EFFECTS OF TEMPORAL AND SPATIAL VARIATIONS IN SESTON FLUX ON GROWTH OF MUSSELS (MYTILUS SPP.), IN SUSPENDED CULTURE IN A BOREAL ENVIRONMENT

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by

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ABSTRACT

The Newfoundland mussel culture industry has experienced significant growth over the last five years and growers are beginning to fully utilize the available space on their tenures or in some of the inshore bays. This has raised questions as to the extent to which a site can be stocked and what are the optimum stocking levels. A reciprocal transplant experiment of three mussel populations was undertaken at three commercial aquaculture sites of different hydrographic and environmental regimes. Variations in growth, survival and production were assessed bimonthly in relation to seston flux, temperature and salinity, which were measured over 2-3 weeks at several stations on each site. Calcium Sulfate cylinders were calibrated with S4 current meters to assess relative current speeds. A strong positive relationship was established between cylinder dissolution and actual current speeds providing a useful index for calculating seston flux. Mussel growth and production varied according to season, populations, site and location within a site (ANOVA, $p < 0.05$). Survival of all mussels exceeded 85% at all sites. Population differences explained variations in survival. Differences in mussel performance were related to the relative seston flux and showed higher as well as more uniform growth and production in areas of higher flux. The importance of relative food flux measurements is discussed in relation to site evaluation criteria and production capacity estimates.

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1.0 INTRODUCTION

1.1 Biology

The blue mussel, *Mytilus edulis*, is distributed in the boreal and temperate regions of the Northern and Southern Hemisphere (McDonald et al., 1991). In the Southern Hemisphere *M. edulis* occurs along the west coast of South America, the Falkland and Kerguelen Islands (McDonald et al., 1991). In the Northern Hemisphere, the species occurs on the west coast of the Atlantic extending from the Atlantic Provinces of Canada to Cape Hatteras in North Carolina. In European waters it occurs in the White Sea and along the Atlantic coast of southern France (Varivo et al., 1988). The waters off the coast of Newfoundland are home to two species of Mytilids, the blue mussel *M. edulis* and *M. trossulus*. The two species are not visibly distinguishable from each other in sympatric populations and there is little hybridization (Innes and Bates, 1999, Penney et al., 2002). The only accurate method of classification is by electrophoresis and DNA gel analysis. Therefore unless stated, any reference to "blue mussels" will include both species of Mytilids (Figure 1).

Mytilids are bivalves, which inhabit a wide range of estuarine and marine environments. Mussels attach to rocks, jetties and piers and sometimes form dense beds on sandy flat substrates. They can be found from the low tide level to a depth of 50 meters (McDonald et al., 1991). The blue mussel has a wide temperature tolerance; sustaining optimal growth to a maximum temperature of 20°C (Almada-Villela et al., 1982), growth is compromised at 0°C yet remains significant below 5°C in the presence of adequate food levels (Loo and Rosenberg, 1983, Mallet and Carver, 1993). Mussels

are suspension feeders. They feed by filtering particles from the water. The main source of food is phytoplankton while decomposed macrophytes or resuspended detritus may also supplement their diet.

Figure 1: Blue mussels, *Mytilus* spp. from Newfoundland, Canada (Photo credit, Sean Macneill).

Mussels are dioecious. They are easily distinguished, as male gonads appear creamy white while females are slightly orange. The orange color is due to oil droplets in the developing eggs (Gosling, 1992). Blue mussels are broadcast spawners; therefore fertilisation occurs in the water column. In this environment, successful fertilisation is very low and the fecundity of these animals is extremely high. A single female mussel may produce between 5 and 12 million eggs in a year (Thompson, 1979). In Newfoundland, spawning occurs predominantly in late June (Sutterlin et al., 1981, Macneill et al., 1999). This is typically a single annual occurrence however the present study, as well as others have found evidence of a secondary-spawning events later in the year in blue mussel populations (King et al., 1989, Pryor et al., 1999). This is considered to be characteristic of mussels under more favourable nutritional conditions during the fall and early spring (Rodhouse et al., 1984).

The ontogenetic larval development of mussels is similar to other marine bivalves. Once fertilised, it takes five hours at 18°C for the embryo to develop small cilia and begin to swim freely. The life cycle is affected by temperature (Baird, 1966) and an embryo requires 100 hours to reach the veliger stage at 8°C. The planktotrophic larvae feed on small phytoplankton cells and begin to develop the larval shell, which has a distinct D shape and measures approximately 95 μm in length (Schweinitz and Lutz, 1976). In 3 weeks, the mussel grows to over 200 μm (Bayne, 1965, Penney, 1993). The late stage larva is referred to as a pediveliger and may be distinguished by the development of a foot and eyespot. The timing of this stage is negatively correlated with temperature (Bayne, 1965). At this time the mussel searches for a suitable substrate for

settlement such as a rock, wharf or collector. The larva then extends the foot and anchors itself to the surface and undergoes metamorphosis, after which it develops into a juvenile and mature adult.

1.2 Mussel Culture in Newfoundland

Culture of the blue mussel is a developing and expanding industry in Newfoundland. Presently mussels account for the largest cultivated shellfish production in Newfoundland and in Canada. The industry in the province has been involved in commercial efforts to produce mussels since the early 1980's. Initial yield for the province was a mere 70 tonnes in 1989. However, the industry has since expanded producing 1,700 tonnes in 1999 (Government of Newfoundland and Labrador, Fisheries and Aquaculture Production Statistics, 2000). Newfoundland's projections for 2003 however, are estimated at a total of 4,500 tonnes (Burke Consulting Inc., 2000). As the industry continues to grow and expand there will be concerns related to mussel growth rates and site carrying capacity. To address these potential constraints, studies examining improved husbandry practices and the development of production capacity models that account for available food, rate of delivery, population densities and environmental factors will be beneficial to the mussel culture industry.

1.3 Seston Availability

The amount of available seston in a given volume of water is never constant even in the absence of grazers (Navarro and Thompson, 1995). It is a dynamic food source,

consisting primarily of phytoplankton. However, bacteria, decomposed macrophytes or resuspended detritus also constitute part of the natural seston available as food to bivalves. Food availability, both planktonic and particulate, has been demonstrated to significantly control the seasonally changing metabolism of mussels regardless of water temperature (Hatcher et al., 1997).

1.3.1 Effect of Temporal Variations in Seston Availability on Mussel Growth

1.3.1.1 Variations and Effects of Annual Seston Availability on Growth

Seston concentration is greatly influenced by oceanographic processes and factors such as currents, availability of light and nutrients. By considering the inter-annual variations in temperature, wind and nutrient availability due to run off, annual production measured in a body of water year after year can vary greatly (Navarro and Thompson, 1995). In addition, long term studies of phytoplankton availability in the North Sea indicate that new production in coastal waters may have increased by 25% in recent decades (Richardson and Pedersen, 1998).

Annual variations in seston availability affect the reproductive output of bivalves (MacDonald and Thompson, 1985b), which in turn contribute to variations in total annual production. Mussels have an opportunistic reproductive strategy in which they invest excess energy into gametes when favorable conditions allow, ensuring continued prosperity in an unpredictable environment (Thompson 1979, MacDonald and Thompson, 1985b). Somatic growth is not associated with improved environmental conditions (MacDonald and Thompson, 1985a). This conservative effort utilises the

surplus energy without creating the nutritional demands of additional body mass, which may not be supported in subsequent years.

1.3.1.2 Variations and Effects of Seasonal Seston Availability on Growth

Seston availability fluctuates seasonally (Navarro and Thompson, 1995). Despite the high degree of variability in the planktonic habitat, there are regular occurrences of blooms in seasonal cycles. The exact timing of a bloom is however subject to climatic as well as hydrodynamic variables and therefore is difficult to predict. The occurrence of a "Spring bloom" which occurs in populations previously light limited, is often dependent upon the stratification of the water column (Riley, 1947, Sverdrup, 1953, Legendre, 1990, Pitcher and Calder, 1998), which is caused by warming at the surface and run-off (Richardson and Pedersen, 1998). As a result phytoplankton are retained in the surface layer where conditions for development are more favorable. The timing of this occurrence can vary greatly from year to year by a matter of weeks (Yin et al., 1997) or even months (Smayda, 1998). These blooms can also be interrupted or hindered by the breakdown of the stratification by energy inputs such as wind, tidal currents and cooling.

Quite often in subarctic regions such as Newfoundland, autumn blooms occur. Cooling of the surface layer and subsequent autumn turnover can initiate this process. This mixing provides an input of nutrients from resuspended bottom material to drive the bloom similar to those, which occur as a result of upwelling (Legendre, 1990, Pitcher and Calder, 1998).

Seasonal influxes of primary production in a system have been correlated with mussel growth suggesting that phytoplankton is the main source of food (Widdows et al., 1979, Page and Hubbard, 1987, Mallet and Carver, 1989, Deslous-Paoli et al., 1990, Page and Ricard, 1990, Grant, 1996). The correlations are often made under the assumption of a time lag, which reflects the time required for metabolic conversion of absorbed energy from the bloom into growth, which is specific to the size of the animal (Page and Hubbard, 1987, Page and Ricard, 1990).

During months when phytoplankton populations are light limited by day length and ice cover, primary production is low and mussels may exhibit signs of food deprivation (Hatcher et al., 1997).

1.3.1.3 Variations and Effects of Tidal Seston Availability on Growth

Further fluctuations in seston concentration and composition occur as well on shorter temporal scales. Seston supply is influenced by its rate of delivery. On spring tides (large tides) the turnover of seston is greater. Conversely, on neap tides there is less of an exchange of seston. Considerable tidal variability has been found with higher levels of total particulate matter (TPM) during the spring tides due to resuspension (Hawkins et al., 1996, Barillé et al., 1997). Barillé et al. (1997) reported an extreme range of seston (20-350 $mg \cdot L^{-1}$) over a spring-neap cycle in an oyster estuary.

Temporal variations in food supply have been reported as well over a tidal period (Litaker et al., 1987, 1993, Fegley et al., 1992, Muschenheim and Newell, 1992, Zurberg et al., 1994, Hawkins et al., 1998), with the increased velocity of ebb and flood tide

currents, the relative contribution of resuspended microalgae, detritus and silt increased (Verity et al., 1998) near bottom. Chlorophyll concentrations may be lower during ebb than flood tides, which has been ascribed to the feeding activity of bivalves (Smaal and Haas, 1997). The range of seston concentrations measured in a single tide can be as great as the range of seston recorded at the same site for an entire year (Fegley et al., 1992, Newell et al., 1998).

Short-term variability in phytoplankton availability, that is less than 24 hours, will depress the assimilation efficiency of Mytilids (Fréchette and Bourget, 1987). Providing that this occurs daily in accordance with the tidal cycle, it stands to reason that growth and production would be limited.

1.3.1.4 Variations and Effects of Storm Induced Seston Availability on Growth

On a more unpredictable level, short-term fluctuations in food available to suspension feeders may occur during storm events including periods of increased wind velocities and wave action (Bock and Miller, 1995, Pedersen et al., 1995, Smaal and Haas, 1997, Cranford et al., 1998, Pitcher and Calder, 1998), as well as river discharge (Yin et al., 1997) and coastal upwelling (Pitcher and Calder, 1998). These inputs of energy can break the stability of stratification and interrupt phytoplankton blooms or enhance it further by adding inputs of nutrients from resuspended bottom material. Cranford et al. (1998) studied seston during a wind-induced resuspension event and reported large fluctuations in seston availability (1 to 30 $mg \cdot L^{-1}$).

The interruption or hindrance of a regular seasonal bloom by storm events can seriously depress the growth and production of a bivalve population as the food stores, which are relied upon for reproductive output and somatic growth are not available. Storm events more frequently result in a decrease of seston quality conditions as opposed to increasing seston availability. This will be discussed further in the section on "Variations in Seston Quality".

1.3.2 Effects of Spatial Variation in Seston Availability on Bivalve Growth

The supply of seston to a population of bivalves is a result of the larger scale patterns of the seston concentration and the hydrodynamics of the water body (Cahalan et al., 1989). For this reason, spatial variations in seston availability may exist within kilometers of each other (MacDonald and Thompson, 1985a, b, Page and Ricard, 1990, Stirling and Okumus, 1994), within mussel beds (Carlson et al., 1984, Wildish and Kristmanson, 1984, Okamura, 1986, Newell, 1990, O'Riordan et al., 1993, Svane and Ompi, 1993), within the water column (Page and Hubbard, 1987, Fréchette and Grant, 1991, Smaal and Haas, 1997, Andreassen and Wassmann, 1998, Sarà et al., 1998), within suspended raft culture (Blanco et al., 1995, Pérez Camacho et al., 1995, Mueller, 1996, Navarro et al., 1996) and within suspended longline culture (Rodhouse et al., 1985).

1.3.2.1 Variation and Effects of Seston Availability amongst Experimental Sites on Growth

MacDonald and Thompson (1985a) in a study of four sites around the island of Newfoundland and one in New Brunswick, reported differences in seston availability among study sites. Similar findings noted differences in phytoplankton biomass between two experimental sites along the coast of California (Page and Ricard, 1990) and two Scottish sea lochs (Stirling and Okumus, 1994). Inshore areas have a tendency to have higher total seston concentrations than offshore areas (Page and Ricard, 1990). Stirling and Okumus (1994) suggested the lower phytoplankton biomass at one of their sites was due to its high level of enclosure, limited light penetration due to mountains and tidal currents. These studies reported differences within their own sites however, by comparing the studies to each other, the results also indicate large spatial variations in seston concentration owing to their extensive geographic range.

Spatial variation in seston availability affects the growth and nutritional condition of filter feeding species (Page and Ricard, 1990, Stirling and Okumus, 1994). Mussel growth is typically elevated at sites with greater chlorophyll-*a* concentrations (Page and Ricard, 1990, Stirling and Okumus, 1994). MacDonald and Thompson (1985a, b) found that not only somatic growth but total production due to reproductive output was enhanced at sites with greater food availability. Grant (1999) predicts that a more variable food environment will result in greater variability in growth of shellfish.

1.3.2.2 Variation and Effects of Seston Availability within Mussel Beds on Growth

Bivalves, in dense populations, demonstrate the ability to deplete the "near-bed-environment" of organic seston particles in flume studies (O'Riordan et al., 1993, Prins et al., 1995, Rheault and Rice, 1996) and in field studies (Fréchette and Bourget, 1985a, b, Rodhouse et al., 1985, Smaal et al., 1986, Newell and Shumway, 1988, Fréchette et al., 1989). Similarly, in tidally reversing flows, animals positioned on the "upstream edge" of the relative flood tide, which receive the flow first may deplete the available seston to a level that inhibits the growth of mussels on the "downstream edge" (Carlson et al., 1984, Karayuecel and Karayuecel, 2000). The extent to which the seston is reduced is inversely proportional to its delivery rate by the tide in most studies on mussels.

Variations in seston availability due to competition from other bivalves result in limited growth and production (Fréchette and Bourget, 1985b, O'Riordan et al., 1993, Rheault and Rice, 1996). It should not be assumed however that growth and production increase/decrease over a wild bed or culture site at the same rate. Growth in dense populations of bivalves may be greater on the edge of large mussel beds where there is less depletion of seston by other mussels (Wildish and Kristmanson, 1984, Okamura, 1986, Newell, 1990, O'Riordan et al., 1993, Svane and Ompi, 1993). Each of these studies measured characteristically low average current speeds. Therefore, growth in a population of bivalves is not simply a function of seston concentration or flow velocity, but instead, a result of these two components acting in combination, i.e., seston flux. Seston depletion over dense mussel beds may therefore be compensated for by higher flux rates (Grant, 1999). Areas with characteristically higher current may support a higher

biomass of mussels (Fréchette and Bourget, 1985b, Fréchette et al., 1989, Newell, 1990, Rheault and Rice, 1996, Campbell and Newell, 1998, Fréchette and Bacher, 1998, Newell et al., 1998). Growth rates within benthic populations of wild bivalves have been correlated to seston fluxes in field situations (Wildish and Kristmanson, 1985, Eckman, 1987).

1.3.2.3 Variation and Effects of Seston Availability with Depth of Bed on Growth

In Eastern Newfoundland larger seston rations are representative of shallow water environments (MacDonald and Thompson, 1985a, b). Similar findings were reported off Otsuchi Bay, Japan (Nakaoka, 1992) with shallow water experimental sites indicating characteristically higher seston biomass than their deep-water counterparts. This is due largely to increased primary productivity is likely due to warmer water temperatures and greater light penetration.

Improved shell growth, notably somatic growth and greater production in bivalves have been reported in shallow water sites owing to higher food availability (MacDonald and Thompson, 1985a, b, Nakaoka, 1992).

1.3.2.4 Variation and Effects of Seston Availability within the Water Column on Growth

Studies comparing seston availability within the water column have yielded varying results. Page and Hubbard (1987) in an offshore study off California found higher chlorophyll-*a* and phaeopigment concentration at 9 and 18 m than at 2 m. A period of thermal stratification occurred in both years of the study from late May through

September. Water temperatures could vary by as much as 4°C from a depth of 2 m to 18 m. In this study, mussel growth rate was associated with phytoplankton abundance, but not water temperature. In a similar open ocean system in the southern Mediterranean, at comparable time of year, higher phytoplankton abundance occurred at 5 m as opposed to 15 m (Sarà et al., 1998).

Suspension culture is designed to utilise more of the water column, taking advantage of not only horizontal flux but vertical flux as well. By utilising the water column suspension culture allows more water to flow past the mussels in order to maximise production (Thorarinsdóttir, 1996). However, variations in seston availability have occurred locally in both high-density raft culture (Navarro et al., 1991, Blanco et al., 1995, Pérez Camacho et al., 1995, Heasman et al., 1998) and longline culture (Rodhouse et al., 1985).

Several studies have shown that growth of mussels as a function of height off the bottom is related to the concentration of organic matter as opposed to mere seston concentration (Fréchette and Bourget, 1985b, Page and Hubbard, 1987, Sarà et al., 1998). This will be discussed further in the section concerning spatial variations in seston quality.

Studies of high-density raft culture have reported "edge effects" similar to those found in benthic beds, the result of intraspecific competition and decreased flow (Navarro et al., 1991, Fuentes et al., 1994, Mueller, 1996, Navarro et al., 1996, Heasman et al., 1998). These farms were not placed in areas of low flow. The problem occurred following the placement of the farms. Current flow through a dense raft is not laminar

(Blanco et al., 1995). The majority of the flow is diverted around the raft, within a raft, the flow aligns along its major axes and is greatly reduced (Boyd and Heasman, 1998). In the study by Boyd and Heasman (1998) flow was reduced by over 82% inside the raft. Seston flux values decreased, reducing growth and production. Growth rates were 8% higher and the percentage of marketable mussels was 30% higher on rafts with increased rope spacing (Heasman et al., 1998).

Similar growth patterns were encountered with longline suspension culture (Rodhouse et al., 1985, Grant, 1999). Like raft culture, longline systems deflect currents away from the farm reducing flow through the farm by 30% or more of ambient with the rest of the flow being forced around the farm or below it (Gibbs et al., 1991). Mussel growers, by adjusting the spatial organization of their suspension culture may reduce the deflection of currents around and under their farms thereby manipulating food availability to mussels.

1.4 Effect of Seston Quality on Bivalve Growth

Growth patterns of bivalves are not affected by the quantity of total particulate matter (TPM) available or the measure of particulate organic matter (POM) but usually the proportion between these two variables (Bayne and Worrall, 1980, Bayne et al., 1987, Page and Ricard, 1990) until an asymptote is reached (MacDonald et al., 1998). There is a positive relationship between the pulse-like growth of mussels, which alternates between growth, and de-growth phases with fluctuations in the POM:TPM (Sarà et al., 1998). Bivalves select organic particles and reject inorganic particles regardless of the

total seston concentration. However this relationship diminishes as the percentage of the organic content of the seston decreases (Bacon et al., 1998). Variations in the filtration rates of mussels have been attributed to a decrease in clearance rate due to increasing TPM (Prins et al., 1994). In addition to a reduction of clearance when exposed to increasing seston concentrations, bivalves increase pseudofaeces production resulting in maximum ingestion rates that are predetermined by the species (Clausen and Riisgård, 1996, Arifin and Bendell-Young, 1997, Bacon et al., 1998).

1.4.1 Temporal Variation in Seston Quality

1.4.1.1 Seasonal Variation and Effects in Seston Quality on Growth

Seston quality can vary seasonally, similar to seston availability. During the spring bloom, the energy content of seston is at its peak (MacDonald and Thompson, 1985a). The percentage of organic matter in the seston is often at its highest concentration at this time while relatively low during winter (MacDonald and Thompson, 1985a, Prins et al., 1994, Navarro and Thompson, 1995, Sarà et al., 1998). Studies under similar conditions to this one reported 43% POM in Bellevue, NL at 0 to 15°C (Thompson, 1984) and 35 to 55% in Whitehead, NS at 9 to 18°C (Carver and Mallet, 1990). In some situations, spring run-off or re-suspension (Sarà et al., 1998) may dilute this influx of POM.

Bivalves will flourish during the spring bloom, translating the high quality seston into reproductive and somatic growth (Sarà et al., 1998). Elevated levels of POM:TPM, greater than 40%, generally result in higher seasonal growth patterns (Bayne and Worrall,

1980). However, during periods of high-suspended loads, the animals will enter a phase of "de-growth" until the ratio of POM to TPM increases (Sarà et al., 1998).

1.4.1.2 Variation and Effects of Seston Quality Due to the Tidal Cycle on Growth

In shallow tidal estuaries spring tides have been reported to deliver higher levels of seston than neap tides due to the enhanced shear forces acting on the bottom (Barillé et al., 1997). The resulting available seston is therefore greatly due to resuspension in near bottom situations (Grant and Bacher, 1999). Chlorophyll-*a* and POM increase linearly with the increasing seston; however the POM:TPM decreases (Widdows et al., 1979, Berg and Newell, 1986, Hawkins et al., 1996, Barillé et al., 1997).

Chlorophyll-*a* values have been found to be lower on the ebb tide than the flood tide due to the feeding activity of bivalves in dense culture situations (Smaal and Haas, 1997). The organic content of the seston is also lower during low tide due to sedimentation (Smaal and Haas, 1997).

In the event that Mytilids interrupt feeding frequently due to a reduction in the quantity or quality of available food, the production of the mussel population will decline (Deslous-Paoli et al., 1990). Shell growth rate has been found to respond to changes in the percent organic matter on a daily time scale in infaunal clams, with no lag or memory to previous seston parameters (Bock and Miller, 1994).

1.4.1.3 Variation and Effects of Seston Quality Due to Storm Events on Growth

Cranford et al. (1998) reported that resuspension of bottom materials during a storm results in large range of nutritional quality in the seston (25-50% organic content). These data coincide with similar studies on the effects of resuspension by wind-induced waves wherein the organic content of the seston was diluted (Bock and Miller, 1994, Smaal and Haas, 1997).

Absorption efficiency in bivalves following a storm event is closely related to seston quality, declining exponentially with decreasing seston quality (Cranford et al., 1998). Daily growth rates in bivalves have been correlated to seston quality following resuspension by to wind-induced waves (Bock and Miller, 1994). These bivalves responded to changes in POM on a daily time scale with no time lag (Bock and Miller, 1994).

1.4.2 Spatial Variation in Seston Quality

1.4.2.1 Variations and Effects of Seston Quality on Growth

The quality of seston has been shown to vary among sites (MacDonald and Thompson, 1985a, b, Page and Ricard, 1990, Stirling and Okumus, 1994). The percentage of POM is often found to be higher at one experimental site than another, which is also characterised by higher mean chlorophyll-*a* concentrations (Page and Ricard, 1990, Stirling and Okumus, 1994).

Sites characterised by higher percentages of POM have been found to support improved growth (Page and Ricard, 1990, Stirling and Okumus, 1994) and production

(Bayne and Worrall, 1980, MacDonald and Thompson 1985b). In these studies some sites were out-performed in spite of abundant TPM concentration, which suggests that variation in seston quality as opposed to quantity is the limiting factor for growth (Bayne and Worrall, 1980, MacDonald and Thompson, 1985b, Page and Ricard, 1990, Stirling and Okumus, 1994).

1.4.2.2 Variation and Effects of Seston Quality within a Bottom Culture Site on Growth

Measurements taken upstream from and within a mussel bed indicate a large reduction in seston quality directly over a mussel bed (Muschenheim and Newell, 1992), suggesting particle selection processes are at work. Chlorophyll, total diatoms, benthic diatoms and total diatom cell volumes each indicated a reduction directly over the bed when compared to the incoming water from upstream due to filtration of POM by the bivalves (Muschenheim and Newell, 1992). The degree to which POM:TPM is reduced is dependent on patch size and therefore mussel biomass.

Seston quality is reduced as it passes over a dense mussel bed (Muschenheim and Newell, 1992). In a large patch, turbulence is required to replenish TPM levels to prevent food limitation. However, the reliance on turbulence is a reliance on low quality sediment loaded seston (Smaal and Haas, 1997). As a result, animals within the center of a large bed exhibit food limited growth due to the depletion of POM by animals on the edges of a bed (Okamura, 1986, Newell, 1990). The extent of the depletion of POM is dependent upon the size of the patch (Newell, 1990, Svane and Ompi, 1993) and the rate of delivery of seston, i.e., seston flux (Newell, 1990).

1.4.2.3 Variation and Effects of Seston Quality with Depth of Bed on Growth

In a 3 year study, MacDonald and Thompson (1985a, b) reported the energy content of seston was greatest in the shallow water experimental sites for the first half of their study while no pattern existed in later months. In addition to energy content, the particle size spectra also varied greatly with depth wherein the surface layer was composed of predominately phytoplankton while deeper depths were characterised by low seston concentrations with similar volumes of phytoplankton, miscellaneous plankton and detritus (MacDonald and Thompson, 1985a, b).

MacDonald and Thompson (1985a) reported negative correlations between differences in somatic weight and depth at 3 of 5 sites studied. These sites were each characterised by decreasing quality of seston with increasing depth.

1.4.2.4 Variation and Effects of Seston Quality within the Water Column on Growth

Depleted chlorophyll-*a* and phaeopigment concentrations have been recorded just above a mussel bed (Fréchette and Bourget, 1985a). Further reports indicate low levels of organic seston in the benthic boundary layer due to dilution by resuspension of sediment (Sarà et al., 1998). A comparison of surface and bottom samples indicates higher total seston concentrations on the bottom (Smaal and Haas, 1997). However, the quality of this seston is greatly reduced by resuspended inorganic matter (Fréchette and Bourget, 1987, Smaal and Haas, 1997).

Fréchette and Bourget (1985b) reported improved growth in caged mussels held just 1 m above the control animals on the bottom. Animals within the benthic boundary

layer endured food limited growth due to the poor quality of seston caused by sediment loading. A comparison of suspension culture versus bottom culture in Iceland had improved growth and production within the water column as opposed to within the benthos (Thorarinsdóttir, 1996).

1.5 Carrying Capacity

Carrying capacity can be defined as the stocking density at which production levels are maximised without negatively affecting growth rates (Carver and Mallet, 1990). While carrying capacity concerns have not been an issue previously in the relatively new Newfoundland mussel culture industry, as the industry continues its rapid growth, questions of carrying capacity will arise. However carrying capacity has been studied in other areas of the world at varying levels of effect utilising a multitude of approaches, categorised as: global models, empirical models, calculations of budgets and simulation modeling.

Global models provide a simple reliable empirical function of the biomass, based on historical production data (Lawrence, 1996). This model design does not account for inherent temporal or spatial variations in the carrying capacity.

Empirical models represent some view of the dependence between bivalves and ratio of food supply to seston flux (Incze et al., 1981); seston depletion correlated with the density of the bed (Smaal et al., 1986); food supply divided by food demand estimated from in situ measurements (Carver and Mallet, 1990).

Budgets of energy transfers during production (Rosenberg and Loo, 1983, Rodhouse and Roden, 1987, Deslous-Paoli et al., 1990) are useful in assessing the relative importance of several variables in the ecosystem. However, they are limited within spatial and temporal boundaries. They do not account for the impact of shellfish culture on the overall dynamics of the system, or the regeneration of food within the shellfish system (Raillard and Ménesguen, 1994).

Simulation modeling is designed to account for the spatial variability of both biological demand and physical characteristics of the system characterising the role of the filter-feeder by measuring the depletion of phytoplankton as well as their positive effect on nutrient cycling and subsequently primary production. Some models have been based upon energy budgets in which the environment was assigned (Ross and Nisbet, 1990, Fréchette and Bacher, 1998). More recent models are designed to dynamically pair bivalves to their environment (Raillard and Ménesguen, 1994, Grant, 1996, Dowd, 1997).

Creating an accurate forecast of bivalve growth as a function of environmental and oceanographic variables is a complex task. It must account for the influences of spatial and temporal variations in the quantity and quality of the available seston (Schulte, 1975, Fréchette and Bourget, 1985a, b, Fegley et al., 1992, Barillé et al., 1997), fluctuations in flow (Loo and Rosenberg, 1983, Grizzle et al., 1992, Eckman and Duggins, 1993, Claereboudt et al., 1994, Leichter and Witman, 1997) and particle flux (Fréchette et al., 1989, Grizzle and Lutz, 1989, O'Riordan, et al., 1993, Wilson-Ormond et al., 1997, Roegner, 1998). Difficulty in assessing such a predictive model occur even when the variables are known; direct measurements of seston availability are often

complex because the sample is not always representative as to what is accessible by the animal (Abelson et al., 1993). This problem becomes even more difficult when considering sessile animals that can not actively hunt for potential food, but must rely on ambient currents to supply them.

The present empirical study differs from those previously mentioned as it has been conducted in a boreal environment on cultured mussels and in suspension culture. As well, this study encompasses the main concepts of carrying capacity. However, instead of defining the upper limit as the maximum stocking density at which growth rate does not decline, it is defined by the optimal sustainable yield, i.e., production capacity. Production capacity includes economic variables, such as considering the yield per unit cost faced by the grower. This may mean that due to the increased stocking density, growth rates are decreased somewhat but overall, annual production is increased. This is a more practical tool for the grower as it answers: Does the production yield at density "X" warrant the time, effort and equipment cost? The study was designed to develop a basic guideline, which will aid mussel farmers in site selection as well as the estimation of production on a sustainable/optimal basis.

1.6 Reciprocal Transplants

The focus of this study was to examine the effects of environmental factors such as temperature, salinity and seston flux on the growth and production of blue mussels held in suspension culture. However it is important to firmly establish that our findings are the result of environmental influences, and not merely a genetic component of growth

(Koehn and Gaffney, 1984, Rodhouse et al., 1986, Tremblay et al. 2001). Growth performance variations due to genetic effects have been found among animals originating from different oceans (Jamieson and Heritage, 1989), within closer proximity in neighboring seas (Johannesson et al., 1990, Kautsky et al., 1990) and even from sources within kilometers of each other in the same coastal waters (Widdows et al. 1984, Swarbrick et al., 1988, Mallet and Carver, 1989, Stirling Okumus, 1994). Fuentes et al. (1994) using four closely related stocks found significant effects on growth rate despite a slight genetic differentiation. It has been found that family genotype has a clear effect on the competitive influence of each individual on its neighbors and its neighbors and its response to competition from them (Brichette et al., 2001). As a result, it is necessary to employ reciprocal transplants when trying to quantify the extent to which observed differences in growth rate are based on environmental factors or genetic variation (Widdows et al., 1984, Mallet and Carver, 1989, Kautsky et al., 1990, Page and Ricard, 1990, Stirling and Okumus, 1994, Iglesias et al., 1996).

1.7 Objectives

The objectives of this study were:

1. To quantify mussel growth and survival in relation to temporal variations in seston flux, quantity and quality.
2. To quantify mussel growth and survival in relation to spatial variations in seston flux, quantity and quality, within and among sites.

3. To utilize growth and survival as functions of temporal and spatial variations in seston flux to determine if each site has stayed within or exceeded its optimal stocking density.
4. To determine temporal and spatial variations in environmental characteristics (temperature, salinity, current speed and direction) of each site in relation to mussel growth.
5. To test Grant's hypothesis (1999) that a more variable food environment will result in greater variability in growth of mussels.
6. To develop a practical means of monitoring relative current speed utilising the rate of dissolution of plaster cylinders.
7. To develop a basic guideline that will aid mussel farmers in site selection as well as the estimation of production on a sustainable/optimal basis.

The primary hypothesis being tested is that higher seston flux will promote higher growth and production. A secondary hypothesis is sites with characteristically higher seston flux will demonstrate more uniform growth and production.

2.0 MATERIAL AND METHODS

2.1 Study Sites

Experiments described in this study were performed between September 1997 and November 1998. Three sites were selected from a number of culture sites around the island of Newfoundland, on the basis of their hydrographic and geomorphic characteristics as well as accessibility and production history. Burnt Arm South (49° 35' N, 54° 38' W) is located approximately 130 km NE of the Town of Grand Falls-Windsor (Figure 2). This study site was characterised as a shallow semi-enclosed bay. The Reach Run (49° 25' N, 54° 40' W) is located 123 km NE of Grand Falls-Windsor (Figure 2). This study site was characterised as a shallow flow-through system. The Big Island site (49° 29' N, 55° 41' W) is located 63 km NW of Grand Falls-Windsor (Figure 2). This site is also characterised as a shallow flow-through system; however, flow at this site is interrupted by a series of islands. All three sites had a farm production history of at least five years.

2.2 Mussels

Beginning September 17, 1997 and finishing October 7, 1997, blue mussels were stripped from collector ropes from the three grow out sites. Each source was assessed for initial shell length (n=150, nearest 0.1 mm) and condition index (n=30, CI= dry soft tissue wt (g) • dry shell wt (g)$^{-1}$ • 100) prior to placing the animals in socks. Mussels

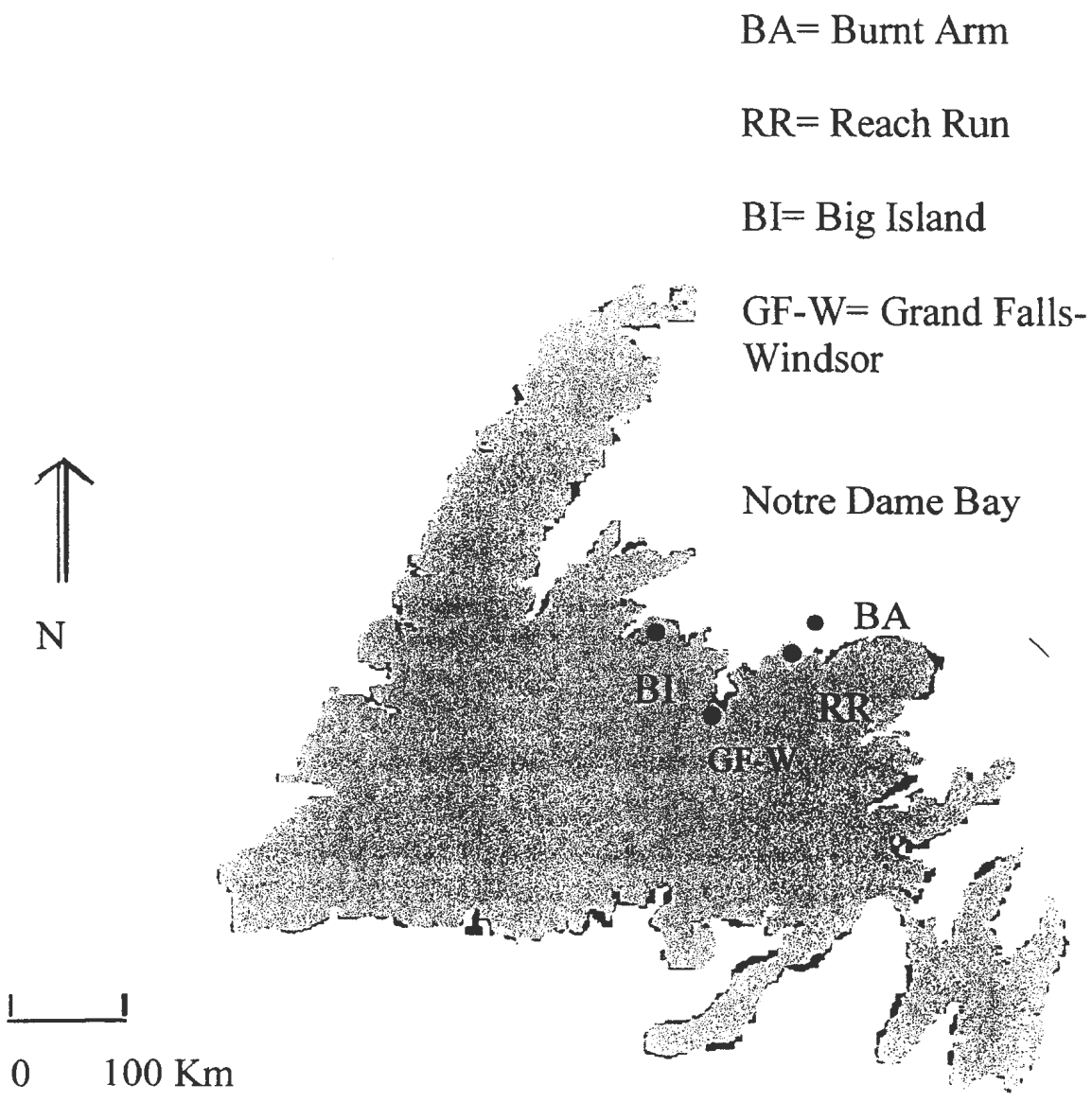

Figure 2. Map of Newfoundland. Dots represent experimental sites.

were placed in 3 meter socks at approximately 200 animals• 30 cm^{-1}. The sock material utilised varied slightly in mesh size depending upon the initial size of the mussels and grower preference but initial densities and sizes of the mussels were comparable. In addition, at each site, mussels were placed in six square-based, pyramidal- shaped pearl nets (mesh size = 6 mm, n=150 mussels• net^{-1}). All pearl nets with animals were hung on existing production lines to await transplantation. This date hinged upon the approval of transfer permits from the Government of Newfoundland and Labrador.

The determination of the ratio of *M. edulis*: *M. trossulus* at the onset of the experiment in each seed source was characterised according to Innes et al. (1999) where species were distinguished by PCR amplification of a diagnostic nuclear DNA marker. The Innes et al. (1999) study sampled spat from the same seed sources and cohort as the present study.

2.3 Transplant Experiment

Two weeks following the completion of placing the mussels in socks, the reciprocal transplant experiment began. On October 19, 1997, all socks, regardless of their destination were removed from experimental longlines and placed in plastic totes. Socks were identifiable by either sock color or identification tags. In total 324 socks from each source were transferred reciprocally to each site (54 socks•$source^{-1}$•$line^{-1}$). Animals were placed on two experimental longlines by the grower and located near the front (stations 1, 2 and 3, Figure 3a-c) and back of each farm (stations 7, 8 and 9, Figure 3a-c). Each line was composed of three experimental stations. A Global Positioning System

(GPS) was used to indicate positions of experimental lines and form the layout of the experiment on each site. Seed sources were dispersed at each station in a standard pattern, one sock from Reach Run, one from Burnt Arm and one from Big Island until a total of 54 socks ($18 \cdot source^{-1}$) were placed at each station. This was done in order to remove any spatial effects on growth within the stations. Continuously recording thermographs were placed in containers with the mussels to record temperatures during the transfer period and throughout the experiment. During the two weeks between placing the animals in socks and transfer, the animals had attached themselves to the socks and mussel loss during transfer was minimal.

A third line devoid of experimental mussels was later chosen in the middle of each farm. This line composed of three sample stations was utilised for environmental sampling.

2.4 Environmental Sampling

Adverse weather conditions limited environmental sampling in November 1997 to CTD casts (SBE 25 Sealogger CTD, Sea-Bird Electronics, Inc., Bellevue Washington) at four stations: a control station outside the farm, one on the front experimental line, middle line and back line. This was repeated every three hours for 9 hours at each site. Due to winter ice and weather conditions, it was not possible to continue sampling beyond November until the following spring. Tony Clemens, a research technician for the Newfoundland Aquaculture Industry Association (NAIA) provided local CTD data for 1997-1998.

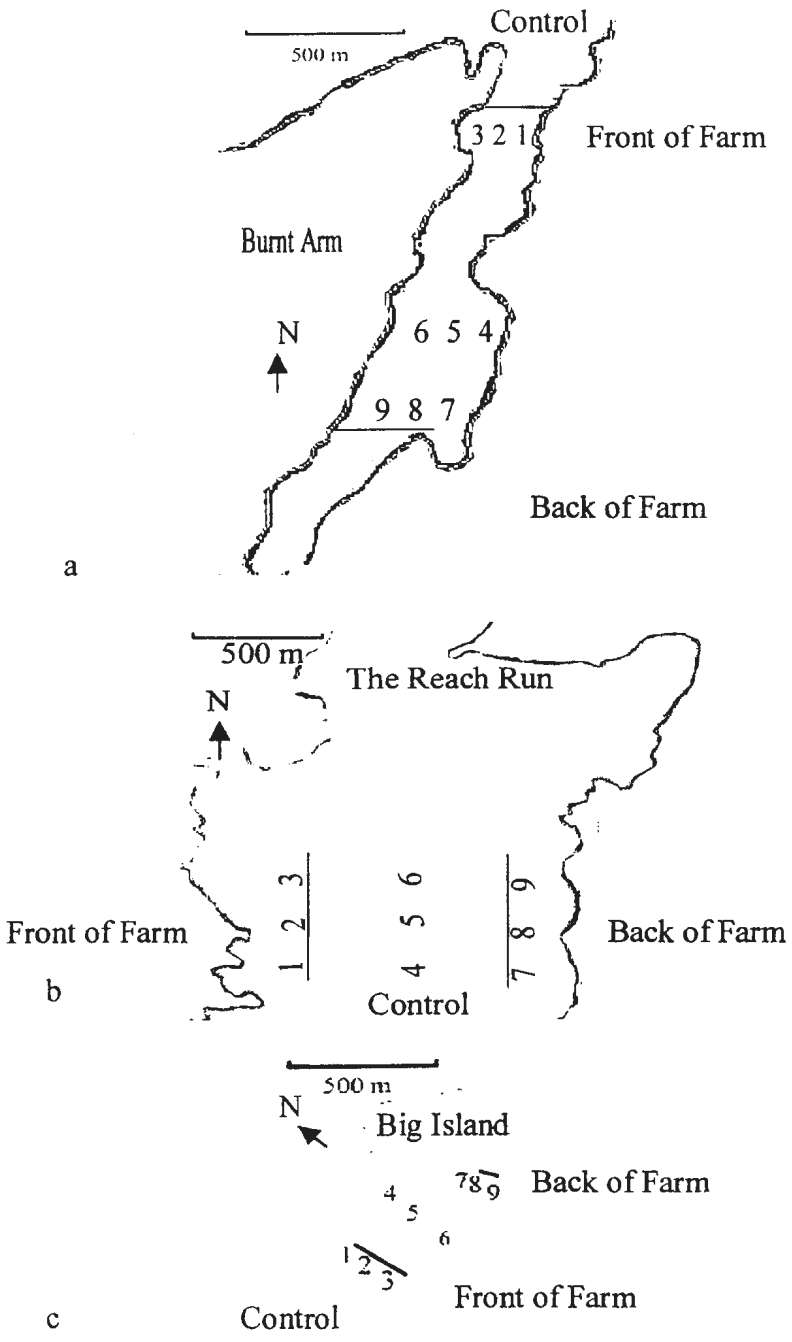

Figure 3. Experimental site set up showing distribution of sampling stations (1-9) at a) Burnt Arm South, b) Reach Run and c) Big Island. The control stations were located approximately 200 meters from the front line at the seaward edge of the site.

In May 1998, sampling resumed (Figure 3). Each site was composed of 10 sampling stations. The "control" station was positioned approximately 200 m outside the site on the seaward edge. This site was utilised to determine the seston concentration and composition in the absence of mussels. Stations 1 through 3 were on the front experimental line, stations 4 through 6 were located on a designated line in the middle of the farm and stations 7 through 9 were located on the back experimental line of each site (Figure 3a-c). There were no experimental animals positioned on the middle line therefore, these stations were utilised merely to determine the variation in seston concentration and composition as flow passed through the farm.

