# Influence of Ice Cover on Sediment Temperature and Implications for Intertidal Benthic Invertebrates on a Bay of Fundy Mudflat

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While the ecology of the intertidal mudflats of the upper Bay of Fundy has been extensively studied during the warmer months of the year, the winter ecology remains largely unknown.  Winter air temperatures average below 0 $^{o}$C for several months of the year, and extensive amounts of sediment-laden ice are present on the mudflats and in the seawater during that time. Benthic macroinvertebrates, such as the amphipod *Corophium volutator*, are an important food source for millions of migrating shorebirds and fish in the summer.  The question arises as to how these invertebrates survive the winter.

In the winter and spring of 1996, environmental conditions and benthic invertebrate density in the upper intertidal zone were monitored at one mudflat in the upper Bay of Fundy to gain an understanding of the winter conditions experienced by infauna and of the presumed recolonization of the mudflat in the spring.  Hourly weather data and subsurface sediment temperatures at 15-min intervals were collected from late January to early June.  Observations of ice on the mudflat were made periodically.  Once the ice had disappeared from the mudflat in mid-March, weekly samples were taken for invertebrates.

Although the air temperature can be substantially colder than the lethal temperature of the invertebrate macrofauna, the sediment temperature is not, which appears to be the result of insulation by ice in or on the sediment.  However, the re-floating of ice which has frozen to the sediment results in the removal of portions of the sediment surface and its infaunal inhabitants.

## 1. Introduction

The upper Bay of Fundy is renowned for having the largest tidal range in the world.  Also characteristic are the extensive intertidal flats, which are an important feeding ground for millions of migrating fish and shorebirds in summer (Hicklin and Smith, 1984; Dadswell *et al.*, 1984; Mawhinney *et al.*, 1993).

Because an estimated 50-95% of the world's population of Semipalmated Sandpipers (*Calidris pusilla*) stop at Bay of Fundy mudflats to feed (Mawhinney *et al.*, 1993), portions of the upper Bay of Fundy have been named as parts of the Bay of Fundy Western Hemisphere Shorebird Reserve (Shepherd *et al.*, 1995). The diet of Semipalmated Sandpipers is composed almost exclusively of the gammaridean amphipod *Corophium volutator* (Hicklin and Smith, 1979; Hicklin and Smith, 1984; Boates and Smith, 1989). *C. volutator* inhabits U-shaped burrows in the sediment and is one important factor determining the stability of the sediments of the intertidal mudflats (Daborn, 1991; Daborn *et al.*, 1993). Densities of *C. volutator* at some mudflats can be as high as 50,000 individuals $m^{-2}$ (Wilson, 1989). Other predators, such as commercially important fish, also prey extensively on *C. volutator* (Imrie and Daborn, 1981).

Other common inhabitants of the mudflats of the upper Bay of Fundy include the tellinid bivalve *Macoma balthica*, the nereid polychaete *Nereis diversicolor*, and the capitellid polychaete *Heteromastus filiformis*. Secondary production in the upper Bay of Fundy is estimated to be 40 g carbon $m^{-2}y^{-1}$ (Gordon, 1994).

A third feature of the upper Bay of Fundy is the large amount of sediment-laden ice transported by the tides and deposited on the shores. The air temperature in winter averages several degrees below 0 °C (Knight and Dalrymple, 1976) and can go as low as –30 °C (Loomis, 1995). Ice may be present from December until March or April (Knight and Dalrymple, 1976; Gordon and Desplanque, 1983). At times, ice covers the entire mudflat or estuary (Hind, 1875; Amos, 1978). Blocks of ice stranded by the tides can grow to over 5 m in height and 7 m in breadth (Hind, 1875). The implications of winter conditions for the invertebrates inhabiting the mudflats in areas subject to ice include: starvation (particularly for those which depend on the diatoms, bacteria, and detritus at the sediment surface for their nutrition); disturbance of habitat due to plowing, scraping, and removal of sediment by ice; and potential freezing injury or death.

Prior to this study, it was assumed that either there was considerable mortality of benthic macrofauna (*Corophium* in particular) in winter (*e.g.*, Wilson, 1989) or possibly that they migrated subtidally during the winter (*e.g.*, Möller, 1986). The few studies which involved sampling during winter, or before and after winter, indicated large declines in *Corophium* abundance over the winter months (Hicklin *et al.*, 1980; Wilson, 1989; Möller, 1986). Research has been done on the freezing tolerance or winter survival of other intertidal invertebrates, though very little or none involving the four species *Corophium volutator*, *Nereis diversicolor*, *Macoma balthica*, and *Heteromastus filiformis*. Other intertidal invertebrates are known either to survive or to avoid freezing, by various mechanisms.

Given the apparent harshness of the winter, the great abundance of *C. volutator* and other species in summer requires explanation. This paper considers the winter ecology of one particular Bay of Fundy mudflat, the Windsor mudflat, particularly with a view to understanding the survival of the benthic macrofauna. It is first necessary to establish what are the winter conditions experienced by the macrofauna. Several aspects of the

physical environment were examined: weather; temperature of the sediment in the layer inhabited by macrofauna; occurrence of ice; and the temperature of the overlying seawater.

## 2. Study Area

The Windsor mudflat was formed by sediment accretion following the 1970 construction of the Windsor Causeway across the formerly tidal Avon River, in Nova Scotia, Canada. The Avon Estuary drains into the Minas Basin of the Bay of Fundy (Figure 1). The mudflat is situated between the causeway and the confluence of the Avon and St. Croix Rivers, centred at latitude 44°59.75' North, longitude 64°08.75' West (Canadian Hydrographic Service, 1994).

After the causeway was constructed, sediment accreted rapidly downstream of the tidal barrier and formed what is now known as the Windsor mudflat. The surface area of the mudflat is estimated to have been 102.4 ha in 1992 (Sangster, 1994).

The portion of the mudflat used in this study lies on the eastern bank of the Avon River, approximately 400 m north of the east end of the Windsor Causeway and about 180 m northwest of the Windsor Tourist Bureau (Figure 2). At the time of the study (January to June, 1996), the study site extended northwest 78 m from the edge of the saltmarsh to the edge of the wastewater-outfall channel and straddled two parallel drainage channels, approximately 60 m apart, which extend perpendicularly from the saltmarsh to the sewage-outfall channel (Figure 2).

## 3. Materials And Methods

*Meteorological conditions*
An Environment Canada meteorological station was installed on top of the dyke at the western end of the Windsor Causeway, 1 km (straight-line distance) from the study area (Figure 2). Meteorological conditions (air temperature, wind speed, wind direction, others) were monitored continuously and recorded hourly from January 26 to June 6, 1996.

*Sediment temperature*
Ten Vemco Minilog®-TR temperature dataloggers were installed at various points on the mudflat to measure sediment temperature every 15 minutes. Each datalogger was inserted into a hole drilled into a 1.2-m length of 5-cm iron channel bar. The iron bar was driven about 1 m into the sediment with a sledge hammer until the bottom of the hole was just above the sediment surface. At that point, the temperature datalogger, wrapped in a plastic bag to keep mud off the infrared transmitter, was inserted into the hole and tethered to the post with a stainless steel cable. The bar was then tapped down until the

sensor lay 2-3 cm below the surface of the sediment.  The datalogger and cable were carefully covered with sediment.  During each subsequent visit to the mudflat, the depth of each datalogger from the sediment surface was measured (except on days on which the stakes were covered by ice).  The dataloggers were retrieved April 5 for downloading data and were reinstalled April 6.

