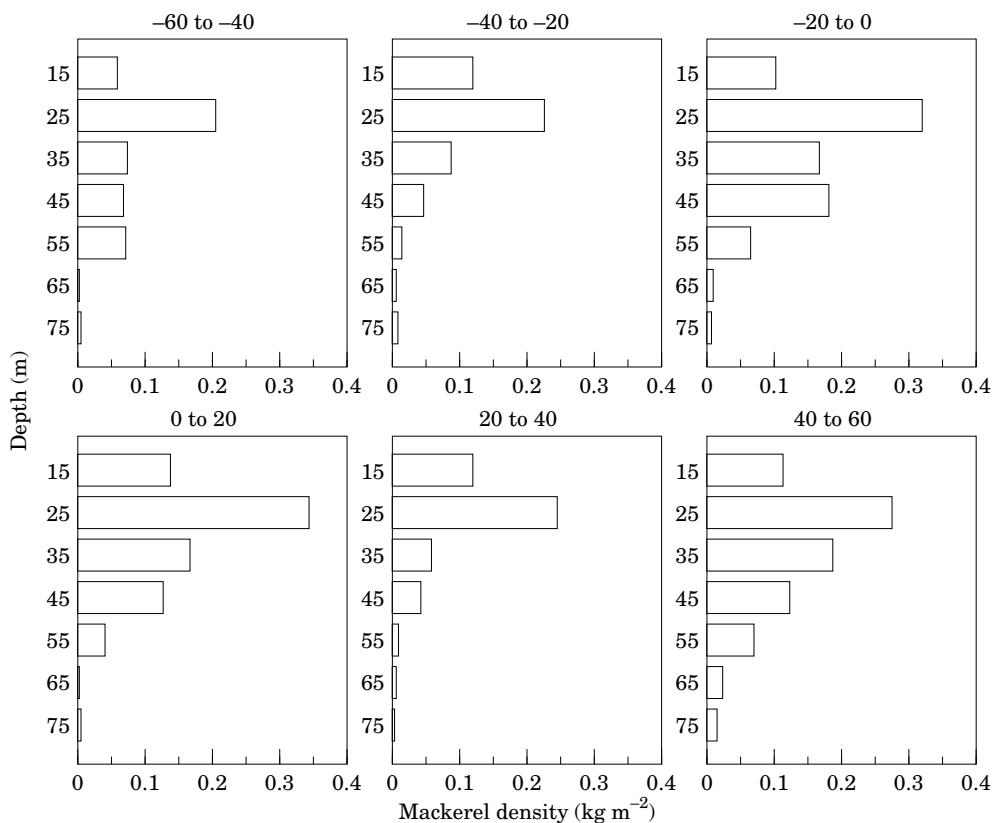


Figure 7. Vertical distribution of mackerel in Cabot Strait for six current conditions expressed as mean mackerel densities (kg m^{-2}) per 10 m depth strata. The six current conditions are defined according to the north/south component (v , cm s^{-1}) of current velocities. The top 11 m of the water column and waters deeper than 80 m were excluded from the analysis.

Strait using STST. The increase of mackerel densities at appropriate slack tides would result from vertical migrations to near-surface waters that we could not detect adequately for two reasons. First, due to their low target strength, we may have had the capability to detect mackerel only when they were near the surface. Foote (1980) estimated that the swimbladder is responsible for 90% of the energy reflected from fish possessing this organ, hence the low target strength of fishes that do not have swimbladders. The noise margin that we used to delete unwanted noise and zooplankton recorded by the EK-500 echosounder (in order to minimize the size of acoustic files) was set too high (Clay and Castonguay, in press); this may have resulted in deleting an increasingly large proportion of mackerel echoes with increasing depth. Hence, schools migrating vertically to the surface may have become fully detectable only when they were in water as shallow as 40–50 m. Furthermore, the deletion of the top 11 m of the water column may have contributed to a masking of vertical migration. This deletion undoubtedly made Z_{mac} values appear deeper than they actually were.