2.4.1 CTD Casts

A profiling SBE 25 CTD was utilised for measurements of temperature, salinity, chlorophyll-*a*, dissolved oxygen, pressure, transmittance, dissolved oxygen, pH and optical backscatterance for casts during the day measuring the entire water column from the surface to within 1 m of the sea floor at each of the 10 stations. Measurements were made over the entire tidal cycle during the day. However, it was not possible to perform regular sampling in the dark, thus the CTD was employed for only a single "Night Cast" to obtain information on short term variations in temperature, salinity and chlorophyll-*a* during this period. This required the CTD to be suspended in the water column at 3.5 m depth on the front experimental line (station 2). Approximately 12 hours later the instrument was retrieved and data downloaded. Due to the extensive operating time required for a Night Cast, the parameters measured had to be limited to temperature,

salinity and chlorophyll-*a* to avoid battery failure overnight. Similar studies have taken environmental samples at one station, once per location (Page and Ricard, 1990) and at three stations, at high and low tide per location (Carver and Mallet, 1990).

2.4.2 Preparation of Water Samples

Water samples were taken with a Niskin sampling bottle at 3.5 m depth in vicinity of mussels and placed in clean 4 L covered containers previously rinsed with seawater. The samples were held in coolers with ice until they could be analysed at the lab that evening. The water was screened through a 300 µm Nitex mesh to exclude debris and large zooplankton. The samples were immediately filtered under a mild vacuum (< 15 PSI) through pre-weighed, pre-combusted Whatman GF/C 47 mm diameter filters for determination of total particulate (TPM), particulate organic (POM) and particulate inorganic (PIM) matter. Blank filters for all the seston analyses were prepared with each set of water samples and assigned the same treatment. Filters were frozen at –20°C until they could be dried and analysed at a later date.

2.4.3 Seston Analysis

Filters containing particulate matter, as well as blanks were rinsed with 10 mL of distilled water. The filters were dried at 60°C for 48 hours, weighed to obtain TPM values, combusted at 450°C for 3 hours and finally re-weighed the nearest 0.1 mg after cooling in a desiccator to assess PIM. The POM value was determined by subtracting the weight of PIM from TPM.

2.4.4 Dissolution Cylinders

Hydrated calcium sulfates have efficiently been utilized as an inexpensive means to quantify water motion (Petticrew and Kalff, 1991, Komatsu and Kawai, 1992, Thompson and Glenn, 1994). There is a strong linear relationship between dissolution and water flow (Petticrew and Kalff, 1991). In this study, plaster cylinders were utilised to obtain a relative index of current speed over the tidal cycle (Appendix 1.0).

2.4.4.1 Preparation of Cylinders

Moulds were made out of 3.81 cm internal diameter ABS pipe, 15.24 cm long. The pipe was split down one side so that it could be later wedged open for the removal of the cylinder. The bottom of the pipe was closed off with a piece of cardboard covered in duct tape. A piece of twine with 2 finishing nails, 2.54 cm long inserted through the twine, went through the pipe with approximately a meter of twine on either side (Petticrew and Kalff, 1991). The twine was later used to tie the cylinder to the frame.

In a clean plastic container, 3.6 L of H_2O and 7.2 kg of Durabond 90R Plaster Patch were mixed using a drill with a paint mixing attachment. The mixture was blended until smooth. It was then poured into moulds. This made approximately 30 cylinders.

The cylinders allowed to dry overnight at room temperature and then were removed from the moulds. The ends of the cylinders were covered in epoxy around the base of the twine to avoid loss of due to friction by the twine when hanging in the water column (Petticrew and Kalff, 1991). Cylinders were then oven-dried for 48 hours at 40°C, weighed and identification tags were attached to the twine.

2.4.4.2 Deployment of Cylinders

Upon arrival at the site, 30 cylinders were attached to 6 ABS square frames (5 per frame) measuring approximately 1 m^2 (Figure 4). The frames were weighted on the bottom to keep them upright in the water column. They were then hung at the front and back of the sites on the experimental longlines at each of the sampling stations (1-3, 7-9) next to mussel socks and pearl nets. Following two complete tidal cycles, the cylinders were retrieved from the water, removed from their frames and carefully transported in the same container to the lab. In the lab, they were lightly rinsed to remove any sludge, which may have collected. They were then dried at 40°C for 48 h (Petticrew and Kalff, (Jokiel and Morrissey, 1993, Claereboudt et al., 1994). Upon cooling the identification tags were removed, and the cylinder weights recorded to the nearest 0.1 mg. Dissolution of plaster cylinders was determined by difference (Petticrew and Kalff, 1991). 1991). Dry weight provides the best determination of weight loss in plaster cylinders.

2.4.4.3 Assessment of Environment on Dissolution

To determine if temperature had an effect on dissolution rates, a small experiment was undertaken. Three tanks of water at 28 ppt salinity, with one suspended cylinder each were tested at 4, 10, 14, 18 and 25°C. The tanks were large enough so that the concentration of the plaster in the water did not over-saturate and affect the dissolution rate. Petticrew and Kalff (1991) studied the effect of tank size on dissolution and found that for a 50 g block, a 20 L tank was sufficient. As the cylinders employed in this study

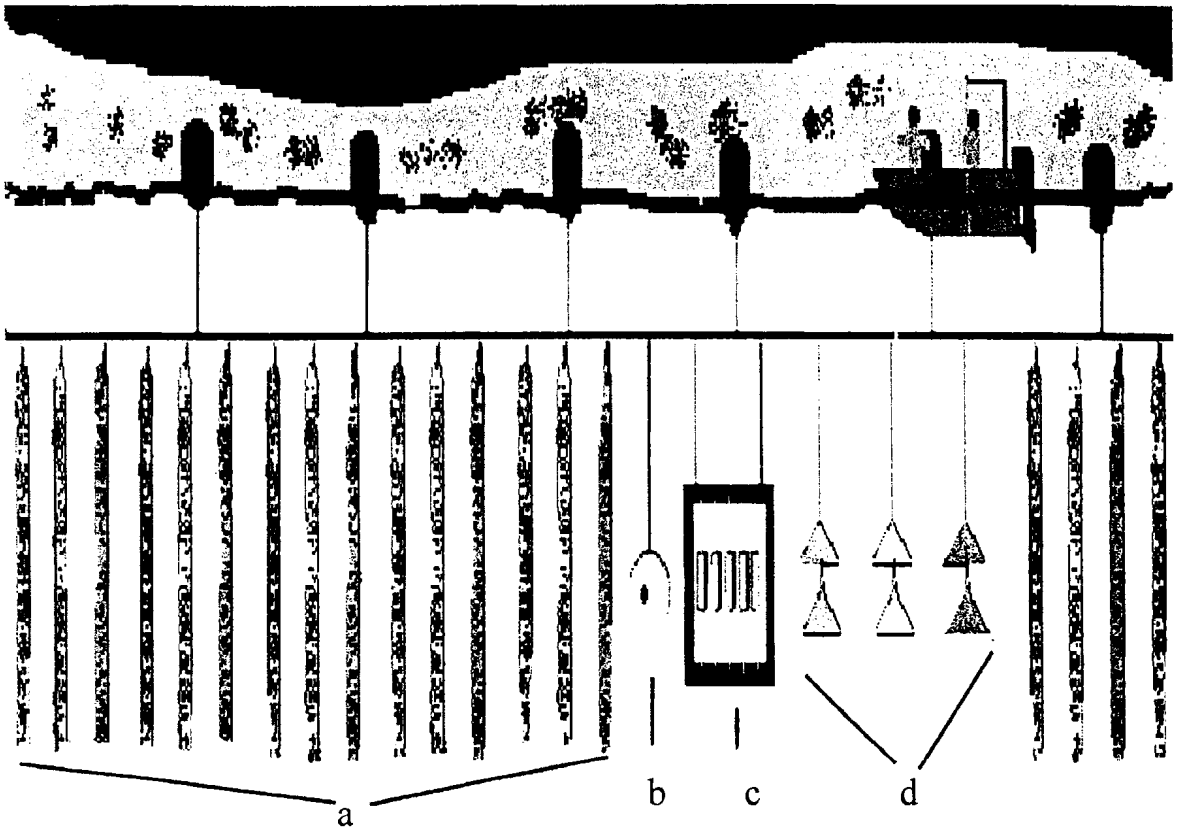

Figure 4. The layout of each experimental station, displaying a) socks, b) S4 current meter, c) dissolution cylinders, and d) pearl nets with mussels from 3 sources. At stations 2 and 8, the cylinders were placed next to the S4 current meters.

averaged 250 g: 100 L tanks were utilised. Cylinders were treated exactly as they were in the field.

With the knowledge that the environment would have a significant effect on the dissolution of the cylinders (Appendix 1.1), environmental data collected by the CTD was included in a stepwise regression using the dissolution data from station 2 and the S4 current meter at the same station. Only data from the S4 at station 2 were utilised for cylinder estimates, as there was uncertainty concerning the calibration of the instrument at station 8. The environmental data were averaged over the time periods that the cylinders were in the water. From the regression equation relative current speeds could then be calculated at six stations on each farm, based on cylinder dissolution rates.

2.4.5 Current Direction

Current direction was measured at each of the 10 stations, every 2 hours for approximately 5 sampling events. Direction was determined by attaching a piece of fluorescent flagging tape approximately 30 cm long to a pole. The pole was lowered to a depth of 3.5 m and secured against the side of the boat. The current direction was noted and mapped immediately. On occasion environmental conditions or lack of available daylight did not allow for current directions to be taken.

2.4.6 Seston Flux

Growth in a population of bivalves is a function of seston flux, which is a product of the concentration of seston and the flow velocity. For this experiment the seston was

measured in terms of chlorophyll-a and PIM:POM. However for the calculation of flux, chlorophyll-a ($\mu g \cdot L^{-1}$) was employed as it was sampled around the tidal cycle at each sample station. These values were multiplied by the relative values of current speed obtained by the dissolution cylinders calculated at each of the six stations (described previously) to assess the spatial and temporal variance of seston flux throughout each farm using the formula:

$$\text{Flux } (\mu g \cdot cm^{-2} \cdot s^{-1}) = \text{chl-}a \cdot \text{relative current speed } (cm \cdot s^{-1})$$

2.5 Biological Sampling

2.5.1 Density and Growth

Sampling of mussels began in November 1997, completing one site at a time. For growth, samples were collected within 7-10 days of each other at all three sites. Sampling continued the following spring with collection of mussel samples in May, July, September and November, 1998. Two socks from each source at each station (n=6) were sampled. The weight of each sock was recorded as well as the weight of 3 sub-samples of 100 mussels, chosen at random from the top middle and bottom of each sock, to determine stocking density • $sock^{-1}$. Biofouling on the socks was minimal. Samples of mussels from each sock were then bagged and labeled for later measurement of shell length and tissue parameters. To determine growth rate (GR), average mussels lengths per source, per station, were compared using the formula:

$GR = (L_{t2} - L_{t1}) \cdot days^{-1}$, where L_{t2} is the average length of the mussels at time 2, L_{t1} is the average length of the mussels at time 1.

Of these samples, 100 mussels from each sock were measured for length to 0.01 mm and 30 were frozen at -20°C for subsequent examination of condition index (CI).

To determine coefficient of variation (CV), sock weight was compared using the formula:

$$CV = \text{standard deviation} \cdot \text{mean sock weight}^{-1}.$$

2.5.2 Condition Index

Condition index was calculated based on the methods described by Walne and Mann (1975). The animals were thawed, cleaned, shucked and dried at 80°C for 48 hours. Shell and soft tissue weights were measured to the nearest 0.1 g for each mussel (n=30 per treatment). Condition index was calculated according to the following equation:

$$CI = \frac{\text{dry soft tissue wt (g) X 100}}{\text{dry shell wt (g)}}$$

2.5.3 Sampling Design

Bimonthly sampling, which was labeled "Comprehensive Sampling," began in May 1998 and consisted of:

1) Deployment of S4 current meters (InterOcean Systems, Inc., San Diego –tilt compensated model), one placed on each of the experimental lines at station 2 and 8 (Figure 3). The current meters were suspended from the main line at a depth of 3.5 m

next to the mussel socks and pearl nets and weighted with a small weight to keep them upright in the water column.

2) Deployment of "plaster dissolution cylinders" placed at 3.5 m depth at each station on the front and back experimental longlines.

3) Spatial/ temporal sampling began as soon as the current measuring equipment was deployed. Seabird casts (SBE 25 Sealogger CTD fitted with additional sensors for chl-a, dissolved O_2, etc.) and current direction were taken at each of the 10 stations, every 2 hours for approximately 5 sample periods during the day depending upon the environmental conditions and available daylight. Current direction collected at the same time.

4) Uploading of the CTD data, new batteries installed and the reconfiguration of the CTD for "Night Sampling". The CTD was then deployed on the front line (station 2) and hung at 3.5 m depth overnight (approximately 12 hours).

5) Retrieval of the CTD the following morning, uploading the data and changing the batteries. In addition, water samples were taken along with one final set of CTD casts and current direction.

6) Retrieval of all field equipment, including cylinders CTD and S4s.

7) Collection of mussel samples and measurement of mussel survival in pearl nets.

2.5.4 Sampling Schedule

During months, which did not include a "Comprehensive sampling", a similar sampling schedule was in place. It was referred to as "Restricted sampling", which entailed the procedures 1 to 6 of the Comprehensive sampling schedule listed above.

At approximately 2 week intervals between major sampling a simple "Spatial sampling" was performed at each site. This sampling regime consisted of a CTD cast, water samples and current direction taken at each of the 10 stations. The Newfoundland Aquaculture Industry Association's environment sampling program provided further supplemental data, as required.

2.5.5 Survival

Each experimental station (1-3, 7-9) at each site contained 6 pearl nets. Two pearl nets containing 150 mussels from each original source at each station. These animals were selected from the same collectors as those animals in the socks and were held at similar densities. These pearl nets were monitored for mortality, counting live and dead animals, beginning in May 1998 and at each subsequent mussel sampling period. This was to determine the losses due to natural mortality as opposed to drop off or dispersion, of each seed source at each location.

2.5.6 Secondary Set

During the course of this study a second set of mussels occurred, raising the density of the mussel socks and lowering the average size of the mussels. To remove the

effects of this "unwanted" cohort. cohort analysis was utilised to identify and separate the normal distribution of the cohorts (Appendix 2.0).

2.6 Additional Data

Additional information such as wind speed, wind direction and precipitation measured at Twillingate, NL were obtained from Environment Canada. Tidal height information was taken from Canadian Tide and Current Tables (1997, 1998). Volume 1, Atlantic Coast and Bay of Fundy.

2.7 Data Analysis

Analysis of variance (ANOVA) procedures (SPSS, 1999) were used to test the effect of site, station, source, and date on the parameters measured in this work: growth (length), production (biomass increases in kg) and survival. Post hoc tests (Bonferroni and Tukey) were conducted to determine difference in means within these factors. Significance was determined at $\alpha = 0.05$.

3.0 RESULTS

3.1 Environmental Data

3.1.1 Temperature

Over the course of the study the temperature at 3.5 m depth varied significantly by site, location within the site and season (ANOVAs, $F= 1536.9, 6.6, 2051.1$, $p< 0.001$ for each). During the sampling events temperatures ranged from -1.1°C to 20.0°C (Figure 5). Thermograph data, which were collected continuously during the experiment, confirmed this range (Appendix 3.0). Reach Run had significantly higher temperatures throughout the study, followed by Big Island and Burnt Arm, respectively (Tukeys HSD, $p< 0.001$). Reach Run had 2346.6 cumulative degree-days followed by Burnt Arm at 1820.5 degree-days and Big Island at 1657.8 degree-days.

Significant seasonal variations occurred over the course of the experiment at each of these sites (Figure 5, Appendix 3.0). Burnt Arm temperatures reached subzero in the January of 1998 (Appendix 3.0) to 17.2°C in September 1997 (Figure 5.1, Appendix 3.0). Temperatures at Reach Run reached subzero a month earlier in December 1997 and rose to 20.0°C in August 1998 (Figure 5.2, Appendix 3.0). The thermal pattern at Big Island ranged from subzero in January 1998 to 14.5°C in August 1998 (Figure 5.3, Appendix 3.0). Short-term temporal variations in temperature occurred on a daily basis at the Burnt Arm site during most sampling events except for November 2-3, 1998 (Table 1, Appendix 4.1-4.6). In Reach Run, short-term temporal variations in temperature occurred during half of the sampling periods (Table 1, Appendix 4.7-4.12). Temporal variations in

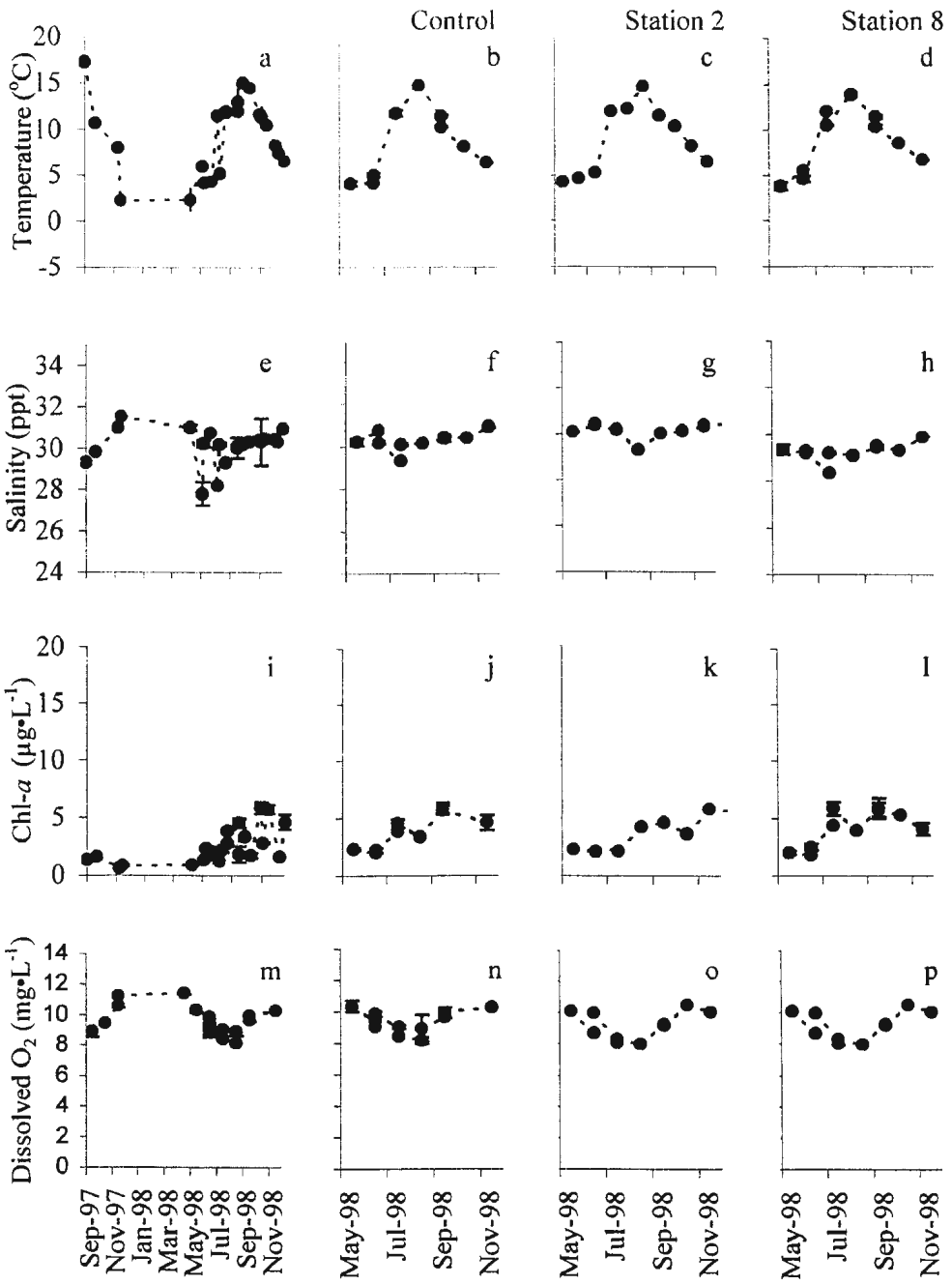

Figure 5.1. Seasonal environmental data collected at Burnt Arm, Sept. 1997 – Nov. 1998 at 3.5 m. Column 1 represents data collected in this study as well as another NAIA sponsored study, column 2 represents data from this study collected at the control station located at the outside each farm, column 3 represents data collected at station 2, positioned at the front of each farm, column 4 represents data collected at station 8 positioned at the back of each farm. Each row represents temperature, salinity, chlorophyll-*a* and dissolved oxygen, respectively (n= 3-5 per point, error bars= standard error).

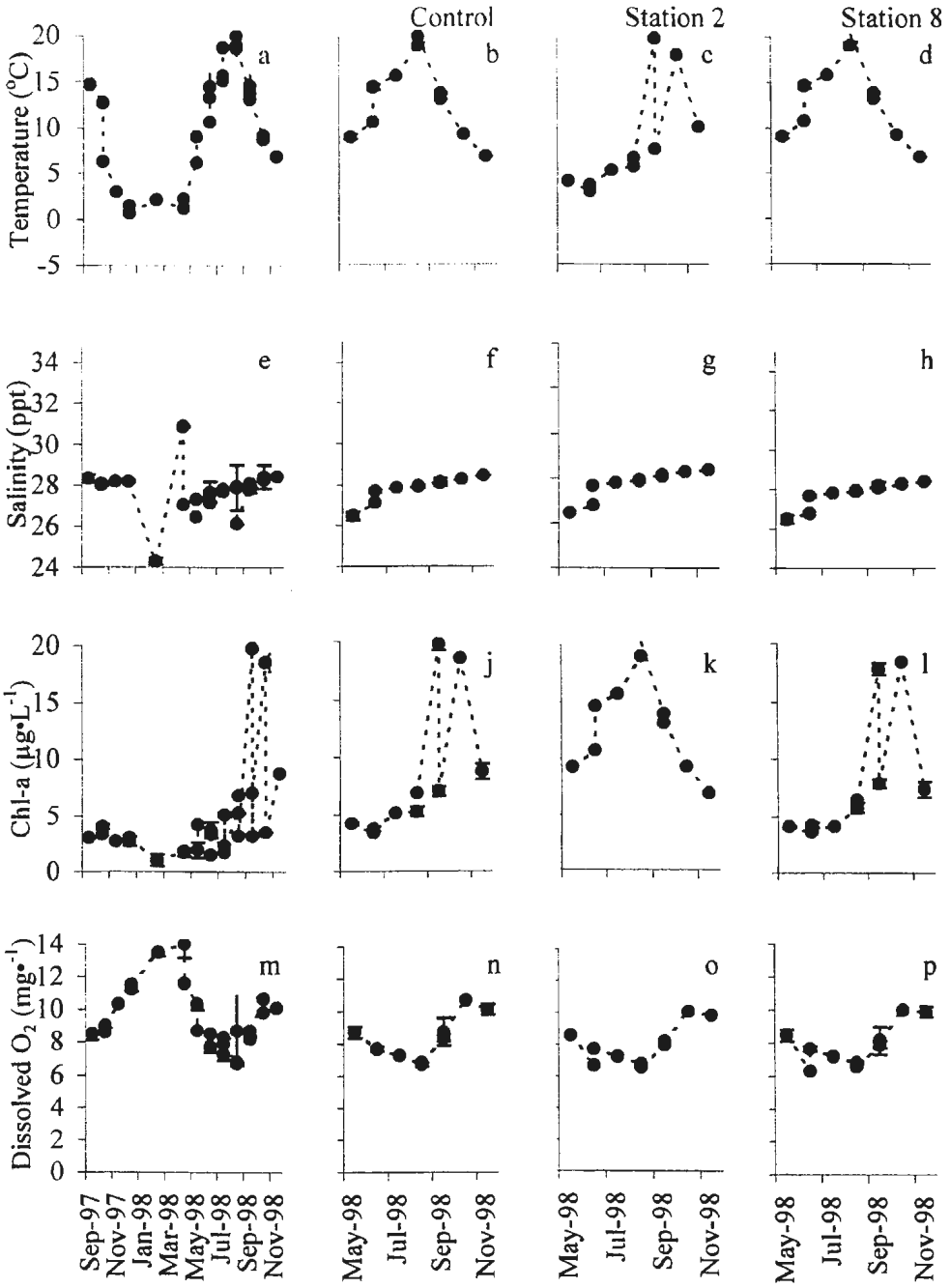

Figure 5.2. Seasonal environmental data collected at Reach Run, Sept. 1997 – Nov. 1998 at 3.5 m. Column 1 represents data collected in this study as well as another NAIA sponsored study, column 2 represents data from this study collected at the control station located at the outside each farm, column 3 represents data collected at station 2, positioned at the front of each farm, column 4 represents data collected at station 8 positioned at the back of each farm. Each row represents temperature, salinity, chlorophyll-*a* and dissolved oxygen, respectively (n= 3-5 per point, error bars= standard error).

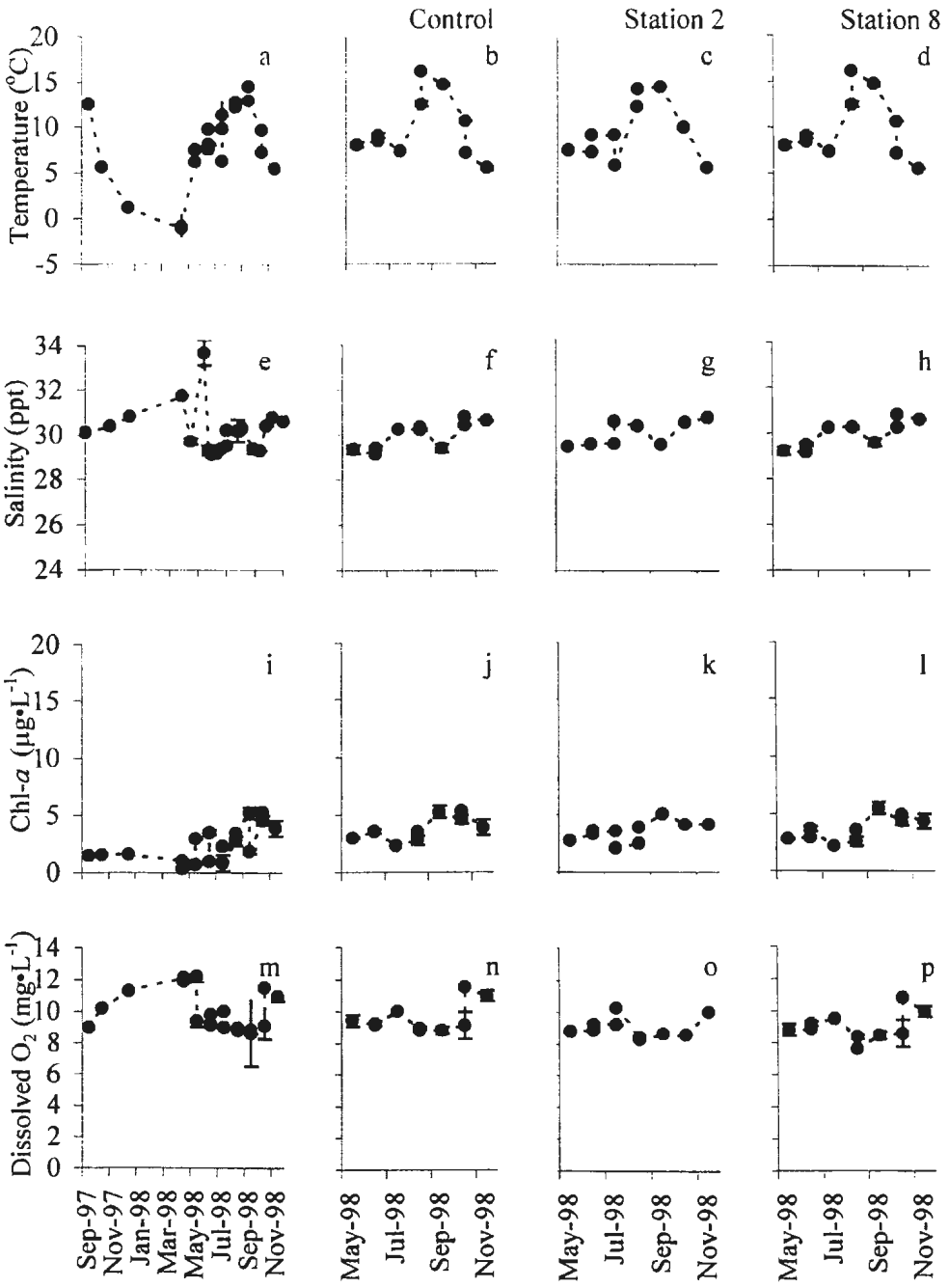

Figure 5.3. Environmental data collected at Big Island, Sept. 1997 – Nov. 1998 at 3.5 m. Column 1 represents data collected in this study as well as another NAIA sponsored study, column 2 represents data from this study collected at the control station located at the outside each farm, column 3 represents data collected at station 2, positioned at the front of each farm, column 4 represents data collected at station 8 positioned at the back of each farm. Each row represents temperature, salinity, chlorophyll-*a* and dissolved oxygen, respectively (n= 3-5 per point, error bars= standard error).

Table 1. Results of ANOVAs of temperature variation over a tidal cycle at each site. Temperatures were averaged for all 10 stations prior to analysis.

Site	Sample Dates	df	F	Significance
Burnt Arm	May 21-22, '98	5	42.517	<0.001
	June 23-24, '98	5	14.546	<0.001
	July 30-31, '98	5	4.677	0.003
	Sept 13-14, '98	5	62.478	<0.001
	Sept 28-29, '98	4	546.016	<0.001
	November 2-3, '98	4	0.613	0.439
Reach Run	May 25-26, '98	6	22.79	<0.001
	June 24-25, '98	5	19.578	<0.001
	August 3-4, '98	5	0.105	0.991
	September 8-9, '98	5	6.304	<0.001
	September 29-30, '98	3	1.658	0.194
	November 4-5, '98	3	2.775	0.057
Big Island	May 28-29, '98	4	6.06	0.001
	June 25-26, '98	4	8.242	<0.001
	August 4-5, '98	5	4.476	0.002
	September 3-4, '98	5	6.854	<0.001
	October 1-2, '98	3	0.934	0.434
	November 7-8, '98	3	0.998	0.405

temperature occurred in the Big Island site during most sample sessions but not October 1-2, 1998 or November 7-8, 1998 (Table 1, Appendix 4.13-4.18).

Spatial temperature variations occurred within each site. Higher mean average temperatures occurred among sample stations on the experimental line at the front of Burnt Arm (Tukey HSD, $p< 0.05$ for each, Figure 5a, Appendix 3.0). In Reach Run, two stations had significantly different temperature patterns. Station 5 indicated significantly higher mean average temperatures than all others except the Control station while temperatures measured at station 9 were lower than all other stations at Reach Run (Tukey HSD, $p< 0.05$ for each, Figure 5b). Spatially, the Big Island site differed only at station 9, which had higher mean temperatures than all other stations (Tukey HSD, $p< 0.05$ for each, Figure 5c).

Thermal stratification near the surface was evident in Burnt Arm from May to August. However, no stratification occurred in September 1998 (Figure 6.1). In Reach Run, thermal stratification in May and July began at depths greater than 5 m (Figure 6.2). Temperatures ranged between 15°C at the surface and 8°C at 8 m depth in September. Samples taken during the months of August, October and November 1998 had no stratification (Figure 6.2). The water column of the Big Island site was stratified in all months with the exceptions of September and November 1998 (Figure 6.3).

3.1.2 Salinity

Salinity ranged from a low of 24.3 ppt at Reach Run to a high of 33.7 near Big Island (Figure 5). Salinity values measured varied by site (ANOVA $F= 2345.7$, $p< 0.001$)

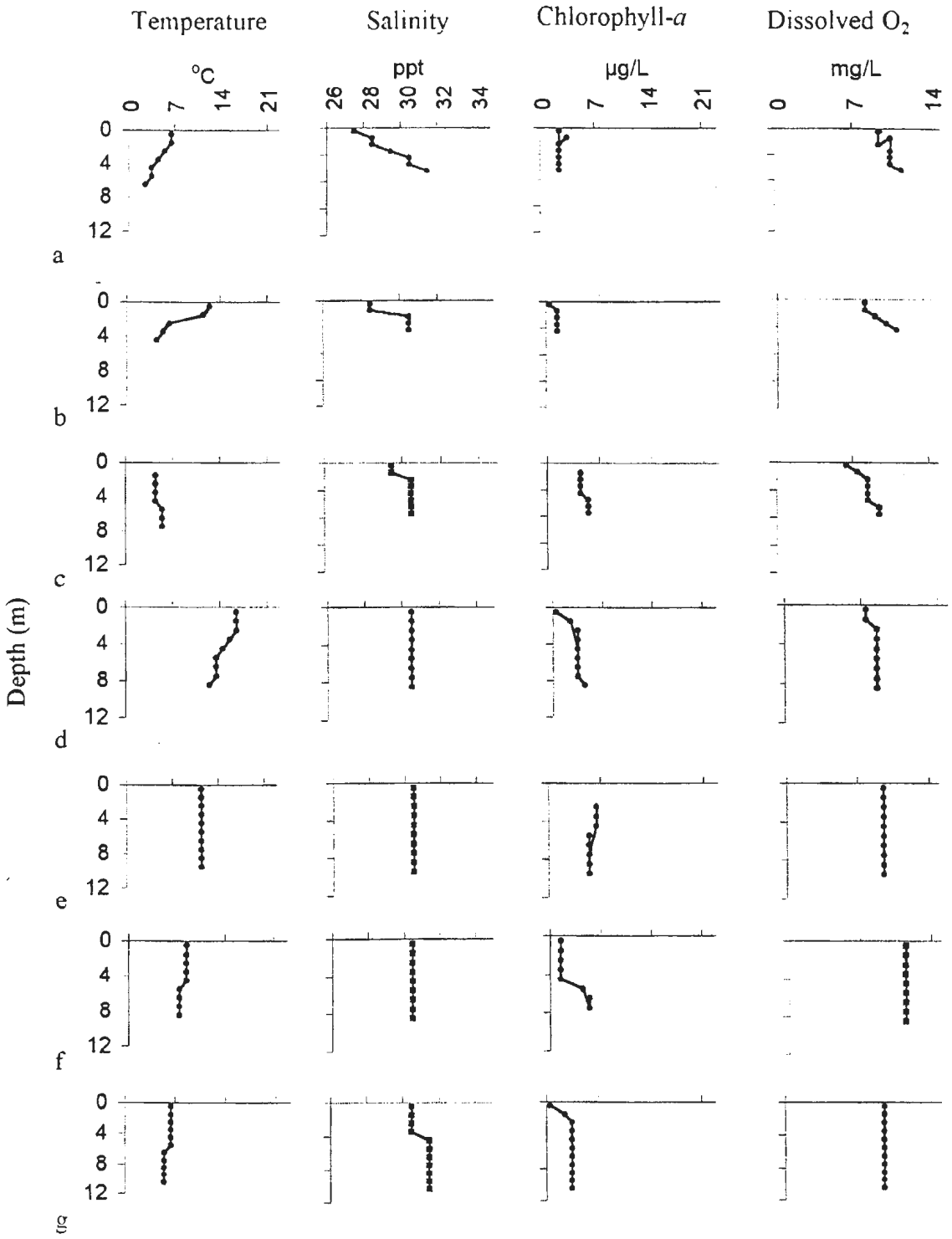

Figure 6.1. Vertical depth profiles of environmental data averaged from all 10 static at Burnt Arm on a) May 21, b) June 23, c) July 04, d) August 10, e) September 13, f) October 17 and g) November 30, 1998.

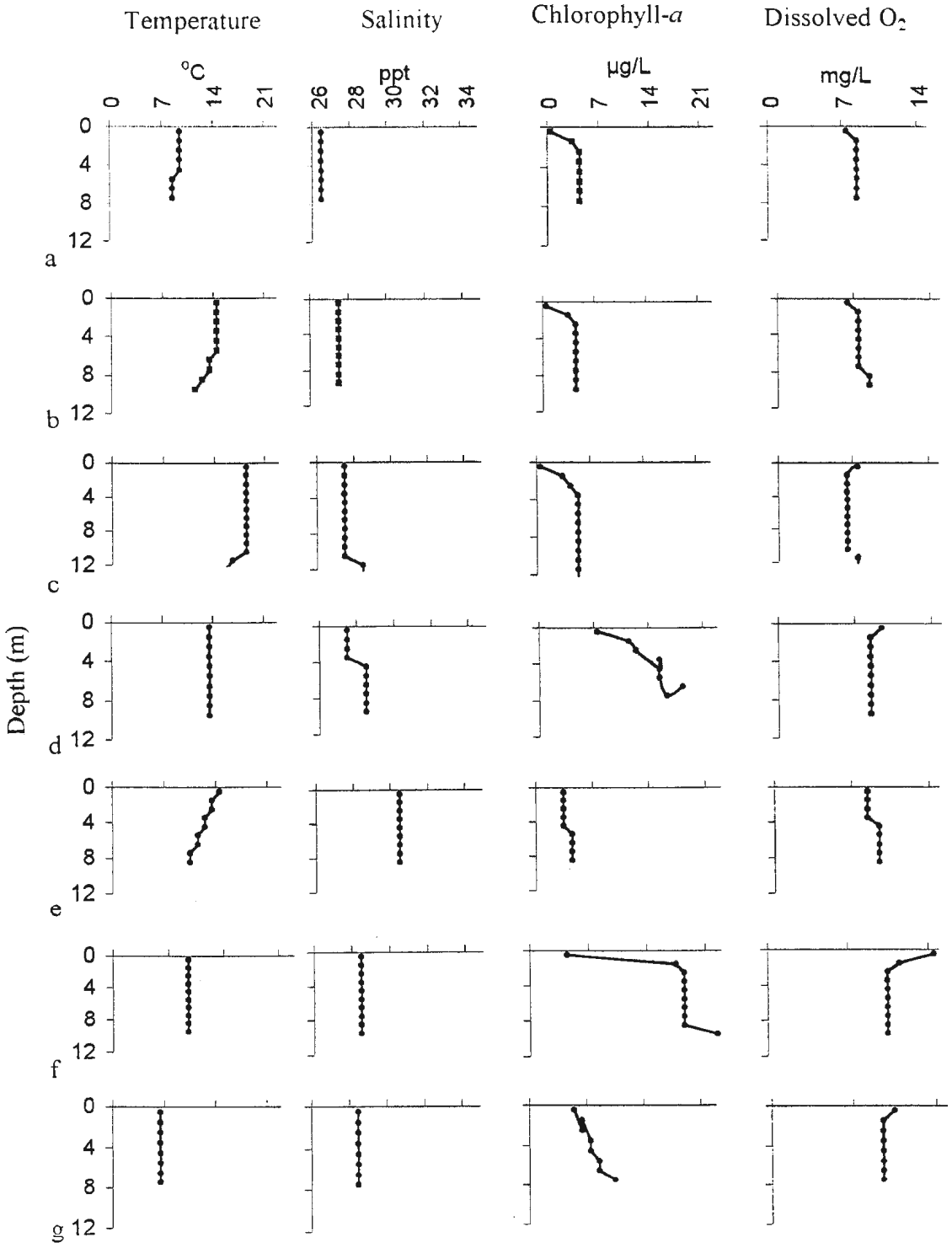

Figure 6.2. Vertical depth profiles of environmental data averaged from all 10 static at Reach Run on a) May 25, b) June 25, c) July 06, d) August 8, e) September 08, f) October 16 and g) November 05, 1998.

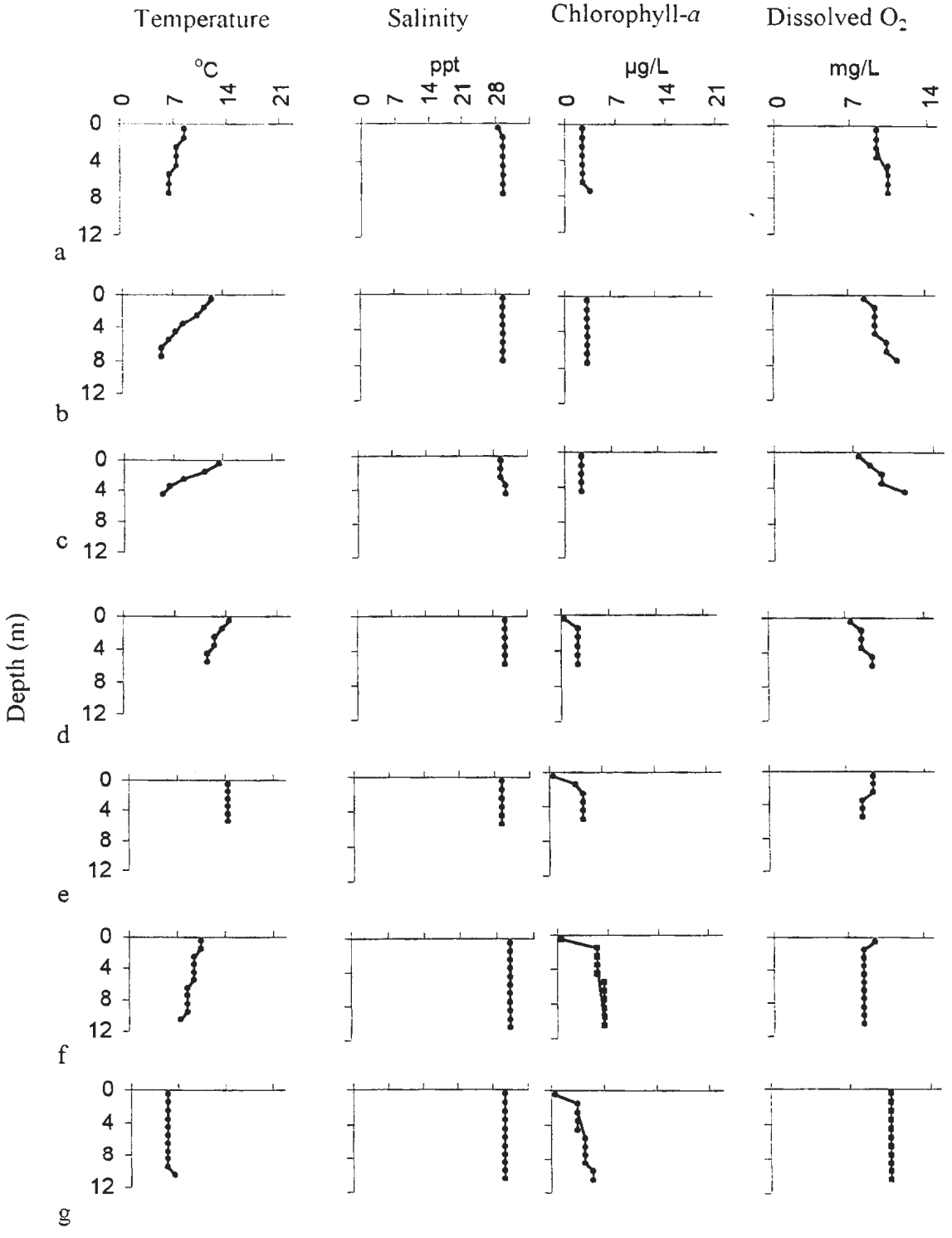

Figure 6.3. Vertical depth profiles of environmental data averaged from all 10 static at Big Island on a) May 30, b) June 26, c) July 8, d) August 5, e) September 3, f) October 2 and g) November 8, 1998.

and season (ANOVA, $F= 44.4$, $p< 0.001$). Burnt Arm had the highest salinities followed by Big Island and Reach Run, respectively (Tukey HSD, $p< 0.001$).

Variations in seasonal temporal patterns of salinity were significant at all three sites (Figure 5). Salinity values recorded at Burnt Arm ranged from a low of 27.8 ppt in May 1998 to 31.5 ppt in December 1997 (Figure 5.1). Reach Run salinity values ranged from 24.3 ppt to 30.9 ppt (Figure 5.2). Salinity at Big Island ranged from 29.3 ppt in April 1998 to 33.7 ppt May 1998 (Figure 5.3).