On February 22, one of the dataloggers (East Small Channel) beside a small stream was found to be uncovered.  Its temperature recordings were used to gauge water temperature when submerged and air temperature near the sediment surface when exposed.

*Ice Presence and Characteristics*
Excursions were made to the Windsor mudflat weekly for the duration of the study, and observations of the environmental conditions were recorded.

*Inferred presence of ice*
Formation of ice in the sediment was inferred by sediment temperatures which dropped below   $-1.6$ °C, then increased either sharply or gradually about 1 °C with the release of latent heat upon freezing of the water, to hold at about $-1$ °C.  The salinity at the head of the Avon Estuary is  28.5 ‰ (Lambiase, 1980); the freezing point of seawater of that salinity is $-1.55$ °C (Doherty and Kester, 1974).  Duration of ice cover was estimated as percent of time between January 20 and April 5 that ice was inferred to be present.

*Sampling for Invertebrates*
Sampling for invertebrates was conducted once during an ice-free period in February, then weekly from mid-March (when most of the ice had disappeared) to the end of the study.  In addition, a few exploratory samples of sediment and ice were collected early in the study.

Sediment cores of 100 cm$^2$ surface area were taken with a square metal sampler measuring 10 cm on a side and 9.8 cm deep.  The sampler was inserted into the substrate to the depth of the soft sediment.  Samples were placed in labeled zipper-type plastic bags and removed to the laboratory to be sieved.

For the random sampling February 24-25, thirty 1-m$^2$ quadrats were selected randomly in a grid 60 m wide by 80 m long.  One sample was taken from the centre of each quadrat.

For the systematic sampling March 18 to June 3, a grid 75 m wide by 75 m long, with 15-m spacing was established.  Sampling was done in checkerboard fashion, with sample locations being visited on alternate weeks.  Two sediment cores were taken a few cm apart at each sample station; two weeks later, the next pair of samples was taken adjacent to the previous pair.

Upon arrival at the laboratory, the sediment cores were refrigerated.  Most cores were sieved within 48 hours, a few within 72 hours.  Each sample was washed with seawater

strained through a 0.177-mm-mesh sieve.  The slurry was gently stirred by hand to near-liquid state, and poured through a 0.25-mm-mesh sieve.

Material remaining in the sieve was washed with strained seawater into a jar.  Enough 37% formaldehyde was added to each jar to result in an end concentration of approximately 4-10% formaldehyde.  A dropperful of Rose Bengal (solution 1 g/l) was added to the samples to highlight small polychaetes.  At a later date, the preserved samples were washed into a tray and the invertebrates picked, identified, enumerated, and placed in vials of 70% ethanol.

For the exploratory samples, two cylindrical sediment cores, each about 90 cm$^2$ in area and 8-10 cm deep, were taken in each of three exposed places at the seaward edge of ice at the fringe of the saltmarsh.  The cores were removed to the laboratory and sieved at 0.5 mm.

*Statistical analysis*
Median counts are reported, and nonparametric tests were used.   Normalizing transformations were not warranted, since nearly all of the counts were in single digits. The Friedman test, blocking by sample location, was employed to test for differences in invertebrate abundance over time.   The Mann-Whitney-Wilcoxon test was used to compare macrofaunal densities in mid-winter (February 24/25 random samples) and early spring (March 18-22 systematic samples).  Graphical methods were used to gain insight into spatial patterns.

Comparison of results for different studies is problematic when all that is reported by other authors are the mean and standard deviation or standard error.    In order to determine whether the results from this study were significantly different from others', Bonferroni-adjusted *t*-confidence intervals were computed and compared.

## 4. Results

*Air Temperature*
Weekly means of average hourly air temperatures were below 0 $^o$C from the beginning of recording at the end of January until mid-March, except for a "February thaw" in mid- to late-February (Figure 3).  From mid-March until recording stopped in early June, the air temperature rose, slowly at first, then more rapidly, plateaued from late April through May, then jumped up sharply in June.  The change in air temperature from sub-zero to above-zero in mid-March coincided with the departure of the ice covering the mudflat.

The lowest air temperature recorded during the study was –22.9 $^o$C (February 5); the highest was 27.7 $^o$C (June 2).  The most rapid change in hourly average air temperature was an increase of 8.5 $^o$C in mid-February, while the most rapid decrease in temperature within one hour was a drop of 4.9 $^o$C in late January.  The largest increase in air temperature within a 24-hour period was almost 21 $^o$C in the span of 9 hours at the

beginning of June, while the largest decrease was an overnight drop of over 21 $^{o}$C in late May.

From mid-March (almost the vernal equinox) to the end of the study, there was very close agreement between the weekly mean air temperatures measured close to the sediment surface by the exposed East Small Channel (East Small Channel) datalogger (tide out) and measured by the weather station.  Prior to that, the air temperatures a few meters higher than the mudflat surface (*i.e.*, those measured by the weather station) were considerably more volatile than air temperatures a few cm above the sediment surface in a small channel.

*Datalogger depth*
The depths of the dataloggers varied throughout the study.  During the winter months, the depths of most of the dataloggers increased considerably, likely due to the weight of overlying ice pushing the stake further into the substrate.  After reinstallation of the dataloggers April 6, past the disappearance of ice on or in the sediment, the depths of most of the dataloggers tended to remain fairly constant.

Erosion or slumping of sediment or sediment removal by ice can be inferred by decreases in the depth of a datalogger.  Increases in depth in the ice-free months may reflect sediment deposition, infilling of excavated areas around the stakes, or possibly additional sinking due to the weight of the iron channel bar in very soft sediment.

Although the sediment-temperature records display a tendency toward an inverse relationship between the depth of the temperature datalogger and the magnitude of short-term changes in temperature, no simple relationship could be determined between the depth of a temperature datalogger and either the average temperature recorded on that day or the maximum change in temperature recorded on that day.

*Sediment temperature*
The pattern of the sediment temperature through the winter includes a period of largely stable, though slightly negative temperature, punctuated by rises of several degrees during the "January thaw" and "February thaw."  From mid-March to mid-April, the sediment temperatures increased overall, though were highly variable (Figure 3).  After a sharp increase in late April, sediment temperature increased more slowly through May (Figure 3).

Sediment temperature was much less volatile than air temperature in winter (Figure 3). In general, the sediment temperature remained essentially constant near –1 $^{o}$C when the air temperature was well below 0 $^{o}$C.  Even from mid-March to early April, the sediment temperature was neither as low nor as high as the air temperature.  From early April until late May, sediment temperature followed air temperature quite closely (Figure 3).

Several patterns in the sediment temperature records can be seen upon close examination. During the winter, while ice was either observed or inferred to be present, the temperature of the sediment was almost constant at about –1 $^{o}$C; the effects of the

environment, such as air temperature, solar radiation, and tidal flooding, were almost nil. When the sediment was free of ice, however, the sediment temperature was a function of air temperature, solar radiation, and seawater temperature.

*Water temperature*
The water temperature, as measured by the exposed East Small Channel datalogger, hovered close to 0 $^o$C from mid-February to mid-March. Water temperature rose to above +1 $^o$C in mid-March and continued to increase for the duration of the study, to an average of 11 $^o$C.