Secondly, some mackerel were found in surface waters when strong currents were flowing out of the Gulf. This may have partially hidden the vertical migration pattern in those fish which do perform vertical migrations. The movement of fish over ground during adverse currents is not known; they may be stationary, leaving the Gulf, or else entering against tidal streams. Cod (*Gadus morhua*) exhibiting STST may at times make progress against an adverse tide if the speed of the water does not exceed the fish's maximum sustainable swimming speed (Arnold *et al.*, 1994). He and Wardle (1988) reported the maximum sustainable swimming speed of mackerel to be 3.5 body-lengths s^{-1} (123 cm s^{-1} for a 35 cm mackerel), i.e. faster than the maximum tidal streams measured. This could explain how mackerel could have entered the Gulf under adverse currents. Variability in STST behaviour may be related to fish condition. Herring in poor condition swim more slowly than herring in good condition (Robinson and Pitcher, 1989). Mackerel condition is lowest at the beginning of the migratory period, when large (35–40 cm) and old (5–11 year-old) mackerel enter the Gulf of St Lawrence (Grégoire *et al.*,

1994). Fishermen in Cabot Strait describe the first mackerel of the season as weak, and also occasionally report mortalities on shores (K. Fitzgerald, pers. comm.). STST might be especially advantageous for weak mackerel but not so important for later mackerel that arrive in better condition.

STST has previously been documented in demersal species in the North Sea and in juvenile eels but never in pelagic fish (see Arnold *et al.*, 1994 for a review). Herring tracked with ultrasonic tags in the St Lawrence Estuary during their prespawning migration also appear to use STST (J. Munro, unpubl.). Moreover, STST has been reported in several larval crustaceans (e.g. DeVries *et al.*, 1994). It is energetically advantageous in areas of strong tidal flow (Weihs, 1978; Metcalfe *et al.*, 1990). It may also lessen the need for precise orientation (Arnold and Cook, 1984).

STST will result in semi-diurnal vertical migrations (i.e. two vertical migration cycles per 24 h 50 min period) provided that semi-diurnal tidal currents are the dominant component of the overall flow pattern. These conditions are met in the North Sea, where all the above STST evidence in fishes has been gathered, except for the work on eels. Hence, Arnold and Cook's (1984) definition stated that STST is accomplished through semi-diurnal vertical migrations. McCleave and Wipfelhauser (1987) extended this definition by demonstrating that juvenile American eels migrating up an estuary using STST do not exhibit a semi-diurnal vertical migration pattern; they remain in the water column for only an average of 190 min during the flood tide before seeking refuge near the bottom until the next flood tide.

In this study, water current reversals and mackerel density increases (and hence inferred vertical migrations) did not occur on a regular semi-diurnal basis, in synchrony with M_2 , the main lunar component of tides. For example, the time elapsed between appropriate slack tides at the 2 km mooring varied between 7.5 and 16 h over the period 4–7 June 1993 instead of the 12.4 h periodicity (M_2 tidal periodicity) of semi-diurnal tides. Such variability is due to two factors. First, tides in Cabot Strait are categorized as “mixed, mainly semi-diurnal”, not “semi-diurnal”, as is the case in the North Sea. A measure of the relative importance of diurnal and semi-diurnal tides is given by the form ratio $F = (K_1 + O_1) / (M_2 + S_2)$, the ratio of major diurnal to major semi-diurnal tidal constituents (Pond and Pickard, 1983; p. 267). Harmonic analysis of the tide gauge record from the 2 km mooring yielded $F = 0.50$, hence the above tidal category for Cabot Strait. This means that there are large inequalities in range and time between the highs and lows each day. In contrast, the tides at Lowestoft in the North Sea have a more semi-diurnal character ($F = 0.29$), possibly explaining why authors working there found STST on a regular

semi-diurnal basis (e.g. Greer Walker *et al.*, 1978). Second, continental shelf currents are not only affected by tidal motions, but also by other types of motions that have a broad range of time scales. Wind-induced motions, horizontal currents associated with internal waves, and coastal trapped waves, for example, all contribute to the observed currents, and are often comparable to or even larger than tidal effects. These non-tidal components of the flow are much less deterministic than tides and could therefore be partly responsible for the irregularity in the time elapsed between successive slack currents at a particular site.