In Burnt Arm, short-term temporal variations in salinity occurred during almost all sampling sessions with the exception of July 30-31, 1998 (Table 2, Appendix 4.1-4.6). The Reach Run site had short-term variations in salinity when sampled during all sample sessions except September 29-30, 1998 (Table 2, Appendix 4.7-4.12). Short-term temporal variations of salinity in the Big Island site occurred during only the May 28-29, 1998, June 25-26, 1998 and September 3-4, 1998 sample sessions (Table 2, Appendix 4.13-4.18).

Within Burnt Arm, salinity did not vary spatially at a depth of 3.5 m (ANOVA $F= 0.5$, $p= 0.897$, Figure 3a); however, a halocline was present during sampling in May, June, July and November 1998 (Appendix 4.1). Station 9, 3.5 m depth, Reach Run, had significantly lower salinities than all other sites, while station 5, recorded salinities lower than all sites except station 1 and 9 (Tukey HSD, $p< 0.05$ for each, Figure 3b). A halocline was present at depths greater than 5 m during the July and August sampling events (Appendix 4.2). The Big Island site, differed only at station 9 wherein higher mean average salinities were recorded (Tukey HSD, $p< 0.05$ for each, Figure 3c). The

Table 2. Results of ANOVAs of salinity variations over a tidal cycle at each site.

Salinities were averaged for all 10 stations prior to analysis.

Site	Sample Dates	df	F	Significance
Burnt Arm	May 21-22, '98	5	36.994	<0.001
	June 23-24, '98	5	34.735	<0.001
	July 30-31, '98	5	1.973	0.115
	Sept 13-14, '98	5	180.877	<0.001
	Sept 28-29, '98	4	222.476	<0.001
	November 2-3, '98	4	4.365	0.043
Reach Run	May 25-26, '98	6	19.492	<0.001
	June 24-25, '98	5	18.540	<0.001
	August 3-4, '98	5	0.617	0.688
	September 8-9, '98	5	4.150	0.003
	September 29-30, '98	3	0.431	0.732
	November 4-5, '98	3	7.692	0.001
Big Island	May 28-29, '98	4	2.987	0.029
	June 25-26, '98	4	5.402	0.001
	August 4-5, '98	5	2.127	0.076
	September 3-4. '98	5	4.066	0.003
	October 1-2, '98	3	1.631	0.199
	November 7-8, '98	3	0.362	0.781

water was slightly less saline at the surface during the May and July sampling sessions (Appendix 4).

3.1.3 Chlorophyll-a

Throughout the study the chlorophyll-*a* concentration at 3.5 m depth varied significantly by site and season (ANOVAs, $F= 275.7, 195.0$, $p< 0.001$). Reach Run had significantly higher chlorophyll-*a* values during the study, followed by Burnt Arm and Big Island, respectively (Tukey HSD, $p< 0.05$ for each). During the study chlorophyll-*a* concentrations ranged from a low of 0.31 $\mu g \cdot L^{-1}$ to 19.75 $\mu g \cdot L^{-1}$ (Figure 5.1, 5.2, 5.3).

Significant seasonal temporal variations of chlorophyll-*a* occurred over the course of the experiment at each site (Figure 5). Burnt Arm chlorophyll-*a* values ranged from a low of 0.60 $\mu g \cdot L^{-1}$ in April 1998 to 5.88 $\mu g \cdot L^{-1}$ in September 1998 (Figure 5.1). Chlorophyll-*a* values at Reach Run ranged from 1.0 $\mu g \cdot L^{-1}$ in February 1998 to 19.75 $\mu g \cdot L^{-1}$ in September 1998 (Figure 5.2). Chlorophyll-*a* at Big Island ranged from 0.31 $\mu g \cdot L^{-1}$ in May 1998 to 5.30 $\mu g \cdot L^{-1}$ in October 1998 (Figure 5.3).

Short-term temporal variations in chlorophyll-*a* concentration occurred over the tidal cycle in Burnt Arm during all sampling periods with the exception of May 21-22, 1998 (Table 3, Appendix 4.1-4.6). Chlorophyll-*a* levels at 3.5 m depth correlated with tidal height during the May, June and July sample sessions (Table 4). In Reach Run (Table 3, Appendix 4.7-4.12) and Big Island (Table 3, Appendix 4.13-4.18) short-term temporal variations of chlorophyll-*a* occurred on a daily basis during each sampling period. In Reach Run, chlorophyll-*a* concentration could vary by 2-3 fold over the tidal

Table 3. Results of ANOVAs of chlorophyll-*a* variation over a tidal cycle at each site. Chlorophyll-*a* values were averaged for all 10 stations prior to analysis.

Site	Sample Dates	df	F	Significance
Burnt Arm	May 21-22, '98	5	2.380	0.052
	June 23-24, '98	5	17.180	<0.001
	July 30-31, '98	5	2.779	0.038
	Sept 13-14, '98	5	25.774	<0.001
	Sept 28-29, '98	4	121.707	<0.001
	November 2-3, '98	4	4.994	0.032
Reach Run	May 25-26, '98	6	25.601	<0.001
	June 24-25, '98	5	52.447	<0.001
	August 3-4, '98	5	34.649	<0.001
	September 8-9, '98	5	36.394	<0.001
	September 29-30, '98	3	4.046	0.014
	November 4-5, '98	3	6.603	0.001
Big Island	May 28-29, '98	4	8.733	<0.001
	June 25-26, '98	4	78.970	<0.001
	August 4-5, '98	5	2.524	0.040
	September 3-4. '98	5	37.718	<0.001
	October 1-2, '98	3	30.516	<0.001
	November 7-8, '98	3	14.846	<0.001

Table 4. Results of correlations between tidal height and chlorophyll-*a* levels at 3.5 m depth. Chlorophyll-*a* values were averaged for all 10 stations prior to analysis.

Site	month			height (m)	chla
Burnt Arm	1.00	height (m)	Correlation		.141
			P value		.325
	2.00	height (m)	Correlation	1.000	.686
			P value	.	.000
	3.00	height (m)	Correlation	1.000	.257
			P value	.	.043
	4.00	height (m)	Correlation	1.000	.267
			P value	.	.030
	5.00	height (m)	Correlation	1.000	-.068
			P value	.	.620
	6.00	height (m)	Correlation	1.000	-.319
			P value	.	.035
Reach Run	1.00	height (m)	Correlation		.443
			P value	.	.000
	2.00	height (m)	Correlation	1.000	.755
			P value	.	.000
	3.00	height (m)	Correlation	1.000	.772
			P value	.	.000
	4.00	height (m)	Correlation	1.000	.482
			P value	.	.000
	5.00	height (m)	Correlation	1.000	-.811
			P value	.	.000
	6.00	height (m)	Correlation	1.000	.064
			P value	.	.700
Big Island	1.00	height (m)	Correlation	1.000	-.156
			P value	.	.249
	2.00	height (m)	Correlation	1.000	.177
			P value	.	.192
	3.00	height (m)	Correlation	1.000	.266
			P value	.	.031
	4.00	height (m)	Correlation	1.000	.772
			P value	.	.000
	5.00	height (m)	Correlation	1.000	.355
			P value	.	.017
	6.00	height (m)	Correlation	1.000	-.551
			P value	.	.000

cycle (Appendix 4.7-4.12). During the months of May, June and August, chlorophyll-*a* levels at 3.5 m depth correlated with tidal height in Reach Run (Table 4). At Big Island chlorophyll-*a* concentrations chlorophyll-*a* levels at 3.5 m depth correlated with tidal height in July and September and October (Table 4).

There were no spatial differences in chlorophyll-*a* among the stations of Burnt Arm (ANOVA, $F= 0.46$, $p= 0.997$, Figure 3a); however, chlorophyll-*a* concentrations increased with increasing depth during the May to August sampling (Figure 6.1). In Reach Run, there were no significantly different spatial patterns of chlorophyll-*a* increased with increasing depth during each sampling event from May 1998 to November 1998 (Figure 6.2). The Big Island site differed only at station 9, which had higher mean chlorophyll-*a* concentration than all other stations (Tukey HSD, $p< 0.05$ for each, Figure 3c). Chlorophyll-*a* concentrations increased with increasing depths from May 1998 to July 1998 (Figure 6.3).

3.1.4 Dissolved Oxygen

Throughout the study the dissolved oxygen concentrations at 3.5 m depth varied significantly by site, location within each site and season (ANOVAs, $F= 496.2, 8.5, 361.0$, $p< 0.001$ for each, Figure 5). Burnt Arm had significantly higher dissolved oxygen values during this study, followed Big Island and Reach Run, respectively (Tukey HSD, $p< 0.001$). During the study dissolved oxygen concentrations ranged from a low of 6.8 $mg \cdot L^{-1}$ to 14.0 $mg \cdot L^{-1}$ at 3.5 m depth (Figure 5). The corresponding range in saturation was 75% to 100%.

Significant seasonal temporal variations in dissolved oxygen occurred over the course of the experiment at 3.5 m depth at each site (Figure 5). Burnt Arm dissolved oxygen values ranged from a low of 8.1 $mg \cdot L^{-1}$ in August 1998 to 11.4 $mg \cdot L^{-1}$ in April 1998 (Figure 5.1). The corresponding saturation was 80% to 85 %. Dissolved oxygen concentrations at Reach Run ranged from a low of 6.8 $mg \cdot L^{-1}$ in August 1998 to 14.0 $mg \cdot L^{-1}$ in April 1998 (Figure 5.2). The corresponding saturation was 75% to 100 %. Dissolved oxygen concentration patterns at Big Island ranged from a low 8.6 $mg \cdot L^{-1}$ in September 1998 to 12.2 $mg \cdot L^{-1}$ in April 1998 (Figure 5.3). The corresponding saturation was 83% to 85 %.

Short-term temporal variations in dissolved oxygen in Burnt Arm occurred on a daily basis during all except two sample sessions (Table 5, Appendix 4.1-4.6). In Reach Run daily temporal variations in dissolved oxygen occurred at each sampling session with the exception of September 29-30, 1998 (Table 5, Appendix 4.7-4.12). Big Island had short-term temporal variations in dissolved oxygen during all sample periods except May 28-29, 1998 (Table 5, Appendix 4.13-4.18).

In Burnt Arm, the control station recorded higher dissolved oxygen concentrations than stations 3 (Tukey HSD, $p= 0.018$) and 6 (Tukey HSD, $p= 0.015$) and dissolved oxygen concentrations increased with increasing depth during the May to August sampling (Figure 6.1). The greatest variation in dissolved oxygen for Burnt Arm occurred in July, ranging from 6 $mg \cdot L^{-1}$ (47% saturation) near the surface, to 9 $mg \cdot L^{-1}$ (75% saturation) at 7.5 m depth. There were significantly different spatial patterns of dissolved oxygen in the Reach Run (ANOVA, $F= 2.5$, $p= 0.011$). The control station and

Table 5. Results of ANOVAs of dissolved oxygen variation over a tidal cycle at each site. Dissolved oxygen values were averaged for all 10 stations prior to analysis.

Site	Sample Dates	df	F	Significance
Burnt Arm	May 21-22, '98	5	6.875	<0.001
	June 23-24, '98	5	2.795	0.026
	July 30-31, '98	5	2.118	0.094
	Sept 13-14, '98	5	15.857	<0.001
	Sept 28-29, '98	4	16.983	<0.001
	November 2-3, '98	4	2.287	0.139
Reach Run	May 25-26, '98	6	5.039	<0.001
	June 24-25, '98	5	23.821	<0.001
	August 3-4, '98	5	2.442	0.046
	September 8-9, '98	5	3.016	0.018
	September 29-30, '98	3	0.475	0.701
	November 4-5, '98	3	4.897	0.007
Big Island	May 28-29, '98	4	1.934	0.121
	June 25-26, '98	4	4.328	0.005
	August 4-5, '98	5	4.072	0.003
	September 3-4. '98	5	12.572	<0.001
	October 1-2, '98	3	9.987	<0.001
	November 7-8, '98	3	11.797	<0.001

station 9 had significantly higher dissolved oxygen concentrations than stations 5 (Tukey HSD, $p< 0.001$), 6 (Tukey HSD, $p= 0.007$), 7 (Tukey HSD, $p= 0.01$) and 8 (Tukey HSD, $p= 0.0035$). Dissolved oxygen concentrations increased with increasing depth during each sampling event from May 1998 to August 1998. The greatest variation in dissolved oxygen for Reach Run occurred in June, ranging from 6 $mg \cdot L^{-1}$ (57% saturation) near the surface, to 8.5 $mg \cdot L^{-1}$ (78% saturation) at 8.5 m depth. However, the water column was well-mixed through the autumn months (Figure 6.2). There were significantly different spatial patterns of dissolved oxygen in the Big Island site (ANOVA, $F= 18.8$, $p< 0.001$). The control station had significantly higher dissolved oxygen concentrations than stations 1-9, while station nine had significantly lower concentrations than stations 0-8 (Tukey HSD, $p< 0.05$ for each). Dissolved oxygen concentrations increased with increasing depths during sampling from May 1998 to August 1998 (Figure 6.3). The greatest variation in dissolved oxygen for Big Island occurred in July, ranging from 7.5 $mg \cdot L^{-1}$ (70% saturation) near the surface, to 11 $mg \cdot L^{-1}$ (81% saturation) at 7.5 m depth.

3.1.5 Particulate Organic Matter

Throughout the study the particulate organic matter (POM) concentrations at 3.5 m depth varied significantly by site, location within each site and season (ANOVAs, $F= 126.0, 35.6, 212.8$, $p< 0.001$, Figure 7). Particulate organic matter concentrations ranged from 0 mg to 11.3 $mg \cdot L^{-1}$. The highest concentrations of POM throughout the study were at Big Island averaging 3.52 $mg \cdot L^{-1}$, followed closely by Reach Run at 3.51 $mg \cdot L^{-1}$, and finally Burnt arm at 2.76 $mg \cdot L^{-1}$. Burnt Arm had significantly higher POM percentages

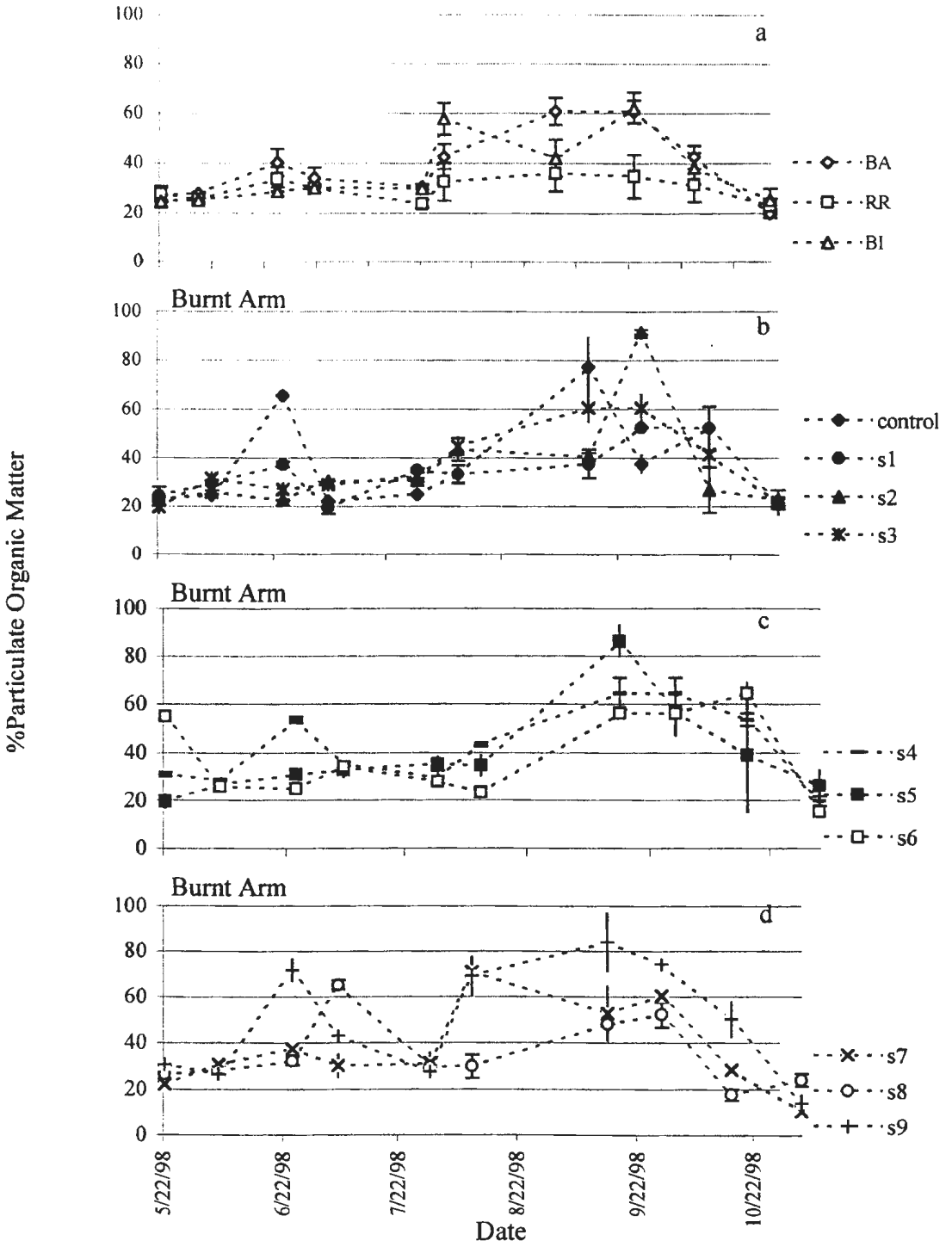

Figure 7.1. a) Percent POM averaged over all stations at Burnt Arm (BA), Reach Run (RR) and Big Island (BI) at 3.5 m, %POM in Burnt Arm at station b) control, 1, 2 and 3 c) 4, 5 and 6 and d) 7, 8 and 9, respectively (error bars= standard error).

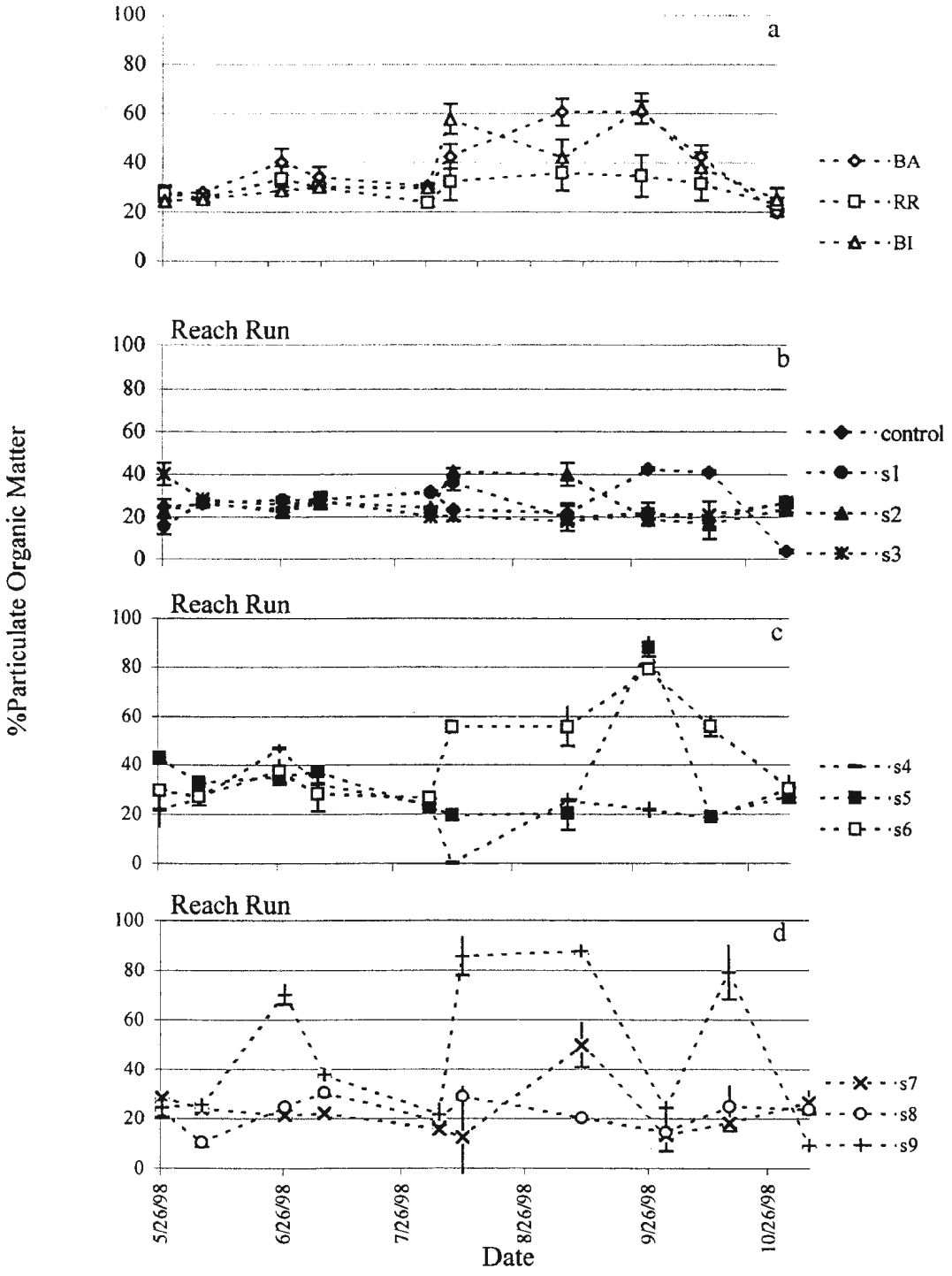

Figure 7.2. a) Percent POM averaged over all stations at Burnt Arm (BA), Reach Run (RR) and Big Island (BI) at 3.5 m, %POM in Reach Run at station b) control, 1, 2 and 3 c) 4, 5 and 6 and d) 7, 8 and 9, respectively (error bars= standard error).

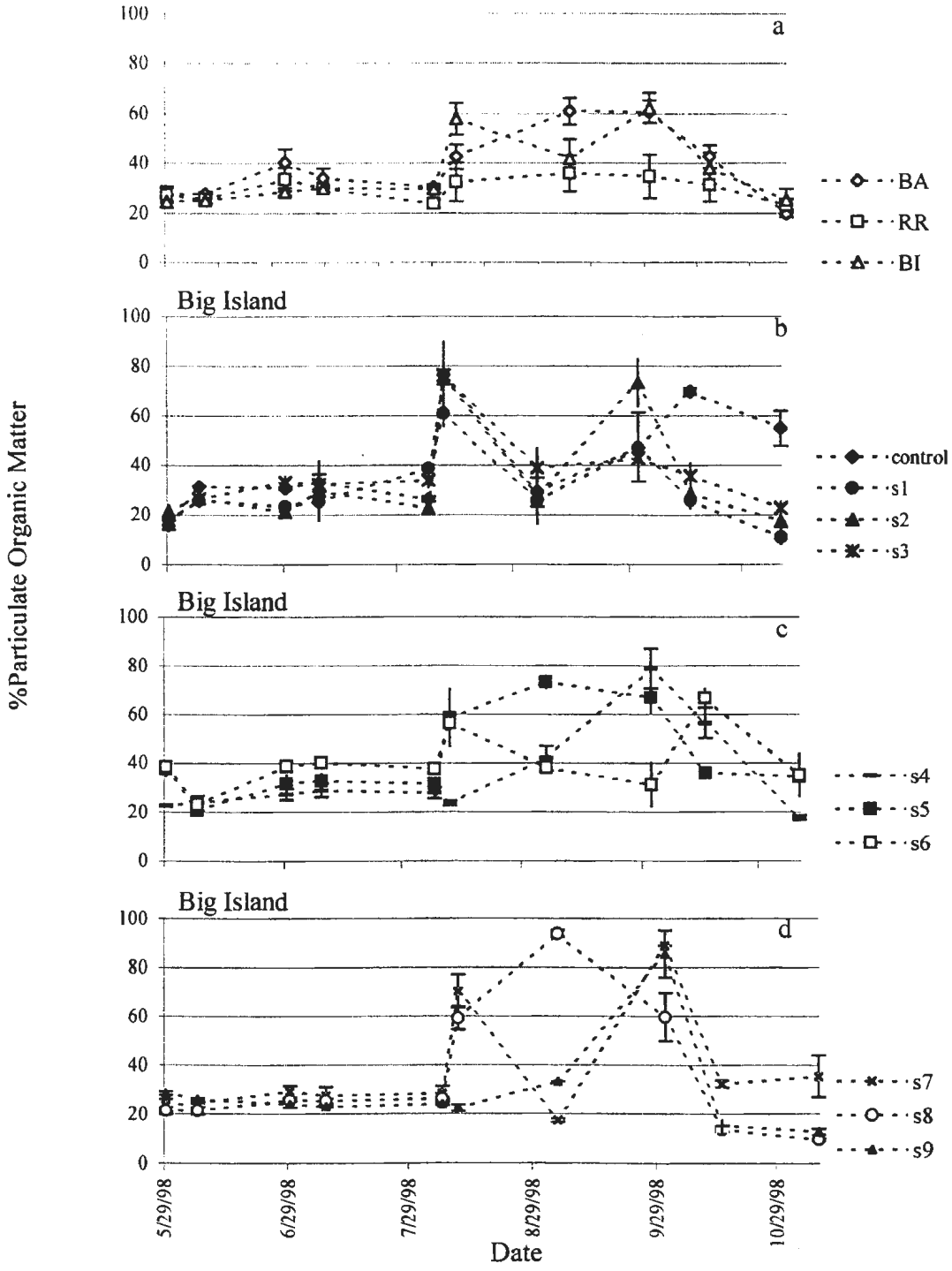

Figure 7.3. a) Percent POM averaged over all stations at Burnt Arm (BA), Reach Run (RR) and Big Island (BI) at 3.5 m, %POM in Big Island at station b) control, 1, 2 and 3 c) 4, 5 and 6 and d) 7, 8 and 9, respectively (error bars= standard error).

during this study, followed by Big Island and Reach Run, respectively (Tukey HSD, $p < 0.001$ for each, Figure 7).

Significant seasonal temporal variations in POM occurred over the course of the experiment at each site (ANOVAs, $F = 155.1, 18.4, 171.0$, $p < 0.001$ for each, Figure 7.1). Concentrations of POM in Burnt Arm ranged from 0.2 $mg \cdot L^{-1}$ in May, 1998 to 8.65 $mg \cdot L^{-1}$ in June, 1998 while %POM in Burnt Arm ranged from a low of 10.47% in late November 1998 to 31.61% in October 1998 (Figure 7.1). Reach Run concentrations of POM ranged from 0.2 $mg \cdot L^{-1}$ in August, 1998 to 9.4 $mg \cdot L^{-1}$ in June, 1998, however, Reach Run %POM ranged from a low of 0% in August 1998 to 88.2 % in October 1998 (Figure 7.2). Big Island POM ranged from, 0.5 $mg \cdot L^{-1}$, in September 1998 to 8.3 $mg \cdot L^{-1}$ in July 1998. Percent POM patterns at Big Island ranged from 9.54% in November 1998 to 93.8% in September 1998 (Figure 7.3).

Percent organic matter varied spatially within all study sites (ANOVAs, $F = 15.3, 55.5, 17.6$, $p < 0.001$ for each). In Burnt Arm, the control station recorded higher %POM than station 9, while all other stations had higher %POM than stations 4 and 9 (Tukey HSD, $p < 0.05$ for each, Figure 7.1). As well, station 9 had the lowest concentration of POM, 1.9 $mg \cdot L^{-1}$, throughout the study, while the control station and stations on the front line had the highest concentrations averaging 3.15 $mg \cdot L^{-1}$. In the Reach Run, the control station, stations 1-4 and 7-8 had significantly lower %POM than stations 5, 6 and 9. In addition, station 5 had lower %POM than stations 6 and 9 but higher %POM than all other stations, station 6 had higher %POM than all stations with the exception of station 9, which was higher in %POM than all stations (Tukey HSD, $p < 0.05$ for each, Figure

7.2). However, the absolute values of POM are highest at station 3, 4 and 5, averaging 4.3, 4.4 and 4.8 $mg \cdot L^{-1}$ and lowest at stations 6 and 9 averaging 2.2 $mg \cdot L^{-1}$ for each. At the Big Island site the control station had significantly higher %POM than stations 1-4 and stations 8-9 (Tukey HSD, $p < 0.05$ for each, Figure 7.3). Station 1 was lower than the control as well as stations 3, 5, 6 and 7 (Tukey HSD, $p < 0.05$ for each, Figure 7.1). Station 2 had %POM values less than the control station, as well as stations 5 and 6 but higher vales than station 9 (Tukey HSD, $p < 0.05$ for each, Figure 7.1). Stations 3, 4 and 8 have similar results to station 2 with the addition of lower %POM than station 1, station 9 had higher %POM values than all stations throughout the study (Tukey HSD, $p < 0.05$ for each, Figure 7.1). Absolute values of POM are highest at stations 5, 6 and 7 with average concentrations of 4.2, 4.65 and 4.15 $mg \cdot L^{-1}$ respectively throughout the study.

3.2 Currents

3.2.1 S4 Current Meter

In Burnt Arm, hourly current speeds ranged between 0.9 and 6.8 $cm \cdot s^{-1}$ at 3.5 m depth throughout the study and averaged 2.35 $cm \cdot s^{-1}$ (Appendix 5.1). Current speed at 3.5 m depth did not correlate with daily average wind speed (Pearson Correlation= 0.053, p= 0.544, Table 6, Appendix 5.1) but was negatively correlated with current direction (Pearson Correlation= -0.259, p= 0.0020, Table 6, Appendix 5.1) and daily wind direction (Pearson Correlation= 0.261, p= 0.002, Table 6, Appendix 5.1). Current direction was not a simple tidally driven force. In many cases, regardless of changing tidal activity, current direction remained constant (Appendix 6.1).

Table 6. Results of S4 current meter correlations with wind data. Wind data = average daily values from Environment Canada.

Site			Current Direction	Wind Speed	Wind Direction
Burnt Arm	Current Speed	Correlation	-0.259	0.053	-0.003
		Sig	0.002	0.544	0.969
		N	138	131	133
	Current Direction	Correlation		-0.107	0.261
		Sig		0.225	0.002
		N		131	133
	Wind Speed	Correlation			0.244
		Sig			0.010
		N			131
Reach Run	Current Speed	Correlation	0.102	-0.198	-0.222
		Sig	0.228	0.023	0.011
		N	142	131	130
	Current Direction	Correlation		0.030	0.153
		Sig		0.735	0.083
		N		131	130
	Wind Speed	Correlation			0.266
		Sig			0.002
		N			128
Big Island	Current Speed	Correlation	-0.495	-0.018	0.179
		Sig	<0.001	0.840	0.040
		N	134	132	133
	Current Direction	Correlation		0.343	-0.015
		Sig		<0.001	0.864
		N		132	133
	Wind Speed	Correlation			0.322
		Sig			<0.001
		N			131

Current speeds in Reach Run ranged between 0.8 cm $\bullet s^{-1}$ and 8.7 cm $\bullet s^{-1}$, averaging 3.7 cm $\bullet s^{-1}$ over the study (Appendix 5.2). Current speeds in Reach Run correlated negatively with both wind speed (Pearson Correlation= -0.198, p= 0.023, Table 6, Appendix 5.2) and direction (Pearson Correlation= -0.222, p= 0.011, Table 6, Appendix 5.2). Reach Run current directions did not correlate with wind speed (Pearson Correlation= 0.030, p= 0.735, Table 6, Appendix 5.2) or direction (Pearson Correlation= 0.153, p= 0.083, Table 6, Appendix 5.2). Current direction was not a simple tidally driven force. In many cases, regardless of changing tidal activity, current direction remained constant (Appendix 5.2).

The Big Island site had the lowest recorded hourly current speeds, ranging from 0.6 cm $\bullet s^{-1}$ to 4.1 cm $\bullet s^{-1}$. Average current speed during the study was 1.8 cm $\bullet s^{-1}$ (Appendix 5.3). Current speeds at the Big Island site correlated negatively with current direction (Pearson Correlation= -0.495, p = 0.018, Table 6, Appendix 5.3) and positively with wind direction (Pearson Correlation= 0.179, p= 0.040, Table 6, Appendix 5.3) but was not correlated wind speed (Pearson Correlation= -0.018, p= 0.840, Table 6, Appendix 5.3). Big Island current directions correlated with wind speed (Pearson Correlation= 0.343, p< 0.001, Table 6, Appendix 5.3) but not direction (Pearson Correlation= -0.015, p= 0.864, Table 6, Appendix 5.3). Current direction was not a simple tidally driven force. The position of the islands in relation to the mainland topography seemed to have an effect on the current flow (Appendix 6.3).

3.2.2 Relative Current Speed

The relationship of the S4 current meter data at station 2 with cylinder dissolution at the same station is represented by the following regression equation:

$C = (D + 1.257 \cdot 10^{-2} - 2.398 \cdot 10^{-4} \cdot (Temp) - 4.202 \cdot 10^{-4} \cdot (ppt)) \cdot (4.147 \cdot 10^{-4})^{-1}$

Where C= current speed ($cm \cdot s^{-1}$), D= dissolution ($mg \cdot cm^{-2} \cdot h^{-1}$), Temp= temperature ($^{o}C$) and ppt= Salinity (ppt).

(R square= 0.752, F= 56.562, $p < 0.001$, Figure 8).

From this equation, relative current speeds were calculated at six stations on each farm (Figure 9). Relative current speed at the test sites varied significantly by site and season (ANOVAs, F= 7.1, p= 0.001, F= 83.8, $p < 0.001$). Reach Run had the highest relative current speeds, followed by Burnt Arm and Big Island, respectively (Tukey HSD, $p < 0.05$ for each, Figure 9). The highest relative current speeds were found over the course of the entire study to be in November followed by the sampling in May and finally June and September, which were not significantly different from one another (Tukey HSD, $p < 0.05$ for each, Figure 9). Relative current speeds measured in July were high at Reach Run while significantly lower than any other sample period in the study at Burnt Arm and Big Island (Tukey HSD, $p < 0.05$ for each, Figure 9), however, wind speeds in July were not low (Figure 9).

On a smaller scale, within site differences existed in Burnt Arm, Reach Run and Big Island (ANOVAs, F= 7.8, 31.153, 6.399, $p < 0.001$ for each, Figure 9). Relative

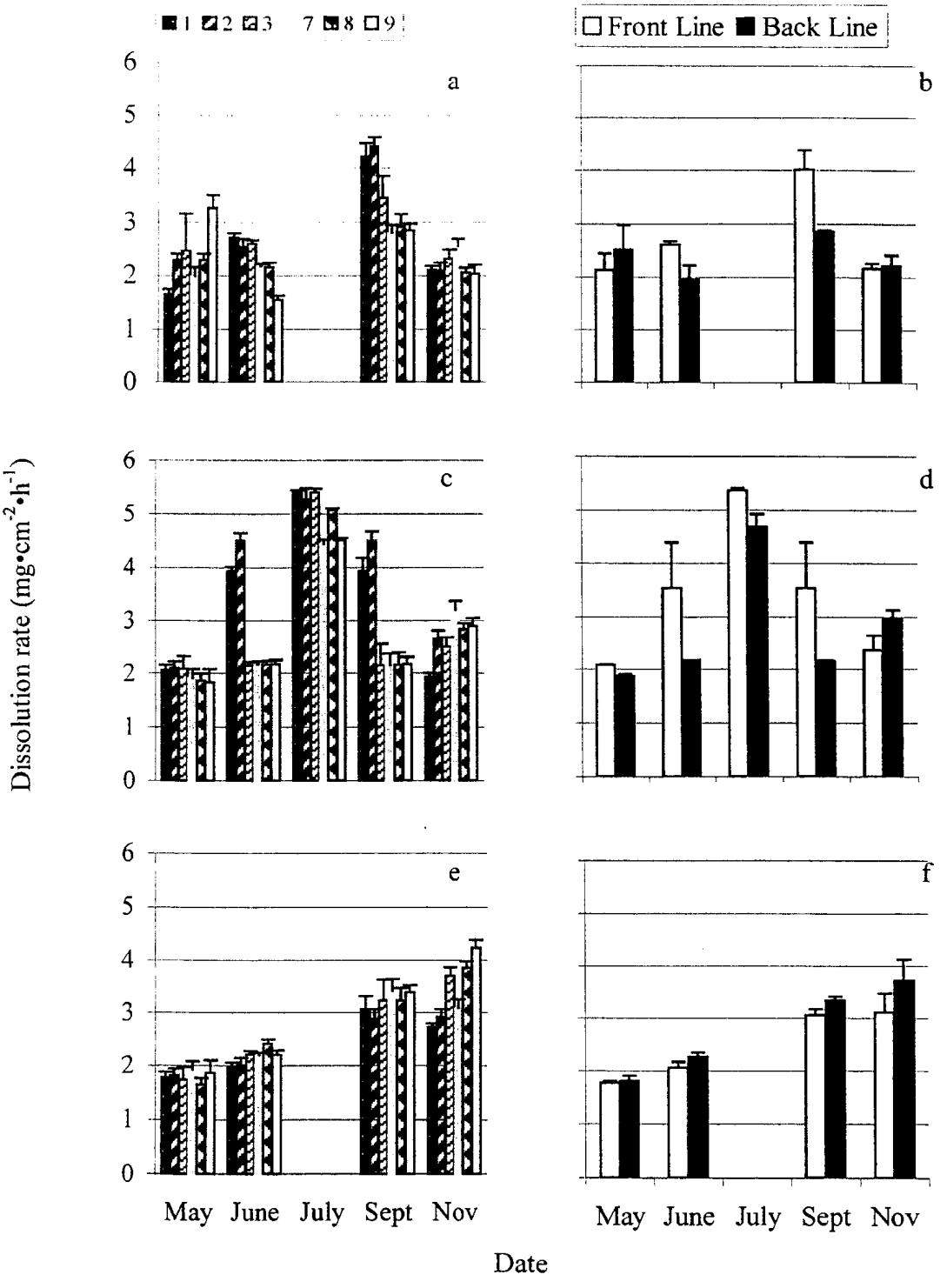

Figure 8. Seasonal dissolution rates ($mg \cdot cm^{-2} \cdot h^{-1}$) of cylinders placed at 3.5 m (a, c, e) at stations 1-3 and 7-9 in a) Burnt Arm c) Reach Run and e) Big Island. Experimental longline averages at 3.5 m (b, d, f) in b) Burnt Arm, d) Reach Run and f) Big Island (n=5, error bars= standard error).

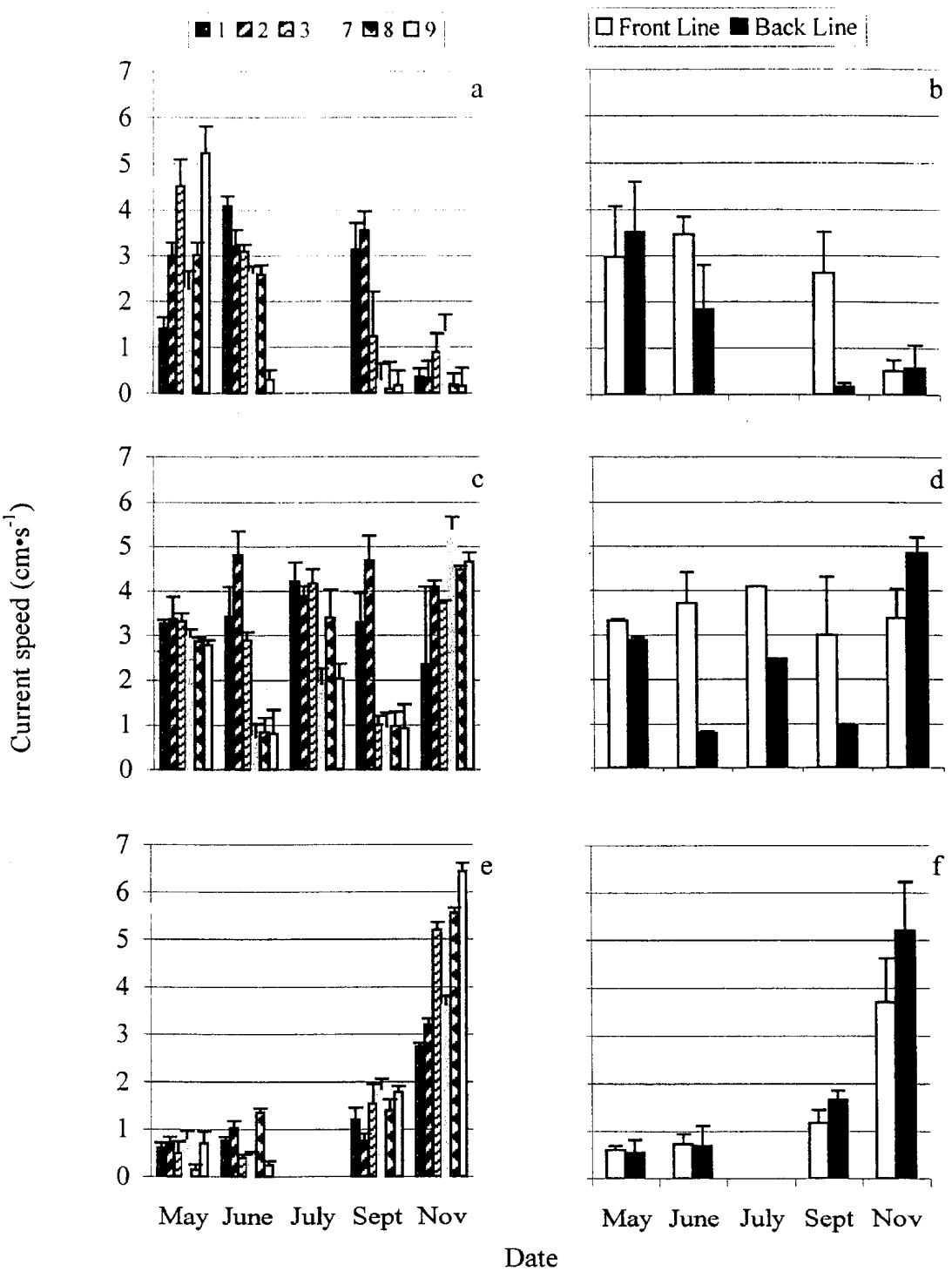

Figure 9. Relative current speed (cm •s^{-1}) at 3.5 m (a, c, e) stations 1-3 and 7-9 measured with dissolution cylinders in a) Burnt Arm, c) Reach Run and e) Big Island, (n=5, error bars =standard error. Experimental long line averages at 3.5 m (b, d, f), in b) Burnt Arm, d) Reach Run and f) Big Island (n=15, error bars= standard error).

current speed in Burnt Arm was significantly higher at stations at the front of the farm (Tukey HSD, $p< 0.05$ for each, Figure 9). Similarly in Reach Run, the highest relative current speeds occur at stations 1 and 2 at the front of the farm (Tukey HSD, $p< 0.05$ for each, Figure 9). The Big Island site had its highest relative current speeds at stations 8 and 9, at the back of the farm (Tukey HSD, $p< 0.05$ for each, Figure 9).

Temporally, relative current speed varied amongst the sites as well. The highest relative current speeds in Reach Run and Big Island occurred in November (Tukey HSD, $p< 0.05$ for each, Figure 9). These currents correspond with high wind speeds in November (Appendix 5). Relative current speeds were greatest in Burnt Arm in the month of May (Tukey HSD, $p< 0.05$ for each, Figure 9). These speeds do not correspond with high wind speeds (Appendix 5). Although there was no precipitation reported for this time period (Table 7) the current speed may be explained by river discharges due to run off from the spring thaw.

3.3 Seston Flux

Seston flux rates over the entire study ranged from 0.0 $\mu g \cdot cm^{-2} \cdot s^{-1}$ to 117.3 $\mu g \cdot cm^{-2} \cdot s^{-1}$. Seston flux values at the test sites varied by site and season (ANOVAs, $F= 389.3, 15.0$, $p< 0.001$ for each, Figure 10). Reach Run had the highest relative seston flux (calculated using relative current speed values), followed by Big Island and Burnt Arm, respectively (Tukey HSD, $p< 0.05$ for each, Figure 10). The highest current speeds were found over the course of the entire study to be in November followed by the sampling in July, September and finally May and June, which were not significantly different from one another (Tukey HSD, $p< 0.05$ for each, Figure 10).