*Observations of ice*
The study began during the annual "January thaw" — a few days of relatively warm weather — during which the study area was free of ice. After that, the amount of ice in or on the sediment increased. In late January-early February, the weather became quite cold, enough to form ice up to 2 cm thick on the outgoing tide. As winter progressed, the ice cakes on the mudflat grew larger, more irregular, and muddier. Ice cakes were layered with thin lamellae of ice containing sediment. Some ice cakes were carrying a thick (up to 15 cm) underlayer of sediment. The ice vanished within two days during the "February thaw" but returned again with the colder weather. After a large snowstorm in mid-March, there was a sudden increase in the amount and whiteness of ice. Rafted ice cakes lifted 3-4 cm off large areas of the surface of the study area (Figure 4). After that, no more ice was observed on top of the mudflat surface.

Several different types of ice were observed during the study: ice sheet, formed by the freezing of the outgoing tide; ice crystals within the sediment; lacy ice on top of the mudflat surface; cake or drift ice; frozen snow; icefoot, or shorefast ice; frozen crust, ice in or bonded to the upper layer of sediment (Knight and Dalrymple, 1976); and mixtures. On four occasions (January 27, February 11, February 22, and March 13), cakes of drift ice with up to 15 cm of sediment attached were observed.

*Inferred presence of ice*
Those sediment temperature datalogger locations closest to channels appear to have experienced the most freezing; those closest to the saltmarsh appear to have experienced the least freezing, even though the dataloggers may have been buried more shallowly than at other locations. However, the percent of time that ice was inferred to be present was not statistically significantly different among the dataloggers (Kruskal-Wallis H = 12.89, df = 9, P-value = 0.167).

Except during the coldest part of the winter, no ice was inferred to be present at depths below 5 cm; *i.e.*, the sediment temperatures remained above –1.6 $^o$C deeper than 5 cm below the surface of the mudflat, except during the period January 27 to February 22, when the lowest air temperatures recorded were below –12 $^o$C. A weak concordance was found between percent of time ice was inferred to be present and depth of temperature datalogger (Kendall's tau$_b$ = 0.308, P-value = 0.000). There was no linear relationship between percent of time ice was inferred to be present and depth of temperature datalogger, even when the view was restricted to depths of less than 5 cm. No

statistically significant relationships were found between rate of sediment temperature change and datalogger depth for the depth-measurement dates (multiple ANCOVAs, Bonferroni family significance level 0.05).

*Invertebrates*
In virtually all samples, only four species of macroinvertebrates were found: the polychaetes *Nereis diversicolor* and *Heteromastus filiformis*, the bivalve *Macoma balthica*, and the amphipod *Corophium volutator*. Occasionally a sample would contain one or two of a spionid polychaete, *Streblospio benedicti*, or a phyllodocid polychaete, *Eteone* sp.

*Exploratory sampling, February 11*
Only *Nereis* and *Corophium* were found. The numbers of *Nereis* in the 90-cm$^2$ samples ranged from 1 to 31, corresponding to densities of up to 3400 individuals m$^{-2}$. *Corophium* ranged from 6 to 98 per 90-cm$^2$ sample, corresponding to densities of 660 to 10,800 individuals m$^{-2}$. These results must be viewed with caution, as the samples do not constitute random or representative sampling.

*Random sampling, February 24/25*
*Nereis* was numerically dominant in the February 24/25 samples; *Heteromastus* was scarce at that time. With the exception of a single sample containing 66 *Nereis*, the numbers of *Nereis* per sample ranged from 1 to 14. The median number of *Nereis* per 100-cm$^2$ sample was 3.5, corresponding to a density of 350 individuals m$^{-2}$ (Figure 5a). Fourteen of the 30 samples contained no *Macoma*. The median number of *Macoma* per sample was 1, corresponding to a density of 100 individuals m$^{-2}$; the maximum number of *Macoma* in a sample was 4 (Figure 5b). The median number of *Corophium* per sample was 0; *i.e.*, more than half of the samples (18 of 30) were devoid of *Corophium*. Another seven samples had only a single *Corophium*, and the counts in the remaining samples ranged from 2 to 8 (Figure 5c). Very few *Heteromastus* were found — of the 30 samples, 25 had no *Heteromastus*, four had a single individual, and one had 3 (Figure 5d).

*Systematic sampling, March 18 - June 3*
The number of *Nereis diversicolor* per sample ranged from 0 to 15, with the median consistently 2 organisms per sample, or a density of 200 individuals m$^{-2}$, during most weeks (Figure 5a). Density of *Nereis* did not change during the study period (Friedman S = 5.94, df = 5, P-value = 0.313).

For all 12 weeks of sampling, the median number of *Macoma balthica* per sample was 1, corresponding to a density of 100 individuals m$^{-2}$. With the exception of two relatively large values, of 26 organisms in one sample in week 9 and of 41 organisms in one sample in week 12, the range of per-sample counts was 0-8 (Figure 5b). The abundance of *Macoma* remained essentially unvarying during the period of study (Friedman S = 3.61, df = 5, P-value = 0.607).

The median number of *Corophium volutator* per sample was 0 in all weeks except the last, when the median increased to 1.5, or about 150 individuals m$^{-2}$. Most samples had no more than 10 *Corophium* (Figure 5c), with a few very high values: 26 (March 22), 35 (May 16), 113 and 142 (May 24), and 23 and 45 (June 3). The two large values of 113 and 142 *Corophium* per sample found May 24 were the counts from a single pair of samples taken at the same location at the edge of the saltmarsh; in that sample pair, 98 of the 113 *Corophium* and 132 of the 142 *Corophium*, respectively, were newly-hatched young. The median number of *Corophium* per sample increased significantly in the last two-week set of samples (Friedman S = 17.82, df = 5, P-value = 0.003).

The median number of *Heteromastus filiformis* per sample was 0 for the first 6 weeks, then fluctuated between 1 and 0 for the last 6 weeks (Figure 5d). The spread and extreme (high) values increased over the course of the study; however, there was no significant difference in the median number of *Heteromastus* per sample over time (Friedman S = 43.43, df = 5, P-value = 0.000).

*Comparison of February 24/25 and March 18/22 densities*
Except in the case of *Nereis*, invertebrate densities in late February were not significantly different from those in mid- to late March (Mann-Whitney test, *Macoma*: P-value = 0.40; *Corophium*: P-value = 0.62; *Heteromastus*: P-value = 0.23). The density of *Nereis* was significantly higher in late February than in mid- to late March (Mann-Whitney W = 1194.5, P-value = 0.0145). Even with the removal of the high outlier (6600 *Nereis* m$^{-2}$) observed in February, the density of *Nereis* was still significantly higher in February than in March (Mann-Whitney W = 1016.5, P-value = 0.0234).

## 5. Discussion

*Low-temperature survival*
Mills and Fish (1980) reported the mean lethal temperature of overwintering *C. volutator* in the U.K. to be approximately −8.4 °C, and −3.3 °C for summer animals, with no significant difference by sex or adult/juvenile stage. Mortality increased as temperature decreased (Mills and Fish, 1980). Moreau (1995) found the supercooling point of juvenile *C. volutator* from Minas Basin to be −8.5 to −10 °C, with differences in that range measured for animals from different locations and different seasons. She also found that the *Corophium* did not survive being frozen (Moreau, 1995). Holmstrom *et al.* (1981) found that the freezing point of *Corophium* varied between −6.6 and −9.9 °C, depending on age, season, and prior acclimation conditioning. Based on finding that the melting point of the hemolymph of *Corophium* was about −0.015 °C, essentially the same as seawater, for both summer and winter animals, Holmstrom *et al.* (1981) concluded that there is no evidence of cryodepressing compounds in the hemolymph of *C. volutator* (Holmstrom *et al.*, 1981).