Besides being irregular at a particular site, tidal currents also exhibit a great deal of spatial variability. During their 1000–2000 km migration along the continental shelf towards their spawning site in the southern Gulf of St Lawrence (Sette, 1950; Parsons and Moores, 1974), mackerel may encounter significant tidal streams in Cabot Strait, on George's Bank, and on some of the shallow banks of the Scotian Shelf, but certainly not in every body of water through which they migrate.

Why would mackerel use STST? So far, we have implied that the primary reason for this behaviour would pertain to the energy savings it may provide the exhausted fish at their lowest condition of the year. However, it is also possible that mackerel use STST as a clue (sensu Harden Jones, 1984), providing information on the direction of migration rather than for energy savings, as suggested by Arnold and Cook (1984). Mackerel may need clues to reach their spawning grounds because, in contrast to tuna and other pelagic fish to whom “home” may be a specific set of environmental conditions whose geographic coordinates may change from year to year (Neill, 1984; Cury, 1994), mackerel always seem to spawn in the same geographic area, as shown by annual egg surveys (Ouellet, 1987; Grégoire, 1993). In addition, mackerel always enter the Gulf around the same date, 27 May \pm 3 days (mean \pm s.d.; $n = 10$) (Castonguay and Beaulieu, 1993). This precise migratory timing has remained the same for the past century, as a fisheries officer from a town near Cabot Strait reported in 1895 that, “Mackerel appeared as usual on May 28th” (Anon., 1896). Such spatio-temporal precision of movement argues for strongly orientated prespawning migrations. STST may be a mechanism for providing orientational information to mackerel in areas where tidal streams are strong. In contrast, postspawning feeding migration of mackerel may be accomplished primarily through behavioural enviroregulation (the behavioural regulation of immediate environmental conditions) (Castonguay *et al.*, 1992), as has been proposed for tuna (Neill, 1984). This suggests that postspawning feeding migration of fish is generally less well orientated than prespawning, as Cury (1994) remarked in the case of the Pacific salmon (*Oncorhynchus* spp.).

Several questions remain unanswered. Do mackerel migrate upward from underneath the CIL, do they perform a horizontal movement from Aspy Bay without vertical migration, or do they rather take advantage of tidal currents through both horizontal and vertical movements? If most mackerel are, as we believe, in deep waters near the bottom when current conditions are unfavourable, does the detection of slack water by fish sufficiently close to the bottom to receive rheotactic stimuli serve as a cue for the fish to ascend the water column at the appropriate time? What cues are used to descend the water column when currents reverse towards the inappropriate direction? Do the fish swim while near the surface or are they passively transported? Is the individual variability in the expression of STST behaviour related to the variability of fish condition? Do other fishes, such as cod, use STST to reach their spawning grounds in the Gulf of St Lawrence?

In summary, we have presented data which suggest that mackerel use STST to enter the Gulf of St Lawrence, although we have yet to document the vertical migrations through which STST would be accomplished. Our data also indicate that this possible case of STST does not involve semi-diurnal vertical migrations because of the irregularity of tidal currents. Moreover, the width of the mackerel migratory corridor seems to depend upon the width of the current entering the Gulf. Future surveys will attempt to address the above questions. Several potential ways to solve the acoustic detection problem of deep-water mackerel need to be investigated, such as using a longer pulse length (i.e. sending more energy in the water), avoiding using the noise margin, and sounding with a 38 kHz frequency in addition to or instead of the 120 kHz currently used, as the sound wave is less attenuated by water at lower frequencies. Holding position at a single station in the centre of the migratory corridor for 12.5 or 25 h might allow us to sample the vertical migration better. Harmonic analysis of tidal currents (see Pond and Pickard, 1983) will allow us to predict the time of slack waters, and hence will maximize our future sampling of current reversals. STST has been documented primarily through ultrasonic tracking (e.g. Greer Walker *et al.*, 1978) and midwater trawling (e.g. de Veen, 1978). We could also apply these techniques in this case.

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