Table 7. Daily precipitation in Twillingate NL, 1998. Data were provided by Environment Canada (N/A indicates missing data).

Twillingate, NL 1998						Total Precipitation (mm)						
Day	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	0.0
2	0.0	0.0	N/A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	0.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A
4	N/A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	N/A
5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	N/A	0.0	N/A
6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	N/A
7	0.0	N/A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	N/A
8	N/A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	N/A
9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A
10	0.0	0.0	N/A	N/A	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
11	0.0	0.0	0.0	N/A	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	N/A
13	0.0	0.0	N/A	N/A	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
14	5.0	N/A	0.0	N/A	0.0	0.0	0.0	0.0	N/A	N/A	0.0	N/A
15	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	N/A	0.0	N/A
16	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	N/A	N/A	N/A
17	N/A	0.0	0.0	N/A	0.0	0.0	0.0	N/A	N/A	0.0	0.0	N/A
18	N/A	0.0	0.0	0.0	0.0	0.0	0.0	N/A	N/A	N/A	0.0	N/A
19	N/A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
20	0.0	4.0	N/A	0.0	0.0	0.0	0.0	0.0	N/A	N/A	0.0	N/A
21	9.0	N/A	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
22	6.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
23	0.0	0.0	0.0	0.0	0.0	N/A	0.0	N/A	N/A	0.0	0.0	N/A
24	N/A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
25	15	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A
26	0.0	3.0	0.0	0.0	0.0	0.0	N/A	N/A	N/A	0.0	0.0	N/A
27	0.0	8.0	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
28	0.0	0.0	N/A	0.0	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
29	0.0	N/A	0.0	0.0	0.0	0.0	0.0	0.0	N/A	0.0	0.0	N/A
30	0.0	N/A	0.0	0.0	0.0	0.0	0.0	N/A	N/A	0.0	0.0	N/A
31	N/A	N/A	0.0	N/A	0.0	N/A	0.0	0.0	N/A	0.0	N/A	N/A

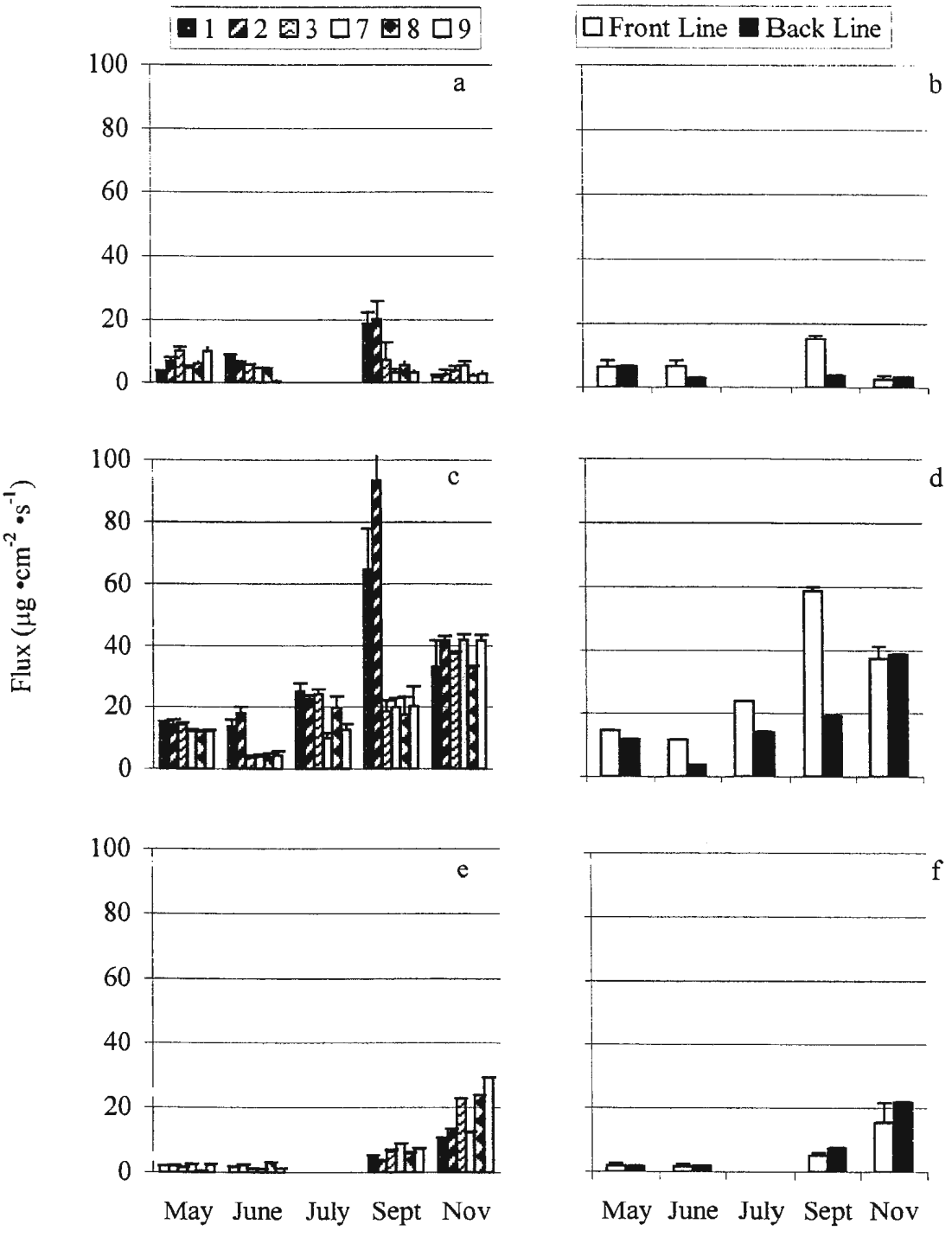

Figure 10. a), c) and e) Flux ($\mu g \cdot cm^{-2} \cdot s^{-1}$) at 3.5 m, stations 1-3 and 7-9 calculated using data from dissolution cylinders and chlorophyll-*a* concentrations in a) Burnt Arm, c) Reach Run and e) Big Island, (n= 5, error bars= standard error. Experimental long line averages at 3.5 m (b, d, f), in b) Burnt Arm, d) Reach Run and f) Big Island (n= 15, error bars= standard error).

On a smaller scale, within site differences existed in Burnt Arm, Reach Run and Big Island (ANOVAs, $F= 7.6, 26.5, 9.68$, $p< 0.001$ for each, Figure 10). Seston flux rates in Burnt Arm were significantly higher at the front of the farm (Tukey HSD, $p< 0.05$, Figure 10). Stations 1 and 2 in Reach Run had significantly higher seston flux rates than other stations (Tukey HSD, $p< 0.05$ for each, Figure 10). The Big Island site had the highest seston flux rates at stations 8 and 9, located at what is considered the back of the farm (Tukey HSD, $p< 0.05$ for each, Figure 10).

Temporally, relative seston flux varied among the sites as well. The highest seston flux values in Burnt Arm and Reach Run occurred in September (Tukey HSD, $p< 0.05$ for each, Figure 10), while the seston flux rates were greatest in Big Island in the month of November (Tukey HSD, $p< 0.05$ for each, Figure 10).

3.4 Mussel Growth, Density and Survival

3.4.1 Growth Rates (Length)

Growth rates over the entire study ranged from 0 to 383.3 $\mu m \cdot d^{-1}$, and averaged 74.8 $\mu m \cdot d^{-1}$. This rate varied by site, source and season (ANOVAs, $F= 8.8$, $p< 0.001$, $F= 4.3$, $p< 0.015$, $F= 32.9$, $p< 0.001$, Figure 11). The Big Island site had the highest seasonal average growth rates, significantly higher than Burnt Arm (Tukey HSD, $p= 0.004$, Figure 11) and Reach Run (Tukey HSD, $p< 0.001$, Figure 11), which were not significantly different from one another (Tukey HSD, $p= 0.737$, Figure 11). The best performing seed source with respect to average shell growth originated from Reach Run followed by the Big Island and finally Burnt Arm. However, the growth rate of the Reach Run and Big

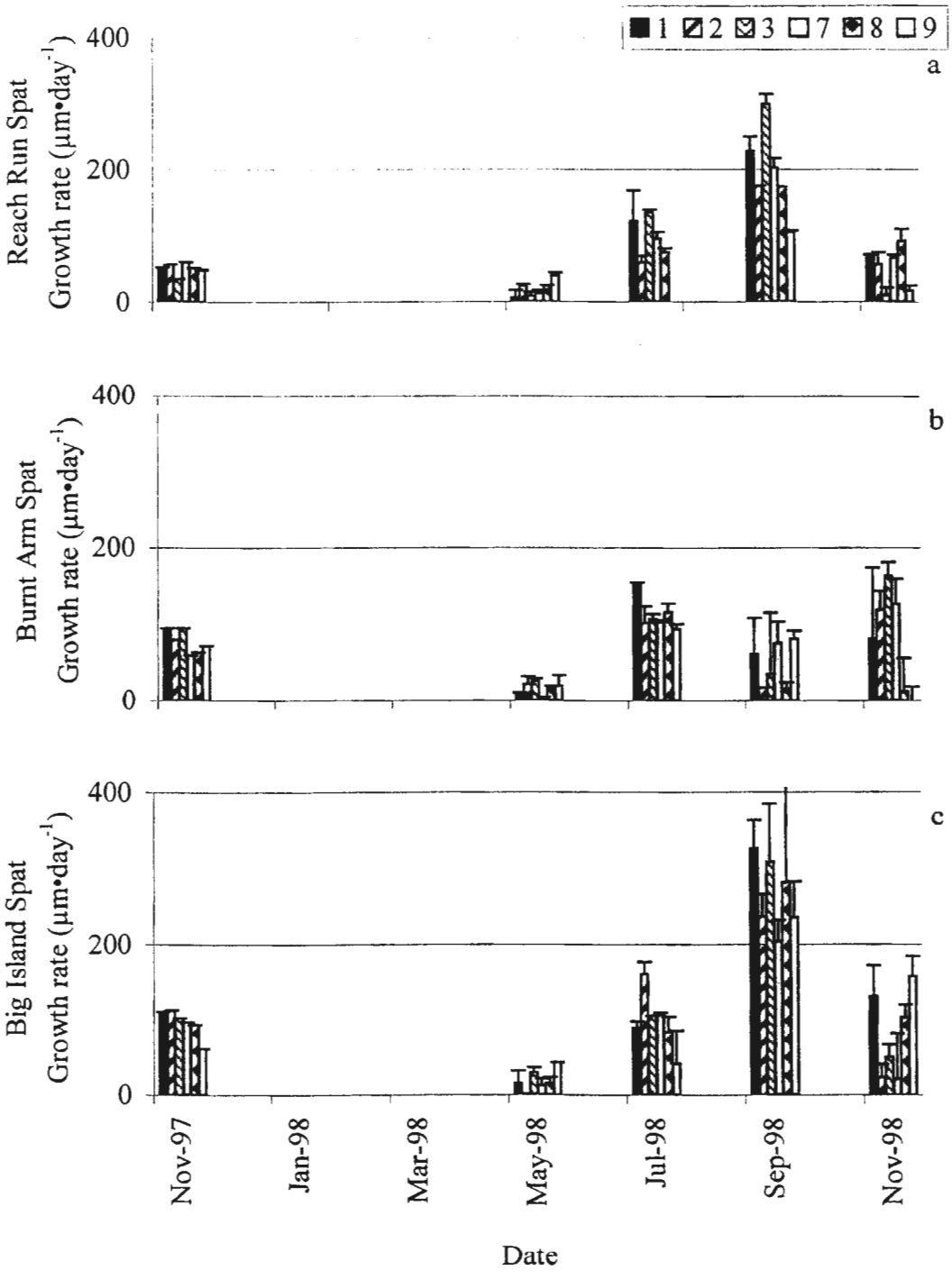

Figure 11.1. Average growth rate ($\mu m \cdot d^{-1}$) per station for Reach Run spat (a), Burnt Arm spat (b) and Big Island spat (c), transplanted to Burnt Arm (n= 100 mussels, error bars= standard error).

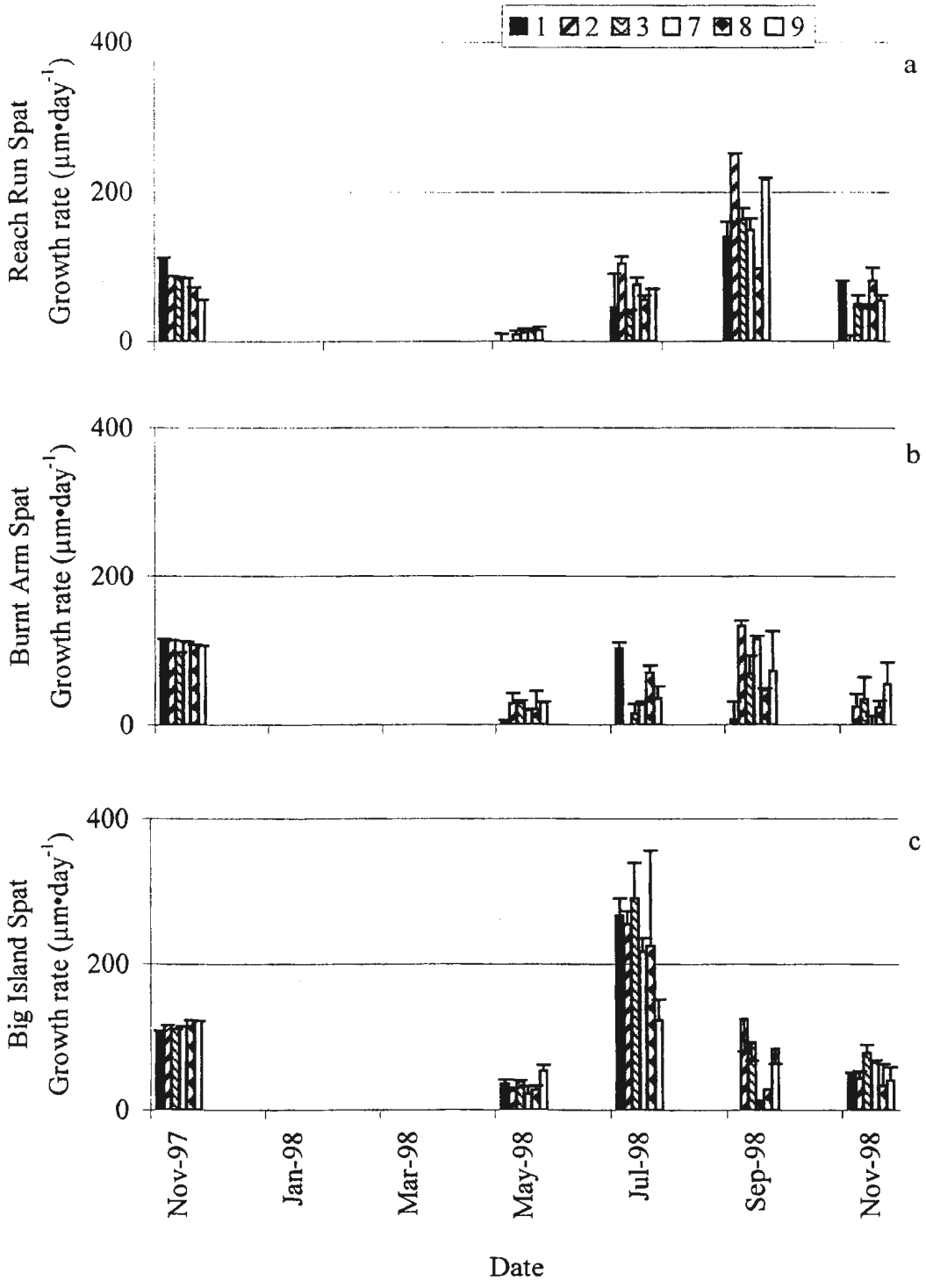

Figure 11.2. Average growth rate ($\mu m \cdot d^{-1}$) per station for Reach Run spat (a), Burnt Arm spat (b) and Big Island spat (c), transplanted to Reach Run (n= 100 mussels, error bars= standard error).

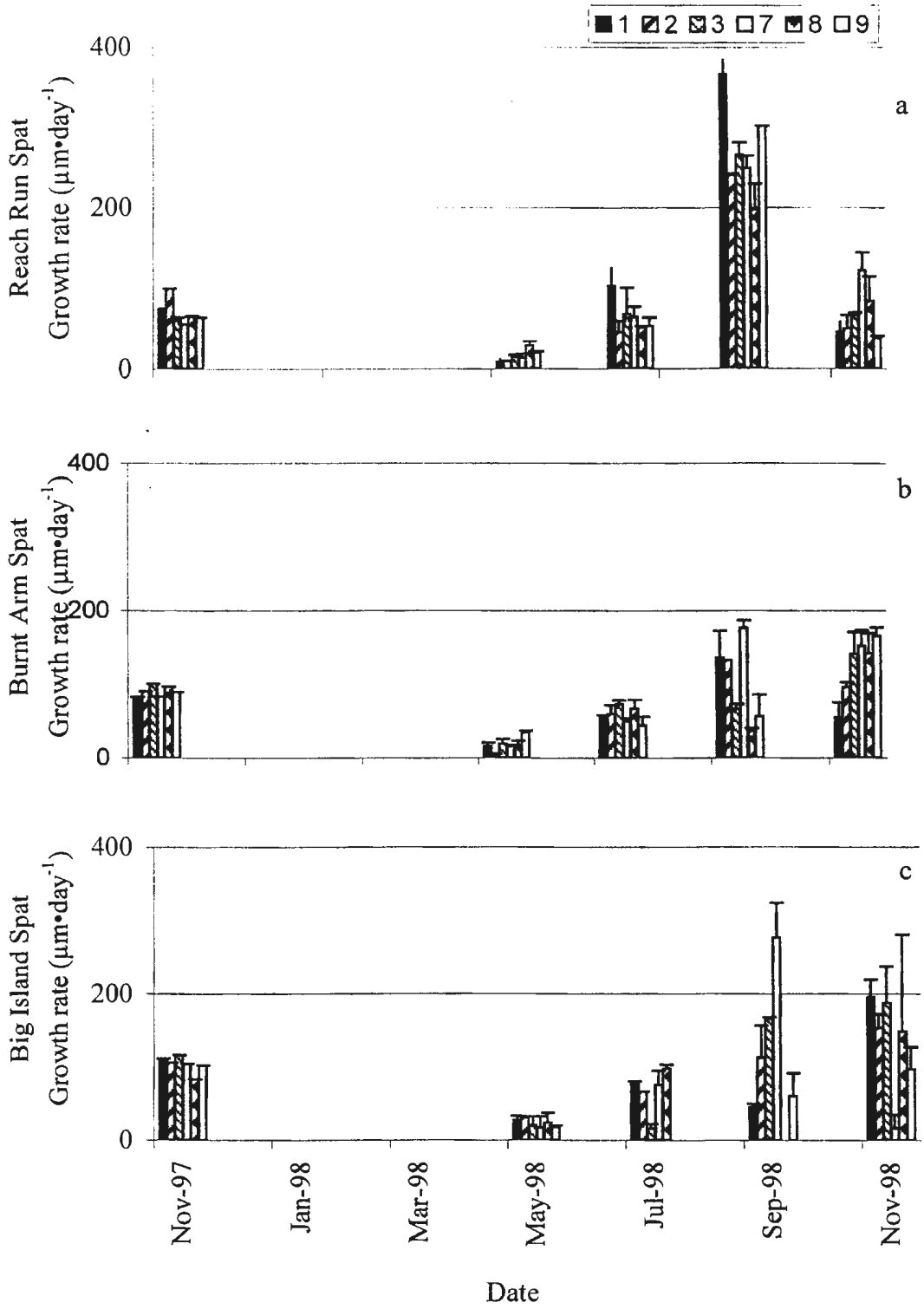

Figure 11.3. Average growth rate ($\mu m \cdot d^{-1}$) per station for Reach Run spat (a), Burnt Arm spat (b) and Big Island spat (c), transplanted to Big Island (n= 100 mussels, error bars= standard error).

Island seed sources were not significantly different from one another (Tukey HSD, p= 0.051 Figure 11). Over the course of the study, the highest growth rates occurred between July and September while the lowest growth rates were found following winter in May (Tukey HSD, $p < 0.05$ for each, Figure 11).

Analysis of each site individually gave differing results. At Burnt Arm growth rates did not vary by source or station (ANOVAs, F= 0.8, p= 0.455, F= 1.1, p= 0.380, Figure 11.1). In Reach Run, growth rates were significantly different among sources but not stations (ANOVAs, F= 16.5, $p < 0.001$, F= 2.1, p= 0.69, Figure 11.2). The Reach Run source performed the best at Reach Run followed by Big Island (Tukey HSD, p= 0.005, Figure 11.2) and Burnt Arm (Tukey HSD, $p < 0.001$ all cases, Figure 11.2). Growth rates at Big Island were significantly different for both source and station (Figure 11.3, ANOVAs, F= 5.4, p= 0.006, F= 2.8, $p < 0.020$). Again, the Reach Run source out performed the other two. However, it was not significantly higher than the Big Island source (Tukey HSD, p= 0.261, Figure 11.3). The station variation was due to higher rates at the back of the farm (Tukey HSD $p < 0.05$ for each, Figure 11.3).

3.4.2 Biomass

Biomass (sock weight) of mussels within the experiment correlated positively with density, chlorophyll-*a*, salinity, dissolved oxygen and food flux (Table 8). There was a significant negative correlation between biomass and condition index (Table 8).

Biomass measurements varied by site, source, station and date (ANOVAs, F= 9.8, 125.0, 4.3, 761.0, $p < 0.001$ all cases, Figure 12.1). Burnt Arm biomass was significantly

Table 8. Results of mussel growth correlations with environmental data, biomass (kg), density (number of animals•30 cm^{-1}), condition index (CI), (growth rate, $g•d^{-1}$), temperature (^{o}C), salinity (ppt), dissolved oxygen (DO, $mg•l^{-1}$), current speed ($cm•s^{-1}$, dissolution), food flux (FF, chlorophyll-*a*• relative current speed). N= 432 for all.

		Density	CI	$g•d^{-1}$	Chla	Temp	ppt	DO	$cm•s^{-1}$	FF
Biomass	Corr	.322	-.276	-.094	.320	.017	.280	.121	.040	.246
	Sig.	< 0.001	< 0.001	.052	< 0.001	.721	< 0.001	.012	.406	< 0.001
Density	Corr		-.180	-.090	.381	.212	-.181	-.058	.028	.312
	Sig.	.	< 0.001	.060	< 0.001	< 0.001	< 0.001	.231	.560	< 0.001
CI	Corr			.127	-.397	-.751	-.067	-.003	.158	-.134
	Sig.		.	.008	< 0.001	< 0.001	.162	.954	.001	.005
$g•d^{-1}$	Corr				-.087	-.172	.084	.104	-.061	-.073
	Sig.			.	.072	< 0.001	.082	.030	.209	.128
Chla	Corr					.327	-.356	-.348	.063	.656
	Sig.				.	< 0.001	< 0.001	< 0.001	.193	< 0.001
Temp	Corr						-.350	-.159	-.316	.021
	Sig.						< 0.001	.001	< 0.001	.670
ppt	Corr							.534	-.173	-.335
	Sig.						.	< 0.001	< 0.001	< 0.001
DO	Corr								-.181	-.357
	Sig.							.	< 0.001	< 0.001
$cm•s^{-1}$	Corr									.662
	Sig.								.	< 0.001

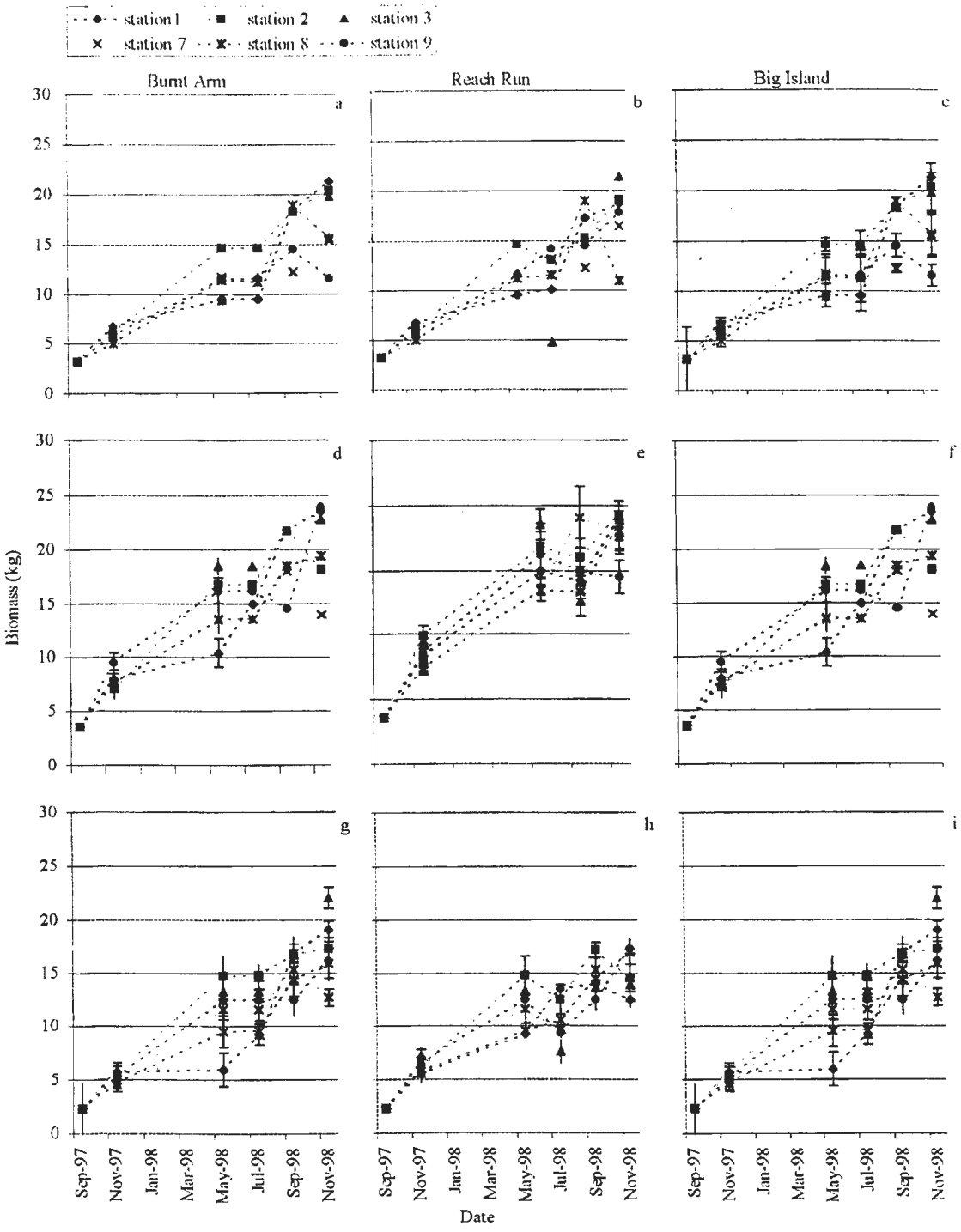

Figure 12.1: Summary of increasing biomass by sock weight (kg) of Reach Run mussels (a-c); Burnt Arm mussels (d-f); Big Island mussels (g-i) transplanted to Burnt Arm (column 1), Reach Run (column 2) and Big Island (column 3), respectively (n= 2, error bars= standard error).

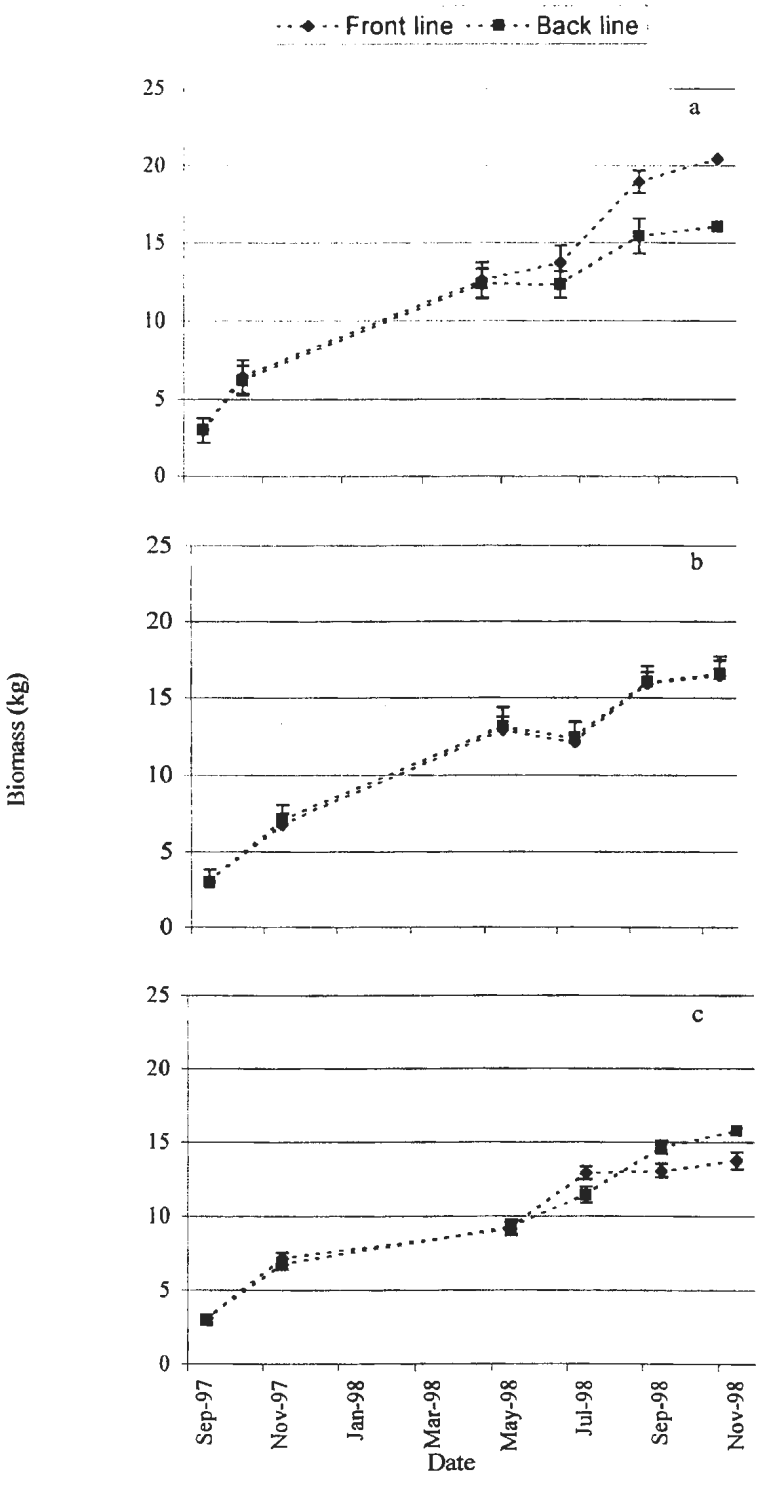

Figure 12.2. Summary of yield of all mussels grown at a) Burnt Arm, b) Reach Run and c) Big Island on the front and back longline of the experimental area (error bars= standard error, n=18).

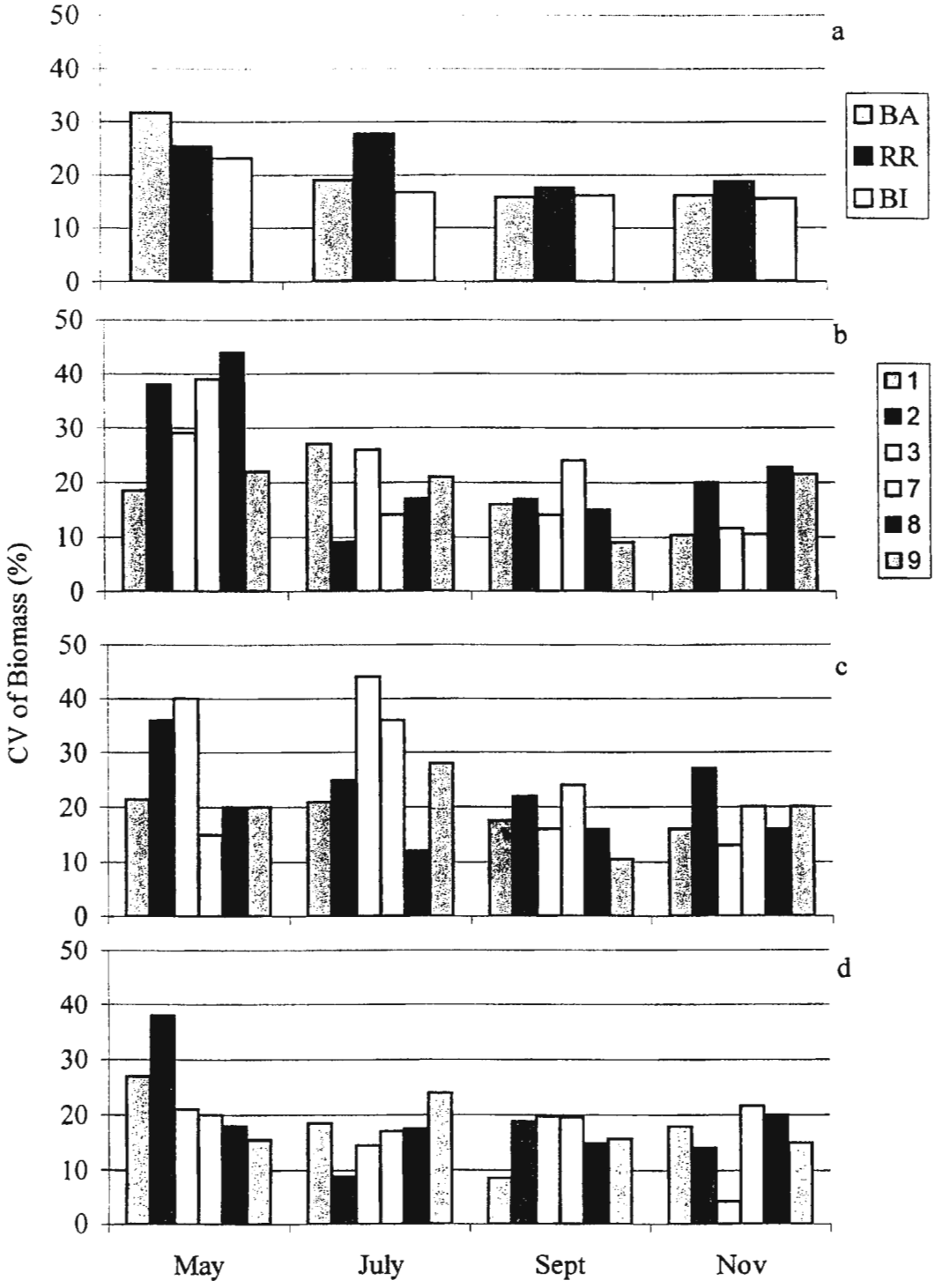

Figure 13. Coefficient of variation (CV= standard deviation•mean^{-1}) of mussel biomass at a) all three sites, at sample stations at b) Burnt Arm, c) Reach Run, and d) Big Island.

higher than the Big Island site (Tukey HSD, $p< 0.001$, Figure 12.1). Burnt Arm biomass was also higher than Reach Run biomass; however the difference was not significant (Tukey HSD, $p= 0.780$, Figure 12.1). Seed source analysis showed that the animals originating from Burnt Arm had the highest biomass (Tukey HSD, $p< 0.001$, Figure 12.1) followed by Reach Run and Big Island, which were not significantly different from each other (Tukey HSD, $p= 0.573$, Figure 12.1).

Analyzing the coefficient of variation (CV= standard deviation •mean sock weight^{-1}) of biomass values, variation ranged from 34% at Burnt Arm in May to 18% in Big Island in September (Figure 13), the differences amongst sites however were not significant (ANOVA, $F= 0.731$, $p= 0.736$). Coefficient of variation decreased over time. In May there was a difference of 12% CV between Burnt Arm and Big Island (Figure 13). At the end of the experiment, the difference in CV between Burnt Arm and Big Island was only 4%. Within each site, differences occurred in the coefficient of variance results; however, these statistics were not significant in Burnt Arm, Reach Run or Big Island, respectively (ANOVAs, $F= 0.230$, $p= 0.994$, $F= 1.376$, $p= 0.280$, $F= 0.596$, $p= 0.704$). Coefficient of variation averaged 23.8% for seed originating from Reach Run, while seed from Burnt Arm and Big Island averaged 16.0 and 15.7, respectively (Figure 13.1).

Individual site analysis indicated that Burnt Arm biomass differed significantly by seed, station and date (Figure 13.1, ANOVAs, $F= 24.1, 10.8, 119.6$, $p< 0.001$ all cases, Figure 12.1). Animals originating from Burnt Arm had a higher biomass than the Big Island mussels (Tukey HSD, $p= 0.014$, Figure 12) and the Reach Run mussels (Tukey

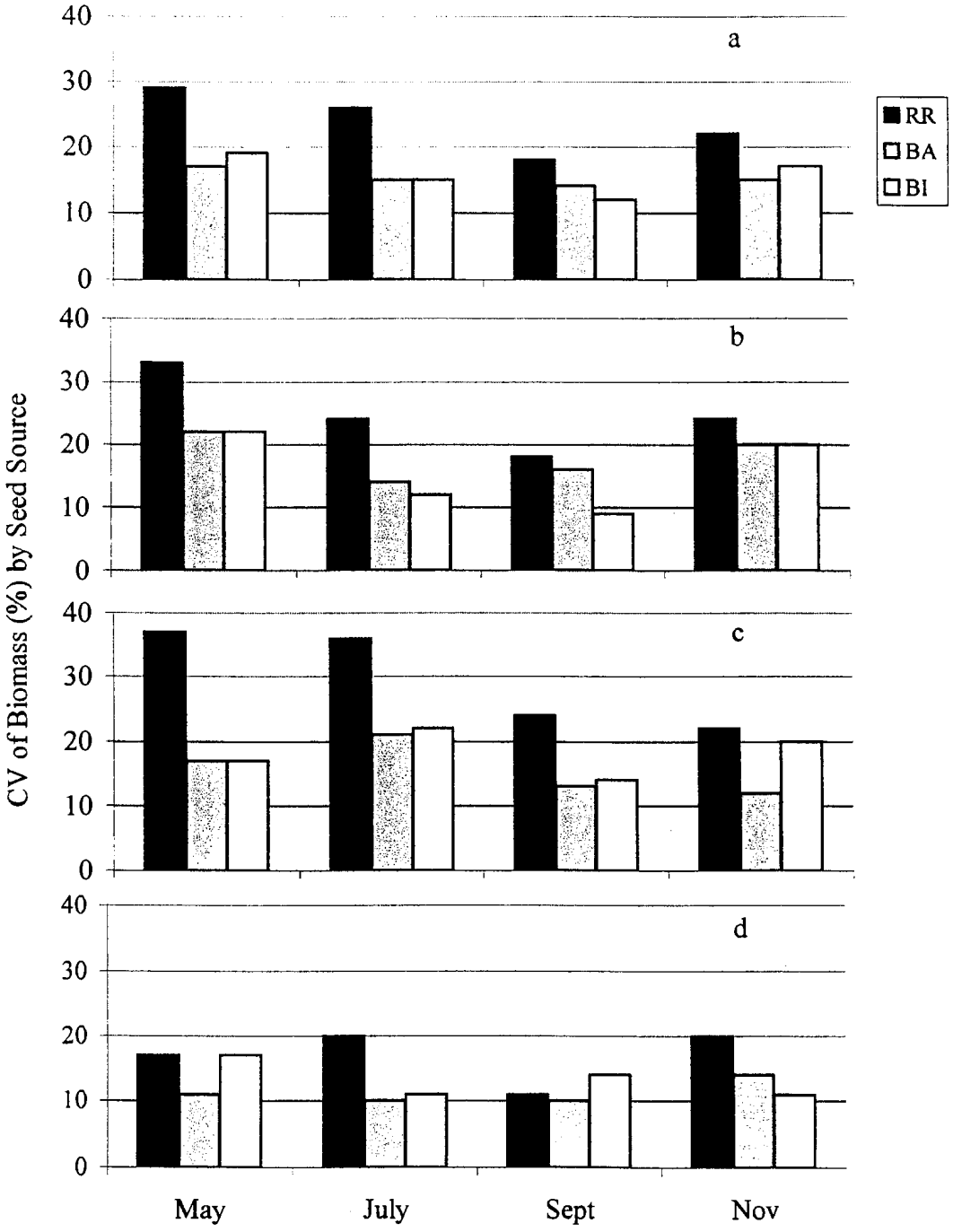

Figure 13.1. Coefficient of variation (CV= standard deviation•mean^{-1}) of mussel biomass by seed source at a) all three sites, at sample stations at b) Burnt Arm, c) Reach Run, and d) Big Island.

HSD, $p < 0.001$, Figure 12.1) at this site. Increases in biomass in Burnt Arm were significantly higher at stations at the front of the farm (Tukey HSD, $p < 0.05$, Figure 12.2). A separate analysis comparing the front experimental line to the back experimental line of Burnt Arm (ANOVA, $F = 36.5$ $p < 0.001$, Figure 12.2) indicated a significant line factor.

At Reach Run, biomass varied significantly by source and date (ANOVAs, $F = 21.4, 75.1$, $p < 0.001$ for each, Figure 12.1) but not station (ANOVA, $F = 1.4$, $p = 0.250$, Figure 12.1). At this site, animals originating from Burnt Arm performed better than animals from Reach Run and Big Island (Tukey HSD, $p < 0.001$ for each, Figure 12.1). Biomass of mussels at the Big Island site differed significantly by source and date (ANOVAs, $F = 70.0, 101.8$, $p < 0.001$ for each, Figure 12.1) but not station (ANOVA, $F = 1.3$, $p = 0.256$, Figure 12.1). Although individual stations were not significantly different at the Big Island site, a separate analysis comparing the front experimental line to the back experimental line of Big Island (ANOVA, $F = 4.8$ $p = 0.030$, Figure 12.2) showed a significant line factor.