Since *C. volutator* does not survive freezing (*i.e.*, formation of ice in the tissues) in the laboratory (Moreau, 1995), one would predict that it would not tolerate freezing in the wild.

*Air Temperature*
The weather over the period of the study covered a wide range of conditions and at times varied rapidly. Since the benthic macrofauna inhabit burrows beneath the surface of the mudflat, some of the effects of the weather conditions are indirect, rather than direct.

Air temperatures affect the formation and melting of ice, as well as the temperature of the sediment. Indirect effects of air temperatures would include effects of ice on the mudflat and the infauna, such as ice-related mortality, unavailability of food, mobility of poikilothermic organisms, and the timing of reproduction for organisms and their food items.

*Sediment temperature*
The sediment-temperature results obtained in this study were consistent with those of Ratcliffe *et al.* (1981).

*Corophium* are reported to survive conditions of frozen sediment (Mills and Fish, 1980), though in what condition and in what numbers are not known. There is no contradiction with the earlier statement that *C. volutator* itself does not survive freezing — the freezing of sediment is actually the freezing of water in the sediment, which is a function of the salinity of the porewater. The freezing point of seawater of salinity 36‰ is about $-2\ ^{\circ}$C (Doherty and Kester, 1974). As ice forms in seawater, salts are excluded, rendering the water beneath the ice hypersaline, and thus lowering its freezing point (Neumann and Pierson, 1966).

Environmental effects from the freezing of seawater, specifically the porewater in the substrate, to which infauna would be subject, include increase in salinity, potential mechanical injury due to ice formation, and sudden temperature increases caused by the release of latent heat upon the freezing of the water. On the other hand, the fact that the sediment temperatures remained constant when ice was present indicates that the presence of ice effectively insulates the sediment, and the invertebrates therein, from extremes of temperature. Furthermore, even though temperatures as low as $-2$ to $-4.4\ ^{\circ}$C were recorded and assumed to be associated with the initial formation of ice deep within the sediment, they were rare, extremely brief, and still always several degrees above the lethal temperature of the infaunal animal of primary interest, *Corophium volutator* (Figure 3).

The fact that the sediment temperatures remained constant at about $-1\ ^{\circ}$C when ice was present suggests that the presence of ice effectively insulates the sediment, and the invertebrates therein, from extremes of temperature. Thus it appears, from the sediment-temperature results presented in this study, not to be necessary that *Corophium* be freeze-tolerant (*i.e.*, to survive freezing of the tissues). Even though the air temperatures would be lethally cold, *Corophium* can survive in its burrow because the sediment temperature remains higher than the amphipod's lethal temperature.

However, although the animals themselves may not freeze, one may conjecture that they could experience ice-related injury or mortality resulting from jagged ice crystals, pressure due to expansion of ice, and sudden temperature changes associated with the initial formation of ice. Further study would be required to verify this hypothesis.

*Water temperature*
The water-temperature results obtained in this study were consistent with those of Clément *et al.* (1998), whose measurements of sub-ice seawater temperature off the coast of northern New Brunswick varied between $-1.05$ $^{o}$C and $-1.61$ $^{o}$C. It should be noted, though, that the water whose temperature was measured by the exposed East Small Channel datalogger was very shallow and likely warmed by the mudflat, *i.e.*, that the water of Minas Basin, in general, was likely not that warm.

Water temperatures affect timing of reproduction of the benthic macroinvertebrates (Dales, 1950; Shaffer, 1983; Cranford *et al.*, 1985).

*Ice*
Shorefast ice forms high in the intertidal zone and, as its name implies, tends to remain there for the duration of the winter (Knight and Dalrymple, 1976). Shorefast ice protects the mudflat surface underneath from erosion (Knight and Dalrymple, 1976). At the seaward edge of the ice, however, the sediment will be prone to erosion by the energy of the tide and waves hitting the ice edge (Sasseville and Anderson, 1976).

Drift ice, particularly large cakes, can scrape and plow the sediment surface as it is transported by the tidal waters, resulting in sediment disturbance, resuspension, and erosion. Estimates of time to recovery of the sediment from ice-scouring damage range from two months (Sasseville and Anderson, 1976) to over three years (Bleakney, 1972).

It is the frozen crust which is removed from the mudflat by ice-rafting, when drift ice freezes to the crust and subsequently is lifted by buoyancy on the rising tide (Knight and Dalrymple, 1976). In cohesive sediments, such as on mudflats, the removal of frozen crust results in abrupt, shallow but broad, holes in the surface (Knight and Dalrymple, 1976; Figure 4). The exposed sediment is not frozen and is therefore vulnerable to erosion. Tidal or groundwater can also force frozen crust apart from the sediment, leaving the crust to be melted or floated away (Knight and Dalrymple, 1976).

The sediment removed from the surface of a mudflat may fall to the estuary bed as the ice melts (Sasseville and Anderson, 1976), thereby contributing to sedimentation or to suspension of sediment in the water column, or it may be transported to another location, where it is deposited when the ice cake carrying it is stranded and melts. Sediment deposited by melting ice cakes is usually quite consolidated and remains as a lump above the surface of the mudflat.

Effects of ice-scouring and ice-rafting on benthic macroinvertebrates include: direct mortality (*e.g.*, by crushing); indirect mortality (or at least environmental stress) by removal of habitat and food sources; and disruption of community structure and

recruitment, by removal and transport of the animals themselves. Organisms in saltmarshes or high in the intertidal zone might be less likely to experience mortality and exportation by ice-rafting. Ice-rafting can also result in importation of saltmarsh thatches and sediment, possibly including immigrant macrofauna.

Hicklin *et al.* (1980) attributed large reductions in the densities of *Corophium* and *Macoma* to ice. Wilson (1989) estimated winter mortality to be over 70% at the nearby location of Avonport Beach, suggesting that the ice conditions were the primary cause, though he also reported about 35% winter mortality in the laboratory. On the other hand, Wilson (1991) claimed that there was no decline in the abundance of other species, including *Heteromastus*, due to winter ice. In the latter paper, however, he did not address mortality in the laboratory.

Except during the coldest part of the winter, no ice was inferred to be present at depths below 5 cm. Since it is the frozen crust, which is formed by a combination of the freezing of porewater and the accumulation of surface ice, which is rafted by ice cakes, that suggests that except during the coldest weather, burrows deeper than 5 cm may be safe from ice rafting. Sediment up to 15 cm thick on the undersides of some ice cakes was observed during the coldest part of the winter, which was also when freezing was inferred to have occurred down to at least 15 cm.

Perhaps the water content is greater in sediment close to channels, which one could hypothesize as an explanation for why there was slightly more freezing inferred close to channels. As well, it is reasonable to conjecture that more sediment-rafting takes place at the edges of channels than on the adjacent flat area, in part because the flooding tidal water would be deeper in the channel, thus providing greater buoyancy.

Slightly less freezing was inferred from the sediment temperatures close to the saltmarsh than elsewhere, even though the dataloggers were not quite as deep there.