Biomass increases measured in g $\bullet d^{-1}$ of sock weight varied significantly by date, source, site (ANOVAs, $F = 26.6, 17.1, 29.9$, $p < 0.001$ all cases, Figure 14) and experimental line (ANOVA, $F = 5.6$, $p = 0.019$, Figure 14). Biomass increases correlated positively with condition index and dissolved oxygen, while correlating negatively with temperature (Table 8). The Burnt Arm site had a higher biomass increases per day than Big Island (Tukey HSD, $p < 0.001$, Figure 14) but not Reach Run (Tukey HSD, $p = 0.780$, Figure 14). The animals originating from Burnt Arm had significantly higher biomass

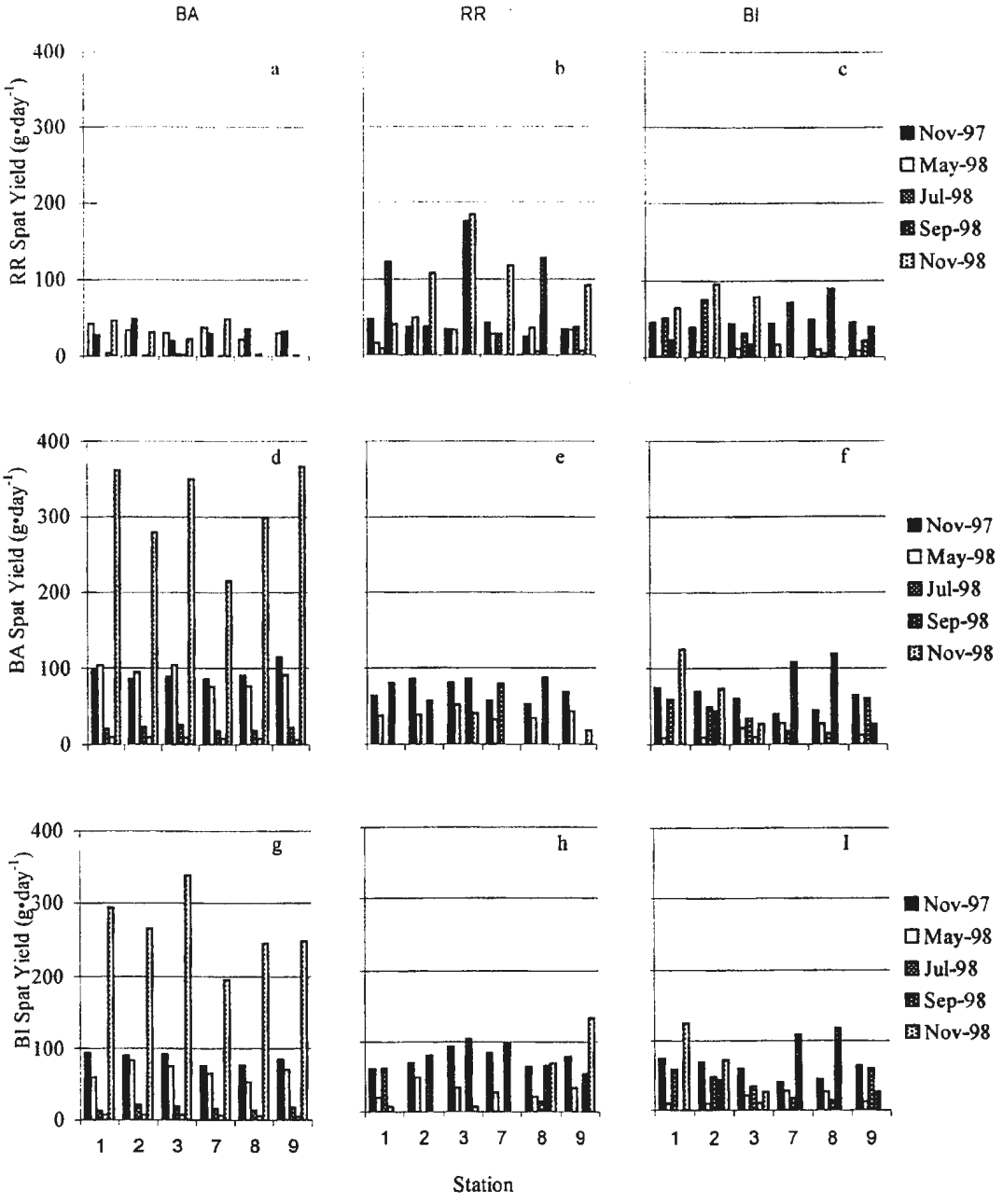

Figure 14. Daily increases of biomass ($g \cdot d^{-1}$) of Reach Run mussels (a-c), Burnt Arm mussels (d-f), Big Island mussels (g-i) transplanted to Burnt Arm (column 1), Reach Run (column 2) and Big Island (column 3), respectively.

increases than animals from Reach Run (Tukey HSD, $p < 0.001$, Figure 14) but not higher than animals from Big Island (Tukey HSD, $p = 0.573$, Figure 14).

Analyzing each site individually indicated significant differences in biomass increases at the Burnt Arm site for date, source (ANOVAs, $F = 217.9$, 143.9, $p < 0.001$ for each, Figure 14) and experimental longline, ($F = 8.9$, $p = 0.004$, Figure 14). At this site, the Burnt Arm source out-performed the other two in daily biomass increases (Tukey HSD, $p < 0.001$ for each, Figure 14). The Reach Run site varied only by date (ANOVA, $F = 6.5$, $p < 0.001$, Figure 14). The Big Island site varied by date (ANOVA $F = 6.5$, $p < 0.001$, Figure 14) and experimental line (ANOVA $F = 5.3$, $p < 0.025$, Figure 14) due to the higher increases on the back line (Figure 14).

3.4.2.1 Model

A model was developed using the biomass data in this study. We used a stepwise regression including, site, seed source, station, date, temperature, salinity, chlorophyll-*a*, current speed (by dissolution) and seston flux. The best equation to predict biomass included only date, site, temperature, salinity, and seston flux (by dissolution) (R Square= 0.537, n= 432):

Biomass= 4.135+0.161•(date)+0.186•(site)+0.37•(temperature)+0.0142•(salinity)+ 0.012• (seston flux)

The date variable contributed the most, explaining 48.75% of the variance followed by site at 2.67%, temperature at 1.22%, salinity at 0.56% and lastly, seston flux at 0.53%.

3.4.3 Condition Index

The condition index of all animals measured in the experiment ranged from 86 to 292. This index varied by site and date (ANOVAs, $F= 86.4$, 1651.2, $p< 0.001$ for each, Figure 15) but not source (ANOVA, $F= 2.745$, $p= 0.64$, Figure 15). Condition index of animals within the experiment correlated negatively with biomass, density, chlorophyll-*a*, temperature, salinity, and food flux while correlating positively with relative current speed (Table 8). Over all, the Big Island site had the highest condition indices followed by Burnt Arm and Reach Run, respectively (Tukey HSD, $p< 0.001$ for all cases, Figure 15).

Condition index at the Burnt Arm site ranged from 133.9 to 292. At this site, condition differed significantly by date, source and station (ANOVAs, $F= 337.3$, $p< 0.001$, $F= 3.6$, $p< 0.029$, $F= 16.5$, $p< 0.001$, Figure 15). Condition peaked in May at all sites and was lowest in July following spawning (Figure 15). In Burnt Arm, the source originating from Big Island had the highest average condition indices, averaging 4.0 indices points higher than the Burnt Arm source (Tukey HSD $p= 0.197$, Figure 15) and 6.16 points higher than Reach Run (Tukey HSD $p= 0.024$, Figure 15). Condition indices at stations the front of Burnt Arm averaged 14.9 points higher than stations at the back of the farm (Tukey HSD $p< 0.05$ all cases, Figure 15).

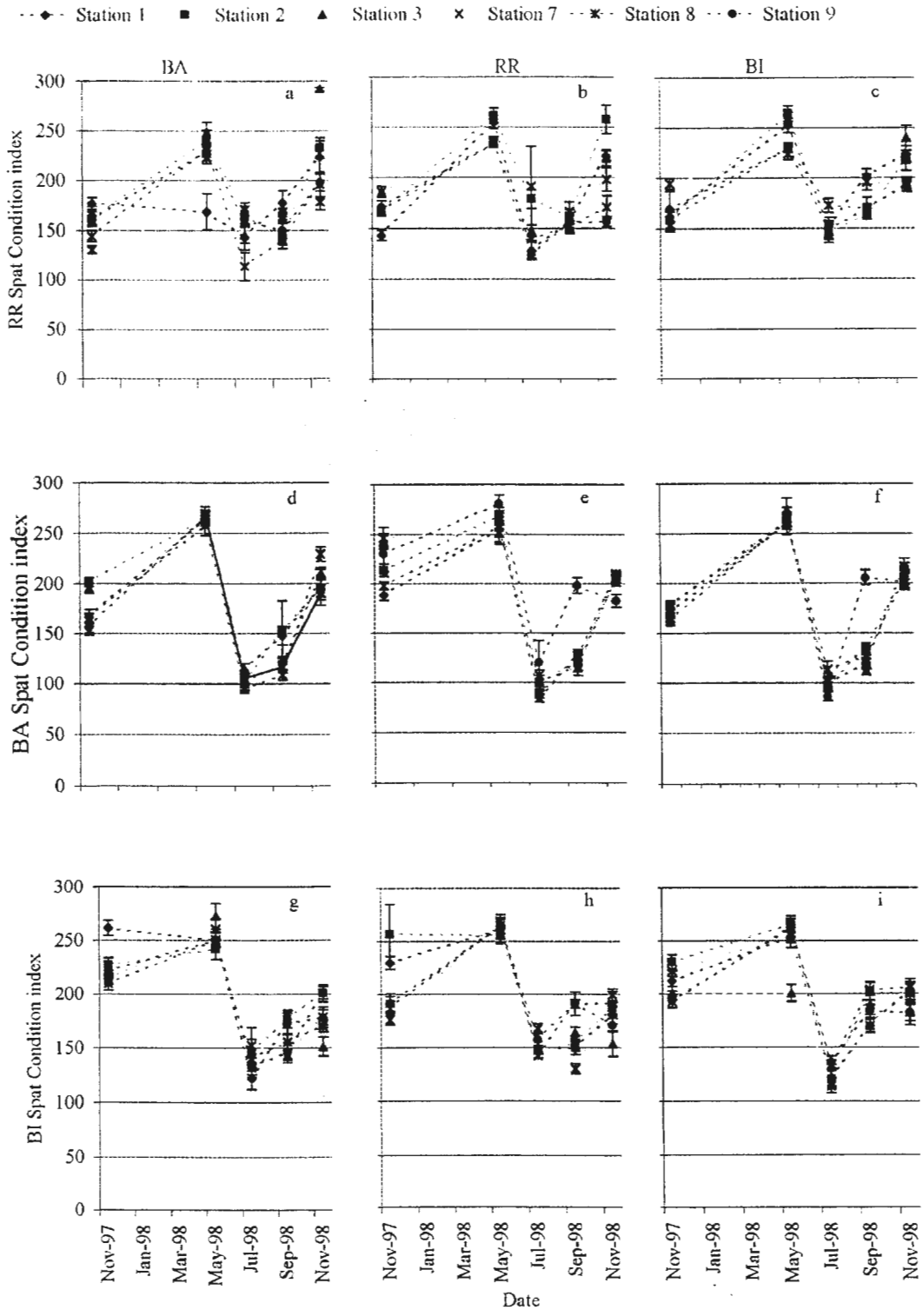

Figure 15. Condition indices of Reach Run mussels (a-c), Burnt Arm mussels (d-f), Big Island mussels (g-i) transplanted to Burnt Arm (column 1), Reach Run (column 2) and Big Island (column 3), respectively (error bars= standard error, n=30).

The Reach Run site condition indices ranged from 86.0 to 280.0. The values were significant different by date and source (ANOVAs, $F= 1216.2, 6.7, p< 0.001$ for each, Figure 15) but not station (ANOVA, $F= 1.1, p= 0.355$ Figure 15). In Reach Run, the Burnt Arm source had the highest average condition indices, averaging 5.8 points over the Reach Run source (Tukey HSD, $p= 0.014$, Figure 15) and 7.1 points over the Burnt Arm source (Tukey HSD, $p= 0.002$, Figure 15). Condition indices in the Big Island site ranged from 114.7 to 272.0. These values varied by date and station (ANOVAs, $F= 572.2, 4.43, p< 0.001$ for each, Figure 15) but not source (ANOVA, $F= 1.213, p< 0.298$, Figure 15). The station differences involved station 2 at the front of the farm, which had a higher condition index than stations 3, 7 and 9 (Tukey HSD, $p< 0.05$ for all cases, Figure 15).

3.4.4 Density

3.4.4.1 Secondary Set

A notable observation in our experiment was the presence of a secondary set, which may have resulted from larval settlement or small drifting juveniles (Appendix 2). It was assumed that the set occurred within the two weeks between placing the mussels in socks and transfer to other sites as all socks transplanted from Reach Run increased in density. As well, socks from other sites, which were transferred to the Reach Run, received a later set (Appendix 2.4 and 2.6). To distinguish between experimental mussels and newly settled mussels, histograms were produced and the cohorts were separated for growth analysis (Appendix 2).

Initial density values ranged from 201 animals•30cm^{-1} to 220 animals•30cm^{-1} (Figure 16). During the study these values differed significantly by source, station, site and month (ANOVAs, F= 56.828, 6.907, 48.399, 69.629, p< 0.001, Figure 16). Density of animals in the study correlated positively with biomass, chlorophyll-*a*, temperature, salinity and food flux while, correlating negatively with condition index (Table 8). Overall the Reach Run site had the highest densities averaging 21.5 and 56.1 animals per foot more than Burnt Arm and Big Island, respectively (Bonferroni, p< 0.05 each case, Appendix 4.32). As well, the Reach Run source had the highest density overall averaging 37.7 and 27.8 animals per foot higher than Burnt Arm and Big Island (Bonferroni, p< 0.05, Figure 16). Investigating each site individually had the same results as the overall analysis. Each site varied by source, station and month (ANOVAs, F= 18.2, 6.1, 34.9, p< 0.001 all cases, Figure 16). The Reach Run source had the highest densities at all sites (Bonferroni, p< 0.05 each case, Figure 16). Within site density variations existed in Burnt Arm and Reach Run; socks at the front of these farms have higher densities than those at the back (Bonferroni, p< 0.05 each case, Figure 16).

3.4.5 Survival

The final survival of the animals ranged from 86.1 % to 96.1 %. Survival differed significantly by site, source, month (ANOVAs, F= 19.8, 51.9, 549.3, p< 0.001 all cases, Figure 17) and station (Figure 22, ANOVA, F= 2.9, p< 0.014, Figure 17). Reach Run had the highest survival rate (Tukey HSD, p< 0.001 for each, Figure 17), followed by Burnt Arm and Big Island (Tukey HSD, p= 0.456, Figure 17). Individually, survival at the sites

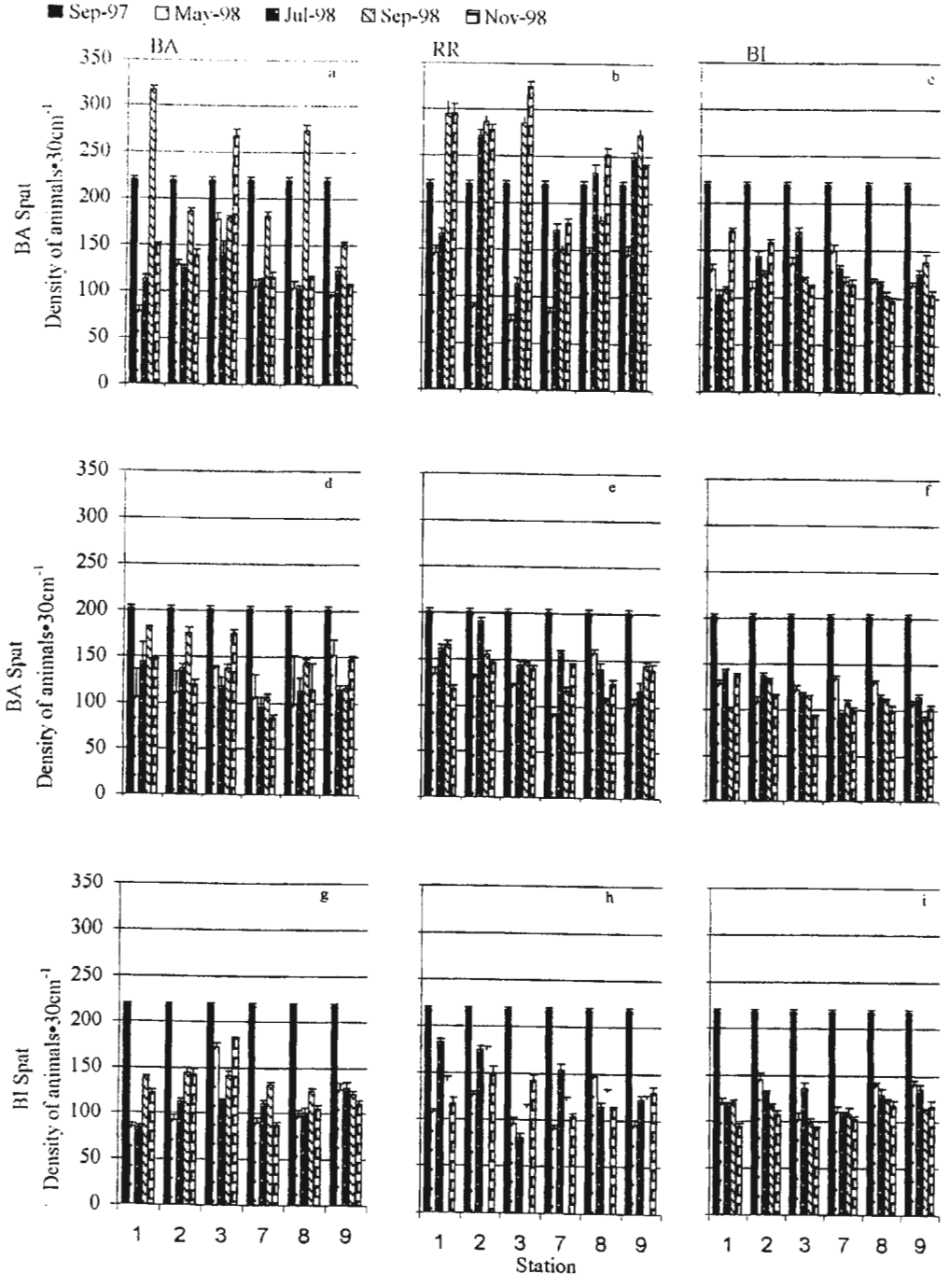

Figure 16. Sock densities of mussels originating from Reach Run (a-c), Burnt Arm (d-f), Big Island (g-i) transplanted to Burnt Arm (column 1), Reach Run (column 2) and Big Island (column 3), respectively (density=mussels•30 cm^{-1} n=2, error bars= standard error).

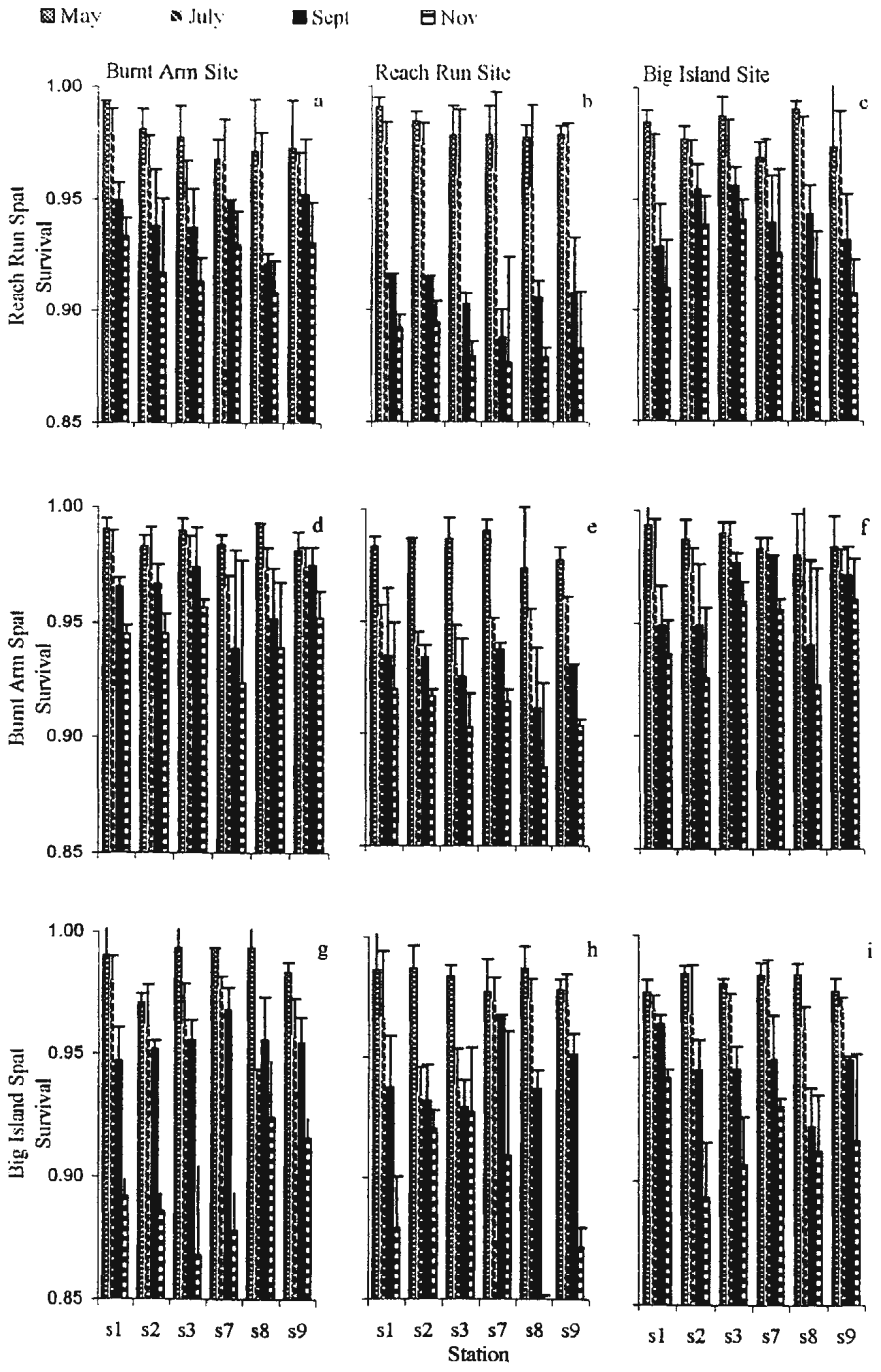

Figure 17. Survival (no. alive / no. at start) of mussels originating from Reach Run (a-c), Burnt Arm (d-f), Big Island (g-i) transplanted to Burnt Arm (column 1), Reach Run (column 2) and Big Island (column 3), respectively, (n= 2, error bars = standard error).

varied by source and date (ANOVAs, Burnt Arm $F= 18.9, 209.6$ $p< 0.001$ for each; Reach Run, $F= 30.9, 101.0$ $p< 0.001$; Big Island, $F= 5.7$, $p= 0.004$, $F= 296.1$, $p< 0.001$, Figure 17). In Burnt Arm and Big Island, the Big Island source had the highest survival rate, while at the Reach Run site, the Reach Run source had the highest survival rate (Tukey HSD, $p< 0.05$ for each, Figure 17). The seed source with the lowest survival was from Burnt Arm (Tukey HSD, $p< 0.05$ for each, Figure 17). This source was composed of 90% *M. edulis* and 10% *M. trossulus* at the time of placement in the socks, while the other sources were composed of 100% *M. edulis* (Innes et al., 1999). Only the Big Island site had variation in the survival within the farm, which indicated slight differences in survival between stations 7 and 8 (Tukey HSD, $p< 0.019$, Figure 17). Seasonally, the mortality increased greatly in all groups from July to September, following spawning and again from September to November (Figure 17).

4.0 DISCUSSION

4.1 Environmental Data

4.1.1 Temperature

Due to the broad annual range of temperature at these three sites, -1.1°C to 20.2°C, mussels were exposed to their upper and lower performance limits. However, studies have shown that filtration and growth are not limited at temperatures as low as –1°C provided there is sufficient food available (Loo, 1992). Hatcher et al. (1997) found that in areas covered by winter ice, as was the case in this study, mussels suspended in longline culture respired less due to inadequate food rather than low temperatures. Temperatures of 20°C and above as found in Reach Run, are an exception along the coast of Newfoundland. Previous work on this site found the maximum temperature to be 13°C (Dabinett and Clemens, 1997, Clemens et al., 1999).

Given time to acclimatise, Widdows (1976) showed that the processes of feeding and respiration in *Mytilus edulis* could function independently of the temperature within a fluctuating range of 11 to 19°C. However, growth in *M. edulis* has been shown to decrease considerably at sites where water temperatures exceeded 20°C (Incze et al., 1980). This could have been a factor in the lower than expected growth rates in Reach Run as water temperature peaked beyond this upper limit for two weeks in the month of August. However, variations in degree-days of exposure to elevated temperatures did not influence mortality as Reach Run had the highest survival rate of the three sites. This supports Incze et al. (1980) who found sites with temperatures elevated above 20°C to

have decreased growth but not increased mortality. The seed source originating from Reach Run performed the best under the wide range of thermal conditions in Reach Run. Previous studies examining seed sources have shown that some stocks which have not had the "previous thermal history" are less able to acclimatise their metabolic rates to high habitat temperatures (Bayne et al., 1975, Thompson and Newell, 1984, Tremblay et al., 1998).

All three sites had a slight thermal stratification throughout the spring and early summer. This thermocline which isolated the mussels from the nutrient rich waters below, likely caused a depletion of nutrients and a reduction in phytoplankton biomass and as a result a reduction in growth and biomass of the mussels. Over the course of the summer, the thermocline slowly sank deeper until the water column became mixed in September. At this time, there were high increases in growth as a result of the increase in phytoplankton biomass, which in turn was due to an influx of nutrients following the breakdown of stratification. Previous studies on these sites by Dabinett and Clemens (1997) found similar patterns and are typical for inshore, protected areas along the Newfoundland coast.

4.1.2 Salinity

Large variations in salinity can be lethal to *M. edulis*. However, if given the opportunity to acclimatise *M. edulis* can live at salinities as low as 7 ppt (Kautsky et al., 1990). Salinities in the vicinity of mussels, ranged from 24.3 ppt at Reach Run to a high of 33.7 ppt near Big Island and little daily fluctuations were observed. Typically the

salinity remained around 28 ppt. However, on February 15, 1998, salinity dropped to a low of 24.3 ppt in Reach Run. This decline may have been the result of heavy precipitation. 15 mm on January 25 and 9 mm February 3, 1998. There were no samples taken at the other two sites at this time. The next sample date was April 5. At this time the salinity measured 31.5 ppt in Burnt Arm, 30.9 ppt in Reach Run and 33.7 ppt in Big Island. This rise in salinity was likely due to the lack of precipitation in the month of March and beginning of April. Within the range of salinity observed, it is concluded that salinity had no negative impact on mussel performance (Mallet and Myrand, 1995).

4.1.3 Dissolved Oxygen

Throughout the study the dissolved oxygen concentrations at 3.5 m depth varied by site, location with each site and season. The higher D.O. at Burnt Arm followed Big Island and Reach could be explained by average site temperature. Reach Run, had the highest average site temperature and therefore had the lowest dissolved oxygen concentration, followed by Big Island and finally Burnt Arm, which had lower average temperatures. The dissolved oxygen concentrations did however, follow a similar pattern. Likewise, the concentration varied annually, ranging from 6.8 $mg \cdot L^{-1}$ to 14.0 $mg \cdot L^{-1}$ or 70 to 100% saturation. Solely, 70% saturation may not affect mussel growth however, when combined with temperatures above 20°C, it is possible the mussels were stressed as at 20°C, the metabolism of the mussels is greatly enhanced requiring more O_2 than at lower temperatures (Widdows, 1976). It was fortunate that the salinity was relatively stable at this time as salinity has also been found to influence the clearance rate and

oxygen consumption (Frenette et al., 2002). The decline of D.O. in the spring and rise in autumn occurred in response to the annual temperature variations.

Spatially, the control station at Big Island, at which there were no mussels, had a significantly higher concentration of D.O. than several stations at this site. This was the case as well for the Reach Run site in which the layout is parallel to the flow. This was possibly due to the respiration of the suspended mussels near the experimental stations. It is unlikely that these variations caused any decrease in mussel performance, as percent saturation was still relatively high. The vertical profiles from the control station sampling in late spring and early summer indicated higher concentrations of dissolved oxygen at depths below the mussel socks, which was unlikely due to depletion by the mussels as the control station showed a similar pattern and did not contain mussels. It was more likely due to the cooler waters present at lower depths with higher O_2 content as the D.O. gradient between the surface and deeper waters becomes nonexistent as the temperature in the water column becomes homogenous.

4.1.4 Chlorophyll-a and Particulate Organic Matter

4.1.4.1 Temporal Variations

Temporal variations in the concentration and composition of seston available to filtering bivalves can be detailed by regular monitoring (Navarro and Thompson, 1995). Unfortunately, our CTD data were sporadic and as a result data for the spring bloom were not available. However, the three study sites had similar trends of chlorophyll-*a* concentration. The trends found in this study were similar to previous work by Thompson

(1984), Dabinett and Clemens (1997) and Clemens et al., (1999). However, for the months of September and October the chlorophyll-*a* levels were exceptionally high in Reach Run as chlorophyll-*a* values reached levels of 19.75 $\mu g \cdot L^{-1}$. An autumn bloom at this time in Notre Dame Bay is not unusual (Dabinett and Clemens, 1997, Clemens et al., 1999). However, the level attained was extraordinary as previous autumn blooms had been reported at 4 to 5 $\mu g \cdot L^{-1}$(Dabinett and Clemens, 1997). This was likely the result of the abnormally warm water temperatures that season. As well, the winds in Notre Dame Bay may have contributed to a sizeable autumn bloom. In the months of August and September leading into the bloom, winds had been fairly moderate averaging 20.8 $km \cdot hr^{-1}$. However, beginning in the early morning of September 5, winds averaged 53.54 $km \cdot hr^{-1}$ and continued all day September 6 at 77.58 $km \cdot hr^{-1}$. The wind event may have mixed the water column and resuspension of nutrient rich sediments, resulting in the final disappearance of the sinking thermocline. This vertical mixing likely created an influx of nutrients to which the phytoplankton responded shortly after the wind event. Similar wind induced phytoplankton blooms have been observed in British Columbia reaching a maximum of 63 $mg \cdot m^{-2}$ chlorophyll-*a* (Yin et al., 1997) and the South Atlantic Bight reaching a maximum of 13 $\mu g \cdot L^{-1}$ chlorophyll-*a* (Verity et al., 1998). Run-off was not a contributing factor to this bloom, as precipitation levels were low throughout the months of August and September, 1998.

Seasonal growth in mussels has been attributed to the seasonal proportion of particulate organic matter and total particulate matter (Bayne and Worrall, 1980, Bayne et al., 1987, Page and Ricard, 1990) until an asymptote is reached (MacDonald et al., 1998).

Percent POM peaked in September, averaging approximately 60, 38 and 42% organic matter in Burnt Arm, Reach Run and Big Island, respectively. This was due to the presence of the phytoplankton bloom as indicated by chlorophyll-*a* levels. Mussels have pulse-like growth, alternating between growth and de-growth phases with fluctuations in the POM: TPM (Sarà et al., 1998). As a result, it would be expected that a large increase in growth following the autumn bloom and subsequent rise in POM: TPM would occur and this was observed at all 3 sites in terms of shell growth, sock biomass and condition indices. The total POM in the present study ranged from 0.2 $mg \cdot L^{-1}$ to 8.65 $mg \cdot L^{-1}$ and was well within normal range of POM values found in temperate waters (Dabinett and Clemens, 1993).

In addition to annual and seasonal variations, relatively large variations in seston flux can occur over a tidal period (Fegley et al., 1992, Barillé et al., 1997, Smaal and Haas, 1997, Wilson-Ormond et al., 1997, Roegner, 1998). Our data had significant variations in the chlorophyll-*a* concentration, as well as several correlations between tide height and chlorophyll-*a* concentration. This phenomenon was most apparent in Reach Run where in the months of May, June and August, chlorophyll-*a* increased with increasing tidal height. This finding agrees with Fegley et al. (1992) where seston concentrations were found to be lower during the ebb tide than during the flood tide. In September and October, during the bloom, chlorophyll-*a* concentration was diluted on the flood tide. This may be evidence that the bloom was localized to the warm shallow waters of the Reach Run. This may explain some of the variation between the chlorophyll-*a* concentrations at each site. The present study confirms earlier findings that

environmental parameters vary on scales from hours to months and must be considered when attempting to explain production performance in a culture setting.

4.1.4.2 Spatial Variations

The quantity of chlorophyll-*a* varied greatly among sites mainly due to the considerably higher concentrations found in Reach Run. Chlorophyll-*a* values were greater at this site during the entire study period. The autumn bloom led to a maximum concentration of 19.75 $\mu g \cdot L^{-1}$ in Reach Run, which was over three times that of the other sites. Such a bloom has not been previously reported off Newfoundland. It was likely the result of favorable conditions such as unusually warm water temperatures and a wind event, which stirred up nutrients from the shallow depths.

On a smaller scale many studies have reported within-site depletion of available food by filter feeding bivalves in wild populations (Smaal et al., 1986, Peterson and Black, 1987, Nakaoka, 1992), bottom culture (Newell, 1990, Muschenheim and Newell, 1992), raft culture (Navarro et al., 1991, Fuentes et al., 1994, Blanco et al., 1995, Pérez Camacho et al., 1995, Mueller, 1996, Navarro et al., 1996, Heasman et al., 1998, Karayuecel and Karayuecel, 2000) and longline culture (Rodhouse et al., 1985). This within-site depletion can lead to localized food limited growth. Food limitation was not an issue within the present study as no consistent patterns of depletion existed among stations at any site. Thus it would initially appear that from this information that carrying capacity had not been exceeded at any of the study sites or locations within-sites as the

food supply, as measured by chlorophyll-*a* and POM, was not depleted as the water currents travel from one end of the farm to the other.

The percentage of particulate organic matter varied significantly by site and location within each site. Burnt Arm had the highest average percentage of POM:TPM at 38.6%, while Reach Run, which had the highest chlorophyll-*a* concentration had the lowest average POM:TPM at 29.8%. This would suggest large concentrations of inorganic matter in the Reach Run considering the extremely high concentrations of chlorophyll-*a*. Bivalves select organic particles and reject inorganic ones independent of seston concentration, resulting in growth phases, which follow POM:TPM (Sarà et al., 1998). However, this selection by mussels diminishes as the organic content of the seston decreases (Bacon et al., 1998). From this, one could assume that feeding was more efficient at the Burnt Arm and Big Island sites as the mussels have to process less inorganic matter. This may explain why Reach Run which has extraordinarily higher seston flux rates did not produce extraordinary growth.

There were within-site variations of POM with particular stations having higher concentrations than others. However, there was no consistent pattern with respect to higher POM at stations on the front line versus stations on the back line of any site.

4.2 Current Speed and Seston Flux

As food limited growth occurs predominantly in high mussel density situations, this can be a serious concern for mussel farmers in bottom, raft or longlines culture. Studies have suggested that increases in flow rates compensate for either low seston

concentration or higher densities by replenishing available seston; that is, increased seston flux may support a higher biomass of mussels (Fréchette and Bourget, 1985b, Fréchette et al., 1989, Newell, 1990, Rheault and Rice, 1996). The effects of flow on bivalve mussels may not be clear until we fully understand the animal's ability to filter and ingest food particles under "natural conditions" (Manuel and Lobsiger, 1999). Reach Run, which had the highest average current speed of 3.695 cm $\cdot s^{-1}$, also had the greatest range extending from 0.785 to 8.735 cm $\cdot s^{-1}$. Thus it would be expected that this site with its previously mentioned high food levels and combined higher current speeds would support the highest production of the three sites. However, this was not the case. There may in fact have been periods where food levels were too high for mussels to ingest and digest and utilise (Newell et al., 2000).

Similarly, our plaster cylinder dissolution study indicated within-site differences in current speed. Burnt Arm for instance, had higher relative current speeds at the front of the farm as opposed to the back of the farm as ambient flow is diverged (Rodhouse et al., 1985). As chlorophyll-*a* levels did not vary among stations throughout this farm and we know that the flux rate was higher at the front and therefore would assume that the front of the farm would support higher biomass or faster growth than the back of the farm (Fréchette and Bourget, 1985b, Fréchette et al., 1989, Newell, 1990, Rheault and Rice, 1996). The present findings support this, as there was a 25-30% increase in biomass on the front line compared the rear line. Also according to the cylinder data, Big Island had higher relative current speeds at stations 8 and 9, which according to the locations of these stations, was expected, as this area is a narrow channel between the land and Big

Island itself. These stations as well would be expected to support higher biomass or faster growth, as was observed (Fréchette and Bourget, 1985b, Fréchette et al., 1989, Newell, 1990, Rheault and Rice, 1996).

4.3 Growth, Density and Survival

4.3.1 Shell Growth Rates (length •unit time^{-1})

Daily growth rates averaged 74.95 μm •day^{-1} or 2.33 mm •month^{-1}, slightly higher than that for mussels in a Nova Scotia site (Mallet and Carver, 1989). Variations in growth rate as determined by shell length have been attributed to site and season (Dickie et al., 1984, Mallet and Carver, 1989, 1993, Mallet et al. 1987, Sukhotin and Maximovich, 1994), source (Stirling and Okumus, 1994), chlorophyll-*a* (Page and Hubbard, 1987, Page and Ricard, 1990, Thorarinsdóttir, 1996), current speed and salinity (Dolmer, 1998) and seston flux (Pérez Camacho et al., 1995). In the present study, season and site influenced mussel shell length in keeping with previous studies

The suitability of shell length as an index of production, has often come into question, as it does not give evidence of tissue condition. Shell length on its own may provide misleading information, as it does not respond to food limitation, as does soft tissue (Fréchette and Bourget 1985b, Fuentes et al., 1994). Moreover, shell and tissue growth are generally uncoupled in mussels (Hilbish, 1986) and scallops (Penney and Mckenzie, 1996). In the present study, shell length did not show significant differences among the stations of Burnt Arm. However, our data indicated that biomass and condition were reduced at the back of the farm. Lewis and Cerrato (1997) in a study of

soft-shell clams concluded that shell growth is coupled to metabolic activity and is not a measure of somatic tissue production. Therefore, the present study's observation that the season and site factors account for the majority of the variability in growth rates according to length is reasonable as seasons and environment govern metabolic activity.

Mallet and Carver (1989) found seed source and seed source by season to be the largest contributors to variance in their reciprocal transplant experiment. However in the present study, species composition was quite similar, hence less likely to differ on this basis.

4.3.2 Biomass, Condition and Density

4.3.2.1 Site Effects

The variation in final biomass or sock weight is mainly due to season and source although site and station did play a significant role. Biomass was positively correlated with density, chlorophyll-*a*, salinity, dissolved oxygen and food flux, while there was a negative correlation between biomass and condition index. This negative correlation is likely due to the spawning event, which took place. Early in the experiment when biomass was low, condition index was increasing. Following the spawning event, condition plummeted while biomass did not. This is likely due to the fact that shell growth and soft tissue growth do not occur simultaneously (Hilbish, 1986, Borrero and Hilbish, 1988). Total experimental biomass was highest in Burnt Arm; however this result was not significantly higher than Reach Run. This was unexpected as Reach Run had considerably warmer temperatures, higher chlorophyll-*a* values, seston flux and as

well, higher current speeds. However, contributing factors to biomass increases over time ($g \cdot day^{-1}$), were very different as the ANOVA and regression model indicated. According to the regression model, date, site, temperature, salinity and seston flux were the best predictors of biomass increases. Daily biomass increases were positively correlated with condition index. Daily biomass increases were highest in Burnt Arm, however these increases were not significantly higher than the Reach Run site. These results were not predicted as Reach Run had what was thought to have significantly more favorable conditions. As well, condition index was at a maximum at the Big Island site, followed by Burnt Arm. Again, Reach Run results were not as expected given the higher flux values.

Burnt Arm and Reach Run which have higher flux values than Big Island, have higher biomass increases supporting our primary hypothesis being tested that higher seston flux will promote higher growth and production. Contradicting this of course is the fact that the Reach Run, which has higher flux than Burnt Arm, did not have the most rapid growth and production.

Upon closer examination of this site we find that although chlorophyll-*a* values were considerably higher, the ratio of POM:TPM was the lowest of all three sites. At its peak during the autumn bloom, the site averaged only 34.6% POM to TPM. This value coupled with a peak of chlorophyll-*a* of 19.75 $\mu g \cdot L^{-1}$ infers a great deal of inorganic matter. Throughout the year, the ratio of POM to TPM was only 29.8%. Part of the explanation for unexpected lower growth rates in Reach Run may lie in that there may be

periods when there is simply too much food for the mussels to use/ingest/digest (Newell et al.. 2000).

Bayne and Worrall (1980) stated that seasonal growth patterns are not a function of total particulate matter or particulate organic matter but their relative proportion. As organic matter becomes diluted by inorganic matter food becomes 'available with difficulty' for suspension feeders (Sarà et al., 1998). Recent field studies suggest that throughout short term periods of low POM:TPM, bivalves clear more water of particles as TPM increases, rejecting PIM as pseudofaeces. Selection efficiency improves retaining organic matter proportional to the clearance rate. As a result, nutrient intake remains balanced (Cranford, 1995, Hawkins et al., 1996). Our data however suggest that the POM:TPM ratio throughout the year in Reach Run was the lowest of all the sites. This is not to say that it was detrimentally low or that the mussels there were "food limited". Rather, mussels at the other sites were exposed to higher quality food and therefore had higher corresponding growth rates (g $\bullet day^{-1}$), biomass and condition.

Another possible explanation as to why biomass, growth rates (g $\bullet day^{-1}$) and condition may be lower in Reach Run was the density. Initially mussels were placed in socks in Reach Run at 201 mussels $\bullet 30\ cm^{-1}$. A secondary set occurred in Reach Run between the time of placement in the socks and transfer in October 1997. Initially the second set was undetected, as it was likely very small "pepper seed" (<1 mm in size). Length-frequency histograms indicated a rise in density in socks originating from Reach Run at each of the three sites after deployment. In September 1998, Reach Run received a subsequent set increasing the density of mussels in the experimental socks further. The

impact of density on growth has been well documented, indicating "edge effect" in beds (Wildish and Kristmanson, 1984, Okamura, 1986, Newell, 1990, O'Riordan et al., 1993, Svane and Ompi, 1993) and raft culture (Navarro et al., 1991, Fuentes et al., 1994, Blanco et al., 1995, Pérez Camacho et al., 1995, Mueller, 1996, Navarro et al., 1996, Heasman et al., 1998). This situation could be analogous to intra-specific competition in an individual sock. Therefore although animals may not be "food limited" in terms of the site or line, localized limitations may exist decreasing the overall sock biomass, growth and condition. This process has been described as "self thinning" and is well recognized in cultured mussel populations (Fréchette and Lefaivre, 1990).

The presence of this secondary set however was indicative of a site with favorable conditions, such as warm temperatures and high food levels, which support redevelopment of the gonads (Thorarinsdóttir, 1996). It is unknown whether the seed, which settled on the socks originated in Reach Run; however, the increased density may have contributed to the low condition indices of the mussels in the presence of abundant food.

4.3.2.2 Within-site Effects

Biomass and condition in Burnt Arm had a marked difference between stations at the front of the farm versus stations at the back of the farm. According to our model seston flux was a significant predictor of growth (partial correlation= 0.108). Although food levels do not diminish from the front to the back, flow was diverted around the farm; within a farm, flow aligns along its major axes and is reduced (Boyd and Heasman,

1998). The result of lower current speed is reduced flux, which in turn results in lower biomass and condition (Fréchette and Bourget, 1985b, Fréchette et al., 1989, Newell, 1990, Pérez Camacho et al., 1995, Rheault and Rice, 1996). This supports our hypothesis of higher flux areas yielding higher growth and production, and alternatively, lower flux yielding lower production.

Similarly the Big Island site had higher biomass on the back line of the farm in the location of higher current speeds due to the narrowing flow-through area between the land and Big Island. This combined with the higher chlorophyll-*a* at station 9 resulted in higher flux, and consequently higher biomass.

The Reach Run did not vary by location within the farm or source, a result quite likely prompted by the higher flux levels supporting our secondary hypothesis that sites with characteristically higher seston flux will demonstrate more uniform growth and production (Grant 1999). The layout of the farm, which is parallel to the current may also reduce variation in mussel growth and production by not impeding flow. Our coefficient of variance data support this hypothesis as the coefficient of variance differences were not significant among stations within the site.

4.3.2.3 Seed Source Effects

Seed source has been shown to be an important factor in the growth rate and production in bivalve populations (Dickie et al., 1984, Mallet and Carver, 1993). Other studies have noted the importance of seed source on growth rate and production of blue mussels based on the ratio of *M. edulis* to *M. trossulus* (Mallet and Carver, 1995) as well

as physiological energetics (Labarta et al., 1997). The highest performing source in terms of biomass, originated in Burnt Arm. However, the difference between the Burnt Arm source and the Reach Run source was not significant. It is interesting that the Burnt Arm seed source was initially composed of 90% *M. edulis* and 10% *M. trossulus*, while the Reach Run source was 100% *M. edulis*. Mallet and Carver (1989) found that while source and site variations were important factors in the variance of shell growth, tissue growth was almost solely a function of the site factor (i.e., environment). Our results are in agreement as source was outweighed by the effect of site, location within the site, temperature and relative current speed in terms of relative importance in explaining growth. As well, source was not a significant factor in the condition indices of the mussels on the whole; however, it did contribute on a local scale at each farm. This result supports the raft culture findings of Iglesias et al. (1996), who reported condition index was dependent on raft position, reflecting the spatial variability in the quality of available food as well as origin effects.