*Invertebrate life histories*
*Nereis* is reported to spawn in late winter to early spring in the U.K., "after a sharp rise in temperature" to $5 - 8.8\ ^{\circ}C$ (Dales, 1950) and in both spring and autumn in La Rance estuary in France (Brenot and Retière, 1997). The densities of *Nereis* as determined by the systematic samples in the current study fail to indicate an increase in numbers indicative of recruitment, and water temperatures in the range $5 - 8.8\ ^{\circ}C$ were not achieved until quite suddenly in the middle of April. However, some *Nereis* only a few mm in length were present in early to mid-April. Animals that small could have passed through the sieve and thus be underrepresented in the survey. They may indicate a spring spawning. As well, occasional "damaged" *Nereis* were found in samples from mid-March to mid-April, with the greatest number in late March. It is possible that those bodies represented post-spawning mortality, which, if true, would lend support to some spawning having taken place.

The 66 *Nereis* in one February 24 sample were quite a mixture of sizes, indicating a mixture of ages, more than only brooding females and their just-hatched young. The

small *Nereis* in that sample were about 6 mm in length.  Even if the polychaetes had not grown over the fall and winter, this evidence suggests the possibility of a cohort produced at a time other than in the late winter to early spring.   Further investigation is warranted.

*Macoma* spawns in the early summer in the upper Bay of Fundy, coinciding with water temperatures around 12-13 $^{o}$C (Cranford *et al.*, 1985).  Spat settle passively at first; however, it is argued that they later actively migrate by byssus-drifting (Beukema, 1993).  The mean and median seawater temperatures measured by the exposed East Small Channel datalogger during tidal immersion reached only 10-11 $^{o}$C by the end of this study.  The densities of *Macoma* over the course of this study did not reflect substantial recruitment, though spat were occasionally present in samples beginning at the end of March.  Thus, unless spat too small to be found on a 0.25-mm-mesh sieve had settled by the end of the study, it is likely that large-scale settlement, and perhaps spawning, had not yet taken place.

Previous research has indicated that *Corophium* has two generations per year.  The overwintering generation reproduces in late May to late June.  The early-summer generation reproduces in mid-July to mid-August, and those progeny become the next overwintering generation (Peer *et al.*, 1986).

The beginnings of the spring recruitment were apparent in the samples, with ovigerous females and juveniles present toward the end of the study.  The samples taken at the edge of the saltmarsh on May 24 contained *Corophium* in numbers which were 1-2 orders of magnitude greater than in other samples; furthermore, most of those animals were juveniles.

*Heteromastus* spawns once a year.  Adults are observed to have ripe gametes during the winter, and settlement of the planktonic larvae begins approximately late winter-early spring in South Carolina (Shaffer, 1983).  Since spawning is a function of water temperature for many polychaetes, and since the temperature of the seawater would be colder in the Bay of Fundy than off the coast of South Carolina, one would expect spawning in the Bay of Fundy to occur somewhat later.  Population densities are fairly constant throughout autumn and winter, then increase sharply in spring and decline steadily until the fall (Shaffer, 1983).  Cadée (1979), however, argues that population structure varies from year to year.

Although the mean and median densities of *Heteromastus* remained fairly constant, the 75$^{th}$ percentile and maximum increased over the course of the study.  This suggests that limited spawning may have been taking place.  Further study would be required to establish details of *Heteromastus* recruitment in the upper Bay of Fundy.

*Comparison with other studies*
A few studies of the Windsor mudflat were performed in the summers of the late-1970s.  Risk *et al.* (1977) found the dominant organism at Windsor at that time to be *Heteromastus*.  *Corophium* and *Macoma* densities were described as being considerably lower than at other mudflats in the upper Bay of Fundy (Risk *et al.*, 1977; Turk *et al.*,

1980).  Very few nereid polychaetes were found at all at Windsor in the late 1970s (Hirtle, 1978; Yeo, 1978).  The only recent surveys of the Windsor mudflat were those of Sangster (1994) and Miner (1997).

It is difficult to compare results of studies which employed different methods and were carried out in different years and seasons.  Changes have taken place over the past 20-30 years at the Windsor mudflat and at other mudflats in the upper Bay of Fundy (Shepherd *et al.*, 1995).  Only Miner (1997) sampled the same part of the Windsor mudflat as this study — the east bank of the Windsor mudflat was essentially nonexistent in the 1970s.  As well, comparison of results obtained with different sieve mesh sizes is unreliable.  Turk *et al.* (1980) sampled the Windsor mudflat in 1976, 1977, and 1979, using a large-mesh sieve (1.0 mm); therefore, their density figures would be negatively biased (Bachelet, 1990).

Comparison of the invertebrate densities reported in other studies by means of checking for non-overlap in Bonferroni-adjusted *t*-confidence intervals for the mean densities without correcting for sieve mesh size suggests that *Macoma* was more abundant at the Windsor mudflat in the 1970s than in the 1990s.  Since bivalves are more likely than other organisms to be underrepresented when larger mesh sizes are used (Bachelet, 1990), this comparison is likely conservative.  Whether *Corophium* abundance has increased cannot be determined, due to the difference in the sieve mesh sizes employed in the different studies.  The abundance of *Nereis* at the Windsor mudflat has increased dramatically from the 1970s, when it was almost nonexistent, to the 1990s.

Other mudflats in the upper Bay of Fundy have been studied extensively, though predominantly in the late 1970s-mid-1980s (*e.g.*, Hicklin, 1981; Gratto, 1979) and predominantly in the summer months.  The study by Hicklin *et al.* (1980) is relevant because it was one of the few studies which have included year-round sampling.  At three locations in Chignecto Bay monitored monthly from May 1978 to April 1979, the authors found 7,000-10,000 *Corophium* m$^{-2}$ in summer or fall and about 40-1340 *Corophium* m$^{-2}$ in winter (Hicklin *et al.*, 1980).  There were no consistent patterns over the year in *Macoma* density, which averaged 10 to 1800 individuals m$^{-2}$.  Density of *Heteromastus* was low (generally below about 250 individuals m$^{-2}$) and essentially constant (Hicklin *et al.*, 1980).

*Winter disappearance*
The *Corophium* densities estimated from the February 11 (1996) exploratory samples are in the range of the summer density figures, while the densities from the February 24/25 random samples and from the March 18 - June 3 systematic samples are one to two orders of magnitude lower.  Again, the exploratory samples do not constitute a proper sampling regime, so the results from that date must be viewed with caution.  That said, the relatively low *Corophium* density over the remainder of the winter and spring (until reproduction began in late spring) certainly suggests a large decline in *Corophium* abundance in late winter.

The results of the study by Hicklin *et al.* (1980) indicate the density of *Corophium volutator* to be 20 to 30 times higher at its peak in summer or autumn than at its low in late winter to early spring. However, the sampling effort in January and February of 1979 was severely limited due to ice (Hicklin *et al.*, 1980), so the density estimates from January and February in that study must be viewed cautiously. The probable cause ascribed to the winter mortality was ice scouring (Hicklin *et al.*, 1980). Hicklin *et al.* (1980, p. 5) state that "Large reductions in numbers of *Corophium* and *Macoma* were also noted soon after the occurrence of heavy ice in January and February." While their data support such a statement for *Corophium*, their data do not in fact support such a statement for *Macoma*.

Based on comparison of invertebrate samples taken in early December 1985 and early April 1986, Wilson (1989) estimated winter mortality to be over 70% at the nearby location of Avonport Beach, though he also reported about 35% winter mortality in the laboratory. In that paper, Wilson concluded that *Corophium* experiences significant winter mortality due to ice (Wilson, 1989). In a 1991 paper stemming from the same research, Wilson claimed that there was no decline in the abundance of any species due to winter ice at Porter Point, based on similar densities of organisms in April in the field and in sediment which had been removed to the laboratory the previous December (Wilson, 1991). No mention in the latter paper was made of mortality in the laboratory.