4.3.3 Survival

Survival was high for all experimental animals averaging >85% in all cases compared with studies conducted in the Canadian Maritimes (Mallet et al., 1993). Variations were explained mainly by season and source. Site and station were also significant factors but to a lesser extent. Similar findings in a reciprocal transplant experiment in Nova Scotia by Mallet and Carver (1989) found source to account more for mortality patterns. This suggests that genetics influence mortality. Our data concerning

species indicated that Big Island and Reach Run spat from 1996, which were used in this study were both 100% *M. edulis*. The Burnt Arm spat used in the experiment, which had a significantly lower survival rate than the other two, was composed of 90% *M. edulis* and 10% *M. trossulus*. It is possible that the source's slightly lower ratio of *M. edulis: M. trossulus* was responsible for the increased level of mortality (Mallet and Carver, 1995, Penney and Hart, 1999); however we did not ascertain species composition at the end of the experiment, and can not confirm this postulate. Evidence of a genotype dependent survival has been reported in *Mytilus* spp. populations in Newfoundland (Penney and Hart, 1999). Penney et al. (2002) have recommended the transplantation and growout of unispecific *M. edulis* seed sources in place of indigenous mixed-species stocks.

Seasonal mortality increased over time; however, there was a marked increase in mortality for all groups between July and September and again from September to November. This could be the result of expended energy reserves and low food levels following spawning (Myrand et al., 2000) and is common in bivalves, including cultured mussels in Newfoundland (Sutterlin et al., 1981).

5.0 CONCLUSIONS

Variations of seston flux in Notre Dame Bay occurred over a tidal cycle in the same magnitude as on a seasonal or even on annual scale. A comparison of the three sites studied within Notre Dame Bay found that variations existed in quantity and quality of seston. Within each site, local variations in the concentration and composition of seston also occurred. In addition to seston variation, environmental and hydrological parameters were not only site specific but in many cases varied within sites considerably.

There was little evidence of reductions in phytoplankton quantity (chlorophyll-*a*) and POM throughout the farms. Therefore it is concluded that production capacity was not exceeded in each of the three farms. However, the physical arrangement of lines in Burnt Arm, perpendicular to flow, did appear to affect the flow patterns and subsequent seston flux from the front to back.

Site was the most important factor in the prediction of biomass increases ($g_{-} \cdot day^{-1}$) in socks. This was followed by temperature, location of the experimental line, relative current speed and finally seed source. Biomass increases at the Burnt Arm and Reach Run site were not significantly different from each other which was not expected considering the higher flux values recorded at Reach Run. This was possibly a result of food quality versus food quantity or a consequence of the secondary set at Reach Run.

Growth rates and production at Reach Run did not vary within the farm by area or source, which supports the hypothesis that sites with characteristically higher seston flux will have more uniform growth and production. Conversely, the Burnt Arm site showed

reduced production at the back of the farm, where flux levels were decreased as a result of lower relative current speeds.

Survival of experimental mussels was high at all sites. Seed source differences accounted for the greatest variation in survival rates. Sites with a mixed population of *M. edulis* and *M. trossulus* had lower survival than the pure *M. edulis* source from Big Island.

Plaster cylinders were found to provide a good relative index of average current speed at mussel culture sites in a boreal environment. These sites are relatively poor in resuspended sediments.

5.1 Implications of Study to the Industry

Seed source is important in mussel performance but in this study, site was shown to be a more important factor in growth and production. Therefore, site evaluations are critical to success. Environmental and hydrological parameters should be considered and assessed not only for site selection purposes prior to set up but also during production to determine the effects of the placement of the farm on currents patterns, available seston and growth, particularly when considering production expansions. This regular appraisal of the environmental conditions could prevent losses or delays in production. In the event that such services are not available an assessment is possible through means of accurate production records. From such records, growth rates, uniformity of grade and mortalities can provide a good indication if production capacity has been exceeded or not at a given site.

Caution is always advised when production expansions are proposed for a farm. In addition to record keeping, proper husbandry practices, i.e., attention to stocking density/ sock, spacing between socks and spacing between lines are good assurances of staying within a site's production level. This study demonstrated the importance of proper line spacing, as it has shown that the physical arrangement of lines at sites affects food patterns and food supplies. Also, lines arranged parallel to current flow resulted in reduced variation in mussel growth/production and therefore, less variation in quality.

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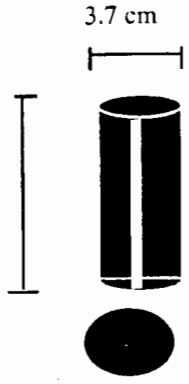
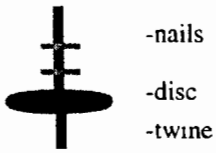
Appendix 1.0 How to make plaster cylinders.

ABS cylinder with slit cut down one side.



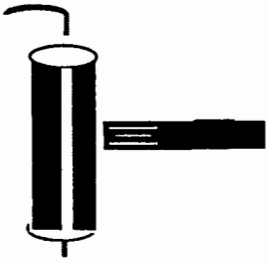
Duct tape covering cardboard disc 3.7 cm diameter.

Cardboard bottom covered in duct tape with orange twine through it.
Also nails placed in twine. (Not to scale).



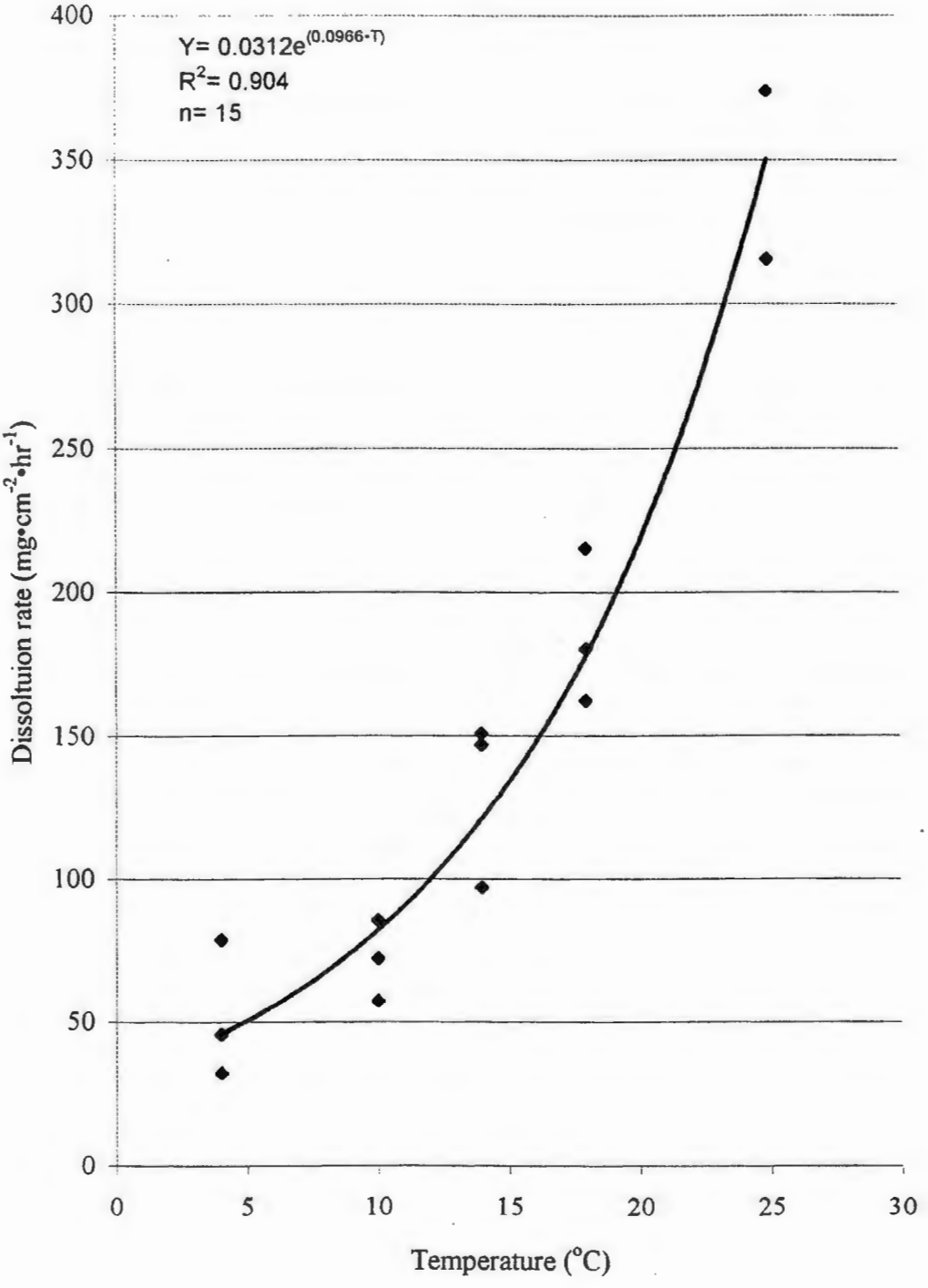
Cylinder with twine in place and edges sealed.

Cylinder with plaster poured and twine secured so that it is centered in the cylinder. Mix 7.2 kg of plaster with 3.6 L of H_2O.



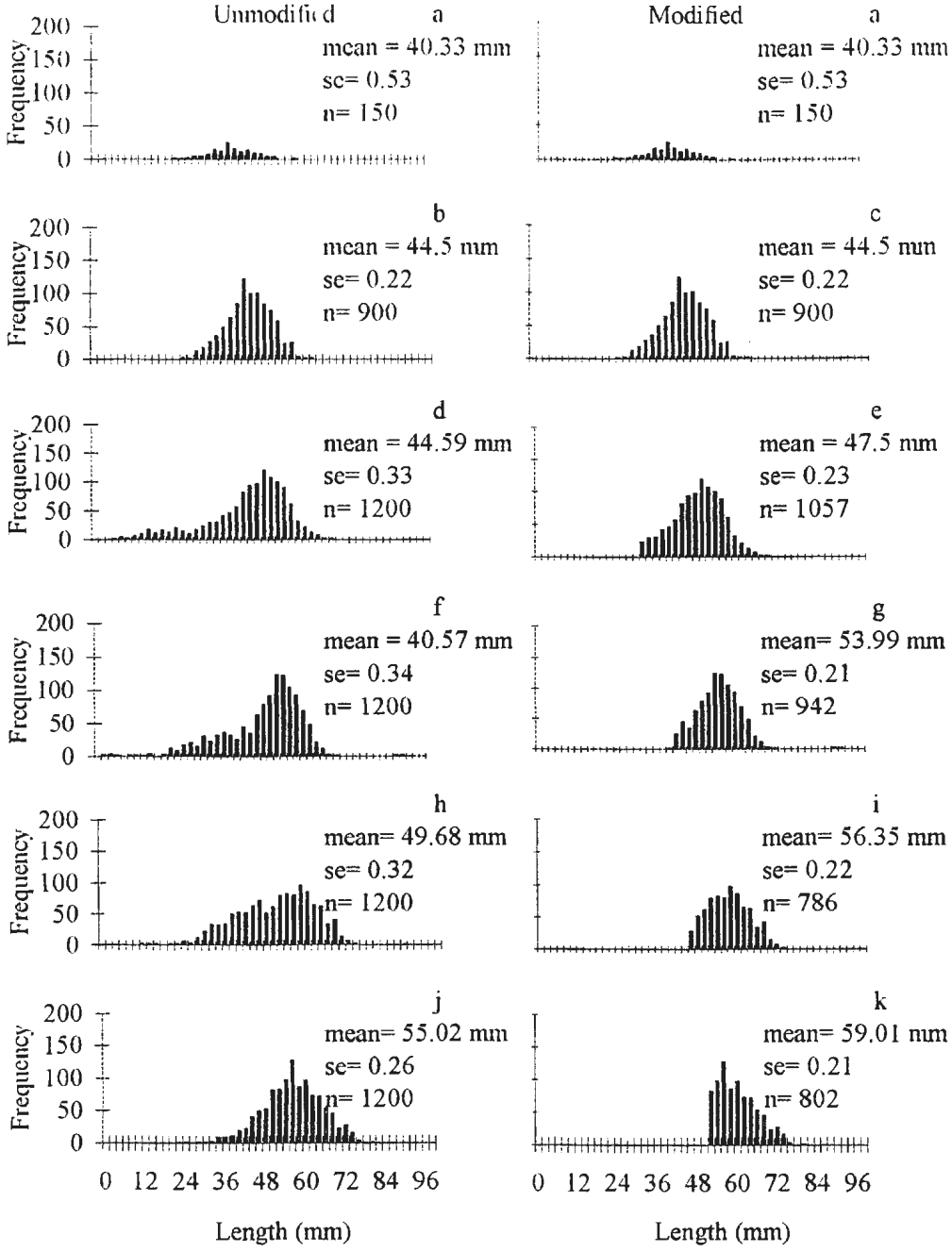
To remove cylinder. Pry pipe open with a chisel.

Dry at 40°C.
Keep twine away from heat



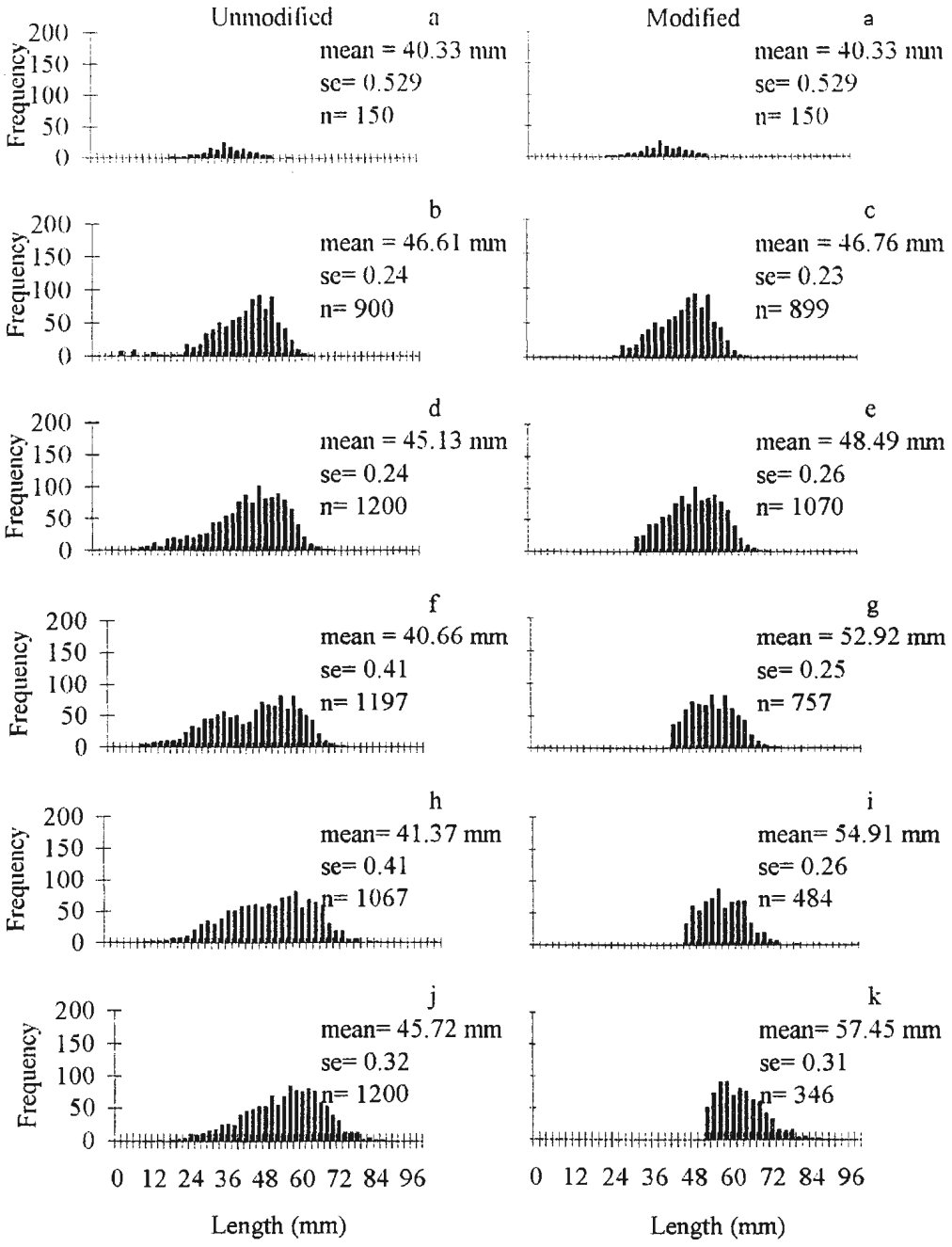
Appendix 1.1: The effects of temperature on dissolution of plaster cylinders. Dissolution based on weight of loss of dry cylinders per unit surface area per hour.

Appendix 2.0: Shell length frequency distribution.



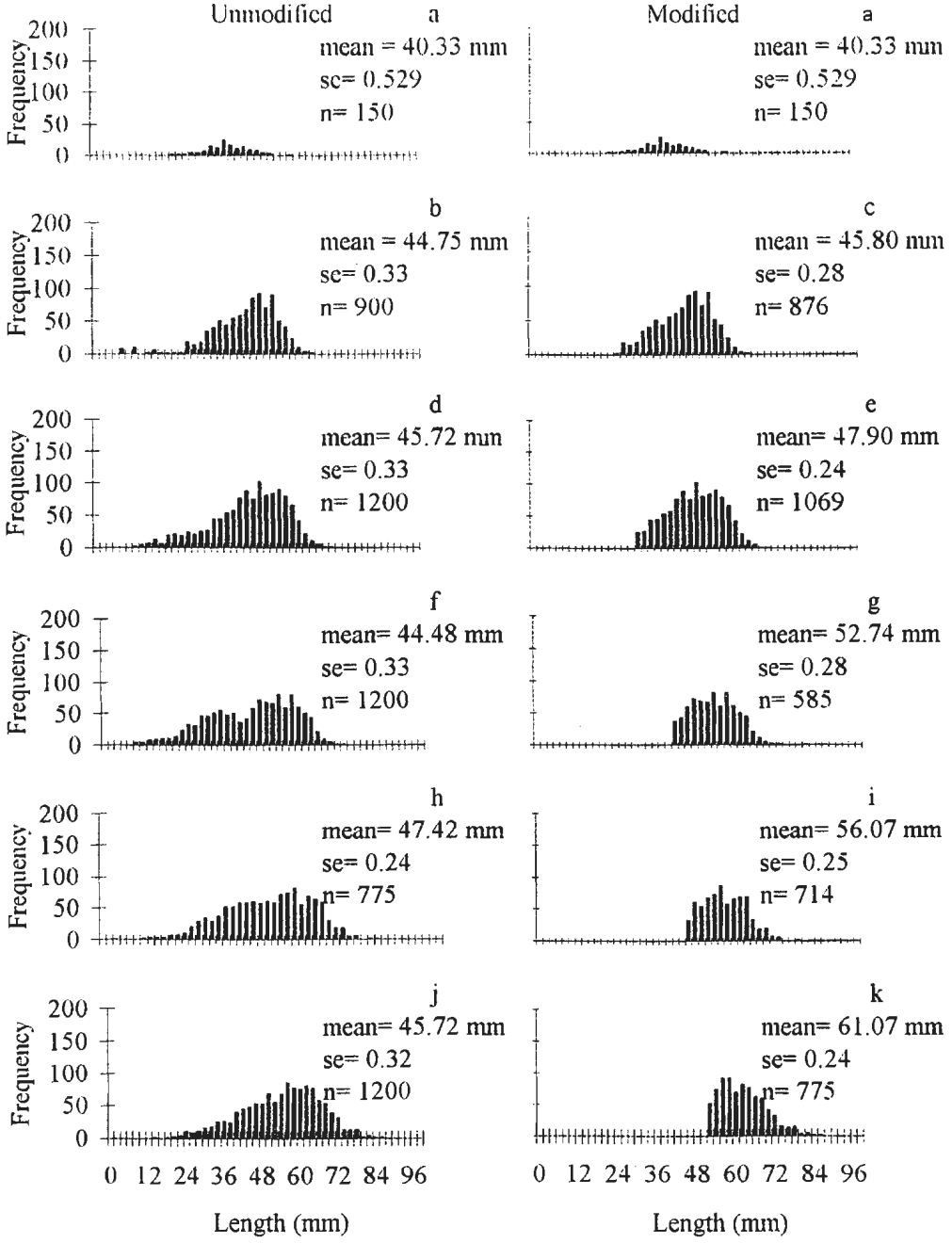
Appendix 2.1: Shell length frequency distribution of Reach Run spat transplanted in Burnt Arm measured a) Sept. 1997 b) Nov. 1997 c) Nov. 1998 modified d) May 1998 e) May 1998 modified f) July 1998, g) July 1998 modified h) Sept. 1998 i) Sept. 1998 modified j) Nov. 1998 k) Nov. 1998 modified (se= standard error, n= number of mussels, modified= data from secondary set removed).

Appendix 2 continued.



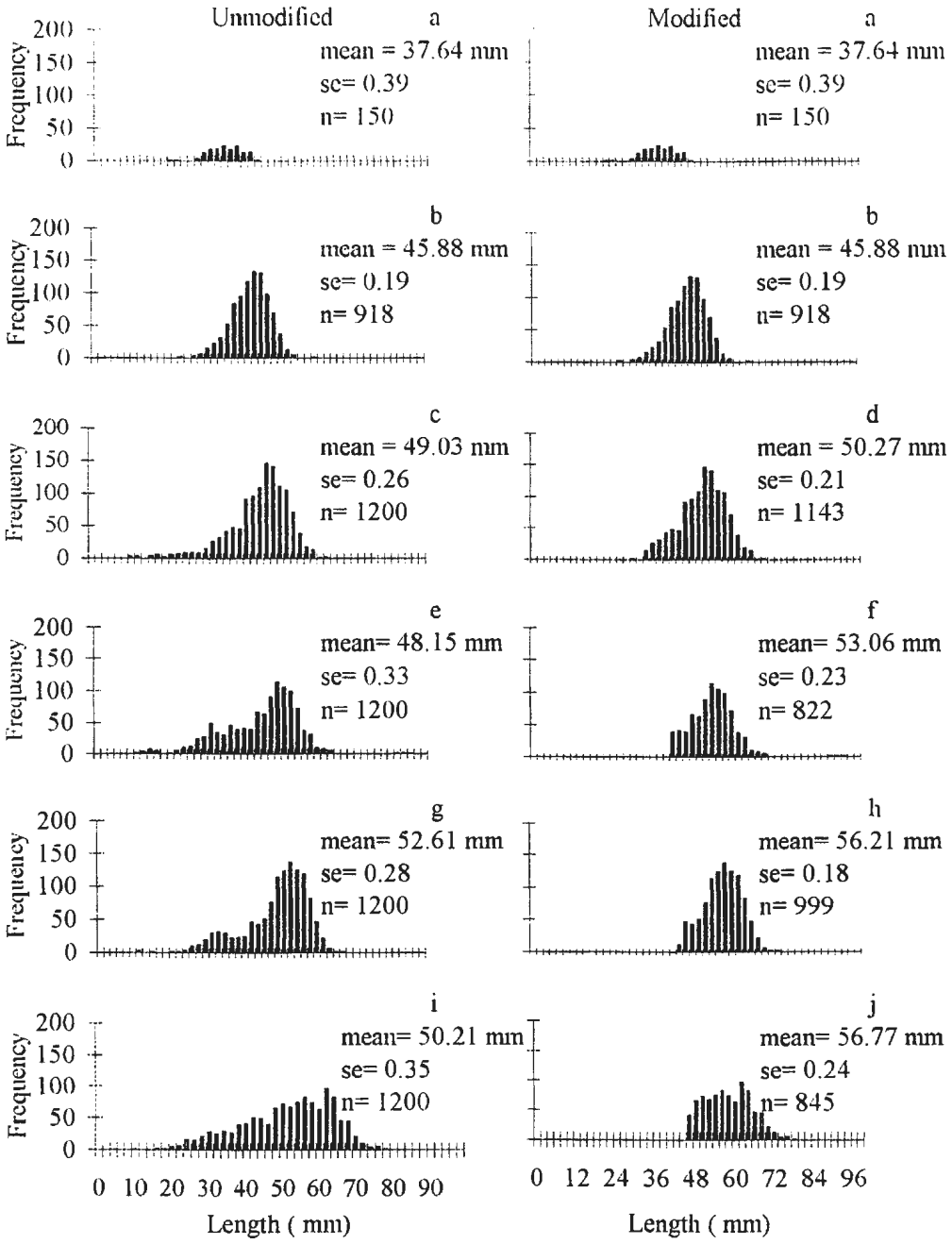
Appendix 2.2: Shell length frequency distribution of Reach Run spat transplanted in Reach Run measured a) Sept. 1997 b) Nov. 1997 c) May 1998 d) May 1998 modified e) July 1998, f) July 1998 modified g) Sept. 1998 h) Sept. 1998 unmodified modified i) Nov. 1998 j) Nov. 1998 modified (se= standard error, n= number of mussels, modified= data from secondary set removed).

Appendix 2 continued.



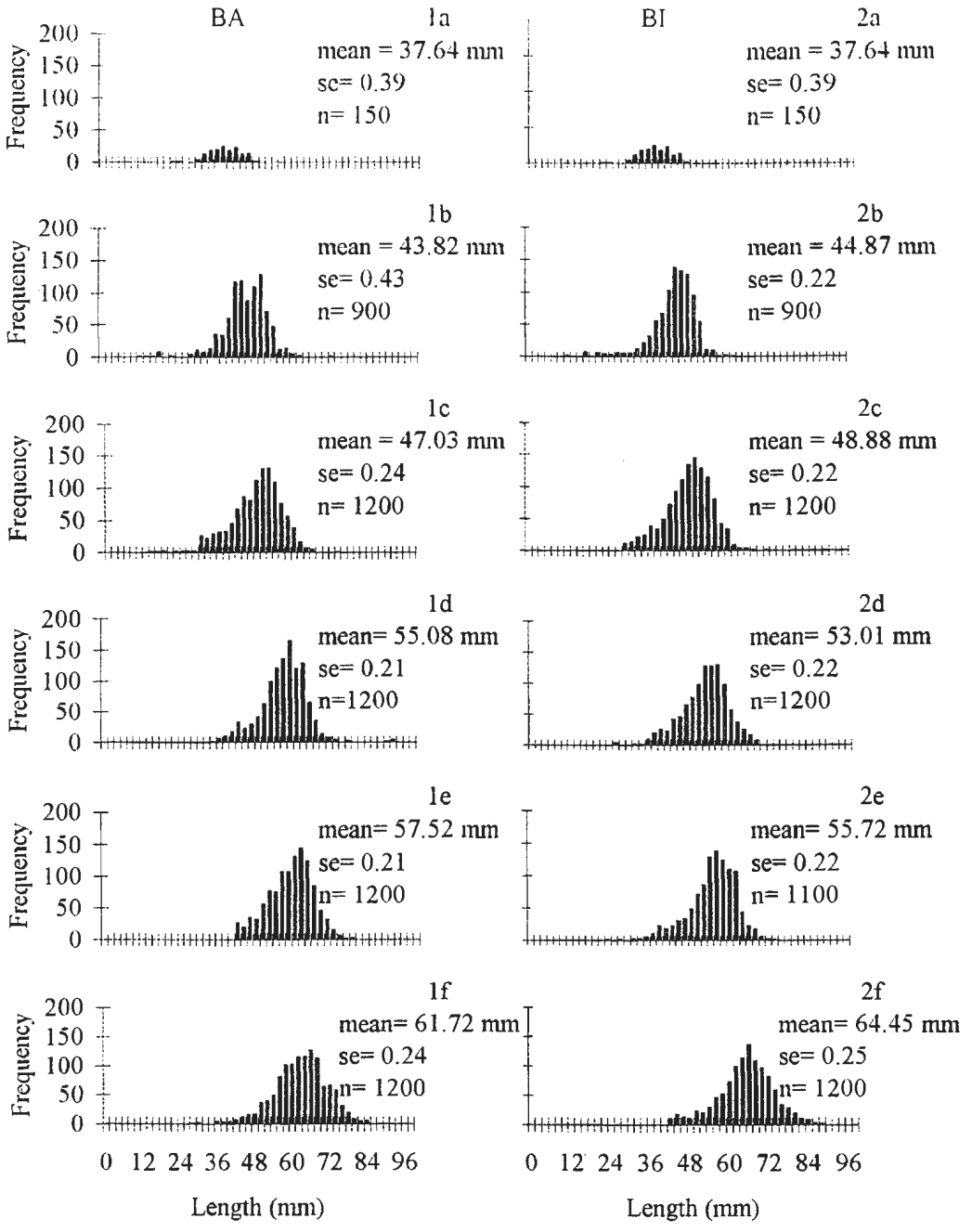
Appendix 2.3: Shell length frequency distribution of Reach Run spat transplanted near Big Island measured a) Sept. 1997 b) Nov. 1997 c) May 1998 d) May 1998 modified e) July 1998, f) July 1998 modified g) Sept. 1998 h) Sept. 1998 unmodified modified i) Nov. 1998 j) Nov. 1998 modified (se= standard error, n= number of mussels, modified= data from secondary set removed).

Appendix 2.0 continued



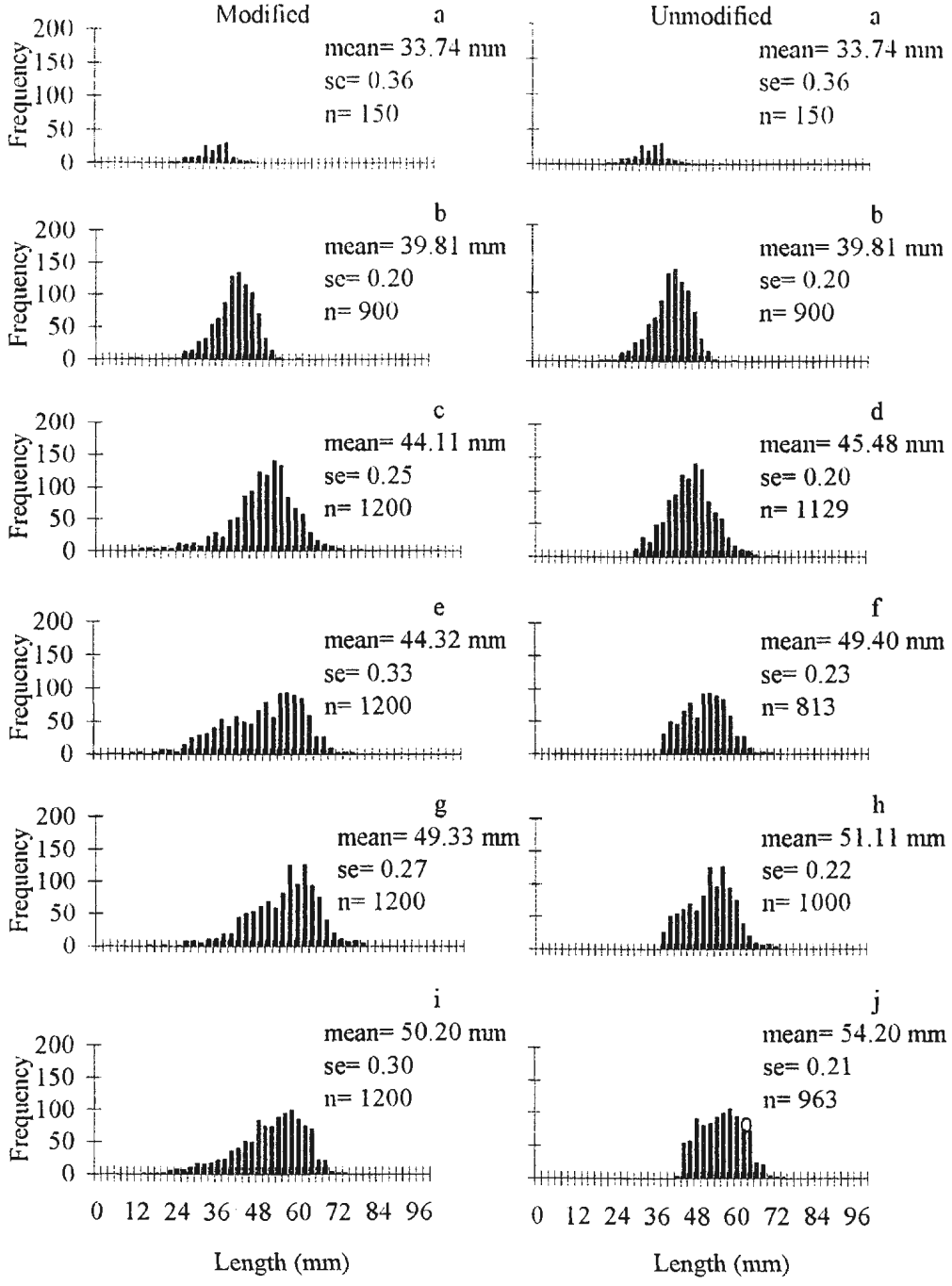
Appendix 2.4: Shell length frequency distributions of Burnt Arm spat transplanted in Reach Run measured a) Sept. 1997, b) Nov. 1997, c) May 1998, d) May 1998 modified, e) July 1998, f) July 1998 modified, g) Sept. 1998, h) Sept. 1998 modified i) Nov. 1998, j) Nov. 1998 modified (se= standard error, n= number of mussels, modified= data from secondary set removed).

Appendix 2 continued



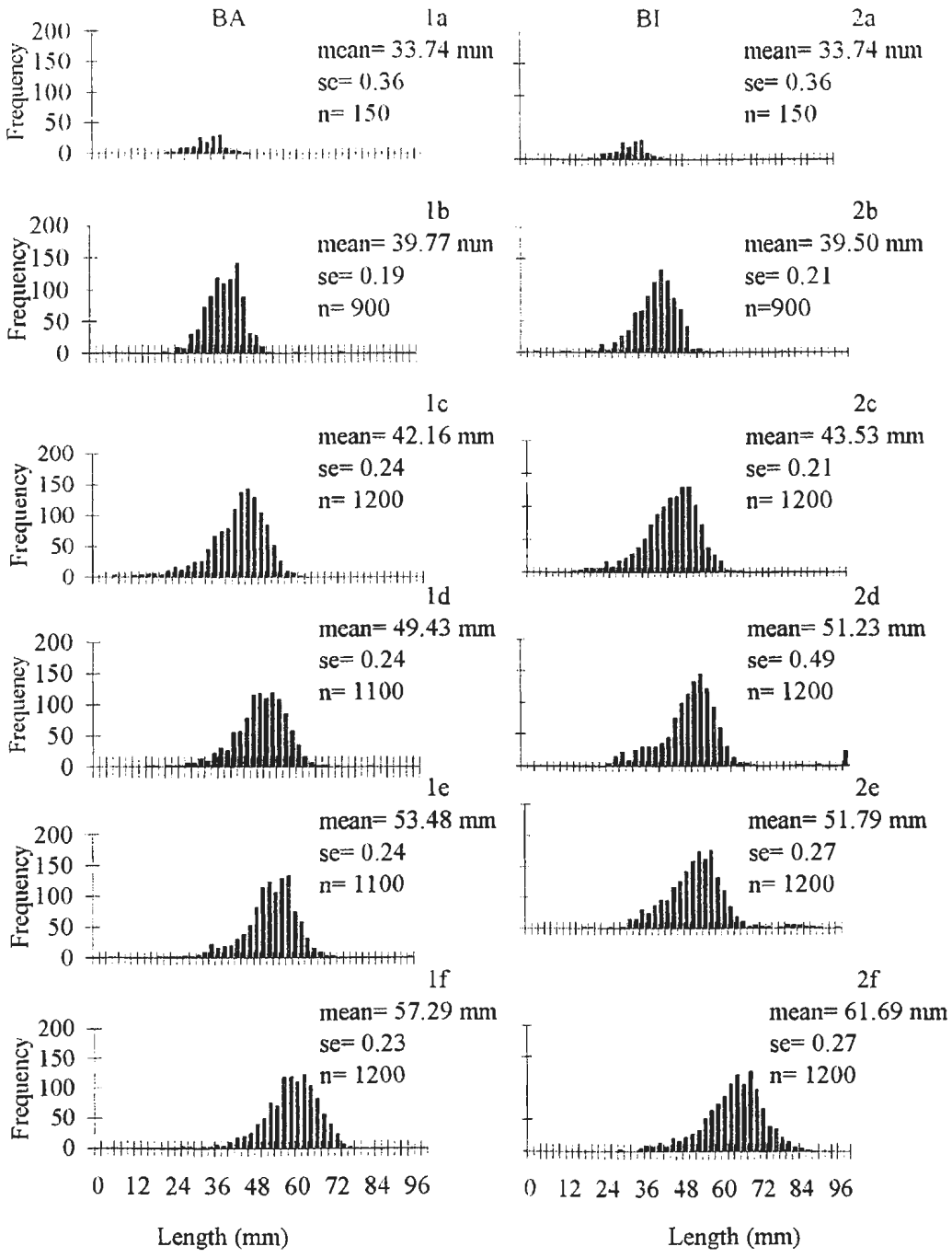
Appendix 2.5: Shell length frequency distribution of Burnt Arm spat transplanted to; 1) Burnt Arm 2) Big Island, measured a) Sept. 1997 b) Nov. 1997 c) May 1998 d) July 1998 e) Sept. 1998 f) Nov. 1998 (se= standard error n= number of mussels).

Appendix 2 continued.



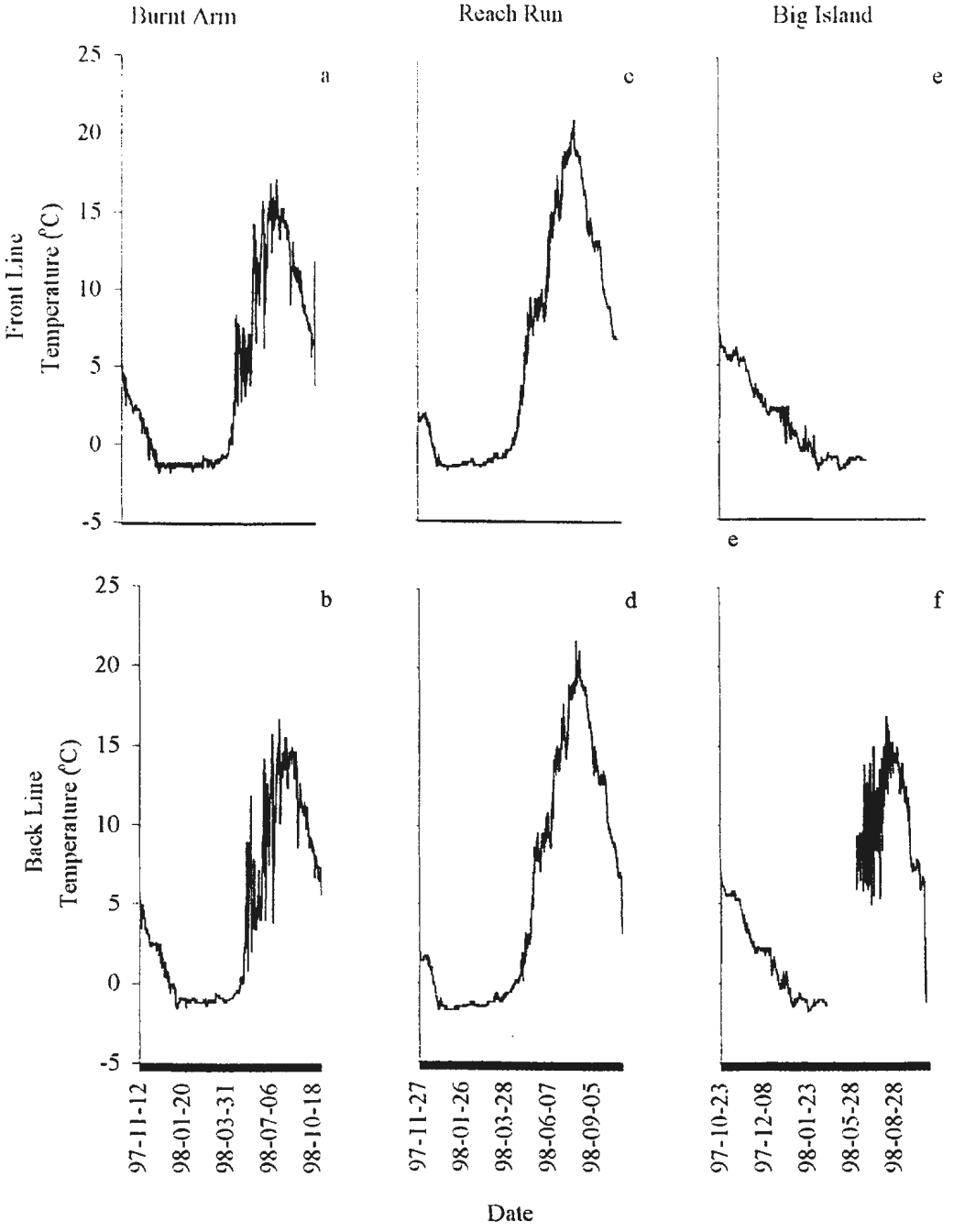
Appendix 2.6: Shell length frequency distribution of Big Island spat transplanted to Reach Run measured a) Sept. 1998, b) Nov. 1998, c) May 1998, d) May 1998 modified, e) Jul 1998, f) Jul 1998 modified, g) Sept. 1998, h) Sept. 1998 modified, i) Nov. 98, j) Nov. 1998 modified (se= standard error, n= number of mussels measured, modified= data from secondary set removed).

Appendix 2 continued.

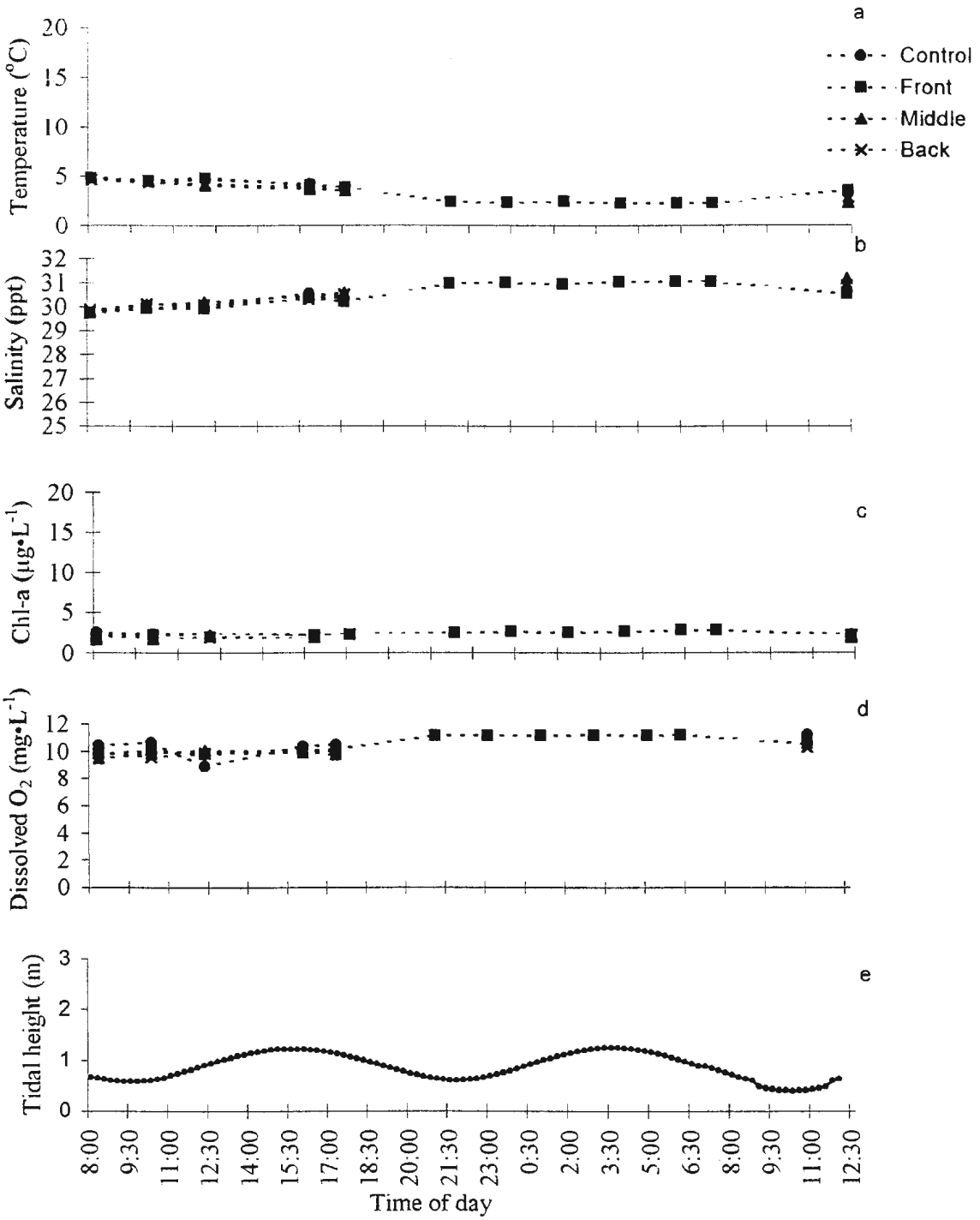


Appendix 2.7: Shell length frequency distribution of Burnt Arm spat transplanted to; 1) Burnt Arm 2) Big Island, measured a) Sept. 1997 b) Nov. 1997 c) May 1998 d) July 1998 e) Sept. 1998 f) Nov. 1998 (se= standard error n= number of mussels).

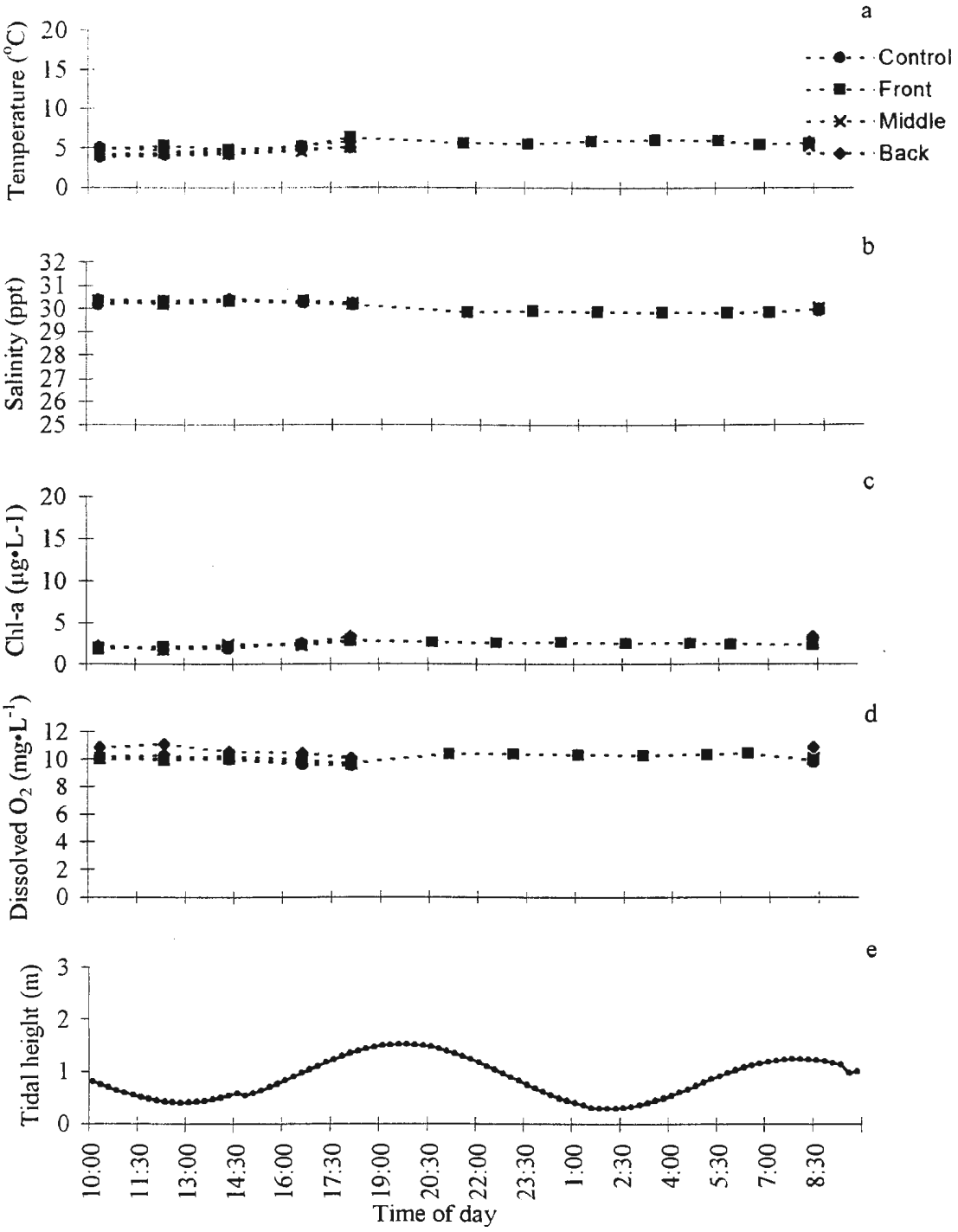
Appendix 3.0 Thermograph data.



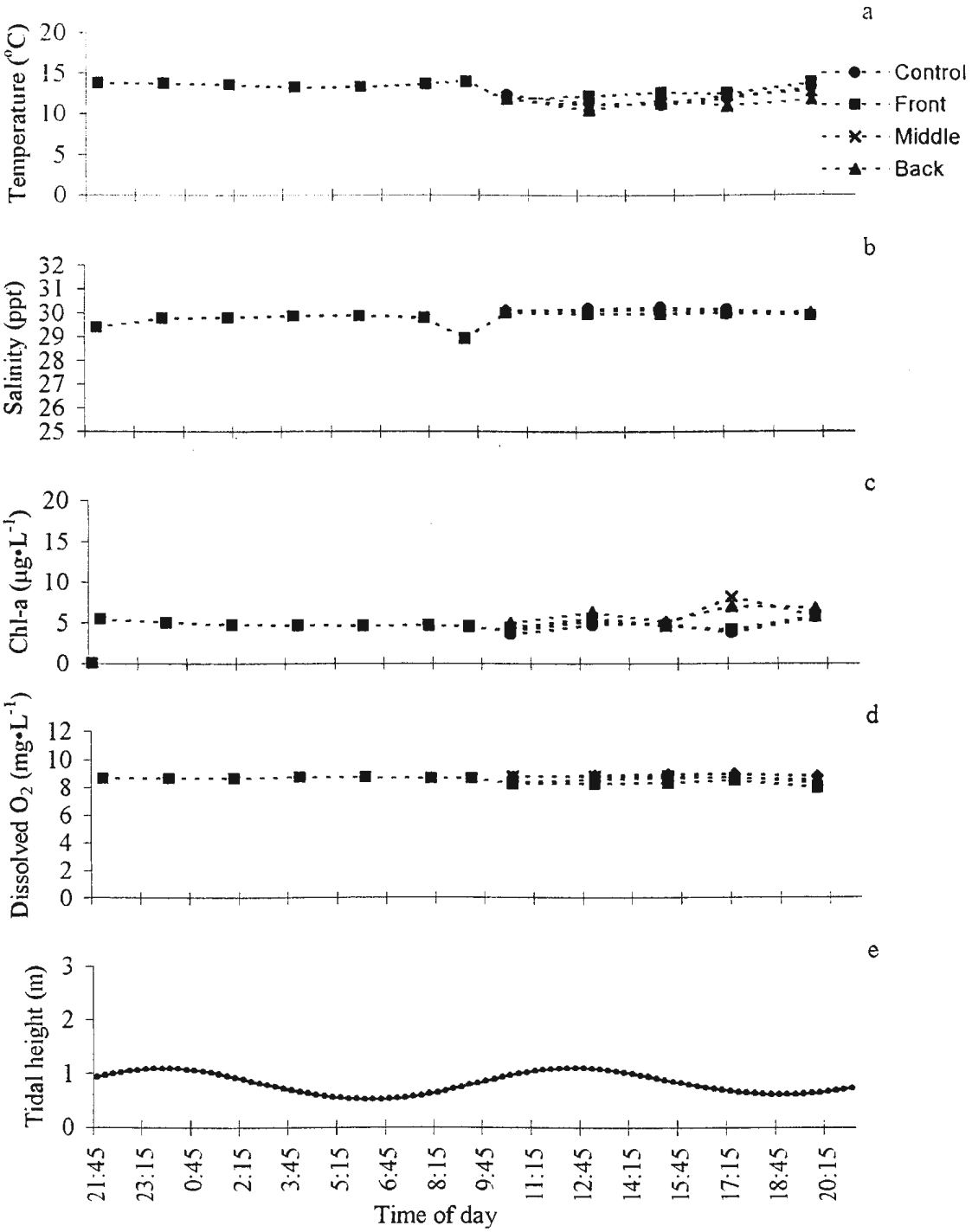
Appendix 3.0. Summary of hourly thermograph data (°C) collected at 3.5 m at the (a, b and c) front experimental line and (d, e and f) back experimental line of Burnt Arm (column 1), Reach Run (column 2) and Big Island (column 3).



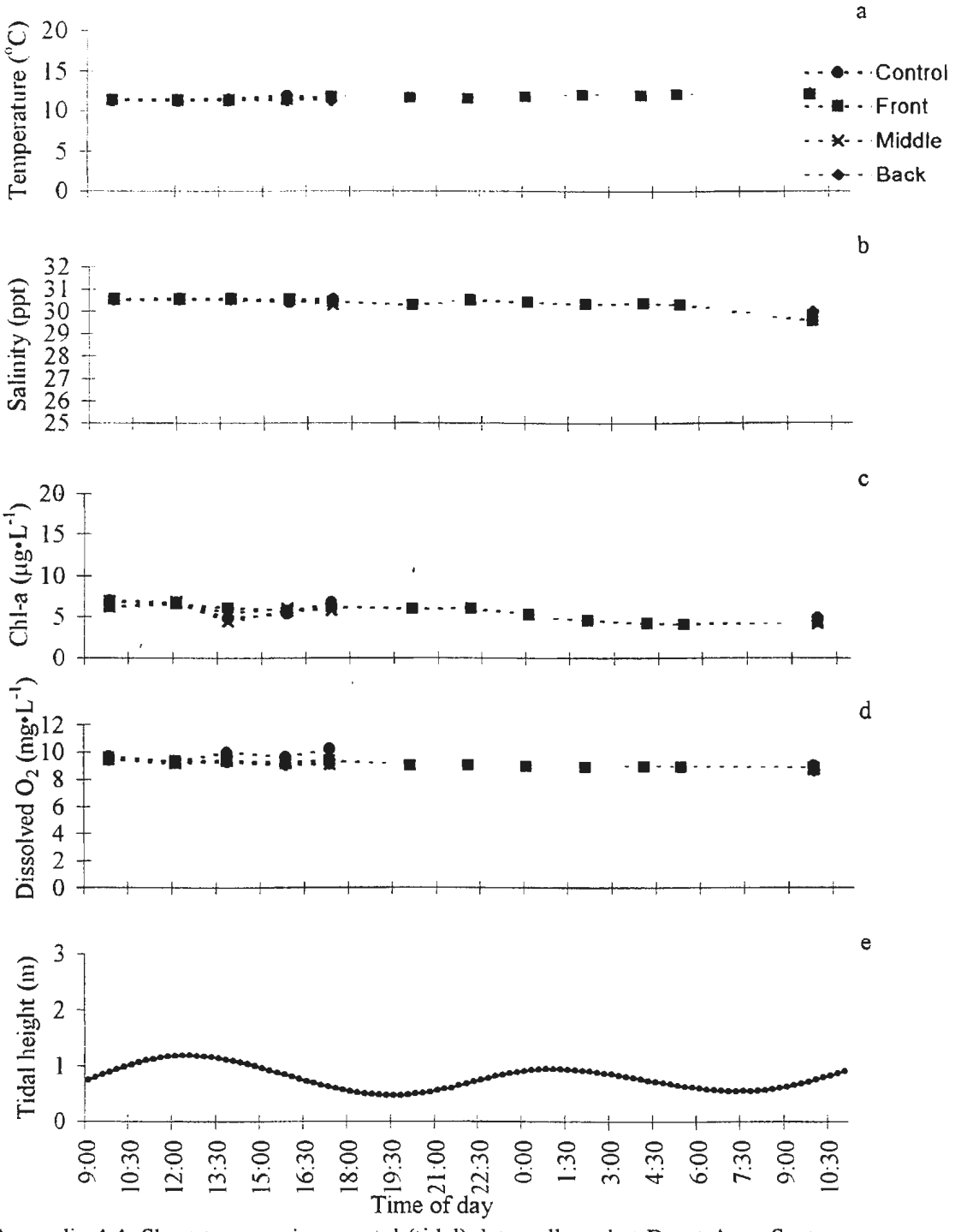
Appendix 4.1: Short-term environmental (tidal) data collected at Burnt Arm, May 21-22, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



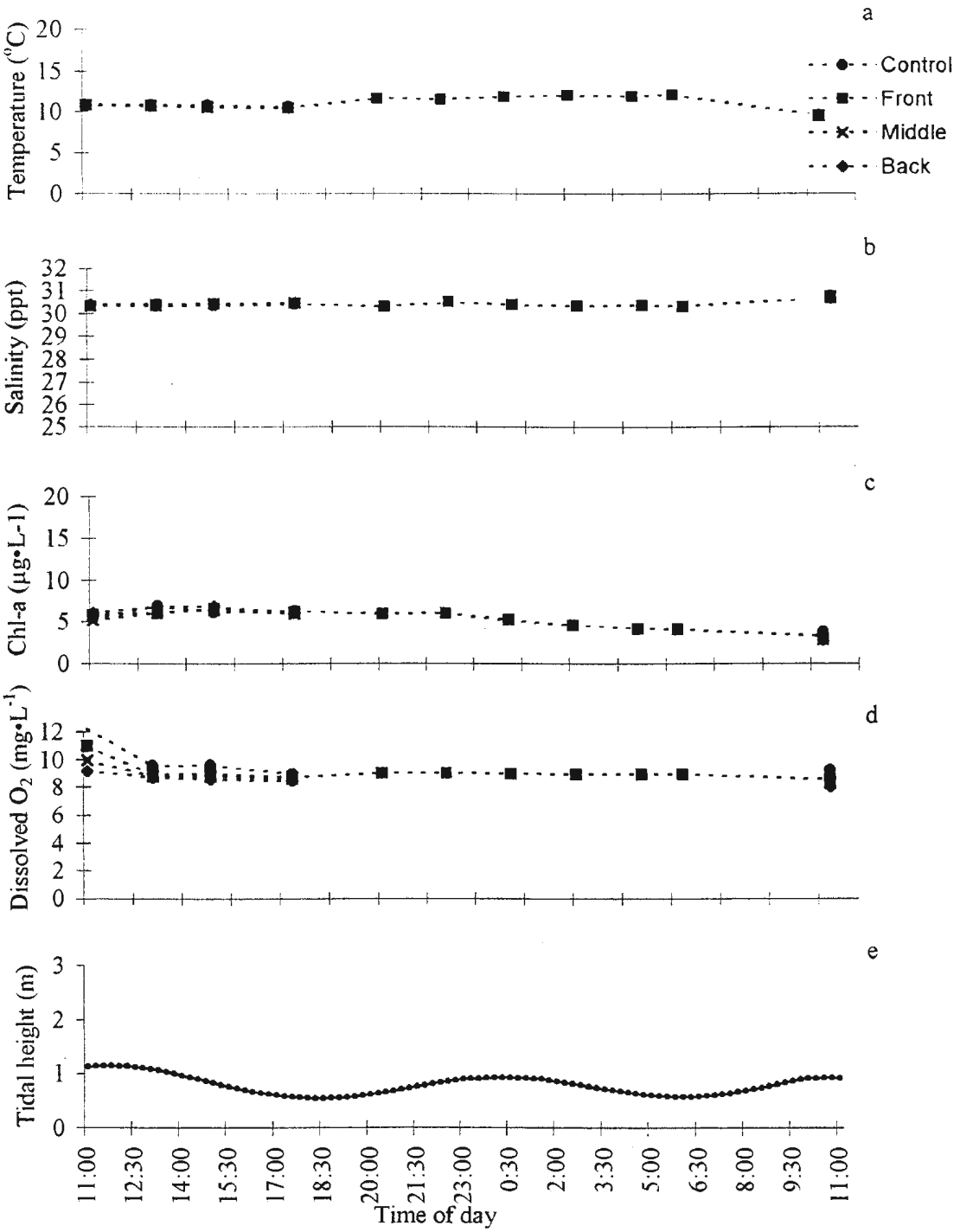
Appendix 4.2: Short-term environmental (tidal) collected at Burnt Arm, June 23-24, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



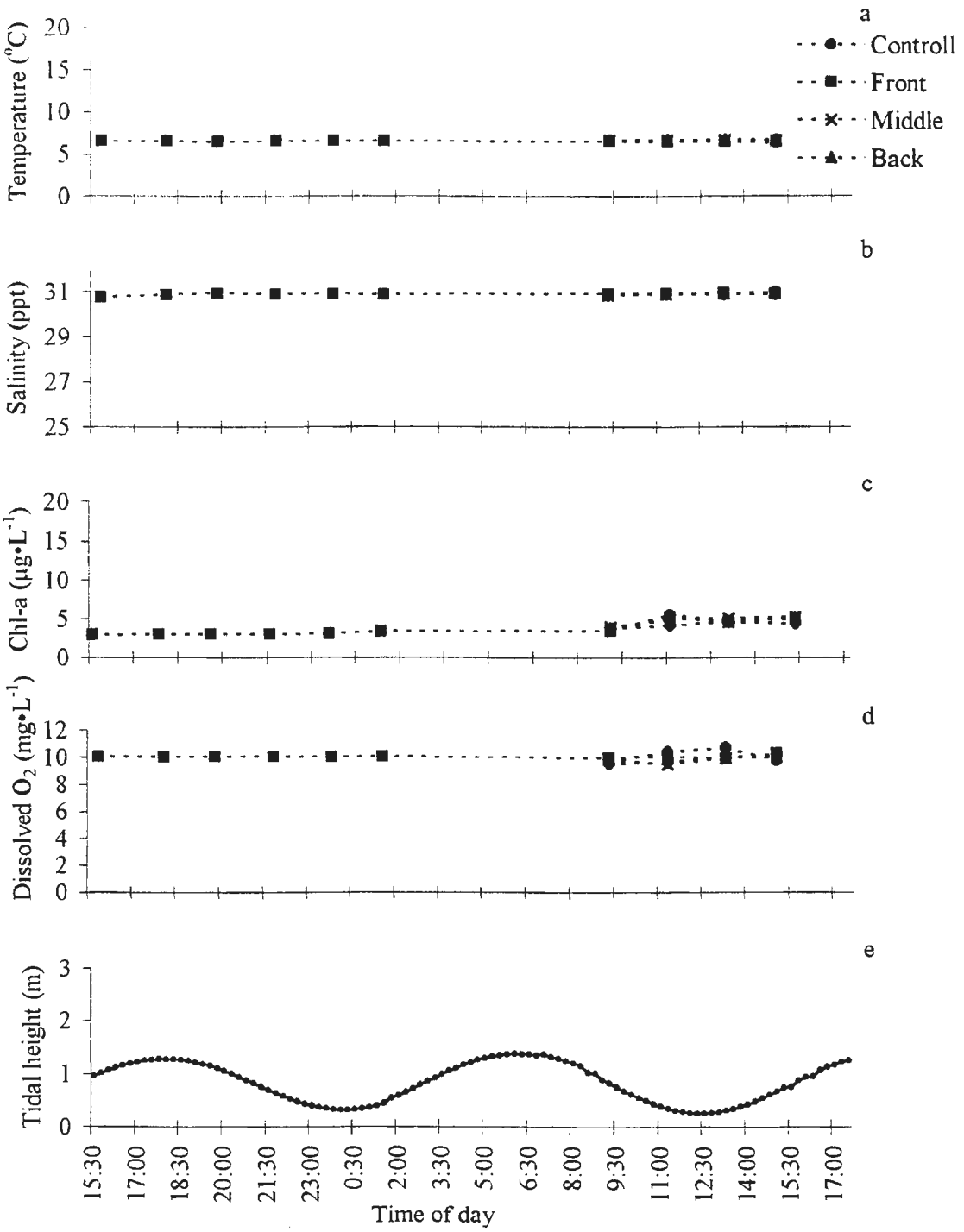
Appendix 4.3: Short-term environmental (tidal) data collected at Burnt Arm, July 30-31, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



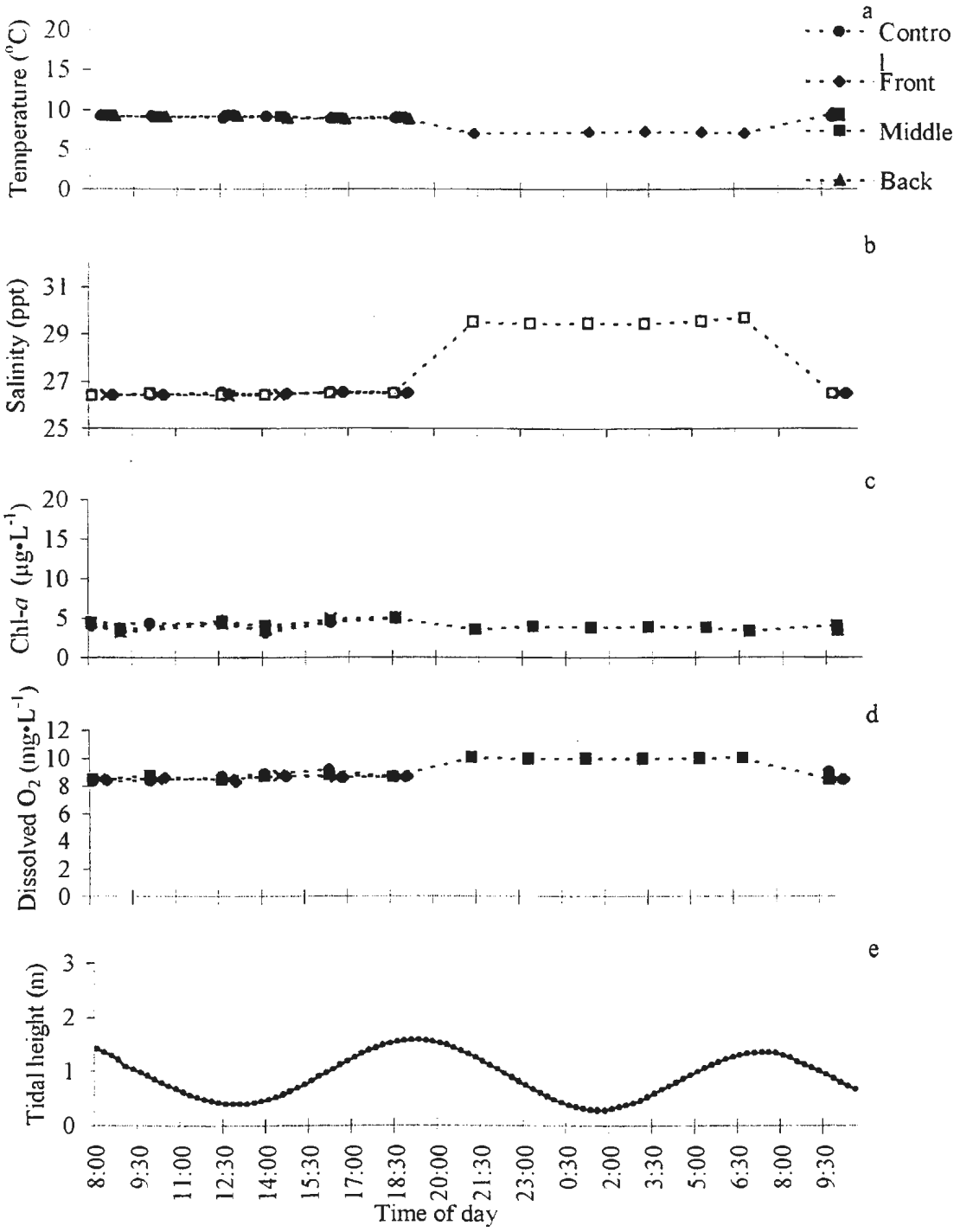
Appendix 4.4: Short-term environmental (tidal) data collected at Burnt Arm, Sept. 13-14, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



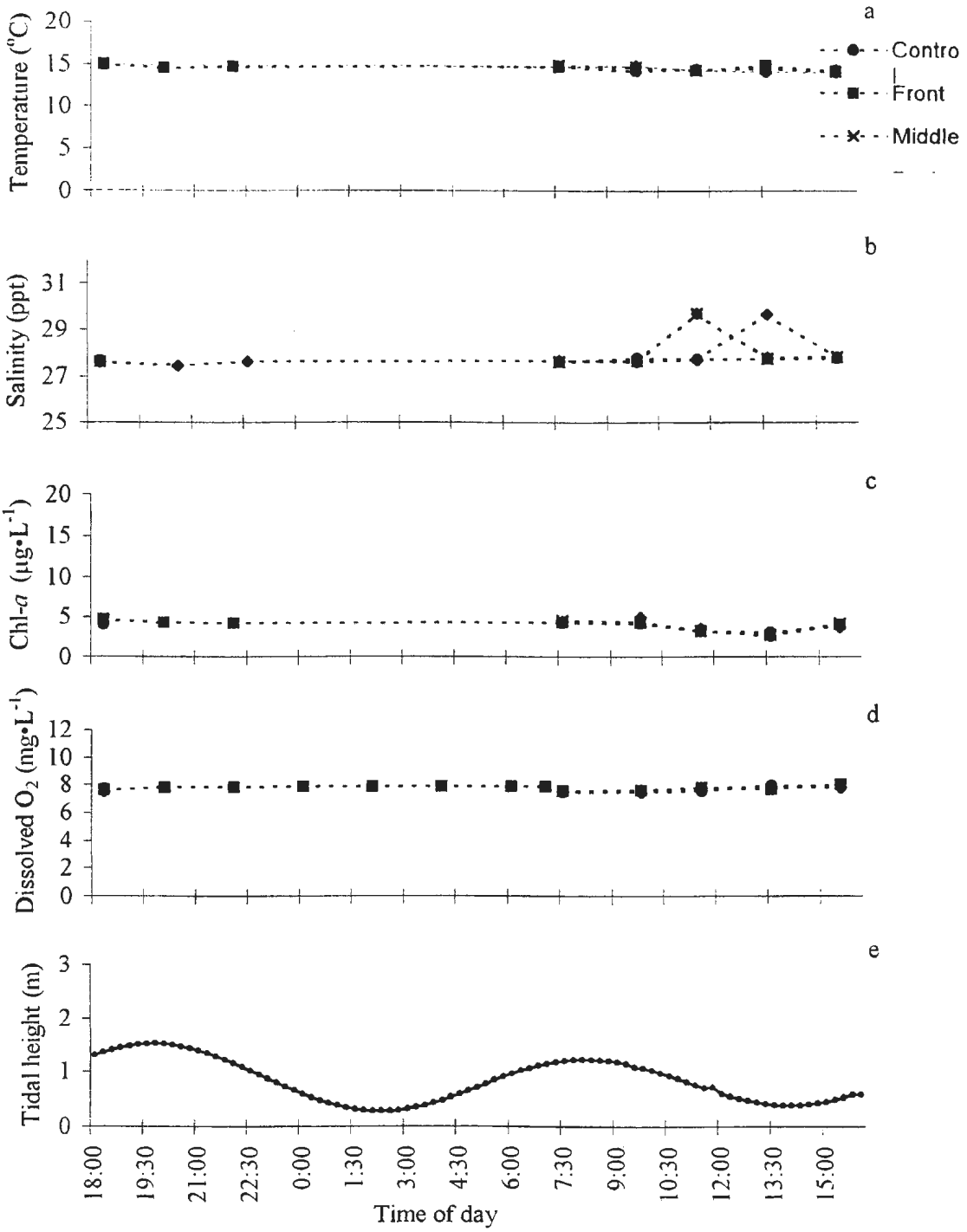
Appendix 4.5: Short-term environmental (tidal) data collected at Burnt Arm, Sept. 28-29, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



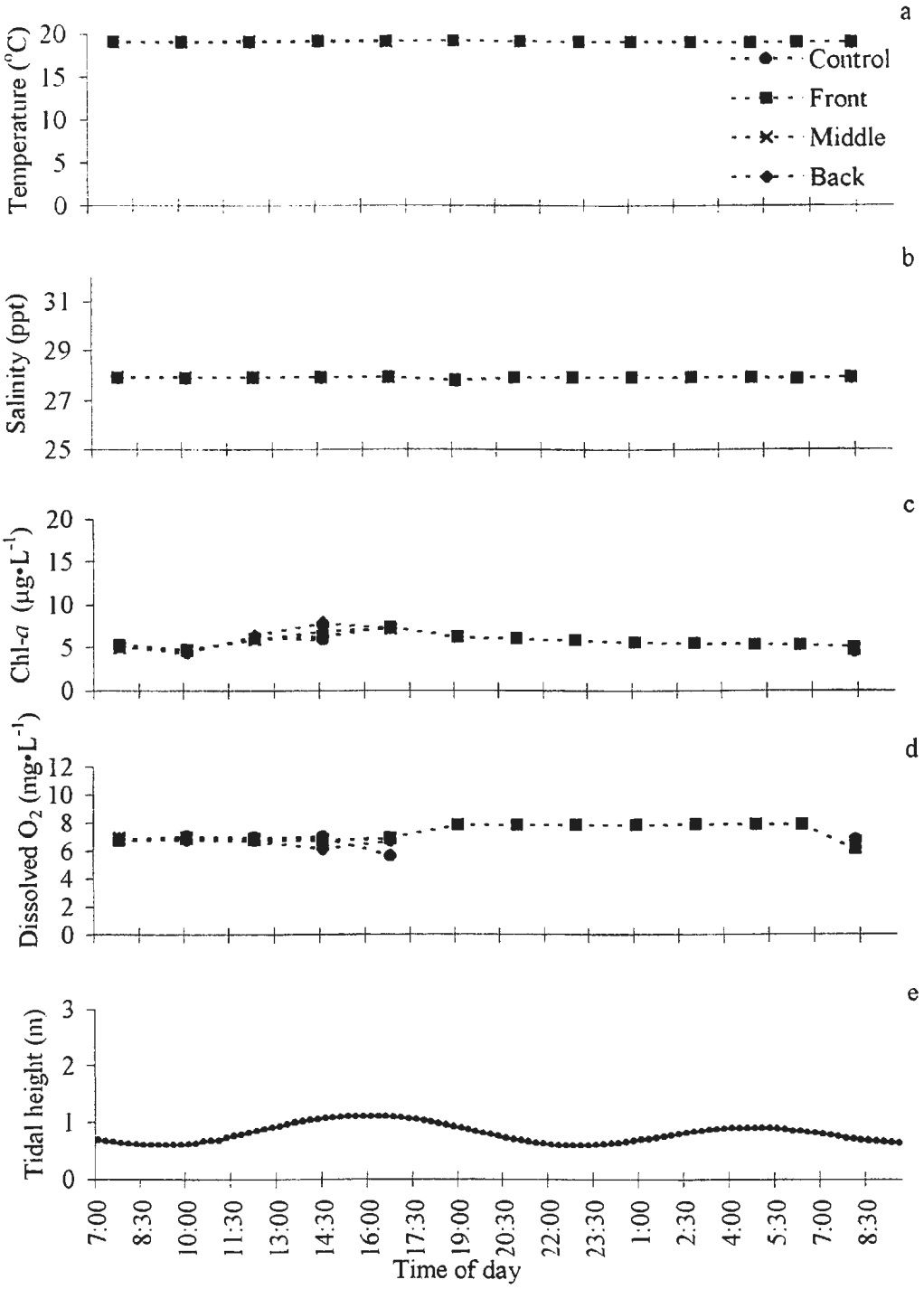
Appendix 4.6: Short-term environmental (tidal) data collected at Burnt Arm, Nov. 2-3, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



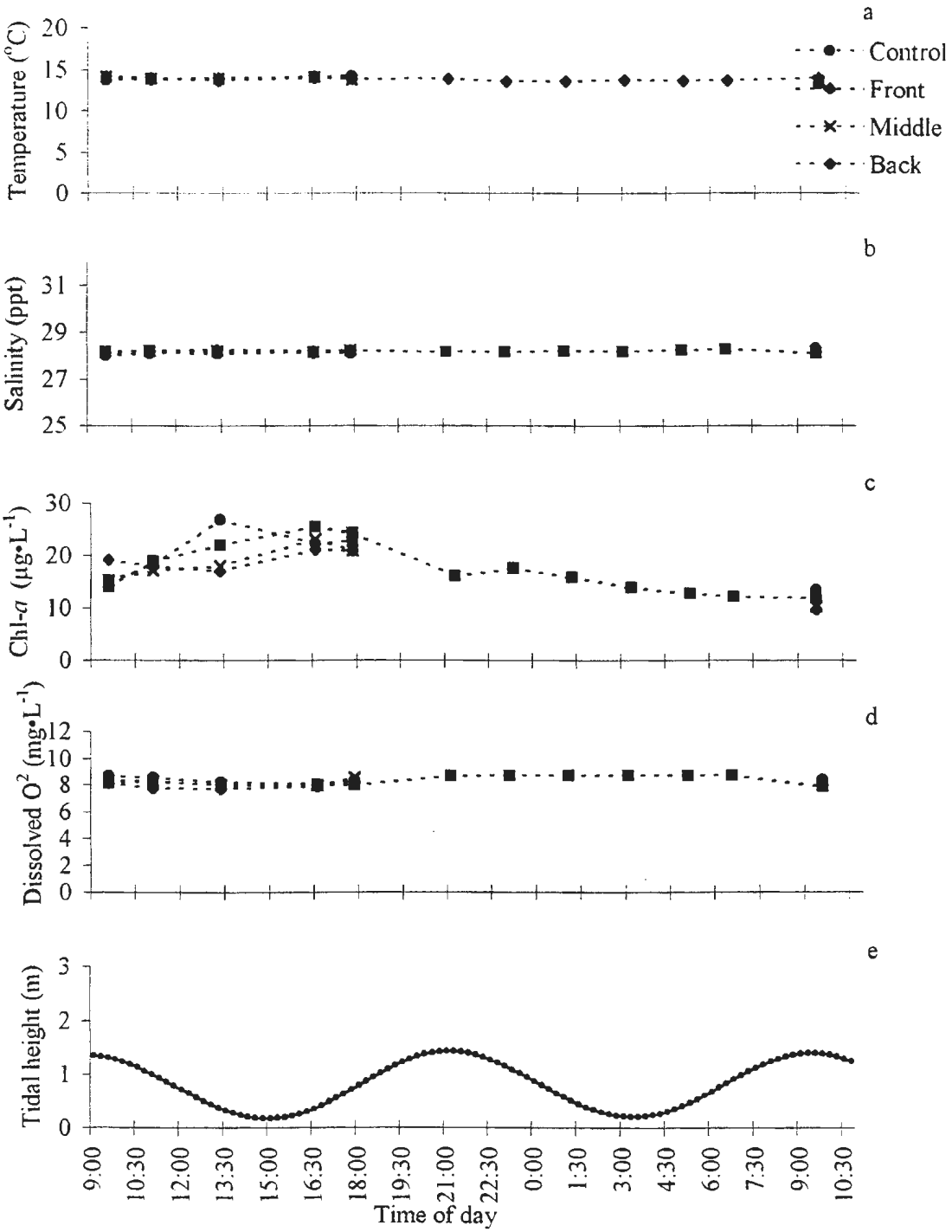
Appendix 4.7: Short-term environmental (tidal) data collected at Reach Run, May 25-26, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



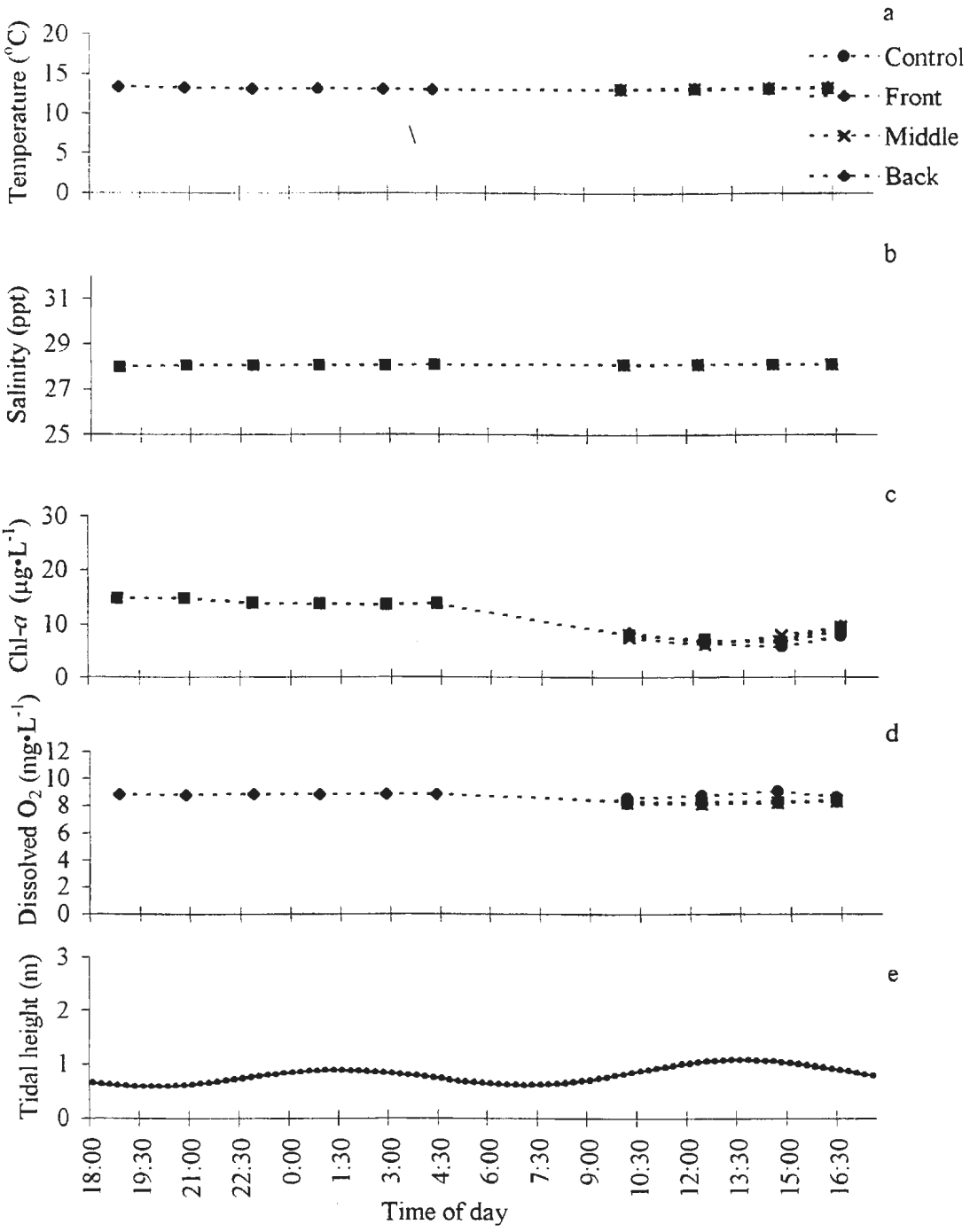
Appendix 4.8: Short-term environmental (tidal) data collected at Reach Run, June 24-25, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



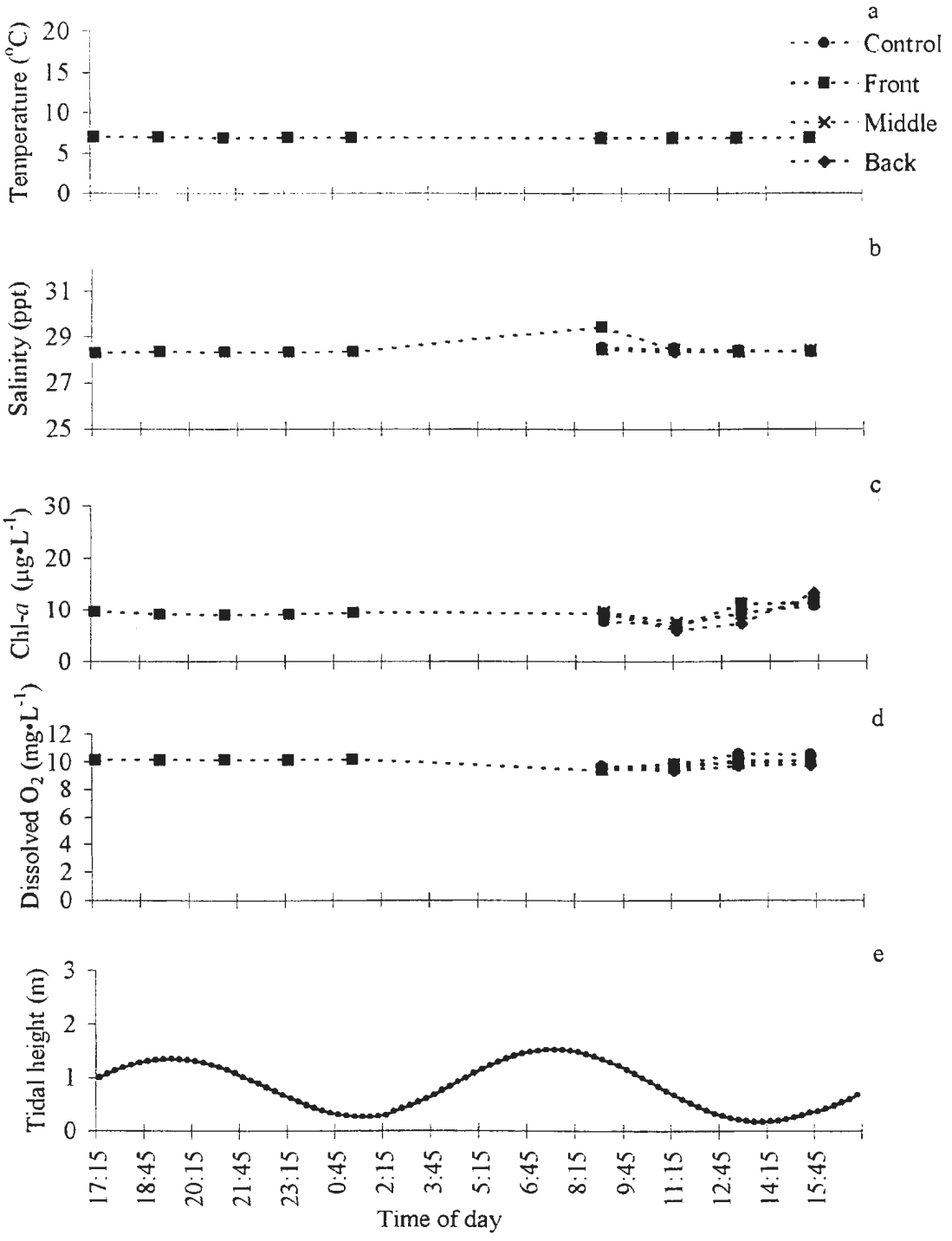
Appendix 4.9: Short-term environmental (tidal) data collected at Reach Run, Aug. 3-4,1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