Gordon and Desplanque (1983) speculate that *Corophium* mortality in the winter is due to instability of the sediment. Gratto (1979) hypothesized that extensive erosion over the fall and winter was responsible for the large decrease in *Corophium* density that he observed.

*Corophium lateral-migration hypothesis (Peer)*
It has been suggested that *Corophium* migrate laterally and congregate in unfrozen depressions in the mudflat (Gordon and Desplanque, 1983, quoting D. L. Peer; Peer, *pers. comm.*). Gordon and Desplanque (1983) further speculate that such a mechanism may explain the clumped distribution of *Corophium* in the spring. The possibility of lateral migration has not been eliminated, but it is unlikely, for several reasons. First, *Corophium* is a poikilotherm and may effectively be immobilized by cold temperatures, thus making it unlikely that the animal would leave its burrow to crawl over the sediment to a new area. The seawater is not very warm, either — the average seawater temperatures measured by the exposed datalogger were below 0 $^{o}$C from mid-February to mid-March, quite similar to the sediment temperatures.

In a clarification of his statement that was quoted by Gordon and Desplanque (1983), Don Peer (*pers. comm.*) hypothesized that the reason he had found more *Corophium* in unfrozen depressions than elsewhere could have been that the individuals in those depressions would have avoided, or had already avoided, selective pressures such as the removal of sediment by ice. This hypothesis is more credible, based on the observations in this study. The exploratory samples taken February 11, 1996 suggest no difference in occurrence of *Corophium* between "puddles" and open areas on the mudflat. As stated

before, the exploratory samples did not constitute a controlled study, and too few samples were taken to draw conclusions, but the results do raise questions for further study.

Although lateral migration by *Corophium* is unlikely, the design of the current study was such that it is not possible to rule out emigration. Future studies to test that hypothesis are needed.

*Ice-rafting*
Immediately prior to the commencement of systematic sampling for invertebrates, much of the entire surface of the study site was removed by ice, to a depth of 3-4 cm (based on the edges; *cf*. Figure 4). There were very few organisms in any of the samples throughout the entire spring sampling period, which initially suggested that the surface-sediment removal by the ice was largely responsible for the low population numbers. But in fact, except for the polychaete *Nereis diversicolor*, there was no difference between the macrofaunal populations February 24/25 and March 18/22. Had the March-13 sediment-removal event been the controlling factor, the populations of all of the animals living in the sediment should have decreased.

Ice cakes with anywhere from a few cm to as much as 15 cm of sediment attached were observed on four separate occasions, three prior to March 13 (the occasion mentioned above). It is possible that portions of the *Corophium* and *Macoma* populations had been removed by one or more of those ice-rafting events. The exploratory samples taken January 27 and February 11 suggest that the *Corophium* population was larger in late January to mid-February than it was from late February until mid-May. While the exploratory samples do not constitute random or representative samples of the entire study area, the results do suggest macrofaunal disappearance earlier than that March 13 sediment-removal event, *i.e.*, that the March 13 event was not the proximal cause of the disappearance.

*Nereis* burrow more deeply than *Macoma* do; and *Nereis*, *Macoma*, and *Heteromastus* all burrow more deeply than does *Corophium* (Turk *et al.*, 1980). If there had been a sediment-removal event in mid-February which resulted in the disappearance of a large portion of the *Corophium* population, it seems possible that further sediment removal by the mid-March event (if not an earlier event) would have removed the next several centimeters of sediment and taken *Nereis* which had managed to avoid the earlier sediment-removal event. Even with the outlying sample of 66 *Nereis* not included in the analysis, there still remained a significant reduction in the abundance of *Nereis* from late February to the latter half of March.

Unexplained is the exceptional case of relatively large numbers of *Corophium* and *Macoma* found on isolated occasions at the bottom of a deep, narrow channel. Perhaps it is less likely that ice would remove sediment at or close to the bottom of a large channel; if so, organisms in those locations would likely be spared the obliterative effects of the lifting ice cakes.

If the water was sufficiently shallow at high tide to prevent or to minimize the lifting of ice frozen into the mud, then those ice cakes would tend to stay in place and melt, depositing rather than removing sediment. Because the saltmarsh at the study site was high in the intertidal zone, organisms in or near the saltmarsh might be less likely to experience mortality and exportation by ice-rafting.

*Burrow depth*
Survival of ice-rafting may be a function of burial depth. There appears to be some relationship (though not linear) between ice in the sediment (inferred) and depth. It is the frozen crust (composed of frozen porewater and overlying ice) which is removed by ice-rafting. If this hypothesis were true, then because *Nereis* burrows more deeply than *Corophium*, the polychaete would be less likely to be removed by ice-rafting. Unless a spring immigration to the mudflat occurs, those animals that survive the winter are inherently the basis of recruitment during the spring and summer.

*Corophium* inhabits U-shaped burrows in the upper 5 cm of the mudflat (Smith *et al.*, 1996). *Nereis* lives in Y-, U-, or J-shaped burrows (Davey, 1994) which can range in depth from 15 to 40 cm (Hughes and Gerdol, 1997; Meadows and Tait, 1989). *Heteromastus* inhabits vertical or inverted-Y-shaped burrows 5 to 30 cm deep (Cadée, 1979; Shaffer, 1983). *Macoma* burrows are a function of the size of the animal and, in the U.K. at least, a function of season (Reading and McGrorty, 1978). Reading and McGrorty (1978) reported that in June, most burrows are less than 3 cm deep, whereas in December, virtually all burrows are less than 7.5 cm deep. However, Davey and Partridge (1997) found *Macoma* 9-12 cm deep, and occasionally below that, in April, also in the U.K.

*Corophium*, *Macoma*, and *Nereis* are reported to burrow more deeply in winter than in summer in the U.K., where ice usually does not form in the intertidal zone (Reading and McGrorty, 1978; Esselink and Zwarts, 1989). In Sweden, however, where ice does form in the intertidal zone, Möller and Rosenberg (1982) found that *Corophium* did not burrow more deeply in winter than in summer. The authors concluded that the large drop in *Corophium* abundance over the winter was evidence of emigration (Möller and Rosenberg, 1982; Möller, 1986). Hicklin *et al.* (1980) suggested that large *Macoma* individuals were more likely to survive winter conditions than smaller individuals (Hicklin *et al.*, 1980). Since *Macoma* burial depth is partly a function of the size of the animal (Reading and McGrorty, 1978), that hypothesis seems likely. Möller (1986) attributed winter survival of *Nereis* on Swedish shores to its ability to burrow deeply. Since *Heteromastus* can also burrow deeply (Shaffer, 1983), it would be reasonable to conjecture that it also would be capable of surviving the winter. In comparing benthic invertebrate densities at one Minas Basin mudflat for early December 1985 and early the following April, Wilson (1991) found an increase in the abundance of *Heteromastus*.

Since *Nereis* burrow more deeply than the other macrofauna do, it may have a competitive advantage with respect to surviving the environmental conditions at the Windsor mudflat. Although it evidently was not one of the initial colonizers of the Windsor mudflat (Turk *et al.*, 1980), perhaps *Nereis* is less affected than some other

organisms by sediment instability and thus may be able to establish burrows in ice-disturbed areas.  *Nereis* juveniles begin their burrows as extensions of the parental burrow (Marty and Retière, 1999), which may be an advantage in colonizing an area (as opposed to competing on the surface).

*Sediment disturbance*

Infauna are affected by sediment disturbance stemming from various causes:  ice-scouring, ice-rafting, storm-caused erosion, human disturbance (including, in this study, researcher-caused disturbance), and bioturbation.  Effects of physical disturbance of the sediment, whether due to human activity or to meteorological or geological events, include direct mortality; habitat removal; burial; and interference with feeding.  The topic of animal-sediment relations has been addressed in depth by a number of researchers; Hall (1994) provides an extensive literature review of physical disturbance and marine communities.

*Natural mortality*

The possibility of natural mortality of benthic macrofauna has not been eliminated.  There may also be sub-lethal effects on the invertebrates due to the winter environmental conditions, which may weaken individuals against further environmental stresses.  Further study would be required to elucidate the degree to which natural mortality is a factor in the decline in abundance of benthic macrofauna over the winter.

*Summary*

The aim of this research was to describe the winter conditions at intertidal mudflats of the upper Bay of Fundy, particularly with reference to those conditions experienced by the macrofauna.   The environmental conditions within the sediment at the level inhabited by benthic macrofauna have been found in this study to vary less than above the surface.  The results show that sediment temperatures remained fairly constant around $-1\ ^{\circ}$C under cover of ice while air temperatures fluctuated in the range of about $-20$ to $0\ ^{\circ}$C.

Organisms that are successful in colonizing intertidal mudflats must have the ability to withstand not only wide ranges of temperatures and other environmental parameters, but also rapid changes in these environmental parameters.  Ice presents additional selective pressures at the mudflats of the upper Bay of Fundy.  All indications are that benthic macroinvertebrates, especially *Corophium* and *Nereis*, remain at the mudflat throughout the winter.  It appears to be the case for *Macoma* and *Heteromastus* as well.

**6. Acknowledgments**

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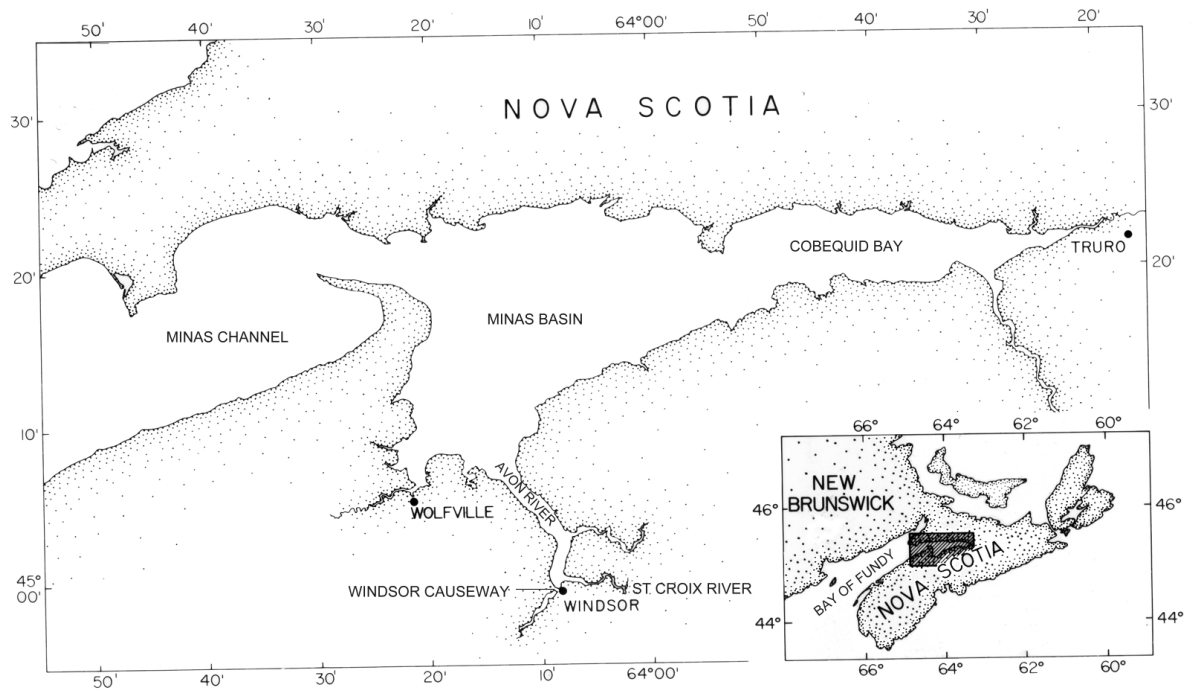
Figure 1. Map of Nova Scotia (inset) and Minas Basin, indicating location of Windsor Causeway. Map by A. Cosgrove.
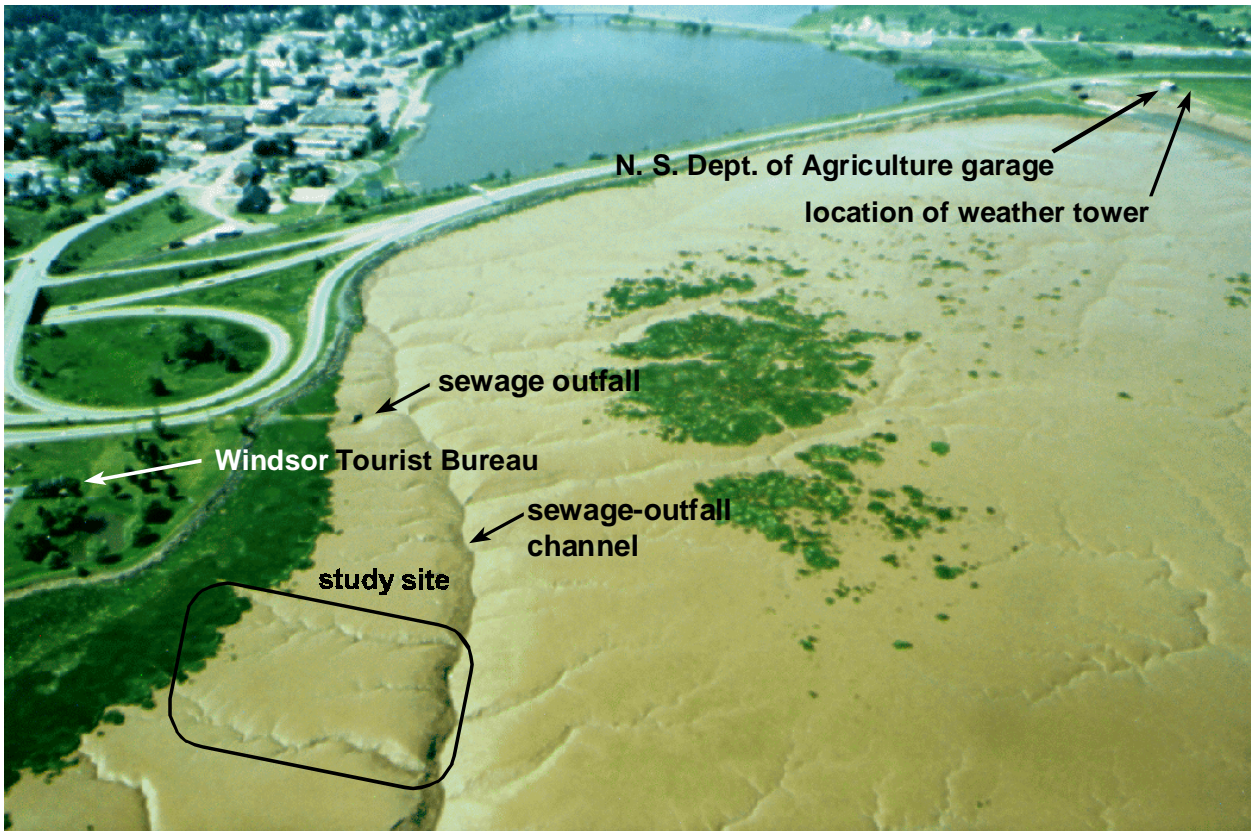
Figure 2. Oblique aerial view of the Windsor mudflat in 1996, indicating locations of study site and weather station. The perspective is from the north-northeast, facing south-southwest toward the Windsor Causeway (seen in the background). The Windsor Causeway is 0.73 km long.