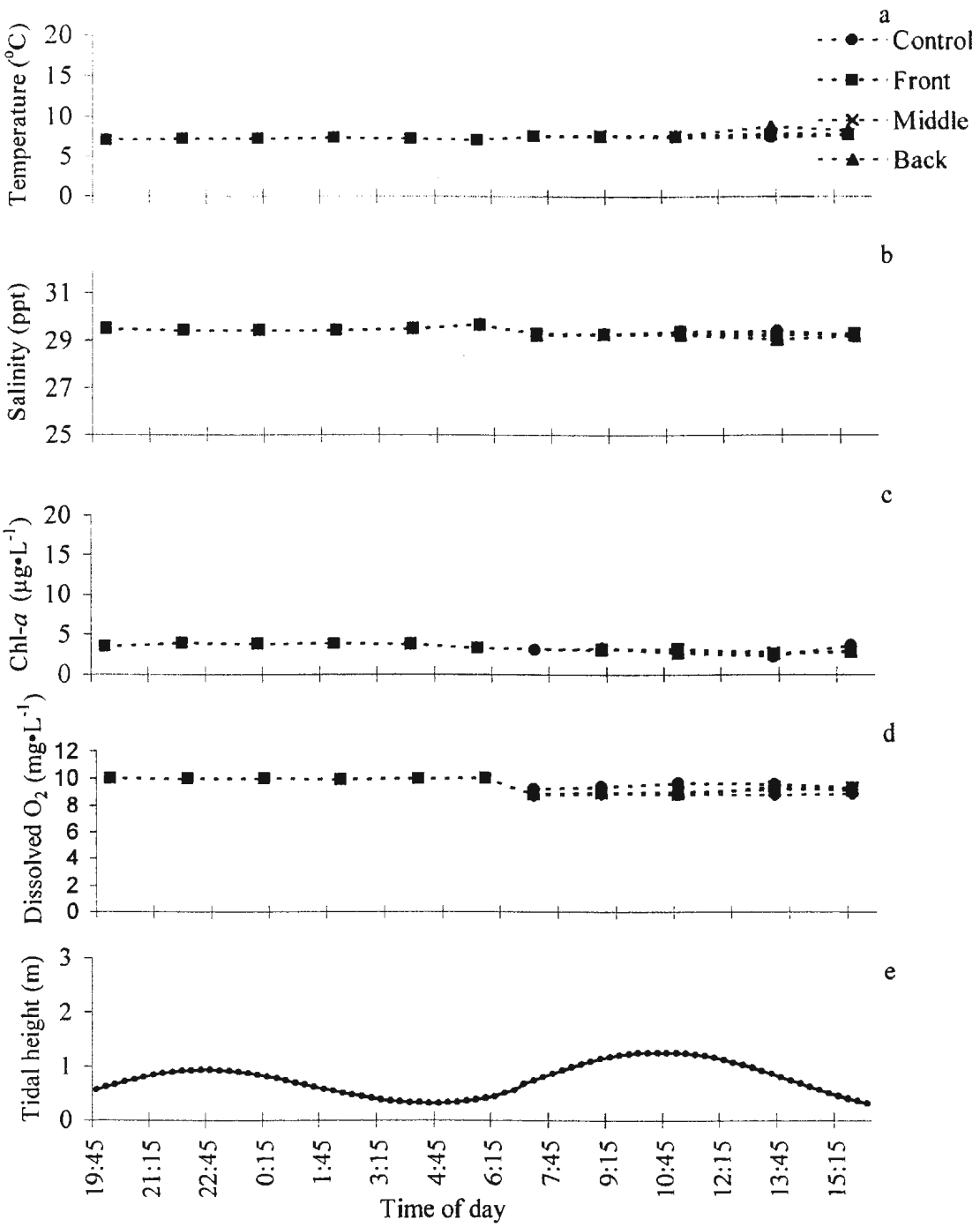
Appendix 4.10: Short-term environmental (tidal) data collected at Reach Run, Sept. 8-9, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



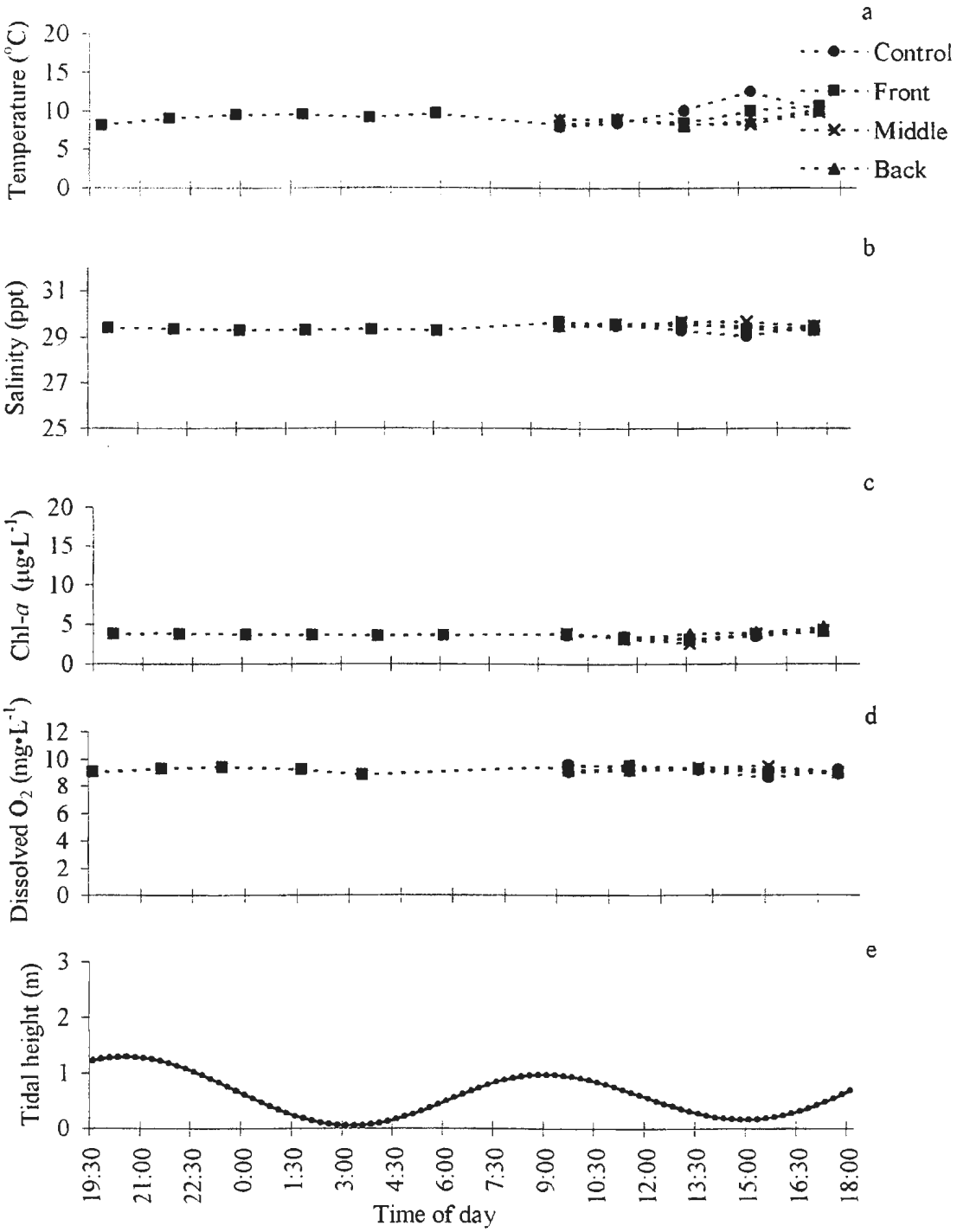
Appendix 4.11: Short-term environmental (tidal) data collected at Reach Run, Sept. 29-30, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



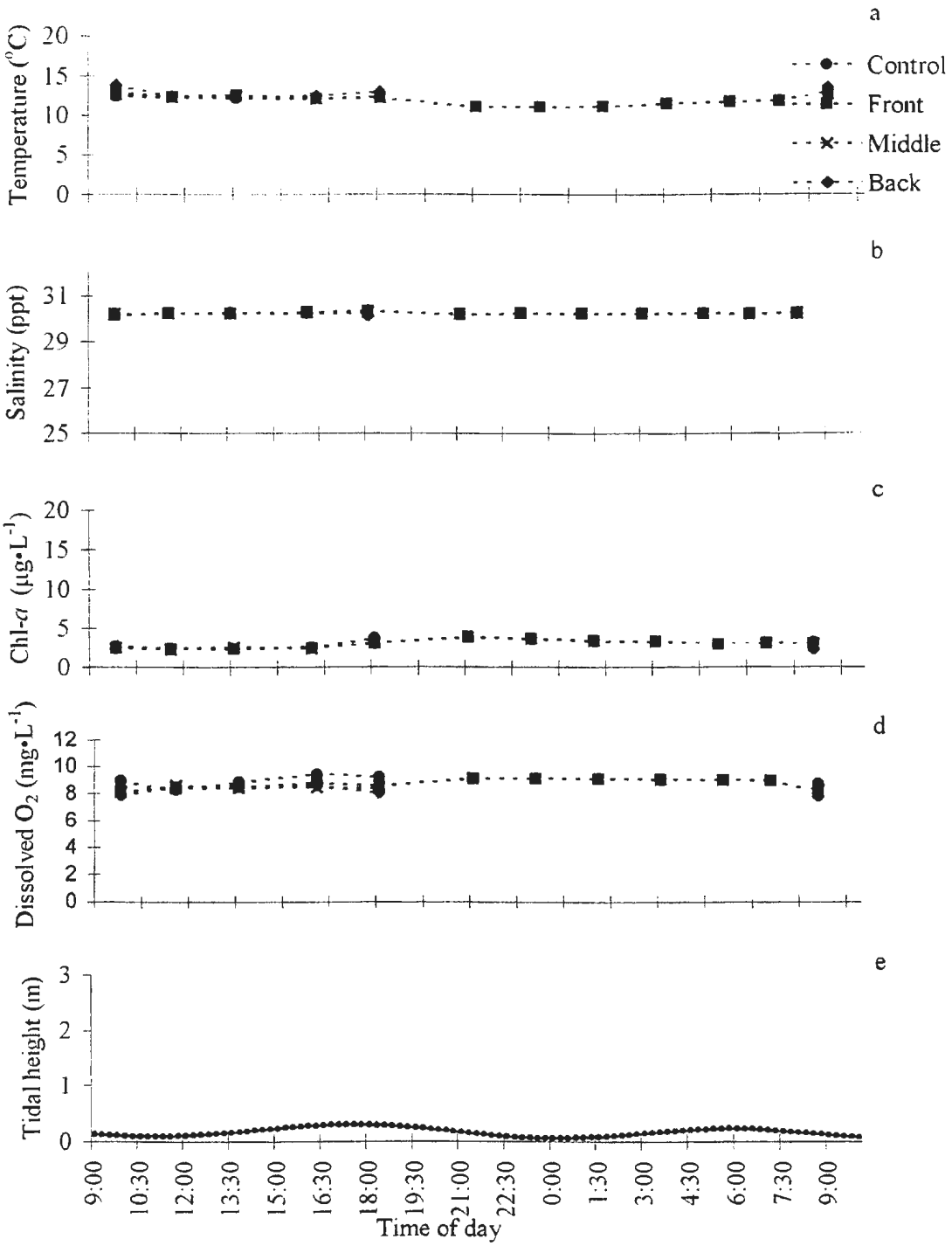
Appendix 4.12: Short-term environmental (tidal) data collected at Reach Run, Nov. 4-5, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



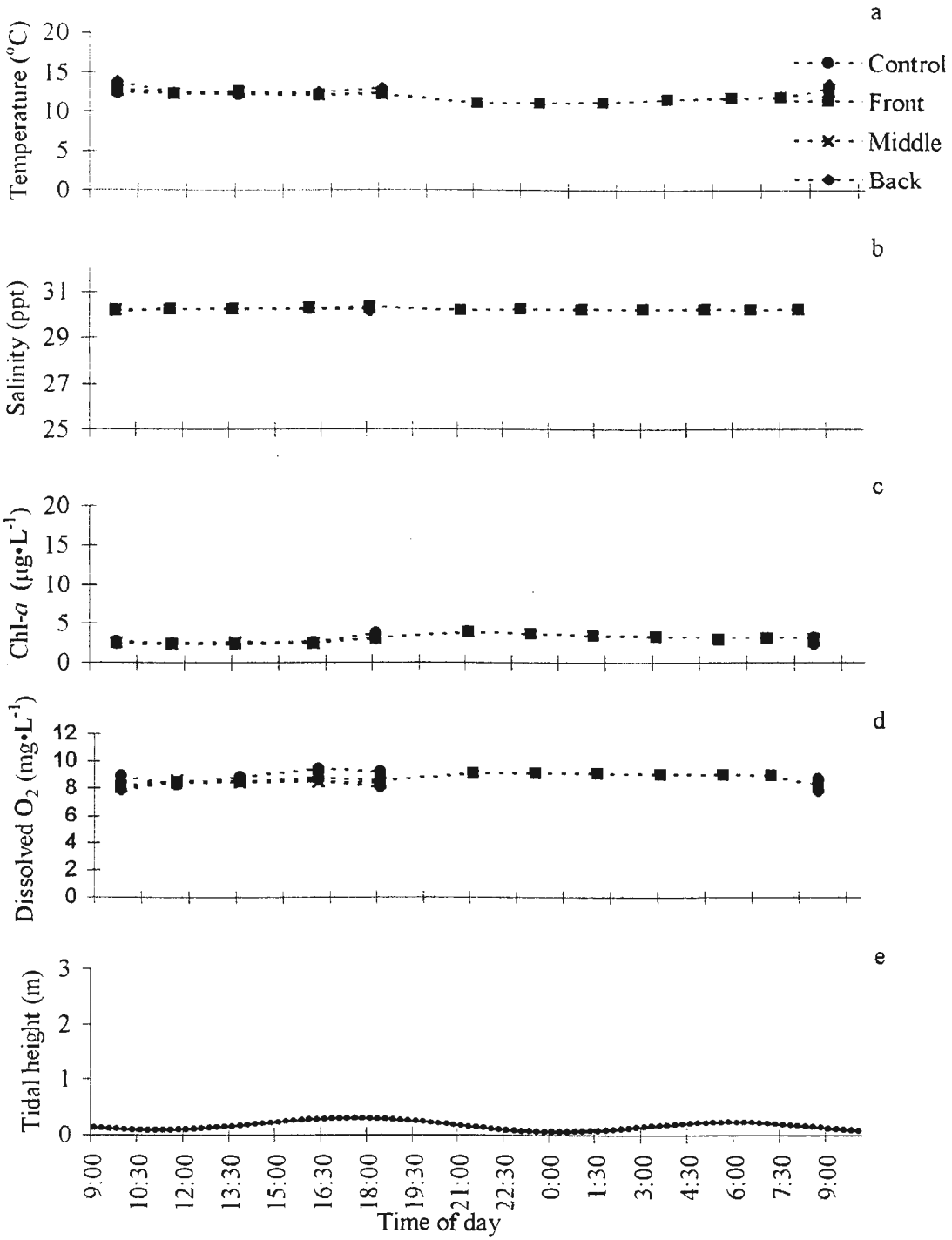
Appendix 4.13: Short-term environmental (tidal) data collected at Big Island, May 28-29, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



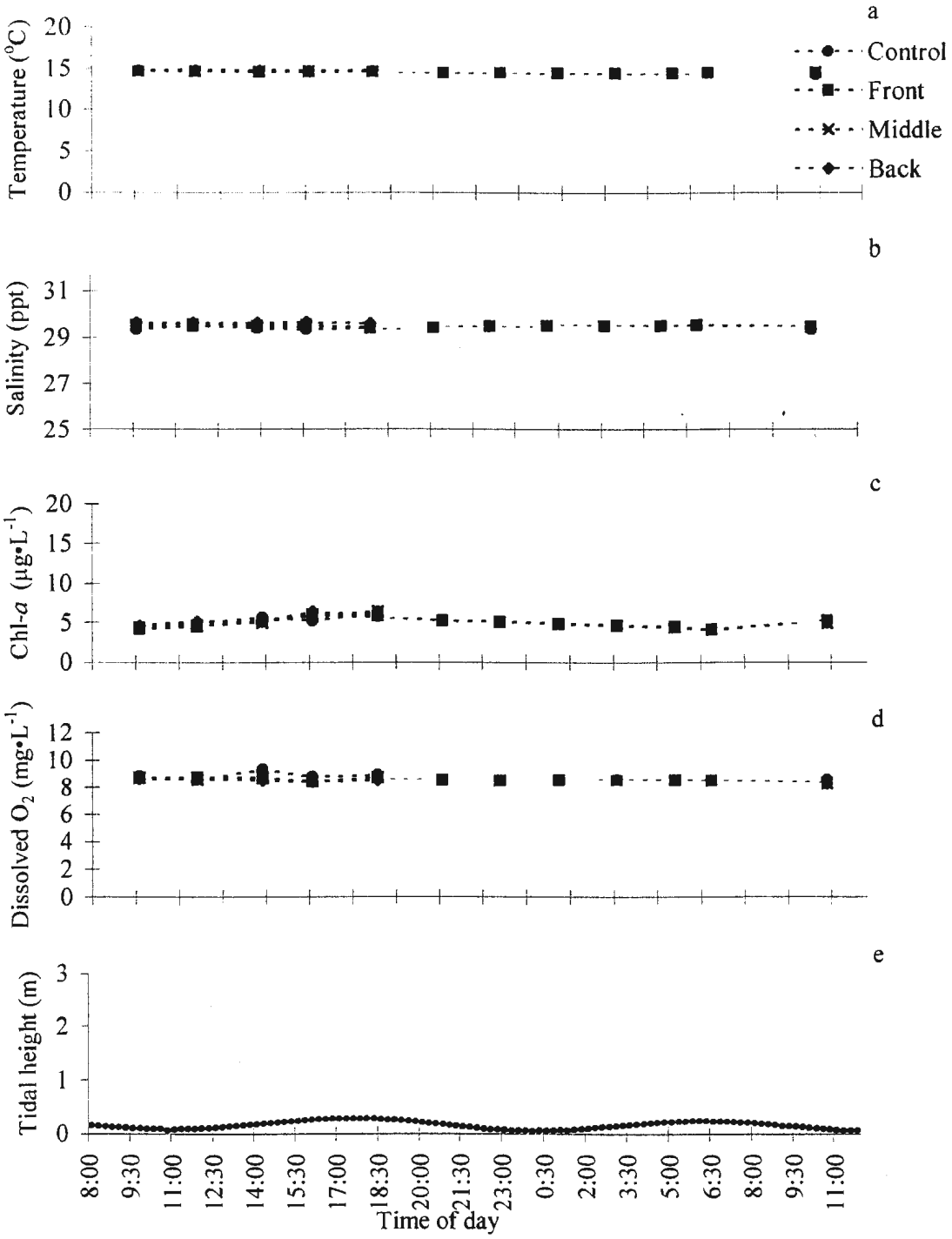
Appendix 4.14: Short-term environmental (tidal) data collected at Big Island, June 25-26, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



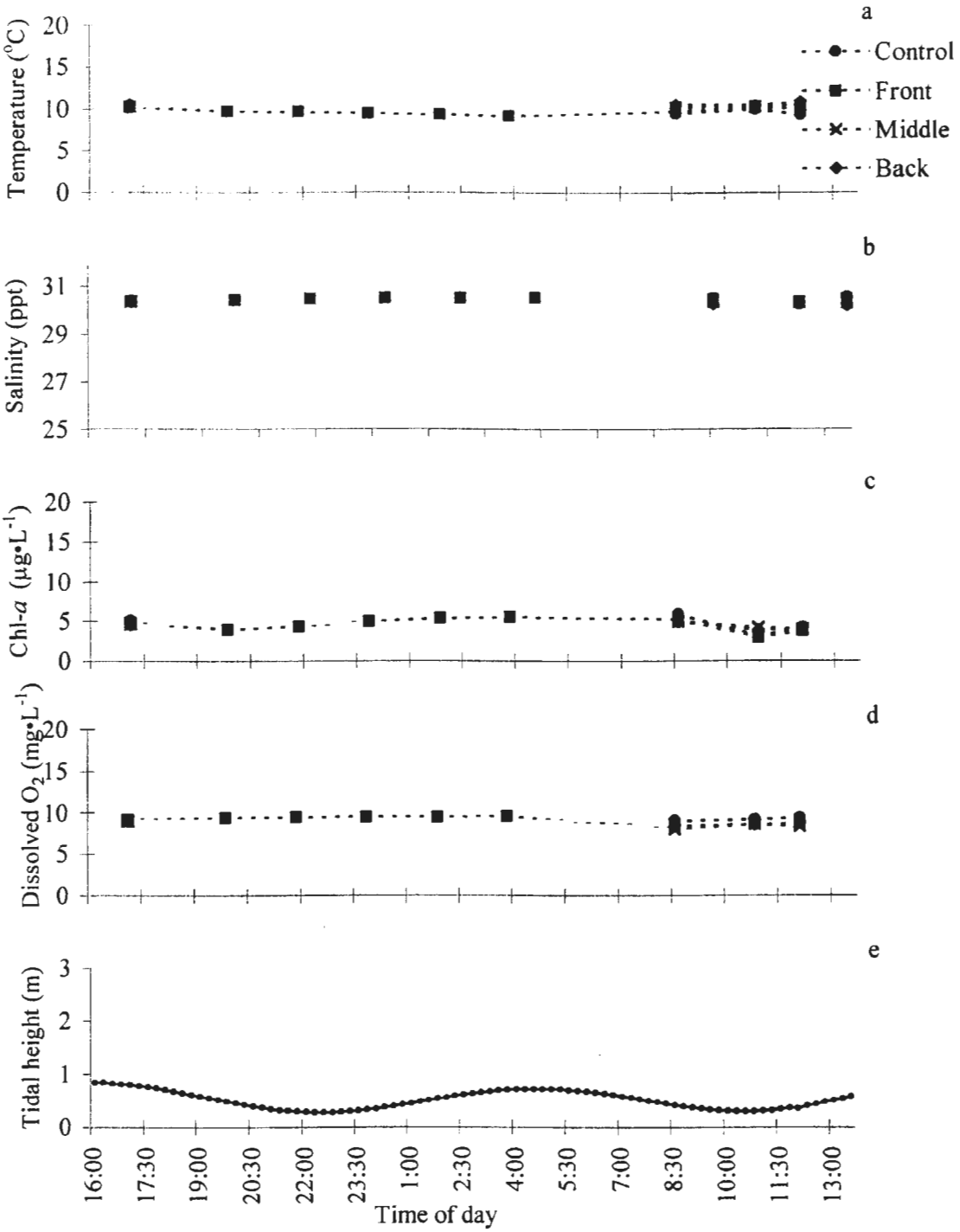
Appendix 4.15: Short-term environmental (tidal) data collected at Big Island, Aug. 4-5, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



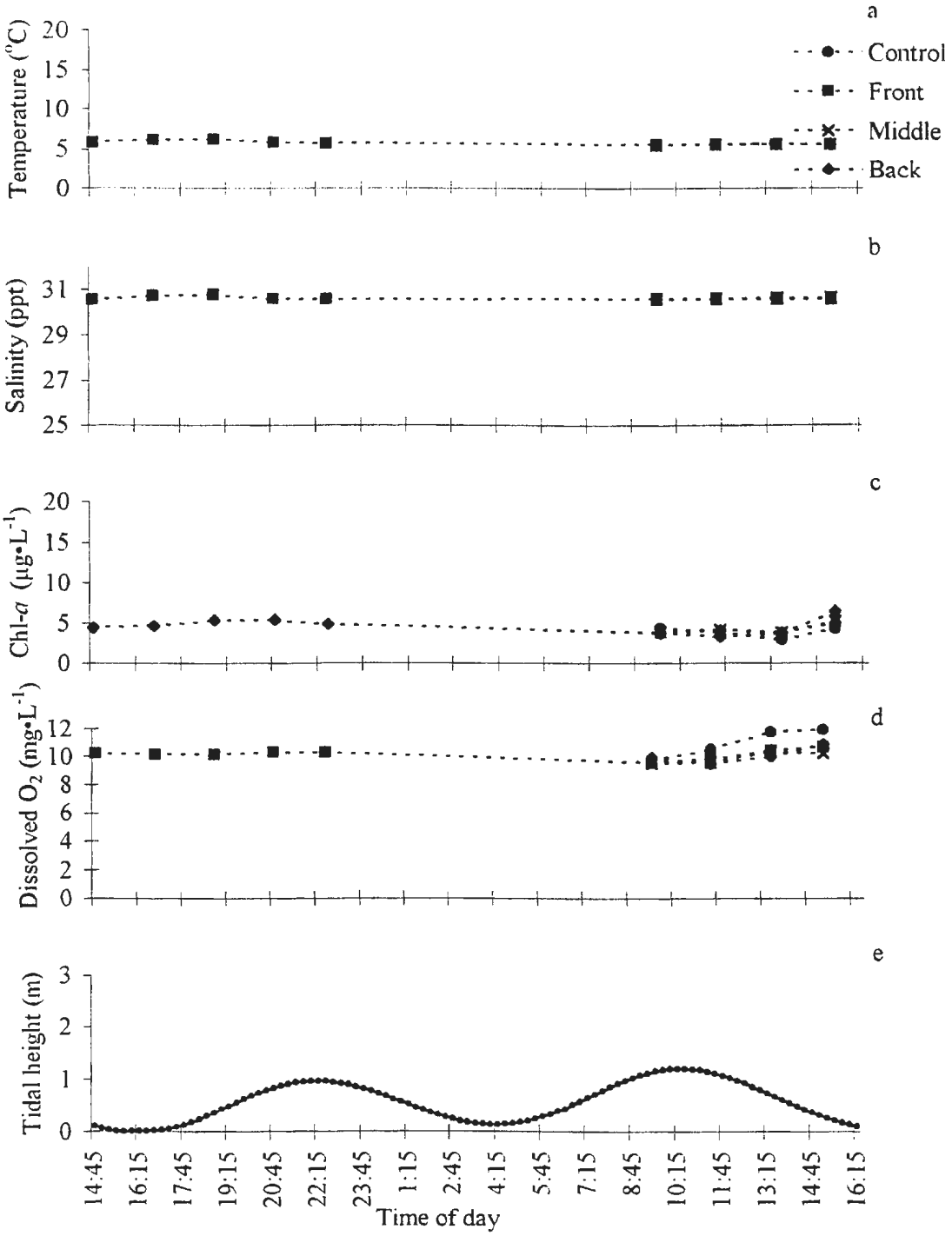
Appendix 4.15: Short-term environmental (tidal) data collected at Big Island, Aug. 4-5, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.



Appendix 4.16: Short-term environmental (tidal) data collected at Big Island, Sept. 3-4, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.

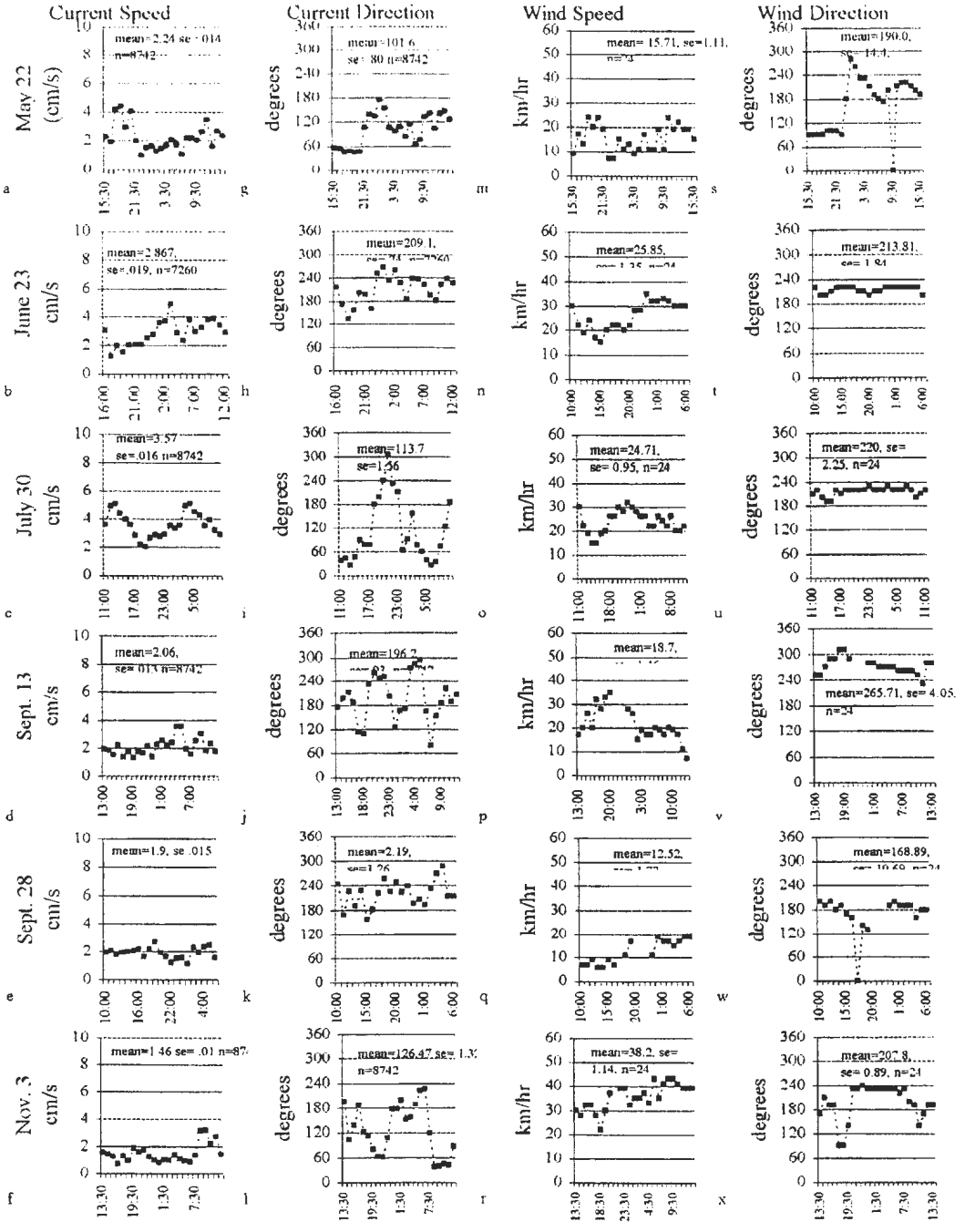


Appendix 4.17: Short-term environmental (tidal) data collected at Big Island, Oct. 1-2, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.

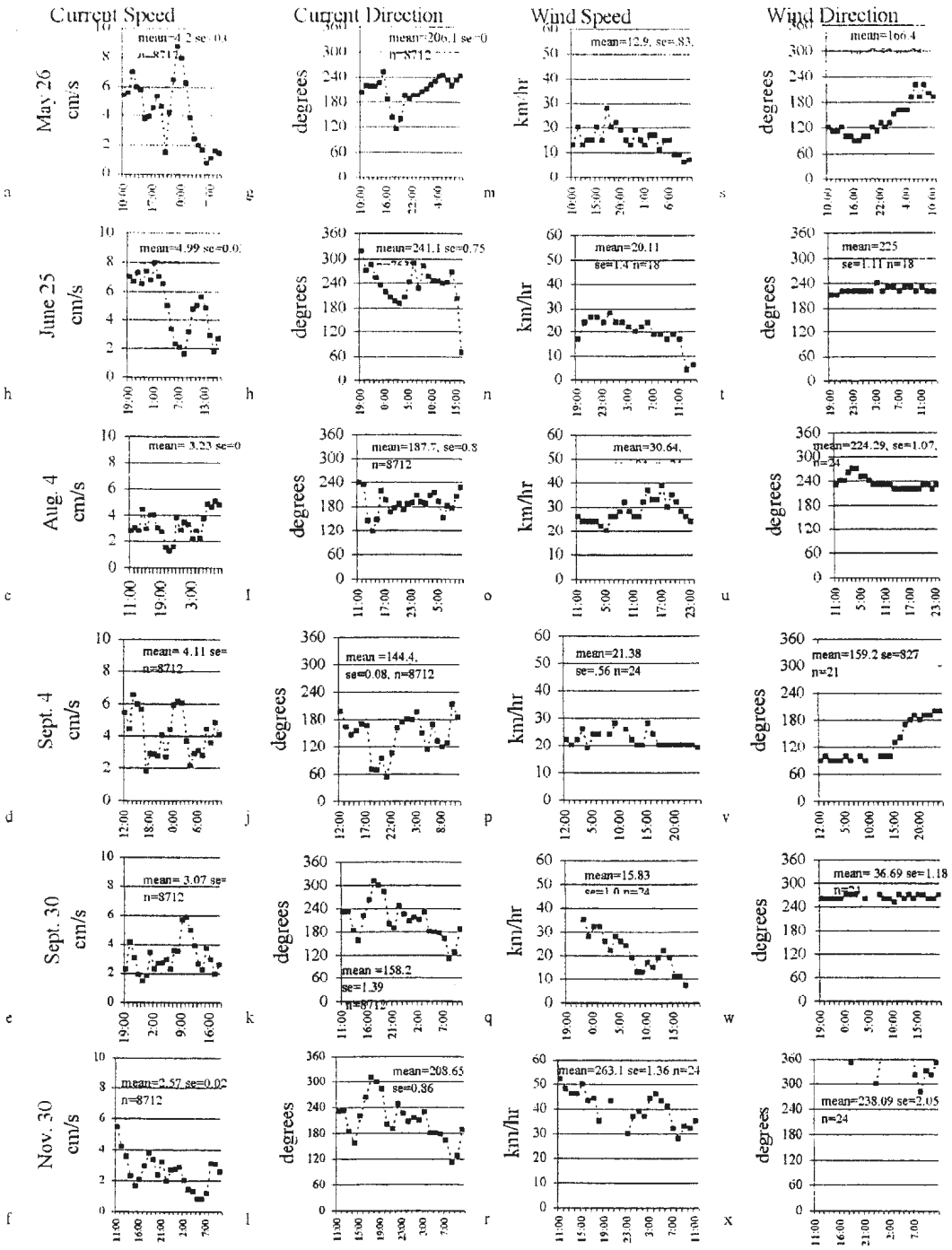


Appendix 4.18: Short-term environmental (tidal) data collected at Big Island, Nov. 7-8, 1998; measured at the control station and three lines in the front, middle and back of the farm at 3.5 m depth with a CTD, a) temperature, b) salinity, c) chlorophyll-a, d) dissolved oxygen e) tidal height at time of sampling.

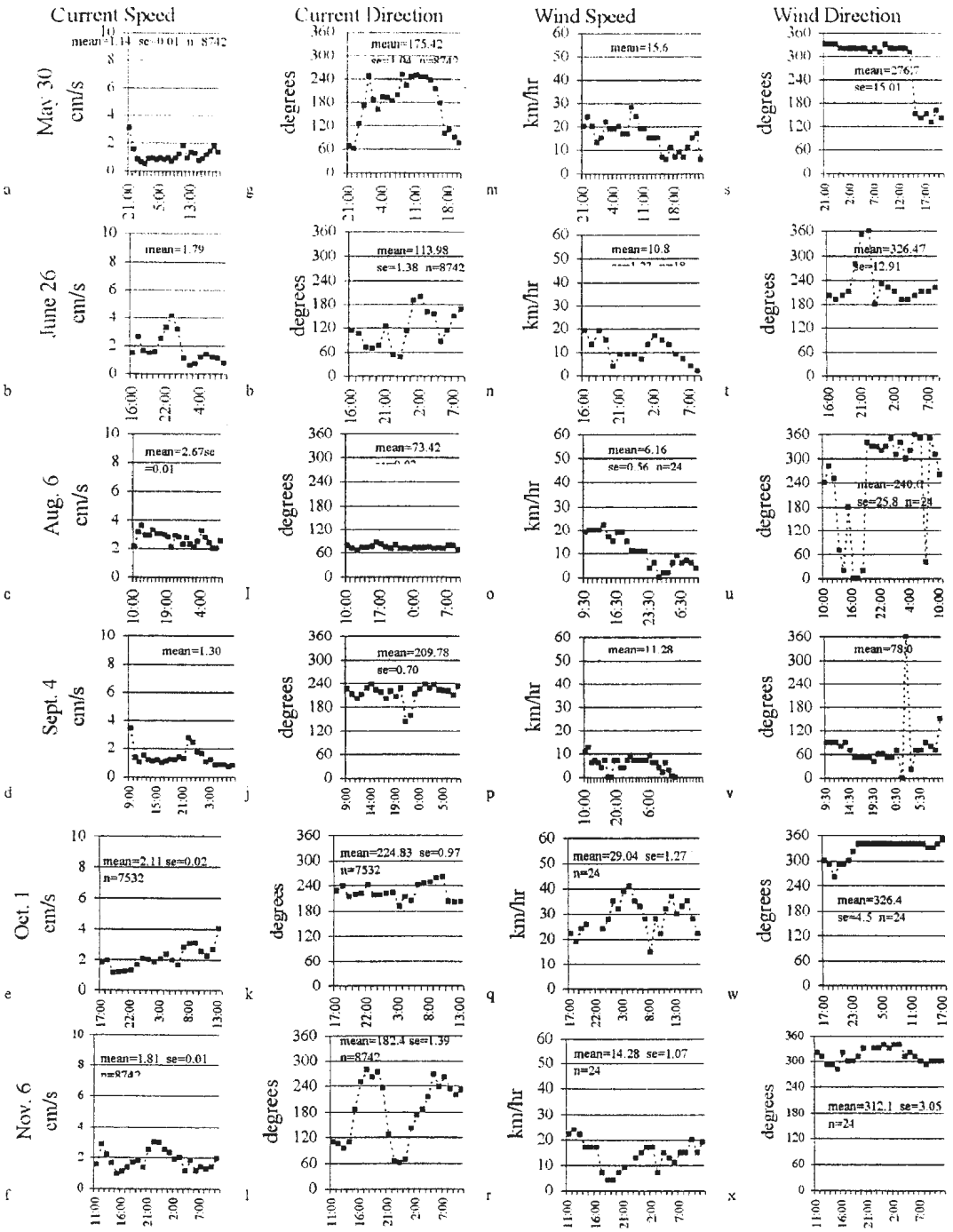
Appendix 5.0 Hourly current direction/speed and wind direction/speed.



Appendix 5.1: Hourly current speed a)-f) and current direction g)-l) measured with an S4 current meter in Burnt Arm, Notre Dame Bay, NL (station 2) on May 22, June 23, July 30, Sept. 13, Sept. 28 and Nov. 3, respectively; Hourly wind speed m)-r) and direction s)-x) collected in the Twillingate, NL on the above dates (source Environment Canada, Twillingate, NL, n= 3 per point).



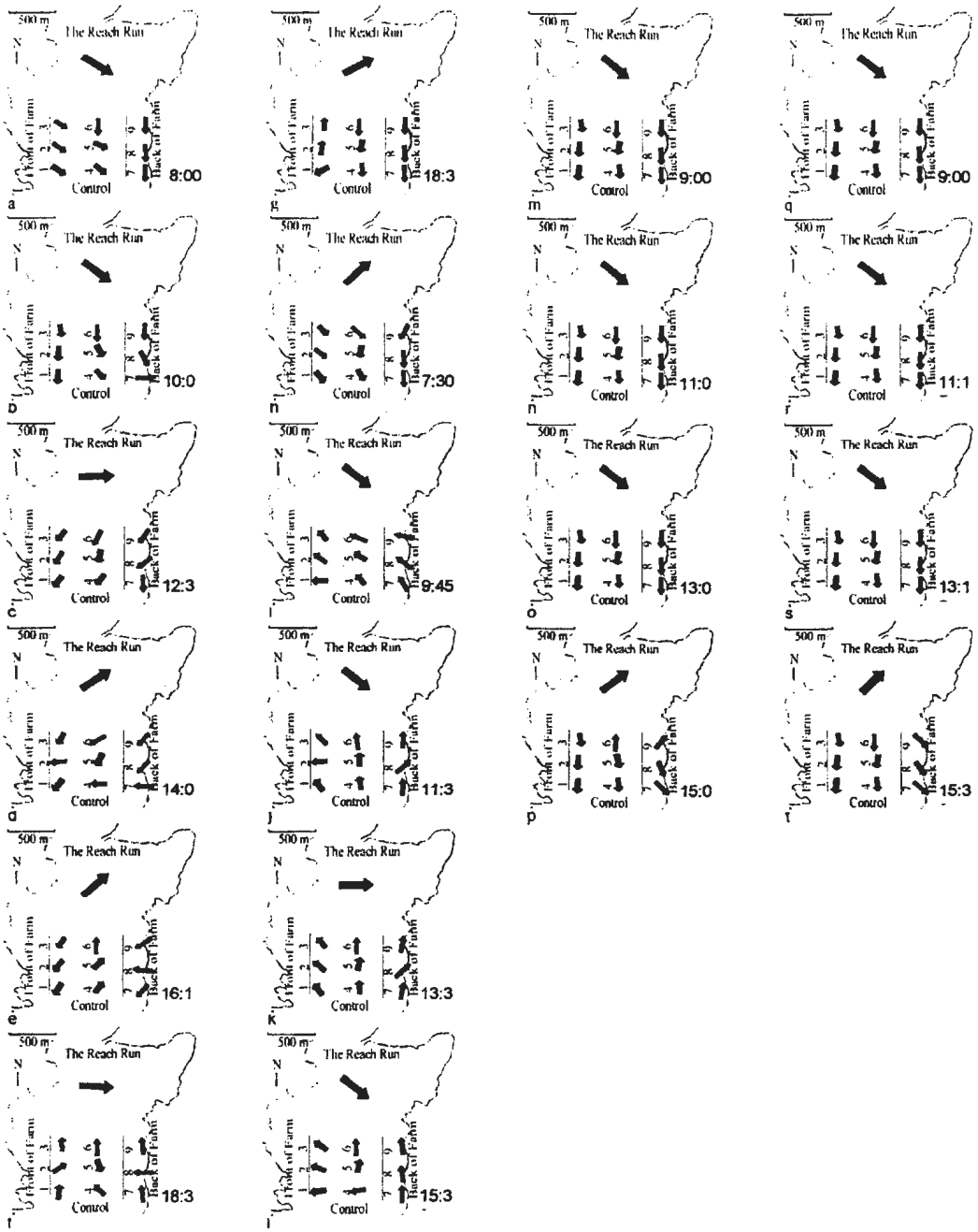
Appendix 5.2: Hourly current speed a)-f) and current direction g)-l) measured with an S4 current meter in Reach Run, Notre Dame Bay, NL (station 2) on May 26, June 25, Aug. 4, Sept. 9, Sept. 30 and Nov. 5th, respectively; Hourly wind speed m)-r) and direction s)-x) collected in the Twillingate, NL on the above dates (source Environment Canada, Twillingate, NL, n= 3 per point).



Appendix 5.3: Hourly current speed a)-f) and current direction g)-l) measured with an S4 current meter near Big Island, Notre Dame Bay, NL (station 2) on May 30, June 26, Aug. 6, Sept. 4, Oct. 1 and Nov. 6th, respectively; Hourly wind speed m)-r) and direction s)-x) collected in the Twillingate, NL on the above dates (source Environment Canada, Twillingate, NL, n= 3 per point).

Appendix 6. Current Direction

Appendix 6.1. Layout of experiment on a mussel farm in Burnt Arm, 49° 35'N, 54° 43'W. Dark lines indicate positioning of experimental mussel lines. Numbers 1-9, indicate sample stations. Small arrows indicate current direction as determined with flagging tape on a pole, lowered to 3.5 m. Time of day is located in the bottom right corner. Large arrow indicates tidal activity, rising ↗, falling ↘ or slack tide →. Current direction was measured. a-e) May 21, '98, f-j) June 23, '98, k-o) July 30, '98, p-u) Sept. 13, '98, v-y) Nov. 3, '98. Current direction could not be monitored Sept. 28, '98 due to high winds.



Appendix 6.2. Layout of experiment on a mussel farm in Reach Run, 49° 21'N, 54° 44'W. Dark lines indicate positioning of experimental mussel lines. Numbers 1-9, indicate sample stations. Small arrows indicate current direction as determined with flagging tape on a pole, lowered to 3.5 m. Time of day is located in the bottom right corner. Large arrow indicates tidal activity, rising ↗, falling ↘ or slack tide →. Current direction was measured. a-f) May 26, '98, g-l) June 25, '98, m-p) Sept. 8, '98, q-t) Nov. 5, '98. Current direction could not be monitored Aug. 3-4 or Sept. 30, '98 due to high winds.