**Sediment and Air Temperatures**
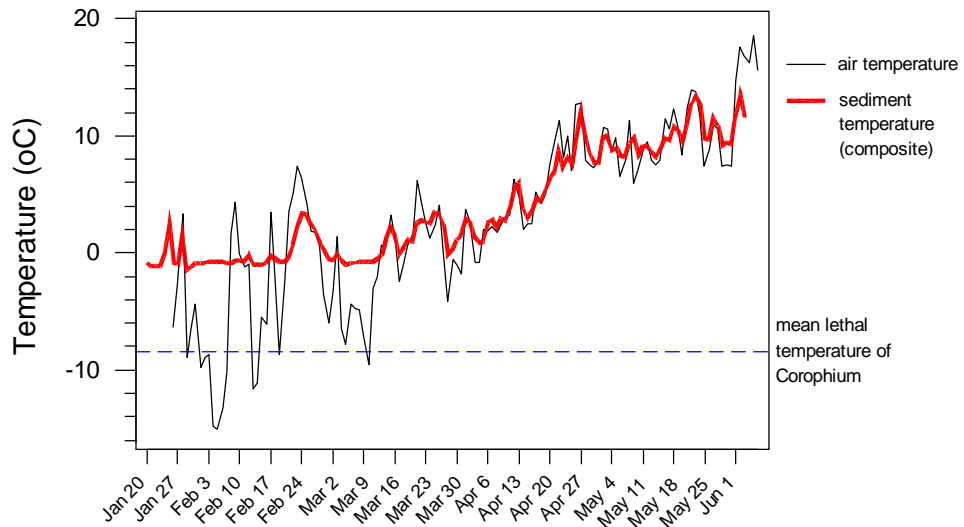
Windsor Mudflat, January to June, 1996

Figure 3.   Daily mean of hourly average air temperatures and daily mean sediment subsurface temperatures.  Also shown is the mean lethal temperature for overwintering *Corophium volutator* (Mills and Fish, 1980).

Figure 4. Tipped-up ice cake, with sediment attached and matching hole in mudflat surface (March 13, 1996).
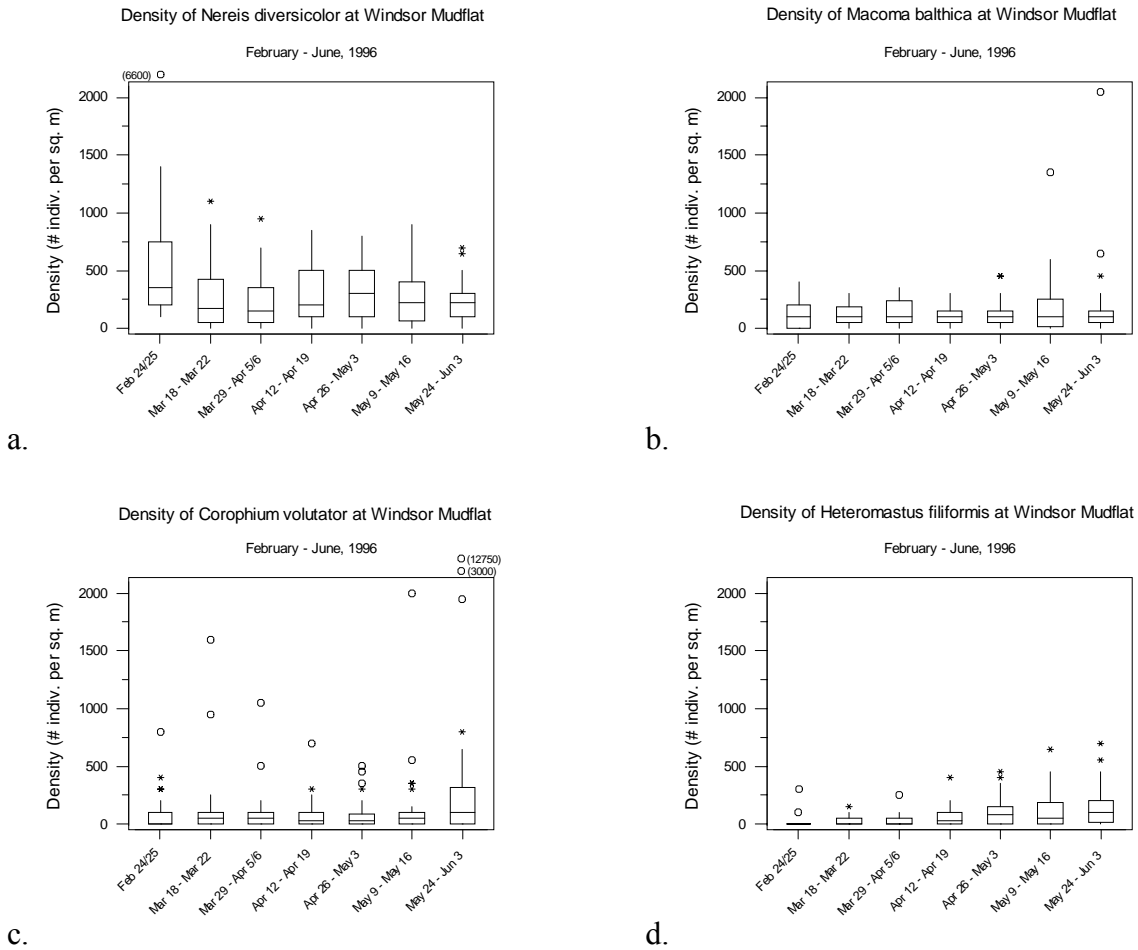
Density of Nereis diversicolor at Windsor Mudflat

February - June, 1996

Density of Macoma balthica at Windsor Mudflat

February - June, 1996

a.

b.

Density of Corophium volutator at Windsor Mudflat

February - June, 1996

Density of Heteromastus filiformis at Windsor Mudflat

February - June, 1996

c.

d.

Figure 5.   Invertebrate densities (individuals $m^{-2}$ surface area) determined from the February 24/25 random samples and weekly systematic samples March 18 to June 3.  All of the graphs have been drawn to the same scale.  Boxplots indicate median (line across box), middle 50% of data (ends of boxes, depicting $25^{th}$ and $75^{th}$ percentiles), and range of values (ends of whiskers or outermost points).  Unusually high or low values, relative to the middle 50%, are called outliers and are depicted by asterisks (if mild) or circles (if extreme).